

Original Article

A new classification of the family Ariidae (Osteichthyes: Ostariophysi: Siluriformes) based on combined analyses of morphological and molecular data

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ABSTRACT

We present a new classification of the catfish family Ariidae based on a total-evidence hypothesis, which incorporates data from the examination of 249 morphological and 5603 molecular characters from 131 species. The named taxa in the proposed classification represent groups of species found in the Maximum Parsimony, Maximum Likelihood, and Bayesian Inference analyses or, in some cases, two of the three methods. Each named taxon is provided with a diagnosis derived from a comprehensive summary of the morphological characters and their character-state transformations, as interpreted from the most parsimonious version of the total-evidence tree. Taxa newly named herein are: Cathoropsini, new tribe; Genidentini, new tribe; Sciadeini, new tribe; *Acerioichthys*, new genus (type species *Arius dioctes* Kailola, 2000); *Blekeriella*, new genus (type species *Arius leptaspis* Bleeker, 1862); *Betancurichthys*, new genus (type species *Arius madagascariensis* Vaillant, 1894); *Jayaramichthys*, new genus (type species *Arius leptanotacanthus* Bleeker, 1849); *Kyataphisa*, new genus (type species *Pimelodus nenga* Hamilton, 1822); *Megalosciades*, new genus (type species *Arius augustus* Roberts, 1978); *Paracinetodus*, new genus (type species *Arius carinatus* Weber, 1913); *Papuaris*, new genus (type species *Arius latirostris* Macleay, 1883); and *Pseudosciades*, new genus (type species *Arius sona* Hamilton, 1822). A key to the genera of Ariidae is presented.

Keywords: biodiversity; catfish; systematics; taxonomy.

INTRODUCTION

Catfish of the family Ariidae, with more than 130 species, are the only representatives of the order Siluriformes with a circumglobal distribution (Marceniuk and Menezes 2007). Representatives of the family are common especially in estuaries and coastal areas of the eastern Pacific and western Atlantic (New World), the eastern Atlantic (West Africa), and the Indo-Pacific (eastern Africa, Madagascar, Asia, Australia, and New Guinea) (Betancur-R 2009). Although predominantly estuarine or nearshore marine, the family also includes exclusively marine species found to 150 m deep, as well as species restricted to freshwater that have been found up to 500 km from river mouths (Marceniuk and Menezes

2007). The Ariidae are characterized by a specialized reproductive habit, wherein males incubate eggs and embryos in the oral cavity (Rimmer and Merrick 1983). The reproductive habits of the Ariidae are associated with their low dispersal capacity and high level of endemism, a condition addressed in studies that describe recent speciation processes related to vicariance events (allopatric speciation), or adaptation to environments with different selective pressure (parapatric speciation) (Betancur-R et al. 2010, Marceniuk et al. 2017a, 2019a). Ariidae are characterized by their large size, abundance, and good quality meat, representing an important component of industrial and subsistence fishing throughout their distribution (Betancur-R 2009).

Recognition of the family Ariidae has been widely acknowledged (e. g., Regan 1911, Sheldon 1937, Berg 1940, Tilak 1965, Greenwood *et al.* 1966, Chardon 1968) since the group was named by Bleeker (1862) as 'Phalanx Arii'. Its monophyly has been corroborated in a number phylogenetic and cladistic studies (Mo 1991, de Pinna 1993, Kailola 2004, Hardman 2005, Sullivan *et al.* 2006, Betancur-R 2009, Marceniuk *et al.* 2012). In contrast, the validity and species composition of many of the genera of the family have been remarkably unstable, making the Ariidae the family with the greatest taxonomic instability within the order Siluriformes (Ferraris 2007). In the 19th and 20th centuries, the great diversity and wide distribution of the Ariidae, as well as the morphological similarity between the species and their poor representation in zoological collections, were the biggest obstacles to carrying out comprehensive studies dealing with the systematic delimitation of the genera. Relatively subtle differences in external morphology required early taxonomists to use inconsistent morphological characters, such as the shape of dental plates (Günther 1864, Eigenmann and Eigenmann 1890, Jordan and Evermann 1896, 1898, Weber and De Beaufort 1913, Meek and Hildebrand 1923, Herre 1926, Jayaram and Dhanze 1978, Roberts 1978, Taylor and Menezes 1978, Taylor 1986, Kailola and Bussing 1995) as diagnostic characters at the generic level.

Over the past two decades, several efforts were undertaken to improve our understanding of the phylogenetic relationships of catfishes of the family Ariidae, and produce a classification of the family based on that phylogeny. The earliest of these efforts was a morphology-based study by Kailola (2004), which produced the first comprehensive classification of ariids since those proposed by Bleeker (1858) and Günther (1864). A new classification of the family was proposed by Marceniuk and Menezes (2007), based on a preliminary version of a morphological phylogenetic study later published by Betancur-R *et al.* (2007), Marceniuk *et al.* (2012) and Betancur-R (2009) produced phylogenetic hypotheses of the family based primarily on mitochondrial and nuclear sequence data, with a new classification of New World ariids proposed in Acero and Betancur-R (2007), Betancur-R *et al.* (2007) proposed the first subfamily-level classification of the Ariidae based on combined molecular and morphological evidence.

More recently generated phylogenetic hypotheses were often incongruent with respect to the higher-level relationships within the family (e. g., Betancur-R 2009, Marceniuk *et al.* 2012). The validity of some genera and their relationships were shared in the various analyses, but differed markedly in other aspects of the hypothesized relationships. That inconsistency resulted in markedly different classifications among various studies, which ill-served the readership. The objective of this study was to use all previously published morphological and molecular data in order to produce a classification of the Ariidae that best fits the available information and provides names for all uncovered monophyletic groups and, in some cases, groups that have been named previously and found herein to be clearly not polyphyletic.

Materials and methods

The analysis of relationships within the Ariidae was based on the examination of 249 morphological and 5603 molecular characters

with 131 species in the ingroup (Supporting Information, Material S1) and five species in the outgroup. A total-evidence matrix was constructed with morphological characters described by Kailola (2004), Betancur-R *et al.* (2007), and Marceniuk *et al.* (2012), and DNA sequences (*cytochrome b*, ATP synthase 8/6, Rag1, Rag2, Myh6, 12S, and 16S) produced by Betancur-R and Acero (2004), Hardman (2002, 2005), Sullivan *et al.* (2006), Betancur-R *et al.* (2007), Betancur-R (2009), Betancur-R and Armbruster (2009), and Marceniuk *et al.* (2019b, c), all of which are available in GenBank (www.ncbi.nlm.nih.gov/genbank/). The final matrix was analysed by Maximum Parsimony, Bayesian Inference, and Maximum Likelihood methods. Morphological and molecular matrixes were concatenated into a single matrix with two sections. The 0–9 state model for standard, discrete morphological characters was used for the morphological data, assuming equal rates of character change (following Nylander *et al.* 2004). For molecular data, MEGA X (Kumar *et al.* 2018) was used to select the best model of nucleotide substitution for each gene and codon partition using the Akaike Information Criterion (Supporting Information, Material S2).

Morphological data

The complete list of examined morphological characters is presented in the 'Character List' (Supporting Information, Material S3), where the number of the character from a source study is listed following our characters (e. g., our character 1 is character 15 of Kailola 2004, and character 1 in Marceniuk *et al.* 2012). The characters and their various character states are briefly summarized herein and more detailed descriptions, often with illustrations, can be found in the source publications. The character state assignment for each taxon is based primarily on the observations of one of us (A.P.M.). Specimens analysed and illustrated in this study belong to different fish collections and the acronyms are listed in Sabaj (2020).

Polarity for morphological character states was determined by outgroup comparison through the parsimony analysis as described in Nixon and Carpenter (1993). The rooting point was established in Diplomystidae, with other catfish families used for outgroup comparison being Anchariidae, Cetopsidae, Ictaluridae, and Pimelodidae (Fink and Fink 1981, Mo 1991, de Pinna 1993, Britto 2002). In cases of ambiguous optimizations, the alternative that maximized reversals rather than convergences was chosen, preserving as much as possible of the original hypotheses of primary homology (de Pinna 1991). Character state distributions were inferred based on Maximum Parsimony analysis. The majority consensus tree was examined through accelerated transformation optimization using WinClada 1.00.08 (Nixon 2002).

Maximum parsimony

Maximum Parsimony (MP) analysis was applied using TNT (Goloboff *et al.* 2008). Morphological data reversals and convergences were considered as equally possible (Swofford and Maddison 1987). Multistate characters were analysed as unordered inasmuch as the practice of ordering multistate characters is inappropriate if congruence with other characters is being examined (Hauser and Presch 1991). The data matrix was assembled with the aid of Mesquite (Maddison and Maddison 2007). '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. Despite claims of Nixon and Davis (1991), the interpretations obtained herein, using different computer programs, were considered equivalent and treated as 'missing data'. Thus, 'missing' and 'not applicable' data are coded as dashes ('-') in the analysed data matrix.

In TNT, a traditional heuristic search was initially performed using the stepwise addition algorithm associated with tree bisection-reconnection (TBR) in a total amount of 10 000 samples, each one loading sectorial searches, 10 ratchet interactions, and 10 tree-drift interactions. After all replicates, 10 tree-fuse interactions were performed. A final round of TBR with all resulting trees was performed. The different topologies found in the fundamental cladograms were summarized in a strict consensus tree.

Maximum Likelihood and Bayesian Inference

The Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were run using morphological data and concatenated molecular sequences. ML analyses were conducted in RAxML (Stamatakis 2006), including all best-fit models for molecular data as detailed in Supplementary Material II. The trees were constructed using the rapid bootstrap algorithm, with node support being estimated by 1000 nonparametric bootstrap replicates (Felsenstein 1985). BI was run in MrBayes v.3.2.7 (Ronquist *et al.* 2012) including all best-fit models as detailed in Supplementary Information S2. Four independent runs were conducted, each with four Markov chains run for 3×10^8 generations. The Bayesian tree was constructed based on a majority rule consensus analysis with random initial trees, which were sampled every 100 000 generations. Conservatively, 25% of the first trees sampled in each MCMC run were discarded as burn-in. The log-likelihood scores were examined in Tracer v.1.6 (Rambaut *et al.* 2014) to assess convergence among runs and run performance. The post-burn-in samples were used to construct a consensus tree. Phylogenetic analyses were performed on the Cipres Science Gateway webserver (Miller *et al.* 2010) and the final tree was edited in FigTree v.1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree>).

Morphological diagnoses

In the diagnoses of named taxa, character states with unambiguous optimizations are presented first, followed by those with ambiguous optimization. Following the character state description is the character number and its transformation. As the derived condition was sometimes not found in some terminals of the branch, reversals to the plesiomorphic condition or acquisition of the different condition within the clade are mentioned. Transformations in bold type represent autapomorphies. Diagnoses distinguish taxa from the remaining named taxa of the immediate more-inclusive taxon.

Within each taxon account, the list of included taxa represents those that are considered valid herein. The originally proposed name of the listed taxa, synonyms (if any), and relevant nomenclatural details (type locality, primary type(s), and details of

the publication that made the name available) can be found in Marceniuk and Menezes (2007) or one of the more recent publications cited in the introduction (Betancur-R 2009, Marceniuk *et al.* 2012). Asterisks (*) that follow names of valid species indicate species that were not included in the phylogenetic analyses.

Recognizable groups of species that are not treated here as named taxa are diagnosed in the remarks section of their more inclusive named taxon. The method of presentation of unambiguous and ambiguous character states is the same as that for named taxa.

RESULTS

Phylogenetic reconstruction

MP analysis yielded 695 equally parsimonious trees with 13 271 steps, a consistency index of 23, and a retention index of 64 (Fig. 1). ML (Fig. 2) and BI (Fig. 3) analyses resulted in well supported trees with mostly concordant groups. In those cases where conflicts among different methods were observed we follow as rule: (1) recognize the monophyletic groups when they were found in two analyses; (2) consider the taxon as *incertae sedis* in cases where conflicts in all analyses were observed. These criteria preserve as much as possible previous classifications and taxa with strong morphological support. The ranks tribe and subtribe were recognized to express monophyly and biogeography, seeking to follow biogeographic precepts established in Betancur-R (2009).

In the new classification of the Ariidae, three subfamilies, four tribes, two subtribes, and 43 genera are recognized. Additionally, eight genera are recognized for the first time and four others recognized as having an *incertae sedis* relationship within the broader taxa. For each taxon a parenthetical annotation is presented summarizing the support indexes for the branch.

NEW CLASSIFICATION OF THE ARIIDAE

Family Ariidae Bleeker, 1858

MP 100, BI 1, ML 100

Type genus: *Arius* Valenciennes, 1840.

Included subfamilies

Ariinae Bleeker 1858

Bagreinae Schultz, 1944

Galeichthyinae Acero & Betancur-R, 2007.

Diagnosis (all non-ambiguous)

Contact face between lateral ethmoid and frontal through two facets that delimit a fenestra (**14, 2 > 3**), state 0 in *Ketengus*; bony blade anteriorly connecting nasal tubules present (**21, 0 > 1**), reversed in *Osteogeneiosus*; posterior cranial fontanel formed exclusively frontals (25, 0 > 1), reversed in *Arius*, *Aspistor*, *Betancurichthys*, *Cathorops dasycephalus*, *Cephalocassis*, *Cinetodus*, *Cryptarius*, *Doiichthys*, *Hemiarius*, *Hemipimelodus*, *Ketengus*, *Nedystoma*, *Nemapteryx*, *Neoarius* (except *Neoarius hainesi*), *Notarius*, *Pachyula*, *Paracinetodus*, *Pauparius*, and *Potamosilurus*; epioccipital posterior process present (**42, 0 > 1**); accessory tooth plates present (58, 0 > 1), reversed in *Hemipimelodus*,

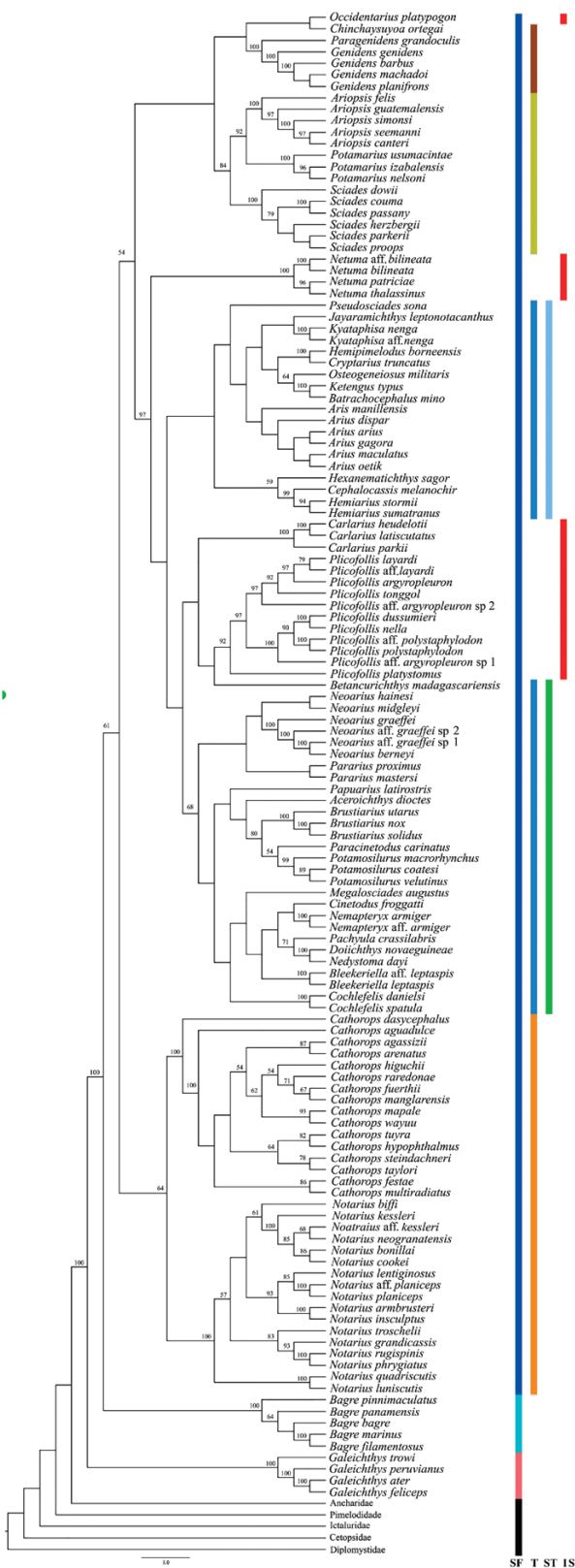


Figure 1. MP analysis. Subfamilies (SF) Galeichthyinae (pink), Bagreinae (bright blue), and Ariinae (dark blue). Tribe (T) Ariini (blue), Cathopsini (orange), **Genidentini tribe nov.** (brown), and **Sciadeini tribe nov.** (light green). Subtribe (ST) Ariina (light blue) and Doiichthyina (green). *Incertae sedis* taxa (IS) (red). Numbers over branches correspond to the bootstrap support.

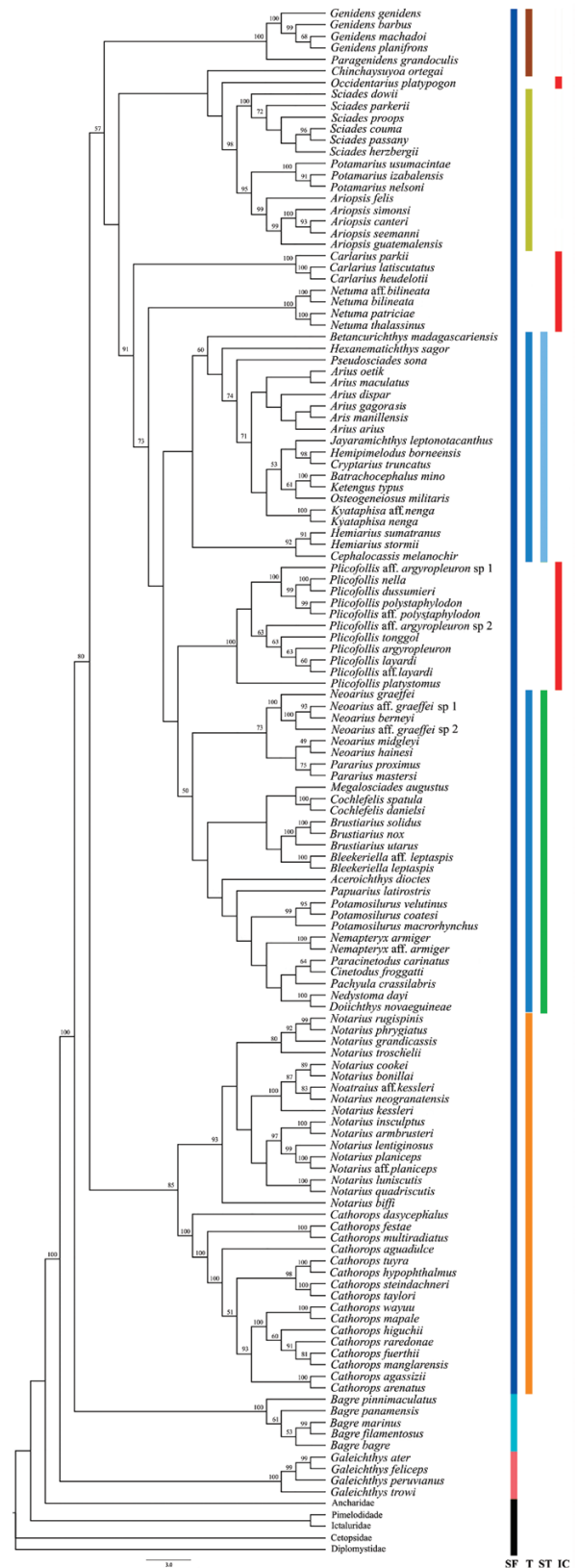


Figure 2. ML analysis. Subfamilies (SF) Galeichthyinae (pink), Bagreinae (bright blue), and Ariinae (dark blue). Tribe (T) Ariini (blue), Cathopsini (orange), **Genidentini tribe nov.** (brown), and **Sciadeini tribe nov.** (light green). Subtribe (ST) Ariina (light blue) and Doiichthyina (green). *Incertae sedis* taxa (IS) (red). Numbers over branches correspond to the bootstrap support.

