



# Phylogenetic analysis of the family Ariidae (Ostariophysi: Siluriformes), with a hypothesis on the monophyly and relationships of the genera

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Ariid monophyly and intrafamilial relationships are investigated based on cladistic analysis of 230 morphological characters. Terminal taxa examined include whenever possible type-species, or the most morphologically similar species to the type-species of the nominal genera, and the largest possible number of species, including cleared and stained specimens, available in zoological collections. Previous hypotheses about monophyly of the Ariidae are strongly corroborated by new synapomorphies discovered in the present study. The subfamily Galeichthyinae and the remaining ariids are strongly supported by new morphological characters. The monotypic subfamily Bagreinae is recognized as the sister group to all nongaleichthyin ariids, supported by a large series of exclusive synapomorphies. A new concept of Ariinae is presented: the subfamily is found to be unequivocally monophyletic and includes all ariid genera, except *Galeichthys* and *Bagre*. New data supporting the monophyly of the genera included in the Ariinae are introduced and previous hypotheses of monophyly, species composition, morphological definition, and relationships are reviewed and discussed.

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ADDITIONAL KEYWORDS: Ariinae – Bagreinae – Galeichthyinae – morphological evidence – new hypotheses of relationships – phylogeny – sea catfishes.

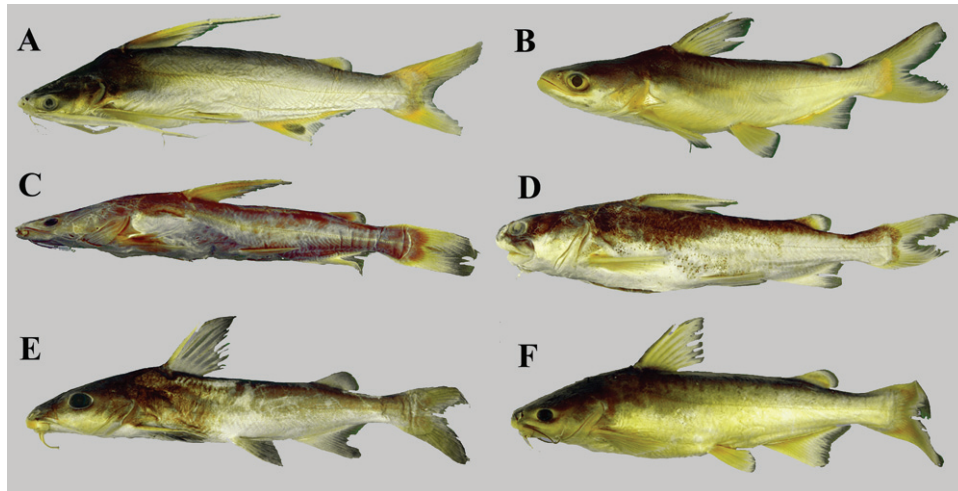
## INTRODUCTION

The Ariidae, predominantly marine catfishes, is the most widespread group of the order Siluriformes, and has considerable commercial importance throughout its range (Fig. 1). Ariid species are common in tropical and temperate areas of the world, and are especially abundant in mangroves and estuaries as well as coastal waters of the continents. The marine species are sometimes caught at depths of 100 m or beyond,

and freshwater species can be found 500 km distant from river mouths. Species such as *Doiichthys novae-guineae* Weber, 1913 reach only 15 cm standard length (SL), but *Hemiaris stormii* (Bleeker, 1858) grows beyond 200 cm SL (Kailola, 2004). Females produce few, large eggs that after fertilization are incubated in the oral cavity of males until the vitelline sac is absorbed by the young (Rimmer & Merrick, 1983).

Since the group was first named by Bleeker (1862) as *Phalanx Arii*, its limits and definition has been little questioned in pre-cladistic studies (Regan, 1911; Shelden, 1937; Berg, 1940; Tilak, 1965; Greenwood

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**Figure 1.** A sample of ariid species to show morphological variation within the family. A, *Bagre pinnimaculatus*; FMNH 62447, 202 mm total length (TL) (western America, predominantly marine); B, *Batrachocephalus mino*, FMNH 68052, 178 mm TL (south and South-East Asia, marine and brackish waters); C, *Cryptarius truncatus*, ANSP 60768, 168 mm TL (South-East Asia, brackish waters); D, *Ketengus typus*, ANSP 60704, 162 mm TL (south and South-East Asia, brackish waters); E, *Potamarius nelsoni*, AMNH 25684, 214 mm TL (Atlantic drainages from México and Guatemala, freshwater); F, *Potamosilurus velutinus*, USNM 217321, 186 mm TL (Indonesia and Papua New Guinea, freshwater).

*et al.*, 1966; Chardon, 1968) and its monophyly widely corroborated by cladistic studies (Mo, 1991; de Pinna, 1993; Kailola, 2004; Hardman, 2005; Sullivan *et al.*, 2006; Betancur-R, 2009). However, characterization and delimitation of ariid genera have always been great challenges to ichthyologists and matters of conflict and controversy during the 19<sup>th</sup> and 20<sup>th</sup> centuries (Günther, 1864; Eigenmann & Eigenmann, 1890; Jordan & Evermann, 1896, 1898; Weber & de Beaufort, 1913; Meek & Hildebrand, 1923; Herre, 1926; Jayaram & Dhanze, 1978; Roberts, 1978; Taylor & Menezes, 1978; Taylor, 1986; Kailola & Bussing, 1995), and prevailed until recently (Kailola, 2004; Betancur-R *et al.*, 2007; Marceniuk & Menezes, 2007). The great diversity and wide distribution of the group, as well as overall morphological similarity amongst the species and rarity of some in museum collections represent major difficulties for a more comprehensive study involving species relationships and systematic delimitation of the genera. Systematic studies have been geographically limited in scope and do not take into account many of the known genera. Kailola's (2004) cladistic analysis of the group, based on morphological data, discussed the relationships and zoogeography of species from New Guinea and Australia, and Betancur-R *et al.* (2007) analysed only genera and species from Colombia and adjacent regions. Both studies included very few species from the occidental region of Africa, South America, and the Indian Ocean, and did not investigate the monophyly of the large genus *Arius* Valenciennes, 1840, in which many phylogenetically unrelated species have

been placed. Although many species have been individually studied both taxonomically and morphologically, a more inclusive morphological revision aiming at establishing the limits and species composition of all genera was undertaken by Marceniuk & Menezes (2007). More recently, Betancur-R (2009) added new information on relationships within the Ariidae based on mitochondrial and nuclear sequence data compiled from a comprehensive sample of taxa. Betancur-R (2009) discussed previous classifications, but proposes no taxonomic or systematic changes.

In this work, previous hypotheses about ariid monophyly are reviewed, and the relationships, morphological definition, and species composition of genera and subfamilies are presented based on new morphological evidence compiled from the most comprehensive set of ariid taxa analysed to date.

## MATERIAL AND METHODS

### PHYLOGENETIC PROCEDURES

Hypotheses of relationships and monophyly were proposed according to the cladistic or phylogenetic method firstly proposed by Hennig (1950, 1966) and subsequently developed by several authors (e.g. Wiley, 1981; Rieppel, 1988; Wiley *et al.*, 1991; Amorim, 1997; Kitching *et al.*, 1998; Page & Holmes, 1998; Scotland & Pennington, 2000).

Parsimony analysis was applied using the computer program HENNIG86 1.5 (Farris, 1988; Platnick, 1989) associated with TREE GARDENER 2.2 (Ramos, 1998) and NONA 2.0 (Goloboff, 1993) associ-

ated with WinClada 100.08 (Nixon, 2002), and TNT (Goloboff *et al.*, 2008). Reversals and convergences were considered as equally possible in the heuristic algorithms employed (Swofford & Maddison, 1987). In HENNIG86 a combination of heuristic algorithms 'mhennig' and 'branch breaker' was used, and in NONA 10 000 replicates were applied using 'Mult\*N' (in each replicate the order of the taxa was altered). 'Tree bisection reconnection' was employed to allow for a new exchange of branches and 100 trees were 'saved' by replicate using 'hold'. In TNT, a traditional heuristic search was initially performed using the stepwise addition algorithm associated with tree bisection reconnection in a total amount of 10 000 samples. After that, a new search was employed using the 'new technologies'. In the matrix, it was performed on 10 000 samples, each one loading sectorial searches, ten ratchet interactions, and ten tree-drift interactions. After all replicates, ten tree-fuse interactions were performed. The different topologies found in the fundamental cladograms were summarized in a strict consensus, and the same result was obtained from all software.

Polarity for character states was determined by outgroup comparison through a single parsimony analysis as explained by Nixon & Carpenter (1993). The rooting point was established in Diplomystidae, considered either the basalmost family of all Siluriformes (Fink & Fink, 1981; Mo, 1991; de Pinna, 1993; Britto, 2002), or of Siluriformes minus Loricarioidei (Sullivan *et al.*, 2006). However, we comprised character-state variation amongst nondiplomystid, noncetopsid catfish outgroups to test more accurately the transformation series information within the Ariidae accordingly to its closest catfish families (Prendini, 2001; Pollock *et al.*, 2002; Zwickl & Hillis, 2002). Hypotheses of relationships within Siluriformes advanced by Mo (1991), Lundberg (1993), de Pinna (1993), Britto (2002), Diogo (2004), Hardman (2005), and Sullivan *et al.* (2006) were used for establishing the most appropriate outgroup taxa. Other catfish families used for outgroup comparison are Anchariidae, Austroglanididae, Claroteidae, Cranglanididae, Doradidae, Horabagridae, Mochokidae, Pangasiidae, Schilbidae, Bagridae, Heptapteridae, and Ictaluridae.

Most multistate characters were analysed as ordered ('minimally connected', Slowinski, 1993), except when it was not possible to detect an explicit morphological sequence amongst character states. In such cases, character states were treated as unordered. In cases of ambiguous optimizations the alternative that maximized reversals rather than convergences was chosen, preserving as much as possible original hypotheses of primary homology (de Pinna, 1991). Bootstrap and jackknife resamplings

(10 000 replicates each) were conducted using TNT software (Goloboff *et al.*, 2008). The decay index (Bremer, 1994) was calculated using a script in the TNT software using the default standards.

The examined characters are described in the section 'Character description' and characters coded for the terminals are summarized in Appendix 1. The data matrix was assembled with the aid of TREE GARDENER 2.2 (Ramos, 1998). 'Missing' was applied in the description of the characters for the terminals in which the character states are not observed because of the poor condition of the material or doubtful cases of polymorphism, and 'not applicable' was used when the terminals in question do not have the structure described in the corresponding character. In spite of the considerations of Nixon & Davis, (1991), the interpretations herein obtained, using different computer programs, were considered equivalent and treated as 'missing values'. Thus, 'missing' and 'not applicable' data are presented independently as dashes ('-') in the data matrix. Therefore, in the matrix loaded in HENNIG86, all missing entries were coded as a dash. The presentation of these conditions in the matrix is only to allow better discrimination of the data.

#### DELIMITATION OF TERMINAL TAXA

The impossibility of examining representatives of all known ariid species led us to choose the most representative terminal taxa for analysis. Whenever feasible, type-species of nominal genera were used in conformity with article 42c of the International Code of Zoological Nomenclature. Examined taxa include the type species of all nominal genera of the Ariidae, except for the following: *Potamarius nelsoni*, type-species of *Potamarius* (Hubbs & Miller, 1960) and *Plicofollis argyropleuron*, type-species of *Plicofollis* (Kailola, 2004). Of the genera treated as valid in Marceniuk & Menezes (2007), only *Amissidens* Kailola, 2004, is not represented in this study by any examined specimens.

When the type-species was not available for study, the species most similar to the type species was used based on the assumption that it would have the essential characteristics of the genus. Thus, *Potamarius izabalensis* was examined instead of *Potamarius nelsoni*, type-species of *Potamarius* (Hubbs & Miller, 1960) and *Plicofollis dussumieri*, *Plicofollis nella*, and *Plicofollis polystaphylodon* instead of *Pl. argyropleuron*, type-species of *Plicofollis* (Kailola, 2004). No representative material of the genera *Amissidens* (Kailola, 2004), *Ariodes* (Müller & Troschel, 1849), *Leptarius* (Gill, 1863), *Pararius* (Whitley, 1940), or *Tetranesodon* Weber, 1913 was examined because of the unavailability of cleared and stained and skeletal

specimens in zoological collections. Additional nontype species were chosen based on validity as confirmed in recent publications, its systematic, biological or commercial importance, and availability of specimens. The genera and their species composition herein recognized are consistent with those in Marceniuk & Menezes (2007).

#### MATERIAL EXAMINED

Examined material is presented in Appendix 2.

#### ANATOMICAL PREPARATIONS

For examination of bone and cartilage, specimens were cleared and counter-stained using the method of Taylor & Van Dyke (1985) and then dissected following the method of Weitzman (1974). Osteological preparations were also obtained through digestion of body tissues by dermestid beetles.

#### TERMINOLOGY

Names of bones are those used by Weitzman (1962), Lundberg & Baskin (1969), and Mo (1991) with the following exceptions: 'parietosupraoccipital' instead of 'supraoccipital' (Arratia & Gayet, 1995), 'sesamoid bone I' (*sensu* Diogo, Oliveira & Chardon, 2001), instead of 'endopterygoid' of Arratia (1992), 'sesamoid bone II' (*sensu* Diogo *et al.*, 2001), instead of 'ectopterygoid' of Arratia (1992), 'autopalatine' instead of 'palatine' (Fink & Fink, 1981; Arratia & Schültze, 1991), and 'scapulocoracoid' instead of 'coracoid' (Lundberg, 1970). The terminology for myological characters follows Winterbottom (1974).

#### INSTITUTIONAL ABBREVIATIONS

Abbreviations for institutional names are those of Levinton *et al.* (1985) and Levinton & Gibbs (1988).

#### CHARACTER DESCRIPTION

The characters recognized as phylogenetically informative are discussed according to the body systems to which they belong. A brief statement defining the character is followed by its condition maximally or minimally connected (when more than two states are defined for the character) and by the respective character states. For each character state the terminals sharing the condition are listed. The condition of the feature is presented first in outgroup taxa and then in ariid genera alphabetically ordered. Character numbers correspond to those in the data matrix. Finally, when necessary, a more detailed description of the structure is presented emphasizing the variation of character states and the plesiomorphic and/or apomorphic condition in the Ariidae.

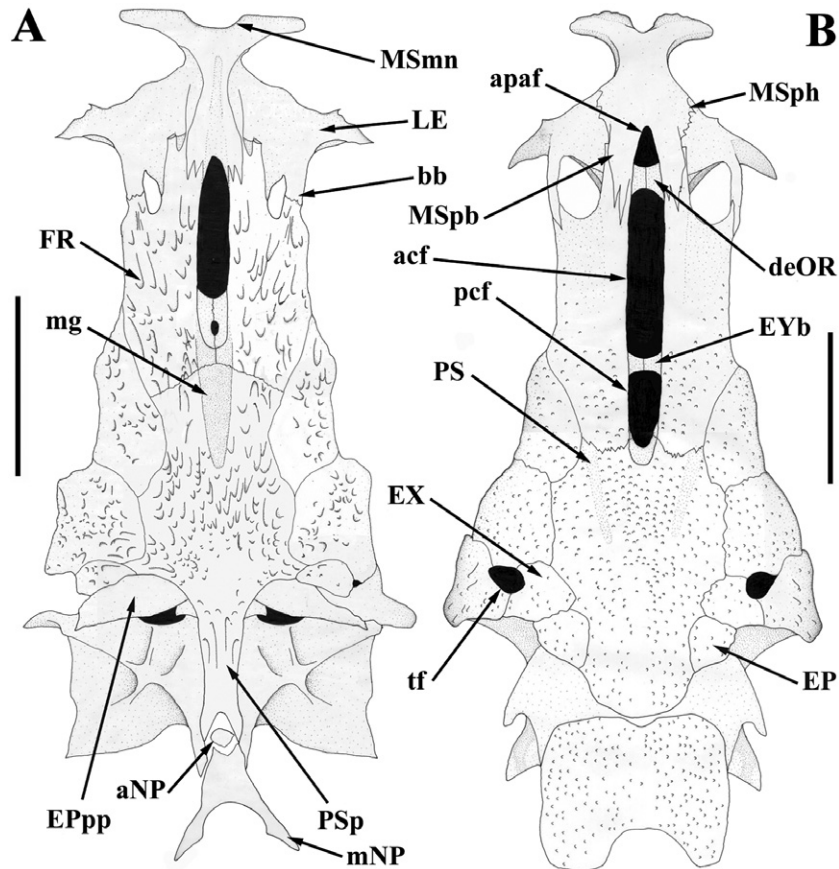
#### NEUROCRANIUM

1. *Form of mesethmoid medial notch*: large and shallow (state 0; Figs 2A, 3B, 4B, 5B); narrow and deep (state 1; Figs 2B, 3A, 4A, 5A, 6A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Horabagridae, Mochokidae, Pangasiidae, Schilbidae, *Bagre*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Ketengus*, and *Pachyula*. State 1: Bagridae, Heptapteridae, Ictaluridae, *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma bilineata*, *Notarius* (except *Notarius grandicassis*), *Occidentarius*, *Plicofollis*, *Potamarius*, *Potamosilurus* (except *Potamosilurus macrorhynchus*), and *Sciades* (except *Sciades parkeri* and *Sciades proops*).

The anterior part of the mesethmoid is characterized by the presence of a pair of horns mesially delimiting a semicircular notch that is inconspicuous and poorly delimited in several catfish families and some genera of Ariidae. A very pronounced and deep notch between mesethmoid horns represents the condition shared by most ariids, and also observed in bagrids, heptapterids, and ictalurids. Not applicable in *Batrachocephalus*, *Netuma thalassina*, *No. grandicassis*, *Osteogeneiosus*, *Potamosilurus macrorhynchus*, *S. parkeri*, and *S. proops*.

2. *Mesethmoid median portion (minimally connected)*: very narrow (state 0; Figs 3A, 4A, 5A); moderately wide (state 1; Figs 2A, B, 6A, B); very wide (state 2; Figs 3B, 5B). State 0: Austroglanididae, Diplomystidae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, *Arius* (except *Arius caelatus* and *Arius madagascariensis*), *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Pachyula*, and *Potamarius*. State 1: Anchariidae, Horabagridae, *Amphiarius*, *Ar. caelatus*, *Ar. madagascariensis*, *Aspistor*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Plicofollis*, *Potamosilurus*, *Sciades assimilis*, *Sciades bonillai*, *Sciades felis*, *Sciades sagor*, and *Sciades seemanni*. State 2: Ictaluridae, Pangasiidae, Schilbidae, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Doiichthys*, *Sciades couma*, *S. parkeri*, *Sciades guatemalensis*, *Sciades herzbergii*, *Sciades leptaspis*, *Sciades passany*, and *S. proops*.

Tilak (1965), studying ariid species from the Indian Ocean, recognized that variation in the shape of the



**Figure 2.** Neurocranium, dorsal view. A, *Galeichthys feliceps*, MZUSP 87694; B, *Aspistor luniscutis*, MZUSP 87696. Abbreviations: acf, anterior cranial fontanel; aNP, anterior nuchal plate; apaf, anterior portion of anterior cranial fontanel; bb, bony bridge; deOR, dorsal expansion of orbitosphenoid; EP, epioccipital; EPpp, epioccipital posterior process; EYb, epioccipital bar; EX, extrascapular; FR, frontal; LE, lateral ethmoid; mg, medial groove; mNP, median nuchal plate; MSpb, mesethmoid posterior branches; MSmn, mesethmoid medial notch; MSph, mesethmoid posterior horn; pcf, posterior cranial fontanel; PS, parietosupraoccipital; PSp, parietosupraoccipital process; tf, temporal fossa. Scale bars = 10 mm.

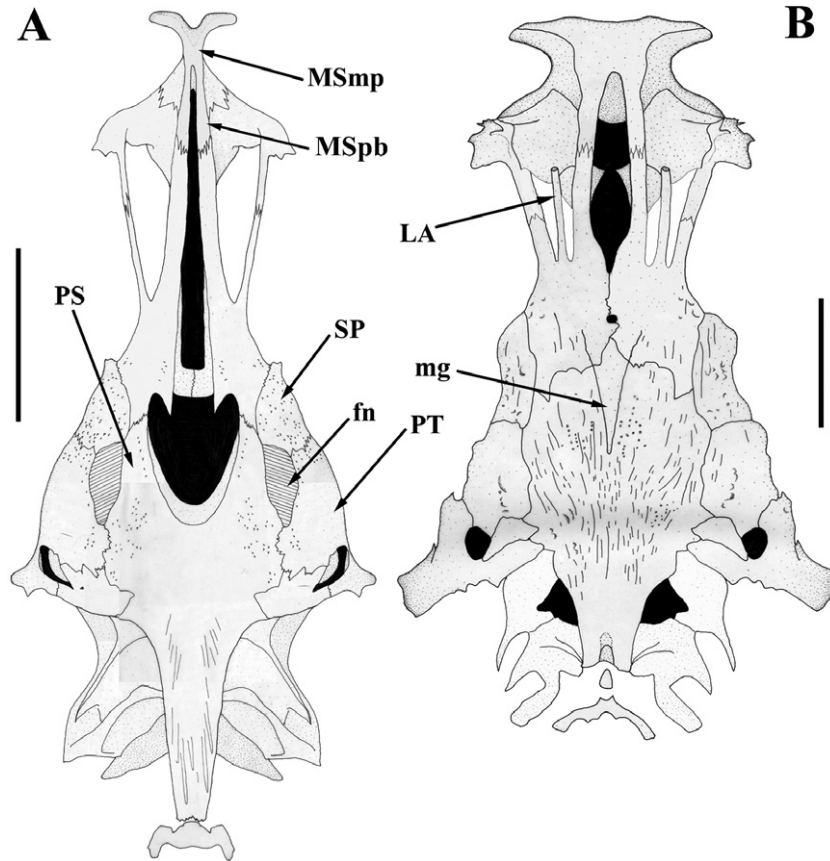
mesethmoid would be useful for identification of genera. Higuchi (1982), however, expressed a different opinion considering that each western South Atlantic species has a peculiar shape and the character therefore could not be used in generic diagnoses. The mesethmoid median portion, delimited by the anterior and posterior horns, is variable in the Ariidae. A moderate width represents a condition observed in several catfish families and some *Arius* species. A mesethmoid narrowing at the median region represents the condition in *Arius* (except *Ar. caelatus* and *Ar. madagascariensis*), *Cathorops*, *Cephalocassis*, *Cinetodus*, *Ketengus*, *Osteogeneiosus*, *Pachyula*, and *Potamarius*. A very wide median region of mesethmoid present in *Bagre*, *Batrachcephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Doichthys*, *S. couma*, *S. parkeri*, *S. guatemalensis*, *S. herzbergii*, *S. leptaspis*, *S. passany*, and *S. proops* defines an extreme of the latter condition. Missing in the Mochokidae and *Arius dispar*.

3. *Fenestra delimited by mesethmoid and lateral ethmoid*: absent (state 0; Figs 2A, B, 3A, B, 5A, B, 6A, B); present (state 1; Fig. 4A, B). State 0: all outgroups and all ariids, except *Ketengus* and *Cathorops* (except *Cathorops dasycephalus*). State 1: *Cathorops* (except *Cat. dasycephalus*), and *Ketengus*.

In most Ariidae a fenestra delimited by the mesethmoid and the lateral ethmoid is not present. Within the Ariidae, *Cathorops* (except *Cat. dasycephalus*) and *Ketengus* show a fenestra delimited by the posterior horn of the mesethmoid.

4. *Fenestra delimited by mesethmoid and lateral ethmoid*: small, not filled with cartilage (state 0; Fig. 4A); large, filled with cartilage (state 1; Fig. 4B). State 0: *Cathorops* (except *Cat. dasycephalus*). State 1: *Ketengus*.

Two very distinct conditions are represented. In *Cathorops* (except *Cat. dasycephalus*), the meseth-



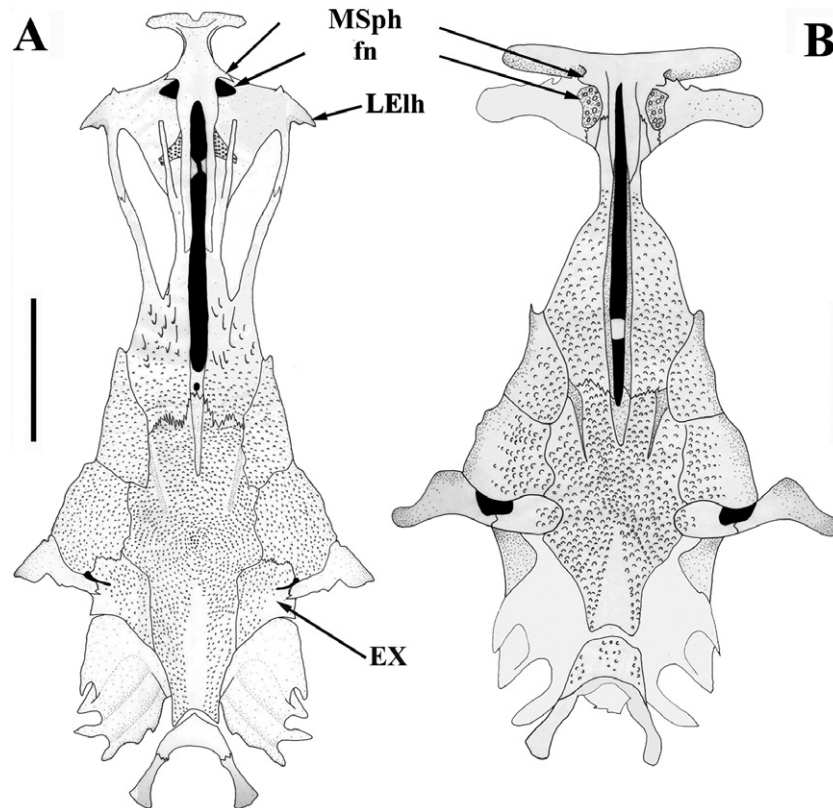
**Figure 3.** Neurocranium, dorsal view. A, *Cephalocassis melanochir*, CAS 49426; B, *Bagre bagre*, MZUSP 35843. Abbreviations: fn, fenestra; LA, lachrymal-antorbital; mg, medial groove; MSmp, mesethmoid median portion; MSpb, mesethmoid posterior branches; PS, parietosupraoccipital; PT, pterotic; SP, sphenotic. In *Cephalocassis melanochir*, the shading of the fenestra represents cartilage. Scale bars = 10 mm.

moid and the lateral ethmoid delimit a small fenestra not filled with cartilage. A large fenestra entirely filled with cartilage is exclusively found in *Ketengus*. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

5. *Form of mesethmoid posterior horn*: depressed, very wide and short (state 0; Figs 2A, B, 3A, B, 5A, B, 6A, B); tubular, narrow, and elongate (state 1; Fig. 4A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae,

*Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* (excluding *Cat. dasycephalus*) and *Ketengus*.

The posterior horns of the mesethmoid are lateral expansions at the origin of the posterior branches of the same bone that are lateroposteriorly sutured to the lateral ethmoids. In most Ariidae and several catfish families, the posterior horns of the mesethmoid are wide and depressed, connected to the lateral ethmoid through a large contact area. In *Ketengus* and *Cathorops* (except *Cat. dasycephalus*), the tubular, narrow, and elongate posterior horns of the mesethmoid contact the lateral ethmoid through a very small area.



**Figure 4.** Neurocranium, dorsal view. A, *Cathorops agassizii*, MZUSP 37232; B, *Ketengus typus*, ANSP 60704. Abbreviations: EX, extrascapular; fn, fenestra; LElh, lateral ethmoid lateral horn; MSph, mesethmoid posterior horn. Scale bars = 10 mm.

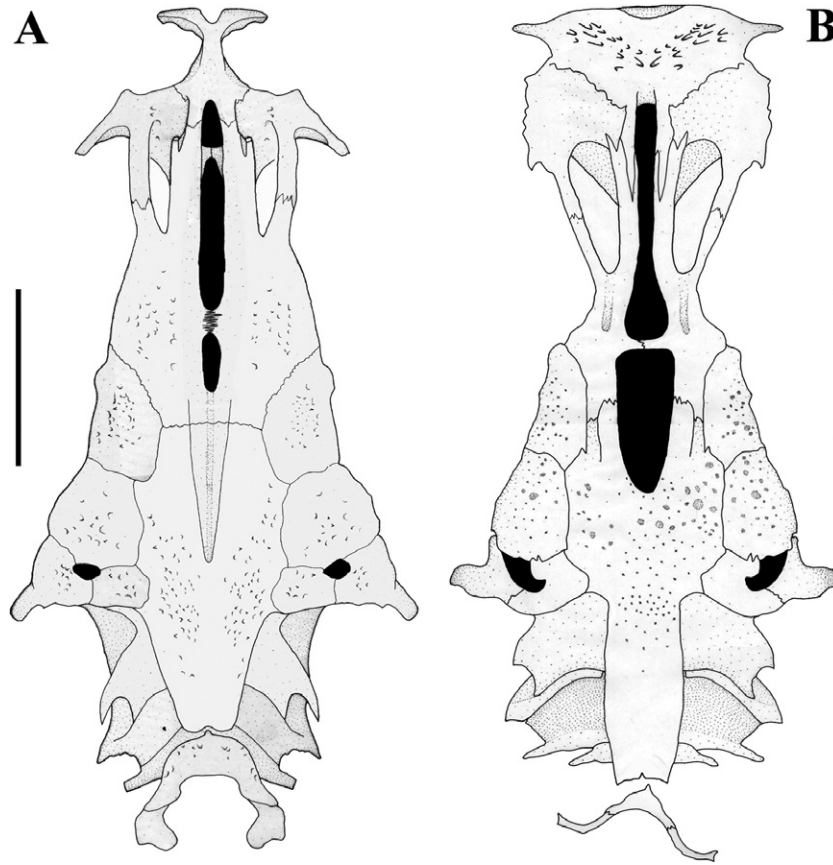
6. *Width of posterior branches of mesethmoid*: wide (state 0; Figs 2A, B, 5A, 6A, B); narrow (state 1; Figs 3A, B, 4A, B, 5B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre panamensis*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nearius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre* (except *Bagre panamensis*), *Cathorops*, *Cephalocassis*, *Doiichthys*, *Ketengus*, *Nedystoma*, and *Nemapteryx*.

Amongst ariids, there are two conditions concerning the posterior branches of mesethmoid, wide or slender (see discussion of character 7).

7. *Relationships between posterior branches of mesethmoid*: divergent posteriorly (state 0; Figs 2A, B, 3B, 5A, 6A, B); posterior branches parallel throughout their entire extension

(state 1; Figs 3A, 4A, B, 5B). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nearius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Diplomystidae, *Cathorops*, *Cephalocassis*, *Doiichthys*, *Ketengus*, *Nedystoma*, and *Nemapteryx*.

The mesethmoid posterior portion bifurcates into two branches interdigitated with frontals, delimiting the anterior part of the anterior cranial fontanel. In several catfish families and representatives of the Ariidae the mesethmoid posterior branches progressively diverge from each other, the internal distance between the two branches always conspicuously larger along the posterior portion than the anterior third, forming an inverted V-shape. However, in the Diplomystidae, *Cathorops*, *Cephalocassis*, *Doiichthys*, *Ketengus*, *Nedystoma*, and *Nemapteryx*, the meseth-



**Figure 5.** Neurocranium, dorsal view. A, *Potamarius izabalensis*, UMMZ 177252; B, *Doiichthys novaeguineae*, AMS I. 27416-002. Scale bars = 10 mm.

moid posterior branches are parallel along their entire length, the internal distance along the posterior portion equal to or a just little larger than the anterior third. Missing in the Cetopsidae and Cranoglanididae.

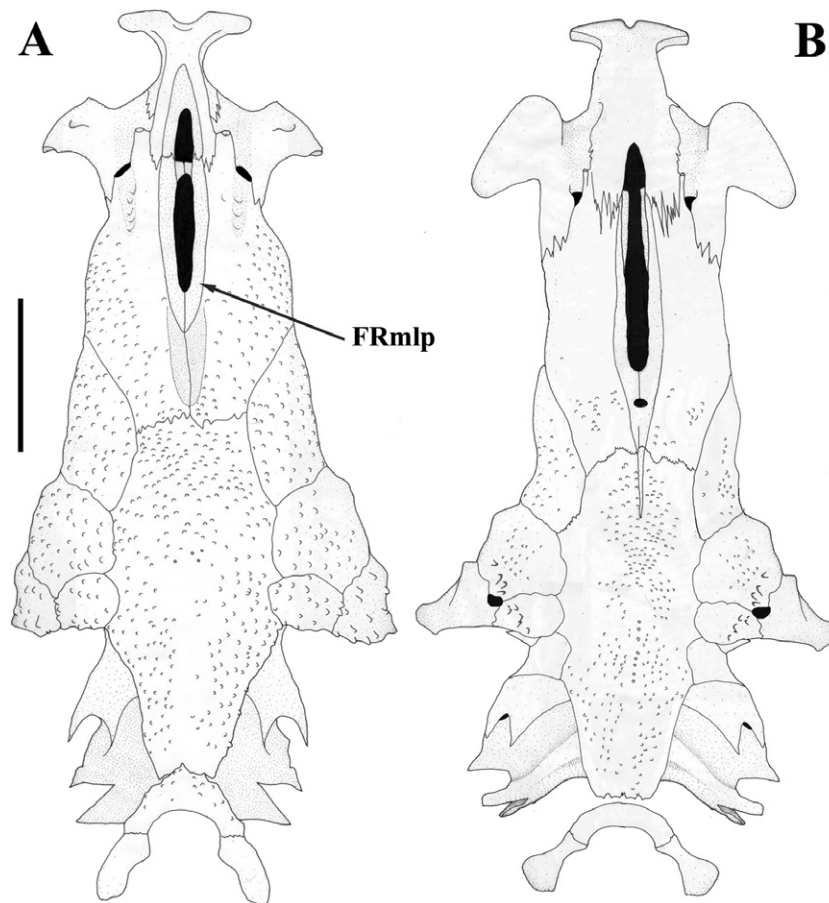
8. *Length and contribution of posterior branches of mesethmoid to delimitation of anterior cranial fontanel (maximally connected):* short, delimiting anteriorly about one quarter of length of antero-cranial fontanel (state 0; Figs 2A, B, 3A, 4B, 5A, B, 6A, B); moderately long, delimiting between one quarter and half of length of anterior cranial fontanel (state 1; Fig. 3B); very long, delimiting half of length of anterior cranial fontanel (state 2; Fig. 4A). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Amphiarius*, *Arius*, *Aspistor*, *Cathorops dasycephalus*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*,

*Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Schilbidae* and *Bagre*. State 2: *Cathorops* (except *Cat. dasycephalus*), and *Nemapteryx*.

The mesethmoid posterior branches and the frontals delimit the anterior cranial fontanel. Three conditions could be observed in the Ariidae and catfish outgroups described herein. In one condition, the posterior branches of mesethmoid are short, delimiting about one quarter of the total length of the anterior cranial fontanel. Exclusively in *Bagre*, the branches are moderately long, delimiting between one quarter and half of the total length of the anterior cranial fontanel. Additionally, in *Cathorops* (except *Cat. dasycephalus*) and *Nemapteryx* the mesethmoid posterior branches are very long, delimiting half of the total length of the anterior cranial fontanel.

9. *Shape of lateral ethmoid:* not expanded (state 0; Figs 2A, B, 3A, B, 4A, 5A, B, 6A); expanded





**Figure 6.** Neurocranium, dorsal view. A, *Sciades herzbergii*, MZUSP 51695; B, *Plicofollis dussumieri*, LACM 3811-48. Abbreviation: FRmlp, frontal mesial laminar projection. Scale bars = 10 mm.

(state 1; Fig. 6B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Ampharius*, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis platystomus*, *Plicofollis tenuispinis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Plicofollis dussumieri*, *Plicofollis nella*, and *Plicofollis polystaphilodon*.

The lateral ethmoids are anteriorly sutured to the mesethmoid, posterodorsally to the frontals, and posteroventrally to the orbitosphenoid and the parasphenoid. In the Ariidae the anterior part of the lateral ethmoid is triangular or cuneiform; only in some species of *Plicofollis* is the anterior part of lateral ethmoid bulky, globular.

10. *Lateral horn of lateral ethmoid*: inconspicuous (state 0; Fig. 4B); conspicuous (state 1; Figs 2A, B, 3A, B, 4A, 5A, B, 6A, B). State 0: Diplomystidae, *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*. State 1: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Ampharius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Amongst the Ariidae, absence of a conspicuous horn on the lateral ethmoid is a condition shared only by *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*. Missing in the Bagridae, Doradidae, and Schilbidae.

11. *Shape of lateral horn of lateral ethmoid*: slightly compressed and acute (state 0); very compressed and spatulate (state 1). State 0: Anchariidae,

Austroglanididae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Amphiarius*, *Aspistor*, *Bagre panamensis*, *Bagre pinnimaculatus*, *Brustiarius*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Plicofollis platystomus*, *Pl. tenuispinis*, *Potamosilurus macrorhynchus*, *S. parkeri*, *S. passany*, and *S. proops*. State 1: Cranoglanididae, *Arius*, *Bagre bagre*, *Bagre marinus*, *Carlarius*, *Cathorops*, *Cinetodus*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Pachyula*, *Pl. dussumieri*, *Pl. nella*, and *Pl. polystaphilodon*, *Potamarius*, *Potamosilurus* (except *Potamosilurus macrorhynchus*), and *Sciades* (except *S. parkeri*, *S. passany*, and *S. proops*).

The shape of the lateral ethmoid horn in ariids is variable, but two main distinct character states can be recognized: lateral horn of lateral ethmoid little differentiated, slightly compressed, and acute vs. conspicuously present as a compressed, truncate structure like a spatula. Missing in the Bagridae, Doradidae, Schilbidae, and *Notarius troschelii* and not applicable in the Diplomystidae, *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*.

12. *Length and disposition of lateral horn of lateral ethmoid (minimally connected)*: short and laterally orientated (state 0; Figs 2A, 3B); moderately long and lateroposteriorly orientated (state 1; Figs 2B, 3A, 4A, 6A); long and posteriorly orientated (state 2; Figs 5A, B, 6B). State 0: Horabagridae, *Ar. caelatus*, *Bagre*, *Brustiarius*, *Cochlefelis danielsi*, *Galeichthys*, *Pl. tenuispinis*, *S. parkeri*, *S. passany*, and *S. proops*. State 1: Cranoglanididae, *Amphiarius*, *Aspistor*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis spatula*, *Cryptarius*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis platystomus*, *Potamosilurus*, and *Sciades* (except *S. parkeri*, *S. passany*, and *S. proops*). State 2: *Arius* (except *Ar. caelatus*), *Doiichthys*, *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), and *Potamarius*.

In *Horabagrus* and several ariid genera the lateral horn of the lateral ethmoid is short and laterally orientated. Another condition is represented by a lateral horn of moderate length that is posteriorly orientated. An additional condition is characterized by a lateral horn very long and posteriorly orientated. Not applicable in the Diplomystidae, *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* and missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae,

Claroteidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

13. *Shape of external posterior branch of lateral ethmoid*: columnar (state 0); depressed (state 1). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Pachyula*, *Potamarius*, and *Potamosilurus*. State 1: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Batrachocephalus*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, and *Sciades*.

A columnar external posterior branch of the lateral ethmoid (i.e. as high as broad) is an exclusive condition in the Ariidae. Not applicable in the Cetopsidae, Diplomystidae, Doradidae, Mochokidae, and *Ketengus*.

14. *Contact face between lateral ethmoid and frontal (minimally connected)*: absent (state 0, Fig. 4B); through a single facet (state 1); through two facets without the presence of a fenestra (state 2); through two facets that delimit a fenestra (state 3; Figs 2A, B, 3A, B, 4A, 5A, B, 6A, B). State 0: *Ketengus*. State 1: Diplomystidae, Cetopsidae, Doradidae, and Mochokidae. State 2: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, and Ictaluridae. State 3: Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The contact between lateral ethmoid and frontal through a single facet represents the plesiomorphic condition in the Siluriformes in relation to other otophysans (de Pinna, 1993). Amongst ariids, this condition is present only in *Ketengus*. In the derived condition the lateral ethmoid and the frontal are connected through two facets (de Pinna, 1993). A frontal anterolateral extension (or external anterior process) contacts a posterior lateral ethmoid extension that forms a bony bridge delimiting a slight depression. In most Ariidae the extreme condition of the character is reached, the external posterior branch of the lateral ethmoid and the external anterior process of the frontal are developed and more laterally displaced in the cranium, delimiting a con-

spicuous window or fenestra sometimes visible even in specimens not cleared and stained.

15. *Composition of bony bridge formed by lateral ethmoid and frontal (minimally connected)*: lateral ethmoid is main component (state 0; Figs 2B, 5A, 6A, B); lateral ethmoid and frontal are equally represented (state 1; Figs 2A, 3B, 5B); frontal is main component (state 2; Figs 3A, 4A). State 0: *Arius*, *Aspistor*, *Batrachocephalus*, *Carlarius*, *Genidens*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: Pangasiidae, Schilbidae, *Brustarius*, *Bagre*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Nedystoma*, *Neoarius*, *Nemapteryx*, and *Pachyula*. State 2: *Amphiarius*, *Cathorops*, *Cephalocassis*, and *Hemiaris*.

The lateral ethmoids interdigitate with the frontal external anterior processes through their external posterior branches forming a continuous bridge in which a fenestra is mesially delimited. The extension and thickness of this bony bridge are variable in the Ariidae, and the equal participation of both bones is shared with some catfish families. However, one of these bones as the main component of the bony bridge is exclusive of the Ariidae (states 0 and 2, above express). Not applicable in the Diplomystidae, Cetopsidae, Doradidae, Mochokidae, and *Ketengus* and missing in the Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, and Ictaluridae.

16. *Thickness of bony bridge formed by lateral ethmoid and frontal*: thick to moderately thick (state 0; Figs 2A, 3B, 5A, 6A, B); very thin (state 1; Figs 2B, 3A, 4A, 5B). State 0: Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Amphiarius*, *Aspistor*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, and *Nemapteryx*.

In most ariids, the bony bridge formed by the lateral ethmoid and the frontal is moderately thick. In another condition, the external posterior branch of the lateral ethmoid and the external anterior process of the frontal are very thin, making the bony bridge a very fragile structure. Not applicable in the Diplomystidae, Cetopsidae, Doradidae, Mochokidae, and *Ketengus* and missing in the Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, and Pangasiidae.

17. *Size of fenestra delimited by lateral ethmoid and frontal (minimally connected)*: very small or indistinct (state 0; Fig. 6A, B); moderately large (state 1; Figs 2A, B, 3B, 5A); very large (state 2; Figs 3A, 4A, 5B). State 0: *Batrachocephalus*, *Cochlefelis*, *Netuma*, *Occidentarius*, *Plicofollis*, and *Sciades*. State 1: Pangasiidae, Schilbidae, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cinetodus*, *Galeichthys*, *Genidens*, *Neoarius*, *Notarius*, *Pachyula*, *Potamarius*, and *Potamosilurus*. State 2: *Amphiarius*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, and *Osteogeneiosus*.

The fenestra between lateral ethmoid and frontal is well differentiated in many Ariidae. The extreme condition of the character is represented by a very large fenestra, clearly visible in specimens not cleared and stained, in *Amphiarius*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, and *Osteogeneiosus*. In *Batrachocephalus*, *Cochlefelis*, *Netuma*, *Plicofollis*, and *Sciades* the fenestra is very reduced and sometimes partially closed during ontogenetic development, with an intermediate condition represented by state 1. Not applicable in the Diplomystidae, Cetopsidae, Doradidae, Mochokidae, and *Ketengus* and missing in the Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, and Ictaluridae.

18. *Position of nasal in relation to mesethmoid*: parallel (state 0); perpendicular (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Ketengus*.

The nasal bones are attached by ligaments to the anterior and posterior horns of the mesethmoid and are parallel to the main axis of the latter. Exclusively in *Ketengus* they are perpendicular to the anteroposterior axis of the cranium. Missing in *Batrachocephalus*.

19. *Shape of nasal (maximally connected)*: shaped like a hockey club (state 0); shape not well defined (state 1); fan shaped (state 2). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglani-

didae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Doiichthys*. State 2: *Batrachocephalus*.

In the Siluriformes (Lundberg, 1982; Arratia, 1987) the nasals are long, laminar, and slightly curved and expanded along their anterior third, similar to a hockey club. In the Ariidae, two conditions are defined as expressed by state characters 1 and 2 above.

20. *Nasal anterior curvature*: little pronounced (state 0); very pronounced (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Osteogeneiosus*.

Nasal anterior part with a very pronounced lateral curvature, almost in form of a straight angle, is a condition exclusively found in *Osteogeneiosus* (see discussion of character 21). Missing in *Doiichthys*.

21. *Bony blade anteriorly connecting nasal tubules*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Osteogeneiosus*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the anterior portion of the nasal bone two tubules are present: one short and dorsally orientated, the second longer and anteriorly directed. In most Siluriformes, these tubules are well developed and free. In the Ariidae (except *Osteogeneiosus*) another condition is represented by the presence of a

bony blade connecting the tubules. Not applicable in *Doiichthys* and missing in the Diplomystidae and Cetopsidae.

22. *Relationship between lachrymal–antorbital and frontal*: coalesced or only partially differentiated (state 0; Figs 2A, B, 3A, 4A, B, 5A, B, 6A, B); distinct from each other (state 1; Fig. 3B) State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Occidentarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Pangasiidae, Schilbidae, and *Bagre*.

A lachrymal–antorbital tubular bone distinct from the frontal bone is an exclusive condition of *Bagre*, amongst ariids, and shared with Schilbidae and the Pangasiidae.

23. *Frontal mesial laminar projection*: absent (state 0; Figs 2A, B, 3A, 4A, 5A, B); present (state 1; Fig. 6A, B). State 0: Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Heptapteridae, Ictaluridae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Potamarius*, and *Potamosilurus latirostris*. State 1: Anchariidae, Claroteidae, Horabagridae, Pangasiidae, Schilbidae, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamosilurus* (except *Potamosilurus latirostris*), and *Sciades*.

The mesial region of the frontal bone is characterized by absence of any projections in the Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Heptapteridae, Ictaluridae, Mochokidae, and several ariid genera. However, in Anchariidae, Claroteidae, Horabagridae, Pangasiidae, Schilbidae, and other ariids, the mesial margin of the frontals has a laminar projection that brings the inner margins of the frontals close together, partially covering the anterior cranial fontanel. Missing in the Austroglanididae and Doradidae.

24. *Anterior portion of anterior cranial fontanel*: not delimited by dorsal expansion of orbitosphenoid (state 0; Figs 2A, 3A, 4B, 5B); partially or totally

delimited by dorsal expansion of orbitosphenoid (state 1; Figs 2B, 3B, 4A, 5A, 6A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Galeichthys*, *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Ketengus*, *Nedystoma*, and *Nemapteryx*. State 1: Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Genidens*, *Hemiarius*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The grooved orbitosphenoid is part of the anterior floor of the neurocranium. Its dorsal portion is uncovered under the cranial fontanel, forming a bony block partially covered by the frontals and the mesethmoid, delimiting the cranial cavity and the anterior quarter of the cranial fontanel (Higuchi, 1982). Amongst the Ariidae, in *Galeichthys*, *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Ketengus*, *Nedystoma*, and *Nemapteryx*, the dorsal part of the orbitosphenoid is not exposed and is excluded from the anterior portion of the cranial fontanel.

25. *Bones associated with formation of posterior cranial fontanel*: frontals and parietosupraoccipital (state 0; Figs 2B, 3A, 4B, 5B); exclusively frontals (state 1; Figs 2A, 3B, 4A, 5A, 6B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Cathorops dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Neoarius*, *Nemapteryx*, *Notarius*, *Pachyula*, and *Potamosilurus*. State 1: Claroteidae, Mochokidae, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Galeichthys*, *Genidens*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, and *Potamarius*.

The participation of the frontals in the delimitation of the posterior cranial fontanel was considered by Tilak (1965) to be an important diagnostic character for ariid genera. This fontanel in the Ariidae is mostly delimited by both the frontals and the parietosupraoccipital. However, in some ariid genera it is delimited only by the frontals. Not applicable in *Batrachocephalus*, and *Sciades* and missing in the Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, and *Ar. caelatus*.

26. *Posterior cranial fontanel*: absent (state 0; Fig. 6A); present (state 1; Figs 2A, B, 3A, B, 4A, B, 5A, B, 6B). State 0: Heptapteridae, Horabagridae, *Batrachocephalus*, and *Sciades*. State 1:

Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus*.

In most Siluriformes two openings are visible dorsally on the cranium (Lundberg, 1970; Mo, 1991; de Pinna, 1991). Most Siluriformes have a posterior cranial fontanel at some stage of its ontogenetic development and participation of the frontals and the parietosupraoccipital is variable. Amongst ariids, only in *Batrachocephalus* and *Sciades* is the posterior cranial fontanel always absent.

27. *Size of posterior cranial fontanel (minimally connected)*: reduced to a small opening (state 0; Figs 2A, 3A, 4A, 6B); relatively narrow and long (state 1; Figs 4B, 5A); wide and long (state 2; Fig. 2B); very wide and long (state 3; Figs 3A, 5B). State 0: Claroteidae, Cranoglanididae, *Bagre*, *Brustiarius*, *Cathorops* (excluding *Cat. dasycephalus*), *Galeichthys*, *Genidens*, *Netuma*, and *Plicofollis* (except *Pl. platystomus*). State 1: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Ictaluridae, Pangasiidae, Schilbidae, *Arius*, *Carlarius*, *Cat. dasycephalus*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Ketengus*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis platystomus*, *Potamarius*, and *Potamosilurus* (except *Potamosilurus latirostris*). State 2: Mochokidae, *Amphiarius*, *Aspistor*, *Hemiarius*, and *Potamosilurus latirostris*. State 3: *Cephalocassis*, *Doiichthys*, *Nedystoma*, and *Nemapteryx*.

The size and shape of the posterior cranial fontanel are variable in the Ariidae. They can be represented by a minute to small rounded opening, sometimes partially or totally obliterated by superficial ossifications in advanced stages of development of representatives of taxa sharing character state 0 above. State characters 1, 2, and 3 express three additional conditions related to a gradually increase of the posterior cranial fontanel size in relation to cranial roof bones. Not applicable in *Batrachocephalus*, *Cinetodus*, and *Sciades* and missing in the Doradidae, Heptapteridae, and Horabagridae.

28. *Epiphyseal bar*: conspicuous (state 0; Figs 2A, B, 3A, B, 4A, B, 5A, B, 6B); indistinct (state 1; Fig. 6A). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Clar-

oteidae, Cranoglanididae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus*. State 1: Doradidae, *Batrachocephalus*, and *Sciades*.

Primitively in the Ostariophysi the frontals are mesially connected by a bony bar, denominated epiphyseal bar, that separates the cranial fontanel in anterior and posterior portions. Even in taxa where superficial ossifications obliterate the posterior cranial fontanel this bar can be visualized through a small fenestra where the bar should be located (Bockmann, 1998). Its absence in *Batrachocephalus* and *Sciades* is unique in the Ariidae. Missing in the Horabagridae.

29. *Size of epiphyseal bar*: transversely short and longitudinally wide (state 0; Figs 2A, 3B, 4A, B, 5A, 6B); transversely elongate and longitudinally narrow (state 1; Figs 2B, 3A, 5B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius* (except *Arius arius* and *Arius gogora*), *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus* (except *Potamosilurus latirostris*). State 1: *Amphiarius*, *Ar. arius*, *Ar. gogora*, *Aspistor*, *Cephalocassis*, *Doiichthys*, *Hemiaris*, *Notarius*, *Nedystoma*, *Nemapteryx*, and *Potamosilurus latirostris*.

Amongst ariids and outgroup catfishes, two conditions are observed in relation to the size of the epiphyseal bar: a short and wide inconspicuous bar in contrast to the relatively long and narrow form. Not applicable in *Sciades* and missing in the Horabagridae.

30. *Medial groove of cranium*: present (state 0; Figs 2A, 3B, 4A,B, 5A, 6A, B); absent (state 1; Figs 2B, 3A, 5B). State 0: Anchariidae, Cranoglanididae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius planiceps*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus* (except *Potamosilurus latirostris*), and *Sciades*. State 1: Austro-

glanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Cephalocassis*, *Cinetodus*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Notarius* (except *No. planiceps*), *Pachyula*, and *Potamosilurus latirostris*.

The medial groove is formed by a depression of the frontal mesial faces that extends posteriorly until the anterior portion of the parietosupraoccipital. Its presence could be observed in most ariid taxa, shared with the Anchariidae and the Cranoglanididae, amongst catfish outgroups. However, the absence of a medial groove is a condition shared by most of the catfish families and the ariid representatives studied.

31. *Form of medial groove of cranium*: shallow with margins not very conspicuous (state 0; Figs 2A, 6A); deep with margins very conspicuous (state 1; Figs 3B, 4A, B, 5A, 6B). State 0: *Bag. panamensis*, *Bag. pinnimaculatus*, *Cochlefelis*, *Galeichthys*, *No. planiceps*, *S. couma*, *S. herzbergii*, *S. guatemalensis*, *S. leptaspis*, and *S. passany*. State 1: Anchariidae, Cranoglanididae, *Arius*, *Bag. bagre*, *B. marinus*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cryptarius*, *Genidens*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus* (except *Potamosilurus latirostris*), and *Sciades* (except *S. couma*, *S. herzbergii*, *S. guatemalensis*, *S. leptaspis*, and *S. passany*).

Amongst catfishes with a medial groove on the cranial roof, the most common condition is a deep and very conspicuous groove. However, in *Bag. panamensis*, *Bag. pinnimaculatus*, *Cochlefelis*, *Galeichthys*, *No. planiceps*, *S. couma*, *S. herzbergii*, *S. guatemalensis*, *S. leptaspis*, and *S. passany* the groove is shallow and inconspicuous. Not applicable in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Cephalocassis*, *Cinetodus*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Notarius*, *Pachyula*, and *Potamosilurus latirostris*.

32. *Delimitation of medial groove (minimally connected)*: delimited mainly by parietosupraoccipital (state 0; Figs 2A, 3B, 4A, B, 5A, 6B); delimited mainly by frontals (state 1); delimited exclusively by frontals (state 2; Fig. 6A). State 0: Anchariidae, Cranoglanididae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*,

and *Potamosilurus* (except *Potamosilurus latirostris*). State 1: *Occidentarius* and *Sciades* (except *S. couma*, *S. herzbergii*, *S. guatemalensis*, *S. leptaspis*, and *S. passany*). State 2: *S. couma*, *S. herzbergii*, *S. guatemalensis*, *S. leptaspis*, and *S. passany*.

Delimitation of the medial groove by the frontals and the parietosupraoccipital varies in the Ariidae and three character states are recognizable. Medial groove delimited mainly by the parietosupraoccipital represents the condition in the Anchariidae, Cranoglanididae, and several ariid genera. Participation mainly or exclusively by the frontals represents the two additional conditions. Not applicable in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Cephalocassis*, *Cinetodus*, *Doiichthys*, *Hemiarius*, *Nedystoma*, *Notarius*, *Pachyula*, and *Potamosilurus latirostris*.

33. *Bones forming cephalic shield*: smooth or grooved (state 0; Figs 2A, 3B); granulated (state 1; Figs 2B, 3A, 4A, B, 5A, B, 6A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Claroteidae, Pangasiidae, Schilbidae, *Bagre*, and *Galeichthys*. State 1: Cranoglanididae, Bagridae, Doradidae, Heptapteridae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Ornamentation of skull roof bones is a well-known characteristic of the Siluriformes (Lundberg, 1992), with the exception of the Diplomystidae and the Cetopsidae in which they are smooth. In the Ariidae the skull roof bones are variously rugose, granulated, and grooved, with the ornamentation following a radial pattern from the central parietal/supraoccipital region. In most members of the family rugosities and granulations are the most common types of ornamentation, usually visible even in specimens not cleared and stained. Exclusively in *Bagre* and *Galeichthys*, the bones of the cephalic shield are ornamented only with grooves and slits, a condition not shared with other ariid representatives. Types of ornamentation and thickness of the skin covering skull bones were used in the past by some authors (e.g. Günther, 1864) to differentiate *Arius sensu lato* from *Galeichthys*.

34. *Fenestra delimited by parietosupraoccipital, pterotic, and sphenotic*: absent (state 0; Figs 2A,

B, 3B, 4A, B, 5A, B, 6A, B); present (state 1; Fig. 3A). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: *Cephalocassis*.

In most Siluriformes, the pterotic, sphenotic, and parietosupraoccipital are strongly sutured. Nevertheless, several degrees of articulation could be observed between some of these bones. For example, a temporal fossa is delimited by the parietosupraoccipital, pterotic, and supracleithrum in the Akysidae, Aspredinidae, Chacidae, Erethistidae, and some representatives of Sisoridae and Plotosidae (Mahajan, 1966; de Pinna, 1996; Britto, 2002). Only in *Cephalocassis*, however, a fenestra is delimited by the parietosupraoccipital, pterotic, and sphenotic.

35. *Shape of extrascapular (minimally connected)*: subrectangular (state 0; Figs 2A, 3B, 4B, 6B); subquadrangular (state 1; Figs 2B, 5A, B, 6A); subtriangular (state 2; Fig. 4A). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Claroteidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Galeichthys*, *Genidens*, *Ketengus*, *Osteogeneiosus*, *Plicofollis*, *Potamarius grandoculis*, and *Potamosilurus velutinus*. State 1: *Amphiarius*, *Aspistor*, *Carlarius*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamarius izabalensis*, *Potamosilurus* (except *Potamosilurus velutinus*), and *Sciades*. State 2: *Cathorops* and *Cinetodus*.

The extrascapular, a laminar bone located on the posterodorsal region of the neurocranium (Fink & Fink, 1981; Arratia & Gayet, 1995), is sutured to the parietosupraoccipital, pterotic, and supracleithrum, covering the epioccipital partially or totally in the Ariidae. This bone is subrectangular, transversely elongate, its length at least twice as its width, a common condition in the outgroups and in the genera *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Galeichthys*, *Genidens*, *Ketengus*, *Osteogeneiosus*, *Plicofollis* and in the species *Potamarius grandoculis*, and *Potamosilurus velutinus*. In most ariid representatives, the extrascapular is oval-shaped to subquadrangular,

about as long as wide. Exclusively in *Cathorops* and *Cinetodus* it is very large, subtriangular, weakly articulated with the epioccipital, and its mesial face laterally delimits a large portion of the basal part of the parietosupraoccipital. Not applicable in *Pachyula* and missing in the Cetopsidae, Cranoglanididae, Doradidae, and Mochokidae.

36. *Temporal fossa*: present (state 0; Figs 2A, B, 3A, B, 4A, B, 5A, B, 6B); absent (state 1; Fig. 6A). State 0: Anchariidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *S. leptaspis*. State 1: Cranoglanididae, Doradidae, Mochokidae, *Occidentarius*, and *Sciades* (except *S. leptaspis*).

The temporal fossa is delimited by the pterotic, supracleithrum, extrascapular, and/or parietosupraoccipital, and its size varies greatly in the Ariidae. It is conspicuous in most members of the family and closed or inconspicuous in *Occidentarius* and *Sciades* (except *S. leptaspis*). Missing in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, and Schilbidae.

37. *Size of the temporal fossa*: very reduced (state 0; Figs 2A, 4A, 6B); moderate to very large (state 1; Figs 2B, 3A, 4B, 5A, B). State 0: *Bag. panamensis*, *Bag. pinnimaculatus*, *Brustarius*, *Cathorops*, *Cephalocassis borneensis*, *Cryptarius*, *Galeichthys*, *Genidens*, and *Netuma bilineata*. State 1: Anchariidae, *Amphiarius*, *Arius*, *Aspistor*, *Bag. bagre*, *Bag. marinus*, *Batrachocephalus*, *Carlarius*, *Cephalocassis melanochir*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Net. thalassina*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *S. leptaspis*.

The opening degree of the temporal fossa in the Ariidae allows the recognition of two distinct conditions concerning the character as defined above. Not applicable in the Cranoglanididae, Doradidae, Mochokidae, *Occidentarius*, and *Sciades* (except *S. leptaspis*) and missing in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, and Schilbidae.

38. *Participation of extrascapular in delimitation of temporal fossa*: less than one fifth (state 0;

Figs 2A, B, 3A, B, 4B, 5A, B, 6A, B); more than three fifths (state 1; Fig. 4A). State 0: Anchariidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops dasycephalus*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Net. thalassina*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *S. leptaspis*. State 1; *Cathorops* (except *Cat. dasycephalus*).

The participation of a significant portion of the extrascapular (more than three fifths of its length) in the delimitation of the temporal fossa, is observed only in *Cathorops* (except *Cat. dasycephalus*). Not applicable in the Cranoglanididae, Doradidae, Mochokidae, *Occidentarius*, and *Sciades* (except *S. leptaspis*) and missing in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Cephalocassis borneensis*, and *Netuma bilineata*.

39. *Epioccipital*: not exposed dorsally (state 0; Figs 2A, 3A, B, 4A, B, 5A, B, 6A); dorsally visible (state 1; Figs 2B, 6B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius phrygiatus*, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Doradidae, *Amphiarius rugispinis*, *Aspistor*, *Carlarius*, *Cinetodus*, *Pachyula*, and *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*).

Epioccipital visible in the dorsal part of the cranium was described for the Auchenipteridae and Doradidae by Regan (1911) and Ferraris (1988). Within the Ariidae the dorsally exposed epioccipital is a condition present only in *Am. rugispinis*, *Aspistor*, *Carlarius*, *Cinetodus*, *Pachyula*, and *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*).

40. *Epioccipital posterior process*: absent (state 0); present (state 1; Figs 2A–6B). State 0: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, and Mochokidae. State 1: Anchariidae, Doradidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*,



*Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Primitively in the Siluriformes the epioccipital posterior margin is smooth and no process or any posterior expansion is present. The presence of a laminar posterior process in the epioccipital was first recognized by Regan (1911) as a specialized condition in the Auchenipteridae, Ageneiosidae, Doradidae, and Ariidae, and later on as a synapomorphy for the Ariidae by Kailola (2004). According to de Pinna (1993) the epioccipital posterior process is also present in the Anchariidae, and in large specimens of the Pangasiidae and Schilbidae. In the present study, an epioccipital posterior process was observed in all ariid representatives.

41. *Length of epioccipital posterior process*: short (state 0; Fig. 2A); very long (state 1; Figs 2B–6B). State 0: Anchariidae, Doradidae, Pangasiidae, Schilbidae, and *Galeichthys*. State 1: *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

An epioccipital posterior process short, not connected to the expanded parapophysis of the complex vertebra, is observed only in *Galeichthys* within the Ariidae. In other members of this family, the epioccipital posterior process is long and connected to the expanded parapophysis of the complex vertebra through a strong suture with the crests associated with the neural spine of the fourth vertebra. This is an extreme condition in relation to that observed in the Anchariidae, Auchenipteridae (except some representatives, as assigned in Ferraris, 1988), Doradidae, Pangasiidae, and Schilbidae (de Pinna, 1993). Not applicable in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, and Mochokidae.

42. *Relationship between epioccipital posterior process and crests associated with neural spine of fourth vertebra (minimally connected)*: contacting a small narrow area of the diagonal crest (state 0); contacting both the diagonal and transversal crests (state 1); contacting a large area of diagonal crest (state 2). State 0:

*Amphiaris*, *Aspistor*, *Bagre*, *Cep. melanochir*, *Cinetodus*, *Cryptarius*, *Hemiaris*, *Notarius*, *Occidentarius*, and *Potamarius izabalensis*. State 1: *Batrachocephalus*, *Cathorops*, *Cep. borneensis*, *Doiichthys*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Pachyula*, *Pl. tenuispinis*, and *Pl. platystomus*. State 2: *Arius*, *Brustiaris*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Plicofollis* (except *Pl. tenuispinis* and *Pl. platystomus*), *Potamarius grandoculis*, *Potamosilurus*, and *Sciades*.

The epioccipital posterior process, usually thin and curved, has a laminar expansion that projects toward the medial axis and is sutured to the dorsal crests associated with the neural spine of the fourth vertebra (Regan, 1911; Higuchi, 1982). The degree of development of the transversal and diagonal crests associated with the neural spine of the fourth vertebra, and the extension of the contact area with the epioccipital posterior process, delineates three distinct conditions as defined above. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*.

43. *Relationship between epioccipital posterior process and medial crest associated with neural spine of fourth vertebra*: not connected (state 0); connected (state 1). State 0: Doradidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cryptarius*.

In the Ariidae, except *Cryptarius*, there is a complete separation between the epioccipital posterior process and the medial crest associated with the neural spine of the fourth vertebra. The presence of a bony bridge connecting the process and the crest occurs only in *Cryptarius*. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, and Mochokidae.