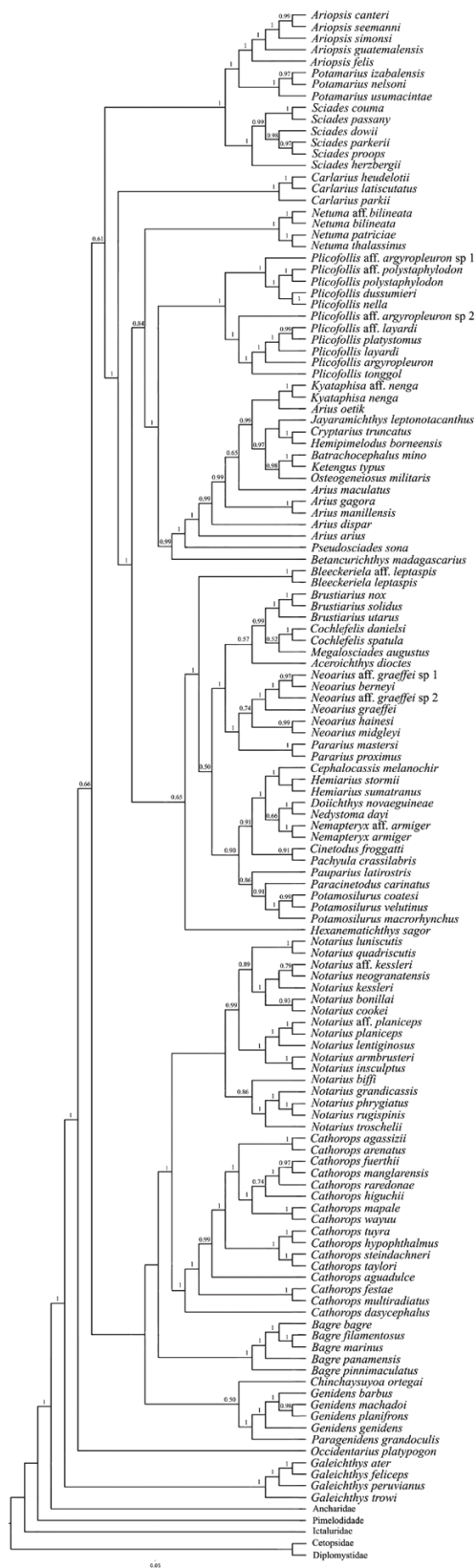


Figure 3. BI analysis. Subfamilies (SF) Galeichthyinae (pink), Bagreinae (bright blue), and Ariinae (dark blue). Tribe (T) Ariini (blue), Cathopsini (orange), **Genidentini tribe nov.** (brown), and **Sciadeini tribe nov.** (light green). Subtribe (ST) Ariina (light blue) and Doichthyina (green). *Incertae sedis* taxa (IS) (red). Numbers over branches correspond to the bootstrap support.

Ketengus, *Nedystoma*, *Pachyula*, *Potamarius* (except *Potamarius usumacintae*), and *Potamosilurus*; otic capsule very large, limited by prootic, pterotic, and exoccipital ($70, 0 > 2$), state 1 in *Sciades* (except *Sciades couma* and *Sciades herzbergii*); lapilli otoliths several times larger than asteriscus and sagitta ($75, 0 > 1$); space between transcapular process and otic capsule moderately large ($89, 0 > 1$), reversed in *Chinchaysuyoa*, *Occidentarius*, *Sciades* (except *Sciades couma* and *Sciades herzbergii*); posterior process of exoccipital present ($90, 0 > 1$), reversed in *Notarius*; posterior infraorbital S-shaped ($97, 0 > 1$), state 2 in *Bagre*; lachrymal-antorbital very wide ($100, 1 > 0$), reversed in *Plicofollis dussumieri*, *Plicofollis layardi*, *Plicofollis nella*, and *Plicofollis polystaphylodon*; dorsal crest of premaxilla present ($125, 1 > 0$), reversed in *Ketengus*; anterior portion of second basibranchial very expanded ($165, 0 > 1$); anterior portion of proximal cartilage of fourth epibranchial about half as wide as posterior portion ($188, 0 > 1$); third pharyngobranchial angled in form of boomerang ($192, 0 > 1$), reversed in *Doichthys*, *Ketengus*, and *Paragenidens*; dorsal processes of upper (pharyngeal) tooth plate long ($197, 0 > 1$), reversed in *Cinetodus* and state 2 in *Doichthys* and *Nedystoma*; anterior and posterior nostrils close together ($232, 0 > 1$).

Remarks

Within the Ariidae, the subfamilies Ariinae and Bagreinae share a suite of molecular and morphological characters not found in the species of the Galeichthyinae. The MP and ML results place the Ariinae plus Bagreinae as the sister group to the Galeichthyinae (Figs 1–2). Morphological character states that are shared by those two subfamilies and absent in Galeichthyinae are as follows: anterior portion of anterior cranial fontanel partially or totally delimited by dorsal expansion of orbitosphenoid ($24, 0 > 1$); enclosure of aortic canal present ($76, 0 > 1$); subvertebral process well developed ($78, 0 > 1$); basioccipital lateral process present ($82, 0 > 1$); sesamoid bone I very long and subtriangular ($145, 0 > 1$); urohyal long $157 (0 > 1)$; posterolateral processes of urohyal short ($160, 0 > 1$); posterolateral processes of urohyal as long as or longer than distal portion of bone ($162, 0 > 1$); distal portion of uncinat process of third epibranchial truncate ($183, 0 > 1$); mesial one-fourth of fourth epibranchial thin, its width about twice its length ($186, 0 > 1$), superficial ventral ossification of Weberian apparatus entirely covering aortic canal ($209, 0 > 1$); 19 or more precaudal vertebrae ($215, 0 > 1$); and protractor muscle of parapophysis of fourth vertebra contacting posterior process of epioccipital ($249, 0 > 1$).

Ambiguous optimization: Mesethmoid median portion moderately wide ($2, 1 > 2$); epioccipital posterior process very long ($43, 0 > 1$); orbitosphenoid and pterosphonoid lateral expansions very narrow and long ($65, 0 > 1$); otolith anteromesial process conspicuous ($72, 0 > 1$); contact face for articulation of transcapular process with basioccipital large and depressed ($85, 0 > 1$); exoccipital bony crest parallel to vertebral column and mesially folded ($92, 1 > 2$); articulation of the autopalatine with lateral ethmoid slightly displaced to anterior portion of bone ($111, 1 > 0$); dorsal crest of urohyal not projected anteriorly ($156, 1 > 0$); Müllerian ramus distal third gently curved ($208, 0 > 1$); 15 or more ribs ($213, 0 > 1$); adipose-fin base very short ($222, 0 > 3$); gas bladder shape cordiform ($239, 0 > 1$), and lateral line not bifurcated, reaching dorsal caudal-fin lobe ($247, 0 > 1$).

Key to subfamilies, tribes, subtribes, and genera of Ariidae

- 1a. Bones forming cephalic shield smooth or grooved; shape of vomerine tooth plates transversely elongate2
- 1b. Bones forming cephalic shield granulated; shape of vomerine tooth plates absent or not elongateAriinae3
- 2a. Posterior process of cleithrum connected by bony blade to second dorsal process of cleithrum; adipose-fin base longer than anal-fin base; maxillary barbel cylindrical; two pairs of mental barbels Galeichthyinae (genus *Galeichthys*)
- 2b. Posterior process of cleithrum free from second dorsal process of cleithrum; adipose-fin base shorter than one-half length of anal-fin base; maxillary barbel compressed; one pair of mental barbels Bagreinae (genus *Bagre*)
- 3a. New World genera of Ariinae 4
- 3b. Old World genera and Subtribes of Ariini 12

Subfamily Galeichthyinae Acero & Betancur-R., 2007

(Figs 1–3)

Type genus: *Galeichthys Valenciennes*, 1840.

Diagnosis (all of ambiguous optimization)

Frontal mesial laminar projection absent (23, 1 > 0); parieto-supraoccipital process base almost as narrow as posterior portion (46, 1 > 0); ventral crest of parieto-supraoccipital process weakly developed, restricted to base of process (48, 1 > 0); anterior margin of otolith irregular, concave (71, ? > 2); transcapular process forming a right angle in relation to body axis (86, 0 > 1); transcapular process very short and thick (87, 0 > 1); bony crest of exoccipital shallow and inconspicuous (91, 0 > 1); posterior branch of lachrymal-antorbital short and little differentiated (99, 1 > 0); maxilla wide for proximal two-thirds with edges parallel, narrow distally, thin and acute posteriorly (102, 0 > 1); autopalatine posterior cartilage as long as anterior cartilage (114, 1 > 0); anterodorsal process of anguloarticular present (118, 0 > 1); opercle posterior portion not well developed posteriorly (129, 1 > 0); second external branchiostegal ray almost as wide as first ray (148, 0 > 1); posterior portion of second basibranchial long and wide (167, 2 > 0); third basibranchial long and narrow (169, 1 > 2); mesial portion of first epibranchial large and depressed (180, 0 > 1); space for insertion of teeth on fifth ceratobranchial very large (194, 1 > 0); median crest associated with neural spine of third vertebra low or absent (201, 1 > 0); seventh vertebra free from ventral superficial ossification (214, 0 > 10); anterior and middle nuchal plates indistinct (217, 1 > 0); posterior process of cleithrum connected by bony blade from second dorsal process of cleithrum (228, 0 > 1); basiptyergium anterior internal process partially connected to bony lamina (231, 0 > 1); gas bladder Müllerian window short (241, 0 > 1).

Included genera

Galeichthys Valenciennes, 1840.

Remarks

The total-evidence analysis corroborates previous morphological and molecular studies and confirms the recognition of a subfamily for the genus *Galeichthys*, as the sister group of all other members of the family Ariidae (Betancur-R. 2009, Marceniuk *et al.* 2012).

Galeichthys Valenciennes, 1840

MP 100, BI 1, ML 100

(Figs 1–3, 4A–5)

Type species: *Galeichthys feliceps* Valenciennes, 1840.

Diagnosis

That of the Galeichthyinae, above.

Included species

Galeichthys ater Castelnau, 1861
Galeichthys feliceps Valenciennes, 1840
Galeichthys peruvianus Lütken, 1874
Galeichthys trowi Kulonowski, 2010 *.

Remarks

Total-evidence analysis corroborated previous morphological (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012) and molecular (Betancur-R. 2009) studies regarding the monophyly and relationship of the genus. Supported by morphological and molecular data, Betancur-R. *et al.* (2007) had the same interpretation of the phylogenetic relationship of *Galeichthys*, examining only *Galeichthys ater* and *Galeichthys peruvianus*, whereas Kailola (2004), based only on morphological evidence, recognized the same species composition, but with a unique hypothesis of phylogenetic relationships.

Habitat and distribution: Marine, southern Africa, and north-western coast of South America (Fig. 4).

Subfamily Bagreinae Schultz, 1944

(Figs 1–2)

Type genus: *Bagre* Cloquet, 1816.

Included genera

Bagre Cloquet, 1816.

Diagnosis

Posterior branches of mesethmoid moderately long, delimiting between one-fourth and one-half length of anterior cranial fontanel (8, 0 > 1); lachrymal-antorbital and frontal distinct from each other (22, 0 > 1); ventral tip of subvertebral process

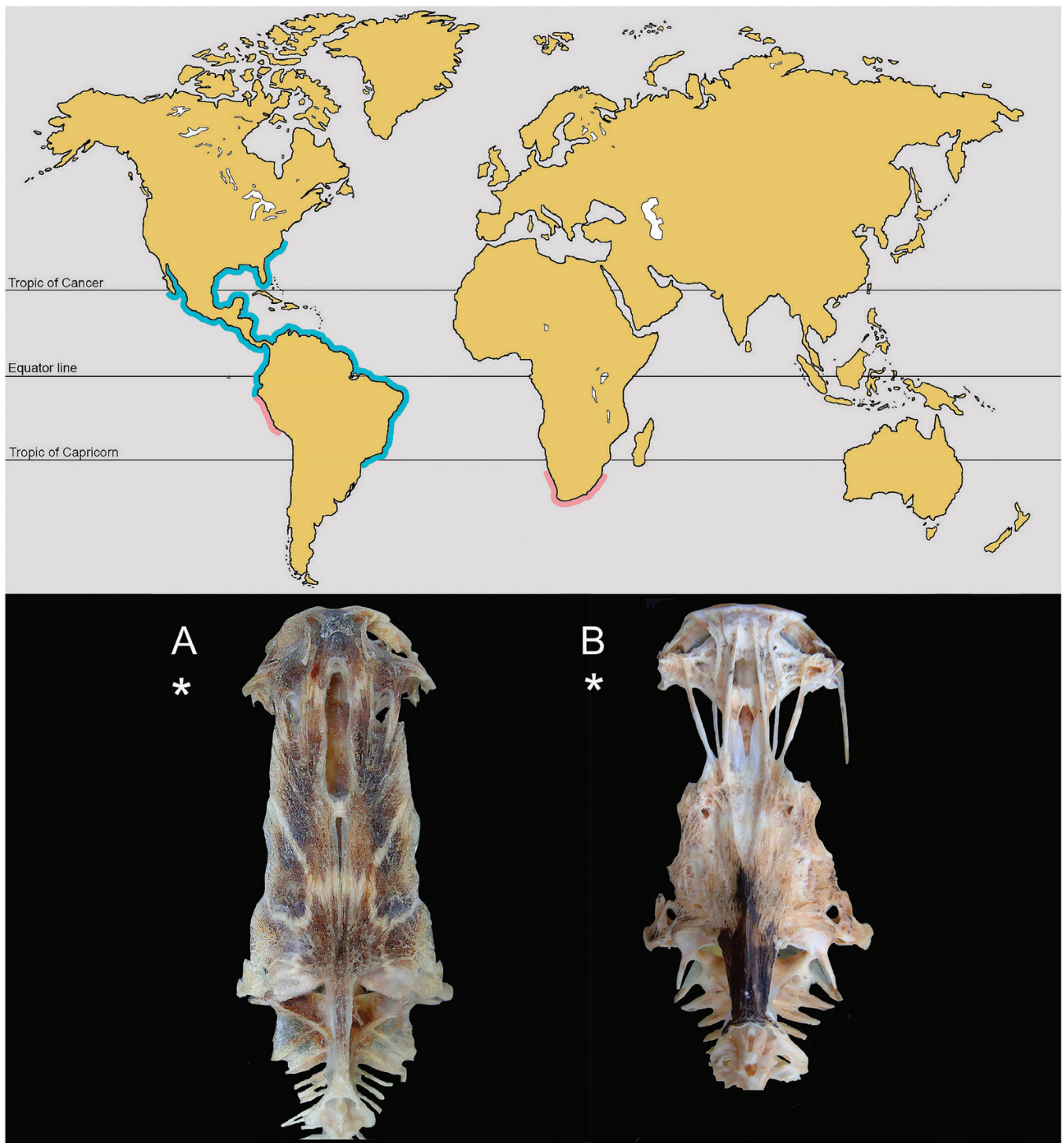


Figure 4. Representative skulls, in dorsal view, and distribution of the subfamilies Galeichthyinae (pink) and Bagreinae (light blue). A, *Galeichthys peruvianus*, MZUSP 94844. B, *Bagre bagre*, MPEG 32804. * marine.

rounded (80, 0 > 1); anterior infraorbital conspicuously curved (96, 0 > 1); posterior infraorbital L-shaped (97, 1 > 2); two anterior branches and one mesial branch in lachrymal-antorbital anterior part (98, 0 > 2); maxilla cylindrical, moderately long and distally acute (101, 0 > 1); maxillary condyle large (103, 1 > 2); autopalatine conical, short, and robust (104, 0 > 1); autopalatine ventral process present and very conspicuous (112, 0 > 1); dorsal crest of premaxilla delimiting contact area with

mesethmoid beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); metapterygoid anterior process very large (139, 0 > 1); posterior ceratohyal long (153, 0 > 1); posterior end of urohyal bifurcate (158, 0 > 1); median constriction of third basibranchial displaced to posterior one-fourth (170, 0 > 1); transverse crest associated with neural spine of fourth vertebra very high (200, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202,



Figure 5. *Galeichthys feliceps*, syntype MNHN A-9363, south-eastern Atlantic and south-western Indian Ocean, type species of the genus.

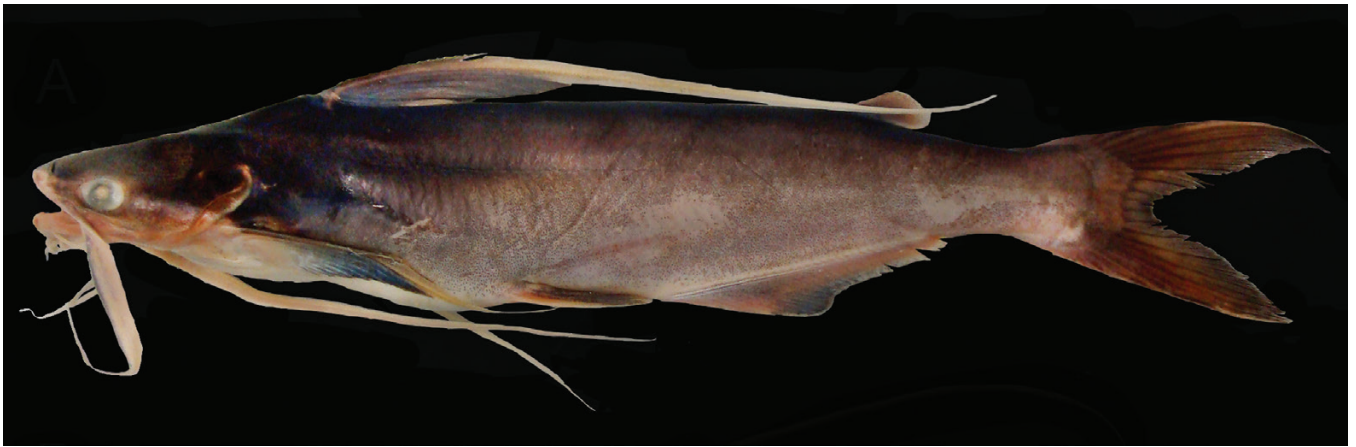


Figure 6. *Bagre bagre*, LBP 30215, western Atlantic, type species of the genus.

0 > 1); Müllerian ramus blade evident only in basal third of length (206, 2 > 1); 39 or more caudal vertebrae (216, 1 > 0); adipose-fin origin vertically above posterior one-half of anal fin (223, 1 > 2); second dorsal cleithral process on lower portion of cleithrum (225, 0 > 1); maxillary barbel compressed (235, 0 > 1); mental barbel one pair (237, 0 > 1); gas bladder lateral diverticula present (243, 0 > 1).

Ambiguous optimization: Posterior branches of mesethmoid narrow (6, 0 > 1), state 0 in *Bagre panamensis*; medial groove of cranium shallow with margins not very conspicuous (31, 1 > 0), state 1 in *Bagre bagre* and *Bagre filamentosus*; dorsal-fin spine prolonged into filament (221, 0 > 1), state 0 in *Bagre panamensis*; lateral line bifurcated, reaching dorsal and ventral caudal-fin lobes (247, 0 > 2).

Bagre Cloquet, 1816

MP 100, BI 1, ML 100

(Figs 1–3, 4A, 6)

Type species: *Silurus bagre* Linnaeus, 1766.

Diagnosis

That of the Bagreinae, above.

Included species

Bagre bagre Linnaeus, 1766
Bagre filamentosus Swainson, 1839
Bagre marinus Mitchill, 1815
Bagre panamensis Gill, 1863
Bagre pinnimaculatus Steindachner, 1876.

Habitat and distribution: Predominantly marine, eastern and western America (Fig. 4).

Remarks

The MP and ML analyses corroborate the morphological diagnosis, species composition, and the hypothesis of phylogenetic relationships of *Bagre* presented in previous morphological studies (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012). With different interpretations of phylogenetic relationships, Kailola (2004), Betancur-R. *et al.* (2007), and Betancur-R. (2009) show the same definition and species composition as found in the total-evidence analysis.

Subfamily Ariinae Bleeker, 1858

MP 100, ML 100

(Figs 1–2)

Type genus: *Arius Valenciennes*, 1840.

Diagnosis

Mesethmoid medial notch narrow and deep (1, $0 > 1$), state 0 in *Cryptarius* and *Ketengus*, state 2 in *Batrachocephalus*, *Bleekeriella*, *Brustarius utarus*, *Cochlefelis*, *Doiichthys*, *Nedystoma*, *Nemapteryx*, *Netuma*, *Notarius grandicassis*, *Osteogeneiosus*, *Pararius mastersi*, *Papuarus*, *Potamosilurus* (except *Potamosilurus velutinus*), *Sciades parkeri*, and *Sciades proops*; bones forming cephalic shield granulated (33, $0 > 1$); vomerine tooth plates rounded (56, $0 > 1$), state 2 in *Brustarius* (except *Brustarius utarus*) and *Pararius proximus*, state 3 in *Aspistor*; accessory tooth plates large, oval to subtriangular (60, $0 > 2$), state 0 in *Acerioichthys*, *Ariopsis guatemalensis*, *Bleekeriella*, *Chinchaysuyoa*, *Cochlefelis*, *Neoarius*, *Paracinetodus*, and *Papuarus*, state 1 in *Brustarius*, *Hexanematichthys*, *Nemapteryx*, *Pararius*, and *Potamarius usumacintae*, state 2 in *Ariopsis* (except *Ariopsis guatemalensis*), *Arius aff. nenga*, *Arius dispar*, *Arius maculatus*, *Arius oetik*, *Carlarius*, *Genidens machadoi*, *Netuma*, *Notarius*, *Occidentarius*, *Pseudosciades*, and *Sciades*, state 3 in *Batrachocephalus*, *Cathorops*, *Cephalocassis*, *Cryptarius*, *Doiichthys*, and *Hemiarus*; distance between optic foramen and trigemino-facialis foramen about twice as large as trigemino-facialis foramen (68, $0 > 1$), state 0 in *Paragenidens* and *Potamosilurus*; articulation of autopalatine with lateral ethmoid moderately large (109, $0 > 1$); anterior cartilage of autopalatine moderately long, one-third to one-fifth as long as bone itself (113, $0 > 1$), state 0 in *Osteogeneiosus* and state 3 in *Batrachocephalus* and *Ketengus*; premaxilla wide and moderately long, its length more than three times in width (120, $0 > 1$), state 0 in *Acerioichthys*, *Brustarius uterus*, and *Cochlefelis*, state 2 in *Arius gagora*, *Cathorops*, *Cephalocassis*, *Hemipimelodus*, *Neoarius hainesi*, *Notarius rugispinis*, *Notarius phrygiatus*, *Paracinetodus*, and *Plicofollis* (except *Plicofollis platystomus*) and state 3 in *Doiichthys*, *Cinetodus*, *Pachyula*, *Paragenidens*, and *Potamarius* (except *Potamarius usumacintae*); anteroventral portion of opercle subtrapezoidal, moderately long (127, $0 > 1$), state 0 in *Acerioichthys*, *Arius leptanotacanthus*, *Arius nenga*, *Arius oetik*, *Bleekeriella*, *Brustarius utarus*, *Cinetodus*, *Hexanematichthys*, *Nedystoma*, *Pararius mastersi*, and *Pseudosciades* and state 2 in *Cathorops*, *Cryptarius*, *Hemiarus*, and *Pachyula*; more than one-half of posterior part of interopercle contacting ventral margin of opercle (131, $0 > 1$), state 0 in *Arius leptanotacanthus*, *Batrachocephalus*, *Bleekeriella*, *Ketengus*, *Neoarius* (except *Neoarius hainesi*), *Notarius* (except *Notarius rugispinis* and *Notarius phrygiatus*), *Plicofollis platystomus*, and *Sciades* (except *Sciades couma* and *Sciades herzbergii*); metapterygoid as deep as long in perpendicular section (135, $0 > 1$), state 0 in *Doiichthys*, state 2 in *Cathorops*, *Cinetodus*, *Chinchaysuyoa*, *Cryptarius*, *Hemipimelodus*, *Pachyula*, *Paragenidens*, *Plicofollis*, and *Potamarius izabalensis*

and state 3 in *Batrachocephalus* and *Ketengus*; first external branchiostegal ray as broad proximally as distally (147, $0 > 1$); second basibranchial mushroom shaped (166, $0 > 1$), state 0 in *Cochlefelis*, *Brustarius*, *Doiichthys*, *Neoarius*, *Notarius* (except *Notarius rugispinis*, *Notarius planiceps*, and *Notarius phrygiatus*), *Osteogeneiosus*, *Sciades couma*, and *Sciades herzbergii*.

Ambiguous optimization: Lateral horn of lateral ethmoid compressed and spatulate (11, $0 > 1$), state 0 in *Aspistor*, *Cephalocassis*, *Cryptarius*, *Hemiarus*, *Hemipimelodus*, *Doiichthyina* (except *Bleekeriella*, *Cinetodus*, *Neoarius*, *Pachyula*, *Paracinetodus*, *Papuarus*, and *Potamosilurus velutinus*), *Notarius* (except *Notarius armbrusteri* and *Notarius biffi*), *Plicofollis platystomus*, *Plicofollis layardi*, and *Sciades* (except *Sciades couma* and *Sciades couma*); lateral horn of lateral ethmoid of variable length and lateroposteriorly oriented (12, $0 > 1$), state 0 in *Acerioichthys*, *Brustarius* (except *Brustarius utarus*), *Cochlefelis danielsi*, *Pararius*, *Plicofollis layardi*, *Sciades* (except *Sciades couma* and *Sciades herzbergii*) and state 2 in *Doiichthys*, *Paragenidens*, *Plicofollis dussumieri*, *Plicofollis nella*, *Plicofollis polystaphylodon*, and *Potamarius* (except *Potamarius usumacintae*); posterior cranial fontanel relatively narrow and long (27, $0 > 1$), state 0 in *Arius leptanotacanthus*, *Arius nenga*, *Brustarius*, *Cathorops* (except *Cathorops dasycephalus*), *Genidentini* (except *Paragenidens*), *Neoarius hainesi*, *Netuma*, *Plicofollis* (except *Plicofollis platystomus*), state 2 in *Aspistor*, *Hemiarus*, *Notarius rugispinis*, *Notarius phrygiatus*, *Papuarus*, and state 3 in *Cephalocassis*, *Doiichthys*, *Hemipimelodus*, *Nedystoma*, and *Nemapteryx*; extrascapular subquadrangular (37, $0 > 1$), state 0 in *Arius*, *Batrachocephalus*, *Betancurichthys*, *Brustarius* (except *Brustarius utarus*), *Genidens*, *Ketengus*, *Notarius* (except *Notarius rugispinis*, *Notarius planiceps*, *Notarius phrygiatus*, and *Notarius troscheli*), *Pararius mastersi*, *Paragenidens*, *Plicofollis*, *Potamarius* (except *Potamarius izabalensis*), *Sciades dowii* and state 2 *Cathorops*, *Cinetodus*, and *Paracinetodus*; temporal fossa moderate to very large (39, $0 > 1$), state 0 in *Arius nenga*, *Bleekeriella*, *Brustarius* (excluded *Brustarius utarus*), *Cathorops*, *Cryptarius*, *Genidens*, *Hemipimelodus*, and *Pararius*; articulation of autopalatine with lateral ethmoid slightly displaced to posterior portion of bone (111, $1 > 2$), state 0 in *Doiichthys*, and state 1 in *Brustarius*, *Cochlefelis*, *Nemapteryx*, and *Neoarius*; dorsal crest of hyomandibula present (140, $0 > 1$); first epibranchial parallel to second epibranchial (179, $1 > 0$), state 1 in *Ketengus*; nuchal plate and parieto-supraoccipital contacting one another through a convex-concave articulation (220, $0 > 1$), state 0 in *Notarius armbrusteri*, *Notarius biffi*, *Notarius kessleri*, and *Notarius neogranatensis* and state 2 in *Aspistor*, *Notarius troscheli*, *Pararius mastersi*, *Sciades* (except *Sciades herzbergii*, *Sciades parkeri*, and *Sciades proops*).

Included tribes

Incertae sedis Ariinae
Ariini Bleeker, 1858
Cathoropsini tribe nov.
Genidentini tribe nov.
Sciadeini tribe nov.

Key to New World genera, *Ariinae*

- 4a. Adipose-fin base long or very short; ventral tip of subvertebral process acute or spatulate; otolith longer than wide; otolith antero-mesial process inconspicuous *Cathoropsini* 5
- 4b. Adipose-fin base moderately long; ventral tip of subvertebral process rounded; otolith almost as long as wide; otolith antero-mesial process conspicuous ... *Incertae sedis*, *Genidentini* and *Sciadeini* 6
- 5a. Accessory tooth plates small, oval; temporal fossa very reduced; anterior margin of otolith markedly irregular, concave; superficial ventral ossification of complex vertebra regularly arched *Cathorops*
- 5b. Accessory tooth plates large, oval to subtriangular; temporal fossa moderate to very large; anterior margin of otolith straight or slightly irregular; otolith posterior margin rounded; superficial ventral ossification of complex vertebra keeled *Notarius*
- 6a. Posterior cranial fontanel absent; epiphyseal bar indistinct 7
- 6b. Posterior cranial fontanel present; epiphyseal bar distinct 8
- 7a. Mesethmoid median portion moderately large; distinct fenestra delimited by lateral ethmoid and frontal; lateral margin of premaxilla with slight concavity; Müllerian ramus distal third gently curved; females with conspicuous pad on pelvic fin ... (*Sciadeini*) *Ariopsis*
- 7b. Mesethmoid median portion very wide; indistinct fenestra delimited by lateral ethmoid and frontal; lateral margin of premaxilla with a very conspicuous concavity; Müllerian ramus distal third straight; females without conspicuous pad on pelvic fin ... (*Sciadeini*) *Sciades*
- 8a. Fenestra delimited by lateral ethmoid and frontal very small or indistinct; temporal fossa absent; subvertebral process indistinct or weakly developed ... (*incertae sedis*) *Occidentarius*
- 8b. Fenestra delimited by lateral ethmoid and frontal distinct and moderately wide; temporal fossa present; subvertebral process well developed 9
- 9a. Posterior cranial fontanel relatively narrow and long; premaxilla very wide and short, as long as wide (except *Paragenidens grandoculis*); mesethmoid median portion very narrow (except *Potamarius usumacintae*); lateral horn of lateral ethmoid long and posteriorly oriented (except *Potamarius usumacintae*); optic foramen very large; distance between optic foramen and trigemino-facialis foramen small, equal to width of trigemino-facialis foramen 10
- 9b. Posterior cranial fontanel reduced to a small opening; premaxilla wide and moderately long, its length more than three times in width; mesethmoid median portion moderately wide; lateral horn of lateral ethmoid variable length and lateroposteriorly oriented; optic foramen moderately large or very reduced; distance between optic foramen and trigemino-facialis foramen large, about twice as large as trigemino-facialis foramen 11
- 10a. Snout very long, snout length 0.5–0.8 times in cephalic shield width at frontal area and 1.6–1.8 times in body width (*Sciadeini*) *Potamarius*
- 10b. Snout moderately long, snout length 1.0–1.5 times in cephalic shield width at frontal area and 2.2–2.7 times in body width ... (*Genidentini*) *Paragenidens*
- 11a. Posterior process of cleithrum moderately long, about one-half vertical length of lateral face of cleithrum; gas bladder with single chamber; temporal fossa very reduced; teeth restricted to mesial two-thirds of dentary; pterotic mesial border with parieto-supraoccipital shorter than anterior border with sphenotic ... (*Genidentini*) *Genidens*
- 11b. Posterior process of cleithrum very long, equal to vertical length of lateral face of cleithrum; gas bladder with three chambers; temporal fossa moderate to very large; teeth restricted to mesial three-fourths of dentary; pterotic mesial border with parieto-supraoccipital longer than anterior border with sphenotic ... (*Genidentini*) *Chinchaysuyoa*.

Ariinae incertae sedis

(Figs 1–3)

Included genera

Occidentarius Betancur-R. & Acero P., 2007.

Remarks

The monotypic genus *Occidentarius* listed here falls within the *Ariinae* in MP and ML analyses, but its position within the subfamily differs markedly among the different analyses. As such, it is treated here as a member of the *Ariinae*, but not included within either of the named tribes.

Occidentarius Betancur-R. & Acero P., 2007

(Figs 1–3, 7–8)

Type species: *Arius platypogon* Günther, 1864.

Diagnosis

Posterior branch of lateral ethmoid depressed (13, 0 > 1); fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, 1 > 0); temporal fossa absent (38, 0 > 1); epioccipital contacting small narrow area of diagonal crest associated with neural spine of fourth vertebra (44, 2 > 0); ventral crest of parieto-supraoccipital process well-developed through entire

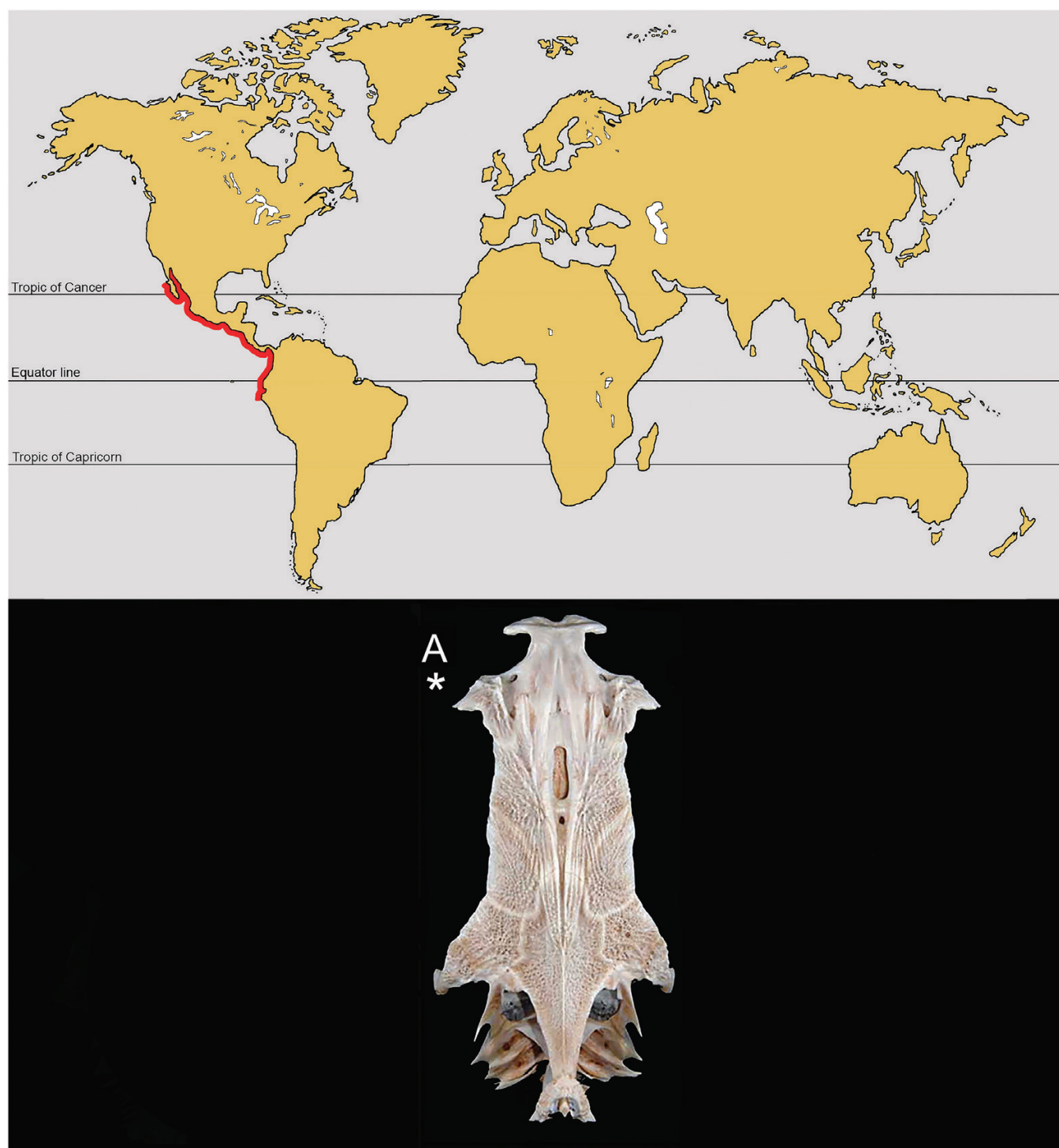


Figure 7. Representative skull, in dorsal view, and distribution of the Ariinae incertae sedis. A, *Occidentarius platypogon*, catfishesbone. acnatsci.org.

extension of process (48, 0 > 1); transverse crest associated with neural spine of fourth vertebra very high (200, 0 > 1); median crest associated with neural spine of third vertebra very high (201, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1). *Ambiguous optimization*: Vomer lateral processes wide (53, 1 > 0); tooth plates associated with vomer present (55, 0 > 1); subvertebral process indistinct or weakly developed (78, 1 > 0); dorsal crest of urohyal projected anteriorly (156, 0 > 1).

Included species

Occidentarius platypogon (Günther, 1864).

Habitat and distribution: Marine, western America (Fig. 7).

Remarks

The genus *Occidentarius* was well defined in previous morphological and molecular studies (Marceniuk and Menezes 2003, Betancur-R. 2009, Marceniuk *et al.* 2012), which was



Figure 8. *Occidentarius platypogon*, BMNH 1864.1.26.316-319, eastern Pacific, type species of the genus.

corroborated in the present analysis, but without consensus regarding its relationships.

Cathoropsini tribe nov.

MP 64, BI 1, ML 85

(Figs 1–3, 9)

ZooBank registration: [urn:lsid:zoobank.org:act:429CBD26-08F8-4207-BB19-13F4260D7CFB](https://zoobank.org/urn:lsid:zoobank.org:act:429CBD26-08F8-4207-BB19-13F4260D7CFB).

Type genus: *Cathorops* Jordan & Gilbert, 1883.

Diagnosis

Mesethmoid median portion very narrow (2, ? > 0), state 1 in *Notarius biffi*, *Notarius kessleri*, and *Notarius neogranatensis*, and state 2 in *Notarius cookei*, *Notarius grandicassis*, and *Notarius troscheli*; bony bridge formed by lateral ethmoid and frontal cylindrical and thin (16, 0 > 1); otolith longer than wide (73, 0 > 1); subvertebral process long and narrow (79, 0 > 1); transcapular process forming a right angle in relation to body axis 86 (0 > 1), state 0 in *Notarius cookei* and *Notarius grandicassis*; exoccipital bony crest parallel to vertebral column and mesially folded (92, 1 > 2), state 3 in *Notarius*.

Ambiguous optimization: Frontal mesial laminar projection present (23, 1 > 0); posterior cranial fontanel formed by frontals and parieto-supraoccipital (25, 1 > 0); pterotic mesial border with parieto-supraoccipital longer than anterior border with sphenotic (36, 0 > 1), reversed in *Notarius*; vomer lateral processes very narrow (53, 0 > 1), reversed in *Aspistor*; otolith anteromesial process inconspicuous (72, 1 > 0), homoplastic in *Galeichthys*; dorsal crest of urohyal projected anteriorly (156, 0 > 1), reversed in *Notarius rugispinis*, *Notarius planiceps*, and *Notarius phrygiatus*; 14 or fewer ribs (213, 1 > 0), reversed in *Notarius*; seventh vertebra free from ventral superficial ossification (214, 0 > 1).

Included genera

Notarius Gill, 1863

Cathorops Jordan & Gilbert, 1883.

Remarks

BI analyses and ML analyses did not recognize *Aspistor* as a valid genus as was reported by Marцениuk and Menezes (2007) and Marцениuk *et al.* (2012) on morphological evidence (see *Notarius* Remarks).

***Cathorops* Jordan & Gilbert, 1883**

MP 100, BI 1, ML 100

(Figs 1–3, 9A–10)

Arius hypophthalmus Steindachner, 1876.