44. *Shape of parietosupraoccipital process (maximally connected)*: base almost as narrow as posterior portion (state 0; Figs 2A, 3A, 5B); base distinctly wider than posterior portion (state 1; Figs 2B, 3B, 4A, B, 5A, 6A, B); base conspicu-

ously narrower than posterior portion (state 2). State 0: Bagridae, *Cep. melanochir*, *Doiichthys*, *Galeichthys*, and *Nedystoma*. State 1: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis borneensis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Hemiarius*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius* (except *No. grandicassis*), *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *No. grandicassis*.

In the Siluriformes, the parietosupraoccipital is larger than in the remaining Otophysi because it is apparently fused with the parietals (Fink & Fink, 1981; Arratia, 1987, 1992). This structure is herein called the parietosupraoccipital in agreement with Arratia & Gayet (1995). The posterior half of the parietosupraoccipital corresponds to its process, which is primitively triangular (broad at base and narrow posteriorly), and sutured to the medial portion of the extrascapular in the Siluriformes (Lundberg, 1992). In ariid representatives, the shape of the parietosupraoccipital process is variable and two additional conditions are recognized. In *Cep. melanochir*, *Doiichthys*, *Galeichthys*, and *Nedystoma* the process width is nearly uniform with parallel lateral margins. Only in *No. grandicassis* is the process strongly constricted at its base, narrower proximally than distally, and with concave lateral margins.

45. *Margin of parietosupraoccipital process contacting nuchal plate*: concave or notched (state 0; Figs 2A, 3A, B, 4A, B, 5A, B, 6A, B); convex (state 1; Fig. 2B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. proops*). State 1: *Aspistor* and *S. proops*.

The posterior margin of the parietosupraoccipital process is fitted to the anterior margin of the nuchal plate in the Ariidae. In most of the studied specimens, the margin of contact of the parietosupraoccipital

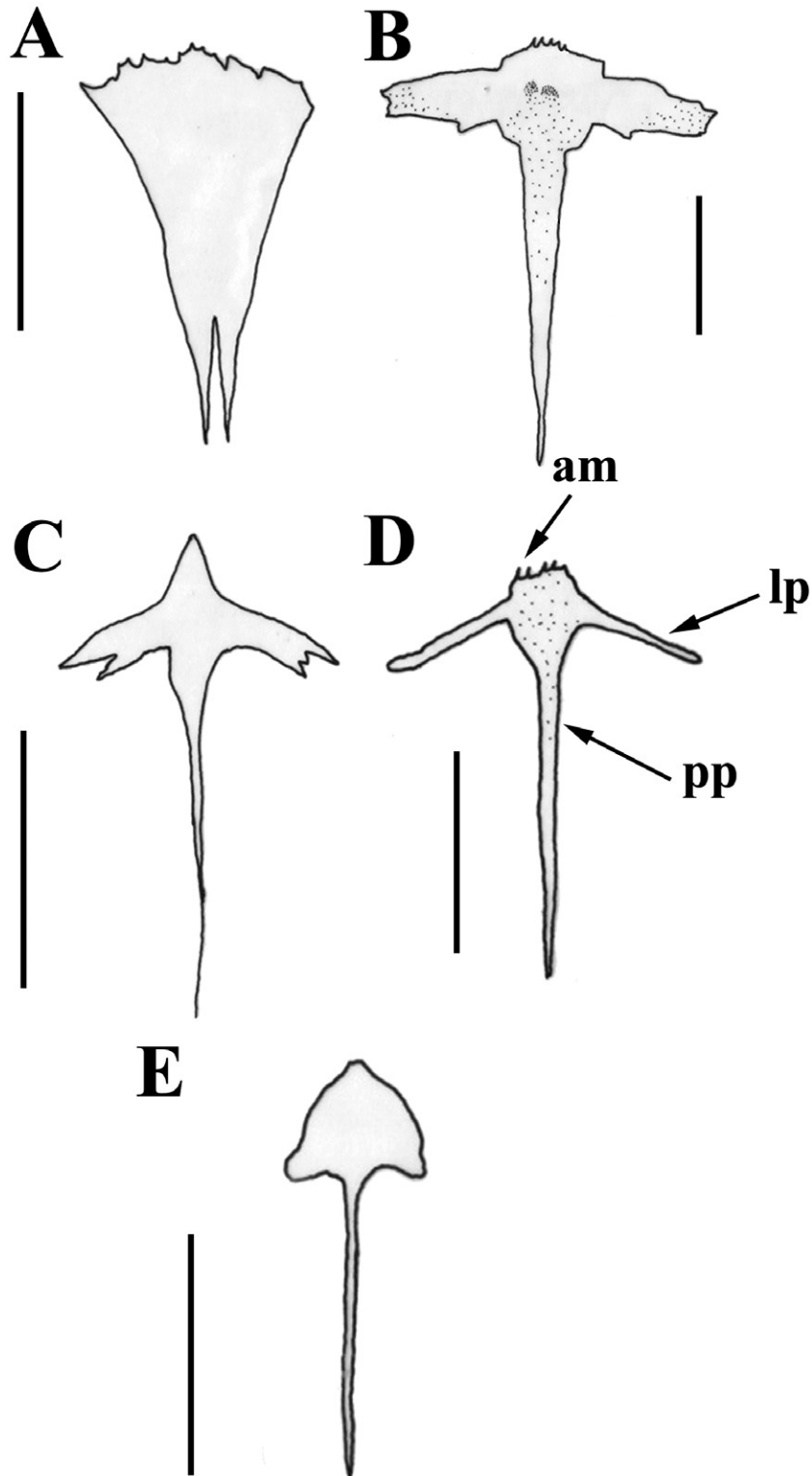
process is concave, notched, or angulated. Exclusively in *Aspistor* and *S. proops* the posterior portion of the parietosupraoccipital process is broadly convex and received by a shallow depression in the anterior margin of the nuchal plate.

46. *Ventral crest of parietosupraoccipital process*: weakly developed, restricted to base of process (state 0); well developed through entire extension of process (state 1). State 0: Bagridae, Doradidae, Mochokidae, *Arius*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Bagre*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Occidentarius*, and *Pachyula*.

The degree of development and extension of the medial bony crest in the ventral face of the parietosupraoccipital process vary in the Ariidae, originating two different conditions as defined above.

47. *General shape of vomer (maximally connected)*: diamond shaped (state 0; Fig. 7A); T-shaped (state 1; Fig. 7B–D); ovoid (state 2; Fig. 7E); arrow-shaped (state 3). State 0: Diplomystidae and *Ketengus*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. tenuispinis*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Plicofollis* (except *Pl. tenuispinis* and *Pl. platystomus*). State 3: *Cryptarius*.

The vomer lies in the anterior part of the cranium, inserted on the medial groove of the mesethmoid ventral face. Arratia (1987) recognized the large diamond-shaped structure present in the Diplomystidae as the plesiomorphic condition in Siluriformes. A diamond-shaped vomer, however, is also observed in *Ketengus*. Mo (1991) considered the T and arrow shapes, determined by the presence of the lateral and the posterior processes, as apomorphic for the Siluriformes minus Diplomystidae. According to Lundberg (1970), primitively in the Ariidae the vomer is



**Figure 7.** Vomer, ventral view. A, *Ketengus typus*, ANSP 60704; B, *Galeichthys feliceps*, MZUSP 87694; C, *Arius arius*, LACM 38129-95; D, *Netuma thalassina*, UMMZ 214630; E, *Plicofollis dussumieri*, LACM 38131-48. Abbreviations: am, anterior margin; lp, lateral processes; pp, posterior process. Scale bars = 4 mm.

T-shaped. In *Plicofollis* (except *Pl. tenuispinis* and *Pl. platystomus*), the central part of the vomer is oval-shaped, its lateral processes short, and the posterior processes very narrow throughout their entire length. A narrow-shaped vomer with very long lateral processes laterally orientated is another condition observed in *Cryptarius*.

48. *Outline of vomer anterior margin*: weakly pronounced and serrated (state 0; Fig. 7A, B, D); very pronounced and acute (state 1; Fig. 7C, E). State 0: Anchariidae, Diplomystidae, Bagridae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *No. planiceps*, *Occidentarius*, *Potamosilurus* (except *Potamosilurus macrorhynchus*), and *Sciades*. State 1: Austroglanididae, Cranoglanididae, Claroteidae, *Amphiarius*, *Arius*, *Aspistor*, *Cephalocassis*, *Cinetodus*, *Potamarius*, *Osteogeneiosus*, *Plicofollis*, *Notarius* (except *No. planiceps*), *Pachyula*, and *Potamosilurus macrorhynchus*.

The vomer anterior margin fits and is entirely interdigitated with a notch in a medial ventral groove of the mesethmoid. A weakly pronounced and serrated anterior margin represents the condition found in the Ariidae and catfish outgroups. Missing in the Cetopsidae.

49. *Vomer lateral processes*: absent (state 0; Fig. 7A); present (state 1; Fig. 7B–E). State 0: Diplomystidae and *Ketengus*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The vomer bearing lateral processes is the most common condition in Siluriformes, except in the Diplomystidae and *Ketengus* (see discussion of character 47). Missing in the Heptapteridae.

50. *Length of vomer lateral processes*: long (state 0; Fig. 7B–D); short (state 1; Fig. 7E). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae,

Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis tenuispinis*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Plicofollis* (excluding *Pl. tenuispinis* and *Pl. platystomus*).

In the Ariidae the lateral processes of the vomer vary greatly in length and width, but they are relatively elongate in most of its representatives. Contrasting with this condition, the processes are short and not well developed in *Plicofollis* (except *Pl. tenuispinis* and *Pl. platystomus*). Not applicable in the Diplomystidae and *Ketengus*, and missing in the Heptapteridae.

51. *Width of vomer lateral processes*: very wide (state 0; Fig. 7B, C); narrow (state 1; Fig. 7D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Cinetodus*, *Galeichthys*, *Nemapteryx*, *Notarius planiceps*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis tenuispinis*, *Pl. platystomus*, *Potamosilurus*, and *Sciades*. State 1: *Amphiarius*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Neoarius*, *Netuma*, *Notarius* (except *No. planiceps*), and *Potamarius*.

A very wide lateral process of the vomer is the condition shared with other catfish families. Not applicable in the Diplomystidae, *Ketengus*, and *Plicofollis* (*Pl. tenuispinis* and *Pl. platystomus*).

52. *Width of anterior portion of posterior process of vomer*: wider than posterior portion (state 0; Fig. 7A–D); as narrow as distal portion (state 1; Fig. 7E). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Pl. tenuispinis*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*.

State 1: *Osteogeneiosus* and *Plicofollis* (excluding *Pl. tenuispinis* and *Pl. platystomus*).

In most Ariidae and other catfishes, the posterior process of the vomer is widest proximally, and progressively narrow distally. In *Osteogeneiosus* and most of *Plicofollis*, the posterior process is uniformly narrow.

53. *Tooth plates associated with vomer*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Ictaluridae, Mochokidae, *Amphiarius*, *Arius*, *Batrachocephalus*, *Carlarius*, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Genidens genidens*, *Ketengus*, *Nedystoma*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Potamosilurus velutinus*. State 1: Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Pangasiidae, Schilbidae, *Aspistor*, *Bagre*, *Brustiarius*, *Cat. dasycephalus*, *Cochlefelis*, *Galeichthys*, *Genidens* (except *G. genidens*), *Hemarius*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Plicofollis* (except *Pl. platystomus*), *Potamosilurus* (except *Potamosilurus velutinus*), and *Sciades*.

Although the presence of teeth associated with the vomer is considered apomorphic in the Siluriformes amongst ostariophysans (de Pinna, 1993), this condition appears to have been lost or independently acquired several times within the order. Amongst Siluriformes, absence of vomerine tooth plates is observed in many ariid representatives.

54. *Shape of vomerine tooth plates (maximally connected)*: transversely elongate (state 0); rounded (state 1); butterfly-shaped (state 2); fused as a single large plate (state 3). State 0: Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Pangasiidae, Schilbidae, *Bagre*, and *Galeichthys*. State 1: *Cat. dasycephalus*, *Cochlefelis*, *Genidens* (except *G. genidens*), *Hemarius*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Plicofollis* (except *Pl. platystomus*), *Potamosilurus* (except *Potamosilurus velutinus*), and *Sciades*. State 2: *Brustiarius*. State 3: *Aspistor*.

The shape of the vomerine tooth plate shows a large array of variation within the Ariidae, which is largely useful for species identification (see character 23). The observed variation allows recognition of four states according to shape and arrangement of the plates. The condition of narrow and transversely elongated plates observed in *Bagre* and *Galeichthys* is shared with other outgroup catfish families. Other

conditions, observed exclusively amongst ariids are: small and rounded plates; plates arranged in a somewhat butterfly shape; and just one large plate. Some taxa may have a secondary fusion between the tooth plates in older individuals, but only *Aspistor* exhibits a large tooth plate in specimens at all developmental stages. Not applicable in Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Ictaluridae, Mochokidae, *Amphiarius*, *Arius*, *Batrachocephalus*, *Carlarius*, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *G. genidens*, *Ketengus*, *Nedystoma*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Potamosilurus velutinus*.

55. *Type of attachment between tooth plates and vomer (minimally connected)*: tooth plates directly attached to vomer (state 0); tooth plates attached to vomer by ligaments (state 1); tooth plates entirely free (state 2). State 0: Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Heptapteridae, Horabagridae, Pangasiidae, Schilbidae, *Aspistor*, *Bagre*, *Brustiarius*, *Cat. dasycephalus*, *Cochlefelis*, *Galeichthys*, *Hemarius*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamosilurus* (except *Potamosilurus velutinus*), and *Sciades*. State 1: *Genidens* (except *G. genidens*). State 2: *Plicofollis* (except *Pl. platystomus*).

In the Ariidae the tooth plates are directly attached to the vomer. Only in *Genidens* (except *G. genidens*) are the plates attached by ligaments. An additional condition is represented by absence of attachment, the plates remaining free below vomer in *Plicofollis* (except *Pl. platystomus*). Kailola (1990) described those plates, in *Plicofollis*, as the second pair of accessory tooth plates. Not applicable in the Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Ictaluridae, Mochokidae, *Amphiarius*, *Arius*, *Batrachocephalus*, *Carlarius*, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Genidens genidens*, *Ketengus*, *Nedystoma*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Potamosilurus velutinus*.

56. *Accessory tooth plates*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Cep. borneensis*, *Ketengus*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus*. State 1: Claroteidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cep. melanochir*, *Cinetodus*,

*Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius grandoculis*, *Potamosilurus latirostris*, and *Sciades*.

Historically, accessory tooth plates have been the main characteristics used to identify ariid species. Tilak (1965) stated that the shape and size of plates and teeth can characterize different species, but this was later contested by several authors who observed ontogenetic changes and differences between sexes (Tobor, 1969; Jayaram & Dhanze, 1978; Marceniuk, 1997). In spite of their structural importance, the origin of accessory plates has been in dispute over a long period of time. Regan (1911), Starks (1926), Bamford (1948), and Bailey & Stewart (1984) interpreted this condition simply as modified dermopalatines; Fink & Fink (1981) interpreted this condition as neomorphic autogenous formations, as they hypothesized that there is no dermopalatine in Otophysi (Fink & Fink, 1996). Grande (1987) considered those tooth plates as ectopterygoid accessory tooth plates. According to de Pinna (1993) the accessory tooth plates represent fragmented extensions of vomerine tooth plates, with which they are connected through ligaments and their presence was interpreted as unique within the Siluriformes. In the Schilbidae, there are no accessory tooth plates in *Laides* and *Siluranodon* (Britto, 2003). Missing in *Potamosilurus macrorhynchus*.

57. *Number of accessory tooth plates (maximally connected)*: one pair (state 0); two pairs (state 1); several small plates (state 2). State 0: Claroteidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens machadoi*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius grandoculis*, *Potamosilurus latirostris*, and *Sciades*. State 1: *Netuma*. State 2: *Genidens* (except *G. machadoi*).

The presence of a single pair of accessory tooth plates in representatives of the Ariidae is a condition shared by the Claroteidae, Pangasiidae, and Schilbidae. Two pairs of accessory tooth plates is a condition found only in *Netuma* and a set of small plates is present exclusively in *Genidens* (except *G. machadoi*). Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Cep. borneensis*, *Ketengus*,

*Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus* and missing in *Potamosilurus macrorhynchus*.

58. *Shape of accessory tooth plates (maximally connected)*: small, transversely elongate, and narrow (state 0, see Kailola, 1999: 868); small and rounded (state 1); large, oval to subtriangular (state 2, see Acero P., 2003: 840, 842); small, vertically oval (state 3, see Acero P., 2003: 849); large, longitudinally elongate (state 4, see Acero P., 2003: 845); moderately large, lateral and irregularly rounded (state 5, see Acero P., 2003: 846). State 0: Claroteidae, Pangasiidae, Schilbidae, *Bagre*, *Galeichthys*, *Cochlefelis*, *Neoarius*, *Potamosilurus latirostris*, *S. guatemalensis*, and *S. leptaspis*. State 1: *Brustiarius*. State 2: *Arius caelatus*, *Ar. dispar*, *Ar. madagascariensis*, *Carlarius*, *G. machadoi*, *Netuma*, *Notarius*, *Occidentarius*, and *Sciades* (except *S. guatemalensis*, *S. leptaspis*, and *S. passany*). State 3: *Batrachocephalus*, *Cathorops*, *Cep. melanochir*, *Cryptarius*, *Doiichthys*, and *Hemiaris*. State 4: *Arius* (except *Ar. caelatus*, *Ar. dispar*, and *Ar. madagascariensis*), *Aspistor*, *Osteogeneiosus*, and *Plicofollis*. State 5: *Amphiarius*.

As previously discussed (see discussion of character 56) even though accessory tooth plates have traditionally been used to distinguish ariid species, variation of their shape is still poorly known. Accessory tooth plates elongate and transversely narrow is the condition found in *Bagre*, *Galeichthys*, *Cochlefelis*, *Neoarius*, *Potamosilurus latirostris*, *S. guatemalensis*, and *S. leptaspis*, and shared with the Claroteidae, Pangasiidae, and Schilbidae. Five character states are found amongst ariids. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Cep. borneensis*, *Ketengus*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus* and missing in *Cinetodus*, *Genidens* (except *Ge. machadoi*), *Nemapteryx*, *Potamarius grandoculis*, *Potamosilurus macrorhynchus*, and *S. passany*.

59. *Shape of accessory tooth plates teeth*: needle-like (state 0); molariform (state 1). State 0: Pangasiidae, Schilbidae, Claroteidae, *Amphiarius*, *Ar. caelatus*, *Ar. madagascariensis*, *Bagre*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamarius grandoculis*, *Potamosilurus latirostris*, and *Sciades*. State 1: *Arius*

(*Ar. caelatus* and *Ar. madagascariensis*), *Aspistor*, *Batrachocephalus*, *Cathorops* (except *Cat. dasycephalus*), *Osteogeneiosus*, and *Plicofollis*.

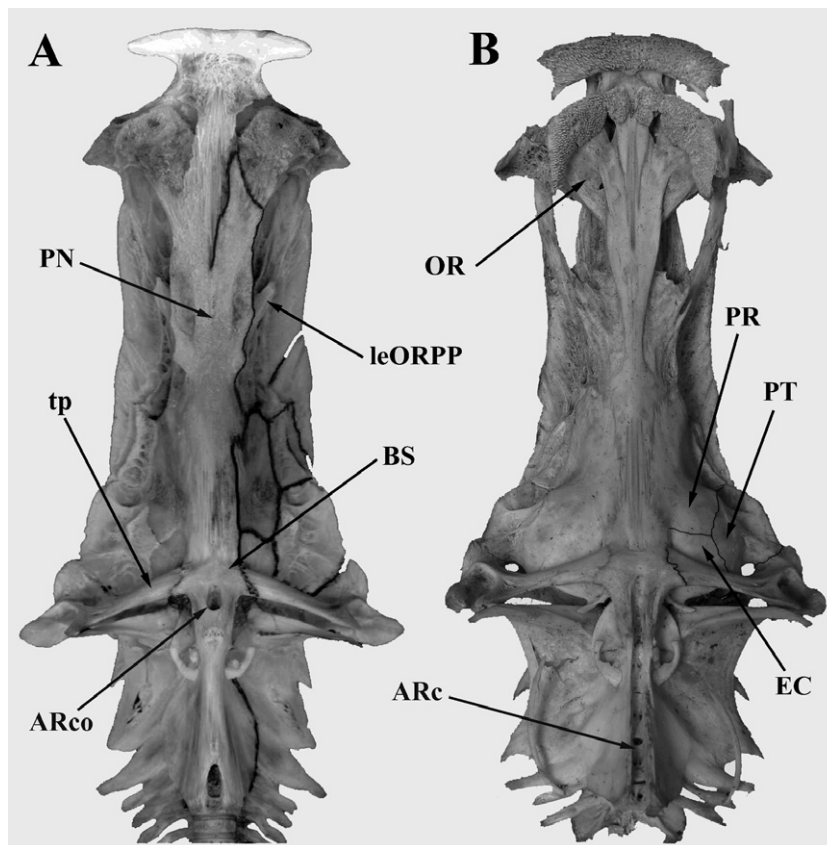
Accessory tooth plates in the Ariidae can have needle-like teeth or more rarely molariform-like teeth. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Cep. borneensis*, *Ketengus*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus* and missing in *Potamosilurus macrorhynchus*.

60. *Location of accessory tooth plates (maximally connected)*: apposed to lateral ethmoid (state 0); apposed to orbitosphenoid and metapterygoid (state 1); situated between premaxilla and lateral ethmoid (state 2). State 0: Pangasiidae, Schilbidae, Claroteidae, *Amphiarius*, *Ar. caelatus*, *Ar. madagascariensis*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Gale-*

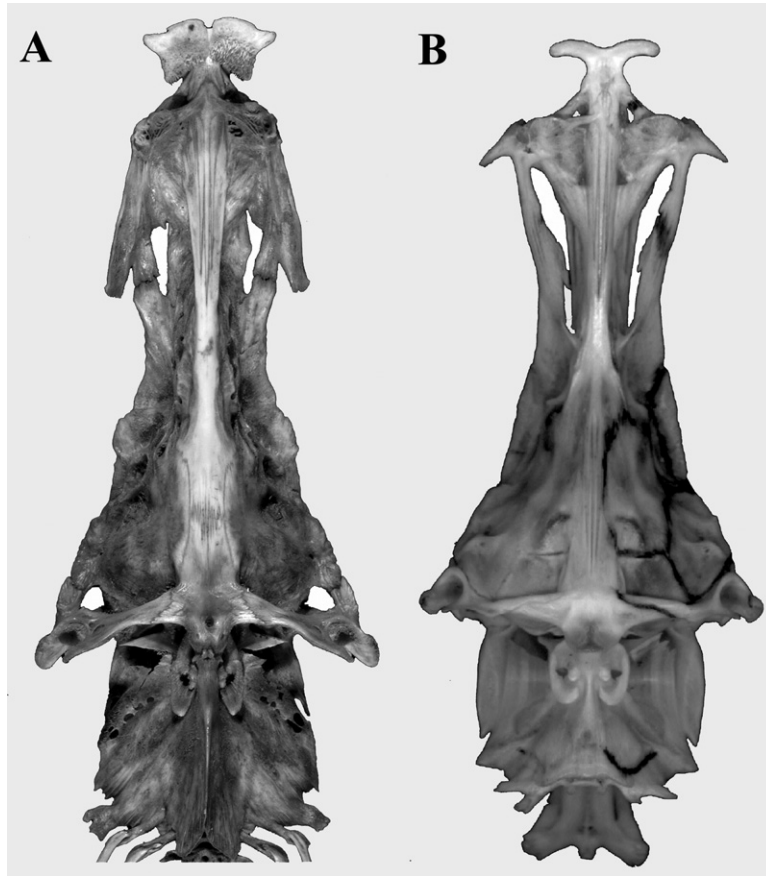
*ichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamosilurus latirostris*, and *Sciades*. State 1: *Arius* (except *Ar. caelatus* and *Ar. madagascariensis*), *Aspistor*, *Osteogeneiosus*, and *Plicofollis*. State 2: *Batrachocephalus*.

In the Ariidae and other catfish outgroups, the accessory tooth plates are apposed to the lateral ethmoid. The locations, as expressed by other character states defined above, are considered unique amongst ariids. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Cep. borneensis*, *Ketengus*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus* and missing in *Potamosilurus macrorhynchus*.

61. *Relationship between lateral margins of orbitosphenoid*: uniformly parallel along their entire length (state 0; Figs 8A, 9A, B); progressively diverging anteriorly (state 1; Fig. 8B). State 0:



**Figure 8.** Neurocranium, ventral view. A, *Sciades dowii*, INVEMAR PEC 6803, 296 mm standard length; B, *Genidens barbatus*, MZUSP (catalogue number not provided), with superficial ossification removed to expose the complex vertebra. Abbreviations: ARc, aortic canal; ARco, aortic canal opening; BS, basioccipital; EC, exoccipital; OR, orbitosphenoid; leORPP, lateral expansions of orbitosphenoid and pterosphenoid; PN, parasphenoid; PR, prootic; PT, pterotic; tp, transcapular process.



**Figure 9.** Neurocranium, ventral view. A, *Potamarius nelsoni*, UMMZ 198713-S, 480 mm standard length (SL); B, *Cathorops multiradiatus*, INVEMAR-PEC 6798, 186 mm SL.

Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Diplomystidae* and *Genidens*.

The orbitosphenoid is ankylosed to the lateral ethmoid, frontal, and parasphenoid, forming the anterior floor of the neurocranium. Amongst catfishes, the orbitosphenoid in ventral view has the lateral margins parallel, except in the *Diplomystidae* and the ariid *Genidens*. In both taxa, the lateral margins of the orbitosphenoid in ventral view progressively diverge posteroanteriorly and anteriorly are considerably separated in relation to the posterior portion of the orbitosphenoid.

62. *Lateral expansions of orbitosphenoid and pterosphenoid*: absent (state 0; Fig. 9A); present (state 1; Figs 8A, B, 9B). State 0: Anchariidae, Austroglanididae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, and *Potamarius*. State 1: Bagridae, Claroteidae, Heptapteridae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamosilurus*, and *Sciades*.

In the majority of siluriforms the orbitosphenoid and the pterosphenoid do not have lateral expansions. Mo (1991) considered the presence of such expansions in the Claroteidae and some Heptapteridae as apomorphic. In the present study, the presence of projections from both the orbitosphenoid and the



pterosphenoid near the optic foramen and surrounding the optic nerves was observed in most Ariidae.

63. *Shape of orbitosphenoid and pterosphenoid lateral expansions (maximally connected)*: two leaf-like short and wide processes (state 0; Fig. 8A, B); very narrow and long (state 1; Fig. 9B); slight projections with sinuous lateral face (state 2); slight projections with straight lateral faces (state 3). State 0: Bagridae, Claroteidae, Heptapteridae, Schilbidae, *Ar. caelatus*, *Ar. madagascariensis*, *Cat. dasycephalus*, *Galeichthys*, *Brustarius*, *Cinetodus*, *Neoarius*, *Genidens*, *Carlarius*, *No. planiceps*, *Netuma*, *Occidentarius*, *Pachyula*, *Pl. platystomus*, *Potamosilurus velutinus*, *Sciades* (except *S. parkeri*, *S. passany*, and *S. proops*). State 1: *Amphiarius*, *Aspistor*, *Bagre*, *Cathorops* (except *Cat. dasycephalus*), *Cochlefelis*, *Hemiaris*, *Notarius* (except *No. planiceps*), *Potamosilurus* (except *Potamosilurus velutinus*), and *S. parkeri*, *S. passany*, and *S. proops*. State 2: *Arius* (except *Ar. caelatus* and *Ar. madagascariensis*). State 3: *Plicofollis* (except *Pl. platystomus*).

In several ariid genera and most outgroups, the two short processes leaving the orbitosphenoid and the pterosphenoid near the optic foramen are leaf-like. A different condition is defined by the presence of very long and narrow lateral processes from the orbitosphenoid and the pterosphenoid. Additionally, two other states are recognized, in *Arius* (except *Ar. caelatus* and *Ar. madagascariensis*) the lateral expansions of the two bones are short and laterally sinuous, and in *Plicofollis* (except *Pl. platystomus*) lateral expansions are short, but clearly straight along the lateral face. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Cranoglanididae, Doradidae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, and *Potamarius*.

64. *Parasphenoid in ventral view*: moderately wide (state 0; Figs 8B, 9A, B); very wide (state 1; Fig. 8A). State 0: Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. couma*, *S. parkeri*, *S. herzbergii*, *S. passany*, and *S. proops*). State 1:

*Amphiarius*, *Aspistor*, *Brustarius*, *Cochlefelis*, *Hemiaris*, *Notarius*, *Plicofollis*, *S. couma*, *S. parkeri*, *S. herzbergii*, *S. passany*, and *S. proops*.

The parasphenoid forms the anterior part of the neurocranium's floor; it is laterally fused to the orbitosphenoid and pterosphenoid, posteriorly bordered, and sutured to prootics and basioccipital. In most ariid representatives and outgroups the parasphenoid in ventral view is elongate and narrow through its entire extension. A second condition present only in the Ariidae is defined by parasphenoid very wide in ventral view, with presence of lateral expansions near the frontal and the lateral ethmoid. Missing in the Anchariidae.

65. *Size of optic foramen (minimally connected)*: very large (state 0); moderately large (state 1); very reduced (state 2). State 0: Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Potamarius*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamosilurus*, and *Sciades*. State 2: Anchariidae, *Cephalocassis*, *Doiichthys*, *Nedystoma*, and *Nemapteryx*.

The primitive condition in the Siluriformes is observed in taxa where the openings for passage of the trigemino-facialis and optic nerves are separate and the optic foramen is considerably larger than the opening for the trigemino-facialis (Bockmann, 1998). Most ariids have the optic foramen moderately large, only slightly larger than the trigemino-facialis opening and extreme reduction of the former in relation to size of the latter is found in *Cephalocassis*, *Doiichthys*, *Nedystoma*, and *Nemapteryx*. Not applicable in the Diplomystidae and missing in the Austroglanididae, Cetopsidae, and Horabagridae.

66. *Distance between optic foramen and trigemino-facialis foramen*: small, equal to width of trigemino-facialis foramen (state 0); large, about twice as large as trigemino-facialis foramen (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Bagre*, *Galeichthys*, and *Potamarius*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*,

*Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamosilurus*, and *Sciades*.

In the outgroups examined and in the genera *Bagre*, *Galeichthys*, and *Potamarius*, the distance between the optic and trigemino-facialis foramina is small, and equals exactly the size of the trigemino-facialis opening. In most Ariidae, this distance is greater, twice or more the size of the trigemino-facialis opening, a unique condition in our analysis. Not applicable in the Diplomystidae and missing in the Cetopsidae.

67. *Otic capsules*: well differentiated (state 0; Figs 8A, B, 9A); weakly differentiated (state 1; Fig. 9B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops*.

Most members of the Ariidae have well-developed otic capsules, in a roughly ampoule-like shape. In *Cathorops*, the capsules are inconspicuous in relation to the ventral face of neurocranium.

68. *Size of otic capsule (minimally connected)*: very small, restricted to prootic (state 0); moderate, limited by prootic, pterotic and exoccipital (state 1; Fig. 8A); very large, limited by prootic, pterotic, and exoccipital (state 2; Figs 8B, 9A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Horabagridae, *Occidentarius*, and *Sciades*. State 2: *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus*.

The utriculus in the Siluriformes is typically a small otolith occupying a restricted area of the prootic. As remarked by Regan (1911) and de Pinna (1993) the utriculus in the Ariidae is well developed, occupying an area corresponding to a great capsule on

each side of the posterior basicranial area formed by portions of the prootic, pterotic, and exoccipital. In the Ariidae, two distinct conditions of the character are defined based on the size of the otic capsules. Exclusively in *Occidentarius* and *Sciades*, the otic capsules are moderately expanded, contrasting with the very large and expanded capsules in the remaining ariid representatives.

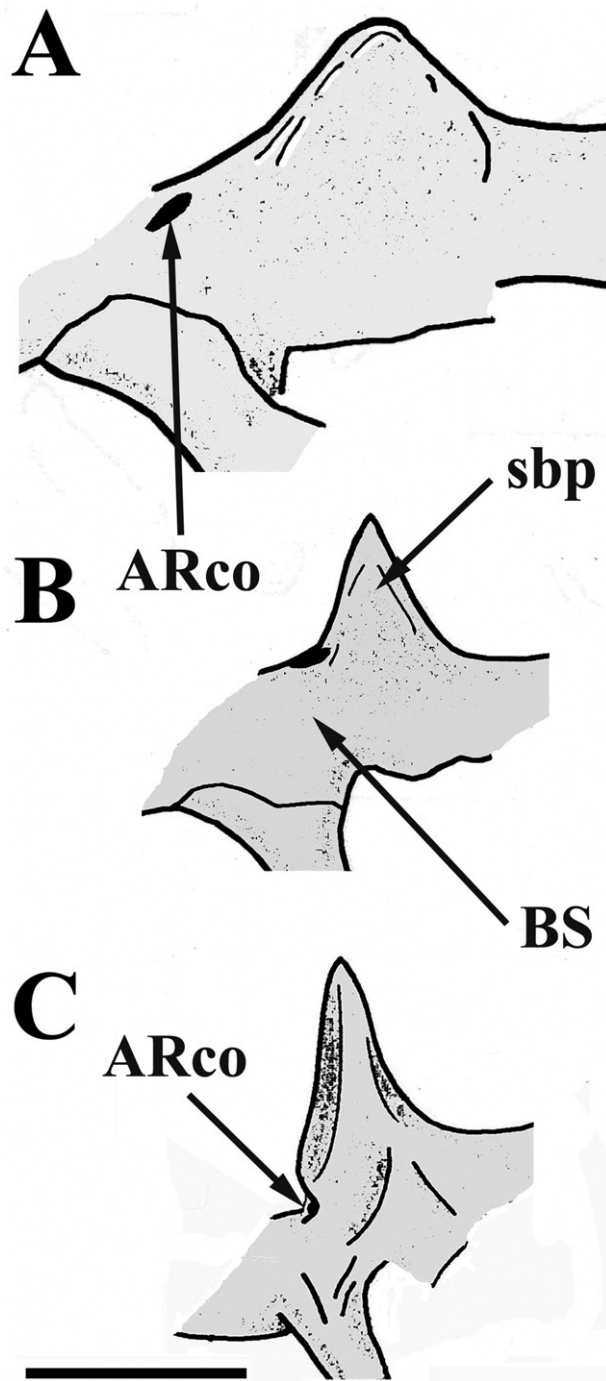
69. *Enclosure of aortic canal*: absent (state 0); present (state 1; Figs 8A, 9A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*. State 1: *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In almost all ariid representatives (*Galeichthys* excluded) bony elements surround the dorsal aorta, forming a closed canal at all developmental stages, with an opening located in front of the base of the subvertebral process in the basioccipital.

70. *Position of anterior opening of aortic canal (minimally connected)*: slightly anterior of subvertebral process and ventrally orientated (state 0; Figs 8A, 9A, 10A); at base of subvertebral process and anteroventrally orientated (state 1; Fig. 10B); within base of subvertebral process and anteriorly orientated (state 2; Fig. 10C). State 0: *Bagre*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Potamarius*, and *Sciades*. State 1: *Amphiarus*, *Arius*, *Aspistor*, *Batrachocephalus*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, and *Potamosilurus*. State 2: *Cathorops*.

The position and orientation of the anterior opening of the aortic canal in the basioccipital varies in relation to the base of the subvertebral process. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*.

71. *Subvertebral process*: indistinct or weakly developed (state 0); well developed (state 1; Fig. 10A–C). State 0: Anchariidae, Austroglanididae,



**Figure 10.** Subvertebral process, ventrolateral view, right side. A, *Genidens barbatus*, MZUSP 51704; B, *Aspistor luniscutis*, MZUSP 51689; *Cathorops (Cathorops) agassizii*, MZUSP 49346. Abbreviations: ARco, aortic canal opening; BS, basioccipital; sbp, subvertebral process. Scale bar = 4 mm.

Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Occidentarius*, and *Sciades*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus*.

The subvertebral process is a conical ventral vertical projection formed by a fusion of the basioccipital and the complex vertebra. In the Ariidae the fused structures are such that the first vertebra lies dorsal to the bony blade that forms the process. Its conspicuous presence represents the condition found in most Ariidae.

72. *Size of subvertebral process*: short and wide (state 0; Fig. 10A); long and narrow (state 1; Fig. 10B, C). State 0: *Arius*, *Bagre*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Neoarius*, *Netuma*, *Plicofollis*, *Potamarius*, and *Potamosilurus*. State 1: *Amphiarius*, *Aspistor*, *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Ketengus*, *Osteogeneiosus*, *Nedystoma*, *Nemapteryx*, *Notarius*, and *Pachyula*.

The subvertebral process can be either cone-shaped, wide at base or represented by a long process, narrow at base. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Occidentarius*, and *Sciades*.

73. *Ventral tip of subvertebral process (minimally connected)*: split (state 0); rounded (state 1); acute (state 2); spatulate (state 3). State 0: *Arius*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*. State 2: *Amphiarius*, *Aspistor*, *Batrachocephalus*, *Cinetodus*, *Cryptarius*, *Ketengus*, *Notarius*, *Osteogeneiosus*, and *Pachyula*. State 3: *Cathorops*, *Cephalocassis*, *Doiichthys*, *Hemiarius*, *Nedystoma*, and *Nemapteryx*.

The ventral tip of the subvertebral process is split in the Ariidae. Exclusively in *Bagre* it is large and rounded. A long and weakly acute ventral tip characterizes an additional feature. The extreme condition, in *Cathorops*, *Cephalocassis*, *Doiichthys*, *Hemiarius*,

*Nedystoma*, and *Nemapteryx*, is represented by the ventral tip of the process clearly compressed antero-posteriorly, shaped like a spatula. Not applicable in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

74. *Anterior margin of subvertebral process*: smooth (state 0; Fig. 10A, B); keeled (state 1; Fig. 10C). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus*. State 1: *Cathorops*.

Contrasting with the condition where the anterior margin of the subvertebral process is smooth, exclusively in *Cathorops*, the anterior portion of the subvertebral process is compressed and keeled. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Sciades*.

75. *Basioccipital lateral process*: absent (state 0); present (state 1; Figs 8A, B, 9A, B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Horabagridae, Ictaluridae, Pangasiidae, Heptapteridae, Schilbidae, *Galeichthys*, and *Cep. melanochir*. State 1: Doradidae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cep. borneensis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the Doradidae and the Mochokidae, and most of the ariids, the basioccipital bears a conspicuous lateral process articulated with the transcapular process. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Cep. melanochir*, and *Galeichthys*.

76. *Basioccipital lateral process*: anterior and posterior portions equally developed (state 0); posterior portion extending further laterally than anterior (state 1; Figs 8A, B, 9A, B). State 0

Doradidae, Mochokidae, *Cinetodus*, and *Pachyula*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cep. borneensis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the Ariidae, the lateral face of the basioccipital lateral process contacting area with the transcapular process is equally developed anteriorly and posteriorly. Another condition is characterized by the lateral margin of the basioccipital lateral process conspicuously more developed posteriorly. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Cep. melanochir*, and *Galeichthys*.

77. *Length of basioccipital lateral process*: short (state 0; Figs 8A, B, 9A); very long (state 1; Fig. 9B). State 0: Doradidae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cep. borneensis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: *Cathorops*.

In the Ariidae, the basioccipital lateral process is short, conspicuously shorter than one third of extension of the bony ridge formed by the former bone and the transcapular process. Only in *Cathorops* the process is very long, representing at least half of the total extension of the same bony bridge. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Cep. melanochir*, and *Galeichthys*.

78. *Contact face for articulation of transcapular process with basioccipital*: small and columnar (state 0; Figs 8A, B, 9A); large and depressed (state 1; Fig. 9B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius* (except *Ar. gagora*, *Ar. maculatus*, *Ar. manillensis*), *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*,

*Pachyula*, *Plicofollis* (except *Pl. platystomus*), *Potamarius*, *Potamosilurus* (except *Potamosilurus latirostris*), and *Sciades*. State 1: *Amphiarius*, *Ar. gagera*, *Ar. maculatus*, *Ar. manillensis*, *Aspistor*, *Bagre*, *Cathorops*, *Cryptarius*, *Doiichthys*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Pl. platystomus*, and *Potamosilurus latirostris*.

The mesial face of the transcapular process columnar and contacting the basioccipital through a small area is a feature present in the Ariidae and several catfish outgroups. A different condition is defined by a mesial portion of the transcapular process depressed, contacting the basioccipital through a relatively large area.

79. *Disposition of transcapular process in relation to body axis*: forming an acute angle (state 0; Figs 8A, B, 9A); forming a right angle (state 1; Fig. 9B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Hora-bagridae, Ictaluridae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cochlefelis*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Doradidae, Mochokidae, *Amphiarius*, *Aspistor*, *Cathorops*, *Cinetodus*, *Cryptarius*, *Galeichthys*, *Nemapteryx*, *Notarius*, and *Pachyula*.

The condition found in the Ariidae and outgroup taxa is defined by the presence of a laterally disposed transcapular process forming an acute angle in relation to the longitudinal body axis. In Doradidae, Mochokidae, *Amphiarius*, *Aspistor*, *Cathorops*, *Cinetodus*, *Cryptarius*, *Galeichthys*, *Nemapteryx*, *Notarius*, and *Pachyula* the process forms a right angle in relation to the body axis.

80. *Length and thickness of transcapular process*: long and thin (state 0; Figs 8A, B, 9A, B); very short and thick (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cinetodus* and *Pachyula*.

In the Ariidae a uniformly long and thin transcapular process is a generalized condition. Only in *Cinetodus* and *Pachyula*, the process is very short and thick.

81. *Shape of transcapular process*: cylindrical or columnar (state 0; Figs 8A, B, 9A); depressed (state 1; Fig. 9B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops*.

In the Ariidae and other siluriforms the transcapular process is cylindrical or columnar. Only in *Cathorops* is this process conspicuously depressed.

82. *Space between transcapular process and otic capsule (minimally connected)*: very large (state 0; Fig. 8A); moderately large (state 1; Figs 8B, 9A); very small (state 2; Fig. 9B). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Occidentarius*, and *Sciades*. State 1: *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Neoarius*, *Netuma*, *Notarius*, *Plicofollis*, *Potamarius*, and *Potamosilurus*. State 2: *Amphiarius*, *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Ketengus*, *Nemapteryx*, *Osteogeneiosus*, and *Pachyula*.

A very large space between the transcapular process and the otic capsule represents the condition in the outgroup, shared with *Occidentarius* and *Sciades*. In members of the Ariidae that share state 2 of character 68, two conditions are present. The free area between the two structures are moderately large or as large as the thickness of the transcapular process, or represented by an extreme condition in which the free space is restricted to the lateral portion, smaller than the thickness of the transcapular process. In some representatives the otic capsule touches the transcapular process at the mesial region.

83. *Posterior process of exoccipital*: absent (state 0); present (state 1). State 0: Anchariidae,

Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Horabagridae, Ictaluridae, *Amphiarius*, *Aspistor*, and *Notarius* (except *No. planiceps*). State 1: Claroteidae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *No. planiceps*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The otic capsule is posteriorly delimited by the exoccipitals. In the Ariidae, Claroteidae, Pangasiidae, and Schilbidae the exoccipital bears a posterior process divergent from the medium axis and parallel to the tripod anterior part above the basioccipital. The presence of the exoccipital posterior process was described by Chardon (1968) who recognized it as a possible ariid synapomorphy. In the present study, the process is absent in *Amphiarius*, *Aspistor*, and *Notarius* (except *No. planiceps*). Missing in the Heptapteridae and Mochokidae.

84. *Bony crest of exoccipital*: well developed and tall (state 0); shallow and inconspicuous (state 1). State 0: *Arius*, *Amphiarius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Notarius* (except *No. planiceps*), *Pachyula*, and *Plicofollis*. State 1: *Brustiarius*, *Carlarius*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Potamarius*, and *Sciades*.

Dorsolateral to the foramen magnum on the posterior part of the exoccipital, there is a compressed vertical expansion, herein defined as exoccipital posterior crest. It is possible to depict two conditions in the Ariidae: a shallow and little differentiated crest and a tall, well-developed crest. Missing in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *No. planiceps*.

85. *Orientation of exoccipital bony crest (maximally connected)*: perpendicular to vertebral column and ventrolaterally directed (state 0); perpendicular to vertebral column and posteriorly directed (state 1); parallel to vertebral column and mesially folded (state 2); parallel to vertebral column and posteriorly directed (state 3). State 0: *Brustiarius*, *Carlarius*, *Cochlefelis*, *Galeichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Netuma*, *Osteogeneiosus*, *Pachyula*,

*Plicofollis*, and *Potamosilurus*. State 1: *Arius*, *Batrachocephalus*, *Bagre*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Pachyula*, and *Plicofollis*. State 2: *Cathorops*. State 3: *Amphiarius*, *Aspistor*, and *Notarius*.

The location and orientation of the exoccipital bony crest vary in the Ariidae, but four distinct and well-defined conditions can be visualized as defined above. Missing in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *No. planiceps*.

86. *Connection between posterior process of exoccipital and Müllerian ramus*: by ligaments (state 0); by suture (state 1). State 0: Claroteidae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *No. planiceps*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius grandoculis*, and *Potamosilurus*. State 1: *Potamarius izabalensis* and *Sciades*.

The exoccipital posterior process in the Ariidae is connected to the base of Müllerian ramus via ligaments. In *Sciades* and *Potamarius izabalensis* the two structures are connected by bony suture. Missing in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Amphiarius*, *Aspistor*, *Notarius* (except *No. planiceps*), and *S. sagor*.

87. *Relationship between exoccipital posterior process and Müllerian ramus*: posterior process not supporting Müllerian ramus (state 0); posterior process supporting Müllerian ramus (state 1). State 0: Claroteidae, Pangasiidae, Schilbidae, *Bagre*, *Brustiarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *No. planiceps*, *Pachyula*, and *Pl. tenuispinis*. State 1: *Arius*, *Batrachocephalus*, *Carlarius*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Osteogeneiosus*, *Plicofollis* (except *Pl. tenuispinis*), *Potamarius grandoculis*, and *Potamosilurus*.

Exclusively amongst ariids, the exoccipital posterior process is modified and expanded to support the base of Müllerian ramus. Not applicable in Anchariidae, Austroglanididae, Doradidae, Heptapteridae,

Horabagridae, Ictaluridae, Mochokidae, *Amphiarius*, *Aspistor*, *Notarius* (except *No. planiceps*), *Occidentarius*, and *Sciades*.

#### INFRAORBITALS

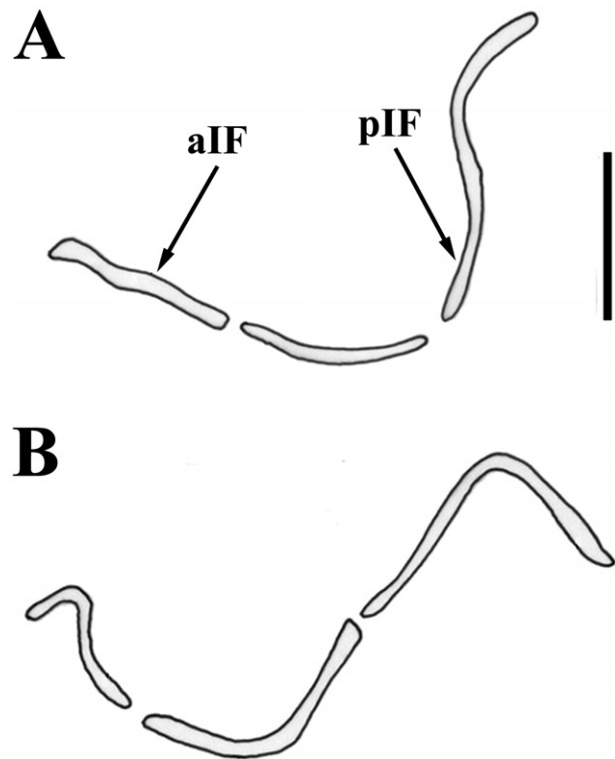
88. *Number of infraorbitals (minimally connected)*: seven (state 0); five (state 1); four (state 2); three (state 3). State 0: Diplomystidae. State 1: Bagridae, Ictaluridae, and *Doiichthys*. State 2: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Cranoglanididae, Horabagridae, Pangasiidae, and Schilbidae. State 3: Mochokidae, Doradidae, Heptapteridae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The infraorbital series is represented by the lachrymal-antorbital (infraorbital one) and the infraorbital ossified tubules forming the infraorbital sensory canal (Bockmann, 1998). The reduced number of three is observed only in the Mochokidae, Doradidae, Heptapteridae and most Ariidae, whereas five infraorbital bones is a condition independently acquired in the Bagridae, Ictaluridae, and *Doiichthys*.

89. *Shape of anterior infraorbital*: straight or slightly curved (state 0; Fig. 11A); conspicuously curved (state 1; Fig. 11B). State 0: Doradidae, Heptapteridae, Mochokidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*.

Basally in the Siluriformes and in the Gymnotiformes, the bones of the orbital series are reduced to ossified tubules, without a laminar portion (Fink & Fink, 1981, 1996). In most of the Ariidae and catfish outgroups, the anterior infraorbital is slightly curved or straight. Only in *Bagre* is the anterior infraorbital markedly curved, giving the bone the shape of the number 7. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, and *Doiichthys*.

90. *Shape of posterior infraorbital (maximally connected)*: C-shaped (state 0); S-shaped (state 1;

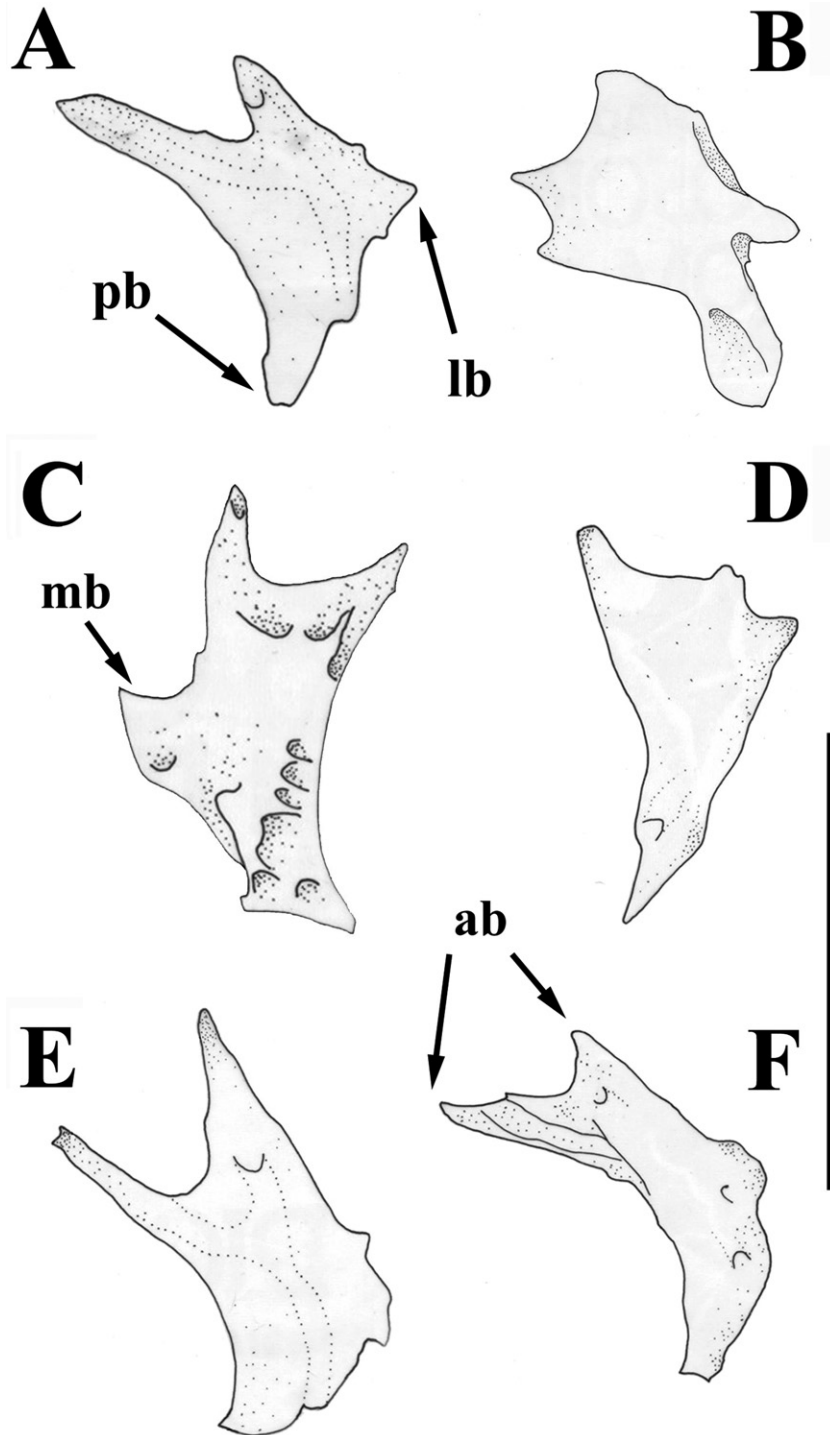


**Figure 11.** Infraorbital ossified tubules, lateral view, right side. A, *Galeichthys feliceps*, MZUSP 87694; B, *Bagre bagre*, MZUSP 35843. Abbreviations: aIF, anterior infraorbital; pIF, posterior infraorbital. Scale bar = 4 mm.

Fig. 11A); L-shaped (state 2; Fig. 11B). State 0: Anchariidae, Bagridae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, and Mochokidae. State 1: Austroglanididae, Claroteidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Bagre*.

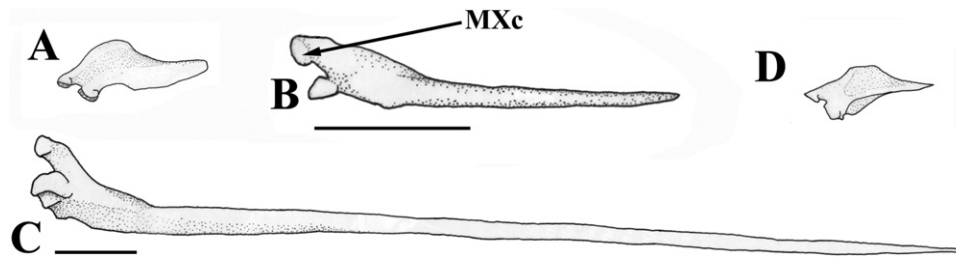
The posterior infraorbital bone is irregularly curved, like an elongated S in most of the Ariidae and some of catfish outgroups. Some of the catfish outgroups examined herein also show a C-shaped infraorbital. Only in *Bagre* is the posterior infraorbital markedly curved, with its two halves forming a right angle. Not applicable in the Diplomystidae, Cetopsidae, and *Doiichthys*.

91. *Number of branches in lachrymal-antorbital anterior part (maximally connected)*: two anterior branches and one lateral (state 0; Fig. 12A);



**Figure 12.** Lachrymal-antorbital, dorsal view, right side. A, *Netuma thalassina*, UMMZ 214630; B, *Osteogeneiosus militaris*, UMMZ 214628; C, *Bagre bagre*, MZUSP 35843; D, *Ketengus typus*, ANSP 60704; E, *Galeichthys ater*, MZUSP 87693; F, *Plicofollis dussumieri*, LACM 38131-48. Abbreviations: ab, anterior branches; lb, lateral branch; mb, mesial branch; pb, posterior branch. Scale bar = 4 mm.





**Figure 13.** Maxilla, mesial view, right side. A, *Genidens genidens*, MZUSP 51721; B, *Bagre bagre*, MZUSP 35843; C, *Osteogeneiosus militaris*, UMMZ 214628; D, *Cochlefelis spatula*, AMS I. 25997-002. Abbreviation: MXc, maxillary condyles. Scale bar = 4 mm.

three anterior branches and one lateral (state 1; Fig. 12B); two anterior branches and one mesial (state 2; Fig. 12C); three anterior branches (state 3; Fig. 12D). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Osteogeneiosus*. State 2: *Bagre* and *Batrachocephalus*. State 3: *Ketengus*.

In the Siluriformes the first element of the infraorbital series results from fusion of antorbital and lachrymals (Kindred, 1919; Gosline, 1961), although some authors raised doubts about its homology (Weitzman, 1962; Bockmann, 1998). This bone is flat, apposed to the lateral ethmoid anterior horn, and with a variable number of branches. In most members of the Ariidae and outgroup taxa, it has one lateral and two long and acute anterior processes in form of a three-pointed star. Character states 1, 2, and 3 are considered unique conditions in the genera listed above. Not applicable in the Diplomystidae and the Cetopsidae.

92. *Posterior branch of lachrymal–antorbital*: short and little differentiated (state 0; Fig. 12E); long and conspicuous (state 1; Fig. 12A–D, F). State 0: *Galeichthys* and *Sciades proops*. State 1: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*,

*Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. proops*).

Posterior branch of the lachrymal–antorbital short and little differentiated, strongly projected mesially, is unique in *Galeichthys* and *S. proops*. Missing in the Diplomystidae, Cetopsidae, and *Doiichthys*.

93. *Width of lachrymal–antorbital*: very wide (state 0; Fig. 12A–E); narrow (state 1; Fig. 12F). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Plicofollis* (except *Pl. platystomus*).

The lachrymal–antorbital is an oblong bone in most Siluriformes. In the Ariidae, excluding *Plicofollis* (except *Pl. platystomus*), it is very large, at least twice as large as the size of the bone in outgroup terminals. Missing in the Diplomystidae and the Cetopsidae.

#### MANDIBULAR ARCH AND ASSOCIATED STRUCTURES

94. *Shape of maxilla (maximally connected)*: laminar and leaf shaped (state 0; Fig. 13A); cylindrical, moderately long, and distally acute (state 1; Fig. 13B); cylindrical, very long, and distally acute (state 2; Fig. 13C); rudimentary and weakly differentiated (state 3). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*,

*Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*. State 2: *Osteogeneiosus*. State 3: *Batrachocephalus* and *Ketengus*.

The maxilla supports and moves the maxillary barbel through muscles and ligaments associated with the premaxilla and the autopalatine (Gosline, 1975). Plesiomorphically in the Siluriformes the maxilla is laminar, slightly concave on the surface where the proximal portion of the maxillary barbel is fixed (de Pinna, 1993). The primitive condition in the Siluriformes defined by de Pinna (1993) is found in most members of the Ariidae. The apomorphic condition in the Heptapteridae defined by de Pinna (1993) and characterized by a tubular or semi-tubular posteriorly cone-shaped maxilla, is also found in *Bagre*. In *Bagre*, the maxilla is relatively long and supports a larger area of the base of the maxillary barbel in comparison with all ariid taxa. In *Osteogeneiosus*, the maxilla is entirely tubular, very long and distally acute, and supports the whole maxillary barbel, which becomes very rigid throughout its total length. An extreme condition is defined by the very reduced maxilla of *Batrachocephalus* and *Ketengus*.

95. *Outline of maxilla (maximally connected)*: mesial and lateral margins parallel in proximal two thirds, converging in distal one third, distal margin truncate (state 0; Fig. 13A); wide for proximal two thirds with edges parallel, narrow distally, and thin and acute posteriorly (state 1); maxilla gradually narrow distally, but lateral and posterior margins rounded (state 2); lateral and mesial margins considerably closer to each other proximally, distally narrow, and pointed (state 3; Fig. 13D). State 0: Bagridae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, *Carlarius heudelotii*, *Genidens*, *Net. thalassina*, *Occidentarius*, and *Plicofollis*. State 1: *Galeichthys*. State 2: Anchariidae, Claroteidae, Horabagridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Carlarius* (except *Car. heudelotii*), *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Net. bilineata*, *Notarius*, *Pachyula*, *Potamosilurus*, and *Sciades*. State 3: Cetopsidae, *Brustarius*, *Cochlefelis*, *Neoarius*, and *Potamarius*.

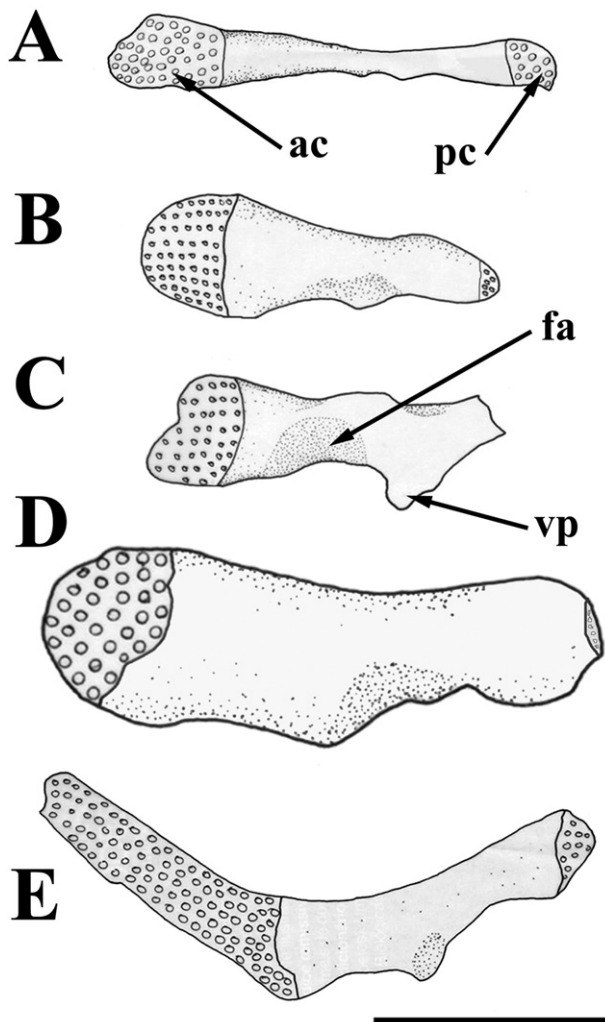
The configuration of the marginal outlines of the laminar portion of the maxilla varies in the Ariidae. Maxilla wide with its edges parallel for proximal two

thirds, narrow distally, and thin and acute posteriorly (state 1) is the unique condition of *Galeichthys*. The lateral and mesial maxillary margins considerably closer to each other proximally, and becoming distally narrow and pointed (state 3) represents the most common condition in the Ariidae. Independent acquisitions of the condition defined as state 0 occur in most members of the examined outgroup and in *Genidens*, *Occidentarius*, *Plicofollis*, *Car. heudelotii*, and *Net. thalassina*, with independent acquisitions of the condition defined as state 3. Not applicable in Austroglanididae, Diplomystidae, *Bagre*, *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*.

96. *Size of maxillary condyles (minimally connected)*: rudimentary (state 0); moderately large (state 1; Fig. 13A, D); large (state 2; Fig. 13B); very large (state 3; Fig. 13C). State 0: Anchariidae, Horabagridae, *Batrachocephalus*, and *Ketengus*. State 1: Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Bagre*. State 3: *Osteogeneiosus*.

Two condyles that articulate with the dorsal and ventral faces of the autopalatine are present at the proximal end of the maxilla and have been described for all the Siluriformes with the exception of the Diplomystidae (Lundberg, 1970) and the Trichomycteridae, Cetopsidae, and Astroblepidae (Mo, 1991). In most Siluriformes the ventral condyle is larger than the dorsal. In the present study the maxillary condyles were found in specimens of all the terminal taxa examined. Presence of moderately large condyles is the common condition in most Ariidae. The presence of large and conspicuous condyles was observed only in *Bagre* and extremely large ones are unique to *Osteogeneiosus*. Extreme condyle reduction occurs in *Batrachocephalus* and *Ketengus*. Not applicable in the Diplomystidae and the Cetopsidae.

97. *General aspect of autopalatine (maximally connected)*: cylindrical, long, and thin (state 0; Fig. 14A); conical, short, and robust (state 1; Fig. 14B, C); cylindrical, very short, and robust (state 2; Fig. 14D); depressed and mesially angled in its anterior third (state 3; Fig. 14E). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Hep-



**Figure 14.** Autopalatine, dorsal view, right side (A, B, D, E), mesial view, right side (C). A, *Genidens genidens*, MZUSP 51721; B–C, *Bagre bagre*, MZUSP 35843; D, *Osteogeneiosus militaris*, UMMZ 214628; E, *Ketengus typus*, ANSP 60704. Abbreviations: ac, anterior cartilage; fa, face for articulation; pc, posterior cartilage; vp, ventral process. In *Bag. bagre* the posterior cartilage was removed. Scale bar = 4 mm.

tapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Brustiarus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*. State 2: *Osteogeneiosus*. State 3: *Batrachocephalus* and *Ketengus*.

The primitive condition in the Siluriformes is represented by a cylindrical autopalatine, anteriorly

rounded or elliptical in cross-section, mesially or dorso-mesially presenting a face for articulation with the lateral ethmoid and narrower posteriorly for articulation with the cranium (de Pinna, 1993). Autopalatine plesiomorphic morphology in Ariidae is similar to the siluriform condition described by de Pinna (1993). In *Bagre* the autopalatine anterior portion is wider, becoming gradually narrow posteriorly, similar in shape to a short and robust cone. In *Osteogeneiosus* it is cylindrical throughout its entire length, short, and very robust. An additional condition is characteristic of *Batrachocephalus* and *Ketengus* wherein the autopalatine is depressed and mesially curved in its anterior third.