Diagnosis

Posterior branches of mesethmoid narrow (6, 0 > 1); posterior branches of mesethmoid parallel throughout their entire extension (7, 0 > 1); frontal as main component of bony bridge formed by lateral ethmoid and frontal (15, 0 > 2); fenestra delimited by lateral ethmoid and frontal very large (17, 1 > 2); epioccipital contacting both diagonal and transversal crests associated with neural spine of fourth vertebra (44, 0 > 1); accessory tooth plates small, vertically oval (60, 2 > 3); otic capsules weakly differentiated (69, 0 > 1); anterior margin of subvertebral process keeled (81, 0 > 1); basioccipital lateral process very long (84, 0 > 1); transcapular process depressed (88, 0 > 1); premaxilla narrow and very long, its length two to three times in width (120, 1 > 2); anteroventral portion of opercle subtrapezoidal, very short (127, 1 > 2); anteroventral margin of opercle concave or almost straight (128, 0 > 1); posterior margin of interopercle straight and inclined (130, 0 > 1); anterior portion of interopercle compressed and bifurcate (132, 0 > 1); metapterygoid anterior process rounded (138, 0 > 2); ventral crest of hyomandibula absent (142, 0 > 1); second external branchiostegal ray almost as wide as first ray (148, 0 > 1); anterior portion of anterior ceratohyal compressed (150, 0 > 1); anterior margin of urohyal not notched (154, 0 > 1); posterolateral processes of urohyal short (160, 1 > 0); transverse crest associated with neural spine of fourth vertebra very high (200, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1); general aspect of superficial ventral ossification of Weberian ossification regularly arched (211, 0 > 1); 18 or fewer precaudal vertebrae (215, 1 > 0); second dorsal cleithral process dorsally directed and parallel to first dorsal process (226, 0 > 1).

Ambiguous optimization: Temporal fossa very reduced (39, 1 > 0); anterior margin of otolith markedly irregular, concave (71, ? > 3); anterior opening of aortic canal within base of subvertebral process and anteriorly oriented (77, ? > 2); ventral tip of subvertebral process spatulate (80, ? > 3).

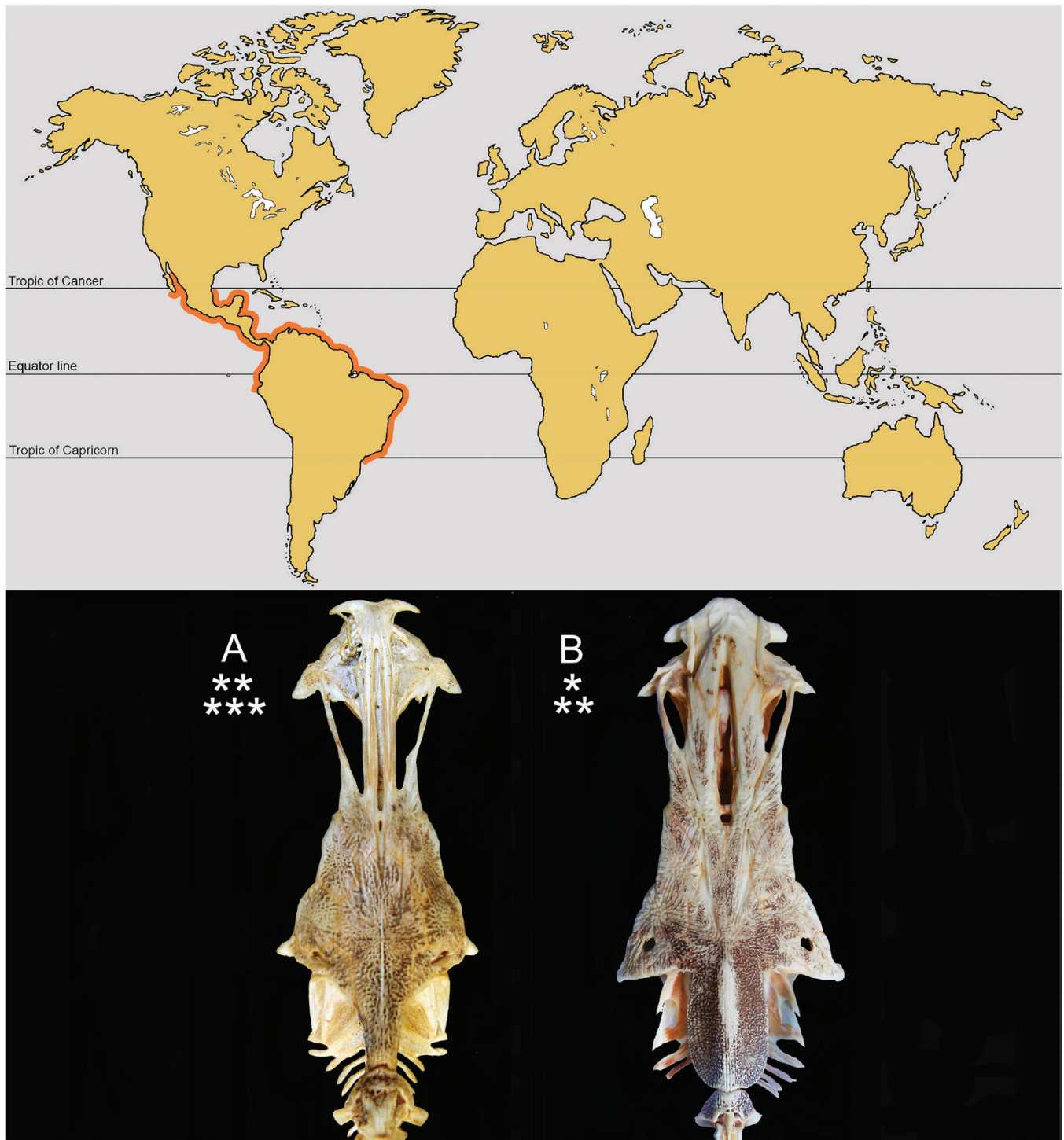


Figure 9. Representative skulls, in dorsal view, and distribution of **Cathoropsini tribe nov.** A, *Cathorops hypophthalmus*, USNM 293275. B, *Notarius grandicassis*, MPEG 30647. * marine, ** brackish waters, *** freshwater.

Included species

Cathorops agassizii (Eigenmann & Eigenmann, 1888)
Cathorops aguadulce (Meek, 1904)
Cathorops arenatus (Valenciennes, 1840)
Cathorops belizensis Marceniuk & Betancur-R., 2008 *
Cathorops dasycephalus (Günther, 1864)
Cathorops festae (Boulenger, 1898)
Cathorops fuerthii (Steindachner, 1876)

Cathorops higuchii Marceniuk & Betancur-R., 2008
Cathorops hypophthalmus (Steindachner, 1876)
Cathorops kailolae Marceniuk & Betancur-R., 2008 *
Cathorops liropus (Bristol, 1897) *
Cathorops manglarensis Marceniuk, 2007
Cathorops mapale Betancur-R. & Acero P., 2005
Cathorops melanopus (Günther, 1864) *
Cathorops multiradiatus (Günther, 1864)



Figure 10. *Cathorops hypophthalmus*, USNM 293275, Panama Pacific drainage rivers, type species of the genus.

Cathorops nuchalis (Günther, 1864) *

Cathorops raredonae Marceniuk, Betancur-R. & Acero P., 2009

Cathorops spixii (Agassiz, 1829) *

Cathorops steindachneri (Gilbert & Starks, 1904)

Cathorops taylori (Hildebrand, 1925)

Cathorops tuyra (Meek & Hildebrand, 1923)

Cathorops wayuu Betancur-R., Acero P. & Marceniuk, 2012.

Habitat and distribution: Fresh and brackish waters, eastern and western Central and South America (Fig. 9).

Remarks

The monophyly *Cathorops* has been shown to be well supported in previous studies (Betancur-R. *et al.* 2007, Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk *et al.* 2012), but there is no consensus regarding their relationships in previous morphological and molecular studies (Betancur-R. *et al.* 2007, Betancur-R. 2009, Marceniuk *et al.* 2012). Results of the total-evidence analysis corroborates the monophyly of *Cathorops* and its sister group relationship with *Notarius* (including *Aspistor*), as postulated in previous molecular studies.

Within *Cathorops*, species share a suite of molecular and morphological characters not found in the species of *Cathorops dasycephalus*. The total-evidence hypothesis presented above places *Cathorops dasycephalus* as the sister group to all remaining *Cathorops*, and was assigned to a separate subgenus *Cathorops (Precathorops)* Betancur-R. & Acero P. (2007). Morphological character states shared by the remaining species, in *Cathorops (Cathorops)*, are as follows: fenestra delimited by mesethmoid and lateral ethmoid present (3, 0 > 1); fenestra delimited by mesethmoid and lateral ethmoid small, not filled with cartilage (4, ? > 0); mesethmoid posterior horn tubular, narrow and elongate (5, 0 > 1); posterior branches of mesethmoid very long, delimiting one-half of length of anterior cranial fontanel (8, 0 > 2); posterior cranial fontanel reduced to a small opening (27, 1 > 0); extrascapular delimiting more than three-fifths of temporal fossa (40, 0 > 1); tooth plates associated with vomer absent (55, 1 > 0); accessory tooth plates molariform (61, 0 > 1); ventral process at symphysis of dentary long and very conspicuous (115,

1 > 2); teeth acicular and molariform on dentary (117, 0 > 1); metapterygoid one and a one-half times longer than deep in perpendicular section (135, 1 > 2); first hypobranchial very elongate transversely, its mesial face well developed and acute 172 (0 > 1); anterior process of first hypobranchial inconspicuous (173, 0 > 1); second hypobranchial very elongate transversely, its mesial face acute (176, 0 > 1); space for insertion of teeth on fifth ceratobranchial very small (194, 1 > 2); cardinal veins at same level of aortic canal (210, 0 > 1); posterior process of cleithrum very short (224, 1 > 0); cleithrum lateral face very narrow (227, 0 > 1).

Ambiguous optimization: Posterior cranial fontanel formed exclusively frontals (25, 0 > 1).

Notarius Gill, 1863

MP 100, BI 1, ML 93

(Figs 1–3, 9B, 11)

Type species: *Arius grandicassius* Valenciennes, 1840.

Diagnosis

Epiphyseal bar transversely elongate and longitudinally narrow (29, 0 > 1); medial groove of cranium absent 30 (0 > 1); vomer anterior margin very pronounced and acute (50, 0 > 1); parasphenoid very wide in ventral view (66, 0 > 1); posterior process of exoccipital absent (90, 1 > 0); exoccipital bony crest parallel to vertebral column and mesially folded (92, 1 > 2); sesamoid bone I irregularly shaped (145, 1 > 2); accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra present (204, 0 > 1).

Ambiguous optimization: Lateral horn of lateral ethmoid acute (11, 1 > 0); interior margin of otolith straight or slightly irregular (71, 0 > 1); anterior opening of aortic canal at base of subvertebral process and anteroventrally oriented (77, ? > 1); ventral tip of subvertebral process acute (80, ? > 2); adipose-fin base long (222, 3 > 1); gas bladder lateral diverticula present (243, 0 > 1).



Figure 11. *Notarius grandicassis*, MNHN A-4608, Atlantic South America, type species of the genus.

Included species

Notarius armbrusteri Betancur-R. & Acero P., 2006
Notarius biffi Betancur-R. & Acero P., 2004
Notarius bonillai (Miles, 1945)
Notarius cookei (Acero P. & Betancur-R., 2002)
Notarius grandicassis (Valenciennes, 1840)
Notarius insculptus (Jordan & Gilbert, 1883)
Notarius kessleri (Steindachner, 1876)
Notarius aff. *kessleri*
Notarius lentiginosus (Eigenmann & Eigenmann, 1888)
Notarius luniscutis (Valenciennes, 1840)
Notarius neogranatensis (Acero P. & Betancur-R., 2002)
Notarius osculus (Jordan & Gilbert, 1883) *
Notarius parmocassis (Valenciennes, 1840) *
Notarius phrygiatus (Valenciennes, 1840)
Notarius planiceps (Steindachner, 1876)
Notarius aff. *planiceps*
Notarius quadriscutis (Valenciennes, 1840)
Notarius rugispinis (Valenciennes, 1840)
Notarius troschelii (Gill, 1863).

Habitat and distribution: Brackish and marine waters, eastern and western Central and South America (Fig. 9).

Remarks

The total-evidence analysis corroborates the monophyly, relationships, and species composition of *Notarius* as previously uncovered by molecular evidence (Betancur-R. et al. 2007; Betancur-R. 2009). The generic names *Amphiarius* and *Aspistor*, recognized as valid in previous morphological analyses (Marceniuk and Menezes 2007, Marceniuk et al. 2012), are treated herein as junior synonyms of *Notarius*.

Genidentini tribe nov.

BI 0.50

(Figs 3, 12, 14)

ZooBank registration: [urn:lsid:zoobank.org:act:0A08A650-D594-4104-8789-89C13E57B3F9](https://zoobank.org/urn:lsid:zoobank.org:act:0A08A650-D594-4104-8789-89C13E57B3F9).

Type genus: *Genidens* Castelnau, 1855.

Diagnosis (all of ambiguous optimization)

Posterior cranial fontanel small (27, 1 > 0), state 1 in *Paragenidens*; pterotic mesial border with parieto-supraoccipital longer than anterior border with sphenotic (36, 0 > 1), reversed in *Genidens*; vomer lateral processes very narrow (53, 0 > 1); tooth plates associated with vomer absent (55, 1 > 0), reversed in *Genidens* (except *Genidens genidens*); maxilla mesial and lateral margins parallel in proximal two-thirds, converging in distal one-third, distal margin truncate (102, 2 > 0), state 3 in *Paragenidens*.

Included genera

Chinchaysuyoa Marceniuk et al. 2019
Genidens Castelnau, 1855
Paragenidens Marceniuk et al. 2019.

Remarks

Within Genidentini, *Genidens* and *Paragenidens* share a suite of molecular and morphological characters not found in *Chinchaysuyoa*. The total-evidence hypothesis places *Genidens* and *Paragenidens* as sister groups, sharing the following morphological character states: lateral margins of orbitosphenoid progressively diverging anteriorly (63, 0 > 1); second basibranchial spindle shaped (166, 1 > 0); second dorsal cleithral process dorsally directed and parallel to first dorsal process (226, 0 > 1).

Ambiguous optimization: Medial groove of cranium delimited mainly by parieto-supraoccipital (32, 1 > 0); extrascapular subrectangular (37, 1 > 0).

Chinchaysuyoa Marceniuk et al. 2019

(Figs 1–3, 12A–13)

Type species: *Arius labiatus* Boulenger, 1898.

Diagnosis

Mesethmoid posterior horn tubular, narrow, and elongate (5, 0 > 1); bony bridge formed by lateral ethmoid and frontal cylindrical and thin (16, 0 > 1); vomer anterior margin very pronounced and acute (50, 0 > 1); accessory tooth plates small, transversely elongate, and narrow (60, 2 > 0); optic foramen

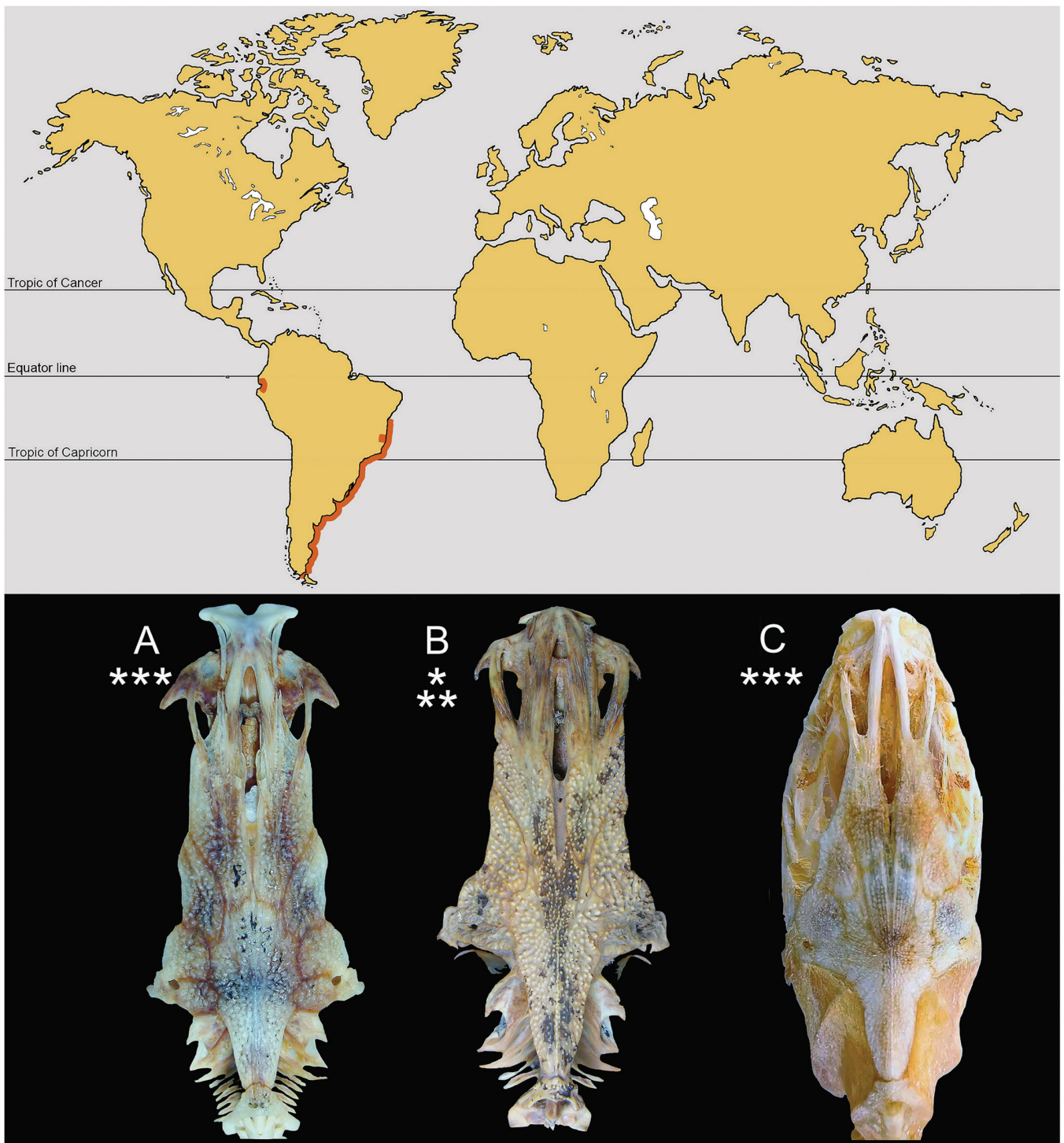


Figure 12. Representative skulls, in dorsal view, and distribution of **Genidentini tribe nov.** A, *Chinchaysuyoa ortegai*, MPEG 35976. B, *Genidens genidens*, MZUSP 51694. C, *Paragenidens grandoculis*, CIUFES 3763. * marine, ** brackish waters, *** freshwater.

very reduced (67, $1 > 2$); anterior opening of aortic canal at base of subvertebral process and anteroventrally oriented (77, $0 > 1$); posterior process of exoccipital connected to Müllerian ramus by suture (93, $0 > 1$); one-half or less of interopercle posterior part contacting ventral margin of opercle (131, $1 > 0$); anterior portion of interopercle compressed and bifurcate (132, $0 > 1$); interopercle anterior portion conspicuously narrow (133, $0 > 1$); metapterygoid one and a one-half times longer than deep in perpendicular section (135, $1 > 2$); uncinat process of third

epibranchial much longer and wider than mesial portion of third epibranchial delimited by uncinat process (182, $0 > 1$); posterior process of cleithrum very long (224, $1 > 2$); gas bladder with three chambers (238, $0 > 2$).

Included species

Chinchaysuyoa ortegai Marceniuk, Marchena, Oliveira & Betancur-R., 2019

Chinchaysuyoa labiata (Boulenger, 1898) *.



Figure 13. *Chinchaysuyoia labiata*, MZUT 1540, western Ecuador Guayas River Basin, type species of the genus.



Figure 14. *Genidens genidens*, western South Atlantic, photograph by Alexandre P. Marceniuk, type species of the genus.

Habitat and distribution: Freshwater, western South America in Ecuador and Peru (Fig. 12).

Remarks

The total-evidence analysis corroborates the monophyly, relationships, and species composition of *Chinchaysuyoia*, as proposed by Marceniuk *et al.* (2019b).

Genidens Castelnau, 1855

MP 100, BI 1, ML 100

(Figs 1–3, 12B, 14)

Type species: *Bagrus genidens* Valenciennes, 1840.

Diagnosis

Temporal fossa very reduced (39, 1 > 0); dentary teeth restricted to mesial two-thirds (116, 1 > 0); posterolateral processes of urohyal short (160, 1 > 0); posterolateral processes of urohyal two-thirds as long as distal portion of bone (162, 1 > 2); posterior portion of second basibranchial short and wide (167, 2 > 3).

Ambiguous optimization: Mesial border with parieto-supraoccipital as long as distal portion of bone (36, 1 > 0); tooth plates attached to vomer by ligaments (57, 0 > 1); otolith posterior margin rounded (74, 1 > 0); posterolateral processes of urohyal as long as or longer than distal portion of bone (162, 0 > 1).

Included species

Genidens barbatus (Lacepède, 1803)

Genidens genidens (Cuvier, 1829)

Genidens machadoi (Miranda Ribeiro, 1918)

Genidens planifrons (Higuchi, Reis & Araújo, 1982).

Habitat and distribution: Brackish and marine waters, east and southern South America (Fig. 12).

Remarks

Total-evidence analysis supports the monophyly of *Genidens*, as reported in previous phylogenetic studies (Betancur-R. 2009, Marceniuk *et al.* 2012), with a new hypothesis of relationships. The species of *Genidens* form a species flock, as evidenced by their shallow genetic divergences (Cerqueira *et al.*, unpublished work).

Paragenidens Marceniuk *et al.* 2019

(Figs 1–3, 12C, 15)

Type species: *Arius grandoculis* Steindachner, 1877.*Diagnosis*

Mesethmoid median portion very narrow (2, 1 > 0); lateral horn of lateral ethmoid long and posteriorly oriented (12, 1 > 2); bony bridge formed by lateral ethmoid and frontal cylindrical and thin (16, 0 > 1); frontal mesial laminar projection absent (23, 1 > 0); anterior margin of vomer very pronounced and acute (50, 0 > 1); lateral expansions of orbitosphenoid and pterosphonoid absent (64, 1 > 0); optic foramen very large (67, 1 > 0), homoplastic in *Potamarius*; distance between optic foramen and trigemino-facialis foramen small, equal to width of trigemino-facialis foramen (68, 1 > 0); contact face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1); transcapular process very short and thick (87, 0 > 1); maxilla lateral and mesial margins considerably closer to each other proximally, distally narrow and pointed (102, 2 > 3); premaxilla very wide and short, only as long as wide (120, 1 > 3); opercle posterior portion well developed posteriorly (129, 0 > 1); interopercle rectangular (134, 0 > 1), homoplastic in *Potamarius*; metapterygoid one and one-half times longer than deep in perpendicular section (135, 1 > 2); metapterygoid anterior process truncate (138, 0 > 1); bony blade connecting posterolateral processes of urohyal absent (159, 0 > 1); third basibranchial long and narrow (169, 1 > 2); third pharyngobranchial funnel shaped (192, 1 > 0); 14 or fewer ribs (213, 1 > 0).

Ambiguous optimization: Posterior cranial fontanel relatively narrow and long (27, 0 > 1).

Included species

Paragenidens grandoculis (Steindachner, 1877).

Habitat and distribution: Fresh and brackish waters, east coast of Brazil (Fig. 12).

Remarks

The total-evidence analysis corroborates the result of a previous morphological and molecular study that supports the recognition of *Paragenidens* (Marceniuk *et al.* 2019c).

Sciadeini tribe nov.

MP 84, BI 1, ML 98

(Figs 1–3, 16)

ZooBank registration: [urn:lsid:zoobank.org:act:02882C05-C5B8-48C9-B796-0339081B8412](https://zoobank.org/urn:lsid:zoobank.org:act:02882C05-C5B8-48C9-B796-0339081B8412).

Type genus: *Sciades* Müller & Troschel, 1849.

Diagnosis

Posterior branch of lateral ethmoid depressed (13, 0 > 1), reversed in *Potamarius izabalensis*; posterior process of exoccipital connected to Müllerian ramus by suture (93, 0 > 1).

Ambiguous optimization: Posterior cranial fontanel absent (26, 1 > 0), reversed in *Potamarius*; epiphyseal bar indistinct (28, 0 > 1), reversed in *Potamarius*; temporal fossa absent (38, 0 > 1); subvertebral process indistinct or weakly developed (78, 1 > 0), reversed in *Potamarius*.

Included genera

Ariopsis Gill, 1861

Potamarius Hubbs & Miller, 1960

Sciades Müller & Troschel, 1849.

Remarks

The total-evidence analysis brings significant results concerning the definition of limits and species composition of *Sciades*. The present analysis supports the hypothesis of monophyly, relationships, and species composition as defined based on previous molecular studies (Betancur-R. *et al.* 2007, Betancur-R. 2009). The inclusion of Old World species in *Sciades* (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012), here assigned to *Hexanematichthys* or *Pseudosciades*, is interpreted as a result of morphological convergence, mainly smaller skull openings (characters 26, 28, and 93).

Ariopsis Gill, 1861

MP 100, BI 1, ML 99

(Figs 1–3, 16A, 17)

Type species: *Arius milberti* Valenciennes, 1840.

Diagnosis (all of ambiguous optimization)



Figure 15. *Paragenidens grandoculis*, LBP 24068, coastal lakes and estuaries of south-eastern Brazil, type species of the genus.

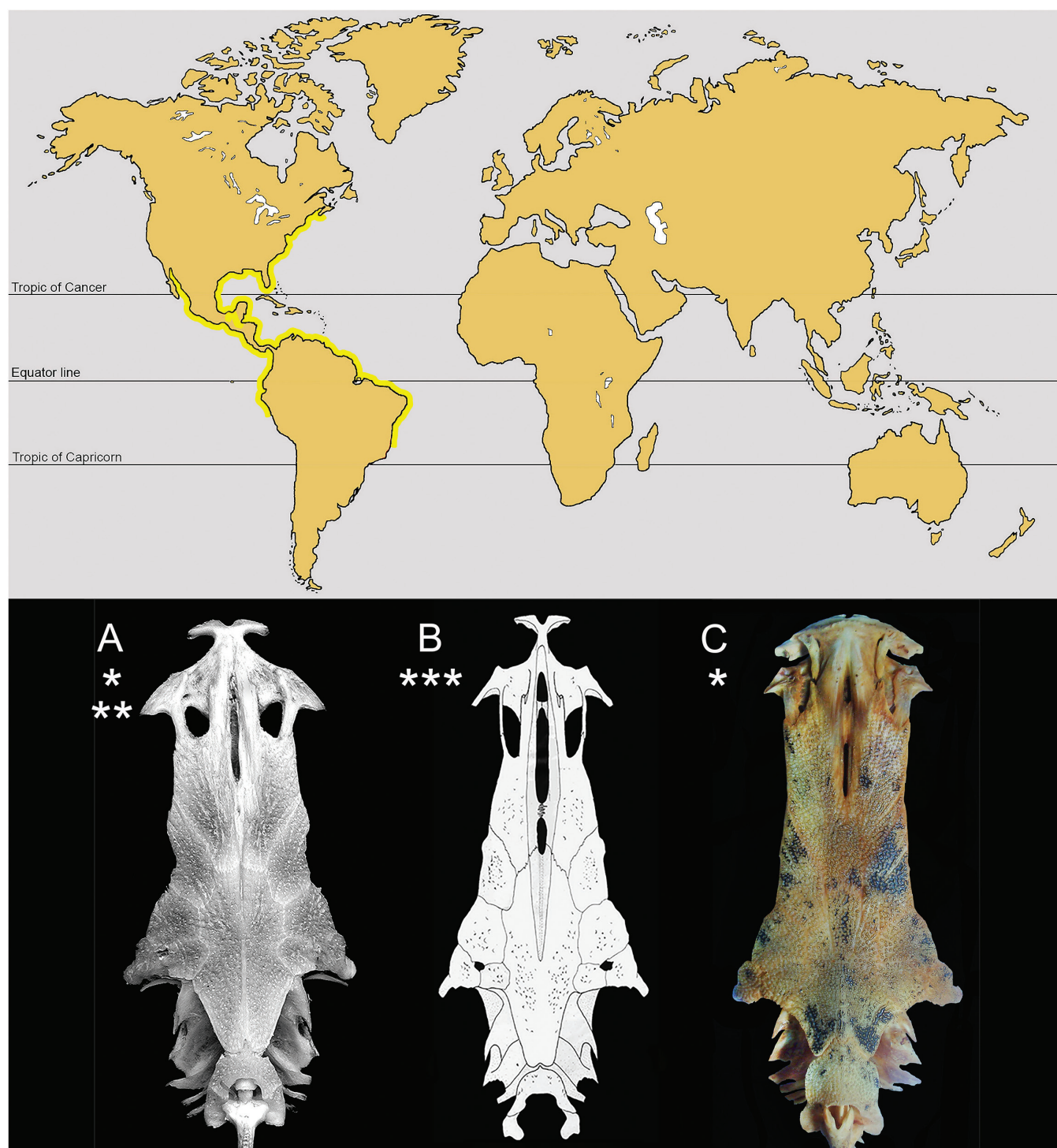


Figure 16. Representative skulls, in dorsal view, and distribution of **Sciadeini tribe nov.** A, *Ariopsis felis*, <http://catfishbone.acnatsci.org>. B, *Potamarius izabalensis*, UMMZ 177252. C, *Sciades parkeri*, MPEG APM 147. * marine, ** brackish waters, *** freshwater.

Third basibranchial chalice shaped (168, 0 > 1), reversed in *Ariopsis guatemalensis*; Müllerian ramus bone blade evident only in basal third (206, 2 > 1), state 2 in *Ariopsis canteri*.

Included species

Ariopsis assimilis Günther, 1864 *

Ariopsis canteri Acero P, Betancur-R. & Marceniuk, 2017

Ariopsis felis Linnaeus, 1766

Ariopsis gilberti Jordan & Williams, 1895 *

Ariopsis guatemalensis Günther, 1864

Ariopsis jimenezi Marceniuk et al., 2017 *

Ariopsis seemanni Günther, 1864

Ariopsis simonsi Starks, 1906.

Habitat and distribution: Freshwater, brackish, and marine waters, North America, Central America and northern South America (Fig. 16).

Remarks

The total-evidence analysis corroborates the monophyly of *Ariopsis* and the relationships established by molecular data (Betancur-R. *et al.* 2007, Betancur-R. 2009), with the same species composition as in the recent revision of the genus (Marceniuk *et al.* 2017b). The overall morphological similarity of *Sciades* and *Ariopsis* is expressed by the synonymy of the genera in previous morphological analyses (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012).

Potamarius Hubbs & Miller, 1960

MP 100, BI 1, ML 100

(Figs 1–3, 16B, 18)

Type species: *Conorhynchos nelsoni* Evermann & Goldsborough, 1902.

Diagnosis

Epioccipital contacting small narrow area of diagonal crest associated with neural spine of fourth vertebra (44, 2 > 0); lateral margins of orbitosphenoid progressively diverging anteriorly (63, 0 > 1); optic foramen very large (67, 1 > 0); distance between optic foramen and trigemino-facialis foramen small, equal to width of trigemino-facialis foramen (68, 1 > 0); contact face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1); opercle posterior portion well developed posteriodorsally (129, 0 > 1); interopercle rectangular (134, 0 > 1).

Ambiguous optimization: Posterior cranial fontanel present (26, 0 > 1); epiphyseal bar conspicuous (28, 1 > 0); temporal fossa present (38, 1 > 0); vomer lateral processes very narrow (53, 0 > 1); subvertebral process well developed (78, 0 > 1); maxilla lateral and mesial margins considerably closer to each other proximally, distally narrow and pointed (102, 2 > 3); metapterygoid anterior process truncate (138, 0 > 1); second basibranchial spindle-shaped (166, 1 > 0); third basibranchial very short and wide (169, 1 > 0); extension of diagonal crest associated with posterior branch of parapophysis of complex vertebra short, reaching transverse crest (199, 1 > 0); opening delimited by epioccipital posterior process and crests of sustentaculum of Weberian apparatus very large (203, 2 > 0); 14 or fewer ribs (213, 1 > 0); second dorsal cleithral process dorsally directed and parallel to first dorsal process (226, 0 > 1); protractor muscle of parapophysis of fourth vertebra originating from ventral surface of parieto-supraoccipital process and posterior process of epioccipital (248, 1 > 0).

Included species

Potamarius izabalensis Hubbs & Miller, 1960

Potamarius nelsoni Evermann & Goldsborough, 1902

Potamarius usumacintae Betancur-R. & Willink, 2007.

Habitat and distribution: Freshwater, eastern Central America (Fig. 16).

Remarks

The total-evidence analysis corroborates the monophyly, relationships and species composition of *Potamarius sensu*



Figure 17. *Ariopsis felis*, MNHN B-0593 (senior synonym of *Arius milberti*), north-western Atlantic, type species of the genus.



Figure 18. *Potamarius nelsoni*, Usumacinta River Basin, Mexico and Guatemala, photograph by Heok Hee Ng, type species of the genus.



Figure 19. *Sciades parkeri* (Traill, 1832), ZMB 2990 [senior synonym of *Bagrus* (*Sciades*) *emphysetus*], coastal rivers from Guyana to northern Brazil, type species of the genus.

Betancur-R. et al. (2007) and Betancur-R. (2009), with results showing that the previous inclusion of *Paragenidens grandoculis* in *Potamarius* (Marceniuk and Menezes 2007, Marceniuk et al. 2012) was the result of morphological convergence (characters 64, 67, 68, 120), apparently the result of secondary invasion of freshwater environments (Marceniuk et al. 2019b, c).

Sciades Müller & Troschel, 1849

MP 100, BI 1, ML 100

(Figs 1–3, 16C, 19)

Type species: *Bagrus* (*Sciades*) *emphysetus* Müller & Troschel, 1849.

Diagnosis

Lateral horn of lateral ethmoid acute (11, 1 > 0), reversed in *Sciades couma* and *Sciades herzbergii*; fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, 1 > 0); orbitosphenoid and pterosphenoid lateral expansions very narrow and long (65, 0 > 1), reversed in *Sciades couma* and *Sciades herzbergii*; parasphenoid very wide in ventral view (66, 0 > 1); otic capsule of moderate size, limited by prootic, pterotic, and exoccipital (70, 2 > 1), reversed in *Sciades couma* and *Sciades herzbergii*; space between transcapular process and otic capsule very large (89, 1 > 0), reversed in *Sciades couma* and *Sciades herzbergii*; one-half or less of interopercle posterior part contacting ventral margin of opercle (131, 1 > 0), reversed in *Sciades couma* and *Sciades herzbergii*; Müllerian ramus distal third straight (208, 1 > 0).

Ambiguous optimization: Mesethmoid median portion moderately wide (2, 1 > 2); autopalatine posterior portion conspicuously compressed (106, 0 > 1); articulation of autopalatine with lateral ethmoid mesoposteriorly oriented (110, 0 > 1); lateral margin of premaxilla with a very conspicuous concavity (123, 1 > 2); sesamoid bone I very long and subrectangular (145, 2 > 3); sesamoid bone II irregularly elongate (146, 0 > 1); first external branchiostegal ray proximally narrow and distally broad (147, 1 > 0); reversed in *Sciades couma* and *Sciades herzbergii*; complex formed by anterior and median nuchal plates shield-like (218, 0 > 1); reversed in *Sciades couma*, *Sciades herzbergii*, and *Sciades passany*; nuchal plate overlaying parieto-supraoccipital (220, 1 > 2); groove connecting posterior nostrils present (233, 0 > 1); reversed in *Sciades parkeri* and *Sciades proops*.

Included species

- Sciades couma* (Valenciennes, 1840)
- Sciades dowii* (Gill, 1863)
- Sciades herzbergii* (Bloch, 1794)
- Sciades passany* (Valenciennes, 1840)
- Sciades parkeri* (Traill, 1832)
- Sciades proops* (Valenciennes, 1840).

Habitat and distribution: Brackish and marine waters, eastern South America, from Colombia to east coast of Brazil and western South and Central America from Panama to Ecuador (Fig. 16).

Remarks

See Tribe Sciadeini Remarks.

Key to Old World genera and subtribes of Ariinae

- 12a. Two pairs of accessory tooth plates ... (*incertae sedis*) *Netuma*
- 12b. One pair accessory tooth plates 13
- 13a. Teeth in premaxilla cuspidate; teeth in dentary spatulate or cuspidate; autopalatine depressed and mesially angled in its anterior third 14
- 13b. Teeth in premaxilla acute; teeth in dentary acicular; autopalatine cylindrical 15
- 14a. Maxillary barbel absent; lateral ethmoid contacts frontal ... (Ariina) *Batrachocephalus*
- 14b. Maxillary barbel present; lateral ethmoid not contacting frontal ... (Ariina) *Ketengus*

15a. Maxillary barbel osseous; mental barbels absent ... (Ariina)	<i>Osteogeneiosus</i>
15b. Maxillary barbel fleshy; mental barbels present	16
16a. Fenestra delimited by lateral ethmoid and frontal distinct and very large; posterior process of cleithrum very short; ventral tip of subvertebral process spatulate	17
16b. Fenestra delimited by lateral ethmoid and frontal indistinct to moderately wide; posterior process of cleithrum moderately long to very long; ventral tip of subvertebral process split or acute	22
17a. Tooth band on fifth ceratobranchial very small; dorsal processes of upper (pharyngeal) tooth plate very long and conspicuous, connected by bony blade	18
17b. Tooth band on fifth ceratobranchial very large to moderate; dorsal processes of upper (pharyngeal) tooth plate very short or absent, not connected by bony blade	19
18a. Accessory tooth plates absent; premaxilla wide and moderately long, its width more than three times its length; upper (pharyngeal) tooth plate very long and narrow, its width more than four times its length ... (Doiichthyina)	<i>Nedystoma</i>
18b. Accessory tooth plates present; premaxilla as long as wide; upper (pharyngeal) tooth plate long and narrow, its width three times its length ... (Doiichthyina)	<i>Doiichthys</i>
19a. Fenestra delimited by parieto-supraoccipital, pterotic and sphenotic present; ventral crest of hyomandibula absent; accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra present	20
19b. Fenestra delimited by parieto-supraoccipital, pterotic and sphenotic absent; ventral crest of hyomandibula present; accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra absent	21
20a. Temporal fossa moderate to very large; lateral line not bifurcated at caudal region, extending to dorsal caudal-fin lobe; superficial ventral ossification of Weberian apparatus keeled ... (Ariina)	<i>Cephalocassis</i>
20b. Temporal fossa very reduced; lateral line bifurcated at caudal region, extending to dorsal and ventral caudal-fin lobes; superficial ventral ossification of Weberian apparatus regularly arched ... (Ariina)	<i>Hemipimelodus</i>
21a. Dorsal-fin spine without filament; optic foramen moderately large; posterior cranial fontanel wide and long (Marceniuk et al. 2012: fig. 2B) ... (Ariina)	<i>Hemiaris</i>
21b. Dorsal-fin spine prolonged into a filament; optic foramen very reduced; posterior cranial fontanel very wide and long (Marceniuk et al. 2012: figs 3A, 5B) ... (Doiichthyina)	<i>Nemapteryx</i>
22a. Cleithrum lateral face very narrow; teeth on dentary restricted to mesial two-thirds; anterior portion of anterior cranial fontanel not delimited by dorsal expansion of orbitosphenoid; vomer arrow shaped ... (Ariina)	<i>Cryptarius</i>
22b. Cleithrum lateral face moderately wide; teeth on dentary restricted to mesial one-third; anterior portion of anterior cranial fontanel partially or totally delimited by dorsal expansion of orbitosphenoid; vomer variable, but not arrow shaped	23
23a. Posterior process of cleithrum very long, equal to vertical length of lateral face of cleithrum; ventral surfaces of parapophyses of fifth and sixth vertebrae conspicuously concave; anterior and posterior portions of basioccipital lateral process equally developed	24
23b. Posterior process of cleithrum very short to moderately long, less than one-third to about one-half vertical length of lateral face of cleithrum; ventral surfaces of parapophyses of fifth and sixth vertebrae straight; posterior portion of basioccipital lateral process extending further laterally than anterior portion	26
24a. Premaxilla narrow and very long, its length two to three times in width; Müllerian ramus slender ... (Doiichthyina)	<i>Paracinetodus</i>
24b. Premaxilla very wide and short, as long as wide; Müllerian ramus robust	25
25a. Epioccipital not exposed dorsally; extrascapular subtriangular; accessory tooth plates present; upper (pharyngeal) tooth plate round, as wide as long ... (Doiichthyina)	<i>Cinetodus</i>
25b. Epioccipital exposed dorsally; extrascapular subquadrangular; accessory tooth plates absent; upper (pharyngeal) tooth plate oval, its width twice in its length ... (Doiichthyina)	<i>Pachyula</i>
26a. Lateral line at caudal region bifurcated, reaching dorsal and ventral caudal-fin lobes; accessory tooth plates with molariform teeth (except <i>Arius manillensis</i> and <i>Arius oetik</i>); vomer anterior margin very pronounced and acute; extrascapular subrectangular	27
26b. Lateral line at caudal region not bifurcated, reaching dorsal caudal-fin lobe (except <i>Neoarius hainesi</i>); accessory tooth plates with needle-like teeth; vomer anterior margin weakly pronounced and serrated (except <i>Potamosilurus</i> and <i>Neoarius hainesi</i>); extrascapular subquadrangular or subtriangular (except <i>Brustarius</i> and <i>Pararius proximus</i>)	31
27a. Vomerine tooth plates present, entirely free from vomer; otolith posterior margin irregular; gas bladder lateral diverticula present; urohyal posterolateral processes as long as or longer than distal portion of bone ... (<i>incertae sedis</i>)	<i>Plicofollis</i>
27b. Vomerine tooth plates absent; otolith posterior margin rounded; gas bladder lateral diverticula absent; urohyal posterolateral processes almost as long as distal portion of bone	28
28a. Fenestra delimited by lateral ethmoid and frontal very small or indistinct; second dorsal cleithral process posteriorly directed and parallel to posterior process; pterotic mesial border with parieto-supraoccipital as long as anterior border with sphenotic	<i>Kyataphisa</i>