98. *Autopalatine anterior portion*: depressed (state 0; Fig. 14E); cylindrical (state 1; Fig. 14A–D). State 0: Cetopsidae, Diplomystidae, *Batrachocephalus*, and *Ketengus*. State 1: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Brustiarus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The autopalatine anterior portion is cylindrical in most Ariidae (see character 97). Only in *Batrachocephalus* and *Ketengus* is it depressed in the part anterior to its articulation with the lateral ethmoid.

99. *Autopalatine posterior portion (maximally connected)*: slightly compressed (state 0; Fig. 14A–D); conspicuously compressed (state 1); conspicuously depressed (state 2; Fig. 14E). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Brustiarus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, *S. assimilis*, *S. bonillai*, and *S. felis*. State 1: *Doiichthys*, *Nedystoma*, *Sciades* (except *S. assimilis*, *S. bonillai*, and *S. felis*). State 2: Cetopsidae, *Batrachocephalus*, and *Ketengus*.

The autopalatine posterior portion slightly compressed, deeper than the anterior portion was first described in the Ariidae by Britto (2002) and

represents the character state that is present in most ariid members. A strongly compressed posterior portion is characteristic of *Nedystoma* and *Sciades* (except *S. assimilis*, *S. bonillai*, and *S. felis*). An additional condition is observed in *Batrachocephalus* and *Ketengus*, defined by the autopalatine posterior portion being conspicuously depressed. Missing in the Diplomystidae.

100. *Autopalatine orientation*: parallel in relation to main body axis (state 0); perpendicular to the main body axis (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Batrachocephalus* and *Ketengus*.

The autopalatine parallel to the main body axis was described by Lundberg (1970) as the typical condition for all the Siluriformes. Exclusively in *Batrachocephalus* and *Ketengus* it is perpendicular to the longitudinal body axis.

101. *Shape of autopalatine at its articulation with lateral ethmoid (maximally connected)*: slightly compressed (state 0; Fig. 14A–D); very compressed (state 1); depressed (state 2; Fig. 14E). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Arius* and *Plicofollis*. State 2: *Batrachocephalus* and *Ketengus*.

In most catfishes the autopalatine is slightly compressed at its articulation with the lateral ethmoid. In *Arius* and *Plicofollis* the autopalatine is clearly compressed at the same region and in *Batrachocephalus* and *Ketengus* it is depressed.

102. *Size of articulation of autopalatine with lateral ethmoid*: very large (state 0; Fig. 14B, C); moderately large (state 1; Fig. 14A, D, E). State 0:

*Bagre* and *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In *Bagre* and *Galeichthys*, the articulation of the autopalatine with the lateral ethmoid is very large, about two and a half to three times the autopalatine length. In all ariid members examined (except *Bagre* and *Galeichthys*) the articulation face is smaller, more than three times the autopalatine length. Missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

103. *Orientation of articulation of autopalatine with lateral ethmoid (minimally connected)*: mesially orientated (state 0; Fig. 14A–C); mesoposteriorly orientated (state 1; Fig. 14D); posteriorly orientated (state 2; Fig. 14E). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, *S. assimilis*, *S. bonillai*, and *S. felis*. State 1: *Osteogeneiosus* and *Sciades* (except *S. assimilis*, *S. bonillai*, and *S. felis*). State 2: *Batrachocephalus* and *Ketengus*.

In the outgroup taxa and most of the Ariidae, the autopalatine articular facet for the lateral ethmoid is mesially orientated. Nevertheless, two additional conditions can be observed within ariids. In *Osteogeneiosus* and *Sciades* (except *S. assimilis*, *S. bonillai*, and *S. felis*), the articular facet directs mesoposteriorly. An extreme, derived condition, in which the facet is posteriorly orientated is shared between *Batrachocephalus* and *Ketengus*.

104. *Position of articulation of the autopalatine with lateral ethmoid (minimally connected)*: slightly displaced to anterior portion of bone (state 0; Fig. 14B, C); in the middle of bone (state 1); slightly displaced to posterior portion of bone (state 2; Fig. 14A, D, E). State 0: *Bagre* and *Doiichthys*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cran-

oglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Brustarius*, *Cochlefelis*, *Galeichthys*, *Nemapteryx*, and *Neoarius*. State 2: *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the outgroup taxa and *Brustarius*, *Cochlefelis*, *Galeichthys*, *Nemapteryx*, and *Neoarius*, the articulation face is displaced in the middle of the autopalatine bone. In the majority of the ariid taxa it is slightly displaced to the posterior portion of the bone, although the articular facet is displaced slightly anteriorly in *Bagre* and *Doiichthys*.

105. *Autopalatine ventral process*: absent (state 0); present and very conspicuous (state 1; Fig. 14C). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*.

Exclusively in *Bagre*, there is a ventral process in the posterior half of the autopalatine.

106. *Length of anterior cartilage of autopalatine (minimally connected)*: very short, less than one third as long as bone itself (state 0; Fig. 14B–D); moderately long, one third to one fifth as long as bone itself (state 1; Fig. 14A); very long, about as long as bone itself (state 2; Fig. 14E). State 0: Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Bagre*, *Galeichthys*, and *Osteogeneiosus*. State 1: Anchariidae, Austroglanididae, Claroteidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Batrachocephalus* and *Ketengus*.

The autopalatine anterior cartilage is short in most Siluriformes, less than half as long as the autopalatine bony portion. It was described by de Pinna (1993) in *Ancharius*, Ariidae, Austroglanididae, and Claroteidae as a well-developed structure, its length equal to or longer than half of the autopalatine. However, opposed to de Pinna (1993), in *Bagre*, *Galeichthys*, and *Osteogeneiosus*, the cartilage is very short, less than one third as long as the autopalatine. An extreme, derived condition in the Siluriformes is defined for *Batrachocephalus* and *Ketengus* wherein the anterior cartilage is as long as the autopalatine itself.

107. *Size of autopalatine posterior cartilage (minimally connected)*: as long as anterior cartilage (state 0); much smaller than anterior cartilage (state 1; Fig. 14A, B, E); reduced to a small dot (state 2; Fig. 14D). State 0: *Galeichthys*. State 1: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Osteogeneiosus*.

Usually in the Siluriformes both the anterior and the posterior autopalatine cartilages are present. Exclusively in *Galeichthys* the posterior cartilage is as long as the anterior. In most Ariidae the posterior cartilage is half as long as the anterior. A very reduced posterior cartilage is characteristic of *Osteogeneiosus*.

108. *Ventral process at symphysis of dentary (minimally connected)*: absent (state 0); short and inconspicuous (state 1); long and very conspicuous (state 2). State 0: Austroglanididae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, and Pangasiidae. State 1: Anchariidae, Claroteidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Cathorops*.

The presence of a small process on the ventral surface of the dentary at the insertion of the intermandibularis muscle is a unique condition amongst the Siluriformes. An extreme condition is found in *Cathorops* in which the dentary ventral process is very long and conspicuous, at least in male specimens.

109. *Distribution of teeth on the dentary (maximally connected)*: restricted to mesial two thirds (state 0); restricted to mesial three quarters (state 1); along entire bone (state 2). State 0: *Cephalocassis*, *Cryptarius*, and *Genidens*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Ketengus*. Missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

The dentaries are curved elongate bones, posteriorly narrow in anterolateral view and mesially articulated at the symphysis. The dorsal surface bears acicular, molariform, spatulate, or cuspidate teeth extending through a variable extension on the bone. Most ariid species have teeth restricted to mesial three quarters of the dorsal portion. In *Cephalocassis*, *Cryptarius*, and *Genidens* the teeth are restricted to the mesial two thirds of the dorsal portion. Exclusively in *Ketengus* a band of teeth extends over the entire dorsal surface of the dentary.

110. *Types of teeth on dentary (maximally connected)*: teeth acicular (state 0); teeth acicular and molariform (state 1); teeth spatulate or cuspidate (state 2). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops*. State 2: *Batrachocephalus* and *Ketengus*.

In the Ariidae and other outgroup catfishes, the dentary bears several rows of acicular teeth on its dorsal surface. Exclusively in *Cathorops* there is a flat

posterior expansion where molariform teeth (at least in females) are implanted whereas in the anterior portion the teeth are acicular. Additionally in *Batrachocephalus* and *Ketengus* there is only a single row of spatulate or cuspidate teeth.

111. *Anterodorsal process of anguloarticular*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: *Galeichthys*

The anguloarticular is a strong and compressed bone at the region of the coronoid process, posteriorly presenting an articulation face with the quadrate anterior process. Only in *Galeichthys* is there a conspicuous process in the anguloarticular, close to the suture with dentary.

112. *Presence of a rod-like structure connecting jaw coronoid process and base of maxillary barbel*: absent (state 0); present (state 1). State 0: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Anchariidae, Claroteidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the Ariidae and the Claroteidae a rod-like structure parallel to the ligamentum primordium was first described by Mo (1991) in representatives of the Auchenoglanididae and later also in the Anchariidae, Claroteidae, and Ariidae by de Pinna (1993) and Britto (2002). According to de Pinna (1993) this connection is lacking in most of the Siluriformes.

113. *Relationship between length and width of premaxilla (maximally connected)*: premaxilla wide and short (state 0); premaxilla wide and moderately long (state 1); premaxilla narrow and very long (state 2); premaxilla very wide and short (state 3). State 0: Anchariidae, Austroglanididae,

Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, *Bagre*, *Brustiarius*, *Cochlefelis*, *Galeichthys*, and *Netuma*. State 1: Horabagridae, Pangasiidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Carlarius*, *Cryptarius*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamosilurus*, and *Sciades*. State 2: Schilbidae, *Cathorops*, *Cephalocassis*, *Cinetodus*, and *Potamarius*. State 3: *Doiichthys*.

In general view, the premaxilla is a depressed, laminar, and subrectangular bone in the Siluriformes (Lundberg, 1970). A premaxilla very narrow or narrower than the mesethmoid was indicated by de Pinna (1993) as a derived condition in the Siluriformes. In the Ariidae the premaxilla presents a large variation related to its width and length. In the Diplomystidae and other catfish families, the premaxilla is wide and short, its length more than three times its width. The condition found in most members of the Ariidae is characterized by a premaxilla moderately long and wide, its length one and a half to two times its width. In *Cathorops*, *Cephalocassis*, *Cinetodus*, and *Potamarius* the premaxilla is very long and narrow, but its width is never larger than the length of mesethmoid lateral process. Exclusively in *Doiichthys* the premaxilla is very wide and short, its length more than four times its width.

114. *Length variation of lateral and mesial portions of premaxilla*: lateral and mesial portions about equally developed (state 0); lateral and mesial portions with different sizes (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Brustiarius*.

The premaxilla is subrectangular in the Siluriformes (see discussion of character 113), with the anterior and posterior margins equally distant from each other for their entire extension in most Ariidae. Only in *Brustiarius* is the lateral third of the premaxilla conspicuously shorter and well differentiated from the two mesial thirds, longer.

115. *Anterior margin of premaxilla*: entire (state 0); fringed (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Nedystoma*.

In the Siluriformes, the anterior border of the premaxilla is devoid of any process or expansion. Exclusively in *Nedystoma* its anterior border presents short and laterally curved processes having a fringed aspect.

116. *Shape of lateral margin of premaxilla (minimally connected)*: straight or slightly convex (state 0); with a slight concavity (state 1); with a very conspicuous concavity (state 2). State 0: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Anchariidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri*, *S. couma*, *S. herzbergii*, *S. passany*, and *S. proops*). State 2: *S. parkeri*, *S. couma*, *S. herzbergii*, *S. passany*, and *S. proops*.

Primitively in the Siluriformes, the lateral margin of the premaxilla is straight or slightly convex (de Pinna, 1993). The condition in the Anchariidae and most Ariidae is characterized by the presence of a concavity in the lateral margin, forming a bilobed structure in this region, the size of the two lobes varying. An additional condition is found in *S. parkeri*, *S. couma*, *S. herzbergii*, *S. passany*, and *S. proops*, in which the lateral margin is conspicuously concave forming a deep groove.

117. *Dorsal crest on the premaxilla delimiting a contact area with mesethmoid*: dorsal crest beginning near or exactly at lateral end of premaxilla anterior margin (state 0); beginning between lateral one third or half of anterior margin (state 1). State 0: *Amphiarius*, *Aspistor*, *Brustiarius*, *Car. parkeri*, *Cathorops*, *Cephalo-*

*cassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Nedystoma*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: *Arius*, *Bagre*, *Batrachocephalus*, *Cochlefelis*, *Hemiarius*, *Nemapteryx*, *Netuma*, and *Potamosilurus velutinus*.

The anterior horns of the mesethmoid contact and cover up a large area of the premaxilla dorsal face corresponding to the anteromesial portion of the bone. The area of the premaxilla free of contact is relatively more restricted and corresponds to the posterolateral portion of the bone. A bony crest oblique and parallel with the posterior margin of the anterior horns of the mesethmoid shows variations concerning its relationships with the anterior margin of the premaxilla. An exclusive condition is characterized by dorsal crest beginning at a point between two thirds and half of the length of the anterior margin of the premaxilla. Missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Carlarius* (except *Car. parkii*), *Ketengus*, and *Potamosilurus* (except *Potamosilurus velutinus*).

118. *Dorsal crest of premaxilla*: present (state 0); absent (state 1). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Ketengus*.

The premaxillae are firmly attached to mesethmoid anterior horns through their dorsal and ventral face. Presence or absence of processes or dorsal crests with variable shapes and dispositions can be detected in siluriform families. Absence of a conspicuous crest parallel with posterior margin of mesethmoid anterior horns is unique in *Ketengus* amongst ariids.

119. *Teeth in the premaxilla*: acute (state 0); cuspidate (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*,

*Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Batrachocephalus* and *Ketengus*.

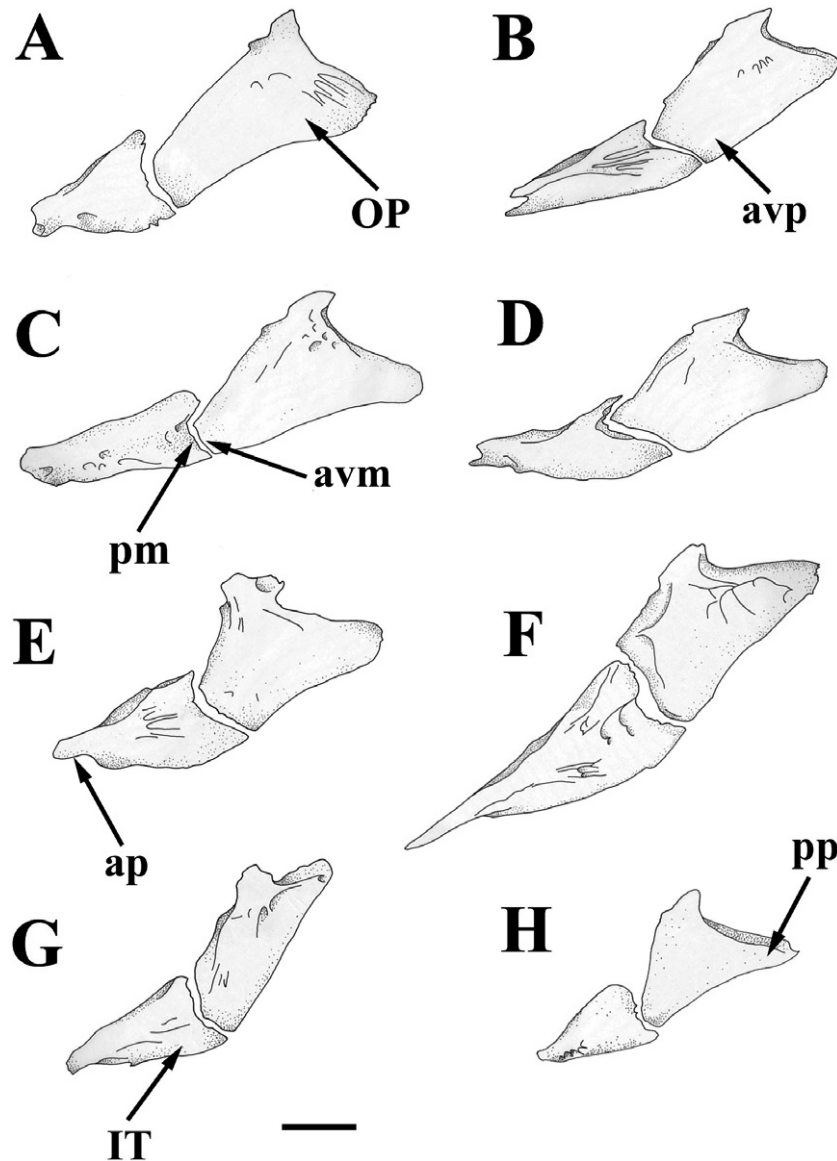
Premaxilla with a single row of spatulate or cuspidate teeth is an exclusive condition present in *Batrachocephalus* and *Ketengus*. In the remaining ariids and outgroups, the premaxilla has many small acute teeth disposed in a continuous band along its entire ventral surface.

#### OPERCULAR SERIES

120. *Shape of anteroventral portion of opercle (maximally connected)*: subtrapezoid, very long (state 0; Fig. 15A); subtrapezoid, moderately long (state 1; Fig. 15B, C); subtrapezoid, very short (state 2; Fig. 15D–F); subrectangular (state 3; Fig. 15G); subtriangular (state 4; Fig. 15H). State 0: Bagridae, Cranoglanididae, Diplomystidae, Doradidae, Ictaluridae, Mochokidae, *Bagre*, *Cinetodus*, *Galeichthys*, and *Nedystoma*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cep. melanochir*, *Doiichthys*, *Genidens*, *Hemiarius*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri*, *S. passany*, and *S. proops*). State 2: *Cathorops*, *Cep. borneensis*, *Cryptarius*, and *Pachyula*. State 3: *Batrachocephalus*. State 4: Anchariidae, Austroglanididae, Claroteidae, Heptapteridae, Pangasiidae, Schilbidae, *Cochlefelis*, *Ketengus*, *S. parkeri*, *S. passany*, and *S. proops*.

The opercle is a subtriangular to subrectangular laminar bone in the Ariidae. Tilak (1965) used variation in shape of the opercle to differentiate species and genera of the taxa that he studied from the Indian Ocean. Later on, Higuchi (1982) recognized that the patterns described by Tilak could not be used to characterize species from the western South Atlantic because of large individual variations or inadequate definitions. In the present study variation of the opercle shape was reviewed and five distinct states are recognized based on variation in shape of the borders of the opercle anteroventral portion delimited by the opercular arm. The subtrapezoid and very long, anteroventral portion of the opercle being about three times the distance between the anteroventral margin and the opercular arm is the condition of the character in the Ariidae, shared with several catfish outgroups. Only in *Batrachocephalus* is the opercle rectangular, very high, and the length of its ventral base almost as long as the opercular bone





**Figure 15.** Opercle and interopercle, lateral view, right side. A, *Galeichthys feliceps*, MZUSP 87693; B, *Plicofollis dussumieri*, LACM 38131-48; C, *Potamarius izabalensis*, UMMZ 177252; D, *Cathorops agassizii*, MZUSP 37232; E, *Cephalocassis borneensis*, UMMZ 181201; F, *Cryptarius truncatus*, ANSP 60768; G, *Batrachocephalus mino*, FMNH 68052; H, *Cochlefelis spatula*, AMS I.25997-002. Abbreviations: ap, anterior portion; avm, anteroventral margin; avp, anteroventral portion; IT, interopercle; OP, opercle; pm, posterior margin; pp, posterior portion. Scale bar = 4 mm.

at the region of the opercular arm. Three additional states are defined: subtrapezoid and moderately long, the opercle anteroventral margin about one and a half to two times that same distance; subtrapezoid and very short, the opercle anteroventral margin as long as distance from opercular anteroventral margin to opercular arm; and the subtriangular shape is characterized by a very short anteroventral margin, its size about three times the opercle length. Missing in the Cetopsidae and Horabagradae.

121. *Shape of anteroventral margin of opercle:* slightly convex (state 0; Fig. 15A, C, E–H); concave or almost straight (state 1; Fig. 15B, D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagradae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*,

*Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* and *Plicofollis* (except *Pl. platystomus*).

*Cathorops* and *Plicofollis* (except *Pl. platystomus*) share a unique condition of the character, defined by a concave or almost straight anteroventral opercular margin (see discussion of character 120).

122. *Opercle posterior portion*: not well developed posteriorly (state 0; Fig. 15A, B); well developed posterodorsally (state 1; Fig. 15C–H). State 0: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Bag. panamensis*, *Carlarius* (except *Car. heudelotii*), *Galeichthys*, *Genidens*, *Ketengus*, *Occidentarius*, *Plicofollis* (except *Pl. platystomus*), and *Sciades* (except *S. couma* and *S. felis*). State 1: Anchariidae, Claroteidae, Heptapteridae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre* (except *Bag. panamensis*), *Batrachocephalus*, *Brustarius*, *Car. heudelotii*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, *S. couma*, and *S. felis*.

Two distinct conditions are defined according to the degree of development and orientation of the opercle posterior portion. Missing in *Ar. caelatus* and *No. troscheli*.

123. *Shape of posterior margin of interopercle*: slightly curved (state 0; Fig. 15A, C, E–H); straight and inclined (state 1; Fig. 15B, D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* and *Plicofollis* (except *Pl. platystomus*).

The interopercle is anterior to the opercle to which it is attached by a thin layer of connective tissue. In

most Ariidae, the interopercle posterior margin is slightly concave.

124. *Contact area between posterior face of interopercle and ventral margin of opercle*: half or less of interopercle posterior part contacting ventral margin of opercle (state 0; Fig. 15A, G, H); more than half of interopercle posterior part contacting ventral margin of opercle (state 1; Fig. 15B–F). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Brustarius*, *Bagre*, *Batrachocephalus*, *Cochlefelis*, *Galeichthys*, *Ketengus*, *Neoarius*, *Notarius*, *Pl. platystomus*, *S. passany*, and *S. proops*. State 1: *Amphiaris*, *Arius*, *Aspistor*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis* (except *Pl. platystomus*), *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. passany* and *S. proops*).

The opercle ventral part fits a notch on the interopercle posterior region. The opercle ventral face contacting an extensive area of the interopercle posterior face, corresponding to more than half of the interopercle posterior part, is a unique condition within the Ariidae.

125. *Anterior portion of interopercle*: columnar and truncate (state 0; Fig. 15A, C, E–H); compressed and bifurcate (state 1; Fig. 15B, D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* and *Plicofollis* (except *Pl. platystomus*).

A clearly compressed, notched or bifurcate interopercle anterior part is a condition found only in *Cathorops* and *Plicofollis*.

126. *Interopercle anterior portion (minimally connected)*: inconspicuous (state 0; Fig. 15A–D, G, H); conspicuously narrow (state 1; Fig. 15E); thin and acute (state 2; Fig. 15F). State 0:

Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Claroteidae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Cranoglanididae, Doradidae, Mochokidae, Heptapteridae, *Cephalocassis*, *Doiichthys*, and *Nedystoma*. State 2: *Cryptarius*.

In most ariids, the interopercle is gradually narrower anteroposteriorly and the bone anterior part not clearly differentiated. Two distinct conditions are defined: in *Cephalocassis*, *Doiichthys*, and *Nedystoma* the anterior quarter of the bone is narrower than the posterior three quarters and in *Cryptarius* the anterior third of the bone is anteriorly very thin and acute. Missing in the Bagridae.

127. *General shape of interopercle (maximally connected)*: subtriangular (state 0; Fig. 15A, D–H); rectangular (state 1; Fig. 15C); subrectangular (state 2; Fig. 15B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamosilurus*, and *Sciades*. State 1: Horabagridae and *Potamarius*. State 2: *Plicofollis* (except *Pl. platystomus*).

In most Ariidae, the interopercle is shaped like a flat funnel of variable length. In *Potamarius* the interopercle is rectangular and moderately long, its length corresponding to the depth of the opercle. An additional condition is represented by a subrectangular and very long interopercle, its length larger than the opercle depth in *Plicofollis* (except *Pl. platystomus*). Missing in the Schilbidae.

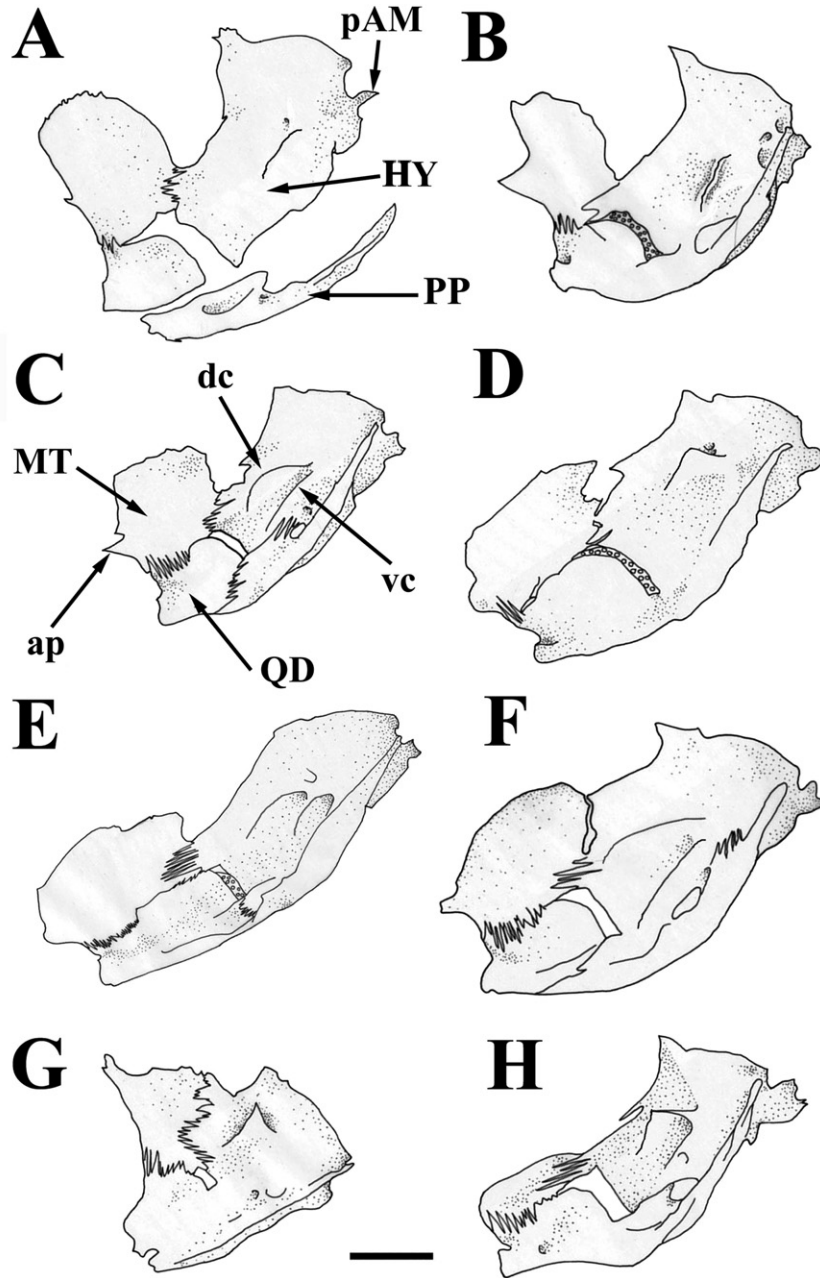
#### SUSPENSORIUM

128. *Shape of metapterygoid in perpendicular section (maximally connected)*: twice as deep as long (state 0; Fig. 16A, B); as deep as long (state 1; Fig. 16C); one and a half times longer than deep (state 2; Fig. 16D–F); subtriangular (state 3;

Fig. 16G); three times longer than deep (state 4; Fig. 16H). State 0: Anchariidae, Doradidae, *Bagre*, *Doiichthys*, and *Galeichthys*. State 1: Mochokidae, Heptapteridae, *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cochlefelis*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamosilurus*, and *Sciades*. State 2: Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Horabagridae, Schilbidae, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Pachyula*, *Plicofollis*, and *Potamarius*. State 3: *Batrachocephalus* and *Ketengus*. State 4: *Osteogeneiosus*.

In siluriforms the metapterygoid is anterodorsally located in relation to the quadrate and not posterodorsally as in the remaining Ostariophysi (Fink & Fink, 1981). de Pinna (1993) considered a metapterygoid as deep as long as plesiomorphic in Siluriformes, a condition illustrated by Lundberg & McDade (1986). In ariids, the metapterygoid is a large laminar bone, sutured to the quadrate and the hyomandibular, its anterodorsal portion extending to the sesamoid bone I and articulating with the posteroventral portion of the corresponding lateral ethmoid, thus connecting the anterior part of the suspensorium with the neurocranium. The condition observed in the sister group of the Ariidae (Anchariidae) and in the ariids *Bagre*, *Doiichthys*, and *Galeichthys* is represented by the metapterygoid at least twice as deep as long. Three other conditions are defined for the character in question (see above) and could be observed in ariid representatives, and other catfish outgroups. In ariid representatives a metapterygoid longer than deep contributes to the head becoming more flattened in the taxa that share this condition. Missing in the Austroglanididae, Claroteidae, Ictaluridae, and Pangasiidae.

129. *Articulation between metapterygoid and quadrate*: by complete interdigitated suture (state 0; Fig. 16A–D, F–H); by interdigitated suture in a small part of contact and by overlapping in the remaining contact area (state 1; Fig. 16E). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cryptarius*.



**Figure 16.** Suspensorium, lateral view, right side. A, *Galeichthys feliceps*, MZUSP 87693; B, *Bagre pinnimaculatus*, FMNH 62447; C, *Arius gadora*, UMMZ 187892; D, *Cathorops agassizii*, MZUSP 37232; E, *Cryptarius truncatus*, ANSP 60768; F, *Plicofollis dussumieri*, LACM 38131-48; G, *Ketengus typus*, ANSP 60704; H, *Osteogeneiosus militaris*, UMMZ 214628. Abbreviations: ap, anterior process; dc, dorsal crest; HY, hyomandibular; MT, metapterygoid; pAM, process for insertion of the adductor mandibulae; PP, preopercle; QD, quadrate; vc, ventral crest. Scale bar = 4 mm.

The condition presented in most otophysans is defined by the metapterygoid and the quadrate connected by synchondral joint. In the Ariidae the extension of the contact area between the metapterygoid and the quadrate is variable, but exclusively in *Cryptarius* the metapterygoid contacts a small part of the quadrate through a interdigitated suture and a larger area by simple overlapping.

130. *Anterior process of metapterygoid*: present (state 0; Fig. 16A–F); absent (state 1; Fig. 16G, H). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Diplomys-tidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*,

*Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Doradidae, Mochokidae, *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*.

The Ariidae are characterized by the presence of a process on the metapterygoid anterior face, variable in shape and size. Its absence is interpreted as unique in *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus*. Missing in the Cetopsidae.

131. *Shape of metapterygoid anterior process (minimally connected)*: acute (state 0; Fig. 16A, B, C); truncate (state 1; Fig. 16F); rounded (state 2; Fig. 16D, E). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Potamosilurus velutinus*, and *Sciades*. State 1: *Cinetodus*, *Cochlefelis*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Potamosilurus* (except *Potamosilurus velutinus*). State 2: *Cathorops* and *Cryptarius*.

An acute anterior process of the metapterygoid is the most common condition in the Ariidae, with two distinct states recognized (see above). Not applicable in *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* and missing in Cetopsidae, *Doiichthys*, and Mochokidae.

132. *Size of metapterygoid anterior process*: small to moderate (state 0; Fig. 16A–C, E, D); very large (state 1; Fig. 16B). State 0: Anchariidae, Bagridae, Heptapteridae, Horabagridae, *Amphiarius*, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Diplomystidae, Claroteidae, Cranoglanididae, Ictaluridae, Pangasiidae, Schilbidae, and *Bagre*.

A metapterygoid anterior process very long and conspicuous is considered a condition present only in representatives of *Bagre* amongst ariids. Not applicable in *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* and missing in the Cetopsidae, Doradidae, and Mochokidae.

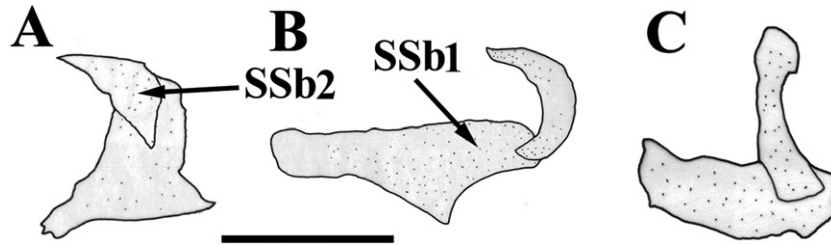
133. *Dorsal crest of hyomandibular*: absent (state 0; Fig. 16A, B); present (state 1; Fig. 16C–H). State 0: Cranoglanididae, Heptapteridae, *Bagre*, and *Galeichthys*. State 1: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Doradidae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The hyomandibular is a large rectangular bone, anteriorly laminar, and posteriorly thicker, possessing on its lateral face a crest in the form of an inverted V where the adductor mandibulae muscles originate. Amongst ariids, a hyomandibular dorsal crest is absent only in *Bagre* and *Galeichthys*. Missing in the Claroteidae.

134. *Shape of dorsal crest of hyomandibular*: long and low (state 0; Fig. 16E, F); short and high (state 1; Fig. 16C, D, G, H). State 0: Bagridae, Diplomystidae, Ictaluridae, Schilbidae, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Nemapteryx*, *Neoarius*, *Net. thalassina*, *Occidentarius*, *Pachyula*, *Plicofollis* (except *Pl. platystomus*), *Potamarius*, and *Sciades*. State 1: Anchariidae, Austroglanididae, Cetopsidae, Doradidae, Horabagridae, Mochokidae, Pangasiidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Cathorops*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Notarius*, *Osteogeneiosus*, *Pl. platystomus*, and *Potamosilurus*.

A low hyomandibular dorsal crest with a long base is shared by Ariidae and several catfish families. The triangular, very high crest, with a short base was observed only in ariid representatives. Not applicable in the Claroteidae, Cranoglanididae, and Heptapteridae.

135. *Ventral crest of hyomandibular*: present (state 0; Fig. 16A–C, E, F, H); absent (state 1; Fig. 16D, G). State 0: Anchariidae, Austroglanididae, Diplomystidae, Cetopsidae, Horabagridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Bagridae, Cranoglanididae,



**Figure 17.** Sesamoid bones, dorsal view, right side. A, *Cochlefelis spatula*, AMS I. 25997-002; B, *Potamarius izabalensis*, UMMZ 177252; C, *Sciades herzbergii*, MZUSP 51695. Abbreviations: SSb1, sesamoid bone I; SSb2, sesamoid bone II. Scale bar = 4 mm.

Doradidae, Heptapteridae, Ictaluridae, Mochokidae, *Cathorops*, *Cephalocassis*, and *Ketengus*.

A second low and long crest parallel to the opercle is part of an inverted V-shaped structure together with the dorsal crest on the hyomandibular lateral crest (see discussion of character 133). Absence of such a crest is unique in *Cathorops*, *Cephalocassis*, and *Ketengus* amongst ariids. Missing in the Claroteidae.

136. *Process of hyomandibular for insertion of the adductor mandibulae*: inconspicuous or absent (state 0); very conspicuous (state 1; Fig. 16A–H). State 0: Austroglanididae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Anchariidae, Bagridae, Claroteidae, Horabagridae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In most members of the Otophysi the adductor mandibulae muscle attaches directly into the hyomandibular mesial face. There is no special modified structure on the surface to receive the muscular fibres. In some siluriforms a small bony projection for insertion of the muscle is present dorsal to the point of articulation with the opercle. The presence of a well-developed process was considered by de Pinna (1993) to be a derived state of the character shared by *Ancharius*, Ariidae, Claroteidae, and Horabagridae. Lundberg (1970) described the same condition of the character in Ariidae and some members of Heptapteridae. In the present study a conspicuous process on the hyomandibular to receive the adductor mandibulae is observed in all the ariids.

137. *Contact face between metapterygoid and hyomandibular*: moderately long (state 0;

Fig. 16A–F, H); very long (state 1; Fig. 16G). State 0: Anchariidae, Bagridae, Claroteidae, Heptapteridae, Horabagridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Cranoglanididae, Cetopsidae, Diplomystidae, Doradidae, Ictaluridae, *Batrachocephalus*, and *Ketengus*.

Primitively in the Siluriformes the metapterygoid and the hyomandibular are connected by a suture (Arratia, 1992). In most ariids the two bones are connected through a narrow area involving half or less than half of the metapterygoid posteroventral portion. In *Batrachocephalus* and *Ketengus* the extensive articulation between the metapterygoid and the hyomandibular involves all the posterior margin of the metapterygoid and a large anterosuperior portion of the hyomandibular. Missing in the Bagridae, Claroteidae, and Mochokidae.

138. *Shape of sesamoid bone I (maximally connected)*: short and triangular (state 0; Fig. 17A); very long and subtriangular (state 1; Fig. 17B); irregularly shaped (state 2); very long and subrectangular (state 3; Fig. 17C). State 0: Anchariidae, Bagridae, Claroteidae, Pangasiidae, Schilbidae, *Am. phrygiatus*, *Bag. panamensis*, *Brustarius*, *Carlarius*, *Cochlefelis*, *Galeichthys*, *Neoarius*, *Netuma*, *Plicofollis*, *Potamosilurus*, *S. bonillai*, and *S. felis*. State 1: *Am. rugispinis*, *Arius*, *Bagre* (except *Bag. panamensis*), *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Occidentarius*, *Pachyula*, *Potamarius*, *S. assimilis*, *S. leptaspis*, *S. guatemalensis*, *S. sagor*, and *S. seemanni*. State 2: *Aspistor*, *Notarius*, and *Osteogeneiosus*. State 3:

*S. couma*, *S. parkeri*, *S. herzbergii*, *S. passany*, and *S. proops*.

In the Siluriformes the sesamoid bone I (*sensu* Diogo *et al.*, 2001) is subtriangular with the mesial and lateral faces little elongate. In most ariid taxa the same bone is subtriangular with the mesial and lateral faces very elongate. In *Aspistor*, *Notarius*, and *Osteogeneiosus* it is rectangular and very elongate anteroposteriorly, whereas in some of the *Sciades* species it is irregularly shaped. Missing in the Austroglanididae, Diplomystidae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, *Batrachocephalus*, and *Ketengus*.

139. *Shape of sesamoid bone II*: half-moon shaped (state 0; Fig. 17A, B); irregularly elongate (state 1; Fig. 17C). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, *Sciades* (except *S. couma*, *S. parkeri*, *S. herzbergii*, *S. passany*, and *S. proops*). State 1: *S. couma*, *S. parkeri*, *S. herzbergii*, *S. passany*, and *S. proops*.

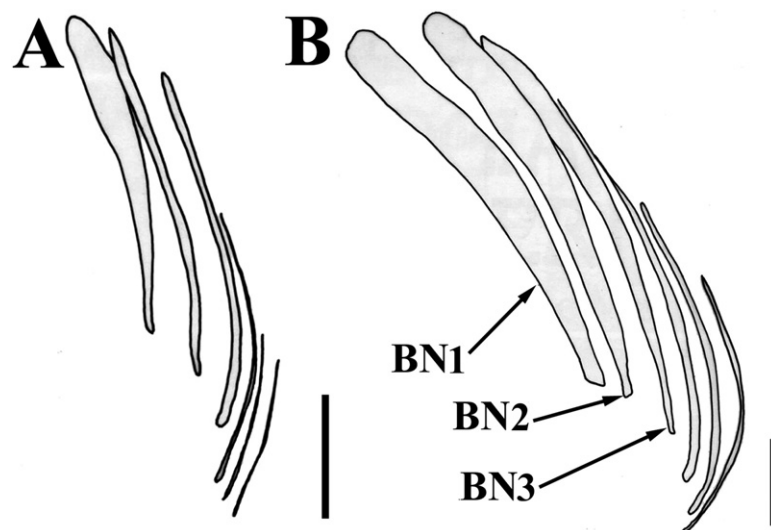
Sesamoid bone II irregularly elongate is a feature exclusive of *S. couma*, *S. herzbergii*, *S. passany*, *S. parkeri*, and *S. proops*. Missing in the Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Hep-

tapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Batrachocephalus*, and *Ketengus*.

#### HYOID ARCH

140. *Shape of first external branchiostegal ray*: proximally narrow and distally broad (state 0; Fig. 18A); as broad proximally as distally (state 1; Fig. 18B). State 0: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Mochokidae, Pangasiidae, Schilbidae, *Ar. caelatus*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius* (except *No. planiceps*), *Osteogeneiosus*, *S. parkeri*, *S. passany*, and *S. proops*. State 1: Bagridae, Ictaluridae, *Amphiarius*, *Arius* (except *Ar. caelatus*), *Aspistor*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *No. planiceps*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri*, *S. passany*, and *S. proops*).

Usually six branchiostegal rays are present in the Ariidae. The four mesial ones are shorter and filamentous, generally associated with the anterior ceratohyal and the two external most are relatively long and distally wide and associated with the posterior ceratobranchial. Two states are defined based on the variation of the basal portion width in relation to the distal portion. Missing in *Ar. madagascariensis* and *Potamosilurus velutinus*.



**Figure 18.** Branchiostegal rays, ventral view, left side. A, *Bagre bagre*, MZUSP 35843; B, *Nedystoma dayi*, AMS I. 25992-001. Abbreviations: BN1, first external branchiostegal ray; BN2, second external branchiostegal ray; BN3, third external branchiostegal ray. Scale bars = 4 mm.

141. *Second external branchiostegal ray*: width less than half that of first ray (state 0; Fig. 18A); almost as wide as first ray (state 1; Fig. 18B). State 0: Anchariidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Diplomystidae, Doradidae, Heptapteridae, *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Galeichthys*, *Ketengus*, and *Nedystoma*.

Two states are defined according to the variation of the second external branchiostegal width in relation with the first external branchiostegal ray.

142. *The distal portion of third external branchiostegal ray*: acute (state 0; Fig. 18A); spatulate (state 1; Fig. 18B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Nedystoma*.

The distal portion of the third branchiostegal ray in the Ariidae is filamentous and acute. Only in *Nedystoma* it is moderately thin and spatulate.

143. *Anterior portion of anterior ceratohyal*: columnar to cylindrical (state 0); compressed (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Cetopsidae, *Cathorops*, and *Cryptarius*.

In most members of the Ariidae the anterior portion of the anterior ceratohyal varies from columnar to cylindrical. Only *Cathorops* and *Cryptarius* have the ceratohyal anterior portion clearly compressed.

144. *Posterior portion of anterior ceratohyal*: compressed and moderately thick (state 0); columnar and very thick (state 1). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Batrachocephalus*.

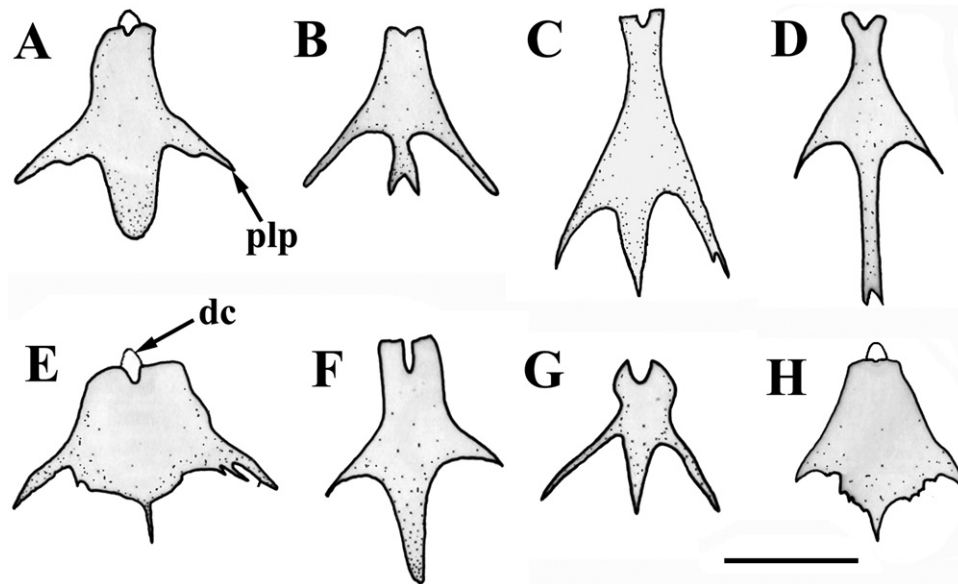
In *Batrachocephalus* the posterior portion of the anterior ceratohyal is columnar and very thick, low, and little differentiated. In all the remaining ariid representatives, the ceratohyal posterior portion is columnar to compressed, large and moderately thick.

145. *Thickness of anterior portion of anterior ceratohyal*: thin to moderately thick (state 0); very thick (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Plicofollis*.

The ariid taxa, in which the anterior portion of the anterior ceratohyal is cylindrical or columnar, have the bone anterior portion thin or moderately thick. Exclusively in *Plicofollis*, the anterior portion of the anterior ceratohyal is very thick. Not applicable in *Cathorops* and *Cryptarius*.

146. *Size of posterior ceratohyal (minimally connected)*: short (state 0); long (state 1); very long (state 2). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryp-*





**Figure 19.** Urohyal, ventral view. A, *Aspistor luniscutis*, M|ZUSP 87696; B, *Bagre bagre*, MZUSP 35843; C, *Brustarius nox*, CAS 637001; D, *Doiichthys novaeguineae*, AMS I. 27416-002; E, *Galeichthys feliceps*, MZUSP 87694; F, *Plicofollis dussumieri*, LACM 38131-48; G, *Potamarius grandoculis*, MZUSP 1004-114; H, *Cathorops agassizii*, MZUSP 37232. Abbreviations: dc, dorsal crest; plp, posterolateral processes. Scale bar = 4 mm.

*tarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Claroteidae, Horabagridae, *Bagre*, *Batrachocephalus*, *Brustarius*, and *Cochlefelis*. State 2: *Doiichthys*.

The posterior ceratohyal is a cuneiform and moderately compressed bone, its distal and angulated portion fitting the interopercle mesial face. In the Ariidae its posterior portion attaches to the anterior ceratohyal through a serrated suture along the superior two thirds and a stripe of cartilage along the inferior one third. In most outgroup taxa and ariid representatives the posterior ceratohyal is relatively short and high, its greatest depth less than one and half times its length. In *Bagre*, *Batrachocephalus*, *Brustarius*, and *Cochlefelis*, the long and low shape is the apomorphic state of the character, its width one and a half to two times its length. Exclusively in *Doiichthys*, the posterior portion of this bone is very long and low, its width more than two times its length, an additional derived condition. Missing in *S. passany*.

147. *Profile of anterior margin of urohyal*: notched (state 0; Fig. 19A–G); not notched (state 1; Fig. 19H). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*,

*Carlarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Not. planiceps*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis* (except *Pl. platystomus*), *Potamarius*, and *Sciades*. State 1: Diplomystidae, Cetopsidae, *Batrachocephalus*, *Cathorops*, and *Pl. platystomus*.

The urohyal is located on the hyoid arch medioventral region. In the Ariidae it bears laminar lateral expansions making its shape triangular in ventral view, dorsally with a well-developed keel along its median portion and a conspicuous notch visible on its anterior margin. In *Batrachocephalus*, *Cathorops*, and *Pl. platystomus*, the urohyal is characterized by the absence of a notch.

148. *Posterolateral processes of urohyal*: absent (state 0); present (state 1; Fig. 19A–H). State 0: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Anchariidae, Claroteidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In most members of the Otophysi laminar lateral expansions are present on the urohyal. In the Siluriformes these expansions are well developed, apomorphically bearing posterolatero processes. The condition recognized as derived in the Siluriformes was first indicated in the Clariidae and the Chacidae by Mo (1991). This same condition was observed herein in the Anchariidae, Claroteidae, and all members of the Ariidae.

149. *Dorsal crest of urohyal*: not projected anteriorly (state 0; Fig. 19B–D, F, G); projected anteriorly (state 1; Fig. 19A, E, H). State 0: Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Anchariidae, Austroglanididae, *Aspistor*, *Cathorops*, *Cep. borneensis*, *Galeichthys*, *Ketengus*, *Notarius* (except *No. planiceps*), and *Occidentarius*.

Presence of an anterior urohyal process is the result of the unusual development of the dorsal crest of this bone. In ventral view the urohyal dorsal crest projects beyond the anterior margin of the bone, partially covering the median notch on this margin, a condition shared by in the Ariidae and several catfish. A unique condition is defined by the urohyal dorsal crest not extending beyond the anterior margin of the bone.

150. *Length of urohyal (minimally connected)*: short (state 0; Fig. 19E); long (state 1; Fig. 19A–C, F–H); very long (state 2; Fig. 19D). State 0: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Ictaluridae, Pangasiidae, *Galeichthys*, and *Osteogeneiosus*. State 1: Bagridae, Heptapteridae, Horabagridae, Mochokidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Neoarius*, *Netuma*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Doiichthys*.

A very short urohyal, shorter than its greatest width, is observed only in *Galeichthys* and *Osteogeneiosus*. In most ariids the urohyal is long, its length equal to or longer than its greatest width. Exclusively

in *Doiichthys* the urohyal is very long, its length two or more times its greatest width.

151. *Posterior end of urohyal*: acute (state 0; Fig. 19A, C, E–H); bifurcate (state 1; Fig. 19B, D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre* and *Doiichthys*.

In *Bagre* and *Doiichthys* the urohyal posterior end is bifurcate or notched, an exclusive state of the character within the Ariidae.

152. *Bony blade connecting posterolateral processes of urohyal*: present (state 0; Fig. 19A–F, H); absent (state 1; Fig. 19G). State 0: Anchariidae, Claroteidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamosilurus*, and *Sciades*. State 1: *Potamarius*.

The most common condition is characterized by a partial or total connection of the urohyal lateral processes by a bony blade. Exclusively in *Potamarius*, the lateral processes are not connected. Not applicable in the Austroglanididae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

153. *Size of posterolateral processes of urohyal*: short (state 0; Fig. 19E, H); long (state 1; Fig. 19A–D, F, G). State 0: Anchariidae, Claroteidae, *Batrachocephalus*, *Cathorops*, *Cep. borneensis*, *Cinetodus*, *Galeichthys*, *Genidens*, *Ketengus*, *Osteogeneiosus*, *Pachyula*, and *Plicofollis* (except *Pl. platystomus*). State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cep. melanochir*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The urohyal posterolateral processes long and conspicuous represent the most common condition within

the Ariidae. Not applicable in the Austroglanididae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

154. *Orientation of posterolateral processes of urohyal*: lateroposteriorly orientated, forming an angle always larger than 70° (state 0; Fig. 19A, B, D–H); posteriorly orientated, forming an angle smaller than 60° (state 1; Fig. 19C). State 0: Anchariidae, Claroteidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre* (except *Bag. panamensis*), *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Net. thalassina*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bag. panamensis*, *Brustarius*, *Cochlefelis*, *Neoarius*, and *Net. bilineata*.

The urohyal posterolateral processes posteriorly orientated, forming an angle smaller than 30°, is the condition observed exclusively in ariid representatives. Not applicable in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

155. *Relationship between length of urohyal and length of posterolateral processes (maximally connected)*: posterolateral processes almost as long as distal portion of bone (state 0; Fig. 19C, E); posterolateral processes as long as or longer than distal portion of bone (state 1; Fig. 19B, G); posterolateral processes two thirds as long as distal portion of bone (state 2; Fig. 19A, H); posterolateral processes more than half as long as distal portion of bone (state 3; Fig. 19F); posterolateral processes one third as long as distal portion of bone (state 4; Fig. 19D). State 0: Anchariidae, Claroteidae, *Amphiarius*, *Brustarius*, *Carlarius*, *Cep. melanochir*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Hemiarius*, *Neoarius*, *Net. bilineata*, *Notarius*, *Occidentarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre* and *Potamarius*. State 2: *Arius* (except *Ar. maculatus*), *Aspistor*, *Batrachocephalus*, *Cathorops*, *Cep. borneensis*, *Cinetodus*, *Genidens*, *Ketengus*, *Nedystoma*, *Net. thalassina*, *Nemapteryx*, *Osteogeneiosus*, and *Pachyula*. State 3: *Plicofollis*. State 4: *Doiichthys*.

In most Ariidae, and the Anchariidae and Claroteidae, the urohyal posterolateral processes are almost as long as the length of the urohyal. Four other states, as listed above, are considered amongst ariids. Not applicable in Austroglanididae, Bagridae, Cetop-

sidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Ar. maculatus*.

156. *Shape of posterior portion of urohyal*: posteriorly narrow and acute (state 0; Fig. 19B–H); as wide distally as proximally (state 1; Fig. 19A). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Aspistor*.

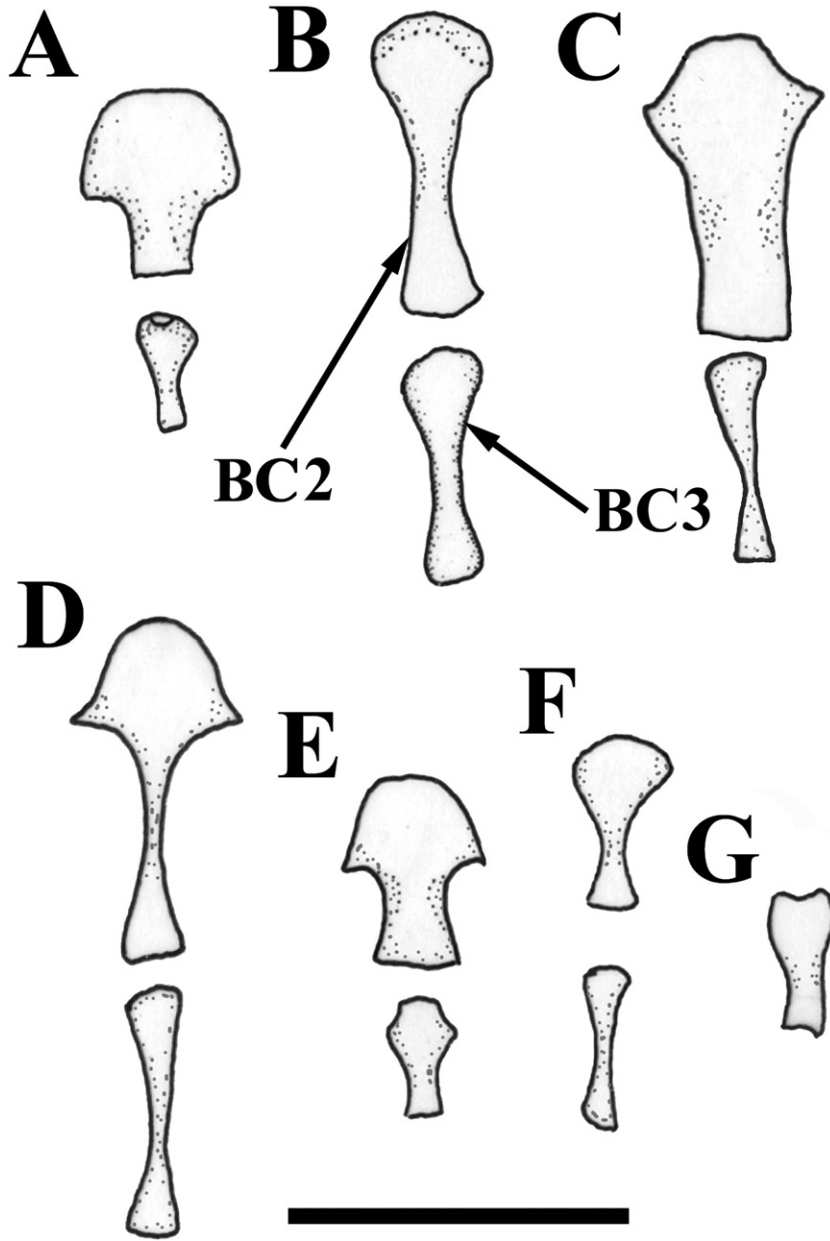
Exclusively in *Aspistor* the urohyal is as wide distally as proximally.

#### BRANCHIAL ARCHES

157. *Number of components of basibranchial series*: two (state 0; Fig. 20A–F); one (state 1; Fig. 20G). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Ketengus*.

As indicated by de Pinna (1993), the first basibranchial is absent in the Siluriformes, where the first component of the series corresponds to the second basibranchial of the remaining Otophysi. In the Ariidae, the second and third basibranchials are ossified and well developed. The presence of a single component was observed only in *Ketengus*. Missing in Doradidae.

158. *Anterior portion of second basibranchial*: not expanded (state 0); very expanded (state 1; Fig. 20A–F). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemi-*



**Figure 20.** Second and third basibranchials, dorsal view. A, *Aspistor luniscutis*, MZUSP 87696; B, *Brustiarius nox*, CAS 63701; C, *Galeichthys feliceps*, MZUSP 87694; D, *Nedystoma dayi*, AMS I. 25992-001; E, *Netuma thalassina*, UMMZ 214630; F, *Potamarius izabalensis*, UMMZ 177252; G, *Ketengus typus*, ANSP 60704. Abbreviations: BC2, second basibranchial; BC3, third basibranchial. Scale bar = 4 mm.

*arius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The second basibranchial in the siluriforms is cylindrical, sometimes with the lateral margins slightly concave and the anterior portion not enlarged, a characteristic interpreted as primitive by de Pinna (1993). The condition characterized by the second basibranchial having its anterior part very expanded, about

one or two times wider than the posterior part, was only observed in the ariid representatives examined. This characteristic was first observed in the Clariidae by de Pinna (1993). Not applicable in the *Ketengus*.

159. *Shape of second basibranchial*: spindle-shaped (state 0; Fig. 20B, C, F); mushroom-shaped (state 1; Fig. 20A, D, E). State 0: *Bagre*, *Batrachochephalus*, *Brustiarius*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*,

*Genidens*, *Neoarius*, *Pachyula*, *Potamarius*, and *Potamosilurus latirostris*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Carlarius*, *Cathorops*, *Doiichthys*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamosilurus* (except *Potamosilurus latirostris*), and *Sciades*.

The expanded anterior portion of the second basibranchial makes its shape at this region variable. One condition in the Ariidae is defined by the basibranchial having its anterior part very expanded with a rounded profile, looking like a mushroom. The other condition is characterized by the profile of anterior part less curved, almost straight, and spindle-shaped. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Ketengus*.

160. *Relationship between length and width of posterior portion of second basibranchial (maximally connected)*: long and wide (state 0; Fig. 20C); very long and narrow (state 1; Fig. 20D); long and wide (state 2; Fig. 20B, F); short and wide (state 3; Fig. 20E); short and narrow (state 4; Fig. 20A). State 0: *Cryptarius* and *Galeichthys*. State 1: *Doiichthys* and *Nedystoma*. State 2: Anchariidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Heptapteridae, Ictaluridae, Schilbidae, *Amphiarius*, *Arius* (except *Ar. gagora* and *Ar. maculatus*), *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Hemiarius*, *Nemapteryx*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 3: *Genidens* and *Netuma*. State 4: *Ar. gagora*, *Ar. maculatus*, *Aspistor*, and *Plicofollis*.

Length and width of the posterior portion of second basibranchial in the Ariidae varies considerably. Five state characters are defined. Not applicable in *Ketengus* and missing in the Austroglanididae, Doradidae, Horabagridae, Mochokidae, and Pangasiidae.

161. *Shape of third basibranchial*: hourglass-shaped (state 0; Fig. 20B–D, F); chalice-shaped (state 1; Fig. 20A, E). State 0: Austroglanididae, Cetopsidae, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Osteogeneiosus*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius*, *Potamosilurus*, *S. parkeri*, *S. guatemalensis*, *S. proops*, *S. passany*, and *S. sagor*. State 1: Diplomystidae, Bagridae, Ictaluridae, Pangasi-

idae, *Arius*, *Amphiarius*, *Aspistor*, *Batrachocephalus*, *Cinetodus*, *Cryptarius*, *Hemiarius*, *Netuma*, *Occidentarius*, *Pachyula*, *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), and *Sciades* (except *S. parkeri*, *S. guatemalensis*, *S. proops*, *S. passany*, and *S. sagor*).

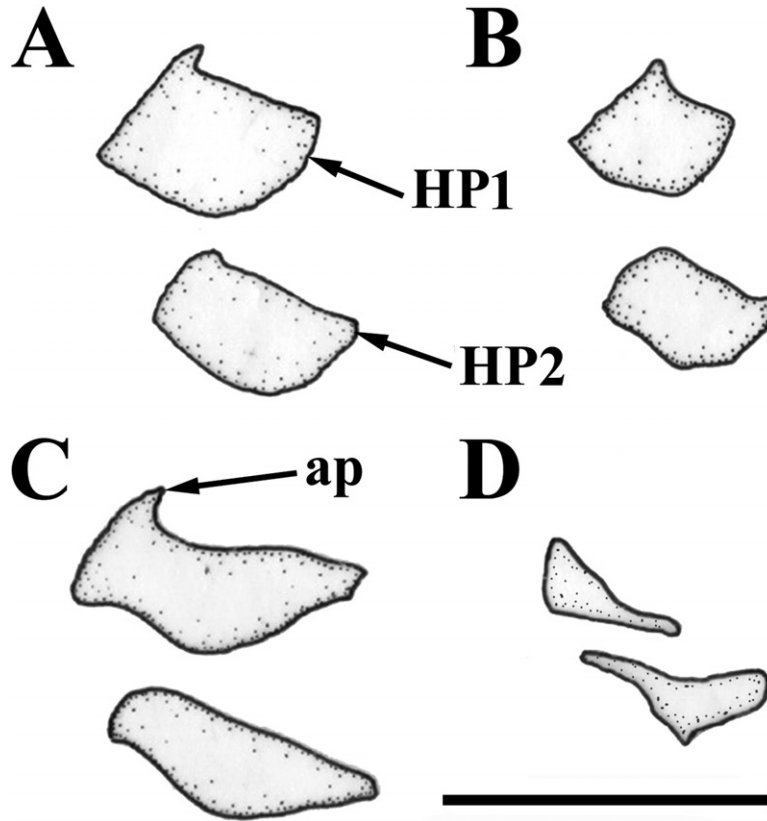
Two distinct shapes of the third basibranchial are evident as a result of the constriction of its margins. One character state is defined by a conspicuous constriction at the median portion, and the anterior and posterior parts enlarged, giving the bone an hourglass appearance. Another condition is the third basibranchial enlarged anteriorly, becoming narrower posteriorly, shaped like a chalice. Missing in the Anchariidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Mochokidae, Schilbidae, and *S. leptaspis*.

162. *Length and width of third basibranchial (maximally connected)*: very short and wide (state 0); moderately long and wide (state 1; Fig. 20A, B); long and narrow (state 2; Fig. 20C, F); very long and narrow (state 3; Fig. 20D). State 0: *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*). State 1: *Arius*, *Amphiarius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Genidens*, *Hemiarius*, *Hemiarium stormii*, *Nemapteryx*, *Neoarius*, *Notarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamosilurus*, and *Sciades*. State 2: *Batrachocephalus*, *Cochlefelis*, *Galeichthys*, and *Potamarius*. State 3: *Doiichthys* and *Nedystoma*.

The third basibranchial is moderately long and wide in most Ariidae. Other states are considered exclusive within the family. Not applicable in Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Ketengus*.

163. *Median constriction of third basibranchial*: approximately at the middle of the bone (state 0; Fig. 20A–F); displaced to posterior quarter (state 1). State 0: Austroglanididae, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Doiichthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Osteogeneiosus*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius*, *Potamosilurus*, *S. parkeri*, *S. guatemalensis*, *S. proops*, *S. passany*, and *S. sagor*. State 1: *Bagre*.

In most taxa where the third basibranchial is hourglass shaped, the median constriction is close to the



**Figure 21.** First and second hypobranchials, dorsal view. A, *Potamarius izabalensis*, UMMZ 177252; B, *Netuma thalassina*, UMMZ 214630; C, *Cathorops (Cathorops) agassizii*, MZUSP 37232; D, *Ketengus typus*, ANSP 60704. Abbreviations: ap, anterior process; HP1, first hypobranchial; HP2, second hypobranchial. Scale bar = 4 mm.

middle of the bone. Exclusively in *Bagre*, the condition is characterized by the constriction being located at the posterior portion, delimiting the posterior fifth of the bone. Missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Amphiarius*, *Aspistor*, *Batrachocephalus*, *Cinetodus*, *Cryptarius*, *Hemiaris*, *Netuma*, *Occidentarius*, *Pachyula*, *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), and *Sciades* (except *S. parkeri*, *S. guatemalensis*, *S. proops*, *S. passany*, and *S. sagor*).

164. *Shape of first hypobranchial*: shell-like (state 0; Fig. 21A–C); club-shaped (state 1; Fig. 21D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*,

*Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Ketengus*.