28b. Fenestra delimited by lateral ethmoid and frontal distinct and moderately wide; second dorsal cleithral process dorsally directed and parallel to first dorsal process; pterotic mesial border with parieto-supraoccipital longer than anterior border with sphenotic	29
29a. Transcapular process depressed; bony blade connecting posterolateral processes of urohyal absent	<i>Jayaramichthys</i>
29b. Transcapular process cylindrical or columnar; bony blade connecting posterolateral processes of urohyal present	30
30a. Orbitosphenoid and pterosphenoid lateral expansions as two short and wide leaf-like processes ... (Ariina)	<i>Betancurichthys</i>
30b. Orbitosphenoid and pterosphenoid lateral expansions as slight projections with straight lateral faces ... (Ariina)	<i>Arius</i>
31a. Posterior cranial fontanel absent	32
31b. Posterior cranial fontanel present	33
32a. Temporal fossa absent ... (Ariina)	<i>Hexanemichthys</i>
32b. Temporal fossa present	35
33a. Accessory tooth plates small, oval to rounded; connection between posterior process of exoccipital and Müllerian ramus by suture; autopalatine posterior portion very compressed ... (Doiichthyina)	<i>Blekeriella</i>
33b. Accessory tooth plates large, oval to subtriangular; connection between posterior process of exoccipital and Müllerian ramus by ligaments; autopalatine posterior portion only slightly compressed	34
34a. Lateral margins of orbitosphenoid progressively diverging anteriorly ... (Doiichthyina)	<i>Pararius</i>
34b. Lateral margins of orbitosphenoid uniformly parallel for entire length ... (Doiichthyina)	<i>Brustarius</i>
35a. Accessory tooth plates absent ... (Doiichthyina)	<i>Potamosilurus</i>
35b. Accessory tooth plates present	36
36a. Posterior branches of mesethmoid very long, delimiting one-half length of anterior cranial fontanel; lateral expansions of orbitosphenoid and pterosphenoid absent ... (Doiichthyina)	<i>Acerichthys</i>
36b. Posterior branches of mesethmoid short, delimiting less than one-half length of anterior cranial fontanel; lateral expansions of orbitosphenoid and pterosphenoid present	37
37a. Accessory tooth plates large, oval to subtriangular	38
37b. Accessory tooth plates small, transversely elongate and narrow or oval to round	39
38a. Margin of parieto-supraoccipital process contacting nuchal plate convex; lateral margins of orbitosphenoid progressively diverging anteriorly ... (Ariina)	<i>Pseudosciades</i>
38b. Margin of parieto-supraoccipital process contacting nuchal plate concave or notched; lateral margins of orbitosphenoid uniformly parallel for entire length ... (<i>incertae sedis</i>)	<i>Carlarius</i>
39a. Accessory tooth plates narrow and oval to rounded ... (Doiichthyina)	<i>Brustarius</i>
39b. Accessory tooth plates transversely elongate and narrow	40
40a. Thirty-nine or more caudal vertebrae; mesial one-fourth of fourth epibranchial robust, almost as wide as long ... (Doiichthyina)	<i>Cochlefelis</i>
40b. Thirty-eight or fewer caudal vertebrae; mesial one-fourth of fourth epibranchial thin, its width about twice its length	41
41a. Posterior cranial fontanel wide and long; articulation of autopalatine with lateral ethmoid slightly displaced to posterior portion of bone ... (Doiichthyina)	<i>Papuaris</i>
41b. Posterior cranial fontanel reduced to a small opening or relatively narrow and long; articulation of autopalatine with lateral ethmoid in middle of bone ... (Doiichthyina)	<i>Nearius</i>

Tribe Ariini Bleeker, 1858

MP 97, BI 1, ML 91

(Figs 1–3)

Type genus: *Arius* Valenciennes, 1840.

Diagnosis (all of ambiguous optimization)

Vomerine tooth plates transversely elongate (56, 1 > 0), state 2 in *Brustarius* (except *Brustarius utarus*) and *Pararius mastersi*; sesamoid bone I short and triangular (145, 1 > 0), state 1 in Ariina, *Betancurichthys*, *Blekeriella*, *Cinetodus*, *Doiichthys*, *Nedystoma*, *Nemapteryx*, and *Pachyula*.

Included subtribes

Incertain sedis Ariini
Ariina Bleeker, 1858
Doiichthyina Weber, 1913.

Remarks

The recognition of the Tribe Ariini corroborates the monophyletic grouping found in the molecular study of *Betancur-R.* (2009), separating the Old World fauna (a monophyletic group within Ariinae, the Tribe Ariini) from the fauna found in the New World (a paraphyletic group within Ariinae). Ariines exhibit a large amount of morphological convergence in taxa occupying similar habitats (e. g., forms restricted to freshwater in general have skulls with more conspicuous openings vs. predominantly marine forms with smaller or no cranial openings).

Ariini incertae sedis

(Figs 1–3, 20)

Included genera

Carlarius Marceniuk & Menezes, 2007
Netuma Bleeker, 1858
Plicofollis Kailola, 2004.

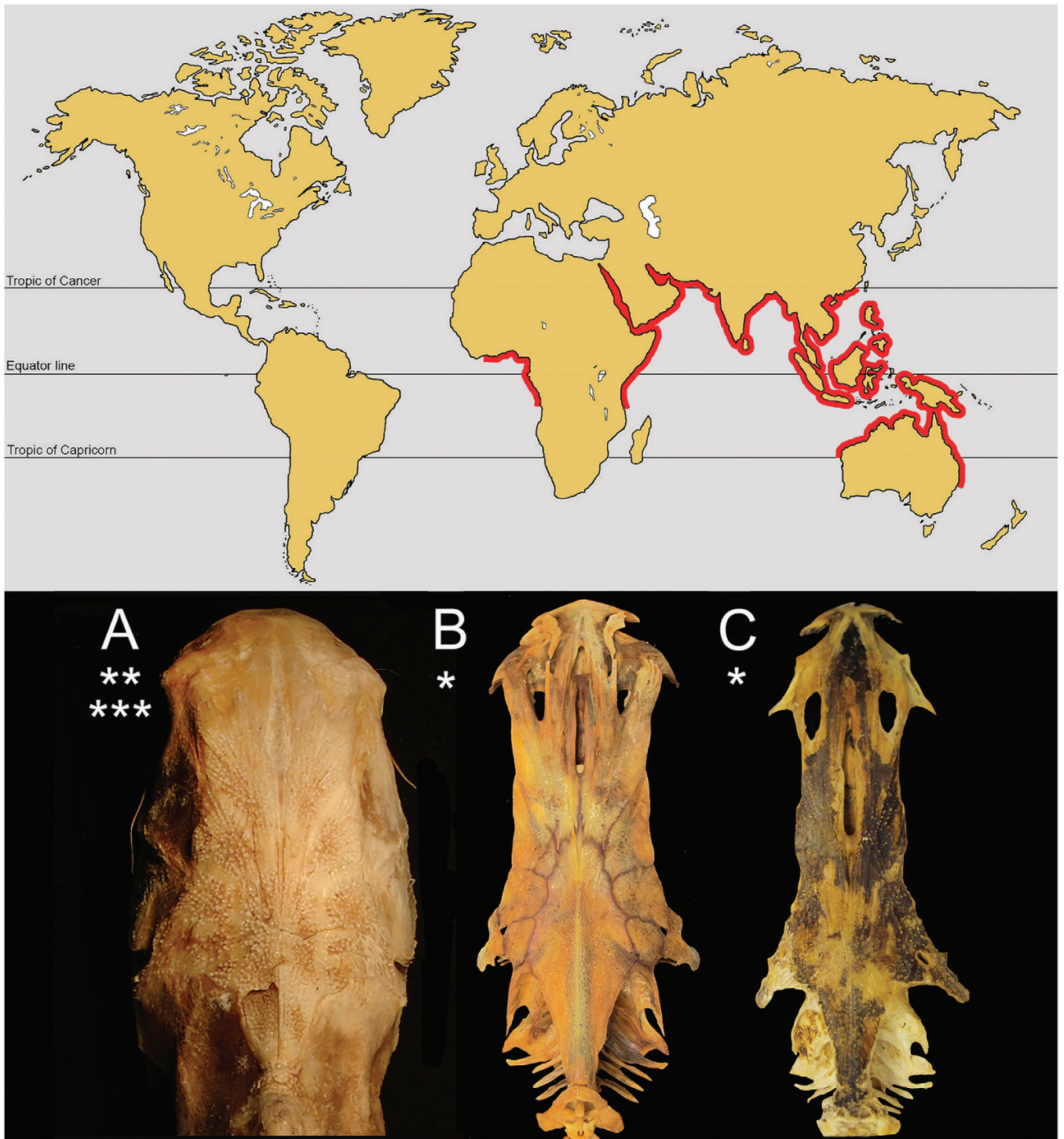


Figure 20. Representative skulls, in dorsal view, and distribution of the Ariini *incertae sedis*. A, *Carlarius heudelotii*, MNHN B-0689. B, *Netuma bilineata*, AUM 47559. C, *Plicofollis argyropleuron*, AUM 44750. * marine, ** brackish water, *** freshwater.

Remarks

The three genera listed here are each monophyletic and all fall within the Ariini, but their positions within that clade differ markedly among the MP, BI, and ML analyses. As such, they are treated here as members of the Ariini, but not included within either of the named subtribes.

Carlarius Marceniuk & Menezes, 2007

MP 100, BI 1, ML 100

(Figs 1–3, 20A, 21)

Type species: *Arius heudelotii* Valenciennes, 1840.



Figure 21. *Carlarius heudelotii*, MNHN B-0689, western-central Africa, type species of the genus.

Diagnosis

Mesial border of pterotic with parieto-supraoccipital longer than anterior border with sphenotic (36, 0 > 1); epioccipital dorsally visible (41, 0 > 1); vomer lateral processes very narrow (53, 0 > 1); tooth plates associated with vomer absent (55, 1 > 0); first external branchiostegal ray proximally narrow and distally broad (147, 1 > 0); posterolateral processes of urohyal almost as long as or longer than distal portion of bone (162, 1 > 0).

Ambiguous optimization: Opercle posterior portion not well developed posteriorly (129, 1 > 0), state 1 in *Carlarius heudelotii*.

Included species

Carlarius gigas (Boulenger, 1911) * *sedis mutabilis*
Carlarius heudelotii Valenciennes, 1840
Carlarius latiscutatus Günther, 1864
Carlarius parkii Günther, 1864.

Habitat and distribution: Fresh and brackish waters, western Africa (Fig. 20).

Remarks

The total-evidence analysis corroborates the monophyly and species composition of *Carlarius* as uncovered previously by morphological and molecular studies (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk et al. 2012), but without consensus regarding its relationships in the MP, BI, and ML analyses.

Netuma Bleeker, 1858

MP 100, BI 1, ML 100

(Figs 1–3, 20B, 22)

Type species: *Bagrus netuma* Valenciennes, 1840.

Diagnosis

Mesethmoid medial notch indistinct, obscured by bone deposition (1, 1 > 2); posterior branch of lateral ethmoid depressed (13, 0 > 1); posterior cranial fontanel reduced to small opening (27, 1 > 0); vomer lateral processes very narrow (53, 0 > 1); accessory

tooth plates two pairs (59, 0 > 1); exoccipital posterior process not supporting Müllerian ramus (94, 1 > 0); dorsal crest of premaxilla beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); metapterygoid anterior process truncate (138, 0 > 1); first external branchiostegal ray narrow proximally and broad distally (147, 1 > 0); posterolateral processes of urohyal posteriorly oriented, forming angle less than 60° (161, 0 > 1); posterior portion of second basibranchial short and wide (167, 2 > 3); third basibranchial chalice shaped (168, 0 > 1); anterior process of first hypobranchial at middle of bone (174, 0 > 1); lateral margin of third pharyngobranchial well developed and acute (193, 0 > 1); adipose-fin base very short (222, 2 > 3); adipose-fin origin vertically above posterior one-half of anal fin (223, 1 > 2); gas bladder lateral diverticula present (243, 0 > 1).

Ambiguous optimization: Mesethmoid median portion moderately wide (2, 2 > 1); lateral line bifurcated, reaching dorsal and ventral caudal-fin lobes (247, 1 > 2).

Included species

Netuma bilineata Valenciennes, 1840
Netuma aff. *bilineata*
Netuma patriciae Takahashi, Kimura & Motomura, 2019
Netuma thalassina Rüppell, 1837.

Habitat and distribution: Brackish and marine waters, eastern Africa, South and Southeast Asia, southern New Guinea, and northern Australia (Fig. 20).

Remarks

Netuma is a well-defined genus that was determined to be monophyletic in previous morphological and molecular studies (Kailola 2004, Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk et al. 2012), a condition corroborated here, but without consensus of its relationships in the MP, BI, and ML analysis.

Plicofollis Kailola, 2004

MP 92, BI 1, ML 100

(Figs 1–3, 20C, 23)

Type species: *Arius argyropleuron* Valenciennes, 1840.



Figure 22. *Netuma thalassina* (Rüppell, 1837), SMF 2627 (senior synonym of *Bagrus netuma*), Red Sea, Indo-West Pacific, East Africa, Persian Gulf east to Philippines, north to southern China, south to Australia, type species of the genus.



Figure 23. *Plicofollis argyropleuron*, South and Southeast Asia, southern New Guinea, and northern Australia, photograph by Ricardo Betancur-R., type species of the genus.

Diagnosis

Posterior branch of lateral ethmoid depressed (13, 0 > 1); parasphenoid very wide in ventral view (66, 0 > 1); maxilla with mesial and lateral margins parallel for proximal two-thirds, converging in distal one-third, distal margin truncate (102, 2 > 0); posterior margin of interopercle straight and inclined (130, 0 > 1); metapterygoid one and one-half times longer than deep in perpendicular section (135, 1 > 2); metapterygoid anterior process truncate (138, 0 > 1); anterior portion of anterior ceratohyal very thick (152, 0 > 1); posterolateral processes of urohyal more than one-half as long as distal portion of bone (162, 2 > 3); gas bladder lateral diverticula present (243, 0 > 1).

Ambiguous optimization: Mesethmoid median portion moderately wide (2, 0 > 1); extension of diagonal crest associated with

posterior branch of parapophysis of complex vertebra short, reaching transverse crest (199, 1 > 0); opening delimited by epioccipital posterior process and crests of sustentaculum of Weberian apparatus moderate (203, 2 > 1).

Included species

Plicofollis argyropleuron Valenciennes, 1840
Plicofollis aff. *argyropleuron* sp 1
Plicofollis aff. *argyropleuron* sp 2
Plicofollis crossocheiros (Bleeker, 1846) * *sedis mutabilis*
Plicofollis dussumieri Valenciennes, 1840
Plicofollis layardi Günther, 1866
Plicofollis aff. *layardi*
Plicofollis magatensis Herre, 1926 *
Plicofollis nella Valenciennes, 1840

Plicofollis platystomus Day, 1877

Plicofollis polystaphylodon Bleeker, 1846

Plicofollis aff. *polystaphylodon*

Plicofollis tenuispinis Day, 1877

Plicofollis tonggol Bleeker, 1846.

Habitat and distribution: Brackish and marine waters, eastern Africa, South and Southeast Asia, southern New Guinea, and northern Australia (Fig. 20).

Remarks

Plicofollis was established by Kailola (2004) based on the examination of *Plicofollis argyroleuron*, *Plicofollis polystaphylodon*, and *Plicofollis nella*. Monophyly of the genus was ratified, and its species composition revised, based on morphological and molecular data (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk et al. 2012, 2017c). The results of the total-evidence analysis corroborate the monophyly of the genus, with the addition of four currently unnamed species, but without consensus on its relationships within the Ariinae (Betancur-R. 2009).

In addition to the diagnostic character states listed above, all species of *Plicofollis* except *Plicofollis platystomus* share the following morphological states. On the basis of this suite of characters, we interpret *Plicofollis platystomus* as the sister to all other species of *Plicofollis*. Posterior cranial fontanel reduced to a small opening (27, 1 > 0); epioccipital dorsally visible (41, 0 > 1); general shape of vomer arrow shaped (49, 1 > 2); vomer lateral processes short (52, 0 > 1); anterior portion of posterior process of vomer as narrow as distal portion (54, 0 > 1); accessory tooth plates large, longitudinally elongate (60, ? > 4); orbitosphenoid and pterosphenoid lateral expansions slight projections with straight lateral faces (65, 0 > 3); lachrymal-antorbital narrow (100, 0 > 1); premaxilla narrow and very long, its length two to three times in width (120, 1 > 2); anteroventral margin of opercle concave or almost straight (128, 0 > 1); anterior portion of interopercle compressed and bifurcate (132, 0 > 1); interopercle subrectangular (134, 0 > 2); posterolateral processes of urohyal short (160, 1 > 0); second basibranchial short and narrow (167, 2 > 4); contact face between first epibranchial and first pharyngobranchial very conspicuous (177, 0 > 1); posterior margin of first epibranchial straight (181, 0 > 1); margin of lateral uncinat process of third epibranchial notched (185, 0 > 1); first pharyngobranchial large and depressed (190, 0 > 1). The following additional morphological character states are shared by species of *Plicofollis* except *Plicofollis platystomus*, but are of ambiguous optimization. Tooth plates associated with vomer present (55, 0 > 1); contact face for articulation of transcapular process with basioccipital small and columnar (85, 1 > 0); exoccipital posterior process not supporting Müllerian ramus (94, 1 > 0); dorsal crest of hyomandibula long and low (141, 1 > 0); posterior end of urohyal truncated (158, 0 > 2); 15 or more ribs (213, 0 > 1); adipose-fin base very short (222, 2 > 3); adipose-fin origin vertically above posterior one-half of anal fin (223, 1 > 2).