Hypobranchials are ossified elements situated between basibranchials and ceratobranchials. In the Siluriformes there is great variation concerning the number of these elements and their degree of ossification. In the Ariidae the first two hypobranchials are ossified and have the appearance of a shell. The first hypobranchial laterally narrow and with its anterior margin concave is a condition observed only in *Ketengus*.

165. *First hypobranchial*: moderately elongate transversely, its mesial face weakly developed and rounded (state 0; Fig. 21A, B); very elongate transversely, its mesial face well developed and acute (state 1; Fig. 21C). State 0: Anchariidae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cat*.

*dasycephalus*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Doradidae, Mochokidae, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cryptarius*, *Doiachthys*, and *Nedystoma*.

A first hypobranchial very elongate transversely, with its mesial face well developed and acute, is a condition shared by *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cryptarius*, *Doiachthys*, and *Nedystoma*.

166. *Anterior process of first hypobranchial*: inconspicuous (state 0; Fig. 21A, B); very conspicuous (state 1, Fig. 21C). State 0: Anchariidae, Austroglanididae, Bagridae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Doiachthys*, and *Nedystoma*.

An anterior margin of the first hypobranchial straight or slightly convex represents a primitive condition in the Siluriformes (de Pinna, 1993). In most Ariidae there is a small acute projection on first hypobranchial anterior margin, short and inconspicuous. Only in *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Doiachthys*, and *Nedystoma*, was the presence of an elongate and conspicuous projection on first hypobranchial anterior margin observed. Not applicable in *Ketengus*.

167. *Position of anterior process of first hypobranchial*: slightly displaced to lateral part of the bone (state 0; Fig. 21A, C); exactly in the middle of the bone (state 1; Fig. 21B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiachthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Neoarius* and *Netuma*.

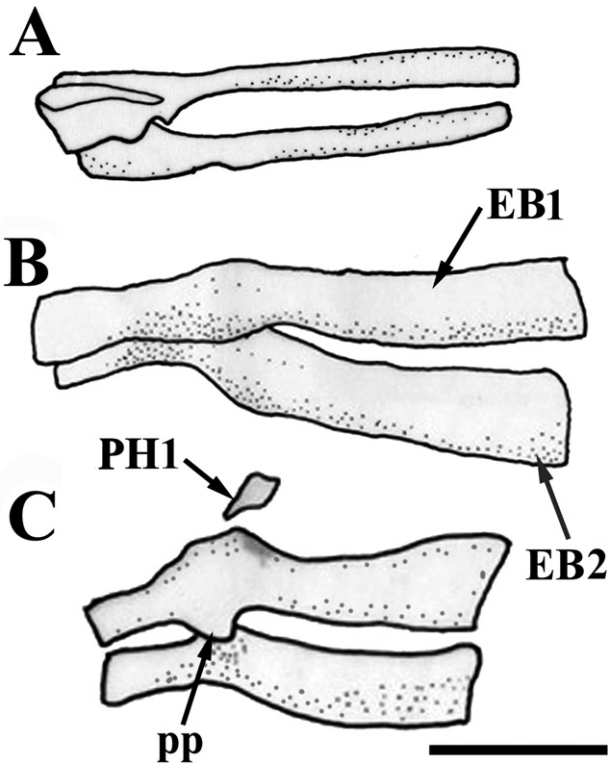
In all catfish outgroups and most ariid representatives the first hypobranchial anterior margin has an acute slight projection located in the mid-lateral portion of the bone. Exclusively in *Neoarius* and *Netuma*, the first hypobranchial anterior process is located in the middle of the bone. Not applicable in *Ketengus*.

168. *Shape of second hypobranchial*: shell-like (state 0; Fig. 21A–C); club-shaped (state 1; Fig. 21D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiachthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Ketengus*.

Exclusively in *Ketengus* the second hypobranchial is curved, club-shaped. In all the remaining species examined the bone is shaped like a bivalve shell (see character 164).

169. *Shape of second hypobranchial*: slightly elongate transversely, its mesial face rounded (state 0; Fig. 21A, B); very elongate transversely, its mesial face acute (state 1; Fig. 21C). State 0: Anchariidae, Bagridae, Cetopsidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Doradidae, Mochokidae, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Doiachthys*, and *Nedystoma*.

The second hypobranchial slightly elongate transversely, its mesial face rounded is the most common condition in the Ariidae. Only *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Doiachthys*, and *Nedystoma*, have the second hypobranchial transversely elongate with its mesial portion narrow and its length more than three times its width. Not applicable in *Ketengus*.



**Figure 22.** First and second epibranchials and first pharyngobranchial, dorsal view, left side. A, *Doiichthys novaeguineae*, AMS I. 27416-002; B, *Galeichthys feliceps*, MZUSP 87694; C, *Plicofollis dussumieri*, LACM 38131-48. Abbreviations: EB1, first epibranchial; EB2, second epibranchial; PH1, first pharyngobranchial; pp, posterior process. Scale bar = 4 mm.

170. *Contact face between first epibranchial and first pharyngobranchial*: inconspicuous (state 0; Fig. 22A, B); very conspicuous (state 1, Fig. 22C). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius* (except *Ar. arius*, *Ar. gagora*, and *Ar. maculatus*), *Aspistor*, *Bagre*, *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Sciades*. State 1: *Ar. arius*, *Ar. gagora*, *Ar. maculatus*, *Brustarius*, *Nedystoma*, *Osteogeneiosus*, *Plicofollis* (except *Pl. platystomus*), and *Potamosilurus*.

In all the representatives of the Siluriformes examined and in most Ariidae, the epibranchials are cylin-

drical, sometimes depressed without projections along their anterior and posterior margins. The anterior margin of the first epibranchial expanded, precisely at the contact area with the first pharyngobranchial, is the condition found only in some ariid taxa. Missing in *Ar. caelatus*.

171. *Shapes of first and second epibranchials*: curved at mesial third (state 0; Fig. 22C, B); straight along their entire extension (state 1; Fig. 22A). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Doiichthys*.

The first and second epibranchials curved, with their mesial third posteriorly orientated is the generalized condition of the character. Only in *Doiichthys*, the first and second epibranchials are straight.

172. *Disposition of first and second epibranchials*: first epibranchial parallel to second (state 0; Fig. 22A, C); first epibranchial overlaying second (state 1; Fig. 22B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*, *Galeichthys*, and *Ketengus*.

The mesial portions of first and second epibranchials are parallel and moderately separated from each other in most ariids. In *Bagre*, *Galeichthys*, and *Ketengus*, the mesial portions of first and second epibranchials are close together and sometimes the first is superimposed to the second.

173. *Mesial portion of first epibranchial (maximally connected)*: tubular and slightly depressed (state 0; Fig. 22C); large and depressed (state 1; Fig. 22B); very large and depressed (state 2; Fig. 22A). State 0: Anchariidae, Austroglanid-



idae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, and *Sciades*. State 1: *Galeichthys*. State 2: *Doiichthys*.

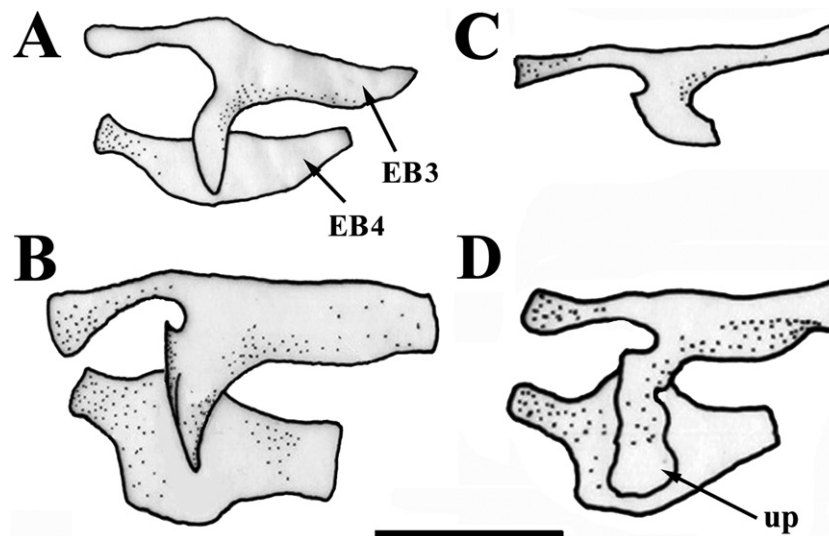
Primitively the epibranchials are cylindrical and slightly depressed in the Siluriformes. The enlargement of the first epibranchial mesial portion was recognized as a derived condition in the Siluriformes (de Pinna, 1993). In the Ariidae, two new states are recognized based on the degree of enlargement and flattening of the first epibranchial mesial portion: large and depressed only in *Galeichthys* and very large and depressed exclusively in *Doiichthys*. Missing in the Mochokidae.

174. *Posterior margin of first epibranchial*: straight (state 0; Fig. 22A, B); mesial one third with a prominent process (state 1; Fig. 22C). State 0: Anchariidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*,

*Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Horabagridae, *Pachyula*, and *Plicofollis* (except *Pl. platystomus*).

Presence of expansions or projections along the first epibranchial posterior margin was interpreted as apomorphic in the Siluriformes (de Pinna, 1993). In most Ariidae the first epibranchial posterior margin is smooth and straight. Another condition, defined by the presence of an irregularly shaped projection along the mesial third of the first epibranchial posterior margin, was observed only in *Plicofollis* (except *Pl. platystomus*).

175. *Size of uncinat process of third epibranchial*: equal or smaller than mesial portion of third epibranchial delimited by uncinat process (state 0; Fig. 23A–C); much longer and wider than mesial portion of third epibranchial delimited by uncinat process (state 1; Fig. 23D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*,



**Figure 23.** Third and fourth epibranchials, lateral view, left side. A, *Cephalocassis melanochir*, CAS 49426; B, *Plicofollis dussumieri*, LACM 38131-48; C, *Doiichthys novaeguineae*, AMS I. 27416-002; D, *Galeichthys feliceps*, MZUSP 87694. Abbreviations: EB3, third epibranchial; EB4, fourth epibranchial; up, uncinat process. Scale bar = 4 mm.

*Pl. platystomus*, *Pl. tenuispinis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*).

The third epibranchial in the Siluriformes is characterized by the presence of an uncinat process whose shape and size varies greatly in ariids. Although the degree of development of the uncinat process of the third epibranchial is variable within the Ariidae, its length and width are always equal or smaller than the third epibranchial mesial portion delimited by the uncinat process. Exclusively in *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), the uncinat process of the third epibranchial is conspicuously longer and wider than its mesial portion delimited by the uncinat process.

176. *Distal portion of uncinat process of third epibranchial*: acute (state 0; Fig. 23A–C); truncate (state 1, Fig. 23D). State 0: Anchariidae, Austroglanididae, Cetopsidae, Claroteidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Genidens*, *Hemiaris sumatranus*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus velutinus*, and *Sciades*.

Two distinct states related to the distal end of the third epibranchial uncinat process as here defined are independently observed in both the outgroup and the ingroup taxa.

177. *Shape of uncinat process of third epibranchial (minimally connected)*: mesially curved and length variable (state 0); straight and elongate (state 1; Fig. 23A, B, D); laterally curved and short (state 2; Fig. 23C). State 0: Austroglanididae, Diplomystidae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, and Mochokidae. State 1: Anchariidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlelelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Doiichthys* and *Nedystoma*.

In most Siluriformes the process is orientated toward the branchial arch mesial region, a condition defined as primitive by de Pinna (1993). This condition was described by de Pinna (1993) only for the Anchariidae and Ariidae. Nevertheless, Britto (2002) considered that, apomorphically in the Anchariidae, Ariidae, Pangasiidae, and Schilbidae, the uncinat process is posteriorly directed. In the present study an additional condition was found in *Doiichthys* and *Nedystoma*, characterized by a very short and laterally orientated process. Missing in the Cetopsidae.

178. *Margin of lateral uncinat process of third epibranchial*: straight (state 0; Fig. 23A–C); notched (state 1; Fig. 23D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlelelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Plicofollis* (except *Pl. platystomus*).

Exclusively in *Plicofollis* (except *Pl. platystomus*) there is a conspicuous notch on the lateral margin of the third epibranchial uncinat process.

179. *Mesial quarter of fourth epibranchial*: robust, almost as wide as long (state 0; Fig. 23B); thin, its width about twice its length (state 1, Fig. 23A, D). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Cochlelelis*, and *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The condition described for *Cochlelelis* and *Galeichthys* is characterized by the mesial quarter of fourth epibranchial being robust, almost as wide as long. Most of the Ariidae representatives have the mesial quarter of the fourth epibranchial thin, its width about twice its length.

180. *Posterior margins of fourth epibranchial*: conspicuously convex, half as wide as long (state 0; Fig. 23B, D); slightly convex, one quarter as wide as long (state 1; Fig. 23A). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cephalocassis*, *Doiichthys*, *Batrachocephalus*, *Ketengus*, and *Nedystoma*.

Fourth epibranchial in the Siluriformes is shorter than first and third epibranchials and usually without well-defined uncinuate process (de Pinna, 1993). In the Ariidae, this bone is broader than first and third epibranchials, with its posterior margin posteriorly projected on its median part and the profile clearly convex. However in *Cephalocassis*, *Doiichthys*, *Batrachocephalus*, *Ketengus*, and *Nedystoma*, it is almost as narrow as the third epibranchial, its posterior margin only slightly projected and its profile slightly convex.

181. *Anterior portion of proximal cartilage of fourth epibranchial*: as large as posterior portion (state 0); about twice narrower than posterior portion (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, and Schilbidae. State 1: *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The absence of a conspicuous morphological difference between the anterior and posterior portions of the proximal cartilage of fourth epibranchial is plesiomorphic for the Siluriformes. The apomorphic condition is characterized by the anterior twice narrower than the posterior portion, a condition observed in all the members of the Ariidae examined. The derived condition was first indicated by de Pinna (1993).

182. *First pharyngobranchial*: present (state 0; Fig. 22A, C); absent (state 1; Fig. 22B). State 0:

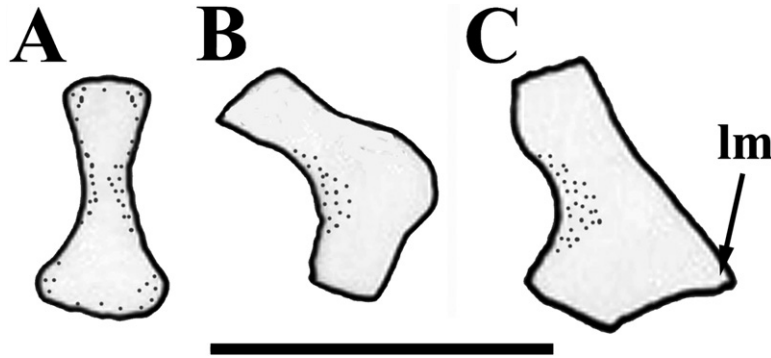
Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Horabagridae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, and *Galeichthys*.

The presence of the first pharyngobranchial was considered a primitive condition in the Siluriformes present in the Ariidae (Mo, 1991; de Pinna, 1993; see discussion of character 183). In *Galeichthys*, the first pharyngobranchial is absent.

183. *Shape of first pharyngobranchial*: long and narrow (state 0; Fig. 22A); large and depressed (state 1; Fig. 22C). State 0: Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Horabagridae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cochlefelis*, *Doiichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cat. dasycephalus*, *Cryptarius*, *Pachyula*, and *Plicofollis* (except *Pl. platystomus*).

Primitively in the Siluriformes the first pharyngobranchial is cylindrical, associated with the anterior margin of first epibranchial, parallel to this bone and with its length equivalent to less than one third of the length of the first epibranchial. Exclusively in *Cat. dasycephalus*, *Cryptarius*, *Pachyula*, and *Plicofollis* (except *Pl. platystomus*), the first pharyngobranchial is depressed and enlarged, in form of a small rectangular to subtrapezoid bony plate. Not applicable in the Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, and *Galeichthys* and missing in *Cinetodus*.

184. *Location of first pharyngobranchial in relation to first epibranchial*: on mesial end of first epibranchial (state 0; Fig. 22A); on mesial two thirds of first epibranchial (state 1; Fig. 22C). State 0: Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Horabagridae, Pangasiidae, Schilbidae, and *Doiichthys*. State 1: *Amphiarus*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*,



**Figure 24.** Third pharyngobranchial, dorsal view, right side. A, *Potamarius grandoculis*, MZUSP 1004-114; B, *Genidens barbatus*, MZUSP 24524; C, *Plicofollis dussumieri* LACM 38131-48. Abbreviation: lm, lateral margin. Scale bar = 4 mm.

*Cinetodus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Hemiarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

All ariid representatives, except *Doiichthys*, have the first pharyngobranchial on the mesial two thirds of the first epibranchial. Not applicable in Anchariidae, Austroglanididae, Cranoglanididae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, and *Galeichthys* and missing in the Heptapteridae.

185. *Shape of third pharyngobranchial*: funnel-like (state 0; Fig. 24A); angled in form of boomerang (state 1; Fig. 24B, C). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Doiichthys*, *Ketengus*, and *Potamarius grandoculis*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius izabalensis*, *Potamosilurus*, and *Sciades*.

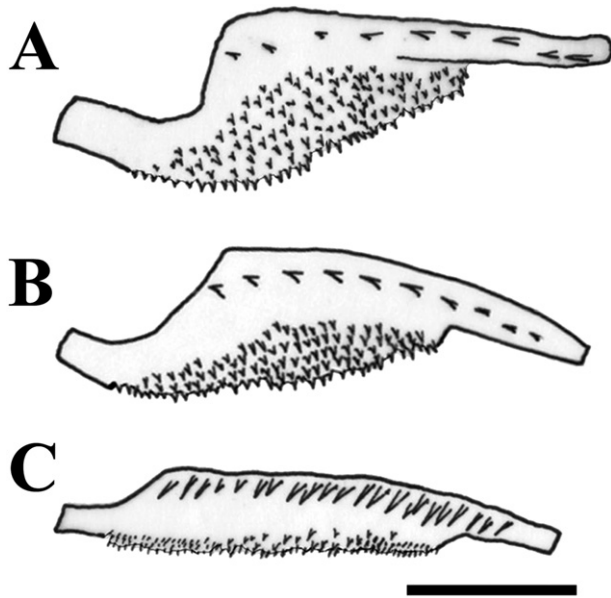
The third pharyngobranchial with its lateral margin well developed was considered synapomorphic for the Ariidae, *Hypophthalmus*, and *Rita* by de Pinna (1993). In the present work the character was reviewed and redefined. In *Doiichthys*, *Ketengus*, *Potamarius grandoculis*, and the outgroup taxa examined, the third pharyngobranchial has its anterior portion very elongate and its posterior portion gradually broader and triangular like a very elongate and depressed funnel. The common condition for most of the ariid representatives is characterized by the ante-

rior and posterior portions equally differentiated and the mesial part of the bone curved and angled.

186. *Lateral margin of third pharyngobranchial*: weakly developed and rounded (state 0; Fig. 24B); well developed and acute (state 1; Fig. 24C). State 0: *Amphiarius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nemapteryx*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius izabalensis*, and *Sciades*. State 1: *Arius*, *Brustiarius*, *Nedystoma*, *Neoarius*, *Netuma*, *Plicofollis*, and *Potamosilurus*.

Two well-defined states as defined above are recognized for the character. Not applicable in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Doiichthys*, *Ketengus*, and *Potamarius grandoculis* and missing in *Ar. dispar* and *Ar. madagascariensis*.

187. *Space for insertion of teeth on fifth ceratobranchial (minimally connected)*: very large (state 0; Fig. 25A); moderate (state 1; Fig. 25B); very small (state 2, Fig. 25C). State 0: *Galeichthys*. State 1: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Hemiarius*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State

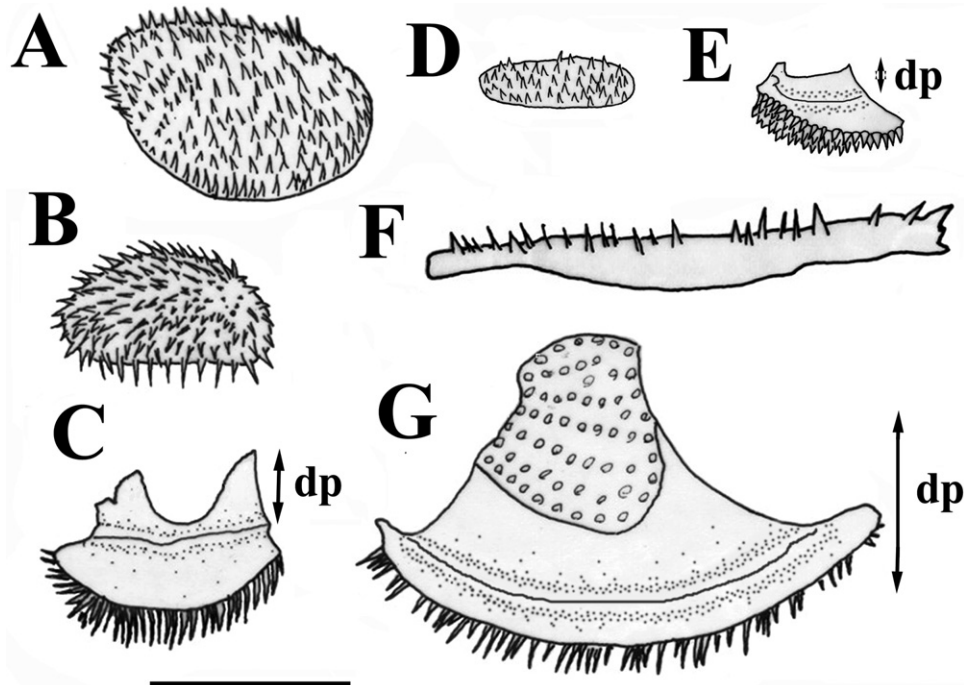


**Figure 25.** Fifth ceratobranchial, dorsal view, right side. A, *Galeichthys feliceps*, MZUSP 87694; B, *Potamarius izabalensis*, UMMZ 177252; C, *Doiichthys novaeguineae*, AMS I. 27416-002. Scale bar = 4 mm.

2: Cetopsidae, *Batrachocephalus*, *Cathorops* (except *Cat. dasycephalus*), *Doiichthys*, *Ketengus*, and *Nedystoma*.

In the Ariidae the fifth ceratobranchial is slightly curved, arrow-shaped, shorter than remaining ceratobranchials, and with a variable number of acicular teeth on its dorsal face (Higuchi, 1982). The presence of a large band of teeth on the dorsal surface of the fifth ceratobranchial was recognized as the primitive condition for the Siluriformes by de Pinna (1993). In *Batrachocephalus*, *Cathorops* (except *Cat. dasycephalus*), *Doiichthys*, *Ketengus*, and *Nedystoma*, the fifth ceratobranchial is conspicuously narrow with a few teeth on its only slightly expanded posterior part. An additional derived condition is found in *Galeichthys* where the posterior portion of fifth ceratobranchial is very expanded with a large band of teeth.

188. Shape of upper (pharyngeal) tooth plate (minimally connected): round, as wide as long (state 0; Fig. 26A); oval-shaped, its width twice its length (state 1; Fig. 26B); long and narrow, its width three times its length (state 2; Fig. 26D); very long and narrow, its width more than four times its length (state 3; Fig. 26F). State 0: *Cinetodus*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae,



**Figure 26.** Pharyngeal tooth plate, ventral view (A, B, D, F) and lateral view (C, E, G). A, *Cinetodus froggatti*, AMS I. 27417-001; B, C, *Genidens genidens*, MZUSP 24524; D, E, *Doiichthys novaeguineae*, AMS I. 27416-002; F, G, *Nedystoma dayi*, AMS I. 25992-001. Abbreviation: dp, dorsal processes. Scale bar = 4 mm.

Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Doiichthys*. State 3: *Nedystoma*.

The most common condition for the Ariidae is characterized by the upper tooth plate associated with the fourth large and oval-shaped pharyngobranchial. Exclusively in *Cinetodus*, the upper (pharyngeal) tooth plate is round, but in *Doiichthys* it is long and narrow and the extreme condition of the character is present in *Nedystoma*.

189. *Dorsal processes of upper (pharyngeal) tooth plate*: free (state 0; Fig. 26C); connected by bony blade (state 1; Fig. 26E, G). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Doiichthys* and *Nedystoma*.

Exclusively in *Doiichthys* and *Nedystoma* the tooth plate dorsal processes are connected by a bony blade along their entire extension (see discussion of character 190). In all the remaining taxa examined the dorsal processes are free. Not applicable in the Diplomystidae.

190. *Length of dorsal processes of upper (pharyngeal) tooth plate (minimally connected)*: very short or absent (state 0); long (state 1; Fig. 26C); very long (state 2; Fig. 26E, G). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Cinetodus*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Doiichthys* and *Nedystoma*.

In the Otophysi there is at least one tooth plate of dermal origin associated with the fourth pharyngobranchial. In most Siluriformes the upper tooth plate is associated with the fourth pharyngobranchial through a dorsal cartilage. In several Siluriformes, there is a pair of dorsal laminar expansions on the dorsal surface of the pharyngeal tooth plates that are connected with the corresponding pharyngobranchials through ligaments (de Pinna, 1993). An extreme condition of the character is present in *Doiichthys* and *Nedystoma* in which the dorsal expansions are very long and conspicuous. Not applicable in the Diplomystidae.

#### AXIAL SKELETON

191. *Diagonal crest associated with posterior branch of parapophysis of complex vertebra*: indistinct (state 0); well developed (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the Ariidae (except *Galeichthys*) the epioccipital laminar posterior process is sutured to the diagonal dorsal crest of the posterior branch of the parapophysis of the complex vertebra. The presence of such a structure is observed in all the Ariidae (except *Galeichthys*).

192. *Extension of diagonal crest associated with posterior branch of parapophysis of complex vertebra*: short, reaching transverse crest (state 0); long, reaching base of Müller's ramus (state 1). State 0: *Amphiarius*, *Aspistor*, *Bagre*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Pachyula*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius izabalensis*, and *Sciades*. State 1: *Arius* (except *Ar. gadora*), *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Occidentarius*, *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), *Potamarius grandoculis*, and *Potamosilurus*.

The degree of variation of the crests associated with the sustentaculum of the Weberian apparatus deter-

mined by how close they are to each other anteriorly, the presence and extension of a median crest, and the development of transverse crests, were used by Tilak (1965) to identify ariid genera and species from the Indian Ocean. The importance of these structures for recognition of supraspecific groups from south-eastern and southern Brazil was confirmed by Higuchi (1982). In some Ariidae the diagonal crest associated with the posterior branch of the parapophysis of the complex vertebra is very elongate, anteriorly close to the longitudinal axis or united to the basal portion of the Müllerian ramus. In some other taxa of the family the diagonal crest is short, anteriorly fused to the neural spine of the third vertebra or to the transverse crests. Not applicable in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys* and missing in *Ar. gagora*, *Ketengus*, and *Osteogeneiosus*.

193. *Transverse crest associated with neural spine of fourth vertebra*: low (state 0); very high (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cochlefelis*, *Doiachthys*, *Galeichthys*, *Genidens*, *Neoarius*, *Netuma*, *Notarius* (except *No. planiceps*), *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Amphiarius*, *Bagre*, *Batrachocephalus*, *Cathorops*, *Cinetodus*, *Cryptarius*, *Ketengus*, *Hemiaris*, *Nemapteryx*, *Nedystoma*, *No. planiceps*, *Occidentarius*, *Osteogeneiosus*, and *Pachyula*.

In the Ariidae on both sides of the base of the neural spine of the fourth vertebra there is a transverse crest of variable height and extension. In one condition, the transverse crests associated with the neural spine of the fourth vertebra are low and little differentiated. Another state is characterized by presence of very high and conspicuous transversal crests.

194. *Median crest associated with neural spine of third vertebra*: low or absent (state 0); very high (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Cryptarius*, *Doiachthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Osteogeneiosus*,

*Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Amphiarius*, *Aspistor*, *Bagre*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Hemiaris*, *Occidentarius*, *Nedystoma*, *Nemapteryx*, and *Pachyula*.

The presence of an inconspicuous median crest associated with the neural spine of the third vertebra or its absence are present in members of the outgroup examined and most taxa of the Ariidae. Missing in the Doradidae.

195. *Median crest associated with neural spine of fourth vertebra*: low or absent (state 0); very high (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cephalocassis*, *Cochlefelis*, *Doiachthys*, *Galeichthys*, *Genidens*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius* (except *No. planiceps*), *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Horabagridae, Heptapteridae, *Amphiarius*, *Bagre*, *Cathorops*, *Cinetodus*, *Cryptarius*, *Hemiaris*, *Occidentarius*, *No. planiceps*, and *Pachyula*.

The presence of a very high and conspicuous median crest anteriorly contacting the crest associated with the neural spine of the fourth vertebra was observed only in the ingroup representatives.

196. *Size of the opening delimited by epioccipital posterior process and the crests of sustentaculum of Weberian apparatus (minimally connected)*: very large (state 0); moderate (state 1); very reduced (state 2). State 0: *Amphiarius*, *Aspistor*, *Bagre*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiachthys*, *Hemiaris*, *Occidentarius*, *Nedystoma*, *Nemapteryx*, *Notarius* (except *No. planiceps*), *Pachyula*, and *Potamarius iza-balensis*. State 1: *Batrachocephalus*, *Ketengus*, *Pl. platystomus*, and *Pl. tenuispinis*. State 2: *Arius*, *Carlarius*, *Brustiarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Osteogeneiosus*, *Plicofollis* (except *Pl. platystomus* and *Pl. tenuispinis*), *Potamarius grandoculis*, *Potamosilurus*, and *Sciades*.

The size of the opening delimited by the epioccipital posterior process and the posterior branch of the parapophysis of the complex vertebra vary in the Ariidae. The size of the opening is primarily defined by the shorter extension of the diagonal crest. The opening delimited by the epioccipital posterior process and by the crests of the sustentaculum can be large,

occupying a large area defined by a short diagonal crest and the crests associated with the neural spines of the third and fourth vertebrae. Two other states of the character are defined by the larger extension of the diagonal crest anterior portion and the transverse and median crests very low. The first is defined by a moderate opening restricted to an area confined to the anterior and mesial portions, anteriorly meeting in the longitudinal axis and delimited by a shorter diagonal crest. The second condition is defined by a very narrow opening, reduced to the anterior portion and delimited by the diagonal crest reaching the base of Müller's ramus. Not applicable in Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Galeichthys*, and *No. planiceps*.

197. *Accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra*: absent (state 0); present (state 1). State 0: Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Amphiarius*, *Aspistor*, *Cephalocassis*, and *Notarius*.

The representatives of the genera *Amphiarius*, *Aspistor*, *Cephalocassis*, and *Notarius* share a conspicuous and high crest connecting the lateral portion of the transverse crest and the median crest associated with the neural spine of the fourth vertebra. Not applicable in *Galeichthys* and missing in the Anchariidae.

198. *Opening delimited by posterior process of epioccipital and crests associated with sustentaculum of Weberian apparatus*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*,

*Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the Ariidae (except *Galeichthys*) the posterior laminar expansion of the epioccipital is sutured to the crests associated with sustentaculum of the Weberian apparatus, delimiting mesoanteriorly an opening (see discussion of character 196). The absence of this opening is observed in the outgroups and *Galeichthys*.

199. *Superficial ventral ossification of the Weberian apparatus*: not or only partially covering the aortic canal (state 0); entirely covering the aortic canal (state 1; Figs 8A, B, 9A, B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bag. marinus*, *Bag. panamensis*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The aorta anteriorly passes through a ventral canal formed by ossifications from the complex vertebra. In the Siluriformes the aortic canal usually remains open at all the developmental stages of representatives of most groups, but in the Ariidae (except *Galeichthys*) exclusively the aorta is enclosed by a canal resulting from the deposition of vertebral bony elements (see more in the discussion of character 201). No sutures allowing recognition of contribution of the vertebrae are visible. Missing in *Bag. bagre* and *Bag. pinnimaculatus*.

200. *Location of cardinal veins in relation to aortic canal*: above level of aortic canal (state 0); at same level of aortic canal (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cat. dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* (except *Cat. dasycephalus*).



In most Ariidae, the cardinal veins pass through the carinae situated between the parapophyses of the anterior vertebrae and adjacent superficial ossification, above the level of the aortic canal. Only in members of the genus *Cathorops* (except *Cat. dasycephalus*) do the cardinal veins run laterally to the aortic canal (see description of character 205).

201. *General aspect of superficial ventral ossification*: keeled (state 0; Figs 8A, B, 9A); regularly arched (state 1; Fig. 9B). State 0: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cep. melanochir*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* and *Cep. borneensis*.

Exclusively in the Ariidae, the superficial ossification lies over the Weberian apparatus reinforcing the anterior portion of the axial skeleton, dorsally fused with the laminar expansion of the parapophyses of the complex vertebra, and ventrally covering the aortic canal. In most Ariidae, the superficial ossification forms a carina fitting precisely the groove located at the dorsomedial depression of the swimbladder. In cross section the structure looks like an inverted triangle in which the aorta is located on the inferior vertex and the cardinal veins on the superior angles. Uniquely in *Cathorops* and *Cep. borneensis*, the superficial ossification is medially cup-shaped, narrower close to the basioccipital and wider posteriorly. The structure is away from the bodies of the anterior vertebrae and the aortic canal is bordered by two large chambers through which pass the cardinal veins; the trabeculae that separate the vessels are formed by fusion of the ventral processes of the anterior vertebrae, a condition first described by Higuchi (1982). Not applicable in Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys*.

202. *Ventral surfaces of parapophyses of fifth and sixth vertebrae*: straight (state 0); conspicuously concave (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Keten-*

*gus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cinetodus* and *Pachyula*.

Ariids have the parapophyses of the fifth and sixth vertebrae projected lateroposteriorly and fused at the proximal portion. The parapophysis of the fifth vertebra is more developed and solidly sutured to the posterior expansion of the complex vertebra. Exclusively in *Cinetodus* and *Pachyula* there is on the ventral face of the parapophyses of the fifth and sixth vertebrae an oval-shaped structure in the form of a large concave bubble on the ventral surface.

203. *Number of ribs*: 14 or fewer (state 0); 15 or more (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustiarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Potamosilurus*. State 1: *Bagre*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Plicofollis* (except *Pl. platystomus*), and *Sciades*.

Presence of 14 or fewer ribs is the most common condition in the Ariidae and catfish outgroups. However, some ariids present 15 or more ribs. Missing in the Cranoglanididae, *No. planiceps*, and *S. seemanni*.

204. *First vertebra free from ventral superficial ossification (minimally connected)*: eighth vertebra (state 0); seventh vertebra (state 1); sixth vertebra (state 2); fifth vertebra (state 3). State 0: *Arius*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Bagridae, Cetopsidae, Doradidae, Horabagridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Aspistor*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, and *Pachyula*. State 2: Anchariidae, Claroteidae, Cranoglanididae, Heptapteridae, and Ictaluridae. State 3: Diplomystidae.

The greatest extension of the ventral superficial ossification and increase in the number of vertebrae firmly articulated with the complex vertebra was con-

sidered the derived condition in the Siluriformes (Roberts, 1973). In the present study the first free vertebra was determined by the unequivocal dissociation of its body from the ventral superficial ossification. Amongst ariids, this feature presents variation characterized by the seventh and/or eighth vertebra totally free from the ventral superficial ossification. Missing in *Ar. arius* and *Bag. bagre*.

205. *Number of precaudal vertebrae*: 18 or fewer (state 0); 19 or more (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Batrachoccephalus*, *Brustiaris nox*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, and *Pachyula*. State 1: *Arius*, *Aspistor*, *Bagre*, *Brustiaris solidus*, *Carlarius*, *Cochlefelis*, *Genidens*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Presence of 18 or fewer precaudal vertebrae is the most common condition in the Ariidae and catfish outgroups. However, some ariids present 19 or more precaudal vertebrae. Missing in the Cranoglanididae and *Potamosilurus macrorhynchus*.

206. *Number of caudal vertebrae*: 39 or more (state 0); 38 or fewer (state 1). State 0: *Bagre* and *Cochlefelis*. State 1: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Batrachoccephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Presence of 38 or fewer caudal vertebrae is the most common condition in the Ariidae and catfish outgroups. However, *Bagre* and *Cochlefelis*, exclusively, present 39 or more caudal vertebrae. Missing in the Cranoglanididae.

#### DORSAL FINS AND ASSOCIATED STRUCTURES

207. *Anterior and middle nuchal plates*: distinct (state 0; Figs 2A, 3B); indistinct (state 1; Figs 2B, 3A, 4A, B, 5A, B, 6A, B). State 0: Austroglanididae, Diplomystidae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Hep-

tapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Bag. bagre*, and *Galeichthys*. State 1: Anchariidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre* (except *Bag. bagre*), *Batrachoccephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

The nuchal plate is formed by the distal expansion of the supraneural, first basal radial, and second basal radial. Distally the supraneural forms the anterior nuchal plate, whereas the first and second basal radials form respectively the middle and posterior nuchal plates (Royero, 1987). The anterior nuchal plate is free and differentiated from the remaining elements that compose the median nuchal plate in most Siluriformes. The Anchariidae and almost all ariids show no suture recognizable between the anterior and middle nuchal plates, which are indistinct (except *Bag. bagre* and *Galeichthys*). Missing in the Cetopsidae.

208. *Shape of complex formed by anterior and median nuchal plates (maximally connected)*: half-moon shaped (state 0; Figs 2A, 3A, B, 4A, B, 5A, B, 6A, B); shield-like (state 1); butterfly shaped (state 2; Fig. 2B). State 0: Anchariidae, *Amphiarius*, *Arius*, *Bagre*, *Batrachoccephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri* and *S. proops*). State 1: *S. parkeri* and *S. proops*. State 2: *Aspistor*.

The most common condition of the character in the Ariidae is defined by a short, half-moon shaped nuchal plate. A shield-like nuchal complex defines the exclusive condition present in *S. parkeri* and *S. proops*. The species of *Aspistor* have an additional condition represented by the typical butterfly shape of the nuchal complex. Not applicable in the Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

209. *Nuchal plate anterior margin (maximally connected)*: convex (state 0; Figs 2A, 3A, B, 4A, B, 5A, B, 6A, B); slightly concave (state 1; Fig. 2B); conspicuously notched (state 2). State 0:

Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarus*, *Arius*, *Bagre*, *Batrachcephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. proops*). State 1: *Aspistor*. State 2: *S. proops*.

The anterior margin of the nuchal plate complex is convex in the Ariidae. The slightly concave and deeply notched condition is exclusive in *Aspistor* and *S. proops*, respectively.

210. *Contact between nuchal plate and parietosupraoccipital (maximally connected)*: contact made through a deeply notched articulation (state 0; Figs 2A, 3B); nuchal plate and parietosupraoccipital contacting one another through a convex–concave articulation (state 1; Figs 3A, 4A, B, 5A, B, 6A, B); nuchal plate overlaying parietosupraoccipital (state 2; Fig. 2B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, Pangasiidae, *Bagre*, and *Galeichthys*. State 1: *Amphiarus*, *Arius*, *Batrachcephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius* (except *No. troschelii*), *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri* and *S. proops*). State 2: *Aspistor*, *No. troschelii*, *S. parkeri*, and *S. proops*.

In the Ariidae, except *Bagre*, and *Galeichthys*, there is a contact between a slightly concave posterior margin of the parietosupraoccipital and a slightly convex anterior margin of the nuchal plate. An additional condition is characterized by the convex anterior margin of the nuchal plate overlaying the posterior portion of the parietosupraoccipital. Not applicable in the Diplomystidae, Doradidae, Mochokidae, and Schilbidae.

211. *Dorsal-fin spine*: without filament (state 0): prolonged into a filament (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae,

*Amphiarus*, *Ar. dispar*, *Ar. gagera*, *Ar. maculatus*, *Aspistor*, *Bag. panamensis*, *Batrachcephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiarus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Arius* (*Ar. dispar*, *Ar. gagera*, and *Ar. maculatus*) and *Bagre* (except *Bag. panamensis*).

Presence of a filament as part of the dorsal-fin spine is exclusive to some species of *Arius* and *Bagre*.

212. *Length of adipose-fin base (minimally connected)*: very long (state 0); long (state 1); moderately long (state 2); very short (state 3). State 0: Anchariidae, Austroglanididae, Bagridae, Claroteidae, Diplomystidae, Doradidae, Heptapteridae, and Mochokidae. State 1: *Amphiarus*, *Aspistor*, *Cephalocassis*, *Cinetodus*, *Galeichthys*, *Hemiarus*, *Notarius*, and *Pachyula*. State 2: Ictaluridae, Cranoglanididae, *Arius*, *Batrachcephalus*, *Carlarius*, *Cochlefelis*, *Doiichthys*, *Genidens*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Occidentarius*, *Osteogeneiosus*, *Pl. platystomus*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 3: Horabagridae, Pangasiidae, Schilbidae, *Bagre*, *Brustiarius*, *Cathorops*, *Cryptarius*, *Netuma*, and *Plicofollis* (except *Pl. platystomus*).

The importance of shape and length of the adipose fin for locomotion in the Siluriformes was discussed by Alexander (1965) and Gosline (1971). Extension and position of the adipose fin in relation to the anal fin is variable in the Ariidae. In the majority of the representatives of the outgroup examined, the adipose fin is very long, its base longer than the anal-fin base. An adipose fin as long as the anal-fin base is unique in the Ariidae. Additional conditions in the family are adipose fin moderately long (its base about half as long as the anal-fin base) or very short (its base shorter than half the length of the anal-fin base). Missing in the Cetopsidae.

213. *Position of adipose-fin origin (minimally connected)*: anterior to anal-fin origin (state 0); vertically above anterior half of anal fin (state 1); vertically above posterior half of anal fin (state 2). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Doradidae, Heptapteridae, and Mochokidae. State 1: Ictaluridae, Cranoglanididae, *Amphiarus*, *Arius*, *Aspistor*, *Batrachcephalus*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Galeichthys*, *Genidens*,

*Hemarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Pl. platystomus*, *Potamarius*, and *Sciades*. State 2: *Horabagridae*, *Pangasiidae*, *Schilbidae*, *Bagre*, *Brustarius*, *Netuma*, and *Plicofollis* (except *Pl. platystomus*).

Apomorphically in the Siluriformes the adipose-fin origin is posterior to a vertical through the anal-fin origin, a condition found in the Ariidae, Ictaluridae, and Cranoglanididae. An adipose-fin origin vertically above the posterior half of the anal fin is exclusive to *Bagre*, *Brustarius*, *Netuma*, and *Plicofollis* (except *Pl. platystomus*). Missing in *Doiichthys*.

#### PECTORAL AND PELVIC GIRDLE

214. *Length of posterior process of cleithrum (minimally connected)*: very short (state 0; Fig. 27A); moderately long (state 1, Fig. 27B, C); very long (state 2; Fig. 27D). State 0: *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Doiichthys*, *Hemarius*, *Nedystoma*, and *Nemapteryx*. State 1: *Anchariidae*, *Claroteidae*, *Diplomystidae*, *Horabagridae*, *Ictaluridae*, *Pangasiidae*, *Schilbidae*, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cat. dasycephalus*, *Cochlefelis*, *Cryptarius*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 2: *Austroglanididae*, *Cranoglanididae*, *Doradidae*, *Cinetodus*, and *Pachyula*.

The length and width of the posterior process of cleithrum, located at the median or superior portions of the bone, is variable. Lundberg (1970) defined four basic conditions for the length and ornamentation of the process in the Siluriformes. According to him, a long and ornamented process is usually found in the Siluriformes and would represent the plesiomorphic state of the character. In the present study, variation in length of the process was evaluated in relation to the vertical length of the lateral face of the cleithrum. A moderate length (about half the vertical length of the lateral face of cleithrum) is the most common condition in the Ariidae. A very long process (equal to the vertical length of the lateral face of cleithrum) is recognized as exclusive in *Cinetodus* and *Pachyula*. An additional condition corresponds to a process very short (less than one third as long as the lateral face of cleithrum). Not applicable in *Galeichthys* and missing in the Cetopsidae, Bagridae, Heptapteridae, and Mochokidae.

215. *Position of the second dorsal cleithral process*: on upper portion of cleithrum (state 0, Fig. 27A, B);

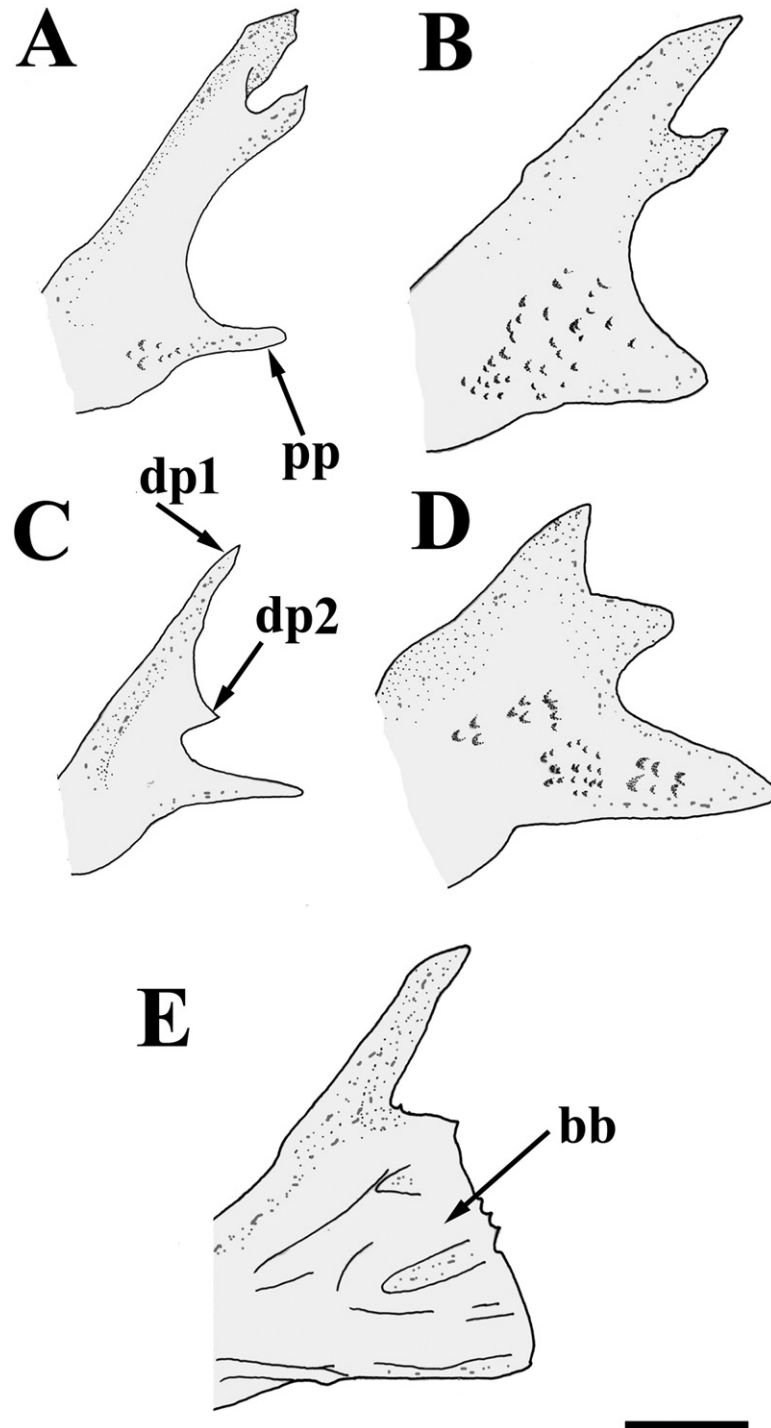
on lower portion of cleithrum (state 1; Fig. 27C). State 0: *Anchariidae*, *Austroglanididae*, *Bagridae*, *Claroteidae*, *Cranoglanididae*, *Diplomystidae*, *Doradidae*, *Horabagridae*, *Ictaluridae*, *Schilbidae*, *Amphiarius*, *Arius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Pangasiidae* and *Bagre*.

The second dorsal process of the cleithrum, located on the ventral part of this bone, constitutes a condition exclusively found in the species of *Bagre*. Not applicable in *Galeichthys* and missing in the Cetopsidae, Heptapteridae, and Mochokidae.

216. *Orientation of the second dorsal cleithral process*: posteriorly directed and parallel to posterior process (state 0; Fig. 27C, D); dorsally directed and parallel to first dorsal process (state 1; Fig. 27A, B). State 0: *Austroglanididae*, *Bagridae*, *Diplomystidae*, *Horabagridae*, *Pangasiidae*, *Schilbidae*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cinetodus*, *Cochlefelis*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Potamosilurus* (except *Potamosilurus velutinus*), and *Sciades*. State 1: *Anchariidae*, *Cranoglanididae*, *Doradidae*, *Ictaluridae*, *Amphiarius*, *Arius*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemarius*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Osteogeneiosus*, *Potamarius*, *Plicofollis*, and *Potamosilurus velutinus*.

Dorsally, the cleithrum bifurcates into two long and acute branches. The first process fits into the articular concavity of the supracleithrum, connecting the pectoral girdle to the cranium. One of the conditions of the character is defined by the main axis of the second dorsal cleithral process parallel to the first dorsal process, its end dorsally orientated. Another condition is represented by the situation in which the second dorsal cleithral process is posteriorly directed and parallel to the posterior process. Not applicable in *Galeichthys* and missing in the Cetopsidae, Heptapteridae, Mochokidae, and *S. passany*.

217. *Cleithrum lateral face*: moderately wide (state 0; Fig. 27B–E); very narrow (state 1, Fig. 27A). State 0: *Anchariidae*, *Austroglanididae*, *Bagridae*, *Claroteidae*, *Cranoglanididae*, *Doradidae*, *Horabagridae*, *Ictaluridae*, *Pangasiidae*, *Schilbidae*, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brus-*



**Figure 27.** Cleithrum, lateral view, left side. A, *Cathorops agassizii*, MZUSP 37232; B, *Plicofollis tenuispinis*, LACM 38128-47; C, *Bagre bagre*, MZUSP 35843; D, *Cinetodus froggatti*, AMS I. 27417-001; E, *Galeichthys feliceps*, MZUSP 87694. Abbreviations: bb, bony blade; dp1, first dorsal process; dp2, second dorsal process; pp, posterior process. Scale bar = 4 mm.

*tiarius*, *Carlarius*, *Cat. dasycephalus*, *Cinetodus*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Ketengus*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, and *Nemapteryx*.

Exclusively amongst ariids, *Cathorops* (except *Cat. dasycephalus*), *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Nedystoma*, and *Nemapteryx* present a dorsoventrally very narrow and elongate lateral face of cleithrum, easily visible even in non-cleared and stained specimens. Missing in the Cetopsidae, Heptapteridae, and Mochokidae.

218. *Relationship between posterior process of cleithrum and cleithrum second dorsal process*: free (state 0; Fig. 27A–C); connected by a bony blade (state 1; Fig. 27E). State 0: Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Claroteidae, Cranoglanididae, Doradidae, Horabagridae, Ictaluridae, Pangasiidae, Schilbidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Heptapteridae, Mochokidae, and *Galeichthys*.

Exclusively present in *Galeichthys* amongst ariids, a bony blade connects the cleithrum second dorsal and posterior processes.

219. *Mesocoracoid loop*: present (state 0); absent (state 1). State 0: Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Doradidae, Anchariidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In most siluriforms, the mesocoracoid is a very thin bone in the form of an arch, its ends fused to the scapulocoracoid. Absence of the mesocoracoid was considered apomorphic in the Siluriformes (Mo, 1991,

Britto, 2003), and Kailola (2004), and is the condition found in all ariids examined in the present study.

220. *Pelvic splint*: absent (state 0); present (state 1). State 0: Anchariidae, Claroteidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Cranoglanididae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae.

The pelvic splint is a small, ossified structure laterally located in relation to the first pelvic-fin rays in the Otophysi (Weitzman, 1962). The homology between the pelvic splint and the pelvic-fin rays was suggested based on the presence of two lepidotrichia-like structures (Lundberg, 1970). Usually the pelvic splint is represented by a reduced pelvic-fin ray-like element. Presence of the pelvic fin splint varies in the Siluriformes and its absence has been interpreted as apomorphic in the Ariidae, Anchariidae, and Claroteidae (Britto, 2002), a condition also observed in all ariids examined in the present study. Missing in the Doradidae and Heptapteridae.

#### MISCELLANEOUS

221. *Distance between nostrils*: anterior nostril distant from posterior (state 0); anterior and posterior nostrils close together (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, and Schilbidae. State 1: Diplomystidae, *Amphiaris*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiaris*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

Amongst otophysans, and several other teleosts, there are two pairs of nostrils situated in the anterior region of the head, showing the posterior pair often close to the orbital rim. Characiforms and cypriniforms display the anterior and posterior nostrils very close to each other, separated just by a minute skin flap. In the Gymnotiformes and other Siluriformes,

both nostrils are well distant from each other, leaving the posterior nostril close to the orbital rim and the anterior close to snout tip. Amongst the catfish groups examined in the present study, this condition is observed only in the Ariidae and Diplomystidae, but in Loricarioidea, state 1 is found in Loricariidae, Scoloplacidae, Astroblepidae, and Corydoradinae, taxa not included as outgroups in the present analysis.

222. *Groove connecting posterior nostrils*: absent (state 0); present (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. couma*, *S. herzbergii*, and *S. passany*). State 1: *S. couma*, *S. herzbergii*, and *S. passany*.

Presence of a groove bordered by a free skin fold connecting the posterior nostrils is a feature exclusively present in *S. couma*, *S. herzbergii*, and *S. passany*. In the remaining ariids, the skin between the posterior nostrils is devoid of groove or skin fold.

223. *Maxillary barbels*: present (state 0); absent (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Batrachocephalus*.

Presence of at least one pair of barbels is typical in the Siluriformes. Lundberg & Baskin (1969), Fink & Fink (1981), and Roberts (1973) considered the presence of a single pair of maxillary barbels the primitive condition for the entire group, and the acquisition of one or two pairs of mental barbels with independent origins (Fink & Fink, 1981) would represent the derived condition. Absence of the maxillary barbels is an exclusive feature of *Batrachocephalus*.

224. *Maxillary barbel*: cylindrical (state 0); compressed (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: *Bagre*.

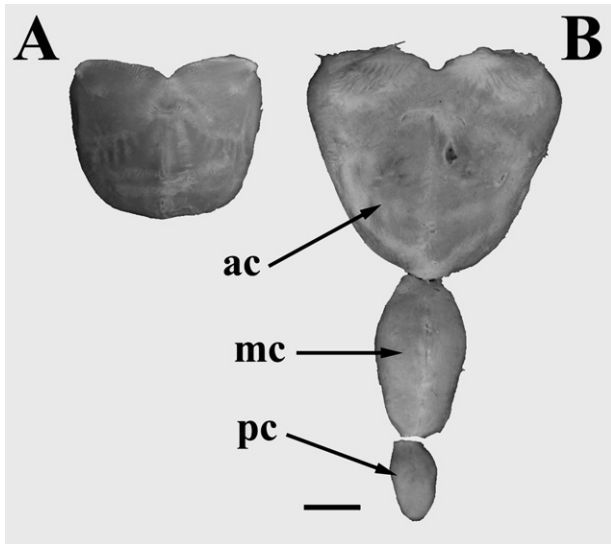
Maxillary barbels very compressed, tape-like, is unique for the species of *Bagre*.

225. *Mental barbels*: present (state 0); absent (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Diplomystidae and *Osteogeneiosus*.

Presence of mental barbels is a feature of the Ariidae, and their absence an exclusive characteristic of *Osteogeneiosus*.

226. *Number of mental barbels*: two pairs (state 0); one pair (state 1). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Schilbidae, *Amphiarius*, *Aspistor*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*. State 1: Pangasiidae and *Bagre*.

Exclusively in the Siluriformes, there is at least one pair of mental barbels, which can be present in the isthmus or lower lip region amongst most of its representatives. Only in *Bagre*, amongst ariids, is there just one pair. Not applicable in Diplomystidae and *Osteogeneiosus*.



**Figure 28.** Swimbladder, ventral view. A, *Aspistor quadriscutis*, MZUSP 48525; B, *Sciades parkeri*, MZUSP 48524. Abbreviations: ac, anterior chamber; mc, middle chamber; pc, posterior chamber. Scale bar = 10 mm.

227. *Swimbladder*: with a single chamber (state 0; Fig. 28A); with three chambers (state 1; Fig. 28B). State 0: Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Galeichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. parkeri* and *S. proops*). State 1: *S. parkeri* and *S. proops*.

The generalized condition of the swimbladder of most siluriforms is represented by a large heart-shaped chamber with rounded borders (Stewart, 1986). Exclusively in *S. parkeri* and *S. proops* two additional posterior chambers are present, the median one elongate and the posterior one very reduced. In the present study the presence of a second chamber in Ictaluridae, Pangasiidae, and Schilbidae (Roberts, 1973) was not confirmed.

228. *Shape of lateral line at caudal region*: not bifurcated (state 0); bifurcated (state 1). State 0: Horabagridae, *Amphiarius*, *Aspistor*, *Brustiarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*,

*Galeichthys*, *Genidens*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Notarius*, *Occidentarius*, *Pachyula*, *Potamarius*, *Potamosilurus*, and *Sciades* (except *S. couma*). State 1: Pangasiidae, *Arius*, *Bagre*, *Batrachocephalus*, *Ketengus*, *Netuma*, *Osteogeneiosus*, *Plicofollis*, and *S. couma*.

In the majority of the Siluriformes the lateral line is continuous, extending to the base of the caudal fin (Lundberg, 1992), where it is slightly bent either dorsally or ventrally. Most ariids have the lateral line bent dorsally reaching or not the base of the caudal fin upper lobe. A different condition found in the Ariidae is represented by a lateral line bifurcated at the caudal region, the dorsal branch reaching the caudal fin upper lobe and the ventral branch the lower lobe of same fin. Missing in the Anchariidae, Austroglanididae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Diplomystidae, Doradidae, Heptapteridae, Ictaluridae, Mochokidae, and Schilbidae.

229. *Origin of protractor muscle of parapophysis of fourth vertebra*: from ventral surface of parieto-supraoccipital process and posterior process of epioccipital (state 0); exclusively from ventral surface of posterior process of epioccipital (state 1). State 0: *Amphiarius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Notarius*, *Pachyula*, and *Potamarius izabalensis*. State 1: *Arius*, *Carlarius*, *Cochlefelis*, *Brustiarius*, *Genidens*, *Neoarius*, *Netuma*, *Osteogeneiosus*, *Plicofollis*, *Potamarius grandoculis*, *Potamosilurus*, and *Sciades*.

In ariids the parapophysis of the complex vertebra is very expanded, forming two projections connected by a delicate, curved bony blade fitting the anterodorsal portion of the swimbladder. The structure is known as the elastic spring apparatus, a sound-generating mechanical system described by Tavalga (1962). The sound-producing mechanism is activated by a muscle originating at the cranium and attaching to the parapophysis of the fourth vertebra and its movement (contraction or expansion) causes the swimbladder to vibrate, producing sound waves (Alexander, 1964; Howes, 1985). According to Howes (1985) sound production is present in the Doradidae, Auchenipteridae, Mochokidae, Malapteruridae, Pangasiidae, and Ariidae. The same mechanism was described by de Pinna (1993) in the Ageneiosidae, Anchariidae, and Centromochlidae. The protractor muscle of the parapophysis of the fourth vertebra, responsible for sound production and part of the



elastic spring apparatus was described by Royero (1987) as a modification of the 'supracarinalis anterior' in the Ariidae, Mochokidae, Doradidae, Auchenipteridae, and Ageneiosidae. Tavalga (1962) and Royero (1987) suggested that the protractor muscle would originate from the ventral face of the parieto-supraoccipital process and from the posterior process of the epioccipital in the Ariidae. Exclusively within the Ariidae, the protractor muscle originates exclusively from the posterior process of the epioccipital. Not applicable in Anchariidae, Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Doradidae, Heptapteridae, Horabagridae, Ictaluridae, Mochokidae, Pangasiidae, Schilbidae, and *Galeichthys* and missing in *No. planiceps* and *Occidentarius*.

230. *Contact between protractor muscle of parapophysis of fourth vertebra and posterior process of epioccipital*: absent (state 0); present (state 1). State 0: Anchariidae, Doradidae, Mochokidae, Pangasiidae, *Galeichthys*. State 1: *Amphiarius*, *Arius*, *Aspistor*, *Bagre*, *Batrachocephalus*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cinetodus*, *Cochlefelis*, *Cryptarius*, *Doiichthys*, *Genidens*, *Hemiaris*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius*, *Netuma*, *Notarius*, *Occidentarius*, *Osteogeneiosus*, *Pachyula*, *Plicofollis*, *Potamarius*, *Potamosilurus*, and *Sciades*.

In the taxa where the elastic spring apparatus is present, the sound-producing mechanism works through the action of the protractor muscle of the parapophysis of the fourth vertebra originating from the parietosupraoccipital and the anterior part of the nuchal plate. In the Ariidae (except *Galeichthys*) the muscle originates from the posterior ventral process of the epioccipital. Not applicable in the Austroglanididae, Diplomystidae, Bagridae, Cetopsidae, Claroteidae, Cranoglanididae, Heptapteridae, Horabagridae, Ictaluridae, and Schilbidae.

#### PHYLOGENETIC RECONSTRUCTION AND DIAGNOSES OF THE CLADES

The analysis of internal relationships within the Ariidae was based on the examination of 230 morphological characters. Parsimony analysis using Hennig86, NONA, and TNT yielded 48 equally parsimonious trees with 960 steps, consistency index 0.34, and retention index 0.81. Relationships within the Ariidae are depicted in the consensus tree (Fig. 29). The data matrix is shown in Appendix 1. The characters in the data matrix correspond to those in the sections 'Character description' and 'Diagnoses of the branches' below. Numbers of the clades herein

recognized are those above each branch of the strict consensus cladogram.

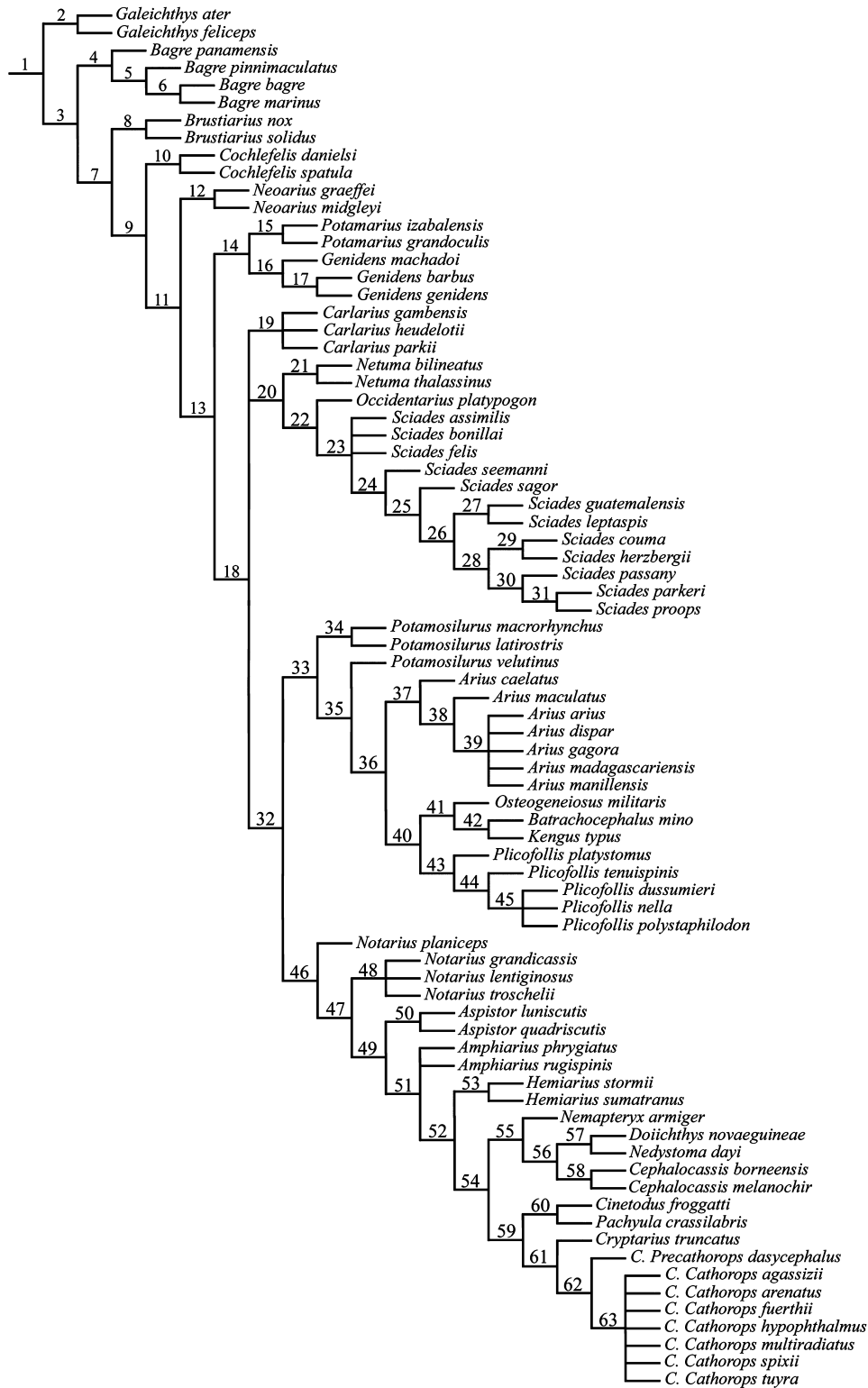
Character state distribution in the strict consensus tree was examined through accelerated transformation optimization using WinClada 1.00.08 (Nixon, 2002). Of the 93 terminal taxa examined, 14 belong to outgroup and 79 to ingroup taxa. As the main purpose of this study was to investigate monophyly of the taxa and the internal relationships within Ariidae, previous hypotheses about relationships of ariid outgroups (Mo, 1991; Lundberg, 1993; de Pinna, 1993, 1998; Britto, 2002; Diogo, 2004; Hardman, 2005; Sullivan, Lundberg & Hardman, 2006) are not discussed. Nevertheless results indicating Ariidae as sister group of the Anchariidae, both forming a monophyletic assemblage including Claroteidae, corroborate previous studies by de Pinna (1993), Britto (2002), Diogo (2004), and Sullivan *et al.* (2006, in part).

For each clade a parenthetical annotation is presented summarizing the internal relationships and the support indexes for the branch (respectively 'bootstrap', 'jackknife' and 'decay index or Bremer'). A brief comment about monophyly of the clade is made, followed by a list of synapomorphies with the apomorphic condition for the clade, the character number, and the character state transition in parentheses. Cases where the derived condition resulted from reversal to the primitive condition observed in the outgroup are shown in square brackets. As the derived condition was sometimes not found in some terminals of the branch, reversals to the plesiomorphic condition within the clade and independent acquisition of the apomorphic condition are mentioned. In the list of synapomorphies characters with non-ambiguous optimizations are separated from the ambiguous ones.

#### MONOPHYLY OF CLADE 1 (ARIIDAE) (GALEICHTHYINAE (BAGREINAE, ARIINAE)) [99 – 100 – 12]

The hypothesis of the monophyly of the family Ariidae is supported by the following synapomorphies, many of which are described for the first time:

1. External posterior branch of lateral ethmoid columnar (13, 1 > 0). Reversed in clades 20 and 40.
2. Lateral ethmoid and frontal connected through two facets with a mesial fenestra between them (14, 1 > 2, Figs 2A, B, 3A, B, 4A, 5A, B, 6A, B). State 0 in *Ketengus*.
3. Nasal anterior tubules connected by a bony blade (21, 0 > 1). Reversed in *Osteogeneiosus*.
4. Epioccipital bearing a posterior process (40, 0 > 1; Figs 2A–6B).



**Figure 29.** Strict consensus tree of 49 trees, length 966, consistency index 0.33, and retention index 0.81, showing the phylogenetic relationships within the family Ariidae based on 230 characters studied, branches with numbers of the clades.

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5. Otic capsules very large, limited by prootic, pterotic, and exoccipital (68, 0 > 2; Figs 8B, 9A, B). State 1 in clade 22.
6. Subvertebral process well developed (71, 0 > 1; Fig. 10A–C). Reversed in clade 22.
7. Space between transcapular process and otic capsule moderately developed (82, 0 > 1; Figs 8B, 9A). State 2 in clades 41 and 51, reversed in clade 22, and convergent in *Hemiaris* and clade 57.
8. Three infraorbitals present (88, 2 > 3, Fig. 11A, B). State 1 in *Doiichthys*.
9. Lachrymal-antorbital very wide (93, 1 > 0; Fig. 12A–E). Reversed in clade 44.
10. Opercle anterior portion subtrapezoid, very long (120, 4 > 0; Fig. 15A). State 1 in clade 7, state 2 in *Cep. borneensis* and clade 59, state 3 in *Batrachocephalus*, reversed in *Cochlefelis*, *Ketengus*, and clade 30, and convergent in *Cinetodus* and *Nedystoma*.
11. Second basibranchial anterior portion well developed and expanded (158, 0 > 1; Fig. 20A–F).
12. Anterior portion of proximal cartilage of fourth ceratobranchial about twice as narrow as posterior portion (181, 0 > 1).
13. Third pharyngobranchial angled, shaped like a boomerang (185, 0 > 1; Fig. 24B, C). Reversed in *Doiichthys*, *Ketengus*, and *Potamarius grandoculis*.
14. Dorsal processes of upper (pharyngeal) tooth plate long (190, 0 > 1; Fig. 26C). State 2 in clade 57 and reversed in *Cinetodus*.
15. Adipose-fin base long, as long as anal-fin base (212, 0 > 1). State 2 in *Nedystoma*, clades 9 and 57, state 3 in *Bagre*, *Brustiarius*, *Netuma*, and clades 44 and 61, and convergent in *Cephalocassis*, and clades 46 and 60.
16. Adipose-fin origin vertically above anterior half of anal fin (213, 0 > 1). State 2 in *Bagre*, *Brustiarius*, *Netuma*, and clade 44, and convergent in clade 9.
17. Anterior and posterior nostrils close together (221, 0 > 1).
20. Accessory tooth plates present (56, ? > 1). State 0 in *Cep. borneensis*, *Ketengus*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus*.
21. Orbitosphenoid and pterosphenoid lateral expansions present (62, ? > 1; Figs 8A, B, 9B). State 0 in *Cryptarius*, *Potamarius*, and clades 41 and 55.
22. Seventh is the first vertebra free from superficial ventral ossification (204, ? > 1). State 0 in clade 3 and convergent in *Ketengus* and clade 49.

MONOPHYLY OF CLADE 2 (GALEICHTHYINAE)  
(*GALEICHTHYS ATER*, *GALEICHTHYS FELICEPS*)  
[100 – 100 – 12]

The subfamily Galeichthyinae is represented only by *Galeichthys* and is a monophyletic group very well defined by the following synapomorphies:

1. Frontal without mesial laminar projection (23, 1 > 0; Figs 2A, B, 3A, 4A, 5A, B). Convergent in *Arius*, *Osteogeneiosus*, *Potamarius*, *Potamosilurus latirostris*, and clade 49.
2. Parietosupraoccipital process nearly as narrow at base as at posterior portion (44, 1 > 0; Figs 2A, 3A, 5B). Convergent in *Cep. melanochir* and clade 57.
3. Transcapular process transversel to main body axis (79, 0 > 1; Fig. 9B). Convergent in clade 46.
4. Lachrymal-antorbital posterior branch short and weakly developed (92, 1 > 0; Fig. 12E). Convergent in *S. proops*.
5. Posterior cartilage of autopalatine as long as anterior cartilage (107, 1 > 0).
6. Anguloarticular with an anterodorsal process (111, 0 > 1).
7. Opercle posterior portion little developed posteriorly (122, 1 > 0; Fig. 15A, B). Convergent in *Bag. panamensis*, *Genidens*, *Ketengus*, *Occidentarius*, *Sciades*, and clade 44.
8. Second external branchiostegal ray almost as wide as first ray (141, 0 > 1; Fig. 18B). Convergent in *Cephalocassis*, *Nedystoma*, and clades 42 and 61.
9. Second basibranchial posterior portion very long and wide (160, 2 > 0; Fig. 20C). Convergent in *Cryptarius*.
10. Mesial portion of first epibranchial large and depressed (173, 0 > 1; Fig. 22B).
11. Space for insertion of teeth on fifth ceratobranchial very large (187, 1 > 0; Fig. 25A).
12. Posterior cleithral process connected with second dorsal process of cleithrum through a bony blade (218, 0 > 1; Fig. 27E).

*Ambiguous optimization*

18. Posterior cranial fontanel delimited exclusively by frontal bones (25, ? > 1; Figs 2A, 3B, 4A, 5A, 6B). State 0 in *Cochlefelis*, *Ketengus*, *Neoarius*, and clade 32, and convergent in *Cathorops* (*Cathorops*), *Osteogeneiosus*, *Plicofollis*, and clade 13.
19. Posterior cranial fontanel reduced to a small opening (27, ? > 0; Figs 2A, 3A, 4A, 6B). State 1 in clade 9, state 2 in *Potamosilurus latirostris* and clade 49, state 3 in clade 55, convergent in *Cathorops* (*Cathorops*), *Genidens*, and clades 22 and 44.

*Ambiguous optimization*

13. Medial groove on top of neurocranium shallow, its margins little differentiated (31, ? > 0; Figs 2A, 6A). Convergent in *Bag. panamensis*, *Bag. pinnimaculatus*, *Cochlefelis*, *No. planiceps*, and clade 26.
14. Parietosupraoccipital ventral crest weakly developed, restricted to base of process (46, ? > 0). Convergent in *Cryptarius*, *Doiichthys*, and clade 7.
15. Maxilla wide at proximal two thirds where its edges are parallel, narrower distally becoming thinner and acute posteriorly (95, ? > 1).
16. Autopalatine anterior cartilage very short, less than one third as long as bone itself (106, ? > 0; Fig. 14B–D). Convergent in *Bagre* and *Osteogeneiosus*.
17. Hyomandibular dorsal crest absent (133, ? > 0; Fig. 16A, B). Convergent in *Bagre*.
18. Third basibranchial long and narrow (162, ? > 2; Fig. 20C–F), Convergent in *Cochlefelis*, *Batrachcephalus*, and *Potamarius*.
19. First epibranchial overlaying second epibranchial (172, ? > 1; Fig. 22B). Convergent in *Bagre* and *Ketengus*.
20. Medial crest associated with neural spine of third vertebra low or absent (194, ? > 0). Convergent in *Cryptarius* and *Doiichthys*.
21. [Reversal] Anterior and median nuchal plates distinct (207, ? > 0; Figs 2A, 3B). Convergent in *Bag. bagre*.

MONOPHYLY OF CLADE 3  
(BAGREINAE, ARIIDAE)  
[94 – 97 – 09]

The subfamily Bagreinae is hypothesized to be the sister group of the subfamily Ariinae based on the following synapomorphies:

1. Mesethmoid median portion very wide (2, 1 > 2; Figs 3B, 5B). State 0 in *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clades 39 and 60, reversed in *Cryptarius* and clade 11, convergent in *Batrachcephalus*, *Carlarius*, *Doiichthys*, and clade 26.
2. Anterior portion of cranial fontanel partially or totally delimited by the dorsal expansion of orbitosphenoid (24, 0 > 1; Figs 2B, 3B, 4A, 5A, 6A, B). Reversed in *Cryptarius*, and clades 42 and 55.
3. Epioccipital posterior process very long, contacting the crests associated with neural spine of fourth vertebra (41, 0 > 1; Figs 2B–6B).

4. Opening of aortic channel present in front of the subvertebral process (69, 0 > 1; Figs 8A, B, 9A, B).
5. Basioccipital bearing a lateral process (75, 0 > 1; Figs 8A, B, 9A, B). Reversed in *Cep. melanochir*.
6. Posterior ceratohyal long (146, 0 > 1). State 2 in *Doiichthys*, reversed in clade 11, and convergent in *Batrachcephalus*.
7. Urohyal dorsal crest not anteriorly projected (149, 1 > 0; Fig. 19B–D, F, G). Reversed in *Aspistor*, *Cathorops*, *Cephalocassis borneensis*, *Ketengus*, *Notarius*, and *Occidentarius* and convergent in clade 51.
8. Urohyal long (150, 0 > 1; Fig. 19A–C, F–H). State 2 in *Doiichthys* and reversed in *Osteogeneiosus*.
9. Urohyal posterolateral processes long (153, 0 > 1; Fig. 19A–D, F, G). Reversed in *Cathorops*, *Cep. borneensis*, *Genidens*, and clades 41, 44, and 60, convergent in *Cryptarius* and *Pl. platystomus*.
10. Uncinate process of third epibranchial truncate (176, 0 > 1; Fig. 23D). Reversed in *H. stormii*, *Potamosilurus*, and clades 56 and 60.
11. Mesial quarter of fourth epibranchial thin, its width about twice its length (179, 0 > 1; Fig. 23A, D). Reversed in *Cochlefelis*.
12. Diagonal crest associated with neural spine of fourth vertebra well developed (191, 0 > 1).
13. Space delimited by epioccipital posterior process and crests associated with neural spine of fourth vertebra present (198, 0 > 1).
14. Aortic channel closed throughout its extension (199, 0 > 1; Figs 8A, 9A, B).
15. Eighth is the first vertebra free from superficial ventral ossification (204, 1 > 0). Reversed in *Ketengus* and clade 49.
16. Precaudal vertebrae 19 or more (205, 0 > 1). Reversed in *Br. nox*, and clades 42 and 51.
17. Protractor muscle of parapophysis of fourth vertebra contacting epioccipital posterior process (230, 0 > 1).

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18. First pharyngobranchial present (182, ? > 0; Fig. 22A, C).
19. First pharyngobranchial located on mesial two thirds of first epibranchial (184, ? > 1; Fig. 22C). State 0 in *Doiichthys*.
20. Anterior and median nuchal plates fused and indistinct (207, ? > 1; Figs 2B, 3A, 4A, B, 5A, B, 6A, B). State 1 in *Bag. bagre*.
21. Cleithrum second dorsal process posteriorly orientated, parallel with cleithrum posterior process (216, ? > 0; Fig. 27C, D). State 1 in clades 14, 35, and 51, convergent in *Batrachcephalus* and clade 60.

MONOPHYLY OF CLADE 4 (BAGREINAE)  
 (BAG. PANAMENSIS (BAG. PINNIMACULATUS  
 (BAG. BAGRE, BAG. MARINUS)))  
 [100 – 100 – 26]

Recognition of the subfamily Bagreinae, exclusively represented by the genus *Bagre*, is strongly supported by 39 synapomorphies, 14 of which are exclusive:

1. Mesethmoid posterior branches moderately long, delimiting between one quarter and half of length of anterior cranial fontanel (8, 0 > 1; Fig. 3B).
  2. Lachrymal tubules differentiated from frontal bones throughout their entire extension (22, 0 > 1; Fig. 3B).
  3. Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, 0 > 1; Fig. 9B). Convergent in *Cathorops* (except *Cat. dasycephalus*), *Cochlefelis*, *Potamosilurus*, and clades 30 and 47.
  4. Ventral face of subvertebral process rounded (73, 0 > 1).
  5. Contact face of transcapular process for articulation with basioccipital large and depressed (78, 0 > 1; Fig. 9B). Convergent in *Pl. platystomus*, *Potamosilurus latirostris*, and clades 39 and 46.
  6. Bony crest of exoccipital well-developed (84, 1 > 0). Convergent in clades 36 and 47.
  7. Bony crest formed by exoccipital posterior process perpendicular to vertebral column and posteriorly orientated (85, 0 > 1). Convergent in clades 36 and 52.
  8. Anterior infraorbital conspicuously curved (89, 0 > 1; Fig. 11B).
  9. Posterior infraorbital L-shaped (90, 1 > 2; Fig. 11B).
  10. Lachrymal-antorbital with two anterior and one mesial branches (91 0 > 2; Fig. 12C). Convergent in *Batrachocephalus*.
  11. Maxilla cylindrical, moderately long and acute (94, 0 > 1; Fig. 13B).
  12. Maxillary condyles large (96, 1 > 2; Fig. 13B).
  13. Autopalatine conical, short, and robust (97, 0 > 1; Fig. 14B, C).
  14. Autopalatine face for articulation with lateral ethmoid slightly displaced to anterior portion of bone (104, 1 > 0; Fig. 14B, C). Convergent in *Doiichthys*.
  15. Autopalatine inferior crest well developed (105, 0 > 1; Fig. 14C).
  16. Premaxilla dorsal crest delimiting the contact area with mesethmoid beginning between one third and half of anterior margin of bone (117, 0 > 1). Convergent in *Arius*, *Batrachocephalus*, *Cochlefelis*, *Hemiarius*, *Nemapteryx*, *Netuma*, and *Potamarius velutinus*.
  17. Metapterygoid anterior process very large (132, 0 > 1; Fig. 16B).
  18. Urohyal posterior end bifurcated (151, 0 > 1; Fig. 19B, D). Convergent in *Doiichthys*.
  19. Urohyal posterolateral processes as long as or longer than distal portion of bone (155, 0 > 1; Fig. 19B, G). Convergent in *Potamarius*.
  20. Third basibranchial median constriction displaced to posterior quarter (163, 0 > 1).
  21. Transversal crest associated with neural spine of fourth vertebra very high (193, 0 > 1). Convergent in *Occidentarius*, *Nedystoma*, *No. planiceps*, and clades 41 and 51.
  22. Medial crest associated with neural spine of fourth vertebra very high (195, 0 > 1). Convergent in *Occidentarius*, *No. planiceps*, and clade 51.
  23. Thirty nine or more caudal vertebrae (206, 1 > 0). Convergent in *Cochlefelis*.
  24. Cleithrum second dorsal process located on lower portion of the bone (215, 0 > 1; Fig. 27C).
  25. Maxillary barbel compressed (224, 0 > 1).
  26. One pair of mental barbels (226, 0 > 1).
  27. Lateral line bifurcated at caudal region (228, 0 > 1). Convergent in *Cep. borneensis*, *Netuma*, *S. couma*, and clade 36.
- Ambiguous optimization*
28. Epioccipital posterior process contacting a small area of diagonal crest associated with neural spine of fourth vertebra (42, ? > 0). Convergent in *Cep. melanochir*, *Cinetodus*, *Occidentarius*, *Potamarius izabalensis*, and clade 46.
  29. [Reversal] Parietosupraoccipital ventral crest well developed, conspicuous throughout extension of process (46, ? > 1). Convergent in *Occidentarius* and clade 49.
  30. Autopalatine anterior cartilage very short, less than one third as long as bone itself (106, ? > 0; Fig. 14B–D). Convergent in *Galeichthys* and *Osteogeneiosus*.
  31. Hyomandibular dorsal crest absent (133, ? > 0; Fig. 16A, B). Convergent in *Galeichthys*.
  32. First epibranchial overlaying second epibranchial (172, ? > 1; Fig. 22B). Convergent in *Galeichthys* and *Ketengus*.
  33. Diagonal crest associated with neural spine of fourth vertebra short, reaching transverse crest (192, ? > 0). Convergent in *Occidentarius*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius izabalensis*, and clade 46.
  34. [Reversal] Medial crest associated with neural spine of fourth vertebra very high (194, ? > 1). Convergent in *Occidentarius* and clade 49.
  35. Opening delimited by exoccipital posterior process and crests associated with fourth vertebra very large (196, ? > 0). Convergent in *Occi-*

*dentarius*, *Potamarius izabalensis*, and clade 47.

36. Fifteen or more ribs (203, ? > 1). Convergent in *Notarius*, and clades 9 and 44.
37. Adipose-fin base very short, smaller than half of anal-fin base (212, ? > 3). Convergent in *Brustiarius*, *Netuma*, and clades 44 and 61.
38. Adipose fin origin vertically above anal fin posterior portion (213, ? > 2). Convergent in *Brustiarius*, *Netuma*, and clade 44.
39. Protractor muscle of parapophysis of fourth vertebra originating from ventral surface of parietosupraoccipital and posterior process of epioccipital (229, ? > 0). Convergent in *Potamarius izabalensis*, and clades 42 and 47.

#### MONOPHYLY OF CLADE 5

(*BAG. PINNIMACULATUS* (*BAG. BAGRE*,  
*BAG. MARINUS*))  
[46 – 47 – 02]

*Bagre pinnimaculatus* is sister species to *Bag. bagre* and *Bag. marinus*, a relationship supported by the following synapomorphies:

1. Mesethmoid posterior branches very thin (6, 0 > 1; Figs 3A, B, 4A, B, 5B). Convergent in *Cathorops*, *Ketengus*, and clade 55.
2. Sesamoid bone I subtriangular and very elongate (138, 0 > 1; Fig. 17B). Convergent in *Arius*, *Occidentarius*, and clades 14, 24, and 51.
3. Dorsal-fin spine prolonged in form of filament (211, 0 > 1). Convergent in *Arius*.

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4. [Reversal] Urohyal posterolateral processes forming an angle always larger than 70° (154, ? > 0; Fig. 19A, B, D–H). Convergent in clade 13.

#### MONOPHYLY OF CLADE 6

(*BAG. BAGRE*, *BAG. MARINUS*)  
[58 – 58 – 02]

The sister-group relationship between *Bag. bagre* and *Bag. marinus* is supported by three synapomorphies:

1. Lateral horn of lateral ethmoid very compressed and spatulated (11, 0 > 1). Convergent in *Cathorops*, and clades 11, 45, and 59.
2. [Reversal] Temporal fossa moderate to very large (37, 0 > 1; Figs 2B, 4B, 3A, 5B). Convergent in clade 9.

#### *Ambiguous optimization*

3. [Reversal] Medial groove on top of cranium deep, its margins well differentiated (31, ? > 1; Figs 3B, 4A, B, 5A, 6B). Convergent in clades 7 and 31.

#### MONOPHYLY OF CLADE 7 (ARIINAE)

(*BRUSTIARIUS* (*COCHLEFELIS* (*NEOARIUS*  
((*GENIDENS*, *POTAMARIUS*)) (*CARLARIUS*)  
(*OCCIDENTARIUS*, *SCIADES*)) (*POTAMOSILURUS*  
(*POTAMOSILURUS VELUTINUS* (*ARIUS*)  
((*OSTEOGENEIOSUS* (*BATRACHOCEPHALUS*,  
*KETENGUS*)) (*PLICOFOLLIS*)))))) (*NO. PLANICEPS*  
(*NOTARIUS* (*ASPITOR* (*AMPHIARIUS* (*HEMIARIUS*)  
((*NEMAPTERYX* (*CEPHALOCASSIS* (*DOIICHTHYS*,  
*NEDYSTOMA*))) (*CINETODUS*, *PACHYULA*)  
(*CRYPTARIUS* (*CATHOROPS*,  
*PRECATHOROPS*))))))))))

[68 – 82 – 05]

The new concept of the Ariinae including all the members of the Ariidae, with the exception of the genera *Bagre* and *Galeichthys*, is well supported by the following synapomorphies:

1. Mesethmoid medial notch narrow and deep (1, 0 > 1; Figs 2B, 3A, 4A, 5A, 6A, B). Reversed in *Cinetodus*, *Cryptarius*, *Doiichthys*, *Ketengus*, and *Pachyula*.
2. Cephalic shield bones granulated (33, 0 > 1; Figs 2B, 3A, 4A, B, 5A, B, 6A, B).
3. Vomer lateral processes narrow (51, 0 > 1; Fig. 7D). Reversed in *Aspistor*, *Nemapteryx*, *No. planiceps*, and clades 22, 33, and 60, and convergent in clades 48 and 51.
4. Distance between the optic foramen and the trigemino-facialis foramen large, about twice as large as trigemino-facialis foramen (66, 0 > 1). Reversed in *Potamarius*.
5. Articulation facet of autopalatine with lateral ethmoid moderately large (102, 0 > 1; Fig. 14A, D, E).
6. Opercle anterior portion subtrapezoid, moderately long (120, 0 > 1; Fig. 15B, C). State 2 in *Cep. borneensis* and clade 59, state 3 in *Batrachcephalus*, state 4 in *Cochlefelis*, *Ketengus*, and clade 30, and reversed in *Nedystoma* and *Cinetodus*.
7. Metapterygoid as long as high (128, 0 > 1; Fig. 16C). State 2 in *Cephalocassis*, *Plicofollis*, *Potamarius*, and clade 59, state 3 in clade 42, state 4 in *Osteogeneiosus*, reversed in *Doiichthys*, and convergent in *Cathorops* (*Precathorops*).
8. Middle nuchal plate fitting parietosupraoccipital through a convex–concave face (210, 0 > 1; Figs 3A, 4A, B, 5A, B, 6A, B). State 2 in *Aspistor*, *No. troschelii*, and clade 31.

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9. Epioccipital posterior process contacting a broad portion of the diagonal crest associated with neural spine of fourth vertebra (42, ? > 2). State 0 in *Cep. melanochir*, *Cryptarius*, *Cinetodus*, *Occi-*

- dentarius*, *Potamarius izabalensis*, and clade 46, state 1 in *Cathorops*, *Pachyula*, and clades 40 and 55, and convergent in clade 45.
10. Parietosupraoccipital ventral crest weakly developed, restricted to base of process (46, ? > 0). State 1 in *Occidentarius* and clade 49, and convergent in *Bagre*, *Cryptarius*, and *Doiichthys*.
  11. Maxilla with lateral and mesial margins considerably closer proximally, distally narrower and pointed (95, ? > 3; Fig. 13D). State 0 in *Car. heudelotii*, *Genidens*, *Net. thalassina*, *Occidentarius*, and *Plicofollis* and state 2 in clade 18.
  12. [Reversal] Autopalatine anterior cartilage moderately long, one third to one fifth as long as bone itself (106, ? > 1; Fig. 14A). State 0 in *Osteogeneiosus* and state 2 in clade 42.
  13. [Reversal] Hyomandibular dorsal crest present (133, ? > 1; Fig. 16C–H).
  14. Hyomandibular dorsal crest long and low (134, ? > 0; Fig. 16E, F). State 1 in *Nedystoma*, *Cathorops*, and clade 32 and convergent in clades 44 and 54.
  15. Urohyal posterolateral processes forming an angle smaller than 60° (154, ? > 1; Fig. 19C). Reversed in clades 5 and 13, convergent in *Net. bilineata*.
  16. [Reversal] First epibranchial parallel to second epibranchial (172, ? > 0; Fig. 22A, C). Reversed in *Ketengus*.
  17. Diagonal crest associated with neural spine of fourth vertebra long, reaching base of Müller's ramus (192, ? > 1). State 0 in *Occidentarius*, *Pl. platystomus*, *P. tenuispinis*, *Potamarius izabalensis*, clade 46, and convergent in clade 45.
  18. Opening delimited by epioccipital posterior process and crests associated with fourth vertebra very reduced (196, ? > 2). State 0 in *Occidentarius*, *Potamarius izabalensis*, clade 47, state 1 in *Pl. platystomus*, *Pl. tenuispinis*, and clade 42 and convergent in *Osteogeneiosus* and clade 42.
  19. Protractor muscle of parapophysis of fourth vertebra originating exclusively from ventral surface of posterior process of epioccipital (229, ? > 1). State 0 in *Potamarius izabalensis*, and clades 42 and 47.

MONOPHYLY OF CLADE 8 (*BRUSTIARIUS*)*(BR. NOX, BR. SOLIDUS)*

[97 – 97 – 04]

The monophyly of the genus *Brustiarius* is defined by ten synapomorphies, two of which are exclusive:

1. Accessory tooth plates small and perfectly round, lateral to vomerine tooth plates (58, 0 > 1).
2. Premaxilla conspicuously wider laterally than mesially (114, 0 > 1).

3. Contact face between first epibranchial and first pharyngobranchial very conspicuous (170, 0 > 1; Fig. 22C). Convergent in *Ar. arius*, *Ar. gagora*, *Nedystoma*, and clade 33.
4. Lateral margin of third pharyngobranchial pointed (186, 0 > 1; Fig. 24C). Convergent in *Nedystoma*, *Neoarius*, *Netuma*, and clade 33.

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5. [Reversal] Medial groove on top of cranium deep, its margins well differentiated (31, ? > 1; Figs 3B, 4A, B, 5A, 6B). Convergent in clades 6, 11, and 31.
6. Tooth plates associated with vomer butterfly-shaped (54, ? > 2).
7. Parasphenoid very wide in ventral view (64, ? > 1; Fig. 8A). Convergent in *Cochlefelis*, *Plicofollis*, and clades 28 and 46.
8. [Reversal] Fourteen or fewer ribs (203, ? > 0). Convergent in *Potamarius*, clades 33 and 49.
9. Adipose-fin base very short, smaller than half of anal-fin base (212, ? > 3). Convergent in *Bagre*, *Netuma*, clades 44 and 61.
10. Adipose fin origin vertically above anal fin posterior portion (213, ? > 2). Convergent in *Bagre*, *Netuma*, and clade 44.

## MONOPHYLY OF CLADE 9

(*COCHLEFELIS* (*NEOARIUS* ((*GENIDENS*, *POTAMARIUS*) (*CARLARIUS*) (*OCCIDENTARIUS*, *SCIADES*) ((*POTAMOSILURUS* (*POTAMOSILURUS VELUTINUS* (*ARIUS*) ((*OSTEOGENEIOSUS* (*BATRACHOCEPHALUS*, *KETENGUS*)) (*PLICOFOLLIS*)))))) (*N. PLANICEPS* (*NOTARIUS* (*ASPITOR* (*AMPHIARIUS* (*HEMIARIUS* ((*NEMAPTERYX* (*CEPHALOCASSIS* (*DOIICHTHYS*, *NEDYSTOMA*))) (*CINETODUS*, *PACHYULA*) (*CRYPTARIUS* (*CATHOROPS*, *PRECATHOROPS*))))))))))

[00 – 00 – 01]

The following synapomorphies support the monophyly of clade 9:

1. [Reversal] Posterior cranial fontanel long and relatively narrow (27, 0 > 1; Figs 4B, 5A). State 2 in *Potamosilurus latirostris* and clade 49, state 3 in clade 55, reversed in *Cathorops* (*Cathorops*), *Genidens*, and clades 20 and 44, and convergent in clade 59.
2. Extrascapular subquadrangular (35, 0 > 1; Figs 2B, 5A, B, 6A). State 2 in *Cinetodus* and *Cathorops*, reversed in *Genidens*, *Potamarius grandoculis*, and clade 35, and convergent in *Cryptarius* and *Potamarius izabalensis*.
3. [Reversal] Temporal fossa moderate to very large (37, 0 > 1;

Figs 2B, 3A, 4B, 5B). Reversed in *Cep. borneensis*, *Genidens*, *Net. bilineata*, and clade 61, and convergent in clade 6.

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4. Tooth plates associated with vomer rounded (54, ? > 1). State 3 in *Aspistor*.
5. Fifteen or more ribs (203, ? > 1). State 0 in *Potamarius*, and clade 33 and 49, and convergent in *Bagre*, *Notarius*, and clade 44.
6. Adipose-fin base moderately long, about half as long as anal-fin base (212, ? > 2). State 1 in *Cephalocassis*, clades 46 and 60, state 3 in *Bagre*, *Brustarius*, *Netuma*, clades 44 and 61, and convergent in *Nemapteryx* and clade 57.
7. Origin of adipose fin vertically above anterior half of anal fin (213, ? > 1). State 2 in *Netuma* and clade 44.

#### MONOPHYLY OF CLADE 10 (*COCHLEFELIS*) (*COC. DANIELSI*, *COC. SPATULA*) [97 – 98 – 05]

Monophyly of *Cochlefelis* is well supported by 11 synapomorphies:

1. Fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, 1 > 0; Fig. 6A, B). Convergent in *Batrachocephalus*, *Plicofollis*, and clade 20.
2. Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, 0 > 1; Fig. 9B). Convergent in *Bagre*, *Cathorops* (*Cathorops*), *Potamosilurus*, and clades 30 and 47.
3. Premaxillary dorsal crest delimiting the contact area with mesethmoid beginning between one third and half of anterior margin of bone (117, 0 > 1). Convergent in *Arius*, *Bagre*, *Batrachocephalus*, *Hemiaris*, *Nemapteryx*, *Netuma*, and *Potamosilurus velutinus*.
4. [Reversal] Opercle anterior portion subtriangular (120, 1 > 4; Fig. 15H). Convergent in *Ketengus* and clade 30.
5. Metapterygoid anterior process truncate (131, 0 > 1; Fig. 16F). Convergent in *Plicofollis*, *Potamarius*, *Potamosilurus*, and clade 59.
6. Third basibranchial long and narrow (162, 1 > 2; Fig. 20C, F). Convergent in *Batrachocephalus*, *Galeichthys*, and *Potamarius*.
7. [Reversal] Mesial quarter of fourth epibranchial robust, almost as wide as long (179, 1 > 0; Fig. 23B).
8. Thirty-nine or more caudal vertebrae (206, 1 > 0). Convergent in *Bagre*.

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9. [Reversal] Posterior cranial fontanel delimited by frontals and parietosupraoccipital (25, ? > 0;

Figs 2B, 3A, 4B, 5B). Convergent in *Ketengus*, *Neoarius*, and clade 32.

10. Medial groove on top of neurocranium shallow, its margins little differentiated (31, 1 > 0; Figs 2A, 6A). Convergent in *Bag. panamensis*, *Bag. pinnimaculatus*, *Galeichthys*, *No. planiceps*, and clade 26.
11. Parasphenoid very wide in ventral view (64, ? > 1; Fig. 8A). Convergent in *Brustarius*, *Plicofollis*, and clades 28 and 46.

#### MONOPHYLY OF CLADE 11 (*NEOARIUS* ((*GENIDENS*, *POTAMARIUS*) ((*CARLARIUS*) (*OCCIDENTARIUS*, *SCIADES*) ((*POTAMOSILURUS* (*P. VELUTINUS* (*ARIUS*) ((*OSTEOGENEIOSUS* (*BATRACHOCEPHALUS*, *KETENGUS*)) (*PLICOFOLLIS*)))))) (*NO. PLANICEPS* (*NOTARIUS* (*ASPISTOR* (*AMPHIARIUS* (*HEMIARIUS* ((*NEMAPTERYX* (*CEPHALOCASSIS* (*DOIICHTHYS*, *NEDYSTOMA*))) ((*CINETODUS*, *PACHYULA*) (*CRYPTARIUS* (*CATHOROPS*, *PRECATHOROPS*))))))))))))) [04 – 06 – 01]

The monophyly of this clade is supported by the following synapomorphies:

1. [Reversal] Mesethmoid median portion moderately wide (2, 2 > 1; Figs 2A, B, 6A, B). State 0 in *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clades 39 and 60, reversed in *Batrachocephalus*, *Carlarius*, *Doiichthys*, and clade 26, and convergent in *Cryptarius*.
2. Lateral horn of lateral ethmoid very compressed and spatulated (11, 0 > 1). Reversed in *Cryptarius*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamosilurus macrorhynchus*, clades 30 and 46, and convergent in *Cathorops*, and clades 6, 45, and 60.
3. Exoccipital process adapted to support Müller's branch (87, 0 > 1). Reversed in *Pl. tenuispinis* and clade 46.
4. Premaxilla long and moderately wide (113, 0 > 1). State 3 in *Doiichthys* and reversed in *Netuma*, state 2 in *Cathorops*, *Cephalocassis*, *Cinetodus*, and *Potamarius*.
5. [Reversal] Posterior ceratohyal short (146, 1 > 0). State 2 in *Doiichthys* and reversed in *Batrachocephalus*.

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6. Lateral horn of lateral ethmoid moderately long and lateroposteriorly orientated (12, ? > 1; Figs 2B, 3A, 4A, 6A). State 2 in *Doiichthys*, *Potamarius*, clades 38 and 45, reversed in *Ar. caelatus*, *Coc. danieli*, *Pl. tenuispinis*, and clade 30, convergent in *Coc. spatula*.



7. [Reversal] Medial groove on top of cranium deep, its margins well differentiated (31, ? > 1; Figs 3B, 4A, B, 5A, 6B). Convergent in clades 6, 11, and 31.
8. [Reversal] Parasphenoid narrow in ventral view (64, ? > 0; Figs 8B, 9A, B). Reversed in *Plicofollis*, and clades 28 and 46, convergent in clade 54.

MONOPHYLY OF CLADE 12 (*NEOARIUS*)  
(*NEOARIUS GRAEFFEI*, *NEOARIUS MIDGLEI*)  
[54 – 49 – 02]

The species of *Neoarius* examined share three synapomorphies:

1. Anterior process of first hypobranchial exactly in the middle of the bone (167, 0 > 1; Fig. 21B). Convergent in *Netuma*.
2. Lateral margin of third pharyngobranchial pointed (186, 0 > 1; Fig. 24C). Convergent in *Brustiarius*, *Nedystoma*, *Netuma*, and clade 33.

*Ambiguous optimization*

3. [Reversal] Posterior cranial fontanel delimited by frontals and parietosupraoccipital (25, ? > 0; Figs 2B, 3A, 4B, 5B). Convergent in *Cochlefelis*, *Ketengus*, and clade 32.

MONOPHYLY OF CLADE 13  
(*GENIDENS*, *POTAMARIUS*) ((*CARLARIUS*)  
(*OCCIDENTARIUS*, *SCIADES*) ((*POTAMOSILURUS*  
(*POTAMOSILURUS VELUTINUS* (*ARIUS*)  
(*OSTEOGENEIOSUS* (*BATRACHOCEPHALUS*,  
*KETENGUS*)) (*PLICOFOLLIS*)))) (*NO. PLANICEPS*  
(*NOTARIUS* (*ASPITOR* (*AMPHIARIUS* (*HEMIARIUS*  
(*NEMAPTERYX* (*CEPHALOCASSIS* (*DOIICHTHYS*,  
*NEDYSTOMA*)))) (*CINETODUS*, *PACHYULA*)  
(*CRYPTARIUS* (*CATHOROPS*, *PRECATHOROPS*)))))))))  
[13 – 14 – 01]

The monophyly of clade 13 is supported by the following synapomorphies:

1. Bony bridge formed by lateral ethmoid and frontal largely represented by lateral ethmoid (15, 1 > 0; Figs 2B, 5A, 6A, B). State 1 in clade 54, state 2 in *Cathorops*, *Cephalocassis*, and clade 51.
2. Accessory tooth plates large, subtriangular to oval-shaped (58, 0 > 2). State 3 in *Batrachcephalus* and clade 52, state 4 in *Aspistor*, and clades 39 and 40, state 5 in clade 51, reversed in *Potamarius latirostris* and clade 27.
3. Autopalatine face for articulation with lateral ethmoid slightly displaced to posterior portion of bone (104, 1 > 2; Fig. 14A, D, E). State 0 in *Doiichthys* and reversed in *Nemapteryx*.
4. More than half of interopercle posterodorsal margin contacting anteroventral margin of opercle

- (124, 0 > 1; Fig. 15B–F). Reversed in *Notarius*, *No. planiceps*, *Pl. platystomus*, *S. passany*, *S. proops*, and clade 42 and convergent in *S. parkeri* and clade 49.
5. [Reversed] Urohyal posterolateral processes forming an angle always larger than 70° (154, 1 > 0; Fig. 19A, B, D–H). Reversed in *Net. bilineata* and convergent in clade 5.

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6. Posterior cranial fontanel delimited only by frontal bones (25, ? > 1; Figs 2A, 3B, 4A, 5A, 6B). State 0 in *Ketengus* and clade 32, and convergent in Ariidae, *Cathorops* (*Cathorops*), *Osteogeneiosus*, and *Plicofollis*.

MONOPHYLY OF CLADE 14  
(*GENIDENS*, *POTAMARIUS*)  
[07 – 08 – 01]

The sister-group relationship between *Genidens* and *Potamarius* is supported by three synapomorphies:

1. Sesamoid bone I subtriangular and very elongate (138, 0 > 1; Fig. 17B). Convergent in *Arius*, *Occidentarius*, and clades 5, 24, and 51.
2. [Reversal] Cleithrum second dorsal process dorsally orientated, parallel with cleithrum first dorsal process (216, 0 > 1; Fig. 27A, B). Convergent in clades 35 and 51.

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3. First external branchiostegal ray almost as large proximally as distally (140, ? > 1; Fig. 18B). Convergent in clades 22 and 32.

MONOPHYLY OF *POTAMARIUS* (CLADE 15)  
(*POTAMARIUS IZABALENSIS*, *POTAMARIUS*  
*GRANDOCULIS*)  
[96 – 99 – 10]

The monophyly and new concept of *Potamarius*, including the South American species *Potamarius grandoculis*, is well supported by 15 synapomorphies, four of which are exclusive:

1. Mesethmoid median portion very narrow (2, 1 > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, and clades 39 and 60.
2. Lateral horn of lateral ethmoid very long and posteriorly orientated (12, 1 > 2; Figs 5A, B, 6B). Convergent in *Doiichthys*, and clades 38 and 45.
3. Frontals without mesial laminar projection (23, 1 > 0; Figs 2A, B, 3A, 4A, 5A, B). Convergent in *Arius*, *Galeichthys*, *Osteogeneiosus*, *Potamosilurus latirostris*, and clade 49.

4. Vomer anterior margin very pronounced and acute (48, 0 > 1; Fig. 7C, E). Convergent in *Cephalocassis*, *Potamosilurus macrorhynchus*, and clades 36, 47, and 60.
5. Vomerine tooth plates absent (53, 1 > 0). Convergent in *Carlarius*, *Genidens genidens*, and clades 35 and 51.
6. [Reversal] Orbitosphenoid and pterosphenoid lateral expansions absent (62, 1 > 0; Fig. 9A). Convergent in *Cryptarius*, and clades 41 and 55.
7. Optic foramen very large (65, 1 > 0).
8. [Reversal] Distance between the optic foramen and the trigeminofacialis foramen small, equal to width of trigeminofacialis foramen (66, 1 > 0).
9. Premaxilla very long and narrow (113, 1 > 2). Convergent in *Cathorops*, *Cephalocassis*, and *Cinetodus*.
10. Interopercle rectangular (127, 0 > 1; Fig. 15C).
11. Metapterygoid one and half longer than high (128, 1 > 2; Fig. 16D–F). Convergent in *Cephalocassis*, *Plicofollis*, and clade 59.
12. Metapterygoid anterior process truncate (131, 0 > 1; Fig. 16F). Convergent in *Cochlefelis*, *Plicofollis*, *Potamosilurus*, and clade 59.
13. Urohyal posterolateral processes not connected by a bony blade (152, 0 > 1; Fig. 19G).
14. Third basibranchial long and narrow (162, 1 > 2; Fig. 20C, F). Convergent *Batrachocephalus*, *Cochlefelis*, and *Galeichthys*.
15. [Reversal] Fourteen or fewer ribs (203, 1 > 0). Convergent in *Brustiarius*, and clades 33 and 49.

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16. Urohyal posterolateral processes as long as or longer than distal portion of bone (155, ? > 1; Fig. 19B, G). Convergent in *Bagre*.

MONOPHYLY OF CLADE 16 (*GENIDENS*)  
(*GENIDENS MACHADOI* (*GENIDENS BARBUS*,  
*GENIDENS GENIDENS*))  
[99 – 99 – 06]

The genus *Genidens*, represented in this study by *G. barbatus*, *G. genidens*, and *G. machadoi*, is a monophyletic assemblage, defined by ten synapomorphies:

1. Posterior cranial fontanel reduced to a small opening (27, 1 > 0; Figs 2A, 3A, 4A, 6B). Convergent in Ariidae, *Cathorops* (*Cathorops*), and clades 20 and 44.
2. Temporal fossa very reduced, sometimes partially closed (37, 1 > 0; Figs 2A, 4A). Convergent in *Cep. borneensis*, *Net. bilineata*, and clade 61.
3. Orbitosphenoid lateral margins progressively more separated from one another anteriorly (61, 0 > 1; Fig. 8B).

4. Maxilla with mesial and lateral margins parallel in proximal two thirds, becoming closer to each other in distal third, posteriorly truncate (95, 3 > 0; Fig. 13A). Convergent in *Car. heudelotii*, *Net. thalassina*, *Occidentarius*, and *Plicofollis*.
5. Teeth on dentary restricted to mesial two thirds of bone (109, 1 > 0). Convergent in *Cephalocassis* and *Cryptarius*.
6. Opercle posterior portion little developed posteriorly (122, 1 > 0; Fig. 15A, B). Convergent in *Bag. panamensis*, *Galeichthys*, *Ketengus*, *Occidentarius*, *Sciades*, and clade 44.
7. [Reversal] Urohyal posterolateral processes short (153, 1 > 0; Fig. 19E, H). Convergent in *Cathorops*, *Cep. borneensis*, and clades 41, 44, and 60.
8. Second basibranchial posterior portion short and wide (160, 2 > 3; Fig. 20E). Convergent in *Netuma*.

#### Ambiguous optimization

9. [Reversal] Extrascapular subrectangular (35, ? > 0; Figs 2A, 3B, 4B, 6B). Convergent in *Po. grandoculis* and clade 35.
10. Vomerine tooth plates connected to vomer by ligaments (55, ? > 1).
11. Urohyal posterolateral processes two thirds as long as distal portion of bone (155, ? > 2; Fig. 19A, H). Convergent in *Aspistor*, *Net. thalassina*, and clades 36 and 54.

MONOPHYLY OF CLADE 17  
(*G. BARBUS*, *G. GENIDENS*)  
[47 – 49 – 01]

*Genidens barbatus* is hypothesized to be the sister species of *G. genidens* based on the following synapomorphy:

1. Accessory tooth plates composed of several small plates (57, 0 > 2).

MONOPHYLY OF CLADE 18  
(*CARLARIUS*) (*OCCIDENTARIUS*, *SCIADES*)  
(*POTAMOSILURUS* (*POTAMOSILURUS VELUTINUS*  
(*ARIUS*) ((*OSTEOGENEOSUS* (*BATRACHOCEPHALUS*,  
*KETENGUS*)) (*PLICOFOLLIS*)))) (*NO. PLANICEPS*  
(*NOTARIUS* (*ASPISTOR* (*AMPHIARIUS* (*HEMIARIUS*  
(*NEMAPTERYX* (*CEPHALOCASSIS* (*DOICHTHYS*,  
*NEDYSTOMA*)))) (*CINETODUS*, *PACHYULA*)  
(*CRYPTARIUS* (*CATHOROPS*, *PRECATHOROPS*)))))))))  
[00 – 00 – 01]

Characterized only by two synapomorphies:

1. [Reversal] Maxilla progressively narrower distally, with lateral and posterior margins rounded (95, 3 > 2). State 0 in *Car. heudelotii*, *Occidentarius*, *Net. thalassina*, and *Plicofollis*.

2. Second basibranchial mushroom-shaped (159,  $0 > 1$ ; Fig. 20A, D, E). Reversed in *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Potamosilurus latirostris*, and clade 60 and convergent in *Cathorops*.

MONOPHYLY OF CLADE 19 (*CARLARIUS*)

(*CAR. LATISCUTATUS*, *CAR. HEUDELLOTII*, *CAR. PARKII*)  
[64 – 72 – 02]

*Carlarius*, as recently defined by Marceniuk & Menezes (2007), is a monophyletic group supported by the following synapomorphies:

1. Mesethmoid median portion very wide (2,  $1 > 2$ ; Figs 3B, 5B). Convergent in *Batrachocephalus*, *Doiachthys*, and clades 3 and 26.
2. Epioccipital dorsally exposed (39,  $0 > 1$ ; Figs 2B, 6B). Convergent in *Aspistor*, *Am. rugispinis*, clades 45 and 60.
3. Vomerine tooth plates absent (53,  $1 > 0$ ). Convergent in *G. genidens*, *Potamarius*, and clades 35 and 51.

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4. [Reversal] First external branchiostegal ray proximally narrow and distally broad (140,  $? > 0$ ; Fig. 18A). Convergent in *Ar. caelatus*, *Doiachthys*, *Netuma*, *Notarius*, and clades 30 and 41.

MONOPHYLY OF CLADE 20

(*NETUMA (OCCIDENTARIUS, SCIADES)*)  
[20 – 24 – 01]

Four synapomorphies have been identified:

1. [Reversal] External posterior branch of lateral ethmoid depressed (13,  $0 > 1$ ). Convergent in clade 40.
2. Fenestra delimited by lateral ethmoid and frontal very small or indistinct (17,  $1 > 0$ ; Fig. 6A, B). Convergent in *Cochlefelis*, *Batrachocephalus*, and *Plicofollis*.
3. Posterior cranial fontanel reduced to a small opening (27,  $1 > 0$ ; Figs 2A, 3A, 4A, 6B). Convergent in Ariidae, *Cathorops (Cathorops)*, *Genidens*, and clade 44.
4. Third basibranchial chalice-shaped (161,  $0 > 1$ ; Fig. 20A, E). Reversed in clade 25 and convergent in *Arius*, *Batrachocephalus*, and clades 29, 45, and 49.

MONOPHYLY OF *NETUMA* (CLADE 21)

(*NET. BILINEATA*, *NET. THALASSINA*)  
[98 – 99 – 08]

*Netuma* is defined by ten synapomorphies:

1. Two pairs of accessory tooth plates (57,  $0 > 1$ ).
2. [Reversal] Premaxilla wide and short (113,  $1 > 0$ ).

3. Premaxilla dorsal crest delimiting the contact area with mesethmoid beginning between one third and half of anterior margin of bone (117,  $0 > 1$ ). Convergent in *Arius*, *Bagre*, *Batrachocephalus*, *Cochlefelis*, *Hemiarius*, *Nemapteryx*, and *Potamosilurus velutinus*.

4. Second basibranchial posterior portion short and wide (160,  $2 > 3$ ; Fig. 20E). Convergent in *Genidens*.

6. Anterior process of first hypobranchial on central portion of bone (167,  $0 > 1$ ; Fig. 21B). Convergent in *Neoarius*.

5. Lateral face of third pharyngobranchial pointed (186,  $0 > 1$ ; Fig. 24C). Convergent in *Brustiarius*, *Nedystoma*, *Neoarius*, and clade 33.

7. Adipose-fin base very short, smaller than half of anal-fin base (212,  $2 > 3$ ). Convergent in *Bagre*, *Brustiarius*, and clades 44 and 61.

8. Adipose-fin origin vertically over posterior half of anal fin (213,  $1 > 2$ ). Convergent in *Bagre*, *Brustiarius*, and clade 44.

9. Lateral line bifurcated at caudal region (228,  $0 > 1$ ). Convergent in *Bagre*, *Cep. borneensis*, *S. couma*, and clade 36.

*Ambiguous optimization*

10. [Reversal] First external branchiostegal ray proximally narrow and distally broad (140,  $? > 0$ ; Fig. 18A). Convergent in *Ar. caelatus*, *Carlarius*, *Doiachthys*, *Notarius*, and clades 30 and 41.

MONOPHYLY OF CLADE 22

(*OCCIDENTARIUS, SCIADES*)  
[66 – 71 – 05]

*Occidentarius platypogon* is sister species of *Sciades*, a condition supported by four unique character states in the Ariidae plus five shared synapomorphies:

1. Medial groove of neurocranium delimited mainly by frontal bones (32,  $0 > 1$ ). Convergent in clade 31, state 2 in clade 26.

2. Temporal fossa very reduced or entirely closed during ontogenetic development (36,  $0 > 1$ ; Fig. 6A). Reversed in *S. leptaspis*.

3. [Reversal] Vomerine lateral processes very wide (51,  $1 > 0$ ; Fig. 7B–D). Convergent in *Aspistor*, *Nemapteryx*, *No. planiceps*, and clades 33 and 60.

4. Otic capsules moderately developed, limited by prootic, pterotic, and exoccipital (68,  $2 > 1$ ; Fig. 8A).

5. [Reversal] Subvertebral process indistinct or little differentiated (71,  $1 > 0$ ).

6. [Reversal] Space between transcapular process and otic capsule very wide (82,  $1 > 0$ ; Fig. 8A).

7. Opercle posterior portion little developed posteriorly (122, 1 > 0; Fig. 15A, B). Reversed in *S. felis* and *S. couma*, and convergent in *Galeichthys*, *Bag. panamensis*, *Genidens*, *Ketengus*, and clade 44.

*Ambiguous optimization*

8. First external branchiostegal ray almost as large proximally as distally (140, ? > 1; Fig. 18B). Convergent in clades 14 and 32.

MONOPHYLY OF *OCCIDENTARIUS*  
(*OCCIDENTARIUS PLATYPOGON*)

*Occidentarius* is a monospecific genus supported by ten new autapomorphies:

1. Epioccipital posterior process contacting a small area of diagonal crest associated with neural spine of fourth vertebra (42, 2 > 0). Convergent in *Bagre*, *Cep. melanochir*, *Cinetodus*, *Cryptarius*, *Potamarius izabalensis*, and clade 46.
2. [Reversal] Parietosupraoccipital ventral crest well developed, conspicuous throughout extension of process (46, 0 > 1). Convergent in *Bagre* and clade 49.
3. Maxilla with mesial and lateral margins parallel in proximal two thirds, becoming closer to each other in distal one third, posteriorly truncate (95, 2 > 0; Fig. 13A). Convergent in *Car. heudelotii*, *Genidens*, *Net. thalassina*, and *Plicofollis*.
4. [Reversal] Urohyal dorsal crest anteriorly projected (149, 0 > 1; Fig. 19A, E, H). Convergent in *Aspistor*, *Cathorops*, *Cep. borneensis*, *Ketengus*, and *Notarius*.
5. Diagonal crest associated with neural spine of fourth vertebra short, reaching transverse crest (192, 1 > 0). Convergent in *Bagre*, *Occidentarius*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamarius izabalensis*, and clade 46.
6. Transversal crest associated with neural spine of fourth vertebra very high (193, 0 > 1). Convergent in *Bagre*, *Nedystoma*, *No. planiceps*, and clades 41 and 51.
7. [Reversal] Medial crest associated with neural spine of third vertebra very high (194, 0 > 1). Convergent in *Bagre* and clade 49.
8. Medial crest associated with neural spine of fourth vertebra very high (195, 0 > 1). Convergent in *Bagre*, *No. planiceps*, and clade 51.
9. Opening delimited by exoccipital posterior process and crests associated to fourth vertebra very large (196, 2 > 0). Convergent in *Bagre*, *Potamarius izabalensis*, and clade 47.

*Ambiguous optimization*

10. Sesamoid bone I subtriangular and very long (138, ? > 1; Fig. 17B). Convergent in *Arius*, and clades 5, 14, 24, and 51.

MONOPHYLY AND INTRAGENERIC RELATIONSHIPS OF  
*SCIADES* (CLADE 23)

((*S. ASSIMILIS*, *S. BONILLAI*, *S. FELIS* (*S. SEEMANNI*  
(*S. SAGOR* ((*S. GUATEMALENSIS*, *S. LEPTASPIS*)  
(*S. COUMA*, *S. HERZBERGII*) (*S. PASSANY*  
(*S. PARKERI*, *S. PROOPS*))))))  
[60 – 63 – 01]

Monophyly of *Sciades*, including representatives of the genera *Sciades* and *Ariopsis* (*sensu* Betancur-R *et al.*, 2007), and two species from southern and South-East Asia, New Guinea, and Australia, is supported by three synapomorphies:

1. Posterior cranial fontanel absent (26, 1 > 0; Fig. 6A). Convergent in *Batrachcephalus*.
2. Epiphyseal bar indistinct (28, 0 > 1; Fig. 6A). Convergent in *Batrachcephalus*.
3. Exoccipital posterior process sutured to Müller's ramus (86, 0 > 1). Convergent in *Potamarius izabalensis*.

MONOPHYLY OF CLADE 24

(*S. SEEMANNI* (*S. SAGOR* ((*S. GUATEMALENSIS*,  
*S. LEPTASPIS*) ((*S. COUMA*, *S. HERZBERGII*)  
(*S. PASSANY* (*S. PARKERI*, *S. PROOPS*))))))  
[81 – 83 – 02]

Supported by three synapomorphies:

1. Autopalatine posterior portion conspicuously compressed (99, 0 > 1). Convergent in clade 57.
2. Articulation face of autopalatine with lateral ethmoid mesoposteriorly orientated (103, 0 > 1; Fig. 14D). Convergent in clade 42.

*Ambiguous optimization*

3. Sesamoid bone I subtriangular and very long (138, ? > 1; Fig. 17B). State 3 in clade 28, convergent in *Arius*, *Occidentarius*, and clades 5, 14, and 51.

MONOPHYLY OF CLADE 25

(*S. SAGOR* ((*S. GUATEMALENSIS*, *S. LEPTASPIS*)  
(*S. COUMA*, *S. HERZBERGII*) (*S. PASSANY*  
(*S. PARKERI*, *S. PROOPS*))))  
[28 – 26 – 01]

Supported by a single homoplastic synapomorphy:

- [Reversal] Third basibranchial hourglass-shaped (161, 1 > 0; Fig. 20B, C, D, F). Reversed in clade 29 and convergent in *Cathorops* and clade 55.

## MONOPHYLY OF CLADE 26

((*S. GUATEMALENSIS*, *S. LEPTASPIS*) (*S. COUMA*,  
*S. HERZBERGII*) (*S. PASSANY* (*S. PARKERI*,  
*S. PROOPS*))))  
[83 – 86 – 03]

Supported by three synapomorphies:

- Mesethmoid median portion very wide (2, 1 > 2; Figs 3B, 5B). Convergent in *Batrachocephalus*, *Carlarius*, *Doiachthys*, and clade 3.
- Medial groove on top of neurocranium shallow, its margins little differentiated (31, 1 > 0; Figs 2A, 6A). Reversed in clade 31 and convergent in *Bag. panamensis*, *Bag. pinnimaculatus*, *Galeichthys*, *Cochlefelis*, and *No. planiceps*.
- Medial groove of neurocranium delimited only by frontal bones (32, 1 > 2; Fig. 6A). Reversed in clade 31.

## MONOPHYLY OF CLADE 27

(*S. GUATEMALENSIS*, *S. LEPTASPIS*)  
[61 – 62 – 01]

The clade represented by *S. guatemalensis* and *S. leptaspis* is supported by the following synapomorphy:

- [Reversal] Accessory tooth plates small, transversely elongate and narrow (58, 2 > 0). Convergent in *Potamarius latirostris*.

## MONOPHYLY OF CLADE 28

((*S. COUMA*, *S. HERZBERGII*) (*S. PASSANY*  
(*S. PARKERI*, *S. PROOPS*)))  
[86 – 93 – 04]

Monophyly of this clade, represented by the species restricted to the north and north-east oriental parts of South America, is supported by three exclusive and one homoplastic synapomorphies. The clade corresponds to the genus *Sciades sensu* Betancur-R *et al.* (2007).

- Parasphenoid very wide in ventral view (64, 0 > 1; Fig. 8A). Convergent in *Brustiarius*, *Cochlefelis*, *Plicofollis*, and clade 46.
- Premaxilla lateral margin deeply concave (116, 1 > 2).
- Sesamoid bone I very long and subrectangular (138, 1 > 3; Fig. 17C).

- Sesamoid bone II irregularly elongate (139, 0 > 1; Fig. 17C).

## MONOPHYLY OF CLADE 29

(*S. COUMA*, *S. HERZBERGII*)  
[40 – 33 – 01]

The sister-group relationship between *S. couma* and *S. herzbergii* is corroborated by two synapomorphies:

- Third basibranchial chalice-shaped (161, 0 > 1; Fig. 20A, E). Convergent in *Arius*, *Batrachocephalus*, and clades 20, 45, and 49.

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- A groove connecting posterior nostrils present (222, ? > 1). Convergent in *S. passany*.

## MONOPHYLY OF CLADE 30

(*S. PASSANY* (*S. PARKERI*, *S. PROOPS*)  
[86 – 92 – 04]

*Sciades passany* is hypothesized to be the sister species of the clade formed by *S. parkeri* and *S. proops*. The monophyly of the group is defined by the following synapomorphies:

- [Reversal] Lateral horn of lateral ethmoid slightly compressed and acute (11, 1 > 0). Convergent in *Cryptarius*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamosilurus macrorhynchus*, and clade 46.
- [Reversal] Lateral horn of lateral ethmoid short and laterally orientated (12, 1 > 0; Figs 2A, 3B). Convergent in *Ar. caelatus*, *Coc. danielsi*, and *Pl. tenuispinis*.
- Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, 0 > 1; Fig. 9B). Convergent in *Bagre*, *Cathorops* (*Cathorops*), *Cochlefelis*, *Potamosilurus*, and clade 47.
- [Reversal] Opercle anterior portion subtriangular (120, 1 > 4; Fig. 15H). Convergent in *Cochlefelis* and *Ketengus*.
- [Reversal] First external branchiostegal ray proximally narrow and distally broad (140, 1 > 0; Fig. 18A). Convergent in *Ar. caelatus*, *Carlarius*, *Doiachthys*, *Netuma*, *Notarius*, and clade 41.

## MONOPHYLY OF CLADE 31

(*S. PARKERI*, *S. PROOPS*)  
[88 – 92 – 04]

The sister-species relationship between *S. parkeri* and *S. proops* is strongly supported by two exclusive and four homoplastic synapomorphies:

- [Reversal] Medial groove on top of cranium deep, its margins well differentiated (31, 0 > 1; Figs 3B,

- 4A, B, 5A, 6B). Convergent in *Brustiarius*, clades 6 and 11.
2. Medial groove of neurocranium delimited mainly by frontal bones (32, 2 > 1). Convergent in clade 22.
  3. Anterior and median nuchal plates forming a shield-like structure (208, 0 > 1).
  4. Nuchal plate overlapping parietosupraoccipital (210, 1 > 2; Fig. 2B). Convergent in *Aspistor* and *No. troschelii*.
  5. Swimbladder with three chambers (227, 0 > 1; Fig. 28B).

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6. [Reversal] A groove connecting posterior nostrils absent (222, ? > 0).

MONOPHYLY OF CLADE 32

((POTAMOSILURUS (POTAMOSILURUS VELUTINUS ((ARIUS) ((OSTEOGENEIOSUS (BATRACHOCEPHALUS, KETENGUS)) (PLICOFOLLIS)))))) (N. PLANICEPS (NOTARIUS (ASPISTOR (AMPHIARIUS (HEMIARIUS ((NEMAPTERYX (CEPHALOCASSIS (DOIICHTHYS, NEDYSTOMA))) ((CINETODUS, PACHYULA) (CRYPTARIUS (CATHOROPS, PRECATHOROPS)))))))))) [00 – 00 – 01]

Clade 32 includes two large groups and is supported by the following synapomorphies:

1. [Reversal] Posterior cranial fontanel delimited by frontals and parietosupraoccipital (25, 1 > 0; Figs 2B, 3A, 4B, 5B). Reversed in *Cathorops* (*Cathorops*), *Osteogeneiosus*, and *Plicofollis* and convergent in *Cochlefelis*, *Ketengus*, and *Neoarius*.
2. Aortic channel opening located on base of subvertebral process and anteroventrally orientated (70, 0 > 1; Fig. 10B). State 2 in *Cathorops*.
3. [Reversal] Hyomandibular dorsal crest short and high (134, 0 > 1; Fig. 16C, D, G, H). Reversed in clades 44 and 54, and convergent in *Nedystoma* and *Cathorops*.

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4. First external branchiostegal ray almost as large proximally as distally (140, ? > 1; Fig. 18B). Convergent in clades 14 and 22.

MONOPHYLY OF CLADE 33

((POTAMOSILURUS (POTAMOSILURUS VELUTINUS ((ARIUS) ((OSTEOGENEIOSUS (BATRACHOCEPHALUS, KETENGUS)) (PLICOFOLLIS)))))) [00 – 00 – 02]

Recognition of monophyly of clade 33 is supported by four synapomorphies:

1. Contact face between first epibranchial and first pharyngobranchial very conspicuous (170, 0 > 1; Fig. 22C). Reversed in *Pl. platystomus*, clade 39 and 42, convergent in *Ar. arius*, *Ar. gagora*, *Brustiarius*, and *Nedystoma*.
2. Lateral margin of third pharyngobranchial pointed (186, 0 > 1; Fig. 24C). Reversed in clade 41 and convergent in *Brustiarius*, *Nedystoma*, *Neoarius*, and *Netuma*.

*Ambiguous optimization*

3. [Reversal] Vomerine lateral processes very wide (51, 1 > 0; Fig. 7B–D). Convergent in *Aspistor*, *Nemapteryx*, *No. planiceps*, clades 22 and 60.
4. [Reversal] Fourteen or fewer ribs (203, ? > 0). Convergent in *Brustiarius*, *Potamarius*, and clade 49.

MONOPHYLY OF POTAMOSILURUS (CLADE 34)  
(POTAMOSILURUS LATIROSTRIS, POTAMOSILURUS MACRORHYNCHUS)  
[58 – 68 – 02]

*Potamosilurus* is considered monophyletic, including only *Potamosilurus latirostris* and *Potamosilurus macrorhynchus* that share the following synapomorphies:

1. Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, 0 > 1; Fig. 9B). Convergent in *Bagre*, *Cathorops* (*Cathorops*), *Cochlefelis*, and clades 30 and 47.
2. Metapterygoid anterior process truncate (131, 0 > 1; Fig. 16F). Convergent in *Cochlefelis*, *Plicofollis*, *Potamarius*, and clade 59.
3. [Reversal] Uncinate process of third epibranchial acute (176, 1 > 0; Fig. 23A, B, C). Convergent in *H. stormii*, and clades 56 and 60.

MONOPHYLY OF CLADE 35

((POTAMOSILURUS VELUTINUS ((ARIUS) ((OSTEOGENEIOSUS (BATRACHOCEPHALUS, KETENGUS)) (PLICOFOLLIS)))))) [00 – 00 – 01]

This is defined by three synapomorphies:

1. [Reversal] Extrascapular subrectangular (35, 1 > 0; Figs 2A, 3B, 4B, 6B). Convergent in *Genidens* and *Potamarius grandoculis*.
2. Vomerine tooth plates absent (53, 1 > 0). Reversed in clade 44 and convergent in *Carlarius*, *G. genidens*, *Potamarius*, and clade 51.
3. [Reversal] Cleithrum second dorsal process dorsally orientated, parallel with cleithrum first

dorsal process (216, 0 > 1; Fig. 27A, B). Reversed in *Batrachocephalus* and convergent in clades 14 and 51.