Subtribe Ariina Bleeker, 1858

(Figs 1–3, 24)

Diagnosis (all of ambiguous optimization)

Posterior cranial fontanel formed by frontals and parieto-supraoccipital (25, 1 > 0), state 1 in *Arius leptanotacanthus*, *Arius nenga*, *Osteogeneiosus*, and *Pseudosciades*; anterior margin of otolith

straight or slightly irregular (71, 0 > 1), state 0 in *Hemiarius stormii*; otolith posterior margin rounded (74, 1 > 0), state 0 in *Hemiarius stormii*; orientation of exoccipital bony crest perpendicular to vertebral column and directed posteriorly (92, 0 > 1), state 0 in *Hexanematichthys*; sesamoid bone I very long and subtriangular (145, 0 > 1), state 2 in *Osteogeneiosus*; 14 or fewer ribs (213, 1 > 0), state 1 in *Hexanematichthys*; second dorsal cleithral process dorsally directed and parallel to first dorsal process (226, 0 > 1), state 0 in *Arius* aff. *nenga*, *Batrachocephalus*, and *Hexanematichthys*.

Included genera

Arius Valenciennes, 1840

Batrachocephalus Bleeker, 1846

Betancurichthys gen. nov.

Cephalocassis Bleeker, 1852

Cryptarius Kailola, 2004

Jayaramichthys gen. nov.

Kyataphisa gen. nov.

Hemiarius Bleeker, 1862

Hemipimelodus Bleeker, 1857

Hexanematichthys Bleeker, 1858

Ketengus Bleeker, 1846

Osteogeneiosus Bleeker, 1846

Pseudosciades gen. nov.

Remarks

The recognition of the subtribe Ariina corroborates the results of a previous molecular study (Betancur-R. 2009), which uncovered a distinct lineage of the Ariinae in Asia vs. that in Papua New Guinea and Australia (Doiichthyina).

Arius Valenciennes, 1840

(Figs 1–2, 24A–25)

Type species: *Pimelodus arius* Hamilton, 1822.

Diagnosis

Bony bridge formed by lateral ethmoid and frontal cylindrical and thin (16, 0 > 1); frontal mesial laminar projection absent (23, 1 > 0); accessory tooth plates ventral to orbitosphenoid and metapterygoid (62, 0 > 1); orbitosphenoid and pterosphenoid lateral expansions slight projections with sinuous lateral face (65, 0 > 2); autopalatine very compressed at articulation with lateral ethmoid (108, 0 > 1); dorsal crest of premaxilla beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); lateral margin of third pharyngobranchial well developed and acute (193, 0 > 1).

Ambiguous optimization: Müllerian ramus bone blade evident only in basal third (206, 2 > 1).

Included species

Arius acutirostris Day, 1877 * *sedis mutabilis*

Arius africanus Günther, 1867 * *sedis mutabilis*

Arius arenarius Müller & Troschel, 1849 * *sedis mutabilis*

Arius arius Hamilton, 1822

Arius brunellii Zollezi, 1939 * *sedis mutabilis*

Arius burmanicus Day, 1870 * *sedis mutabilis*

Arius dispar Herre, 1926

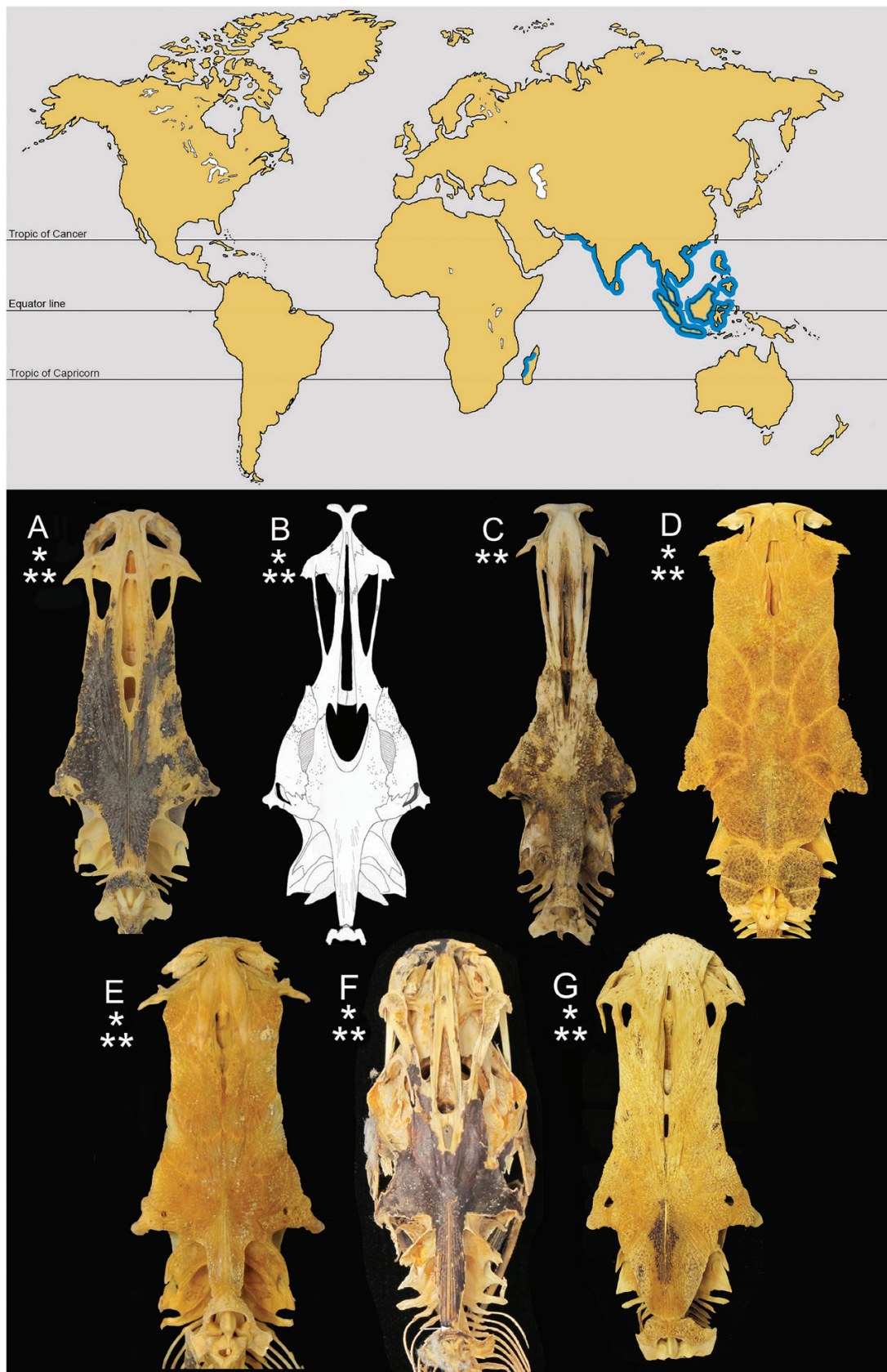


Figure 24. Representative skulls, in dorsal view, and distribution of the subtribe Ariina. A, *Arius maculatus*, AUM 44875. B, *Cephalocassis melanocheir*, CAS 49426. C, *Cryptarius truncatus*, AUM 50243. D, *Hexanematichthys sagor*, AUM 50242. E, *Kyataphisa nenga*, AUM 46280. F, *Osteogeneiosus militaris*, AUM 44880. G, *Pseudosciades sona*, AUM 44861. * marine, ** brackish water, *** freshwater.



Figure 25. *Arius arius*, Indo-West Pacific, photograph by Ricardo Betancur-R., type species of the genus.

Arius gagora Hamilton, 1822

Arius jatius Hamilton, 1822 * *sedis mutabilis*

Arius jella Day, 1877 * *sedis mutabilis*

Arius leptanotacanthus Bleeker, 1849 *sedis mutabilis*

Arius macronotacanthus Bleeker, 1846 * *sedis mutabilis*

Arius maculatus Thunberg, 1792

Arius malabaricus Day, 1877 * *sedis mutabilis*

Arius manillensis Valenciennes, 1840

Arius microcephalus Bleeker, 1855 * *sedis mutabilis*

Arius nenga Hamilton, 1822 *sedis mutabilis*

Arius aff. *nenga* *sedis mutabilis*

Arius oetik Bleeker, 1846

Arius subrostratus Valenciennes, 1840 * *sedis mutabilis*

Arius venosus Valenciennes, 1840 * *sedis mutabilis*.

Habitat and distribution: Fresh and brackish waters, eastern Africa and South to Southeast Asia (Fig. 24).

Remarks

The genus *Arius* undoubtedly has the most complex taxonomy of the Ariidae, serving to accommodate taxa without clear affinities elsewhere (Marceniuk and Menezes 2007). Recent morphological studies have recognized the monophyly of *Arius* with the inclusion of *Betancurichthys madagascariensis* (Marceniuk and Menezes 2007, Marceniuk et al. 2012), an arrangement not supported by Betancur-R. (2009), a molecular study that does not recognize the monophyly of *Arius*. The MP and ML analysis supports the monophyly of *Arius* without *Betancurichthys madagascariensis*.

***Batrachocephalus* Bleeker, 1846**

(Figs 1–3, 26)

Type species: *Batrachocephalus ageneiosus* Bleeker, 1846.

Diagnosis

Mesethmoid median portion very wide (2, 0 > 2); nasal fan shaped (19, 0 > 2); posterior cranial fontanel absent (26,

1 > 0); epiphyseal bar indistinct (28, 0 > 1); sphenotic long and narrow (35, 1 > 0); posterior portion of anterior ceratohyal columnar and very thick (151, 0 > 1); posterior ceratohyal long (153, 0 > 1); anterior margin of urohyal not notched (154, 0 > 1); second dorsal cleithral process posteriorly directed and parallel to posterior process (226, 1 > 0); maxillary barbel absent (234, 0 > 1).

Ambiguous optimization: Anteroventral portion of opercle subtriangular (127, 2 > 3).

Included species

Batrachocephalus mino Hamilton, 1822.

Habitat and distribution: Brackish and marine waters, South and Southeast Asia (Fig. 24).

Remarks

The MP analysis of the data matrix corroborates previous morphological studies (Marceniuk and Menezes 2007, Marceniuk et al. 2012), both in terms of species composition and the relationship of *Batrachocephalus* with *Ketengus* plus *Osteogeneiosus*, which contrasts with the hypothesis of Kailola (2004),

***Betancurichthys* gen. nov.**

(Figs 1–3, 27)

ZooBank registration: urn:lsid:zoobank.org:act:CF91C445-9AA0-4852-8291-6F9FD57C9CD2.

Type species: *Arius madagascariensis* Vaillant, 1894.

Diagnosis

Bony bridge formed by lateral ethmoid and frontal cylindrical and thin (16, 0 > 1); frontal mesial laminar projection absent (23, 1 > 0); posterior cranial fontanel formed by frontals and parieto-supraoccipital (25, 1 > 0); otolith posterior margin rounded (74, 1 > 0); dorsal crest of premaxilla beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); third basibranchial chalice shaped (168, 0 > 1); dorsal-fin spine prolonged into filament (221, 0 > 1).



Figure 26. *Batrachocephalus mino*, FMNH 68052 (senior synonym of *Batrachocephalus ageneiosus*), Indo-West Pacific, type species of the genus.



Figure 27. *Betancurichthys madagascariensis*, MNHN 1894-0002, western Madagascar, type species of the genus.

Ambiguous optimization: Sesamoid bone I very long and subtriangular ($145, 0 > 1$).

Etymology

Named after Colombian ichthyologist Ricardo Betancur-R. for his dedication to the knowledge of the taxonomy, evolution, and biogeography of marine catfishes. Gender: masculine.

Included species

Betancurichthys festinus Ng & Sparks, 2003 * *sedis mutabilis*
Betancurichthys madagascariensis Vaillant, 1894
Betancurichthys uncinatus Ng & Sparks, 2003 * *sedis mutabilis*.

Habitat and distribution: Fresh and brackish waters, western Madagascar (Fig. 24).

Remarks

The genus *Betancurichthys* was established to accommodate species endemic to Madagascar, in the western Indian Ocean, corroborating molecular results presented by [Betancur-R.](#)

(2009). Its inclusion in the Ariina is supported by the BI and ML analyses. The inclusion of *Betancurichthys festinus* and *Betancurichthys uncinatus* in the genus is provisional, based on the distribution and life habits of the species restricted to freshwater in Madagascar.

Cephalocassis Bleeker, 1852

(Figs 1–3, 24B, 28)

Type species: *Arius melanocheir* Bleeker, 1852.

Diagnosis

Posterior branches of mesethmoid narrow ($6, 0 > 1$); posterior branches of mesethmoid parallel throughout their entire extension ($7, 0 > 1$); anterior portion of anterior cranial fontanel not delimited by dorsal expansion of orbitosphenoid ($24, 1 > 0$); fenestra delimited by parieto-supraoccipital, pterotic and sphenotic present ($34, 0 > 1$); parieto-supraoccipital process base almost as narrow as posterior portion ($46, 1 > 0$); vomer anterior margin



Figure 28. *Cephalocassis melanochir*, USNM 230311, Indonesia and Malaysia, type species of the genus.

very pronounced and acute (50, 0 > 1); tooth plates associated with vomer absent (55, 1 > 0); lateral expansions of orbito-sphenoid and pterosphenoid absent (64, 1 > 0); optic foramen very reduced (67, 1 > 2); basioccipital lateral process absent (82, 1 > 0); space between transcapular process and otic capsule very small (89, 1 > 2); teeth on dentary restricted to mesial two-thirds (116, 1 > 0); premaxilla narrow and very long, its length two to three times in width (120, 1 > 2); interopercle anterior portion conspicuously narrow (133, 0 > 1); metapterygoid one and one-half times longer than deep in perpendicular section (135, 1 > 2); ventral crest of hyomandibula absent (142, 0 > 1); second external branchiostegal ray almost as wide as first ray (148, 0 > 1); second basibranchial spindle shaped (166, 1 > 0); first hypobranchial very elongate transversely, with well-developed and acute mesial face (172, 0 > 1); anterior process of first hypobranchial very conspicuous (173, 0 > 1); second hypobranchial very elongate transversely, its mesial face acute (176, 0 > 1); posterior margin of fourth epibranchial slightly convex, one-fourth as wide as long (187, 0 > 1); accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra present (204, 0 > 1).

Ambiguous optimization: Posterior cranial fontanel very wide and long (27, 2 > 3).

Included species

Cephalocassis melanochir Bleeker, 1852.

Habitat and distribution: Freshwater, Southeast Asia (Fig. 24).

Remarks

Hemipimelodus had been treated as a junior synonym of *Cephalocassis* in recent morphological studies (Marceniuk and Menezes 2007, Marceniuk et al. 2012), a condition supported by an extensive list of shared synapomorphies (2, 15, 50, 85, 116, 120, 135, 142, 166, 204, 148, 200, and 222) including an autapomorphy (presence of a fenestra delimited by the supraoccipital, pterotic, and sphenotic). The total-evidence analysis, however, corroborates results of a previous molecular analysis (Betancur-R. 2009), which supports the recognition of *Cephalocassis* and *Hemipimelodus* as valid genera, indicating a strong morphological convergence of lineages restricted to freshwater. The inclusion of *Cephalocassis* in the subtribe Ariina is supported by the MP and ML analyses.

Cryptarius Kailola, 2004

(Figs 1–3, 24C, 29)

Type species: *Arius truncatus* Valenciennes, 1840.

Diagnosis

Mesethmoid medial notch large and shallow (1, 1 > 0); mesethmoid median portion very wide (2, 0 > 2); epioccipital contacting small narrow area of diagonal crest associated with neural spine of fourth vertebra (44, 1 > 0); epioccipital posterior process and medial crest associated with neural spine of fourth vertebra connected (45, 0 > 1); vomer arrow shaped (49, 1 > 3); vomer anterior margin weakly pronounced and serrated (50, 1 > 0); contact face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1); transcapular process at right angle to body axis (86, 0 > 1); articulation between metapterygoid and quadrate by interdigitated suture in small portion of contact and by overlapping in remaining contact area (136, 0 > 1); metapterygoid anterior process rounded (138, 0 > 2); anterior portion of anterior ceratohyal compressed (150, 0 > 1); posterolateral processes of urohyal long (160, 0 > 1); posterolateral processes of urohyal almost as long as distal portion of bone (162, 2 > 0); posterior portion of second basibranchial long and wide (167, 2 > 0); first pharyngobranchial large and depressed (190, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1); gas bladder lateral diverticula present (243, 0 > 1); lateral line not bifurcated, reaching dorsal caudal-fin lobe (247, 2 > 1).

Ambiguous optimization: Interopercle anterior portion thin and acute (133, 0 > 2); transverse crest associated with neural spine of fourth vertebra very high (200, 0 > 1); adipose-fin base very short (222, 2 > 3).

Included species

Cryptarius daugueti Chevey, 1932 * *sedis mutabilis*
Cryptarius truncatus Valenciennes, 1840.

Habitat and distribution: Brackish waters, South and Southeast Asia (Fig. 24).

Remarks

Cryptarius was established by Kailola (2004), and has been recognized as valid by both morphological (Marceniuk and

Menezes 2007, Marceniuk *et al.* 2012) and molecular studies (Betancur-R. 2009), but without consensus on its relationships.

Hemiarus Bleeker, 1862

MP 94, ML 91

(Figs 1–3, 30)

Type species: Cephalocassis stormii Bleeker, 1858.

Diagnosis

Parasphenoid very wide in ventral view (66, 0 > 1); dorsal crest on premaxilla beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); dorsal crest of hyomandibula short and high (141, 0 > 1); third basibranchial chalice shaped (168, 0 > 1); transverse crest associated with neural spine of fourth vertebra very high (200, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1).

Ambiguous optimization: Mesethmoid median portion moderately wide (2, 0 > 1); gas bladder lateral diverticula shallow, rounded bulges (244, 0 > 1).

Included species

Hemiarus bleekeri Popta, 1900 * *sedis mutabilis*
Hemiarus hardenbergi Kailola, 2000 * *sedis mutabilis*
Hemiarus harmandi Sauvage, 1880 * *sedis mutabilis*
Hemiarus manillensis Valenciennes, 1840 * *sedis mutabilis*
Hemiarus stormii Bleeker, 1858
Hemiarus sumatranus Anonymous, 1830
Hemiarus verrucosus Ng, 2003 * *sedis mutabilis*.

Habitat and distribution: Predominantly brackish waters, South and Southeast Asia (Fig. 24).

Remarks

The total-evidence analysis supports the monophyly of *Hemiarus* as observed in previous morphological studies



Figure 29. *Cryptarius truncatus*, South and southeast Asia, photograph by Ricardo Betancur-R., type species of the genus.



Figure 30. *Hemiarus stormii*, BMNH 1863.12.4.65, Thailand, Vietnam, and Indonesia, type species of the genus.

(Marceniuk and Menezes 2007, Marceniuk et al. 2012). The inclusion of *Hemiarius* in the subtribe Ariina is supported by the MP and ML analyses.

Hemipimelodus Bleeker, 1857

(Figs 1–3, 31)

ZooBank registration: [urn:lsid:zoobank.org:act:84D53B59-4ABB-4F76-B370-F9A510BB29F2](https://zoobank.org/urn:lsid:zoobank.org:act:84D53B59-4ABB-4F76-B370-F9A510BB29F2).

Type species: *Pimelodus borneensis* Bleeker, 1851.