#### MONOPHYLY OF CLADE 36

((ARIUS) ((OSTEOGENEIOSUS (BATRACHOCEPHALUS, KETENGUS)) (PLICOFOLLIS)))  
[00 – 02 – 02]

Clade 36 is represented by species from the Indian and western Pacific oceans. Its monophyly is justified by five synapomorphies:

1. Vomer anterior margin very pronounced and acute (48, 0 > 1; Fig. 7C, E). Reversed in clade 42 and convergent in *Cephalocassis*, *Potamarius*, *Potamosilurus macrorhynchus*, and clades 47 and 60.
2. Bony crest of exoccipital well developed (84, 1 > 0). Convergent in *Bagre* and clade 47.
3. Bony crest formed by exoccipital posterior process perpendicular to vertebral column and posteriorly orientated (85, 0 > 1). Convergent in *Bagre* and clade 52.
4. Urohyal posterolateral processes two thirds as long as distal portion of bone (155, 0 > 2; Fig. 19A, H). State 3 in *Plicofollis* and convergent in *Aspistor*, *Genidens*, *Net. thalassina*, and clade 54.
5. Lateral line bifurcated at caudal region (228, 0 > 1). Convergent in *Bagre*, *Cep. borneensis*, *Netuma*, and *S. couma*.

#### MONOPHYLY AND INTRAGENERIC RELATIONSHIPS OF ARIUS (CLADES 37)

(AR. CAELATUS (AR. MACULATUS (AR. ARIUS, AR. DISPAR, AR. GAGORA, AR. MADAGASCARIENSIS, AR. MANILLENSIS)))  
[22 – 21 – 01]

The complex genus *Arius* has its monophyly supported by five homoplastic synapomorphies:

1. Frontals without mesial laminar projection (23, 1 > 0; Figs 2A, B, 3A, 4A, 5A, B). Convergent in *Galeichthys*, *Osteogeneiosus*, *Potamarius*, *Potamosilurus latirostris*, and clade 49.
2. Sesamoid bone I subtriangular and very long (138, 0 > 1; Fig. 17B). Convergent in *Occidentarius*, and clades 5, 14, 24, and 51.
3. Third basibranchial chalice-shaped (161, 0 > 1; Fig. 20A, E). Convergent in *Batrachocephalus*, and clades 20, 29, 45, and 49.

#### Ambiguous optimization

4. Premaxilla dorsal crest delimiting the contact area with mesethmoid, beginning from one third to half the length of anterolateral margin of the latter bone (117, ? > 1). Convergent in *Bagre*, *Batrachoceph-*

*alus*, *Hemiaris*, *Nemapteryx*, *Netuma*, and *Potamosilurus velutinus*.

5. Dorsal-fin spine prolonged in form of filament (211, 0 > 1). Convergent in clade 5, reversed in *Ar. dispar*, *Ar. gagara*, and *Ar. manillensis*.

#### MONOPHYLY OF CLADE 38

(AR. MACULATUS (AR. ARIUS, AR. DISPAR, AR. GAGORA, AR. MADAGASCARIENSIS, AR. MANILLENSIS))  
[06 – 06 – 01]

Monophyly of *Arius*, excluding *Ar. caelatus*, is supported by three synapomorphies, one of them representing a unique condition within the Ariidae:

1. Lateral horn of lateral ethmoid very long and posteriorly orientated (12, 1 > 2; Figs 5A, B, 6B). Convergent in *Doiichthys*, *Potamarius*, and clade 45.
2. Orbitosphenoid and/or pterosphenoid lateral expansions slightly projected, with wavy lateral margins (63, 0 > 2). Reversed in *Ar. madagascariensis*.

#### Ambiguous optimization

3. Autopalatine very compressed at the articulation face with lateral ethmoid (101, ? > 1). Convergent in *Plicofollis*.

#### MONOPHYLY OF CLADE 39

(AR. ARIUS, AR. DISPAR, AR. GAGORA, AR. MADAGASCARIENSIS, AR. MANILLENSIS)  
[07 – 08 – 01]

Clade 39 includes all *Arius* species that have molariform teeth on the accessory tooth plates. They can also be characterized by three additional synapomorphies:

1. Mesethmoid median portion very narrow (2, 1 > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clade 60.
2. Accessory tooth plates large and longitudinally elongate (58, 2 > 4). Reversed in *Ar. dispar*, convergent in *Aspistor* and clade 40.
3. Accessory tooth plates bearing molariform teeth (59, 0 > 1). Convergent in *Aspistor*, *Cathorops* (*Cathorops*), and clade 40.
4. Accessory tooth plates apposed to orbitosphenoid and metapterygoid (60, 0 > 1). Convergent in *Aspistor* and clade 40.

MONOPHYLY OF CLADE 40  
 ((*OSTEOGENEOSUS* (*BATRACHOCEPHALUS*,  
*KETENGUS*)) (*PLICOFOLLIS*))  
 [00 – 01 – 01]

*Plicofollis* is hypothesized to be sister to *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* based on five synapomorphies:

1. [Reversal] External posterior branch of lateral ethmoid depressed (13, 0 > 1). Convergent in clade 20.
2. Epioccipital posterior process contacting the transversal and diagonal crests related with neural spine of fourth vertebra (42, 2 > 1). Reversed in clade 45, convergent in *Cathorops*, *Pachyula*, and clade 55.
3. Accessory tooth plates large and longitudinally elongate (58, 2 > 4). State 3 in *Batrachocephalus* and convergent in *Aspistor* and clade 39.
4. Accessory tooth plates bearing molariform teeth (59, 0 > 1). Convergent in *Aspistor*, *Cathorops* (*Cathorops*), and clade 39.
5. Accessory tooth plates apposed to orbitosphenoid and metapterygoid (60, 0 > 1). State 2 in *Batrachocephalus* and convergent in *Aspistor* and clade 39.

MONOPHYLY OF CLADE 41  
 (*OSTEOGENEOSUS* (*BATRACHOCEPHALUS*,  
*KETENGUS*))  
 [66 – 71 – 03]

Clade 41 includes three monospecific genera well characterized in the literature. *Osteogeneiosus* is hypothesized to be sister group to the clade consisting of *Batrachocephalus* plus *Ketengus*, strongly supported by 11 synapomorphies:

1. Lateral horn of lateral ethmoid inconspicuous (10, 1 > 0; Fig. 4B).
2. [Reversal] Orbitosphenoid and pterosphenoid lateral expansions absent (62, 1 > 0; Fig. 9A). Convergent in *Cryptarius*, *Potamarius*, and clade 55.
3. Space between transcapular process and otic capsule very reduced (82, 1 > 2; Fig. 9B). Convergent in clade 51.
4. Subvertebral process long and thin (72, 0 > 1; Fig. 10A, B). Convergent in clade 46.
5. Ventral face of subvertebral process acute (73, 0 > 2). Convergent in *Cryptarius*, and clades 46 and 60.
6. Articulation face of autopalatine with lateral ethmoid mesoposteriorly orientated (103, 0 > 1; Fig. 14D). State 2 in clade 42 and convergent in clade 24.

7. Metapterygoid anterior process absent (130, 0 > 1; Fig. 16G, H).
8. [Reversal] First external branchiostegal ray proximally narrow and distally broad (140, 1 > 0; Fig. 18A). Convergent in *Ar. caelatus*, *Carlarius*, *Doiichthys*, *Netuma*, *Notarius*, and clade 30.
9. [Reversal] Lateral margin of third pharyngobranchial rounded (186, 1 > 0; Fig. 24B).
10. Transversal crest associated with neural spine of fourth vertebra very high (193, 0 > 1). Convergent in *Bagre*, *Occidentarius*, *Nedystoma*, *No. planiceps*, and clade 51.

*Ambiguous optimization*

11. [Reversal] Urohyal posterolateral processes short (153, ? > 0; Fig. 19E, H). Convergent in *Cathorops*, *Cep. borneensis*, *Genidens*, and clades 44 and 60.

MONOPHYLY OF *OSTEOGENEOSUS*  
 (*OSTEOGENEOSUS MILITARIS*)

*Osteogeneiosus* is well characterized by 20 autapomorphies, many of which are exclusive:

1. Fenestra delimited by lateral ethmoid and frontal very large (17, ? > 2; Figs 3A, 4A, 5B). Convergent in clade 51.
2. Nasal anterior curvature very pronounced (20, 0 > 1).
3. [Reversal] Nasal anterior tubules not connected by bony blade (21, 1 > 0).
4. Frontal without mesial laminar projection (23, 1 > 0; Figs 2A, B, 3A, 4A, 5A, B). Convergent in *Arius*, *Galeichthys*, *Potamarius*, *Potamosilurus latirostris*, and clade 49.
5. Vomer posterior process as narrow at the basal as at the distal portions (52, 0 > 1; Fig. 7E). Convergent in clade 45.
6. Maxillary condyles very large (96, 1 > 3; Fig. 13C).
7. Anterior cartilage of autopalatine very reduced, less than one third as long as bone itself (106, 1 > 0; Fig. 14B–D). Convergent in *Bagre* and *Galeichthys*.
8. Posterior cartilage of autopalatine reduced to a small dot (107, 1 > 2; Fig. 14D).
9. [Reversal] Urohyal short (150, 1 > 0; Fig. 19E).
10. Mental barbels absent (225, 0 > 1).

*Ambiguous optimization*

11. Mesethmoid median portion very narrow (2, ? > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*, *Cephalocassis*, *Ketengus*, *Potamarius*, and clades 39 and 60.
12. Posterior cranial fontanel delimited exclusively by frontal bones (25, ? > 1; Figs 2A, 3B, 4A, 5A,



- 6B). Convergent in *Cathorops* (*Cathorops*), *Plicofollis*, and clade 13.
13. Lachrymal–antorbital with three anterior and one lateral branch (91, ? > 1; Fig. 12B).
  14. Maxilla cylindrical, very long and acute (94, ? > 2; Fig. 13C).
  15. Autopalatine cylindrical, very short and robust (97, ? > 2; Fig. 14D).
  16. [Reversal] Autopalatine slightly compressed at the articulation face with lateral ethmoid (101, ? > 0, Fig. 14A–D).
  17. Premaxilla dorsal crest delimiting the contact area with mesethmoid beginning near or exactly at lateral end of anterior margin of bone (117, ? > 0).
  18. Metapterygoid three times longer than high (128, ? > 4; Fig. 16H).
  19. Sesamoid bone I irregularly shaped (138, ? > 2). Convergent in clade 46.
  20. Opening delimited by exoccipital posterior process and crests associated to fourth vertebra very reduced (196, ? > 2). Convergent in clades 7 and 45.

MONOPHYLY OF CLADE 42  
(*BATRACHOCEPHALUS*, *KETENGUS*)  
[100 – 100 – 16]

The sister-group relationship between *Batrachocephalus* and *Ketengus* is strongly supported by exclusive and homoplastic synapomorphies:

1. Nasal perpendicular in relation to mesethmoid (18, 0 > 1).
2. [Reversal] Anterior portion of anterior cranial fontanel not delimited by a dorsal expansion of orbitosphenoid (24, 1 > 0; Figs 2A, 3A, 4B, 5B). Convergent in *Cryptarius* and clade 55.
3. [Reversal] Vomer anterior margin little pronounced and serrated (48, 1 > 0; Fig. 7A, B, D). Convergent in clade 52.
4. Maxillary condyles rudimentary (96, 1 > 0).
5. Autopalatine anterior portion depressed (98, 1 > 0; Fig. 14E).
6. Autopalatine posterior portion conspicuously depressed (99, 0 > 2; Fig. 14E).
7. Autopalatine transversely situated in relation to main body axis (100, 0 > 1).
8. Articulation between autopalatine and lateral ethmoid posteriorly orientated (103, 1 > 2; Fig. 14E).
9. Autopalatine anterior cartilage very long, about as long as bone itself (106, 1 > 2; Fig. 14E).
10. Dentary teeth spatulate and/or cuspidate (110, 0 > 2).
11. Premaxillary teeth cuspidate (119, 0 > 1).

12. [Reversal] Half or less of interopercle dorsoanterior margin contacting anteroventral margin of opercle (124, 1 > 0; Fig. 15A, G, H). Convergent in *Notarius*, *Pl. platystomus*, *S. passany*, and *S. proops*.
13. Contact face between metapterygoid and hyomandibular very long (137, 0 > 1; Fig. 16G).
14. Second external branchiostegal ray almost as wide as first ray (141, 0 > 1; Fig. 18B). Convergent in *Cephalocassis*, *Galeichthys*, *Nedystoma*, and clade 61.
15. [Reversal] Contact face between first epibranchial and first pharyngobranchial inconspicuous (170, 1 > 0; Fig. 22A, B). Convergent in *Pl. platystomus* and clade 39.
16. Fourth epibranchial posterior margin slightly convex (180, 0 > 1; Fig. 23A). Convergent in clade 56.
17. Space for insertion of teeth on fifth ceratobranchial very reduced (187, 1 > 2; Fig. 25C). Convergent in clade *Cathorops* (*Cathorops*) and clade 57.
18. [Reversal] Eighteen or fewer precaudal vertebrae (205, 1 > 0). Convergent in *Br. nox* and clade 51.
19. Protractor muscle of parapophysis of fourth vertebra originating from ventral surface of parieto-supraoccipital process and posterior process of epioccipital (229, 1 > 0). Convergent in *Bagre*, *Potamarius izabalensis*, and clade 47.

*Ambiguous optimization*

20. Maxilla rudimentary, little differentiated (94, ? > 3).
21. Autopalatine depressed and mesially angled in its anterior third (97, ? > 3; Fig. 14E).
22. Autopalatine depressed at articulation face with lateral ethmoid (101, ? > 2; Fig. 14E).
23. Metapterygoid subtriangular-shaped (128, ? > 3; Fig. 16G).
24. Opening delimited by epioccipital posterior process and crests associated with neural spine of fourth vertebra moderately large (196, ? > 1). Convergent in *Pl. platystomus* and *Pl. tenuispinis*.

MONOPHYLY OF *BATRACHOCEPHALUS*  
(*BATRACHOCEPHALUS MINO*)

The monospecific *Batrachocephalus* is well characterized by the following autapomorphies:

1. Nasal bone fan-shaped (19, 0 > 2).
2. Posterior cranial fontanel absent (26, 1 > 0; Fig. 6A). Convergent in *Sciades*.
3. Epiphyseal bar indistinct (28, 0 > 1; Fig. 6A). Convergent in *Sciades*.

4. Posterior portion of anterior ceratohyal columnar and very thick (144, 0 > 1).
5. Posterior ceratohyal long (146, 0 > 1). Convergent in clade 3.
6. Urohyal anterior margin not notched (147, 0 > 1; Fig. 19H). Convergent in *Cathorops* and *Pl. tenuispinis*.
7. Cleithrum second dorsal process posteriorly orientated, parallel with cleithrum posterior process (216, 1 > 0; Fig. 27C, D). Convergent in clades 3 and 60.
8. Maxillary barbels absent (223, 0 > 1).

#### *Ambiguous optimization*

9. Mesethmoid median portion very wide (2, ? > 2; Figs 3B, 5B). Convergent in *Carlarius*, *Doiichthys*, and clades 3 and 26.
10. Fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, ? > 0; Fig. 6A, B). Convergent in *Cochlefelis*, *Plicofollis*, and clade 20.
11. Accessory tooth plates small and vertically oval (58, ? > 3). Convergent in clade 52.
12. Accessory tooth plates located between premaxilla and lateral ethmoid (60, ? > 2).
13. Lachrymal–antorbital with two anterior and one mesial branch (91, ? > 2; Fig. 12C). Convergent in *Bagre*.
14. Premaxilla dorsal crest delimiting the contact area with mesethmoid beginning between one third and half of anterior margin of bone (117, ? > 1). Convergent in *Arius*, *Bagre*, *Cochlefelis*, *Hemiaris*, *Nemapteryx*, *Netuma*, and *Potamarius velutinus*.
15. Opercle anterior portion subrectangular (120, ? > 3; Fig. 15G).
16. [Reversal] Second basibranchial spindle-shaped (159, ? > 0; Fig. 20B, C, F). Convergent in *Cephalocassis*, *Cryptarius*, *Potamosilurus latirostris*, and clade 60.
17. Third basibranchial chalice-shaped (161, ? > 1; Fig. 20A, E). Convergent in *Arius*, and clades 20, 29, 45, and 49.
18. Third basibranchial long and narrow (162, ? > 2; Fig. 20C, F). Convergent in *Cochlefelis*, *Galeichthys*, and *Potamarius*.
2. Mesethmoid posterior horn tubular, narrow and elongate (5, 0 > 1; Fig. 4A, B). Convergent in *Cathorops* (*Cathorops*).
3. Mesethmoid posterior branches very thin (6, 0 > 1; Fig. 3A, B, 4A, B, 5B). Convergent in *Cathorops* and clades 5 and 55.
4. Mesethmoid posterior branches parallel throughout their entire extension (7, 0 > 1; Figs 3A, 4A, B, 5B). Convergent in *Cathorops* and clade 55.
5. Lateral ethmoid and frontal not connected (14, 2 > 0; Fig. 4B).
6. Vomer diamond-shaped (47, 1 > 0; Fig. 7A).
7. Vomer lateral processes absent (49, 1 > 0; Fig. 7A).
8. [Reversal] Accessory tooth plates absent (56, 1 > 0). Convergent in *Cep. borneensis*, *Nedystoma*, *Pachyula*, *Potamarius izabalensis*, and *Potamosilurus velutinus*.
9. Teeth implanted along entire extension of dentary (109, 1 > 2).
10. Premaxilla dorsal crest absent (118, 0 > 1).
11. Opercle posterior portion little developed posteriorly (122, 1 > 0; Fig. 15A, B). Convergent in *Bag. panamensis*, *Galeichthys*, *Genidens*, *Occidentarius*, *Sciades*, and clade 44.
12. Hyomandibular ventral crest absent (135, 0 > 1; Fig. 16D, G). Convergent in *Cathorops* and *Cephalocassis*.
13. [Reversal] Urohyal dorsal crest anteriorly projected (149, 0 > 1; Fig. 19A, E, H). Convergent in *Aspistor*, *Cathorops*, *Cep. borneensis*, *Notarius*, and *Occidentarius*.
14. Second and third basibranchials fused and indistinct (157, 0 > 1; Fig. 20G).
15. First hypobranchial club-shaped (164, 0 > 1; Fig. 21D).
16. Second hypobranchial club-shaped (168, 0 > 1; Fig. 21D).
17. First epibranchial overlaying second epibranchial (172, 0 > 1; Fig. 22B). Convergent in *Bagre* and *Galeichthys*.
18. [Reversal] Third pharyngobranchial elongate and hourglass-shaped (185, 1 > 0; Fig. 24A). Convergent in *Doiichthys* and *Potamarius grandoculis*.
19. Seventh is the first vertebra free from superficial ventral ossification (204, 0 > 1). Convergent in Ariidae and clade 49.

#### MONOPHYLY OF *KETENGUS*

##### (*KETENGUS TYPUS*)

*Ketengus* is strongly supported by 22 autapomorphies:

1. Mesethmoid and lateral ethmoid delimiting a fenestra (3, 0 > 1; Fig. 4A, B). Convergent in *Cathorops* (*Cathorops*).

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20. [Reversal] Mesethmoid medial notch inconspicuous, large, and shallow (1, ? > 0; Figs 2A, 3B, 4B, 5B). Convergent in *Cryptarius*, *Doiichthys*, and clade 60.
21. Mesethmoid median portion very narrow (2, ? > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*,

- Cephalocassis*, *Osteogeneiosus*, *Potamarius*, clades 39 and 60.
22. Fenestra delimited by mesethmoid and lateral ethmoid large and filled with cartilage (4, ? > 1; Fig. 4B).
  23. [Reversal] Posterior cranial fontanel delimited by frontals and parietosupraoccipital (25, ? > 0; Figs 2B, 3A, 4B, 5B). Convergent in *Cochlefelis*, *Neoarius*, and clade 32.
  24. Lachrymal–antorbital with three anterior branches (91, ? > 3; Fig. 12D).
  25. [Reversal] Opercle anterior portion subtriangular (120, ? > 4; Fig. 15H). Convergent in *Cochlefelis* and clade 30.

MONOPHYLY AND INTRAGENERIC RELATIONSHIPS OF  
*PLICOFOLLIS* (CLADES 43)

(*PL. PLATYSTOMUS* (*PL. TENUISPINIS*

(*PL. DUSSUMIERI*, *PL. NELLA*, *PL. POLYSTAPHYLODON*)  
[87 – 91 – 03]

*Plicofollis* as delimited herein is more inclusive than as defined in recent studies. The species examined share the following synapomorphies:

1. Parasphenoid very wide in ventral view (64, 0 > 1; Fig. 8A). Convergent in *Brustiarius*, *Cochlefelis*, and clades 28 and 46.
2. Anterior portion of anterior ceratohyal very thick (145, 0 > 1).
3. Urohyal posterolateral processes more than half as long as distal portion of bone (155, 2 > 3; Fig. 19F).
4. Second basibranchial posterior portion short and narrow (160, 2 > 4; Fig. 20A). Convergent in *Ar. maculatus*, *Ar. gagora*, and *Aspistor*.

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5. Fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, ? > 0; Fig. 6A, B). Convergent in *Cochlefelis*, *Batrachocephalus*, and clade 20.
6. Posterior cranial fontanel delimited exclusively by frontal bones (25, ? > 1; Figs 2A, 3B, 4A, 5A, 6B). Convergent in *Cathorops* (*Cathorops*), *Osteogeneiosus*, and clade 13.
7. Maxilla with mesial and lateral margins parallel in proximal two thirds, becoming closer to each other in distal third, posteriorly truncate (95, ? > 0; Fig. 13A). Convergent in *Genidens*, *Car. heudelotii*, *Net. thalassina*, and *Occidentarius*.
8. Autopalatine very compressed at the articulation face with lateral ethmoid (101, ? > 1). Convergent in clade 38.
9. Metapterygoid one and a half times longer than high (128, ? > 2; Fig. 16D–F). Convergent in *Cephalocassis*, *Potamarius*, and clade 59.

10. Metapterygoid anterior process truncate (131, ? > 1; Fig. 16F). Convergent in *Cochlefelis*, *Potamarius*, *Potamosilurus*, and clade 59.

MONOPHYLY OF CLADE 44

(*PL. TENUISPINIS* (*PL. DUSSUMIERI*, *PL. NELLA*,  
*PL. POLYSTAPHYLODON*)  
[98 – 99 – 12]

Within clade 47, *Pl. tenuispinis* is considered the sister species of the group including *Pl. dussumieri*, *Pl. nella*, and *Pl. polystaphylodon*, a condition supported by 18 synapomorphies, five of which are exclusive:

1. Posterior cranial fontanel reduced to a small opening (27, 1 > 0; Figs 2A, 3A, 4A, 6B). Convergent in *Cathorops* (*Cathorops*), *Genidens*, and clade 22.
2. [Reversal] Vomerine tooth plates present (53, 0 > 1). Convergent in *Cathorops* (*Precathorops*), *Hemarius*, and *Nemapteryx*.
3. Orbitosphenoid and/or pterosphenoid lateral expansion slightly projected, with straight lateral margin (63, 0 > 3).
4. [Reversal] Lachrymal–antorbital thin (93, 0 > 1; Fig. 12F).
5. Opercle anteroventral margin concave or almost straight (121, 0 > 1; Fig. 15B, D). Convergent in *Cathorops*.
6. Opercle posterior portion little developed posteriorly (122, 1 > 0; Fig. 15A, B). Convergent in *Bag. panamensis*, *Galeichthys*, *Genidens*, *Ketenus*, *Occidentarius*, and *Sciades*.
7. Interopercle posterior margin angled (123, 0 > 1; Fig. 15B, D). Convergent in *Cathorops*.
8. Interopercle anterior portion compressed and bifurcated (125, 0 > 1; Fig. 15B, D). Convergent in *Cathorops*.
9. Interopercle subrectangular (127, 0 > 2; Fig. 15C).
10. Hyomandibular dorsal crest long and low (134, 1 > 0; Fig. 16E, F). Convergent in clades 7 and 54.
11. First epibranchial posterior margin with a prominent process (174, 0 > 1; Fig. 22C). Convergent in *Pachyula*.
12. Lateral face of uncinat process of third epibranchial notched (178, 0 > 1; Fig. 23D).
13. First pharyngobranchial large and depressed (183, 0 > 1; Fig. 22C). Convergent in clade 59.
14. Fifteen or more ribs (203, 0 > 1). Convergent in *Bagre*, *Notarius*, and clade 9.
15. Adipose-fin base very short, smaller than half of anal-fin base (212, 2 > 3). Convergent in *Bagre*, *Brustiarius*, *Netuma*, and clade 61.

16. Adipose fin origin vertically above anal fin posterior portion (213, 1 > 2). Convergent in *Bagre*, *Brustiarius*, and *Netuma*.

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17. Vomerine tooth plates entirely free (55, ? > 2).  
 18. [Reversal] Urohyal posterolateral processes short (153, ? > 0; Fig. 19E, H). Convergent in *Cathorops*, *Cep. borneensis*, *Genidens*, and clades 41 and 60.

MONOPHYLY OF CLADE 45

(*PL. DUSSUMIERI*, *PL. NELLA*, *PL. POLYSTAPHYLODON*)  
 [99 – 99 – 10]

*Plicofollis dussumieri*, *Pl. nella*, and *Pl. polystaphylodon* share the following synapomorphies:

1. Lateral ethmoid very expanded (9, 0 > 1; Fig. 6B).
2. Lateral horn of lateral ethmoid very long and posteriorly directed (12, 1 > 2; Figs 5A, B, 6B). Convergent in *Doiichthys*, *Potamarius*, and clade 38.
3. Epioccipital dorsally exposed (39, 0 > 1; Figs 2B, 6B). Convergent in *Am. rugispinis*, *Aspistor*, *Carlarius*, and clade 60.
4. Epioccipital posterior process contacting a large area of diagonal crest associated with neural spine of fourth vertebra (42, 1 > 2). Convergent in clade 7.
5. Vomer oval-shaped (47, 1 > 2; Fig. 7E).
6. Vomerine lateral processes very short (50, 0 > 1; Fig. 7E).
7. Vomer posterior process as narrow at the basal as at the distal portions (52, 0 > 1; Fig. 7E). Convergent in *Batrachocephalus*.
8. Third basibranchial chalice-shaped (161, 0 > 1; Fig. 20A, E). Convergent in *Arius*, *Batrachocephalus*, and clades 20, 29, and 49.
9. Third basibranchial very short and wide (162, 1 > 0).
10. Uncinate process of third epibranchial longer and wider than mesial portion of same bone delimited by uncinat process (175, 0 > 1; Fig. 23D).

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11. Lateral horn of lateral ethmoid very compressed and spatulated (11, ? > 1). Convergent in *Cathorops*, and clades 6, 11, and 60.
12. Diagonal crest associated with neural spine of fourth vertebra long, reaching base of Müller's ramus (192, ? > 1). Convergent in clade 7.
13. Opening delimited by epioccipital posterior process and crests associated with fourth verte-

bra very reduced (196, ? > 2). Convergent in *Osteogeneiosus* and clade 7.

MONOPHYLY OF CLADE 46

(*NO. PLANICEPS* (*NOTARIUS* (*ASPISTOR* (*AMPHIARIUS* (*HEMIARIUS* ((*NEMAPTERYX* (*NEDYSTOMA*, *DOIICHTHYS*))) ((*CINETODUS*, *PACHYULA* (*CRYPTARIUS*, *CATHOROPS*)))))))))  
 [48 – 58 – 07]

Clade 46 includes species primarily living in estuarine or freshwaters in the Neotropical areas of Asia and New Guinea. Monophyly of the clade is supported by 13 synapomorphies:

1. [Reversal] Lateral horn of lateral ethmoid slightly compressed and acute (11, 1 > 0). Reversed in *Cathorops* and clade 60, and convergent in *Cryptarius*, *Pl. platystomus*, *Pl. tenuispinis*, *Potamosilurus macrorhynchus*, and clade 30.
2. Epiphyseal bar long and narrow (29, 0 > 1; Figs 2B, 3A, 5B). Reversed in clade 59 and convergent in *Ar. arius*, *Ar. gagora*, and *Potamarius latirostris*.
3. Epioccipital posterior process contacting a small area of diagonal crest associated with neural spine of fourth vertebra (42, 2 > 0). State 1 in *Cathorops*, *Pachyula*, and clade 55 and convergent in *Bagre*, *Cep. melanochir*, *Cinetodus*, *Cryptarius*, *Occidentarius*, and *Potamarius izabalensis*.
4. Parasphenoid very wide in ventral view (64, 0 > 1; Fig. 8A). Reversed in clade 54 and convergent in *Brustiarius*, *Cochlefelis*, *Plicofollis*, and clade 28.
5. Subvertebral process long and thin (72, 0 > 1; Fig. 10A, B). Convergent in clade 41.
6. Ventral face of subvertebral process acute (73, 0 > 2). State 3 in *Cathorops*, *Hemiaris*, and clade 55, convergent in *Cryptarius*, and clades 41 and 60.
7. Contact face of transcapular process for articulation with basioccipital large and depressed (78, 0 > 1; Fig. 9B). Reversed in *Cephalocassis*, *Hemiaris*, and clade 60, convergent in *Bagre*, *Pl. platystomus*, *Potamarius latirostris*, and clade 39.
8. Transcapular process transversel to main body axis (79, 0 > 1; Fig. 9B). Reversed in *Hemiaris* and clade 56, and convergent in *Galeichthys*.
9. [Reversal] Exoccipital posterior process without special structure to support Müller's ramus (87, 1 > 0). Convergent in *Pl. tenuispinis*.
10. Sesamoid bone I irregularly shaped (138, 0 > 2). State 1 in clade 51 and convergent in *Osteogeneiosus*.

11. Diagonal crest associated with neural spine of fourth vertebra short, reaching transverse crest (192, 1 > 0). Convergent in *Occidentarius*, *Pl. platystomus*, *Pl. tenuispinis*, and *Potamarius izabalensis*.
12. Accessory crest connecting transversal crest to medial crest associated to neural spine of fourth vertebra present (197, 0 > 1). Reversed in clade 52 and convergent in *Cephalocassis*.
13. Adipose-fin base long, as long as anal-fin base (212, 2 > 1). State 3 in clade 61, reversed in *Nemapteryx* and clade 57, and convergent in *Cephalocassis* and clade 60.

## MONOPHYLY OF CLADE 47

(*NOTARIUS* (*ASPISTOR* (*AMPHIARIUS* (*HEMIARIUS* (*NEMAPTERYX* (*NEDYSTOMA*, *DOIICHTHYS*)) (*CINETODUS*, *PACHYULA*) (*CRYPTARIUS*, *CATHOROPS*))))))  
[00 – 04 – 02]

The following synapomorphies support the monophyly of clade 47:

1. Medial groove of cranium absent (30, 0 > 1; Figs 2B, 3A, 5B). Reversed in *Nemapteryx* and clade 61, and convergent in *Potamosilurus latirostris*.
2. Vomer anterior margin very pronounced and acute (48, 0 > 1; Fig. 7C, E). Reversed in clade 52 and convergent in *Cephalocassis*, *Potamarius*, *Potamosilurus macrorhynchus*, and clades 36 and 60.
3. Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, 0 > 1; Fig. 9B). Reversed in *Cathorops* (*Precathorops*) and clade 60, and convergent in *Cathorops* (*Cathorops*), *Cochlefelis*, *Bagre*, *Potamarius*, and clade 30.
4. [Reversal] Exoccipital posterior process absent (83, 1 > 0). Reversed in clade 54.

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5. Bony crest of exoccipital well developed (84, ? > 0). Convergent in *Bagre* and clade 36.
6. Bony crest formed by exoccipital posterior process parallel to vertebral column and posteriorly orientated (85, ? > 3). State 0 in clade 52, state 2 in *Cathorops*.
7. Opening delimited by epioccipital posterior process and crests associated with fourth vertebra very large (196, ? > 0). Convergent in *Bagre*, *Occidentarius*, and *Potamarius izabalensis*.
8. Protractor muscle of parapophysis of fourth vertebra originating from ventral surface of parietosupraoccipital and posterior process of epioccipital (229, ? > 0). Convergent in *Bagre*, *Potamarius izabalensis*, and clade 42.

MONOPHYLY OF *NOTARIUS* (CLADE 48)

(*NOTARIUS GRANDOCULIS*, *NOTARIUS LENTIGINOSUS*, *NOTARIUS TROSCHELII*)  
[54 – 47 – 01]

*Notarius* is considered monophyletic with *No. planiceps* excluded, by the following six synapomorphies:

1. [Reversal] First external branchiostegal ray proximally narrow and distally broad (140, 1 > 0; Fig. 18A). Convergent in *Ar. caelatus*, *Carlarius*, *Doiichthys*, *Netuma*, and clades 30 and 41.

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2. Vomerine lateral processes narrow (51, ? > 1; Fig. 7E). Convergent in clades 7 and 51, reversed in *Aspistor*, *Nemapteryx*, and clade 60.
3. [Reversal] Half or less of interopercle dorsoanterior margin contacting anteroventral margin of opercle (124, ? > 0; Fig. 15A, G, H). Convergent in *No. planiceps*, *Pl. platystomus*, *S. passany*, *S. proops*, and clade 42.
4. [Reversal] Urohyal dorsal crest anteriorly projected (149, ? > 1; Fig. 19A, E, H). Convergent in *Aspistor*, *Cathorops*, *Cep. borneensis*, *Ketengus*, and *Occidentarius*.
5. Fifteen or more ribs (203, ? > 1). Convergent in *Bagre*, clades 9 and 44.

## MONOPHYLY OF CLADE 49

(*ASPISTOR* (*AMPHIARIUS* (*HEMIARIUS* (*NEMAPTERYX* (*NEDYSTOMA*, *DOIICHTHYS*)) (*CINETODUS*, *PACHYULA*) (*CRYPTARIUS*, *CATHOROPS*))))))  
[07 – 13 – 02]

Defined by the following synapomorphies:

1. Bony bridge formed by lateral ethmoid and frontal very thin (16, 0 > 1; Figs 2B, 3A, 4A, 5B). Reversed in clade 60.
2. Frontals without mesial laminar projection (23, 1 > 0; Fig. 2A, B, 3A, 4A, 5A, B). Reversed in clade 60 and convergent in *Arius*, *Galeichthys*, *Osteogeneiosus*, *Potamarius*, and *Potamosilurus latirostris*.
3. Posterior cranial fontanel long and broad (27, 1 > 2; Fig. 2B). State 0 in *Cathorops* (*Cathorops*), state 3 in clade 55 and convergent in *Potamosilurus latirostris*, reversed in clade 59.
4. [Reversal] Parietosupraoccipital ventral crest well developed, conspicuous throughout extension of process (46, 0 > 1). Reversed in *Cryptarius* and *Doiichthys* and convergent in *Bagre* and *Occidentarius*.
5. Third basibranchial chalice-shaped (161, 0 > 1; Fig. 20A, E). Reversed in *Cathorops* and clade 55 and convergent in *Arius*, *Batrachocephalus*, and clades 20, 29, and 45.

6. [Reversal] Medial crest associated with neural spine of third vertebra very high (194, 0 > 1). Reversed in *Cryptarius* and *Doiichthys* and convergent in *Bagre* and *Occidentarius*.
7. Seventh is the first vertebra free from ventral superficial ossification (204, 0 > 1). Convergent in *Ketengus*.

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8. More than half of interopercle posterodorsal margin contacting anteroventral margin of opercle (124, 0 > 1; Fig. 15B–F). Convergent in *S. parkeri* and clade 13.
9. [Reversal] Fourteen or fewer ribs (203, ? > 0). Convergent in *Brustarius*, *Potamarius*, and clade 33.

MONOPHYLY OF *ASPISTOR* (CLADE 50)  
(*ASPISTOR LUNISCUTIS*, *ASPISTOR QUADRISCUTIS*)  
[99 – 99 – 10]

*Aspistor* is considered monophyletic based on 14 synapomorphies, four of them exclusive:

1. Epioccipital dorsally exposed (39, 0 > 1; Figs 2B, 6B). Convergent in *Am. rugispinis*, *Carlarius*, and clades 45 and 60.
2. Parietosupraoccipital posterior margin convex (45, 0 > 1; Fig. 2B). Convergent in *S. proops*.
3. Tooth plates associated with vomer fused, forming a single large plate (54, 1 > 3).
4. Accessory tooth plates bearing molariform teeth (59, 0 > 1). Convergent in *Cathorops* (*Cathorops*), and clades 39 and 40.
5. Accessory tooth plates apposed to orbitosphenoid and metapterygoid (60, 0 > 1). Convergent in clades 39 and 40.
6. Urohyal posterolateral processes two thirds as long as distal portion of bone (155, 0 > 2; Fig. 19A, H). Convergent in *Genidens*, *Net. thalassina*, and clades 36 and 54.
7. Urohyal posterior portion as wide distally as proximally (156, 0 > 1; Fig. 19A).
8. Second basibranchial posterior portion short and narrow (160, 2 > 4; Fig. 20A). Convergent in *Ar. gagora*, *Ar. maculatus*, and *Plicofollis*.
9. Anterior and median nuchal plates forming a butterfly-shaped structure (208, 0 > 2; Fig. 2B).
10. Anterior margin of nuchal plate slightly concave (209, 0 > 1; Fig. 2B).
11. Nuchal plate overlapping parietosupraoccipital (210, 1 > 2; Fig. 2B). Convergent in *No. troschelii* and clade 31.

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12. [Reversal] Vomerine lateral processes very wide (51, ? > 0; Fig. 7B–D). Convergent in *Nemapteryx*, *No. planiceps*, and clades 22, 33, and 60.

13. Accessory tooth plates large and longitudinally elongate (58, ? > 4). Convergent in clades 39 and 40.
14. [Reversal] Urohyal dorsal crest anteriorly projected (149, ? > 1; Fig. 19A, E, H). Convergent in *Cathorops*, *Cep. borneensis*, *Ketengus*, *Notarius*, and *Occidentarius*.

MONOPHYLY OF CLADE 51

(*AMPHIARIUS* (*HEMIARIUS* ((*NEMAPTERYX* (*NEDYSTOMA*, *DOIICHTHYS*))) ((*CINOTODUS*, *PACHYULA*) (*CRYPTARIUS*, *CATHOROPS*))))  
[17 – 22 – 02]

Supported by the following synapomorphies:

1. Bony bridge formed by lateral ethmoid and frontal mostly represented by latter bone (15, 0 > 2; Figs 3A, 4A). State 1 in clade 54 and convergent in *Cathorops* and *Cephalocassis*.
2. Fenestra delimited by lateral ethmoid and frontal very large (17, 1 > 2; Figs 3A, 4A, 5B). Reversed in clade 60, convergent in *Osteogeneiosus*.
3. Vomerine tooth plates absent (53, 1 > 0). Reversed in *Cathorops* (*Precathorops*), *Hemiaris*, and *Nemapteryx* and convergent in *Carlarius*, *G. genidens*, *Potamarius*, and clade 35.
4. Space between transcapular process and otic capsule very restricted (82, 1 > 2; Fig. 9B). Reversed in *Hemiaris* and clade 57 and convergent in clade 41.
5. Sesamoid bone I subtriangular and very long (138, 2 > 1; Fig. 17B). Convergent in *Arius*, *Occidentarius*, and clades 5, 24, and 14.
6. Transversal crest associated with neural spine of fourth vertebra very high (193, 0 > 1). Reversed in *Cephalocassis* and *Doiichthys* and convergent in *Bagre*, *Occidentarius*, *Nemapteryx*, *No. planiceps*, and clade 41.
7. Medial crest associated with neural spine of fourth vertebra very high (195, 0 > 1). Reversed in clade 55 and convergent in *Bagre*, *Occidentarius*, and *No. planiceps*.
8. [Reversal] Eighteen or fewer precaudal vertebrae (205, 1 > 0). Convergent in *Br. nox* and clade 42.
9. [Reversal] Cleithrum second dorsal process dorsally orientated, parallel with cleithrum first dorsal process (216, 0 > 1; Fig. 27A, B). Reversed in clade 60 and convergent in clades 14 and 35.

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10. Vomerine lateral processes narrow (51, ? > 1; Fig. 7D). Reversed in *Nemapteryx* and clade 60, and convergent in clades 7 and 48.
11. Accessory tooth plates of moderate size, lateral, and irregularly rounded (58, ? > 5).

12. Urohyal dorsal crest not anteriorly projected (149, ? > 0; Fig. 19B–D, F, G). Reversed in *Cathorops* and *Cep. borneensis* and convergent in clade 3.

## MONOPHYLY OF CLADE 52

((HEMIARIUS ((NEMAPTERYX (NEDYSTOMA, DOIICHTHYS))) ((CINETODUS, PACHYULA) (CRYPTARIUS, CATHOROPS))))  
[00 – 05 – 02]

*Hemiaris* is interpreted as the basalmost genus of clade 52, defined by six synapomorphies:

- [Reversal] Vomer anterior margin little pronounced and serrated (48, 1 > 0; Fig. 7A, B, D). Reversed in *Cephalocassis* and clade 60, and convergent in clade 42.
- Accessory tooth plates small and vertically oval (58, 5 > 3). Convergent in *Batrachcephalus*.
- Exoccipital posterior process present (83, 0 > 1). Convergent in Ariidae.
- Bony crest formed by exoccipital posterior process perpendicular to vertebral column and posteriorly orientated (85, 3 > 1). State 2 in *Cathorops* and convergent in *Bagre* and clade 36.
- [Reversal] Accessory crest connecting transversal crest to medial crest associated to neural spine of fourth vertebra absent (197, 1 > 0). Reversed in *Cephalocassis*.
- Cleithrum very narrow (217, 0 > 1; Fig. 27A). Reversed in *Cat. dasycephalus* and clade 60.

MONOPHYLY OF *HEMIARIUS* (CLADE 53)  
(*H. STORMII*, *H. SUMATRANUS*)  
[85 – 83 – 03]

The monophyletic condition of *Hemiaris* is supported by the following synapomorphies:

- [Reversal] Vomerine tooth plates present (53, 0 > 1). Convergent in *Cathorops* (*Precathorops*), *Nemapteryx*, and clade 44.
- [Reversal] Contact face of transcapular process for articulation with basioccipital small and columnar (78, 1 > 0; Figs 8A, B, 9A). Convergent in *Cephalocassis* and clade 60.
- [Reversal] Transcapular process perpendicular to main body axis (79, 1 > 0; Figs 8A, B, 9A). Convergent in clade 56.
- Space between transcapular process and otic capsule moderately developed (82, 2 > 1; Figs 8B, 9A). Convergent in clade 57.
- Dorsal crest delimiting contact area between mesethmoid and premaxilla beginning between one third and half of anterior margin of bone (117,

0 > 1). Convergent in *Arius*, *Bagre*, *Batrachcephalus*, *Cochlefelis*, *Nemapteryx*, *Netuma*, and *Potamosilurus velutinus*.

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- Ventral face of subvertebral process spatulate (73, ? > 3). Convergent in *Cathorops* and clade 55.
- Cleithrum humeral process very short (214, ? > 0; Fig. 27A). Convergent in *Cathorops* (*Cathorops*) and clade 55.

## MONOPHYLY OF CLADE 54

((NEMAPTERYX (CEPHALOCASSIS (NEDYSTOMA, DOIICHTHYS))) ((CINETODUS, PACHYULA) (CRYPTARIUS, CATHOROPS)))  
[00 – 02 – 01]

Supported by the following synapomorphies:

- [Reversal] Bony bridge formed by equal portions of lateral ethmoid and frontal (15, 2 > 1; Figs 2A, 3B, 5B). Reversed in *Cathorops* and *Cephalocassis*.
- [Reversal] Parasphenoid narrow in ventral view (64, 1 > 0; Figs 8B, 9A, B). Convergent in clade 11.
- Hyomandibular dorsal crest long and low (134, 1 > 0; Fig. 16E, F). Reversed in *Cathorops* and *Nedystoma* and convergent in clades 7 and 44.
- Urohyal posterolateral processes two thirds as long as distal portion of bone (155, 0 > 2; Fig. 19A, H). Reversed in *Cep. melanochir* and *Cryptarius*, state 4 in *Doiichthys* and convergent in *Aspistor*, *Genidens*, *Net. thalassina*, and clade 36.

## MONOPHYLY OF CLADE 55

(NEMAPTERYX (CEPHALOCASSIS (NEDYSTOMA, DOIICHTHYS)))  
[62 – 69 – 05]

Monophyly of clade 55, including species mainly found in fresh waters of northern Australia, Indonesia, Malaysia, Thailand, and New Guinea, is well supported by 11 synapomorphies:

- Mesethmoid posterior branches very thin (6, 0 > 1; Figs 3A, B, 4A, B, 5B). Convergent in *Cathorops*, *Ketengus*, and clade 5.
- Mesethmoid posterior branches parallel throughout their entire extension (7, 0 > 1; Figs 3A, 4A, B, 5B). Convergent in *Cathorops* and *Ketengus*.
- [Reversal] Anterior portion of anterior cranial fontanel not delimited by dorsal expansion of orbitosphenoid (24, 1 > 0; Figs 2A, 3A, 4B, 5B). Convergent in *Cryptarius* and clade 42.
- Posterior cranial fontanel very large and long (27, 2 > 3; Figs 3A, 5B).
- [Reversal] Orbitosphenoid and pterosphenoïd lateral expansions absent (62, 1 > 0; Fig. 9A).

Convergent in *Cryptarius*, *Potamarius*, and clade 41.

6. Optic foramen very reduced (65, 1 > 2).
7. [Reversal] Third basibranchial hourglass-shaped (161, 1 > 0; Fig. 20B, C, D, F). Convergent in *Cathorops* and clade 25.
8. [Reversal] Medial crest associated with neural spine of fourth vertebra low or absent (195, 1 > 0).

#### *Ambiguous optimization*

9. Epioccipital posterior process contacting the transversel and diagonal crests related with neural spine of fourth vertebra (42, ? > 1). Convergent in *Cathorops*, *Pachyula*, and clade 40.
10. Ventral face of subvertebral process spatulate (73, ? > 3). Convergent in *Cathorops* and *Hemiaris*.
11. Cleithrum humeral process very short (214, ? > 0; Fig. 27A). Convergent in *Cathorops* (*Cathorops*) and *Hemiaris*.

#### MONOPHYLY OF *NEMAPTERYX* (*NEMAPTERYX ARMIGER*)

*Nemapteryx* is a valid monospecific genus supported by seven autapomorphies:

1. Mesethmoid posterior branches very long, delimiting half of anterior cranial fontanel length (8, 0 > 2; Fig. 4A). Convergent in *Cathorops* (*Cathorops*).
2. [Reversal] Medial groove of cranium present (30, 1 > 0; Figs 2A, 3B, 4A, B, 5A, B, 6A). Convergent in clade 61.
3. [Reversal] Vomerine lateral processes very wide (51, 1 > 0; Fig. 7B–D). Convergent in *Aspistor*, *No. planiceps*, and clades 22, 33, and 60.
4. [Reversal] Vomerine tooth plates present (53, 0 > 1). Convergent in *Cathorops* (*Precathorops*), *Hemiaris*, and clade 44.
5. [Reversal] Autopalatine face for articulation with lateral ethmoid located exactly in the centre of bone (104, 2 > 1).
6. Dorsal crest delimiting contact area between premaxilla and mesethmoid beginning between one third and half of anterior margin of bone (117, 0 > 1). Convergent in *Arius*, *Bagre*, *Batrachocephalus*, *Cochlefelis*, *Hemiaris*, *Netuma*, and *Potamosilurus velutinus*.

#### *Ambiguous optimization*

7. Adipose-fin base moderately long, about half as long as anal-fin base (212, ? > 2). Convergent in clades 9 and 57.

#### MONOPHYLY OF CLADE 56

(*CEPHALOCASSIS* (*NEDYSTOMA*, *DOIICHTHYS*))  
[81 – 90 – 06]

The sister-group relationship between *Cephalocassis* and other two members of this clade (*Doiichthys* and *Nedystoma*) is well supported by seven synapomorphies:

1. [Reversal] Transcapular process perpendicular to main axis of body (79, 1 > 0; Figs 8A, B, 9A). Convergent in *Hemiaris*.
2. Interopercle anterior portion conspicuously narrow (126, 0 > 1; Fig. 15E).
3. First hypobranchial transversely very elongate, its mesial face very pronounced and acute (165–188, 0 > 1; Fig. 21C). Convergent in *Cathorops* (*Cathorops*) and *Cryptarius*.
4. First hypobranchial anterior process very conspicuous (166, 0 > 1; Fig. 21C). Convergent in *Cathorops*.
5. Second hypobranchial transversely very elongate, its mesial face acute (169, 0 > 1; Fig. 21C). Convergent in *Cathorops*.
6. [Reversal] Uncinate process of third epibranchial acute (176, 1 > 0; Fig. 23A–C). Convergent in *H. stormii*, *Potamosilurus*, and clade 60.
7. Fourth epibranchial posterior margin slightly convex (180, 0 > 1; Fig. 23A). Convergent in clade 42.

#### MONOPHYLY OF CLADE 57

(*NEDYSTOMA*, *DOIICHTHYS*)  
[98 – 99 – 08]

The hypothesis of relationship between *Doiichthys* and *Nedystoma* is supported by 11 synapomorphies of which six are exclusive:

1. Space between transcapular process and otic capsule moderately large (82, 2 > 1; Figs 8B, 9A). Convergent in *Hemiaris*.
2. Autopalatine posterior portion conspicuously compressed (99, 0 > 1). Convergent in clade 24.
3. Second basibranchial posterior portion very long and thin (160, 2 > 1; Fig. 20D).
4. Third basibranchial very long and narrow (162, 1 > 3; Fig. 20D).
5. Uncinate process of third epibranchial short and laterally curved. (177, 1 > 2; Fig. 23C).
6. Space for insertion of teeth on fifth ceratobranchial very reduced (187, 1 > 2; Fig. 25C). Convergent in *Cathorops* (*Cathorops*) and clade 42.
7. Pharyngeal tooth plate long and narrow (188, 1 > 2; Fig. 26D).
8. Dorsal processes of upper (pharyngeal) tooth plate connected by a bony blade (189, 0 > 1; Fig. 26E, G).



9. Dorsal processes of upper (pharyngeal) tooth plate very long (190, 1 > 2; Fig. 26E, G).

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10. Parietosupraoccipital nearly as narrow at base as at posterior portion (44, ? > 0; Figs 2A, 3A, 6B). Convergent in *Galeichthys* and *Cep. melanochir*.  
 11. Adipose-fin base moderately long, about half as long as anal-fin base (212, ? > 2). Convergent in *Nemapteryx* and clade 9.

MONOPHYLY OF *NEDYSTOMA*

(*NEDYSTOMA DAYI*)

Characterized by the following autapomorphies:

1. [Reversal] Accessory tooth plates absent (56, 1 > 0). Convergent in *Cep. borneensis*, *Ketengus*, *Pachyula*, *Potamarius izabalensis*, and *Potamosi-lurus velutinus*.
2. Premaxilla anterior margin fringed (115, 0 > 1).
3. Opercle anterior portion subtrapezoid, very long (120, 1 > 0; Fig. 15A). Convergent in *Cinetodus*.
4. [Reversal] Hyomandibular dorsal crest short and high (134, 0 > 1; Fig. 16C, D, G, H). Convergent in *Cathorops* and clade 32.
5. Third external branchiostegal ray spatulate (142, 0 > 1; Fig. 18B).
6. Contact face between first epibranchial and first pharyngobranchial very conspicuous (170, 0 > 1; Fig. 22C). Convergent in *Ar. arius*, *Ar. gagora*, *Brustiarius*, and clade 33.
7. Pharyngeal tooth plate very long and narrow (188, 2 > 3; Fig. 26F).

*Ambiguous optimization*

8. Second external branchiostegal ray almost as wide as first ray (141, ? > 1; Fig. 18B). Convergent in *Cephalocassis*, *Galeichthys*, clades 42 and 61.
9. Lateral margin of third pharyngobranchial pointed (186, ? > 1; Fig. 24C). Convergent in *Brustiarius*, *Neoarius*, *Netuma*, and clade 33.
10. Transversel crest associated with neural spine of fourth vertebra very high (193, ? > 1). Convergent in *Bagre*, *Occidentarius*, *No. planiceps*, and clades 41 and 51.

MONOPHYLY OF *DOIICHTHYS*

(*D. NOVAEGUINEAE*)

*Doichthys* is defined by nine exclusive and 12 homoplastic synapomorphies:

1. [Reversal] Mesethmoid anterior notch inconspicuous, large, and shallow (1, 1 > 0; Figs 2A, 3B, 4B,

5B). Convergent in *Cryptarius*, *Ketengus*, and clade 60.

2. Mesethmoid median portion very wide (2, 1 > 2; Figs 3B, 5B). Convergent in *Carlarius*, *Batrachcephalus*, clades 3 and 26.
3. Lateral horn of lateral ethmoid very long and posteriorly orientated (12, 1 > 2; Figs 5A, B, 6B). Convergent in *Potamarius*, and clades 38 and 45.
4. Nasal bone indefinite-shaped (19, 0 > 1).
5. Parietosupraoccipital ventral crest weakly developed, restricted to base of process (46, 1 > 0). Convergent in *Cryptarius*, *Galeichthys*, and clade 7.
6. Circumorbital series formed by five infraorbitals (88, 3 > 1).
7. Autopalatine face for articulation with lateral ethmoid slightly displaced to anterior portion of bone (104, 2 > 0; Fig. 14B, C). Convergent in *Bagre*.
8. Premaxilla wide and short (113, 1 > 3).
9. [Reversal] Metapterygoid twice as long as high (128, 1 > 0; Fig. 16A, B).
10. [Reversal] First external branchiostegal ray proximally narrow and distally broad (140, 1 > 0; Fig. 18A). Convergent in *Ar. caelatus*, *Carlarius*, *Netuma*, *Notarius*, and clades 30 and 41.
11. Posterior ceratohyal very long (146, 0 > 2).
12. Urohyal very long (150, 1 > 2; Fig. 19D).
13. Urohyal posterior end bifurcated (151, 0 > 1; Fig. 19B, D). Convergent in *Bagre*.
14. Urohyal posterolateral processes one third as long as distal portion of bone (155, 2 > 4; Fig. 19D).
15. First and second epibranchials straight throughout their entire extension (171, 0 > 1; Fig. 22A).
16. Mesial portion of first epibranchial very large and depressed (173, 0 > 2; Fig. 22A).
17. [Reversal] First pharyngobranchial located at mesial end of first epibranchial (184, 1 > 0; Fig. 22A).
18. [Reversal] Third pharyngobranchial elongate and hourglass-shaped (185, 1 > 0; Fig. 24A). Convergent in *Ketengus* and *Potamarius grandoculis*.
19. Medial crest associated with neural spine of third vertebra low or absent (194, 1 > 0). Convergent in *Cryptarius* and *Galeichthys*.

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20. [Reversal] Second external branchiostegal ray less than half width of first ray (141, ? > 0; Fig. 18A).
21. [Reversal] Transversel crest associated with neural spine of fourth vertebra low (193, ? > 0). Convergent in *Cephalocassis*.

MONOPHYLY OF *CEPHALOCASSIS* (CLADE 58)  
(*CEP. BORNEENSIS*, *CEP. MELANOCHIR*)  
[95 – 98 – 10]

*Cephalocassis* including *Cep. borneensis* and *Cep. melanochir* is well defined by 14 synapomorphies:

1. Mesethmoid median portion very narrow (2, 1 > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clades 39 and 60.
2. Bony bridge formed by lateral ethmoid and frontal mostly represented by latter bone (15, 1 > 2; Figs 3A, 4A). Convergent in *Cathorops* and clade 51.
3. Supraoccipital, pterotic, and sphenotic delimiting a fenestra (34, 0 > 1; Fig. 3A).
4. Vomer anterior margin very pronounced and acute (48, 0 > 1; Fig. 7C, E). Convergent in *Potamarius*, *Potamosilurus macrorhynchus*, and clades 36, 47, and 60.
5. [Reversal] Contact face of transcapular process for articulation with basioccipital small and columnar (78, 1 > 0; Figs 8A, B, 9A). Convergent in *Hemiaris* and clade 60.
6. Teeth on dentary restricted to mesial two thirds of bone (109, 1 > 0). Convergent in *Cryptarius* and *Genidens*.
7. Premaxilla very long and narrow (113, 1 > 2). Convergent in *Cathorops*, *Cinetodus*, and *Potamarius*.
8. Metapterygoid one and a half times longer than high (128, 1 > 2; Fig. 16D–F). Convergent in *Plicofollis*, *Potamarius*, and clade 59.
9. Hyomandibular ventral crest absent (135, 0 > 1; Fig. 16D, G). Convergent in *Cathorops* and *Ketengus*.
10. Second basibranchial spindle-shaped (159, 1 > 0; Fig. 20B, C, F). Convergent in *Batrachocephalus*, *Cryptarius*, *Potamosilurus latirostris*, and clade 60.
11. Accessory crest connecting transversel crest to medial crest associated to neural spine of fourth vertebra present (197, 0 > 1). Convergent in clade 46.

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12. Second external branchiostegal ray almost as wide as first ray (141, ? > 1; Fig. 18B). Convergent in *Galeichthys*, *Nedystoma*, and clades 42 and 61.
13. [Reversal] Transversel crest associated with neural spine of fourth vertebra low (193, ? > 0). Convergent in *Doiichthys*.
14. Adipose-fin base long, as long as anal-fin base (212, ? > 1). Convergent in Ariidae, clades 46 and 60.

MONOPHYLY OF CLADE 59  
((*CINETODUS*, *PACHYULA*) (*CRYPTARIUS*  
(*PRECATHOROPS*, *CATHOROPS*)))  
[01 – 07 – 02]

The hypothesis about the monophyly of this clade that includes genera mainly from freshwaters of the Neotropical region, South-East Asia, Indonesia, Papua New Guinea, and Australia is supported by the following synapomorphies:

1. [Reversal] Posterior cranial fontanel long and relatively narrow (27, 2 > 1; Figs 4B, 5A). State 0 in *Cathorops* (*Cathorops*) and convergent in clade 9.
2. [Reversal] Epiphyseal bar short and wide (29, 1 > 0; Figs 2A, 3B, 4A, B, 5A, 6B).
3. Opercle anterior portion subtrapezoid, very short (120, 1 > 2; Fig. 15D–F). State 0 in *Cinetodus* and convergent in *Cep. borneensis*.
4. Metapterygoid one and a half times longer than high (128, 1 > 2; Fig. 16D–F). State 1 in *Cathorops* (*Precathorops*) and convergent in *Cephalocassis*, *Plicofollis*, and *Potamarius*.
5. Metapterygoid anterior process truncate (131, 0 > 1; Fig. 16F). State 2 in clade 61 and convergent in *Cochlefelis*, *Plicofollis*, *Potamarius*, and *Potamosilurus*.
6. First pharyngobranchial large and depressed (183, 0 > 1; Fig. 22C). Reversed in *Cathorops* (*Cathorops*) and convergent in clade 44.

*Ambiguous optimization*

7. [Reversal] Cleithrum humeral process moderately long (214, ? > 1; Fig. 27B, C). State 0 in *Cathorops* and state 2 in clade 60.

MONOPHYLY OF CLADE 60  
(*CINETODUS*, *PACHYULA*)  
[99 – 99 – 11]

The sister-genera relationship between *Cinetodus* and *Pachyula* is well defined by four exclusive ariid characters and 18 homoplastic synapomorphies:

1. [Reversal] Bony bridge formed by lateral ethmoid and frontal moderately thick (16, 1 > 0; Figs 2A, 3B, 5A, 6A, B).
2. [Reversal] Fenestra delimited by lateral ethmoid and frontal moderately large (17, 2 > 1; Figs 2A, B, 3B, 5A).
3. [Reversal] Frontal with a mesial laminar projection (23, 0 > 1; Figs 3B, 4B, 6A, B).
4. Epioccipital dorsally exposed (39, 0 > 1; Figs 2B, 6B). Convergent in *Am. rugispinis*, *Aspistor*, *Carlarius*, and clade 45.
5. Vomer anterior margin very pronounced and acute (48, 0 > 1; Fig. 7C, E). Convergent in

*Cephalocassis*, *Potamarius*, *Potamosilurus macrorhynchus*, and clades 36 and 47.

6. [Reversal] Vomer lateral processes very wide (51, 1 > 0; Fig. 7B–D). Convergent in *Aspistor*, *Nemapteryx*, *No. planiceps*, clades 22 and 33.
7. Basioccipital lateral process with anterior and posterior portions equally developed (76, 1 > 0).
8. [Reversal] Contact face of transcapular process for articulation with basioccipital small and columnar (78, 1 > 0; Figs 8A, B, 9A). Convergent in *Cephalocassis* and *Hemiaris*.
9. Transcapular process very shorter and broad (80, 0 > 1).
10. [Reversal] Uncinate process of third epibranchial acute (176, 1 > 0; Fig. 23A–C). Convergent in *H. stormii*, *Potamosilurus*, and clade 56.
11. Ventral surface of parapophysis of fifth and sixth vertebrae concave (202, 0 > 1).
12. Cleithrum humeral process very long (214, 1 > 2; Fig. 27D).
13. Cleithrum second dorsal process posteriorly orientated, parallel with cleithrum posterior process (216, 1 > 0; Fig. 27C, D). Convergent in *Batrachocephalus* and clade 3.
14. [Reversal] Cleithrum moderately wide (217, 1 > 0; Fig. 27B–E). Convergent in *Cat. dasycephalus*.

#### *Ambiguous optimization*

15. [Reversal] Mesethmoid medial notch inconspicuous, large, and shallow (1, ? > 0; Figs 2A, 3B, 4B, 5B). Convergent in *Cryptarius*, *Doiichthys*, and *Ketengus*.
16. Mesethmoid median portion very narrow (2, ? > 0; Figs 3A, 4A, 5A). Convergent in *Cathorops*, *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clade 39.
17. Lateral horn of lateral ethmoid very compressed and spatulated (11, ? > 1). Convergent in *Cathorops*, and clades 6, 11, and 45.
18. [Reversal] Orbitosphenoid and/or pterosphenoid lateral expansion two leaf-like short and wide processes (63, ? > 0; Fig. 8A, B). Convergent in *Ar. madagascariensis* and *Cathorops (Precathorops)*.
19. Ventral face of subvertebral process acute (73, ? > 2). Convergent in *Cryptarius*, and clades 41 and 46.
20. [Reversal] Urohyal posterolateral processes short (153, ? > 0; Fig. 19E, H). Convergent in *Cathorops*, *Cep. borneensis*, *Genidens*, and clades 41 and 44.
21. Second basibranchial spindle-shaped (159, ? > 0; Fig. 20B, C, F). Convergent in *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, and *Potamosilurus latirostris*.

22. Adipose-fin base long, as long as anal-fin base (212, ? > 1). Convergent in *Cephalocassis* and clade 46.

#### MONOPHYLY OF *CINETODUS* (*CINETODUS FROGGATTI*)

*Cinetodus* is defined by six autapomorphies:

1. Premaxilla very long and narrow (113, 1 > 2). Convergent in *Cathorops*, *Cephalocassis*, and *Potamarius*.
2. Opercle anterior portion subtrapezoid, very long (120, 2 > 0; Fig. 15A). Convergent in *Nedystoma*.
3. Pharyngeal tooth plate rounded (188, 1 > 0; Fig. 26A).
4. [Reversal] Dorsal process of upper (pharyngeal) tooth plate very short (190, 1 > 0).

#### *Ambiguous optimization*

5. Extrascapular subtriangular (35, ? > 2; Fig. 4A). Convergent in *Cathorops*.
6. Epioccipital posterior process contacting a small area of diagonal crest associated with neural spine of fourth vertebra (42, ? > 0). Convergent in *Bagre*, *Cep. melanochir*, *Cryptarius*, *Occidentarius*, *Potamarius izabalensis*, and clade 46.

#### MONOPHYLY OF *PACHYULA* (*PACHYULA CRASSILABRIS*)

*Pachyula* is characterized by three autapomorphies:

1. [Reversal] Accessory tooth plates absent (56, 1 > 0). Convergent in *Cep. borneensis*, *Potamarius izabalensis*, *Potamosilurus velutinus*, *Ketengus*, and *Nedystoma*.
2. First epibranchial posterior margin with a prominent process (174, 0 > 1; Fig. 22C). Convergent in clade 44.

#### *Ambiguous optimization*

3. Epioccipital posterior process contacting the transversal and diagonal crests related with neural spine of fourth vertebra (42, ? > 1). Convergent in *Cathorops*, and clades 40 and 55.

#### MONOPHYLY OF CLADE 61 (*CRYPTARIUS (PRECATHOROPS, CATHOROPS)*)

[22 – 31 – 02]

*Cryptarius* is hypothesized to be the sister group of the Neotropical genus *Cathorops* based on six synapomorphies:

1. [Reversal] Medial groove of cranium present (30, 1 > 0; Figs 2A, 3B, 4A, B, 5A, B, 6A). Convergent in *Nemapteryx*.

2. Temporal fossa very reduced, sometimes partially closed (37, 1 > 0; Figs 2A, 4A). Convergent in *Cep. borneensis*, *Genidens*, and *Net. bilineata*.
3. Metapterygoid anterior process rounded (131, 1 > 2; Fig. 16D, E).
4. Second external branchiostegal ray almost as wide as first ray (141, 0 > 1; Fig. 18B). Convergent in *Cephalocassis*, *Galeichthys*, *Nedystoma*, and clade 42.
5. Anterior ceratohyal mesial portion compressed (143, 0 > 1).
6. Adipose-fin base very short, smaller than half of anal-fin base (212, ? > 3). Convergent in *Bagre*, *Brustiarius*, *Netuma*, and clade 44.

MONOPHYLY OF *CRYPTARIUS*  
(*CRYPTARIUS TRUNCATES*)

The monospecific genus *Cryptarius* is very well defined by 21 autapomorphies:

1. [Reversal] Anterior portion of anterior cranial fontanel not delimited by dorsal expansion of orbitosphenoid (24, 1 > 0; Figs 2A, 3A, 4B, 5B). Convergent in clades 42 and 55.
2. Epioccipital posterior process contacting medial crest associated with neural spine of fourth vertebra (43, 0 > 1).
3. Parietosupraoccipital ventral crest weakly developed, restricted to base of process (46, 1 > 0). Convergent in *Doiichthys* and *Galeichthys*.
4. Vomer arrow-shaped (47, 1 > 3).
5. [Reversal] Orbitosphenoid and pterosphenoid lateral expansions absent (62, 1 > 0; Fig. 9A). Convergent in *Potamarius*, and clades 41 and 55.
6. Teeth on dentary restricted to mesial two thirds of bone (109, 1 > 0). Convergent in *Cephalocassis* and *Genidens*.
7. Interopercle anterior portion thin and acute (126, 0 > 2; Fig. 15F).
8. Metapterygoid articulated with a small area of quadrate through a toothed suture and overlaying remaining part of that bone (129, 0 > 1; Fig. 16E).
9. [Reversal] Urohyal posterolateral processes almost as long as distal portion of bone (155, 2 > 0; Fig. 19C, E). Convergent in *Cep. melanochir*.
10. Second basibranchial posterior portion long and wide (160, 2 > 0; Fig. 20C). Convergent in *Galeichthys*.
11. Medial crest associated with neural spine of fourth vertebra low or absent (194, 1 > 0). Convergent in *Doiichthys* and *Galeichthys*.

*Ambiguous optimization*

12. [Reversal] Mesethmoid medial notch inconspicuous, large, and shallow (1, ? > 0; Figs 2A, 3B, 4B,

- 5B). Convergent in *Doiichthys*, *Ketengus*, and clade 60.
13. [Reversal] Mesethmoid median portion moderately wide (2, ? > 1; Figs 2A, B, 6A, B). Convergent in clade 11.
14. [Reversal] Lateral horn of lateral ethmoid slightly compressed and acute (11, ? > 0). Convergent in *Pl. platystomus*, *Pl. tenuispinis*, *Potamosilurus macrorhynchus*, and clades 30 and 46.
15. Extrascapular subquadrangular (35, ? > 1; Figs 2B, 5A, 6A, B). Convergent in *Potamarius izabalensis* and clade 9.
16. Epioccipital posterior process contacting a small area of diagonal crest associated with neural spine of fourth vertebra (42, ? > 0). Convergent in *Bagre*, *Cep. melanochir*, *Cinetodus*, *Occidentarius*, *Potamarius izabalensis*, and clade 46.
17. [Reversal] Orbitosphenoid and/or pterosphenoid lateral expansions leaf-like, short and wide processes (63, ? > 0; Fig. 8A, B). Convergent in *Ar. madagascariensis* and clade 60.
18. Ventral face of subvertebral process acute (73, ? > 2). Convergent in clades 41, 46, and 60.
19. Urohyal posterolateral processes long (153, ? > 1; Fig. 19A–D, F, G). Convergent in *Pl. platystomus* and clade 3.
20. Second basibranchial spindle-shaped (159, ? > 0; Fig. 20B, C, F). Convergent in *Batrachocephalus*, *Cephalocassis*, *Potamosilurus latirostris*, and clade 60.
21. First hypobranchial transversely very elongate, its mesial face very pronounced and acute (165, ? > 1; Fig. 21C). Convergent in *Cathorops* (*Cathorops*) and clade 56.

MONOPHYLY AND INTRAGENERIC RELATIONSHIPS OF  
GENUS *CATHOROPS* (CLADE 62)

(*CATHOROPS (PRECATHOROPS)*, *CATHOROPS*  
(*CATHOROPS*)  
[99 – 100 – 14])

*Cathorops* is supported by six exclusive and 21 homoplastic synapomorphies:

1. Mesethmoid posterior branches very thin (6, 0 > 1; Figs 3A, B, 4A, B, 5B). Convergent in *Ketengus*, and clades 5 and 55.
2. Mesethmoid posterior branches parallel throughout their entire extension (7, 0 > 1; Figs 3A, 4A, B, 5B). Convergent in *Ketengus* and clade 55.
3. Bony bridge formed by lateral ethmoid and frontal mostly represented by latter bone (15, 1 > 2; Figs 3A, 4A). Convergent in *Cephalocassis* and clade 51.
4. Otic capsules slightly differentiated (67, 0 > 1, Fig. 9B).

5. Aortic channel opening located within base of subvertebral process and anteriorly orientated (70, 1 > 2; Fig. 9B).
6. Anterior margin of subvertebral process keeled (74, 0 > 1; Fig. 10C).
7. Basioccipital lateral process very long (77, 0 > 1; Fig. 9B).
8. Transcapular process depressed (81, 0 > 1; Fig. 9B).
9. Bony crest formed by exoccipital posterior process parallel to vertebral column and mesially folded (85, 1 > 2).
10. Premaxilla very long and narrow (113, 1 > 2). Convergent in *Cephalocassis*, *Cinetodus*, and *Potamarius*.
11. Opercle anteroventral margin concave or almost straight (121, 0 > 1; Fig. 15B, D). Convergent in clade 44.
12. Interopercle posterior margin angled (123, 0 > 1; Fig. 15B, D). Convergent in clade 44.
13. Interopercle anterior portion compressed and bifurcated (125, 0 > 1; Fig. 15B, D). Convergent in clade 44.
14. [Reversal] Hyomandibular dorsal crest short and high (134, 0 > 1; Fig. 16C, D, G, H). Convergent in *Nedystoma* and clade 32.
15. Hyomandibular ventral crest absent (135, 0 > 1; Fig. 16D, G). Convergent in *Cephalocassis* and *Ketengus*.
16. Urohyal anterior margin not notched (147, 0 > 1; Fig. 19H). Convergent in *Batrachocephalus* and *Pl. tenuispinis*.
17. [Reversal] Urohyal dorsal crest anteriorly projected (149, 0 > 1; Fig. 19A, E, H). Convergent in *Aspistor*, *Cep. borneensis*, *Ketengus*, *Notarius*, and *Occidentarius*.
18. [Reversal] Third basibranchial hourglass-shaped (161, 1 > 0; Fig. 20B, C, D, F). Convergent in clades 25 and 55.
19. Superficial ventral ossification arched (201, 0 > 1; Fig. 9B). Convergent in *Cep. borneensis*.
24. Epioccipital posterior process contacting the transversal and diagonal crests related with neural spine of fourth vertebra (42, ? > 1). Convergent in *Pachyula*, and clades 40 and 55.
25. Ventral face of subvertebral process spatulate (73, ? > 3). Convergent in *Hemiaris* and clade 55.
26. [Reversal] Urohyal posterolateral processes short (153, ? > 0; Fig. 19E, H). Convergent in *Cep. borneensis*, *Genidens*, and clades 41, 44, and 60.
27. Second basibranchial mushroom-shaped (159, 0 > 1; Fig. 20A, D, E). Convergent in clade 18.

MONOPHYLY OF SUBGENUS *PRECATHOROPS*  
(*CATHOROPS* (*PRECATHOROPS*) *DASYCEPHALUS*)

Defined by five new autapomorphies:

1. [Reversal] Vomerine tooth plates present (53, 0 > 1). Convergent in *Hemiaris*, *Nemapteryx*, and clade 44.
2. Metapterygoid as long as high (128, 2 > 1; Fig. 16C). Convergent in clade 7.
3. [Reversal] Cleithrum moderately wide (217, 1 > 0; Fig. 27B–E). Convergent in clade 60.

*Ambiguous optimization*

4. [Reversal] Orbitosphenoid and/or pterosphenoid lateral expansion two leaf-like short and wide processes (63, ? > 0; Fig. 8A, B). Convergent in *Ar. madagascariensis* and clade 60.
5. [Reversal] First hypobranchial transversely moderately elongate transversely, its mesial face weakly developed and rounded (165, ? > 0; Fig. 21A, B).

MONOPHYLY OF SUBGENUS *CATHOROPS* (CLADE 63)  
(*CAT. CATHOROPS AGASSIZII*, *CAT. CATHOROPS ARENATUS*, *CAT. CATHOROPS FUERTHII*,  
*CAT. CATHOROPS HYPOPTHALMUS*, *CAT. CATHOROPS MULTIRADIATUS*, *CAT. CATHOROPS SPIXII* AND  
*CAT. CATHOROPS TUYRA*)  
[100 – 100 – 15]

Monophyly of *Cathorops*, with the exception of *Cat. dasycephalus* (of subgenus *Precathorops*), is defined by 19 synapomorphies:

*Ambiguous optimization*

20. Mesethmoid medial notch conspicuous, narrow, and deep (1, ? > 1; Figs 2B, 3A, 4A, 5A, 6A, B). Convergent in clade 7.
21. Mesethmoid median portion very narrow (2, ? > 0; Figs 3A, 4A, 5A). Convergent in *Cephalocassis*, *Ketengus*, *Osteogeneiosus*, *Potamarius*, and clades 39 and 60.
22. Lateral horn of lateral ethmoid very compressed and spatulated (11, ? > 1). Convergent in clades 6, 11, 45, and 60.
23. Extrascapular subtriangular (35, ? > 2; Fig. 4A). Convergent in *Cinetodus*.
1. Mesethmoid and lateral ethmoid delimiting a fenestra (3, 0 > 1; Fig. 4A, B). Convergent in *Ketengus*.
2. Mesethmoid posterior horn tubular, narrow and elongate (5, 0 > 1; Fig. 4A, B). Convergent in *Ketengus*.
3. Mesethmoid posterior branches very long, delimiting half of anterior cranial fontanel length (8, 0 > 2; Fig. 4A). Convergent in *Nemapteryx*.

5. Posterior cranial fontanel delimited exclusively by frontal bones (25, 0 > 1; Figs 2A, 3B, 4A, 5A, 6B). Convergent in *Osteogeneiosus*, *Plicofollis*, and clade 13.
6. Posterior cranial fontanel reduced to a small opening (27, 1 > 0; Figs 2A, 3A, 4A, 6B). Convergent in *Genidens*, and clades 20 and 44.
7. Extrascapular delimiting more than three fifths of temporal fossa (38, 0 > 1; Fig. 4A).
8. Accessory tooth plates bearing molariform teeth (59, 0 > 1). Convergent in *Aspistor*, clades 39 and 40.
9. Ventral process at symphysis of dentary long and very conspicuous (108, 1 > 2).
10. Dentary teeth acicular and molariform (110, 0 > 1).
11. First hypobranchial anterior process very conspicuous (166, 0 > 1; Fig. 21C). Convergent in clade 56.
12. Second hypobranchial transversely very elongate, its mesial face acute (169, 0 > 1; Fig. 21C). Convergent in clade 56.
13. [Reversal] First pharyngobranchial long and narrow (183, 1 > 0; Fig. 22A).
14. Space for insertion of teeth on fifth ceratobranchial very reduced (187, 1 > 2; Fig. 25C). Convergent in clades 42 and 57.
15. Cardinal veins passing at same level as aortic channel (200, 0 > 1).
16. Cleithrum humeral process very short (214, 1 > 0; Fig. 27A). Convergent in *Hemiarius* and clade 55.

#### *Ambiguous optimization*

17. Fenestra delimited by mesethmoid and lateral ethmoid small and not filled with cartilage (4, ? > 0; Fig. 4A).
18. Orbitosphenoid and/or pterosphenoid lateral expansion very narrow and long (63, ? > 1; Fig. 9B). Convergent in *Cochlefelis*, *Bagre*, *Potamarius*, and clades 30 and 47.
19. First hypobranchial transversely very elongate, its mesial face very pronounced and acute (165, ? > 1; Fig. 21C). Convergent in *Cryptarius* and clade 56.

## DISCUSSION

### MONOPHYLY OF THE ARIIDAE

The family Ariidae has been recognized as a natural group since precladistic studies (Regan, 1911; Shelden, 1937; Berg, 1940; Tilak, 1965; Greenwood *et al.*, 1966; Chardon, 1968), a condition never seriously questioned (Weber & de Beaufort, 1913; Berg, 1940; Schultz, 1944; Mo, 1991), and used by several authors (Tilak, 1965; Chardon, 1968; Higuchi, 1982;

Rimmer & Merrick, 1983; Rao & Lakshmi, 1984; Nolf, 1985), especially based on the presence of the strongly developed lapillus (= utricular otolith), occupying the area corresponding to the prootic, pterotic, and exoccipital (character 68, state 2), epioccipital bearing a posterior process (character 40, state 1 in the present study), a well-developed basioccipital ventral process forming a cone-shaped projection (character 71, state 1), anterior and posterior nostrils close together (character 221, state 1), and male mouth-brooding of eggs and embryos (not seen in the present study).

Cladistic studies based on analysis of morphological characters (Mo, 1991; de Pinna, 1993; Oliveira *et al.*, 2002; Marceniuk, 2003; Kailola, 2004; Diogo, 2004) and molecular data (Hardman, 2005; Sullivan *et al.*, 2006; Betancur-R *et al.* 2007; Betancur-R, 2009) support ariid monophyly. Mo (1991) justified the monophyly of the Ariidae based on two synapomorphies: greatly enlarged utriculus otolith that occupies a large median space formed by the prootic, pterotic, and exoccipital bones and extensive superficial ossification on the ventral side of the complex centrum (character 199, state 1, condition herein interpreted as a synapomorphy of Ariinae plus Bagreinae). More evidence of the monophyly of the Ariidae was provided by de Pinna (1993) based on six additional synapomorphies: frontal and lateral ethmoid connected by a lateral bridge of bone mesially delimiting a space (character 14, state 3), last basibranchial with lateral expansions at the region of contact with the proximal cartilaginous tip of the fourth ceratobranchial (not observed in the specimens examined in the present study), third pharyngobranchial strongly protruded laterally (character 185, state 1), anterior cartilage of the fourth ceratobranchial as narrow as or narrower than the lateral process when it is present (character 181, state 1), mesial tip of first and second epibranchials anteriorly covering the anterior tip of the third pharyngobranchial (not examined in the present study), and presence of the Müllerian ramus (condition recognized as derived in the Ariidae, but not included herein). Oliveira *et al.* (2002), in a description of the cephalic and pectoral-girdle muscles of three ariid species, *Ar. heudelotii*, *G. genidens*, and *Bag. marinus*, suggested two putative autapomorphies for the Ariidae: adductor arcus palatini muscle inserted on the mesial margin of both the hyomandibular and the metapterygoid, and also on a significant part of the lateral surface of the metapterygoid; and section Aw (Winterbottom, 1974) of the adductor mandibulae muscle well developed and obliquely orientated bundle, with its posterodorsal fibres significantly dorsal to the upper edge of the coronoid process (not observed in the present study). Kailola (2004) defined the monophyly of the Ariidae through presence of oral incubation (not included in the present analysis

because of the difficulty in examining the habit in all members of the group), absence of a mesocoracoid (herein a synapomorphy of Anchariidae plus Ariidae, character 219, state 1), frontal and mesethmoid meeting at a minimum of two sites (character 14, state 3), possession of strong pelvic musculature (not examined), body naked (not included herein), presence of large otolith (herein character 68 in part, state 2), formation of an aortic tunnel (character 199, state 1), homologous elastic spring apparatus (not examined), extended epioccipital (character 39, state 1), and absence of a supraneural (herein a synapomorphy of Ariinae plus Bagreinae, character 207, state 1). Betancur-R *et al.* (2007) did not point out morphological evidence corroborating monophyly of the Ariidae, and Acero P. & Betancur-R (2007) defined the family based on characters from the literature. In the present contribution previous hypotheses of ariid monophyly are supported by 22 synapomorphies, some not presenting similar conditions in other Siluriformes examined: nasal anterior tubules connected by a bony blade (character 21, state 1, absent in *Osteogeneiosus*); three infraorbitals present (character 88, state 3, five in *Doiichthys*); lachrymal-antorbital very wide (character 93, state 0, narrow in *Plicofollis*, except *Pl. platystomus*, Fig. 12A–E), and second basibranchial anterior portion well developed and expanded (character 158, state 1).

In the past, the main question related to the monophyly of the family was a result of the inclusion or not of the genus *Ancharius* in the Ariidae and of the genera *Bagre* and *Doiichthys* in different families. Mo (1991) postulated that *Ancharius*, endemic to Madagascar and previously included in the Ariidae (Jayaram, 1983), would share exclusive derived features with the Mochokidae and the Doradoidea, and should be considered a member of the Mochokidae. However, de Pinna (1993) considered that in spite of sharing derived characters with Mochokidae and Doradoidea, *Ancharius* is more closely related to the Ariidae as part of a monophyletic group within the Claroteidae, composing the superfamily Arioidea. More recently *Ancharius* was included in its own family, Anchariidae, by Stiassny & Raminosa (1994), a decision also taken by Ng & Sparks (2005) when describing a new genus and three new species in the same family. Diogo (2004) hypothesized Ariidae plus Anchariidae to be the sister group of the Claroteidae, and nested this assemblage together with austroglanidids, ictalurids, cranoglanidids, schilbids, and pangasids in a large, inclusive siluriform clade. A higher-level phylogeny of the Siluriformes based on rag1 and rag2 nuclear gene sequences (Sullivan *et al.*, 2006) also corroborated a close relationship between ariids and *Ancharius*, although this assemblage was nested in a large polytomy together with most of the

catfish families. The analysis herein undertaken indicates a relationship amongst Ariidae, Anchariidae, and Claroteidae, *sensu* Pinna (1993), supported by characters 108 (state 1), 112 (state 1), 122 (state 1), 136 (state 1), 148 (state 1), and 220 (state 0), and a sister-group relationship between Anchariidae and Ariidae supported by characters 2 (state 1), 30 (state 0), 65 (state 1), 116 (state 1), 132 (state 0), 177 (state 1), and 219 (state 1).

Less controversial has been the decision to consider *Bagre* Oken, 1817 (= *Bagre* Cloquet, 1816) and *Doiichthys* Weber, 1913 as belonging to their own families, Bagreidae (Schultz, 1944) and Doiichthyidae (Weber, 1913), respectively. Cladistic analysis based on morphological evidence independently undertaken by Marceniuk (2003) and Kailola (2004) confirmed the monophyletic condition of the Ariidae including members of the two genera, a hypothesis also corroborated by molecular data (Betancur-R, 2009). The condition is also corroborated in the present work.

#### MONOPHYLY AND RELATIONSHIPS OF ARIID SUBFAMILIES AND GENERA

In the strict consensus tree (Fig. 29), the new hypotheses of monophyly and relationships of the subfamilies and genera recognized by Kailola (2004), Marceniuk & Menezes (2007), and Betancur-R *et al.* (2007) are depicted. Of the 33 nominal genera considered valid by those authors, 32 have been herein examined (see Appendix 2) and the ten recognized as monospecific are supported by an extensive series of autapomorphies, many of which represent unique derived conditions in the Ariidae (*Batrachocephalus*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Nedystoma*, *Nemapteryx*, *Ketengus*, *Occidentarius*, *Osteogeneiosus*, and *Pachyula*). Amongst the remaining 22 genera in which two or more species are included, 16 are monophyletic (*Arius*, *Aspistor*, *Bagre*, *Brustarius*, *Carlarius*, *Cathorops*, *Cephalocassis*, *Cochlefelis*, *Galeichthys*, *Genidens*, *Hemiarius*, *Nearius*, *Netuma*, *Plicofollis*, *Potamarius*, and *Sciades*), three are not monophyletic (*Ampharius*, *Notarius*, and *Potamosilurus*), and three (*Ariopsis*, *Guiritinga*, and *Hexanematichthys*) are considered synonyms. Three subfamilies (Ariinae, Bagreinae and Galeichthyinae) and two subgenera (*Cathorops* and *Precathorops*) are recognized.

#### SUBFAMILY GALEICHTHYINAE

The monophyly of *Galeichthys* and its position as sister group of the remaining members of the Ariidae has long been suggested. Acero P. & Betancur-R (2007) proposed the subfamily Galeichthyinae (including only *Galeichthys*) by the presence of a

postcleithral process fused to the posterior dorsal process of the cleithrum, forming a fan-shaped lamina (character 218, state 1), and of a long and narrow supraoccipital process (character 44, state 0), usually grooved along its entire extension (a condition herein interpreted as primitive in the Ariidae, as discussed under character 33). Kailola (2004), even without including *Galeichthys* in its own subfamily, defined the genus through the following derived features: oblique laminae of second and third neural spines high and another lamina extending downwards also from the ventral surface of the supraoccipital (not considered in the present study); posterior cleithral process broad and fan-shaped (character 218, state 1); temporal fossa small (herein not interpreted as synapomorphic for *Galeichthys*, see character 37, state 0); neurocranium nearly smooth, covered by thick skin and/or muscle layers (condition herein interpreted as primitive in the Ariidae, shared by *Bagre* and *Galeichthys*, see character 33, state 0); supraoccipital long and narrow, its sides nearly parallel (character 44, state 0); fin spines moderately thin (condition herein considered variable and phylogenetically not informative); and no pads on inner pelvic-fin rays of mature females (herein not examined).

New morphological evidence herein proposed supports the monophyly of *Galeichthys*. The most relevant characters are unique to the genus: posterior cartilage of autopalatine as long as anterior cartilage (character 107, state 0); anguloarticular with an anterodorsal process (character 111, state 1); mesial portion of first epibranchial large and depressed (character 173, state 1); space for insertion of teeth on fifth ceratobranchial very large (character 187, state 0); and maxilla wide at proximal two thirds where its edges are parallel, narrower distally becoming thinner and acute posteriorly (character 95, state 1). Additionally the currently accepted phylogenetic position of *Galeichthys* (Marceñiuk, 2003; Betancur-R, Acero P. & Mejía-Ladino, 2004; Betancur-R *et al.*, 2007; Betancur-R, 2009; Betancur-R & Armbruster, 2009) is strongly supported by new derived characters shared by all the representatives of the Ariidae (except Galeichthyinae): a distinct opening of the aortic channel present in front of the subvertebral process (character 69, state 1); basioccipital bearing a lateral process (character 75, state 1, absent in *Cep. melanochir*); diagonal crest associated with neural spine of fourth vertebra well developed (character 191, state 1); presence of a space delimited by the epioccipital posterior process and crests associated with the neural spine of fourth vertebra (character 198, state 1); protractor muscle of parapophysis of fourth vertebra contacting the epioccipital posterior process (character 230, state 1); first pharyngobranchial present (character 182, state 0), and first pharyngobranchial located on mesial two thirds of first

epibranchial (character 184, state 1, on two thirds of first epibranchial in *Doiichthys*). The result contrasts sharply with that of Kailola's (2004) phylogenetic analysis in which *Galeichthys feliceps* Valenciennes, 1840, was considered as the sister species of *Sciades emphysetus* (Müller & Troschel, 1849) [= *S. parkeri sensu* Betancur-R *et al.*, 2007] and *Aspistor hardenbergi* (Kailola, 2000) within a large polytomy.

#### SUBFAMILY BAGREINAE

In our analysis the species of *Bagre* represent the most strongly corroborated monophyletic group, defined by 39 synapomorphies. Some of these synapomorphies represent exclusive derived features in the Ariidae herein described for the first time whereas others have been described previously: mesethmoid posterior branches moderately long, delimiting more than one quarter of the anterior cranial fontanel length (character 8, state 1); anterior infraorbital conspicuously curved (character 89, state 1); posterior infraorbital L-shaped (character 90, state 2); maxilla cylindrical, moderately long and acute (character 94, state 1); maxillary condyles large (character 96, state 2); autopalatine conical, short, and robust (character 97, state 1); autopalatine inferior crest well developed (character 105, state 1), metapterygoid anterior process very large (character 132, state 1); and third basibranchial median constriction displaced to the posterior quarter of this bone (character 163, state 1). Although the monophyletic condition of *Bagre* has never been previously questioned (Marceñiuk, 2003; Betancur-R *et al.*, 2004; Kailola, 2004; Betancur-R *et al.*, 2007; Betancur-R, 2009), the relationships of its species with the remaining ariids have been controversial.

The large number of exclusive derived characters herein observed, including some that can be distinguished externally, allows the characterization and recognition of members of *Bagre* in their own subfamily, Bagreinae, proposed by Schultz (1944) as a new family. We adopt this here to express the degree of morphological divergence and the phylogenetic position of this genus in relation to the remaining ariids.

#### SUBFAMILY ARIINAE

In recent published studies (Acero P. & Betancur-R, 2007; Betancur-R *et al.*, 2007; Betancur-R, 2009), all the ariid genera except *Galeichthys* have been included in the subfamily Ariinae based on a series of characters including: posterior process of epioccipital very long and connected to the sustentaculum of the Weberian apparatus (character 41, state 1); ventral process of basioccipital and ventral ossification of complex vertebra mesially closed forming an aortic tunnel (character 199, state 1); presence of an antero-



dorsal bony block of the orbitosphenoids (character 24, state 1, absent in *Batrachocephalus*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, *Nedystoma*, *Nemapteryx*, and *Ketengus*); and anterior nuchal plate absent (character 207, state 1, also observed in *Bag. bagre*). Ariinae (*sensu* Acero P. & Betancur-R, 2007), as here defined includes all the members of the Ariidae with the exception of *Bagre* and *Galeichthys*. The new ariin concept is supported by 18 synapomorphies, some of which are exclusive: cephalic shield bones granulated (character 33 state 1); distance between the optic foramen and the trigeminofacialis foramen large, about twice as large as the trigeminofacialis foramina (character 65, state 1, reversed in *Potamarius*); articulation facet of the autopalatine with the lateral ethmoid moderately large (character 102, state 1); autopalatine anterior cartilage moderately long, one third to one fifth as long as the bone itself (character 106, state 1, reversed in *Osteogeneiosus*); hyomandibular dorsal crest present (character 133, state 1); first epibranchial parallel to second epibranchial (character 172, state 0, reversed in *Ketengus*); and nuchal plate fitting the parietosupraoccipital through a convex-concave face (character 210, state 1).

#### MONOPHYLY AND RELATIONSHIPS OF THE SUBFAMILY ARIINAE GENERA

The results herein obtained partially support the monophyly of the genera recognized in recently proposed classifications (Kailola, 2004; Betancur-R *et al.*, 2007; Marceniuk & Menezes, 2007). Monophyletic hypotheses exclusively based on molecular studies (Betancur-R, 2009) are further supported by additional morphological evidence in spite of conflicting conclusions, especially concerning relationships of genera. In this section differences in species composition of the genera and of the characters used to define them are discussed.

#### GENUS *AMISSIDENS*

No hypothesis of relationships for this genus could be proposed because none of the specimens belonging to the type series was examined. Nevertheless, based on the presence of granulated cephalic shield bones (character 33, state 1) and the middle nuchal plate fitting the parietosupraoccipital through a convex-concave face (character 210, state 1), amongst other external features described by Kailola (2000) to characterize the species, we consider *Amissidens* as belonging to the Ariinae.

#### GENUS *AMPHIARIUS*

As defined by Marceniuk & Menezes (2007), *Amphiarius* included *Am. phrygiatus* and *Am. rugis-*

*pinis* and was characterized by having: accessory tooth plates small to moderate, roughly round and laterally located (character 58, state 5), and bony bridge formed by frontals and lateral ethmoid with frontals as its major component (character 15, state 2). This is contrary to the conclusion of Betancur-R *et al.* (2007) who considered *Amphiarius* synonymous with *Notarius*, based only on molecular data taken from *Am. rugispinis*. Even though the species of *Amphiarius* appear in the consensus cladogram in a trichotomy including clade 52, the genus is characterized by a set of exclusive features in the Ariidae and phylogenetically distinct from *Notarius* (*sensu* Marceniuk & Menezes, 2007).

#### GENUS *ARIUS*

The main issues in ariid systematics have been the definition and delimitation of the genus *Arius* and its recognition as a natural group. In precladistic classifications *Arius* (= *Tachysurus* Lacepède, 1803) was always considered the most diverse and widely distributed genus in the Ariidae, in which species that were not clearly defined were accommodated (Eigenmann & Eigenmann, 1890; Herre, 1926; Fowler, 1936, 1941; Smith, 1945; Chandy, 1953; Misra, 1959; Jayaram, 1982). Even in more recent classifications (Kailola, 1999; Acero P., 2003) the nonmonophyletic condition and the difficulty in defining its limits using external morphological characters were pointed out. In Marceniuk & Menezes (2007), the species included in the genus *Arius*, distributed from eastern Africa, western Madagascar and south and southeastern Asia, are diagnosed through internal morphological characters, as well as a combination of external features that can easily be recognized: bifurcation of the lateral line at the caudal region (vs. lateral line simple, not bifurcated at the caudal region), except for *Bagre* in which, however, there is one pair of mental barbels (vs. two pairs in the *Arius* species). Additionally, *Arius* species can be distinguished from the remaining genera present in south and south-eastern Asia by having the adipose fin of moderate length, about half as long as the anal fin (vs. adipose fin short, less than half the length of the anal fin, characteristic of *Netuma* and *Plicofollis*), maxillary barbels present and always developed (vs. maxillary barbels absent in *Batrachocephalus* and rudimentary in *Ketengus*) and mental barbels present (vs. mental barbels absent in *Osteogeneiosus*).

Kailola's (2004) phylogenetic hypothesis considered *Arius* as a senior synonym of *Ariodes* and *Pseudarius*, and defined the monophyletic condition of the genus based only on the examination of the type-species of the respective genera. Another 13 species considered valid and allocated into the genus, but not used in

Kailola's (2004) phylogenetic analysis, were also included in *Arius* by Marceniuk & Menezes (2007), with the exception of *Ar. platystomus* and *Bagrus sumatranus* included in *Plicofollis* and *Hemiaris*, respectively. In Kailola's (2004) and Marceniuk & Menezes' (2007) works, the *Arius* species are restricted to southern and South-East Asia (at least 18 valid species), eastern Africa (two species), and western Madagascar (three species). By contrast, Betancur's (2009) molecular data, taken from a large number of taxa examined in his phylogenetic analysis, did not indicate *Arius* to be a monophyletic group and most of the species included in this genus by Marceniuk & Menezes (2007) appeared as part of a large polytomy. The monophyly of *Arius* (*sensu* Marceniuk & Menezes, 2007) is herein supported by five homoplastic synapomorphies (see diagnosis of clade 37). With the exclusion of *Ar. caelatus*, the genus *Arius* can be better characterized by the following synapomorphies: lateral horn of lateral ethmoid very long and posteriorly orientated (character 12, state 2, convergent in *Doichthys*, *Potamarius*, and *Plicofollis*, except *Pl. platystomus* and *Pl. tenuispinis*), orbito-sphenoid and/or pterosphenoid lateral expansion slightly projected, with wavy lateral margins (character 63, state 2, reversed in *Ar. madagascariensis* Vaillant, 1894), and autopalatine very compressed at the articulation face with lateral ethmoid (character 101, state 1, condition independently acquired in *Plicofollis*). *Arius* is hypothesized as the sister group of clade 40 that includes *Batrachocephalus*, *Ketengus*, *Osteogeneiosus*, plus *Plicofollis*, from eastern Africa, south and South-East Asia, and north New Guinea, a relationship in part corroborated by Betancur-R (2009), with the exclusion of *Plicofollis* and *Batrachocephalus*, the latter genus not included in the analysis (Betancur-R, 2009).

#### GENUS *ASPISTOR*

The genus *Aspistor*, including *As. luniscutis* and *As. quadriscutis*, is a monophyletic and well-defined taxon characterized by unique derived features in the Ariidae: tooth plates associated with vomer fused, forming a single large plate (character 54, state 3); urohyal posterior portion as wide distally as proximally (character 156, state 1); anterior and median nuchal plates forming a butterfly-shaped structure (character 208, state 2); and anterior margin of nuchal plate slightly concave (character 209, state 1). Based on these morphological characters Marceniuk & Menezes (2007) considered *Aspistor* a valid genus. Nonetheless, Betancur-R *et al.* (2007) treated *Aspistor* as synonymous with *Notarius*, even recognizing the former in some of their analyses as sister group of the latter. Kailola (2004) considered *Aspistor* valid based

only on direct examination of *Arius hardenbergi* Kailola, 2000, from Australia and New Guinea, adding into the genus another seven species from the Americas that were not included in her cladistic analysis.

#### GENUS *BRUSTIARIUS*

The monophyly of *Brustiarius*, as defined by Kailola (2004), is corroborated in the present study. Kailola characterized *Brustiarius* by the following synapomorphies: presence of a small adipose fin (character 212, state 3); adipose fin situated vertically above the posterior end of the anal fin (character 213, state 2); and four patches of teeth on the palate (two vomerine and two autogenous), which are often confluent, sometimes butterfly-shaped (character 54, state 2). She also used in the definition of the genera other characters not examined herein or recognized as synapomorphies in other branches of our cladogram, besides generalized external morphological characters. We propose herein new synapomorphies, three of which are exclusive: tooth plates associated with vomer butterfly-shaped (character 54, state 2), accessory tooth plates small and perfectly round, lateral to vomerine tooth plates (character 58, state 1), and premaxilla conspicuously wider laterally than mesially (character 114, state 1). Marceniuk & Menezes (2007) also included *Arius proximus* Ogilby, 1898, in *Brustiarius* based exclusively on a combination of external characters used to define the genus (species treated as *sedis mutabilis* on page 114). The monophyly of the genus, excluding *Ar. proximus*, was confirmed by Betancur-R (2009). The basal position of the genus within the Ariinae is weakly supported (Betancur-R, 2009).

#### GENERA *BATRACHOCEPHALUS*, *KETENGUS*, AND *OSTEOGENEIOSUS*

The monospecific condition of these three genera has been supported in many precladistic studies (Fowler, 1941; Smith, 1945; Misra, 1959; Wongratana & Bhatia, 1974; Jayaram & Dhanze, 1978; Jayaram, 1982, 1983; Talwar & Jhingran, 1991; Rainboth, 1996; Kailola, 1999) by unique external morphological characters within the Ariidae: pair of mandibular barbels very small and maxillary barbels absent in *Batrachocephalus* (character 223, state 1), mouth opening wide, cleft extending behind orbit, and jaws with a single row of incisor-like teeth on each jaw in *Ketengus* (condition here interpreted as synapomorphic to *Batrachocephalus* plus *Ketengus*, character 110, state 2 and character 119, state 1), and barbels restricted to a stiff semiosseous maxillary pair in *Osteogeneiosus* (character 94, state 2 and character 225, state 1). Jayaram & Dhanze (1985) hypothesized

the relationship of the Indian genera of the Ariidae and recognized *Batrachocephalus* as sister group of *Ketengus*, both representing an independent evolutionary lineage. *Arius* is thought to be the most specialized genus, having evolved from an ancestor near *Osteogeneiosus*, considered the most primitive of the four genera. In Kailola's (2004) phylogenetic analysis, the monospecific genera *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* are recognized as valid. Kailola's strict consensus cladogram shows *Ketengus* as the sister group of all the remaining members of the Ariidae, with *Osteogeneiosus* and *Batrachocephalus* as the last sister group of *Cryptarius* in branches successively more internal. *Batrachocephalus* was not examined by Betancur-R (2009), who recognized the sister-group relationship between *Ketengus* and *Osteogeneiosus* within a large polytomy with *Cryptarius* and *Cep. borneensis*, plus some of the species included in *Arius* by Marceniuk & Menezes (2007).

Monophyly of the clade comprising *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* is herein supported by 11 synapomorphies of which at least two are unique: lateral horn of lateral ethmoid inconspicuous (character 10, state 0) and metapterygoid anterior process absent (character 130, state 1). The sister-group relationship between *Batrachocephalus* and *Ketengus*, as suggested by Jayaram & Dhanze (1985), is strongly corroborated by 14 exclusive and another ten homoplastic synapomorphies many related to the palatine–maxillary system: nasal perpendicular in relation to mesethmoid (character 18, state 1); maxilla rudimentary and little differentiated (character 94, state 3); maxillary condyles rudimentary (character 96, state 0); autopalatine depressed (character 97, state 3); autopalatine anterior portion depressed (character 98, state 0); autopalatine transversely situated in relation to main body axis (character 100, state 1); autopalatine depressed at articulation face with lateral ethmoid (character 101, state 2); articulation between autopalatine and lateral ethmoid posteriorly orientated (character 103, state 2); autopalatine anterior cartilage very long, about as long as bone itself (character 106, state 2); dentary teeth spatulate and/or cuspidate (character 110, state 2); premaxillary teeth cuspidate (character 119, state 1, partially interpreted as a synapomorphy to *Batrachocephalus* plus *Ketengus* by Kailola, 2004); metapterygoid subtriangular-shaped (character 128, state 3); and contact face between metapterygoid and hyomandibular very long (character 137, state 1, partially interpreted as a synapomorphy to *Batrachocephalus* by Kailola, 2004).

The monospecific condition of *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* is corroborated by a large number of features, most of them herein described for the first time. *Batrachocephalus* is sup-

ported by 18 autapomorphies, most of them consisting of unique derived characters: nasal bone fan-shaped (character 19, state 2 also recognized by Kailola, 2004); accessory tooth plates located between premaxilla and lateral ethmoid (character 60, state 2); opercle anterior portion subrectangular (character 120, state 3); posterior portion of anterior ceratohyal columnar and very thick (character 144, state 1); and maxillary barbels absent (character 223, state 1, partially described by Kailola, 2004).

*Ketengus* is defined by an extensive series of autapomorphies, ten of which are unique: fenestra delimited by mesethmoid and lateral ethmoid large and filled with cartilage (character 4, state 1); lateral ethmoid and frontal not connected (character 14, state 0, although Kailola, 2004, considered that the lateral ethmoid contacts the frontal through a single facet); vomer diamond-shaped (character 47, state 0); however, Kailola, 2004, described the vomer of *Ketengus* as T-shaped as in Fig. 7B); vomer lateral processes absent (character 49, state 0); lachrymal–antorbital with three anterior branches (character 91, state 3); teeth implanted along entire extension of dentary (character 109, state 2); premaxilla dorsal crest absent (character 118, state 1); second and third basibranchials fused and indistinct (character 157, state 1); first hypobranchial club-shaped (character 164, state 1); and second hypobranchial club-shaped (character 168, state 1).

*Osteogeneiosus* is also defined by a large number of autapomorphies, 11 of which are unique: nasal anterior curvature very pronounced (character 20, state 1, also described by Kailola, 2004); nasal anterior tubules not connected by bony blade (character 21, state 0); maxillary condyles very large (character 96, state 3); posterior cartilage of autopalatine reduced to a small dot (character 107, state 2); urohyal short (character 150, state 0); mental barbels absent (character 225, state 1, also described by Kailola, 2004); lachrymal–antorbital with three anterior and one lateral projections (character 91, state 1, also described by Kailola, 2004), maxilla cylindrical very long and acute (character 94, state 2, also described by Kailola, 2004); autopalatine cylindrical, very short, and robust (character 97, state 2), premaxilla dorsal crest delimiting the contact area with mesethmoid beginning near or exactly at lateral end of anterior margin of bone (character 117, state 0), and metapterygoid three times longer than wide (character 128, state 4, also described by Kailola, 2004).

There are many difficulties in interpreting Kailola's definitions and relationships of the genera because she does not present a list of the synapomorphies for the branches of her cladogram. It is thus not always possible to be sure whether the characters, from both the external and internal morphology used to

diagnose the genera, are derived or generalized features.

#### GENUS *CARLARIUS*

Described by Marceniuk & Menezes (2007) for the species from the occidental part of the African continent previously included in the paraphyletic genus *Tachysurus* (= *Arius*) (Fowler, 1936; Tobor, 1969), *Carlarius* is monophyletic, a condition also supported by molecular data (Betancur-R, 2009). The following synapomorphies were used by Marceniuk & Menezes (2007) to define *Carlarius*: character 2 (state 2); character 39 (state 1); and character 53 (state 0). A new homoplastic synapomorphy is added herein: first external branchiostegal ray proximally narrow and distally broad (Fig. 18A). The basal position of *Carlarius* in relation to members of clade 32 is weakly supported in the present study.

#### GENUS *CATHOROPS*, AND SUBGENERA *PRECATHOROPS* AND *CATHOROPS*

*Cathorops* has been considered a valid genus by Taylor & Menezes (1978), Castro-Aguirre, Espinosa Pérez & Schmitter-Soto (1999), and Acero P. (2003). The first attempt to define the genus on the basis of derived features was carried out by Marceniuk (1997) and the current species composition defined by Marceniuk (2003), with the inclusion of *Ar. dasycephalus* in *Cathorops*. Higuchi (1982) and Marceniuk (1997) described exclusive morphological characters of *Cathorops*, many of which are recognized as synapomorphies to characterize the monophyly of the genus (Kailola, 2004; Betancur-R *et al.*, 2007), a condition that receives additional support from molecular data (Betancur-R *et al.*, 2007, Betancur-R, 2009). The long list of morphological characters that has been described to define *Cathorops* is here reviewed and new evidence is added to support the monophyletic condition of the genus through 27 synapomorphies, the following six exclusive: otic capsules slightly differentiated (character 67, state 1); aortic channel opening located within base of subvertebral process and anteriorly orientated (character 70, state 2); anterior margin of subvertebral process keeled (character 74, state 1); basioccipital lateral process very long (character 77, state 1); transcapular process depressed (character 81, state 1); and bony crest formed by exoccipital posterior process parallel to vertebral column and mesially folded (character 85, state 2).

R. Betancur-R & A. Acero P. (in Betancur-R *et al.*, 2007), based on morphological and molecular data, erected the subgenera *Precathorops* to include only *Cat. dasycephalus*, and *Cathorops* for the remaining species. *Precathorops* was defined by R. Betancur-R &

A. Acero P. on the basis of a single synapomorphy: presence of bony spinulations on the posterior projections of the mesethmoid, posterolateral process of the lateral ethmoids and anterior portion of the frontals (character not considered in present study, although *Cat. (Precathorops) dasycephalus* is recognized. The subgenus *Cathorops* was defined by those same authors by three exclusive synapomorphies here described as characters 38 (state 1), 59 (state 1), and 200 (state 1). The monophyly of *Cathorops* and the phylogenetic definition and relationships of *Cat. (Precathorops) dasycephalus* were confirmed by Betancur-R (2009). *Precathorops* is herein defined by five new synapomorphies (see monophyly of subgenus *Precathorops*), and subgenera *Cathorops* by 19 synapomorphies, the following ones exclusive: fenestra delimited by the mesethmoid and lateral ethmoid small and not filled with cartilage (character 4, state 0); ventral process at symphysis of dentary long and very conspicuous (character 108, state 2); dentary with acicular and molariform teeth (character 110, state 1); and cardinal veins passing at same level as aortic channel (character 200, state 1).

*Cathorops* is hypothesized as sister group of *Cryptarius*, a condition supported by two exclusive synapomorphies: metapterygoid anterior process rounded (character 131, state 2) and anterior ceratohyal mesial portion compressed (character 143, state 1). This relationship suggests a common origin of both genera, represented by species with geographical distributions widely apart: *Cathorops* in the Neotropical region and *Cryptarius* in Thailand, Indonesia, and Malaysia. *Cathorops* and *Cryptarius*, together with the remaining genera included in clade 52 (*Hemimarius*, *Cinetodus*, *Doiichthys*, *Cephalocassis*, *Nedystoma*, *Nemapteryx*, and *Pachyula*), are represented by species primarily found in estuarine or fresh waters that have a lighter skull, with larger openings and bones thin and longer. This hypothesis was also proposed by Kailola (2004).

#### GENUS *CEPHALOCASSIS*

*Hemipimelodus* was previously considered a valid genus based on the lack of palatine teeth (Herre, 1926; Fowler, 1941; Smith, 1945; Misra, 1959; Desoutter, 1977; Jayaram & Dhanze, 1978; Taylor, 1986; Rainboth, 1996). In Kailola's (2004) phylogenetic analysis, *Cep. melanochir* and *Cep. borneensis* were considered sister species and *Hemipimelodus* was included in the synonymy of *Cephalocassis*. She characterized *Cephalocassis* mainly on the basis of three synapomorphies, also herein recognized: vomer wedge-shaped (character 48, state 1); adipose fin long-based (character 212, state 1); and the pterotic bone thin and cartilaginous anterodorsally, creating a depression in the cranium

between the supraoccipital and the sphenotic (an exclusive character in the Ariidae, character 34, state 1). Eleven new synapomorphies are added to corroborate the monophyly of *Cephalocassis* (*sensu* Kailola, 2004), see diagnosis of clade 58. Despite the strong morphological support for the recognition of the monophyly of *Cephalocassis*, the molecular studies of Betancur-R (2009) did not support this hypothesis and indicated that *Cep. borneensis* is the sister species of *Arius leptanotacanthus* Bleeker, 1849, within a monophyletic clade in which *Cryptarius truncatus* is included, a hypothesis that would allow the recognition of *Cryptarius* as synonymous with *Hemipimelodus*. Additionally, *Cep. halocassis melanochir* was treated as sister to *H. stormii*, in a monophyletic clade with *Pimelodus sagor* in a basal position, suggesting that the nominal genera *Cephalocassis*, *Hexanematichthys*, and *Hemiarius* could be synonymous. The sister-species condition of *Sciades sagor* and *Cep. melanochir*, hypothesized by Betancur-R (2009) based on molecular data, is not supported by our morphological data. The first species shares with the other species of *Sciades* and *Occidentarius* (*sensu* Marceniuk & Menezes, 2007) a compact and heavy skull without fontanels and fenestrae (Ohe, 2006: fig. 9b). The second is characterized by a very light skull composed of thin bones with large fenestrae and fontanels (Fig. 3A), sharing with the other species of *Cephalocassis* many other derived features. Kailola's (2004) finding that *Cephalocassis* is the sister group of *Nedystoma* plus *Doiichthys* (*sensu* Marceniuk & Menezes, 2007) is here strongly supported by seven synapomorphies (see diagnosis of clade 56).

#### GENERA *CINETODUS* AND *PACHYULA*

The hypothesis of phylogenetic relationships of ariid genera proposed by Kailola (2004) shows *Cinetodus* and *Pachyula* (*sensu* Marceniuk & Menezes, 2007) as valid and monophyletic genera, the first including *Cinetodus froggatti* and *Cinetodus carinatus* (Weber, 1913) and the second including *Pachyula crassilabris* and *Pachyula conorhynchus* (Weber, 1913). Nonetheless, even without support from the topology of the consensus tree for the monophyly of *Cinetodus* plus *Pachyula*, Kailola recognized *Pachyula* as synonymous with *Cinetodus*. In Betancur-R (2009) the synonymy between *Pachyula* and *Cinetodus* (*sensu* Kailola, 2004) was not supported. Instead, *Pachyula* was considered sister group of *Doiichthys* plus *Nedystoma*, and *Ci. froggatti* sister species of *Neoarius midgleyi*. In the present study, the sister-species relationship between the type-species of *Cinetodus* and *Pachyula* is strongly supported by 21 synapomorphies, four of which represent a unique condition in the Ariidae: basioccipital lateral process with anterior

and posterior portions equally developed (character 76, state 0); transcapular process very short and broad (character 80, state 1); ventral surface of parapophysis of fifth and sixth vertebrae concave (character 202, state 1); and cleithrum humeral process very long (character 214, state 2). The common possession of these derived characters would justify Kailola's (2004) synonymy, but the presence of different autapomorphic features in *Cinetodus* and *Pachyula* supports their recognition as separate monospecific genera. In *Cinetodus* the upper pharyngeal tooth plate is rounded (character 188, state 0) and the dorsal process of the upper pharyngeal tooth plate very short (character 190, state 0). In *Pachyula* the first epibranchial posterior margin has a prominent process (character 174, state 1, with independent origins in *Pl. dussumieri*, *Pl. nella*, and *Pl. polystaphylodon*).

#### GENUS *COCHLEFELIS*

The monophyly of *Cochlefelis* was independently corroborated by Kailola (2004) and Marceniuk & Menezes (2007), but with a different species composition. Kailola (2004) included *Arius burmanicus* Day, 1870, in the genus, but did not use the species in her cladistic analysis, and Marceniuk & Menezes (2007) tentatively included *Arius dioctes* Kailola, 2000 and *Arius insidiator* Kailola, 2000. In spite of the conflicting species composition of the genus in both studies, *Cochlefelis* is defined only through direct examination of *Coc. danielsi* and *Coc. spatula*. The monophyletic condition of *Cochlefelis*, including *Coc. danielsi* and *Coc. spatula*, is well supported herein by 11 homoplastic synapomorphies, one of them also described by Kailola (2004): the large number of caudal vertebrae (39 or more in our counts and 32–36 according to Kailola's, probably because of a different way of counting) in comparison with the remaining ariid species (a condition independently developed in *Bagre*, see character 206). Even though *Ar. burmanicus* and *Ar. insidiator* were not included, molecular data (Betancur-R, 2009) also support the monophyly of *Cochlefelis*, excluding *Ar. dioctes*. The genus is hypothesized as the second most basal group within the Ariinae, a condition weakly supported.

#### GENUS *CRYPTARIUS*

In Kailola's (2004) consensus cladogram, *Cryptarius* is characterized as a monospecific taxon, in spite of the putative inclusion of *Hemipimelodus daugueti* Chevey, 1932, in it, a decision also taken by Marceniuk & Menezes (2007). The monospecific condition of *Cryptarius* is independently supported in the cladistic analysis of Betancur-R (2009), who considered the

type-species *C. truncatus* the basalmost species of the clade including *Ar. leptanotacanthus* Bleeker, 1849, and *Cep. borneensis*. The following three unique synapomorphies in the Ariidae herein support the monospecific condition of the genus: epioccipital posterior process contacting medial crest associated with neural spine of fourth vertebra (character 43, state 1); vomer arrow-shaped (character 47, state 3, also used by Kailola, 2004); interopercle anterior portion thin and acute (character 126, state 2); and metapterygoid articulated with a small area of quadrangle through a toothed suture and overlaying the remaining part of that bone (character 129, state 1). The inclusion of *H. daugueti* in *Cryptarius* needs confirmation through direct examination of the internal morphology of specimens. *Cryptarius* is here recognized as sister group of *Cathorops* in a more inclusive monophyletic clade represented by species of the genera *Cephalocassis*, *Cinetodus*, *Doiichthys*, *Hemiaris*, *Nedystoma*, *Nemapteryx*, and *Pachyula*, mainly found in freshwaters of South-East Asia and New Guinea and *Cathorops* in freshwaters and estuaries of the Neotropics.

#### GENERA *DOIICHTHYS* AND *NEDYSTOMA*

The sister-group relationship between the species of the monospecific genera *Doiichthys* and *Nedystoma* was pointed out by Kailola (2004) and Betancur-R (2009), despite the lack of agreement about the taxonomic status of both genera recognized as valid by Marceniuk & Menezes (2007). *Doiichthys* and *Nedystoma* are easily diagnosable, having been accepted as valid by Wongratana & Bhatia (1974) and Roberts (1978). Kailola (2004) considered *Doiichthys* as synonymous with *Nedystoma* and defined the genus through a series of external morphological characters not examined in the present study in addition to internal anatomical characters interpreted as synapomorphies in other branches of our cladogram. Previous hypotheses of relationships between the type-species of *Doiichthys* and *Nedystoma* are herein confirmed by new evidence and at least six unique synapomorphies: second basibranchial posterior portion very long and thin (character 160, state 1); third basibranchial very long and narrow (character 162, state 3); uncinat process of third epibranchial short and laterally curved (character 177, state 2); pharyngeal tooth plate long and narrow (character 188, state 2); dorsal processes of upper (pharyngeal) tooth plate connected by a bony blade (character 189, state 1); and dorsal processes of upper (pharyngeal) tooth plate very long (character 190, state 2). We believe that even though *Doiichthys* and *Nedystoma* are monospecific sister groups, their synonymy is not justifiable. *Doiichthys* is characterized by many autapomorphies: nasal bone indefinite-shaped (character 19, state 1); circumorbital series

formed by five infraorbitals (character 88, state 1); premaxilla wide and short (character 113, state 3); posterior ceratohyal very long (character 146, state 2); urohyal very long (character 150, state 2); urohyal posterolateral processes one third as long as distal portion of bone (character 155, state 4); first and second epibranchials straight throughout their entire extension (character 171, state 1); mesial portion of first epibranchial very large and depressed (character 173, state 2); and first pharyngobranchial located at mesial end of first epibranchial (character 184, state 0). *Nedystoma* is also supported by ten autapomorphies, the main ones consisting of: premaxilla anterior margin fringed (character 115, state 1); third external branchiostegal ray spatulate (character 142, state 1); and pharyngeal tooth plate very long and narrow (character 188, state 3).

#### GENERA *GENIDENS*

*Genidens* as defined by Marceniuk & Menezes (2007) is monophyletic, a condition independently found by Betancur-R (2009). The characters used by Marceniuk & Menezes (2007) to define the genus are here confirmed as synapomorphic and the subrectangular shape of the extrascapular (character 35, state 0) is indicated as a new synapomorphy of *Genidens*, hypothesized as sister group of *Potamarius*.

#### GENUS *HEMIARIUS*

Kailola (2004), considered *Hemiaris* as monophyletic including *H. dioctes* (Kailola, 2000), *H. insidiator* (Kailola, 2000), *H. stormii*, and three additional species not included in her phylogenetic analysis. Marceniuk & Menezes (2007) defined the genus based on the characters observed in *H. stormii* and *H. sumatranus*, and three species tentatively assigned to the genus of which only *Arius verrucosus* Ng, 2003, was also included in *Hemiaris* by Kailola (2004). Betancur-R (2009) recognized the type-species of *Hemiaris* as sister species of *Cep. melanochir* (type-species of *Cephalocassis*) in a clade also including *S. sagor*, type-species of *Hexanematichthys* (see comments under *Cephalocassis*). The monophyletic condition of *Hemiaris*, as defined in Marceniuk & Menezes (2007), is herein corroborated by seven homoplastic synapomorphies none of them previously described by Kailola (2004). *Hemiaris* is here considered to be the sister group of the genera represented by freshwater or estuarine species from South-East Asia, New Guinea, and the Neotropical region (see comments under *Cathorops*).

#### GENUS *NETUMA*

The monophyletic condition of *Netuma* is well supported in the studies by Kailola (2004), Marceniuk &

Menezes (2007), and Betancur-R (2009), although the species composition varies. According to Marceniuk & Menezes (2007), the genus would be represented only by *Net. bilineata* and *Net. thalassina*, whereas Kailola (2004) included *Ar. proximus* in *Netuma*. The inclusion of *Ar. proximus*, considered sister group of *G. barbatus* in Kailola's consensus cladogram, makes *Netuma* (*sensu* Kailola, 2004) paraphyletic. The following new synapomorphies supporting the monophyly of *Netuma* (*sensu* Marceniuk & Menezes, 2007) are herein included: premaxilla wide and short (character 113, state 0); second basibranchial posterior portion short and wide (character 160, state 3); anterior process of first hypobranchial on central portion of bone (character 167, state 1); and lateral face of third pharyngobranchial pointed (character 186, state 1). In addition, the following characters described by Kailola (2004) are considered synapomorphies of *Netuma*: 57 (state 1), 212 (state 3), 213 (state 2), and 228 (state 1). The phylogenetic relationship of *Ar. proximus* is uncertain. It was tentatively included in *Brustiaris* by Marceniuk & Menezes (2007), whereas in Betancur-R (2009), it was hypothesized as sister group of *Amissidens hainesi* (Kailola, 2000), in a clade with other two species of *Neoarius* (*sensu* Marceniuk & Menezes, 2007). *Netuma* is herein considered sister group of *Occidentarius* plus *Sciades*.

#### GENUS *NEMAPTERYX*

*Nemapteryx* was defined as monospecific by Marceniuk & Menezes (2007), a condition partially supported in other recent cladistic studies. Kailola (2004) recognized *Nemapteryx armiger* as sister species of *Bagre*, in a clade with members of the genera *Hemiaris* (*sensu* Kailola, 2004) and *Cochlefelis* (*sensu* Marceniuk & Menezes, 2007). Without justification, *Arius augustus* Roberts, 1978, was included by Kailola (2004) in *Nemapteryx*, making this genus paraphyletic. Betancur-R (2009) considered *Nem. armiger* as sister species of the clade in which *Pachyula* is the sister group of *Doiichthys* plus *Nedystoma* and the inclusion of *Ar. augustus* was not corroborated in his strict consensus tree topologies. Other species included in *Nemapteryx* by Kailola (2004), but not considered in her data matrix and also not examined in our and Betancur's (2009) studies, were assigned either to *Cephalocassis* or *Arius* by Marceniuk & Menezes (2007). *Nemapteryx* is herein defined by seven homoplastic autapomorphies and recognized as sister group of members of clade 55. At least in part the sister-group relationship between *Nemapteryx* and *Doiichthys* plus *Nedystoma* was supported in Betancur's (2009) work, the only difference consisting of the replacement of *Cephalocassis* by *Cinetodus* as sister species of *Doiichthys* plus *Nedystoma*.

#### GENUS *NEOARIUS*

The monophyletic condition of *Neoarius* is here supported by derived characters examined in *Neoarius graeffei* and *Neoarius midgleyi*, representing three homoplastic synapomorphies, the main one consisting of the anterior process of first hypobranchial located exactly in the middle of the bone (character 167, state 1, with independent origin in *Netuma*). *Arius augustus*, *Tachysurus (Pararius) berneyi* Whitley, 1941, and *Arius pectoralis* Kailola, 2000, putatively included in *Neoarius* by Marceniuk & Menezes (2007) were not examined herein. Kailola (2004) did not recognize *Neoarius* as valid and included all the above-mentioned species in her polyphyletic genus *Ariopsis*. The monophyly of *Neoarius* was corroborated by Betancur-R (2009), including *Neo. graeffei* and *Neo. berneyi*, but not *Ar. midgleyi* and *Ar. augustus*, but *Ar. pectoralis* was not examined. The species composition of *Neoarius* is still uncertain and the study of the species not directly examined in previous contributions will be decisive for the definition of the genus.

#### GENUS *NOTARIUS*

The monophyly, species composition, and taxonomic status of *Notarius* are very controversial. In the present study the monophyly of *Notarius* (*sensu* Marceniuk & Menezes, 2007), including *Ar. grandoculis* as its type-species, *No. lentiginosus*, and *No. troschelii* is poorly supported and the inclusion of *No. planiceps* makes the genus paraphyletic. By contrast, *Notarius* (*sensu* Betancur-R *et al.*, 2007 and Betancur-R, 2009) is more inclusive, containing the species included by Marceniuk & Menezes (2007) in *Amphiarius* and *Aspistor*. According to Betancur-R *et al.* (2007), *Notarius* is characterized by the following synapomorphies: posterior edge of cranial fontanel posteriorly limited by frontals with participation of parietosupraoccipital (herein a homoplastic condition also observed in many ariid genera, character 25, state 0); angular process of otic capsules (on pterotic) present (not observed by us); and wing-like expansions of parasphenoid present (herein interpreted as orbitosphenoid and pterosphenoid lateral expansions, a homoplastic condition also observed in many ariid genera, character 62, state 1). Kailola (2004) without even examining the type species of the genus, *Ar. grandoculis*, recognized *Notarius* as synonymous with *Hemiaris*, including in this genus six additional species from South-East Asia and New Guinea. In Betancur-R (2009), *Notarius* was hypothesized as a sister group of *Cathorops*, a condition here corroborated in part with the exclusion of the Old World genera of clade 52. The delimitation and monophyly of *Notarius* are yet to be precisely determined (see also the sections on *Amphiarius* and *Aspistor*).

GENUS *OCCIDENTARIUS*

*Occidentarius* was defined as a monospecific genus by R. Betancur-R & A. Acero P. (in Betancur-R *et al.*, 2007), supported by three autapomorphies: cavities of lateral ethmoids greatly developed, bony projection of posterolateral process of lateral ethmoids prominent, completely closing the lateral fenestrae, and basioccipital with a laminar bony crest bordering the anterior foramen of aortic tunnel. These features were herein examined and a different interpretation of the characters given. The variation observed in the remaining Ariidae does not allow us to define the first autapomorphy as a derived condition in the family. The second derived character was also observed in members of the genera *Batrachocephalus*, *Cochlefelis*, *Netuma*, *Plicofollis*, and *Sciades*, and represents a condition that becomes more evident during ontogeny (partially represented as character 17, state 0). The third autapomorphy was not observed in the clear and stained specimen examined. Despite the controversy concerning the state characters recognized as synapomorphies for the genus by R. Betancur-R & A. Acero P., *Occidentarius* is considered a valid genus, characterized by ten new homoplastic synapomorphies (see the diagnosis of the genus in the previous section). Its relationship with *Sciades* (*sensu* Marceniuk & Menezes, 2007) is herein strongly supported by unique characters within the Ariidae: temporal fossa very reduced or entirely closed during ontogenetic development (character 36, state 1, reversed in *Sciades leptaspis*); otic capsules moderately developed (character 68, state 1); subvertebral process indistinct or little differentiated (character 71, state 0); and space between transcapular process and otic capsule very wide (character 82, state 0).

GENUS *PLICOFOLLIS*

The monophyly of *Plicofollis* Kailola, 2004, is well defined and characterized on the basis of derived characters also examined in the present study. As originally proposed it included *Pl. argyropleuron* (Valenciennes, 1840), *Pl. nella*, *Pl. polystaphylodon*, *Plicofollis crossocheilos* (Bleeker, 1846) (= *Arius tonggol* Bleeker, 1846), *Pl. dussumieri*, *Plicofollis layardi* (Günther, 1866), and *Plicofollis magatensis* (Herre, 1926), but only the first three species were included in the cladistic analysis herein undertaken. Kailola (2004) uses to define the genus, among other characters not examined in the present work, the following unique synapomorphies for the Ariidae: presence of short arms on the vomer (character 50, state 1); lachrymal–antorbital bone flattened and with extremely pronounced angles (in part character 93, state 1); epioccipital invading the skull roof in some species (character 39, state 1); metapterygoid

enlarged and extending well beyond the hind margin of the quadrate (in part character 128, state 2); and elongate posterior median fontanel reduced in size with growth (character 27, state 0). The monophyly of *Plicofollis* was confirmed by Betancur-R (2009) using molecular and direct examination of *Pl. argyropleuron*, *Pl. dussumieri*, *Pl. layardi*, *Pl. nella*, *Pl. polystaphylodon*, and *Plicofollis tonggol*. New exclusive synapomorphies are herein introduced adding additional support to define the genus and justifying the inclusion of *Pl. platystomus*: anterior portion of anterior ceratohyal very thick (character 145, state 1), and urohyal posterolateral processes more than half as long as distal portion of bone (character 155, state 3). The basal position of *Pl. platystomus* is corroborated by exclusive derived characters shared with the remaining species of *Plicofollis* (except *Pl. platystomus*): orbitosphenoid and/or pterosphenoid lateral expansions slightly projected, with straight lateral margins (character 63, state 3); interopercle subrectangular (character 127, state 2); lateral face of uncinatate process of third epibranchial notched (character 178, state 1); and vomerine tooth plates entirely free (character 55, state 2). Even though the hypothesis of relationships based on molecular data derived from the examination of a larger number of species, the internal relationship of *Plicofollis* is partially corroborated herein, having *Pl. layardi* (here designated as *Pl. tenuispinis*) as the most external member of the clade including *Pl. dussumieri*, *Pl. nella*, and *Pl. polystaphylodon*. This condition is supported by the following exclusive synapomorphies shared by all the species: lateral ethmoid very expanded (character 9, state 1); vomer oval-shaped (character 47, state 2); vomerine lateral process very short (character 50, state 1); third basibranchial very short and wide (character 162, state 0); and uncinatate process of third epibranchial longer and wider than mesial portion of same bone delimited by uncinatate process (character 175, state 1). *Plicofollis* is hypothesized as sister group of the clade represented by *Batrachocephalus*, *Ketengus*, and *Osteogeneiosus* through five synapomorphies (see diagnosis of clade 40).

GENUS *POTAMARIUS*

The monophyly of this genus was corroborated by Betancur-R *et al.* (2007) and Betancur-R (2009), but with a species composition different from that of Marceniuk & Menezes (2007). In addition to *Potamarius izabalensis* and *Potamarius nelsoni* (Evermann & Goldsborough, 1902), Betancur-R *et al.* (2007) added into the genus *Potamarius usumacintae* Betancur-R & Willink, 2007, whereas Marceniuk & Menezes (2007) considered *Arius grandoculis* Steindachner, 1877, to belong in *Potamarius*. Marceniuk & Menezes' (2007)



decision is herein strongly corroborated by 16 synapomorphies, four of which are exclusive, observed in cleared and stained specimens of *Potamarius izabalensis* and *Potamarius grandoculis*: optic foramen very large (character 65, state 0); distance between the optic foramen and the trigeminofacialis foramen small, equal to width of trigeminofacialis foramen (character 66, state 0, condition shared by *Bagre* and *Galeichthys*); interopercle rectangular (character 127, state 1); and urohyal posterolateral processes not connected by a bony blade (character 152, state 1). Betancur-R *et al.* (2007) recognized two synapomorphies for *Potamarius*, including *Potamarius usumacintae*: fossa between dorsomedial limb of post-temporosupracleithrum, extrascapular and pterotic well developed (not interpreted by us as a synapomorphy for *Potamarius*, see character 37, state 1); and posterior expansion of dentary well developed (not included in our analysis, but observed only in females of *Cathorops*). The same authors also used in the diagnosis of the genus another derived character that they had apparently not seen: lateral cornu of lateral ethmoid long and paddle-shaped, directed posteriorly and forming a very acute angle with the posterolateral process of the bone (a condition here interpreted as a synapomorphy for *Potamarius*, character 12, state 2). *Potamarius usumacintae* was not included in our analysis, but preliminary observation of skeletons of this species (UMMZ 190074) revealed character states different from those here interpreted as derived for *Potamarius* (see diagnosis of clade 15): character 2 (state 1, not state 0), character 48 (state 0, not state 1), character 53 (state 1, not state 0), character 62 (state 1, not state 0); character 66 (state 1, not state 0), character 113 (state 0, not state 2), and character 128 (state 1, not state 2). The decision as to whether or not to include *Potamarius usumacintae* in *Potamarius* cannot be reached without more comprehensive examination of morphological data.

#### GENUS *POTAMOSILURUS*

*Potamosilurus* Marceniuk & Menezes, 2007, is confirmed as a valid genus but with a different species composition from that initially conceived by Marceniuk & Menezes (2007) as a result of the examination of *Hemipimelodus macrorhynchus* and *Arius latirostris*, and putative inclusion of *Arius coatesi* Kailola, 1990, *Arius robertsi* Kailola, 1990, and *Hemipimelodus velutinus*. Betancur's (2009) molecular analysis also indicated the monophyletic condition of *Potamosilurus*, with the inclusion of *Potamosilurus coatesi* and *Potamosilurus velutinus*, and the exclusion of *Ar. latirostris*. In the present study, the monophyly of this genus, including *Potamosilurus macrorhynchus* and *Potamosilurus latirostris*, is supported by three homoplastic synapomorphies and the inclusion of

*Hemipimelodus velutinus*, making *Potamosilurus* paraphyletic. This is another genus that needs to have its monophyletic condition and species composition better defined.

#### GENUS *SCIADES*

In our analysis, the Neotropical genus *Sciades* is considered monophyletic, including the species of *Ariopsis* (*sensu* Betancur-R *et al.*, 2007), and two additional species from south and South-East Asia, New Guinea, and northern Australia, *Hexanematischthys leptaspis* and *Pimelodus sagor* (type-species of *Hexanematischthys* Bleeker, 1858). As opposed to the molecular hypothesis of phylogenetic relationship proposed by Betancur-R (2009) that supports monophyly of the Old World species of Ariidae, the inclusion in *Sciades* of the species from northern Australia, southern New Guinea, south and South-East Asia, and the Americas suggests a common origin of species presently with disjunct geographical distributions. *Sciades* is represented by species essentially found in marine waters that have a very heavy and compact skull with very reduced or even absent fenestrae and fontanels on the dorsal portion. Its monophyletic condition and synonymy are supported by three homoplastic synapomorphies: posterior cranial fontanel absent (character 26, state 0, convergent in *Batrachcephalus*); epiphyseal bar indistinct (character 28, state 1, convergent in *Batrachcephalus*); and exoccipital posterior process sutured to the Müllerian ramus (character 86, state 1, convergent in *Potamarius izabalensis*). According to Betancur-R *et al.* (2007) *Ariopsis* is valid and its monophyly supported by only one synapomorphy: extrascapular subrounded (herein considered a very homoplastic feature in the Ariidae, character 35, state 1). The characterization of *Sciades* by Betancur-R *et al.* (2007) was based on four synapomorphies that do not apply to our branch 28 (= *Sciades sensu* Betancur-R *et al.*, 2007): anterior laminar expansion of frontals covering lateral fenestra present (herein observed also in *Batrachcephalus*, *Cochlefelis*, *Netuma*, *Occidentarius*, and *Plicofollis*, character 17, state 0); posterior portion of supraoccipital process only with endochondral components (not examined); middle nuchal plate overlapping the supraoccipital process (also observed in *Aspistor* and *Notarius* in part, character 210); granulations on cranial surface numerous and blunt (condition herein interpreted as synapomorphic for the Ariinae, character 33, state 1); anterodorsal bony block of orbitosphenoid present and developed (present in several genera within the Ariinae, character 24, state 1), with posterior limbs of mesethmoid not surpassing its posterior end (not examined). As here defined, the species included in *Ariopsis* in part (*sensu* Betancur-R *et al.*, 2007) occupy a basal position in relation to the

species included in *Sciades* (*sensu* Betancur-R *et al.*, 2007) but do not represent a monophyletic group, whereas *Sciades* (*sensu* Betancur-R *et al.*, 2007) is monophyletic (branch 28), a condition corroborated by three exclusive synapomorphies in the Ariidae: premaxilla lateral margin deeply concave (character 116, state 2); sesamoid bone I very long and subrectangular (character 138, state 3); and sesamoid bone II irregularly elongate (character 139, state 1). Here the sister-group relationship between *Occidentarius* and *Sciades* (*sensu* Marceñiuk & Menezes, 2007) is strongly supported (see comments under *Occidentarius*).

### CONCLUSION

A more accurate systematic definition of ariid genera, its limits, and species composition has challenged ichthyologists for many years. The group is widely distributed, represented in all land masses of the world, including fossil records in Africa (six), America (five), Asia (one), and Europe (six), and has species living in coastal marine, estuarine, and fresh waters, as well as the deep sea. Large collections containing representatives of all the members are difficult to assemble, and for this reason regional studies prevailed during the 20<sup>th</sup> century, leading to the imprecise delimitation of genera, characterization and definition of nominal species and taxa, and recognition of useful features for phylogenetic reconstruction. During the last decade, more inclusive studies using the cladistic approach (Marceñiuk, 2003; Kailola, 2004; Betancur-R *et al.*, 2007; Betancur-R, 2009) have greatly contributed to increasing the knowledge of the systematics, relationships, and evolution of the Ariidae.

In the present contribution, new evidence has been presented to support previous hypotheses and to bring new insights into the controversial issue of comparing morphological vs. molecular data (Scotland, Olmstead & Bennett, 2003; Wiens, 2004). New synapomorphies have been discovered to corroborate the monophyly of the Ariidae and to propose a new hypothesis of relationships for *Bagre* (subfamily Bagreinae) and a new phylogenetic definition of the Ariinae. The relationships of basal ariid genera are usually poorly supported, and the evolution of independent lineages because of the occupation of similar environments in different parts of the world may have generated morphological convergence of characters, making the evaluation of relationships in some of the genera confusing.

One of the most important results of this study is the redefinition of the problematical genus *Arius*, always considered as the box where species that fit nowhere else in the recognized genera have been included, making it an ill-defined and artificial genus. It is herein characterized by exclusive features shared

by a more reduced number of species and considered a monophyletic taxon with distribution limited to eastern Africa, western Madagascar, and southern and South-East Asia. Other genera are defined under the same criteria, but much more work is needed to allocate the known ariid species into their proper generic categories, especially those that were not examined and putatively assigned only on the basis of literature information in Kailola (2004) and Marceñiuk & Menezes (2007). In this regard the genera *Cephalocassis*, *Hemiaris*, *Notarius*, *Potamosilurus*, and *Sciades* need to be better characterized, in view of the conflicting results obtained by morphological and molecular studies. Perhaps the combined evidence from both molecular and morphological studies would contribute to better and more stable generic definitions. In this respect, a phylogenetic comparison of molecular and morphological data sets would be helpful, but this approach is beyond the scope of the present work. However, considering that taxonomy and systematics primarily rely on morphological information, we believe that the results herein obtained will improve the knowledge of the group.

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APPENDIX 1  
CHARACTER STATE MATRIX

*Outgroup***Ancharidae**

010-000001	0-12---000	0010011000	1000001000	---1011010
000--0----	00--20000-	0---0--000	000----2-0	0110200100
0-010111-0	010001-104	0100000000	00110100-0	0000000110
00000000-2	---0000000	0000001000	01--0-1100	0-010--000
-002011000	0001010010	0000000--0		

**Austroglanididae**

000-000001	0-12---000	00-0011001	--000---00	---1011110
000--0----	00-0-0000-	0---0--000	000----2-1	0110-10100
0-010110-0	000000-104	0000000-00	0111001--0	1000000010
0----000--	0-00-000-0	0001000000	01--0-1100	0-010-0000
-001010-00	0002000001	0000000---		

**Bagridae**

100-00000-	--12---000	0000011001	--100---00	---0001010
001000----	010000000-	0---0--000	000----1-0	0110010100
0-010010-0	000000-100	00000-0200	001011-0-1	0000000001
0----000-2	1--0000000	0000010000	00000-1100	0-010-0000
-001010-00	000-000001	0000000---		

**Cetopsidae**

000-00-001	0--1---000	-000011001	--00----00	---1011-10
001-00----	00-0--000-	0---0--000	000----2--	---03-0020
0-010010-0	000000-10-	000-00020-	--11001--0	0010001000
0----000-2	0--0000000	000000-000	00000-2100	0-010-0000
-00201--00	0-----01	0000000---		

**Claroteidae**

000-000001	0-12---000	0010110001	--000---00	---1011110
0010010000	010000000-	0---0--000	001--002-1	0110210100
0-010111-0	010000-104	0100000-00	01---1-0-0	0000010110
00000000-2	---0-000-0	0000000000	00000-1100	0-010-0000
-002010-00	0000010000	0000000---		

**Cranoglanididae**

000-00-001	1112---000	0010-10000	1010-1--00	---1011110
000--0----	00-000000-	0---0--000	000----2-0	0110010100
0-010010-0	000000-100	0000010200	010-101--0	0000000000
0----000-2	---0000000	0000010000	01--0-1100	0-010-0000
-0-2--0-00	0212010001	0000000---		

**Diplomystidae**

000-001000	---1---000	-000011001	--000---00	----01000-
-01100----	10-1--000-	0---0--000	000----0--	---0--00-0
0-010010-0	000000-100	00000002-0	0110001--0	1000001000
0----000-2	1--0000000	0000010000	00000-11--	0-010-0000
-003010-0-	0001000001	10001-0---		

APPENDIX 1 *Continued**Outgroup***Doradidae**

000-00000-	---1---000	00-0-0-1-1	--10-1--11	0-01001010
000--0----	00-000000-	0---100010	000----300	0110010100
0-010010-0	000000-100	0000010001	--11101--0	1000000000
0----0-0--	---0100010	0000000000	01--0-1100	0-0-0-0000
-001010-0-	000201000-	0000000--0		

**Heptapteridae**

100-000001	0-12---000	0000-0-001	--100---00	---1011---
001000----	0100-0000-	0---0--000	00----300	0110010100
0-010010-0	000000-104	0100010100	000-100--0	1000000001
0----000-2	---0000000	00000-0000	01--0-1100	0-011-0000
-002010-00	000----10-	0000000---		

**Horabagridae**

010-000001	0012---000	0010-0---1	---00---00	---1011010
001000----	00-0-0010-	0---0--000	000----2-0	0110200100
0-010010-0	001000-10-	0000001200	0011010--0	0000010001
0----000--	---0000000	0001010000	00000-1100	0-011-0000
-001010-00	0321000001	00000000--		

**Ictaluridae**

120-000001	0-12---000	0000011001	---00---00	---1011010
000--0----	00-000000-	0---0--000	000----1-0	0110010100
0-010010-0	000000-100	0000000-00	0110101--1	0000000000
0----000-2	1--0000000	0000000000	01--0-1100	0-010-0000
-002010-00	0211010001	0000000---		

**Mochokidae**

0-0-000001	0--1---000	0000112001	--10-1--00	---1001010
000--0----	00-000000-	0---100010	00----300	0110010100
0-010010-0	000000-100	00000101-1	--1110--0	0000000001
0----000--	---0100010	00-0000000	01--0-1100	0-010-0000
-001010-0-	000----101	0000000--0		

**Pangasiidae**

020-000001	0-13101000	0110011001	--000---01	0-01011010
0010010000	00-000000-	0---0--000	001--002-1	0110210100
0-010010-0	001000-104	0000000-00	01110000-0	0000000000
0----000--	1--0000000	0000001000	00000-1100	0-010-0000
-001010-00	0321100001	00000101-0		

**Schilbeidae**

020-00010-	--13101000	0111011001	--000---01	0-01011010
0010010000	010000000-	0---0--000	001--002-1	0110210100
0-010011-0	002000-104	000000-200	01100000-0	0000000001
0----000-2	---0000000	0000011000	00000-1100	0-010-0000
-001010-0-	0321000001	0000000---		



APPENDIX 1 *Continued**Ingroup**Amphiarius phrygiatus*

110-000001	0103212000	1001012011	--10101001	1001011110
100--10500	0111110211	1120110110	02003--301	0100210100
0102011110	0110010001	0101000100	0011010101	0000000101
0010000112	11-0000000	0000011010	1001101101	1011101110
0001011001	0111010010	1000000001		

*Amphiarius rugispinis*

110-000001	0103212000	1001012011	--10101011	1001011110
100--10500	0111110211	1120110110	02003--301	0100210100
0102011110	0110010001	0101000100	0011010101	0000000101
0010000112	11-0000000	0000011010	1001101101	1011101110
0001011001	0111010010	1000000001		

*Arius arius*

100-000001	1203001000	1001011010	1010001001	1201001110
000--10411	0120110211	1000110000	0110101301	0100210100
1102011110	0110011001	0101000100	0011010101	0000000101
0010200112	11-0000001	0000011010	1001111101	1100020110
000-111001	1211010010	1000000111		

*Arius caelatus*

110-000001	1003001000	1001-11000	1010001001	1201001110
000--10200	0100110211	1000110000	0110101301	0100210100
-102011110	0110011001	0-01000100	0011010100	0000000101
0010200112	11-000000-	0000011010	1001111101	1100020110
0000111001	1211010010	1000000111		

*Arius dispar*

1-0-000001	1203001000	1001011000	1010001001	1201001110
000--10211	0120110211	1000110000	0110101301	0100210100
1102011110	0110011001	0101000100	0011010101	0000000101
0010200112	11-0000000	0000011010	10011-1101	1100020110
0000111001	0211010010	1000000111		

*Arius gagora*

100-000001	1203001000	1001011010	1010001001	1201001110
000--10411	0120110211	1000110100	0110101301	0100210100
1102011110	0110011001	0101000100	0011010101	0000000101
0010200114	11-0000001	0000011010	10011-1101	1-00020110
0000111001	0211010010	1000000111		

*Arius maculatus*

110-000001	1203001000	1001011000	1010001001	1201001110
000--10200	0120110211	1000110000	0110101301	0100210100
1102011110	0110011001	0101000100	0011010-0-	0000000101
0010-00114	11-0000001	0000011010	10011-1101	1100020110
0000111001	1211010010	1000000111		

APPENDIX 1 *Continued**Ingroup**Arius madagascariensis*

100-000001	1203001000	1001011000	1010001001	1201001110
000--10411	0100110211	1000110100	0110101301	0100210100
1102011110	0110011001	0101000100	0011010101	0000000101
0010200112	11-0000000	0000011010	1001111101	1100020110
0000111001	1211010010	1000000111		

*Arius manillensis*

100-000001	1203001000	1001011000	1010001001	1201001110
000--10411	0120110211	1000110100	0110101301	0100210100
1102011110	0110011001	0101000100	0011010101	0000000101
0010200112	11-0000000	0000011010	1001111101	1100020110
0000111001	0211010010	1000000111		

*Aspistor luniscutis*

110-000001	0103011000	1001012011	--10101011	1001111110
0013010411	0111110211	1120110110	01003--301	0100210100
0102011110	0110010001	0101000100	0011010201	0000000111
0010210114	11-0000000	0000011010	1001101101	1001001110
0001111212	0111000010	1000000001		

*Aspistor quadriscutis*

110-000001	0103011000	1001012011	--10101011	1001111110
0013010411	0111110211	1120110110	01003--301	0100210100
0102011110	0110010001	0101000100	0011010201	0000000111
0010210114	11-0000000	0000011010	1001101101	1001001110
0001111212	0111000010	1000000001		

*Bagre bagre*

020-010101	1003101000	1111110000	1000001001	1001011010
0010010000	0110100210	1010110100	0110100312	2101-21100
0000101110	0100011000	0100000000	010-010100	0000010101
1010100102	0110000000	0100011010	1001101101	10111001-0
001-100000	1321100010	1001010101		

*Bagre marinus*

020-010101	1003101000	1111110000	1000001001	1001011010
0010010000	0110100210	1010110100	0110100312	2101-21100
0000101110	0100011000	0100000000	010-010100	0000010101
1010100102	0110000000	0100011010	1001101101	1011100110
0010101000	1321100010	1001010101		

*Bagre panamensis*

020-000101	0003101000	1111110000	0000000001	1001011010
0010010000	0110100210	1010110100	0110100312	2101-21100
0000101110	0100011000	0000000000	010-010000	0000010101
1011100102	0110000000	0100011010	1001101101	1011100110
0010101000	0321100010	1001010101		

APPENDIX 1 *Continued**Ingroup**Bagre pinnimaculatus*

020-010101	0003101000	1111110000	0000000001	1001011010
0010010000	0110100210	1010110100	0110100312	2101-21100
0000101110	0100011000	0100000000	010-010100	0000010101
1010100102	0110000000	0100011010	1001101101	10111001-0
0010101000	1321100010	1001010101		

*Batrachocephalus mino*

-20-000000	--13000120	1010-0-1-0	1010001001	1101001010
000--10312	00-0110211	1120110000	0210101301	2103-03021
2122021112	0110011013	0100000301	--11011--0	1001011101
0000200102	12-0000000	0000011011	1001102101	1110010110
0000011001	0211000010	101-000101		

*Brustiarius nox*

120-000001	0003101000	1011110000	1010000001	1201001010
1012010100	0101110210	1000110000	0111000301	0100310100
0101011110	0101010001	0100000100	0010010000	0000010101
0011000102	0100000001	0000011010	1001111101	1100020110
0000011001	0321000010	1000000011		

*Brustiarius solidus*

120-000001	0003101000	1011110000	1010000001	1201001010
1012010100	0101110210	1000110000	0111000301	0100310100
0101011110	0101010001	0100000100	0010010000	0000010101
0011000102	0100000001	0000011010	1001111101	1100020110
0000111001	0321000010	1000000011		

*Carlarius latiscutatus*

120-000001	1103001000	1011111000	1010101011	1201001010
100--10200	0100110210	1000110000	0111001301	0100210100
0102011110	0110011001	0001000100	0010010000	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Carlarius heudelotii*

120-000001	1103001000	1011111000	1010101011	1201001010
100--10200	0100110210	1000110000	0111001301	0100010100
0102011110	0110011001	0101000100	0010010000	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Carlarius parkii*

120-000001	1103001000	1011111000	1010101011	1201001010
100--10200	0100110210	1000110000	0111001301	0100210100
0102011110	0110010001	0001000100	0010010000	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

APPENDIX 1 *Continued**Ingroup**Cathorops agassizii*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cathorops arenatus*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cathorops dasycephalus*

100-011001	1103212000	1001011000	1010200001	1101011010
1011010300	0100111212	1131111110	1210200301	0100210100
0102011110	0120010002	1111100100	2011110101	1010-01111
0000200112	0100000000	0000011010	1011101101	1011100110
1001011001	0311010010	1000000001		

*Cathorops fuerthii*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cathorops hypophthalmus*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cathorops multiradiatus*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cathorops spixii*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

APPENDIX 1 *Continued**Ingroup**Cathorops tuyra*

1010111201	1103212000	1001110000	1010200101	1101011010
100--10310	0110111212	1131111110	1210200301	0100210100
0102011211	0120010002	1111100200	2011110101	1010-01111
0000200112	0100110010	0000011010	1001102101	1011100111
1001011001	0310011010	1000000001		

*Cephalocassis borneensis*

100-011001	0103212000	1000013011	--11100-01	1101011110
100--0----	00-0210211	1130110000	0210100301	0100210100
0102011100	0120010002	0101010200	0010110101	1000000111
0000200102	0100110010	0000001011	1001101101	1001001110
1001011001	0110011010	1000000101		

*Cephalocassis melanochir*

100-011001	0103212000	1000013011	--11101001	1000011110
100--10300	00-0210211	11300--000	0210100301	0100210100
0102011100	0120010001	0101010200	0010110101	1000000101
0010000102	0100110010	0000001011	1001101101	1001001110
0001011001	0110011010	1000000001		

*Cinetodus froggatti*

000-000001	1103101000	101101-001	--10201011	1001011110
000--10-00	0100110211	1120100011	0210100301	0100210100
0102011110	0120010000	0101000200	1010010101	0000000101
0000200102	11-0000000	0000001010	10-1101000	1011100110
0101011001	0112000010	1000000001		

*Cochlefelis danielsi*

120-000001	0003100000	1011011000	0010101001	1201001010
1011010000	0111110210	1000110000	0111000301	0100310100
0101011110	0100011004	0100000100	1010010000	0000010101
0011000102	0200000000	0000011000	1001101101	1100020110
0010101001	0211000010	1000000011		

*Cochlefelis spatula*

120-000001	0103100000	1011011000	0010101001	1201001010
1011010000	0111110210	1000110000	0111000301	0100310100
0101011110	0100011004	0100000100	1010010000	0000010101
0011000102	0200000000	0000011000	1001101101	1100020110
0010101001	0211000010	1000000011		

*Cryptarius truncatus*

010-000001	0103112000	1000011000	1010100001	1011003010
100--10300	00-0110211	1120110110	0210100301	0100210100
0102011100	0110010002	0101020210	2010010101	1010-00101
0010000100	11-0100000	0000011010	1011101101	1010100110
0001011001	0311011010	1000000001		

APPENDIX 1 *Continued**Ingroup**Doiichthys novaeguineae*

020-011001	020311201-	-000013011	--10101001	1100001010
100--10300	00-0210211	1130110100	01101001--	0-00210110
0100011110	0130010001	0101010000	0010010100	0000020102
1010400111	0300110010	1020002011	10000-2212	1000000110
0001011001	02-0011010	1000000001		

*Galeichthys ater*

010-000001	0003101000	1000110000	0000000001	0-00001010
0010010000	010010020-	10000--010	0111000301	0000110100
0001000110	1100010000	0000000000	000-010000	1000000110
0000000100	0200000000	0110001000	11--100101	0-000--000
-001010000	011---0110	10000000-0		

*Galeichthys feliceps*

010-000001	0003101000	1000110000	0000000001	0-00001010
0010010000	010010020-	10000--010	0111000301	0000110100
0001000110	1100010000	0000000000	000-010000	1000000110
0000000100	0200000000	0110001000	11--100101	0-000--000
-001010000	011---0110	10000000-0		

*Genidens barbatus*

110-000001	1103001000	1011110000	1010000001	1201001010
1011112-00	1100110210	1000110000	0111001301	0100010100
0102011100	0110010001	0001000100	0010010101	0000000101
0000200103	0100000000	0000011010	1001101101	1100020110
0010111001	0211010010	1000000011		

*Genidens genidens*

110-000001	1103001000	1011110000	1010000001	1201001010
100--12-00	1100110210	1000110000	0111001301	0100010100
0102011100	0110010001	0001000100	0010010101	0000000101
0000200103	0100000000	0000011010	1001101101	1100020110
0010111001	0211010010	1000000011		

*Genidens machadoi*

110-000001	1103001000	1011110000	1010000001	1201001010
1011110200	1100110210	1000110000	0111001301	0100010100
0102011100	0110010001	0001000100	0010010101	0000000101
0000200103	0100000000	0000011010	1001101101	1100020110
0010111001	0211010010	1000000011		

*Hemiarius stormii*

110-000001	0103212000	1001012011	--10101001	1001011010
1011010300	0111110211	1130110000	0110100301	0100210100
0102011110	0110011001	0101000100	0011010101	0000000101
0010000112	11-0000000	0000001010	1001101101	1011100110
0001011001	0110011010	1000000001		

APPENDIX 1 *Continued**Ingroup**Hemiaris sumatranus*

110-000001	0103212000	1001012011	--10101001	1001011010
1011010300	0111110211	1130110000	0110100301	0100210100
0102011110	0110011001	0101000100	0011010101	0000000101
0010000112	11-0000000	0000011010	1001101101	1011100110
0001011001	0110011010	1000000-01		

*Ketengus typus*

0011111000	---0---100	1010011000	1010001001	110100000-
-00--0----	00-0110211	1120110000	0210101301	3103-03021
2122021122	011001-114	0000000301	--11111--0	1000000111
0000201---	---1---1-0	0100011011	10010-2101	1-10010110
0001011001	0211010010	1000000101		

*Nedystoma dayi*

110-011001	0103112000	1000013011	--10101001	1100011010
100--0----	00-0210211	1130110100	0110100301	0100210110
0102011110	0110110000	0101010100	0011010101	1100000101
0010200111	0300110011	0000002011	1001112312	1011000110
0001011001	0210011010	1000000001		

*Nemapteryx armiger*

110-011201	0103112000	1000013010	1010101001	1101011010
0011010-00	00-0210211	1130110110	0210100301	0100210100
0101011110	0110011001	0101000100	0010010101	0000000101
0010200112	0100000000	0000011010	1001101101	1011000110
0001011001	0210011010	1000000001		

*Neoarius graeffei*

110-000001	1103101000	1011011000	1010101001	1201001010
1011010000	0100110210	1000110000	0111001301	0100310100
0101011110	0110010001	0100000100	0010010000	0000000101
0011000102	0100001000	0000011010	1001111101	1100020110
0010111001	0211000010	1000000011		

*Neoarius midgleyi*

110-000001	1103101000	1011011000	1010101001	1201001010
1011010000	0100110210	1000110000	0111001301	0100310100
0101011110	0110010001	0100000100	0010010000	0000000101
0011000102	0100001000	0000011010	1001111101	1100020110
0010111001	0211000010	1000000011		

*Netuma bilineata*

110-000001	1113000000	1011110000	1010100-01	1201001010
1011011200	0100110210	1000110000	0111001301	0100210100
0102011110	0100011001	0101000100	001-010000	0000000101
0011000113	11-0001000	0000011010	1001111101	1100020110
0010111001	0321000010	1000000111		

APPENDIX 1 *Continued**Ingroup**Netuma thalassina*

-10-000001	1113000000	1011110000	1010101001	1201001010
1011011200	0100110210	1000110000	0111001301	0100010100
0102011110	0100011001	0101000100	0010010000	0000000101
0010200113	11-0001000	0000011010	1001111101	1100020110
0010111001	0321000010	1000000111		

*Notarius grandicassis*

-10-000001	0103001000	1011011011	--10101001	1002001110
1011010200	0111110211	1120110110	01003--301	0100210100
0102011110	0110010001	0100000100	0011010200	0000000111
0010000112	0100000000	0000011010	1001101101	1000001110
0010111001	0111000010	1000000001		

*Notarius lentiginosus*

110-000001	0103001000	1011011011	--10101001	1001001110
1011010200	0111110211	1120110110	01003--301	0100210100
0102011110	0110010001	0100000100	0011010200	0000000111
0010000112	0100000000	0000011010	1001101101	1000001110
0010111001	0111000010	1000000001		

*Notarius planiceps*

110-000001	0103001000	1011011010	0010101001	1001001010
0011010200	0101110211	1120110110	011--00301	0100210100
0102011110	0110010001	0100000100	0011010201	0000000101
0010000112	0100000000	0000011010	1001101101	10101-1110
00-0111001	0111000010	10000000-1		

*Notarius troschelii*

110-000001	-103001000	1011011011	--10101001	1001001110
1011010200	0111110211	1120110110	01003--301	0100210100
0102011110	0110010001	0-00000100	0011010200	0000000111
0010000112	0100000000	0000011010	1001101101	1000001110
0010111002	0111000010	1000000001		

*Occidentarius platypogon*

110-000001	1113000000	1011110000	111011--01	1001011010
0011010200	0100110110	0-00110000	001100-301	0100010100
0102011110	0110010001	0001000100	0010010101	0000000111
0010000112	11-0000000	0000011010	1001101101	1011100110
0010111001	0211000010	10000000-1		

*Osteogeneiosus militaris*

-00-000000	--13002001	0001111000	1010001001	1101001110
010--10411	00-0110211	1120110000	0210101301	1102-32100
0112002110	0110010001	0101000401	--11010200	0000000100
0000200112	0100000001	0000011010	1001101101	1-10020110
0000111001	0211010010	10001-0111		



APPENDIX 1 *Continued**Ingroup**Pachyula crassilabris*

000-000001	1103101000	1011011001	--10-01011	1101011110
000--0----	0100110211	1120100011	0210100301	0100210100
0102011110	0110010002	0101000200	1010010101	0000000101
0000200102	11-0000000	0001001010	1011101101	1011100110
0101011001	0112000010	1000000001		

*Plicofollis dussumieri*

110-000011	1213000000	1011110000	1010001011	1201002111
0111210411	0131110211	1000110000	0110101301	0110010100
1102011110	0110010001	1011102200	1010010001	0000100101
0000300114	10-0000001	0001111110	1011111101	1100020110
0010111001	0321010010	1000000111		

*Plicofollis nella*

110-000011	1213000000	1011110000	1010001011	1201002111
0111210411	0131110211	1000110000	0110101301	0110010100
1102011110	0110010001	1011102200	1010010001	0000100101
0000300114	10-0000001	0001111110	1011111101	1100020110
0010111001	0321010010	1000000111		

*Plicofollis platystomus*

110-000001	0113000000	1011111000	1010001001	1101001110
000--10411	0101110211	1000110100	0110101301	0100010100
1102011110	0110010001	0100000200	1011010001	0000100101
0010300114	0100000000	0000011010	1001111101	1000010110
0000111001	0211010010	1000000111		

*Plicofollis polystaphylodon*

110-000011	1213000000	1011110000	1010001011	1201002111
0111210411	0131110211	1000110000	0110101301	0110010100
1102011110	0110010001	1011102200	1010010001	0000100101
0000300114	10-0000001	0001111110	1011111101	1100020110
0010111001	0321010010	1000000111		

*Plicofollis tenuispinis*

110-000001	0013000000	1011110000	1010001001	1101001110
0011210411	0131110211	1000110000	0110100301	0110010100
1102011110	0110010001	1011102200	1010010001	0000101101
0000300114	0100000001	0001011110	1011111101	1000010110
0010111001	0321010010	1000000111		

*Potamarius izabalensis*

100-000001	1203001000	1001111000	1010101001	1001001110
100--0----	00-0000210	1000110000	011101-301	0100310100
0102011110	0120010001	0101001200	1010010101	0000000101
0110100102	0200000000	0000011010	1001101101	1000000110
0000111001	0211010010	1000000001		

APPENDIX 1 *Continued**Ingroup**Potamarius grandoculis*

100-000001	1203001000	1001111000	1010001001	1201001110
100--10-0-	00-0000210	1000110000	0111001301	0100310100
0102011110	0120010001	0101001200	1010010101	0000000101
0110100102	0200000000	0000011010	10010-1101	1100020110
0000111001	0211010010	1000000011		

*Potamosilurus latirostris*

110-000001	1103001000	1001012011	--10101001	1201001010
0011010000	0110110211	1000110100	0111001301	0100210100
0102011110	0110010001	0101000100	1011010001	0000000101
0010000102	0100000001	0000001010	1001111101	1100020110
0000111001	0211000010	1000000011		

*Potamosilurus macrorhynchus*

-10-000001	0103001000	1011011000	1010101001	1201001110
00110-----	0110110211	1000110000	0111001301	0100210100
0102011110	0110010001	0101000100	1011010001	0000000101
0010000112	0100000001	0000001010	1001111101	1100020110
0000-11001	0211000010	1000000011		

*Potamosilurus velutinus*

110-000001	1103001000	1011011000	1010001001	1201001010
000--0----	0100110211	1000110000	0111001301	0100210100
0102011110	0110011001	0101000100	001101000-	0000000101
0010000112	0100000001	0000011010	1001111101	1100020110
0000111001	0211010010	1000000011		

*Sciades assimilis*

110-000001	1113000000	1011-0-1-0	111011--01	1201001010
0011010200	0100110110	0-0-110000	001101-301	0100210100
0102011110	0110010001	0001000100	0010010101	0000000101
0010000112	11-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades bonillai*

110-000001	1113000000	1011-0-1-0	111011--01	1201001010
0011010200	0100110110	0-0-110000	001101-301	0100210100
0102011110	0110010001	0001000100	0010010001	0000000101
0010000112	11-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades couma*

120-000001	1113000000	1011-0-1-0	021011--01	1201001010
0011010200	0101110110	0-0-110000	001101-301	0100210110
0112011110	0110020001	0101000100	0010010311	0000000101
0010000112	11-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1100000111		

APPENDIX 1 *Continued**Ingroup**Sciades felis*

110-000001	1113000000	1011-0-1-0	111011--01	1201001010
0011010200	0100110110	0-0-110000	001101-301	0100210100
0102011110	0110010001	0101000100	0010010001	0000000101
0010000112	11-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades guatemalensis*

120-000001	1113000000	1011-0-1-0	021011--01	1201001010
0011010000	0100110110	0-0-110000	001101-301	0100210110
0112011110	0110010001	0001000100	0010010101	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades herzbergii*

120-000001	1113000000	1011-0-1-0	021011--01	1201001010
0011010200	0101110110	0-0-110000	001101-301	0100210110
0112011110	0110020001	0001000100	0010010311	0000000101
0010000112	11-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1100000011		

*Sciades leptaspis*

120-000001	1113000000	1011-0-1-0	0210101001	1201001010
0011010000	0100110110	0-0-110000	001101-301	0100210110
0112011110	0110010001	0001000100	0010010101	0000000101
0010000112	-1-0000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades parkeri*

-20-000001	0013000000	1011-0-1-0	111011--01	1201001010
0011010200	0111110110	0-0-110000	001101-301	0100210110
0112011110	0110020004	0001000100	0010010310	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111102	0211000010	1000001011		

*Sciades passany*

120-000001	0013000000	1011-0-1-0	021011--01	1201001010
0011010-00	0111110110	0-0-110000	001101-301	0100210110
0112011110	0110020004	0000000100	0010010310	00000-0101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	02110-0010	1100000011		

*Sciades proops*

-20-000001	0013000000	1011-0-1-0	111011--01	1201101010
0011010200	0111110110	0-0-110000	001101-301	0000210110
0112011110	0110020004	0000000100	0010010310	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111122	0211000010	1000001011		

APPENDIX 1 *Continued**Ingroup**Sciades sagor*

110-000001	1113000000	1011-0-1-0	111011--01	1201001010
0011010200	0100110110	0-0-110000	00110--301	0100210110
0112011110	0110010001	0001000100	0010010101	0000000101
0010000112	0100000000	0000011010	1001101101	1100020110
0010111001	0211000010	1000000011		

*Sciades seemanni*

110-000001	1113000000	1011-0-1-0	111011--01	1201001010
0011010200	0100110110	0-0-110000	001101-301	0100210110
0112011110	0110010001	0001000100	0010010101	0000000101
0010000112	11-00000000	0000011010	1001101101	1100020110
00-0111001	0211000010	1000000011		

## APPENDIX 2

## MATERIAL EXAMINED

The families, genera, and species are in alphabetical order. The species name and author is followed by an institutional catalogue number, the number of specimens preserved in alcohol (AL), the number of specimens cleared and counterstained for bone and cartilage (CS), and the skeletal material (SK). The number of specimens examined does not necessarily correspond to the total number of specimens in the respective lot.

*Anchariidae*

*Ancharius fuscus* (Steindachner, 1880) – MNHN 1960-237 (1 CS), Madagascar, Ranamafano.

*Ariidae*

*Amphiarius phrygiatus* (Valenciennes, 1840) – USNM 233474 (4 AL and 1 CS), Venezuela, Territorio Federal delta Amacuro, Orinoco River, deep river channel, brazo imataca near Curiapo, 60 nautical miles upstream from sea buoy.

*Amphiarius rugispinis* (Valenciennes, 1840) – FMNH 52852 (4 AL), Guyana, Georgetown Market; MZUSP 87695 (1 CS), Brazil, Maranhão, Ilha de São Luís, Estreito de Coqueiro; MZUSP 25170 (1 AL), Brazil, Pará, Vigia.

*Arius arius* (Hamilton, 1822) – ANSP 60717 (1 AL) Thailand, Bangkok, Siam; ANSP 106800 (4 AL) Baram, North Borneo, Indonesia; CAS 131523 (4 AL and 1 CS), India, Karalla state, Kozhichode, Calicut, research station; LACM 38129-95 (3 AL and 1 SC), Pakistan, Sind, west-north-west of mouth of Korangi.

*Arius caelatus* Valenciennes, 1840 – ANSP 60690 (5 AL and 1 CS), Thailand, Bangkok, Siam; CAS 63619

(5 AL), Thailand, Gulf of Thailand, fishing grounds off Chol Buri City, from Chol Buri market; FMNH 23373 (2 AL), Malaysia, Sabah, Sandakan; LACM 38132-64 (3 AL and 1 CS), Pakistan, Sind, mouth of Turshian Creek, 4 km off Sul, near mouth of Khobar Creek; UMMZ 208844 (3 AL and 1 CS), Bangladesh, Chittagong, Bay of Bengal, just off Kutubdia Island.

*Arius dispar* Herre, 1926 – CAS 127666 (8 AL and 1 CS), Philippines, Rizal Laguna, Luzon Island, Laguna de Bay.

*Arius gogora* (Hamilton, 1822) – UMMZ 187892 (4 AL and 1 CS), Bangladesh, Comilla, River Meghna, Chandpu.

*Arius maculatus* (Thunberg, 1792) – USNM 297128 (5 AL and 1 CS), Sri Lanka, eastern province, Batticaloa district, Batticaloa, tidal lagoon opposite government rest house.

*Arius madagascariensis* Vaillant, 1894 – AMNH 88075 (4 AL and 1 CS), Malagasy Republic, Madagascar, Antsirabe market, from river Tsiribihina.

*Arius manillensis* Valenciennes, 1840 – CAS 138201 (15 AL and 1 CS), Philippines, Rizal province (prov.) Luzon Island Tagig; USNM 138384 (2, 150–223 mm total length), Philippine, San Rogue market, Cavite.

*Aspistor luniscutis* (Valenciennes, 1840) – MZUSP 87696 (3 AL and 1 CS), Brazil, coast of São Paulo; MZUSP 51723 (3 AL), Brazil, Bahia, rio Peruipe, port of Viçosa; MZUSP 51689 (3 SK), Brazil, Paraná, Baía de Paranaguá; MZUSP 51690 (1 SK), Brazil, coast of the São Paulo state; MZUSP 61342 (3 AL), Brazil, Bahia, Caravelas, estuary and mouth of rio Caravelas.

*Aspistor quadriscutis* (Valenciennes, 1840) – FMNH 52850 (5 AL), Guyana, Georgetown Market; MZUSP 87697 (1 CS), Brazil, Sergipe; MZUSP 87698 (1 CS), Brazil, Sergipe; MZUSP 52840 (1 AL), Brazil, Maranhão, São Luís, ilha de São Luís, rio Curuca.

*Bagre bagre* (Linnaeus, 1766) – MZUSP 22691 (3 AL and 1 CS), Brazil, São Paulo, Santos; MZUSP 35843 (2 AL and 1 CS), Brazil, São Paulo, Guarujá, Perequê; MZUSP 51696 (2 SK), Brazil, Espírito Santo, near rio Doce; MZUSP 51697 (1 SK), Brazil, coast of São Paulo; MZUSP 61339 (3 AL), Brazil, Bahia, Caravelas, estuary and mouth of rio Caravelas.

*Bagre marinus* (Mitchill, 1815) – AMNH 52052 (8 AL), USA, Alabama, Mobile Dauphin Island and Vicinity; MZUSP 22201 (2 AL and 1 CS), without collecting data; MZUSP 24489 (1 AL), Brazil, São Paulo, Ubatuba, Ponta Grossa.

*Bagre panamensis* (Gill, 1863) – LACM W55-140 (10 AL and 1 CS), Mexico, Baja California, Almejas Bay; UMMZ 86047 (2 AL), Mexico, Nayarit, San Blas.

*Bagre pinnimaculatus* (Steindachner, 1876) – FMNH 62447 (5 AL and 1 CS), Panama, Panama Bay, offshore between Punta de Hicacal and río Pasiga; USNM 286506 (2 AL), Colombia.

*Batrachocephalus mino* (Hamilton, 1822) – FMNH 68052 (4 AL and 1 CS), Malaysia, Sabah, East Coast Residency, Kinabatangan District, Deramakot Camp, Aquatic station 2.

*Brustiarius nox* (Herre, 1935) – AMS I.27407-002 (1 CS), Papua New Guinea, Angoram, Sepik River; CAS 63701 (6 AL and 1 CS), Papua New Guinea, Madang, Regene roundwater (oxbow lake of Ramu River); UMMZ 214018 (2 AL), Australia, Papua New Guinea, Angoram, Sepik River.

*Brustiarius solidus* (Herre, 1935) – AMNH 58711 (5 AL), Papua New Guinea, east Sepik river, Magendo 2 Village; MZUSP 38658 (3 AL and 1 CS), Papua New Guinea, Sepik River, Magendo Two Village, near Angoram.

*Carlarius latiscutatus* (Günther, 1864) – USNM 188475 (4 AL and 1 CS), Nigeria, off Lagos.

*Carlarius heudelotii* (Valenciennes, 1840) – USNM 293075 (3 AL and 1 CS), Guinea Bissau, 11°38'N, 17°00'W.

*Carlarius parkii* (Günther, 1864) – CAS 115845 (2 AL), Cameroon; USNM 218279 (5 AL and 1 CS), Sierra Leone.

*Cathorops agassizi* (Eigenmann & Eigenmann, 1888) – MZUSP 37232 (17 AL, 1 SK and 2 CS), Brazil, Maceió, Alagoas, Lagoa Mundaú; MZUSP 49346 (4 AL and 2 SK), Brazil, Pará, Baía de Marajó, Ilha do Musquiteiro, Cajueiro; MZUSP 37231 (7 AL and 1 SK), Brazil, Alagoas, Maceió, Lagoa Mundaú; MZUSP 49358 (6 AL and 2 SK), Brazil, Sergipe; MZUSP 37228 (1 SK), Brazil, Maranhão, ilha de São Luís, estreito de Coqueiro.

*Cathorops arenatus* (Valenciennes, 1840) – USNM 233482 (+40 AL and 2 SK), Venezuela, mouth of río Orinoco, 10 nautical miles upstream from sea buoy; USNM 286395 (17 AL), Suriname, off Surinam.

*Cathorops dasycephalus* (Günther, 1864) – FMNH 19143 (5 AL and 1 CS), Panama, Canal Zone, Panama Bay, Balboa; USNM 286481 (7 AL and 1 CS), Colombia, off Cape Manglares, south of Tumaco.

*Cathorops fuerthii* (Steindachner, 1877) – USNM 79398 (12 AL and 2 SK), Panama, Panama Bay, Balboa, Canal Zone.

*Cathorops hypophthalmus* (Steindachner, 1877) – USNM 293275 (2 AL and 1 SK), Panama, Darien prov., río Pirre c. 1/2 km above El Real (Rio Tuyra drainage).

*Cathorops multiradiatus* (Günther, 1864) – USNM 286400 (3 AL and 1 SK), Colombia, off Cape Manglares, south of Tumaco; USNM 79408 (2 AL), Panama, Panama Bay, Balboa, Canal Zone.

*Cathorops spixii* (Agassiz, 1829) – MZUSP 49345 (5 AL and 1 SK), Brazil, Pará, Baía de Marajó; MZUSP 49363 (16 AL and 2 SK), Brazil, Sergipe, rio Sergipe; MZUSP 49353 (31 AL and 2 SK), Brazil, Rio de Janeiro, Pontal de Atafona; MZUSP 23127 (232 AL and 3 SK), Brazil, Rio de Janeiro, baía da Ilha Grande; MZUSP 49362 (38 AL and 2 SK), Brazil, São Paulo, Santos; MZUSP 37240 (6 AL and 2 SK), Brazil, São Paulo, Cananéia; MZUSP 51706 (1 SK), Brazil, Paraná, praia de Pontal do Sul.

*Cathorops tuyra* (Meek & Hildebrand, 1923) – USNM 286466 (9 AL and 2 SK), Panama, río Pirre, 3–5 miles above El Real, purchased (caught on line); USNM 292824 (5 AL), Panama, río Uruseca, 2 miles above El Real.

*Cephalocassis borneensis* (Bleeker, 1851) – ANSP 87374 (2 AL and 1 CS), Thailand, Bangkok, Siam; UMMZ 181201 (4 AL and 1 CS), Cambodia, Mekong River, 15 km north of Phnom Penh.

*Cephalocassis melanochir* (Bleeker, 1852) – CAS 49426 (3 AL and 1 CS), Indonesia, Borneo, Kalimantan Barat, fish market at Sintang (purchased); USNM 230311 (2 AL), Indonesia, Borneo, Sintang market. Purchase.

*Cinetodus froggatti* (Ramsay & Ogilby, 1886) – AMS I. 27417-001 (1 CS), Papua New Guinea, Gulf of Papua; USNM 217080 (3 AL), Papua New Guinea, mainstream of lower fly 1.5 km upstream from elangowan island, 298 km upriver from Toro Pass.

*Cochlefelis danielsi* (Regan, 1908) – AMS I.26972-002 (2 CS), Papua New Guinea, Kubiri Creek.

*Cochlefelis spatula* (Ramsay & Ogilby, 1886) – AMS I.25997-002 (1 CS), Papua New Guinea, mid Purari River.

*Cryptarius truncatus* (Valenciennes, 1840) – ANSP 60768 (3 AL and 1 CS), Thailand, Paknam, Siam, at the mouth of the Me Nam Chao Phya, south of Bangkok; UMMZ 181176 (4 AL and 1 CS), Cambodia, Battambang, Tonle Sap (Great Lake) north-west basin, Mekong dr.; USNM 103189 (2 AL), Thailand, Menam Chao Phya, Koh yYai, Siam.

*Doiichthys novaeguineae* Weber, 1913 – AMS I.27416-002 (1 CS), Papua New Guinea, Era River.

*Galeichthys ater* Castelnau, 1861 – MZUSP 87693 (1 AL and 1 CS), South Africa, Groot Bank.

*Galeichthys feliceps* Valenciennes, 1840 – AMNH 97276 (2 AL), Angola, or Walfish Bay, Namibia; MZUSP 87694 (1 AL and 1 CS), Namibia.

*Genidens barbatus* (Lacépède, 1803) – MZUSP 22780 (1 CS), Brazil, Rio de Janeiro, Pontal de Atafona; MZUSP 24524 (5 AL and 1 CS), Brazil, São Paulo, Ubatuba, praia Dura, mouth of Rio Escuro; MZUSP 51702 (1 SK), Brazil, São Paulo, Juréia; MZUSP 51703 (1 SK), Brazil, São Paulo, Bertioga, 6 miles from coast; MZUSP 51704 (3 SK), Brazil, coast of São Paulo; MZUSP 28275 (1 AL), Brazil, Rio de Janeiro, Itaguaí, mouth of Rio da Guarda.

*Genidens genidens* (Cuvier, 1829) – MZUSP 49319 (12 AL and 1 CS), Brazil, São Paulo, Cananéia; MZUSP 51721 (5 AL and 1 CS), Brazil, Bahia, Rio Peruípe, port of Viçosa; MZUSP 51692 (4 SK), Brazil, coast of São Paulo; MZUSP 51694 (1 SK), Brazil, São Paulo, Juréia; MZUSP 51693 (2 SK), Brazil, São Paulo, between Ilha de Bom Abrigo and Juréia, 16 miles from coast; MZUSP 51691 (1 SK), Brazil, São Paulo, Bertioga, 6 miles from coast; MZUSP 24366 (5 AL), Brazil, São Paulo, Cananéia.

*Genidens machadoi* (Miranda Ribeiro, 1918) – MZUSP 24398 (18 AL and 1 CS), Brazil, 32°28'S–52°15'N; MZUSP 51698 (1 SK), Brazil, São Paulo, Juréia; MZUSP 51699 (1 SK), Brazil, São Paulo, Juréia; MZUSP 51700 (1 SK), Brazil, São Paulo, Bertioga; MZUSP 51701 (3 SK), Brazil, coast of São Paulo; MZUSP 24417 (1 AL), Brazil, 29°43'S–49°55'W.

*Hemiaris stormii* (Bleeker, 1858) – ANSP 60720 (10 AL and 1 CS), Thailand, Bangkok, Siam.

*Hemiaris sumatranus* (Anonymous, 1830) – CAS 140223 (6 AL and 1 CS), Myanmar, Rangoon.

*Ketengus typus* Bleeker, 1847 – ANSP 60704 (3 AL and 1 CS), Thailand, Bangkok, Siam.

*Nedystoma dayi* (Ramsay and Ogilby, 1886) – AMS I.25992-002 (1 CS), Papua New Guinea, Kibi Creek, Wabo; USNM 217082 (3 AL and 1 CS), Papua New Guinea, side channel of Strickland 4 km downstream from massy bakers junction, 450 km upriver from Toro Pass.

*Nemapteryx armiger* (De Vis, 1884) – AMS I.27418-001 (1 CS), Australia, North Territory, Murgens Creek; CAS 60485 (2 AL), Papua New Guinea, Moinamu (Kikori River), Gulf of Papua; NTM F.188 (5 AL), Australia, Northern Territory, west of Alligator River.

*Neoaricus graeffei* (Kner & Steindachner, 1867) – AMNH 51641 (7 AL and 1 CS), Australia, Northern Territory, south Alligator river where it crosses Oenpelli-Darwin road.

*Neoaricus midgleyi* (Kailola & Pierce, 1988) – AMNH 51651 (16 AL and 1 CS), Australia, Northern Territory, south Alligator River on pine Creek-Oenpelli road.

*Netuma bilineata* (Valenciennes, 1840) – ANSP 79487 (2 AL), Philippines, Orion, Bataan Province, Luzon; UMMZ 155785 (5 AL and 1 CS), Indonesia, Java; vicinity of Batavia, Pasan Ikan at Batavia, fish market; MZUSP 38656 (2 AL and 1 CS), Australia, Arafura Sea.

*Netuma thalassina* (Rüppell, 1837) – UMMZ 214610 (4 AL), Vietnam, Bac Lieu, South China Sea, Paknam Station 13, 39 km south-east of Bac Lieu Province, Mekong River Plume; UMMZ 214630 (3 AL and 1 CS), Vietnam, Bac Lieu, South China Sea, Paknam Station 13, 39 km south-east of Bac Lieu Province, Mekong River Plume.

*Notarius grandicassis* (Valenciennes, 1840) – MZUSP 10092–10103 (2 CS), Brazil, Espirito Santo, between São Mateus and the Rio Doce; MZUSP 51695 (1 SK), Brazil, Maceió, Alagoas, lagoa Mundaú; MZUSP 51705 (1 SK), Brazil, São Paulo, Bertioga; MZUSP 61341 (1 AL), Brazil, Bahia, Caravelas, estuary and mouth of Rio Caravelas.

*Notarius lentiginosus* (Eigenmann & Eigenmann, 1888) – USNM 293282 (7 AL and 1 CS), Panama, Darien prov., rio Chucunaque near confluence with rio Tuyra.

*Notarius planiceps* (Steindachner, 1877) – FMNH 19068 (3 AL and 1 CS), Panama, Canal Zone, Panama Bay, Balboa; USNM 79433 (2 AL), Panama, Panama Bay, Balboa.

*Notarius troschelii* (Gill, 1863) – FMNH 57741 (5 AL), Colombia, Tumaco; UMMZ. 194659 (7 AL and 1 CS), Costa Rica, Puntarenas, Gulf of Nicoya, off Puntarenas, Pacific.

*Occidentarius platypogon* (Günther, 1864) – LACM W58-36 (8 AL and 1 CS), Mexico, Nayarit, San Blas, Baia Matenchén.

*Osteogeneiosus militaris* (Linnaeus, 1758) – LACM 38116-36 (4 AL), Pakistan, fish market in Karschi; UMMZ 214628 (10 AL and 1 CS), Vietnam, Ba Xuyen Prov., Mouth of Bassac River, 2.5 km south-east of Truong Binh, Mekong River drainage; USNM 207092 (7 AL), India.

*Pachyula crassilabris* (Ramsay & Ogilby, 1886) – AMS I.27411-001 (1 CS), Papua New Guinea, Kubipara.

*Plicofollis dussumieri* (Valenciennes, 1840) – AMNH 32823 (3 AL), Kenya, Mombasa; LACM 38131-48 (2 AL and 1 CS), Pakistan, Sind, 6–8 km south of Hajambro, Turshian Creek; USNM 297118 (3 AL), Madagascar, north-western coast of Madagascar, baie d'Amboro.

*Plicofollis nella* (Valenciennes, 1840) – UMMZ 214647 (5 AL and 1 CS), Vietnam, South China Sea,

Paknam Station 9A, 34 km south-east of Bac Lieu Province, Mekong River plume.

*Plicofollis platystomus* (Day, 1877) – UMMZ. 208845 (3 AL and 1 CS), Bangladesh, Chittagong, Bay of Bengal, just off Kutubdia Island.

*Plicofollis polystaphylodon* (Bleeker, 1846) – AMS I.27412-001 (1 CS), Indonesia, Jarkarta, Muararakang; AMNH 88024 (12 AL and 1 CS), Malagasy Republic, Madagascar, Mananjary, estuary of river Mananjary, side lagoon behind hotel Jardin de la Mer, c. 100 m from sea; USNM 138376 (3 AL), Indonesia, Celebes, river at Makassar.

*Plicofollis tenuispinis* (Day, 1877) – CAS 127670 (1 AL), Malaysia, Sabah state, Sandakan; LACM 38128-47 (7 AL and 1 CS), Pakistan, Sind, Hawkes Bay, west of Karachi; LACM 38130-80 (13 AL and 1 CS), Pakistan, Sind, 20 km south of Paitiani, creek north of mouth of Turshian Creek.

*Potamarius grandoculis* (Steindachner, 1877) – MZUSP 1004-114 (11 AL, 1 CS and 1 SK), Brazil, Espirito Santo, Linhares, Lagoa Japurunã.

*Potamarius izabalensis* Hubbs & Miller, 1960 – UMMZ 177251 (1 AL), Guatemala, Lago de Izabal near the mouth of río Polochic; UMMZ 177252 (1 CS), Guatemala, Lago de Izabal.

*Potamosilurus latirostris* (Macleay, 1883) – AMS I.30113-001 (1 CS), Papua New Guinea, Laloki River; AMNH 58712 (11 AL), Papua New Guinea, western OK Tedi river at Nigerum; USNM 210858 (6 AL), Papua New Guinea, Papua-central district Laloki drainage Laloki river at Kokoda trail motel. MZUSP 38655 (4 AL and 1 CS), Papua New Guinea, Tedi River, near Ningerum.

*Potamosilurus macrorhynchus* (Weber, 1913) – AMS I.25998-002 (1 CS), Papua New Guinea, Purari River, Kone, Wabo Dam site.

*Potamosilurus velutinus* (Weber, 1907) – AMS I.27410-001 (1 CS), Papua New Guinea, Angoran, Sepik River, fish market; CAS 63536 (3 AL), Papua New Guinea, Madang, Ramu River where it is crossed by bridge on Brahman Road. north side near Usema village; freshwater; elevation (elev.) 125 m; CAS 63411 (4 AL and 1 CS), Papua New Guinea, Madang, just south of boat launch area, Bunapas Mission, 45 km upstream, elevation 5 m; USNM 217321 (3 AL), Papua New Guinea, Ramu river near Mt Otto.

*Sciades assimilis* (Günther, 1864) – AMNH 35070 (6 AL and 1 CS), Guatemala, Izabal, río Nimblaja, 1 km above mouth into Rio Sarstun; FMNH 103770 (3 AL), Belize, Belizean Beach, 4.5 miles on Western Highway; UMMZ 197214 (7 AL and 1 CS), Guatemala, Izabal, río Nimblaja, 1 km above mouth in río Sarstun, 3.5 km (by air) east of Modesto Mendez, elevation c. 2 m, Atlantic drainage.

*Sciades bonillai* (Miles, 1945) – USNM 292999 (3 AL and 1 CS), Colombia, Magdalena, Cienaga Grande

de Santa Marta, east side near south-east end of highway bridge; USNM 286488 (4 AL), Colombia, amongst mangroves at boca la Boquilla.

*Sciades couma* (Valenciennes, 1840) – CAS 122460 (6 AL and 1 CS), Brazil, Pará; FMNH 98033 (5 AL), Guyana, Georgetown Market.

*Sciades felis* (Linnaeus, 1766) – AMNH 52073 (7 AL and 1 CS), USA, Alabama, Mobile, Dauphin Island and Vicinity; AMNH 85099 (6 AL), USA, Alabama, Gulf of Mexico, Theodore Ship Channel; FMNH 37916 (4 AL), USA, South Carolina, Charleston Harbor.

*Sciades guatemalensis* (Günther, 1864) – UMMZ 178475 (2 AL and 1 CS), Mexico, Guerrero, Laguna Coyuca, c. 10 miles north-west of Acapulco – 3 miles north-west of military airport on south-west side of the lagoon, Pacific drainage.

*Sciades herzbergii* (Bloch, 1794) – CAS 153484 (4 AL), Brazil, Pernambuco; MZUSP 48951 (3 AL and 1 CS), Brazil, Maranhão, São Luís, Rio Curuca; MZUSP 87700 (1 CS), Brazil, Sergipe; MZUSP 51695 (4 AL and 2 SK), Brazil, Maceió, Alagoas, Lagoa Mundaú.

*Sciades leptaspis* (Bleeker, 1862) – AMS I.27420-001 (1 CS), Australia, Northern Territory, Jabiru, Long Harry's Billabong; AMNH 58993 (4 AL), Papua New Guinea, Madang, Ramu river at Bunapas mission, boat launch area, 45 km upstream of mouth; UMMZ 214017 (1 AL), Papua New Guinea, Mira Point, Purari River delta.

*Sciades parkeri* Müller & Troschel, 1849 – USNM 215204 (2 AL), Brazil, 01°04'N, 48°06'W; MZUSP 48524 (1 AL) Brazil, Pará, Baía de Marajó, Cabo Maguari; MZUSP 87699 (1 CS), Brazil, Maranhão, Ilha de São Luís, Estreito do Coqueiro.

*Sciades passany* (Valenciennes, 1840) – MZUSP 87701 (1 CS), Brazil, Pará.

*Sciades proops* (Valenciennes, 1840) – MZUSP 87702 (1 AL), Brazil, Pará, Vigia, Fish Market; MZUSP 52846 (1 AL), Brazil, Maranhão, São Luís, Ilha de São Luís, rio dos Cachorros; MZUSP 87703 (1 CS) Brazil, Pará.

*Sciades sagor* (Hamilton, 1822) – UMMZ 225447 (2 AL and 1 CS), Thailand, Prachuab Khiri Khan Gulf of Thailand shore at Ban Khlong Wan.

*Sciades seemanni* (Günther, 1864) – FMNH 19791 (2 AL), Panama, Chame Point; LACM W58-32 (12 AL and 1 SC), Mexico, Nayarit, San Blas.

#### *Austroglanididae*

*Austroglanis barnardi* (Skelton, 1981) – MNHN 1981-857 (1 CS), South Africa, Noordhoeks.

#### *Bagridae*

*Bagrus bajad* (Forsskall, 1775) – USNM 229884 (1 CS), Nigeria, Sokoto-Rima floodplain at Sokoto.

*Heterobagrus bocourti* (Bleeker, 1864) – MNHN 1974-20 (1 CS), Cambodge, Snoc Trou, Mekong River drainage, Tonlé Sap River.

*Mystus malabaricus* (Jerdon, 1849) – NRM 12137 (1 CS), India, Kerala, Indduki distr., Periyar River drainage, Deviyar River at Mannambandam.

#### Cetopsidae

*Cetopsis coecutiens* (Lichtenstein, 1819) – ANSP 137558 (2 CS), Metica River, upstream from entrance to Lake Mozambique, halfway to entrance to Laguna Arrotas.

*Hemicetopsis morenoi* (Fernandez-Yépez, 1972) – MBUCV 15891 (1 CS), Ajuaro River.

#### Claroteidae

*Bathylabus tetranema* (Bailey & Stewart, 1984) – UMMZ 196086 (1 CS), Zambia, Lake Tanganyika, west of Mutondwe Island.

*Chrysichthys auratus* (Geoffroy Saint-Hilaire, 1809) – MNHN 1967-119 (4 CS), Congo, Loeme River.

*Clarotes laticeps* (Rüppell, 1855) – MNHN 1968-53 (1 CS), Senegal, Richard Toll, River Senegal drainage, Taw ey River.

*Gephyroglanis longipinnis* (Boulenger, 1899) – FMNH 55346 (1 CS), Congo, Stanleyville.

*Lophiobagrus aquilus* (Bailey & Stewart, 1984) – UMMZ 199929 (2 CS), Zambia, Northern prov., Lake Tanganyika, east side, Nyika Bay.

*Phyllonemus filinemus* (Worthington & Ricardo, 1937) – MRAC 90257 (1 CS), Lake Tanganyika, Kajowa River.

#### Cranoglanididae

*Cranoglanis boudierus* (Richardson, 1846) – USNM 094590 (1 CS), China, Wuchow.

#### Diplomystidae

*Diplomystes* sp. – MZUSP 36953 (1 CS), Chile.

#### Doradidae

*Doras carinatus* (Linnaeus, 1766) – AMNH 91335 (1 CS), Venezuela, Bolivar, río Lima, tributary of río Carapo, along south face of Cero Guaiquinima.

#### Horabagridae

*Horabagrus brachysoma* (Günther, 1864) – CAS-SU 41071 (1 CS), India, Pamoin, Goa.

#### Ictaluridae

*Noturus gyrinus* (Mitchill, 1817) – FMNH 42269 (2 CS), USA, Florida, Okeechobee County, stream from Lake Annie to Lake Placid.

*Trogloglanis pattersoni* (Eigenmann, 1919) – UMMZ 211191 (1 CS), USA, Texas, Bexar, irrigation ditches from artesian well on Mitchell Ranch, north-east edge of Von Ormy.

#### Mochokidae

*Mochokus niloticus* (Joannis, 1835) – USNM 229657 (1 CS), Nigeria.

*Synodontis clarias* (Linnaeus, 1758) – USNM 229746 (2 CS), Nigeria, North-Western, Pumping station at bridge over Rima River.

#### Pangasiidae

*Helicophagus waandersii* (Bleeker, 1858) – UMMZ 186797 (1 CS), Thailand, Market at Ubol.

*Pangasius pangasius* (Hamilton, 1822) – UMMZ 208434 (2 CS), Bangladesh, Noakhali, Shabaspur River, just north of Hatia Island, Meghna River drainage.

#### Heptapteridae

*Phreatobius cisternarum* (Goeldi, 1905) – MNRJ 11569 (1 CS), Brazil, state of Amapá, well in Macapá.

*Rhamdiopsis moreirai* (Haseman, 1911) – MZUSP 35841 (1 CS), Brazil, state of Minas Gerais, city of Cordisburgo, Salitre Cave.

#### Schilbidae

*Ailia coila* (Hamilton, 1822) – UMMZ 208442 (3 CS), Bangladesh, Barisal, Meghna River at Gazipur Char.

*Clupisoma garua* (Hamilton, 1822) – UMMZ 208355 (3 CS), Bangladesh, Comilla, Megha River, upstream from Chandpur, just downstream from Gumti River mouth at Kanudi.

*Eutropiichthys vacha* (Hamilton, 1822) – UMMZ 208330 (1 CS), Bangladesh.

*Laiides hexanema* (Bleeker, 1852) – UMMZ 186798 (2 CS), Thailand, market at Ubol.

*Silonia silondia* (Hamilton, 1822) – UMMZ 208460 (1 CS), Bangladesh, Dacca, Meghna River, just downstream from Gazaria.