Diagnosis

Posterior branches of mesethmoid narrow (6, 0 > 1); posterior branches of mesethmoid parallel along entire extension (7, 0 > 1); fenestra delimited by lateral ethmoid and frontal very large (17, 1 > 2); frontal mesial laminar projection absent (23, 1 > 0); posterior cranial fontanel very wide and long (27, 1 > 3); epiphyseal bar transversely elongate and longitudinally narrow (29, 0 > 1); medial groove of cranium absent (30, 0 > 1); fenestra delimited by parieto-supraoccipital, pterotic and sphenotic present (34, 0 > 1); ventral crest of parieto-supraoccipital process well developed through entire extension of process (48, 0 > 1); accessory tooth plates absent (58, 1 > 0); optic foramen very reduced (67, 1 > 2); ventral tip of subvertebral process spatulate (80, 2 > 3); premaxilla narrow and very long, its length two to three times in width (120, 1 > 2); ventral crest of hyomandibula absent (142, 0 > 1); dorsal crest of urohyal projected anteriorly (156, 0 > 1); anterior process of first hypobranchial inconspicuous (173, 1 > 0); second hypobranchial transversely elongate, its mesial face acute (176, 0 > 1); distal portion of uncinat process of third epibranchial acute (183, 1 > 0); posterior margins of fourth epibranchial slightly convex, one-fourth as wide as long (187, 0 > 1); median crest associated with neural spine of third vertebra very high (201, 0 > 1); accessory crest connecting transverse and median crests associated with neural spine of fourth vertebra present (204, 0 > 1); general aspect of superficial ventral ossification regularly arched (211, 0 > 1); posterior process of cleithrum very short (224, 1 > 0).

Ambiguous optimization: Frontal as main component of bony bridge formed by lateral ethmoid and frontal (15, 0 > 2); third basibranchial hourglass shaped (168, 1 > 0); transverse crest associated with neural spine of fourth vertebra low (200, 1 > 0).

Included species

Hemipimelodus borneensis (Bleeker, 1851).

Habitat and distribution: Freshwater, South and Southeast Asia (Fig. 24).

Remarks

See Remarks of *Cephalocassis*.

Hexanematichthys Bleeker, 1858

(Figs 1–3, 24D, 32)

Type species: *Bagrus sondaicus* Valenciennes, 1840.

Diagnosis

Posterior branches of mesethmoid moderately long, delimiting between one-fourth and one-half of length of anterior cranial fontanel (8, 0 > 1); posterior branch of lateral ethmoid depressed (13, 0 > 1); posterior cranial fontanel absent (26, 1 > 0); epiphyseal bar indistinct (28, 0 > 1); temporal fossa absent (38, 0 > 1); accessory tooth plates small, oval to rounded (60, 2 > 1); lateral margins of orbitosphenoid progressively diverging anteriorly (63, 0 > 1); autopalatine posterior portion conspicuously compressed (106, 0 > 1); articulation of autopalatine with lateral ethmoid mesoposteriorly oriented (110, 0 > 1); lateral and mesial portions of premaxilla with different sizes (121, 0 > 1); anteroventral portion of opercle subtrapezoidal, very long (127, 1 > 0); Müllerian ramus distal third markedly curved (208, 1 > 2).

Ambiguous optimization: Exoccipital bony crest perpendicular to vertebral column and ventrolaterally directed (92, 1 > 0); 15 or more ribs (213, 0 > 1); second dorsal cleithral



Figure 31. *Hemipimelodus macrocephalus* Bleeker, 1858, junior synonym of *Hemipimelodus borneensis* Bleeker, 1851, BMNH 1863.12.4.78, Sundaland, Malaysia to Vietnam, type species of the genus.

process posteriorly directed and parallel to posterior process (226, 1 > 0).

Included species

Hexanemichthys sagor Hamilton, 1822.

Habitat and distribution: Brackish and marine waters, South and Southeast Asia (Fig. 24).

Remarks

The total-evidence analysis supports the validity of *Hexanemichthys*, corroborating the result of a previous molecular study (Betancur-R. 2009) that reveals a strong morphological convergence between *Hexanemichthys* and *Sciades* (characters 26, 28, 93, 106, and 110), which had resulted in them having previously been treated as synonyms (Marceniuk *et al.* 2012).

Jayaramichthys gen. nov.

(Figs 1–3, 33)

ZooBank registration: urn:lsid:zoobank.org:act: 84D53B59-4ABB-4F76-B370-F9A510BB29F2.

Type species: *Arius leptotacanthus* Bleeker, 1849.

Diagnosis

Bony bridge formed by lateral ethmoid and frontal equally represented (15, 0 > 1); accessory tooth plates large, longitudinally elongate (60, 3 > 4); face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1); transcapular process at right angle to body axis (86, 0 > 1); transcapular process depressed (88, 0 > 1); bony blade connecting posterolateral processes of urohyal absent (159, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1).



Figure 32. *Hexanemichthys sagor* (senior synonym of *Bagrus sondaicus*), Indo-West Pacific, photograph by Ricardo Betancur-R., type species of the genus.



Figure 33. *Jayaramichthys leptotacanthus*, Indonesia and Thailand, photograph by Ricardo Betancur-R., type species of the genus.

Ambiguous optimization: Space between transcapular process and otic capsule very small (89, 1 > 2); contact area between interopercle and opercle no more than one-half of interopercle posterior face (131, 1 > 0).

Etymology

Named for the Indian ichthyologist Kottore Chidambaram Jayaram (1926–2011) who contributed greatly to our understanding of the taxonomy, evolution, and biogeography of ariids from the Indian subcontinent. Gender: masculine.

Included species

Jayaramichthys leptotacanthus Bleeker, 1849.

Habitat and distribution: Brackish and marine waters, Southeast Asia (Fig. 24).

Remarks

Jayaramichthys is established to accommodate *Jayaramichthys leptotacanthus*, not examined in a previous morphological study (Marceniuk et al. 2012), but treated as valid (as *Arius leptotacanthus*) in a previous molecular study in Betancur-R. (2009).

***Ketengus* Bleeker, 1846**

(Figs 1–3, 34)

Type species: *Ketengus typus* Bleeker, 1846.

Diagnosis

Mesethmoid medial notch large and shallow (1, 2 > 0); fenestra delimited by mesethmoid and lateral ethmoid present (3, 0 > 1); fenestra delimited by mesethmoid and lateral ethmoid large, filled with cartilage (4, ? > 0); mesethmoid posterior horn tubular, narrow and elongate (5, 0 > 1); posterior branches of mesethmoid narrow (6, 0 > 1); posterior branches of mesethmoid parallel throughout their entire extension (7, 0 > 1); lateral ethmoid not contact frontal (14, 3 > 0); vomer diamond shaped (49, 1 > 0); vomer lateral processes absent (51, 1 > 0); accessory tooth plates absent (58, 1 > 0); three anterior branches in lachrymal-antorbital anterior part (98, 2 > 3); teeth on dentary along entire bone (116, 1 > 2); dorsal crest of premaxilla present (125, 0 > 1); opercle posterior portion not well developed posteriorly (129, 1 > 0); ventral crest of hyomandibula absent (142, 0 > 1); dorsal crest of urohyal projected anteriorly (156, 0 > 1); one basibranchial

series (164, 0 > 1); first hypobranchial club shaped (171, 0 > 1); second hypobranchial club shaped (175, 0 > 1); first epibranchial overlaying second epibranchial (179, 0 > 1); third pharyngobranchial funnel shaped (192, 1 > 0); seventh vertebra free from ventral superficial ossification (214, 0 > 1).

Included species

Ketengus typus Bleeker, 1846.

Habitat and distribution: Brackish waters, South and Southeast Asia (Fig. 24).

Remarks

The close relationship of *Ketengus* plus *Osteogeneiosus* established in previous morphological and molecular studies (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk et al. 2012) is further supported by the results of the total-evidence analysis.

***Kyataphisa* gen. nov.**

MP 100, BI 1, ML 100

(Figs 1–3, 24E, 35)

ZooBank registration: urn:lsid:zoobank.org:act: 2981DCA4-DDB0-49A5-BE7A-6D05DD7E750.

Type species: *Pimelodus nenga* Hamilton, 1822.

Diagnosis

Ambiguous optimization: Posterior branches of mesethmoid moderately long, delimiting between one-fourth and one-half of length of anterior cranial fontanel (8, 0 > 1); fenestra delimited by lateral ethmoid and frontal very small or indistinct (17, 1 > 0); pterotic mesial border with parieto-supraoccipital as long as anterior border with sphenotic (36, 1 > 2); temporal fossa much reduced (39, 0 > 1); accessory tooth plates small, vertically oval (60, 3 > 2); exoccipital posterior process not supporting Müllerian ramus (94, 1 > 0); lateral and mesial portions of premaxilla of different sizes (121, 0 > 1); Müllerian ramus bone blade evident only basally (206, 2 > 1); dorsal-fin spine prolonged into filament (221, 0 > 1); second dorsal cleithral process posteriorly directed and parallel to posterior process (226, 1 > 0).

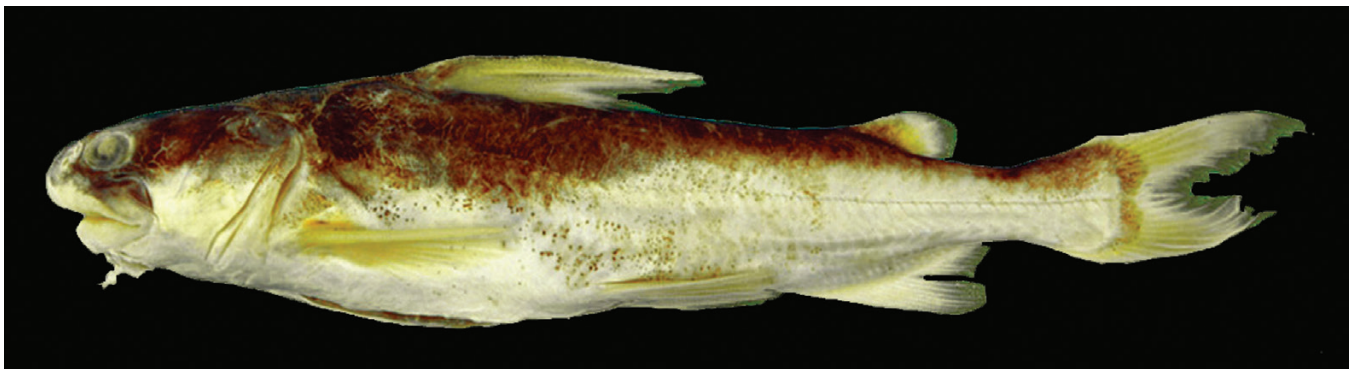


Figure 34. *Ketengus typus*, ANSP 60704, eastern Indian Ocean, type species of the genus.

Etymology

Kyataphisa is from the Bengali, meaning catfish.

Included species

Kyataphisa nenga Hamilton, 1822.

Habitat and distribution: Brackish and marine waters, South and Southeast Asia (Fig. 24).

Remarks

Kyataphisa is established to accommodate *Kyataphisa nenga* and a second species (*Kyataphisa* aff. *nenga*) that was not examined in a previous morphological study (Marceniuk *et al.* 2012), corroborating a previous morphological study (as *Arius caelatus* in Marceniuk *et al.* 2012) and a molecular study (as *Arius nenga* in Betancur-R. 2009).

Osteogeneiosus Bleeker, 1846

(Figs 1–3, 24F, 36)

Type species: *Osteogeneiosus militaris* Linnaeus, 1758.

Diagnosis

Nasal anterior curvature very pronounced (20, 0 > 1); bony blade not connecting nasal tubules anteriorly (21, 1 > 0); frontal mesial laminar projection absent (23, 1 > 0); anterior portion of posterior process of vomer as narrow as posterior portion (54, 0 > 1); accessory tooth plates large, longitudinally elongate (60, 3 > 4); accessory tooth plates situated between premaxilla and lateral ethmoid (62, 1 > 2); maxilla cylindrical, very long and distally acute (101, 0 > 2); autopalatine cylindrical, very short and robust (104, ? > 2); anterior cartilage of autopalatine very short, less than



Figure 35. *Kyataphisa nenga*, Indo-West Pacific, photograph by Ricardo Betancur-R., type species of the genus.



Figure 36. *Osteogeneiosus militaris*, UMMZ 214628, Indo-West Pacific, type species of the genus.

one-third length of bone (113, 1 > 0); autopalatine posterior cartilage reduced to small sphere (114, 1 > 2); anteroventral portion of opercle subtriangular (127, 3 > 4); metapterygoid three times longer than deep (135, 3 > 4); urohyal short (157, 1 > 0); contact face between first epibranchial and first pharyngobranchial very conspicuous (177, 0 > 1); Müllerian ramus distal one-third markedly curved (208, 1 > 2); mental barbel absent (236, 0 > 1); gas bladder lateral diverticula present (243, 0 > 1); gas bladder diverticula present anterolaterally (246, 0 > 1).

Ambiguous optimization: Anterior portion of anterior cranial fontanel partially or totally delimited by dorsal expansion of orbitosphenoid (24, 0 > 1); posterior cranial fontanel formed exclusively frontals (25, 0 > 1); maxillary condyle very large (103, 1 > 3); anteroventral portion of opercle subtrapezoidal, moderately long (127, 2 > 1); second external branchiostegal ray width less than one-half that of first ray (148, 1 > 0); second basibranchial mushroom shaped (166, 0 > 1); third basibranchial hourglass shaped (168, 1 > 0); 19 or more precaudal vertebrae (215, 0 > 1); gas bladder lateral diverticula with diverticula (244, 0 > 1); protractor muscle of parapophysis of fourth vertebra originating exclusively from ventral surface of posterior process of epioccipital (248, 0 > 1).

Included species

Osteogeneiosus militaris (Linnaeus, 1758).

Habitat and distribution: Brackish and marine waters, South and Southeast Asia (Fig. 24).

Remarks

The close relationship of *Osteogeneiosus* with *Ketengus* that was reported in previous morphological and molecular studies (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk *et al.* 2012) is supported by the results of the total-evidence analysis.

Pseudosciades gen. nov.

(Figs 1–3, 24G, 37)

ZooBank registration: urn:lsid:zoobank.org:act: 0A403C08-B65C-4292-B708-2B7E1AC9456D.

Type species: *Arius sona* Hamilton, 1822.

Diagnosis

Posterior branches of mesethmoid moderately long, delimiting between one-fourth and one-half of anterior cranial fontanel length (8, 0 > 1); epioccipital dorsally visible (41, 0 > 1); margin of parieto-supraoccipital process contacting nuchal plate convex (47, 0 > 1); lateral margins of orbitosphenoid progressively diverging anteriorly (63, 0 > 1); lateral and mesial portions of premaxilla of different sizes (121, 0 > 1); anteroventral portion of opercle subtrapezoidal, very long (127, 1 > 0); metapterygoid anterior process truncate (138, 0 > 1); posterior end of urohyal truncated (158, 0 > 2); posterolateral processes of urohyal posteriorly oriented, forming an angle smaller than 60° (161, 0 > 1); Müllerian ramus distal one-third markedly curved (208, 1 > 2); nuchal plate anterior margin slightly concave (219, 0 > 1).

Ambiguous optimization: Posterior cranial fontanel formed exclusively within frontals (25, 0 > 1).

Etymology

Pseudo from Latin, meaning false, in reference to its convergent morphology with the Neotropical genus *Sciades*. Gender: masculine.

Included species

Pseudosciades sona (Hamilton, 1822).

Habitat and distribution: Brackish and marine waters, South and Southeast Asia (Fig. 24).

Remarks

Pseudosciades sona is an Old World species that shares with *Sciades parkeri* (type species of the New World genus *Sciades*) a medial groove of neurocranium delimited mainly by frontal bones, anterior and median nuchal plates forming a shield-like structure, and nuchal plate overlapping parietosupraoccipital, but were shown to be not closely related in the total-evidence analysis or in a previous molecular study (Betancur-R. 2009).



Figure 37. *Pseudosciades sona*, Indo-West Pacific, photograph by Ricardo Betancur-R., type species of the genus.

Subtribe Doiichthyina Weber, 1913

MP 68, BI 1, ML 50

(Figs 1–3, 38)

Type genus: Doiichthys Weber, 1913.*Diagnosis*

Accessory tooth plates small, transversely elongate and narrow (60, 2 > 0), state 3 in *Doiichthys*. *Ambiguous optimization*: Mesethmoid medial notch large and shallow (1, 1 > 0), reversed *Brustarius* (except *Brustarius utarus*), *Cinetodus*, *Neoarius*, *Pachyula*, *Pararius mastersi*, and *Potamosilurus velutinus*; posterior cranial fontanel formed by frontals and parieto-supraoccipital (25, 1 > 0).

Remarks

The recognition of the subtribe Doiichthyina corroborates the results of a previous molecular study (Betancur-R. 2009), which recognized two distinct lineages of Ariina, one in Papua New Guinea and Australia (Doiichthyina) and the other in Asia (Ariina).

Included genera

Aceroichthys gen. nov.
Blekeriella gen. nov.
Brustarius Herre, 1935
Cinetodus Ogilby, 1898
Cochlefelis Whitley, 1941
Doiichthys Weber, 1913
Nedystoma Ogilby, 1898
Nemapteryx Ogilby, 1908
Neoarius Castelnau, 1878
Megalosciades gen. nov.
Pachyula Ogilby, 1898
Paracinetodus gen. nov.
Pararius Whitley, 1940
Papuarius gen. nov.
Potamosilurus Marceniuk & Menezes, 2007.

Aceroichthys gen. nov.

(Figs 1–3, 38E, 39)

Type species: Arius dioctes Kailola, 2000.*Diagnosis*

Posterior branches of mesethmoid very long, delimiting one-half of length of anterior cranial fontanel (8, 0 > 2); lateral horn of lateral ethmoid variable length and laterally oriented (12, 1 > 0); posterior branch of lateral ethmoid depressed (13, 0 > 1); lateral expansions of orbitosphenoid and pterosphenoid absent (64, 1 > 0); parasphenoid very wide in ventral view (66, 0 > 1); exoccipital posterior process not supporting Müllerian ramus (94, 1 > 0); premaxilla wide and short, its length more than four times in width (120, 1 > 0); anteroventral portion of opercle subtrapezoidal, very long (127, 1 > 0); no more than one-half of posterior part of interopercle contacting ventral margin of opercle (131, 1 > 0); posterolateral processes of urohyal almost as long as distal portion of bone (162, 2 > 0).

Etymology

Named after the Colombian ichthyologist Arturo Acero P. (b. 1954) to honour his valuable contributions to ariid taxonomy. Gender: masculine.

*Included species**Aceroichthys dioctes* Kailola, 2000.

Habitat and distribution: Fresh and brackish waters, southern New Guinea and northern Australia (Fig. 38).

Remarks

Aceroichthys is established based on morphological and molecular evidence to accommodate *Aceroichthys dioctes*, with phylogenetic relationships first reported in a molecular study (Betancur-R. 2009).

Blekeriella gen. nov.

MP 100, BI 1, ML 100

(Figs 1–3, 40)

ZooBank registration: [urn:lsid:zoobank.org:act:8CB66BDD-FB43-495E-B45A-EBF42667194F](https://zoobank.org/urn:lsid:zoobank.org:act:8CB66BDD-FB43-495E-B45A-EBF42667194F).

Type species: Arius leptaspis Bleeker, 1862.*Diagnosis (all of ambiguous optimization)*

Posterior branch of lateral ethmoid depressed (13, 0 > 1); posterior cranial fontanel absent (26, 1 > 0); epiphyseal bar indistinct (28, 0 > 1); medial groove of cranium absent (30, 0 > 1); temporal fossa very reduced (39, 1 > 0); posterior process of exoccipital sutured to Müllerian ramus (93, 0 > 1); autopalatine posterior portion conspicuously compressed (106, 0 > 1); articulation of autopalatine with lateral ethmoid posteromesially oriented (110, 0 > 1); lateral and mesial portions of premaxilla with different sizes (121, 0 > 1); anteroventral portion of opercle subtrapezoidal, very long (127, 1 > 0); one-half or less of interopercle posterior part contacting ventral margin of opercle (131, 1 > 0); sesamoid bone I very long and subtriangular (145, 0 > 1); Müllerian ramus bone blade evident only basally (206, 2 > 1); Müllerian ramus distal third markedly curved (208, 1 > 2).

Etymology

Named for the Dutch ichthyologist Pieter Bleeker (1819–1878) who contributed greatly to our understanding of the taxonomy of ariids from the Indo–Malaysian archipelago. Gender: feminine.

*Included species**Blekeriella leptaspis* Bleeker, 1862*Blekeriella* aff. *leptaspis*.

Habitat and distribution: Predominantly brackish waters, southern New Guinea and northern Australia (Fig. 38).

Remarks

Arius leptaspis was previously included in *Ariopsis* Kailola 2004 or *Sciades* (Marceniuk and Menezes 2007, Marceniuk et al. 2012),

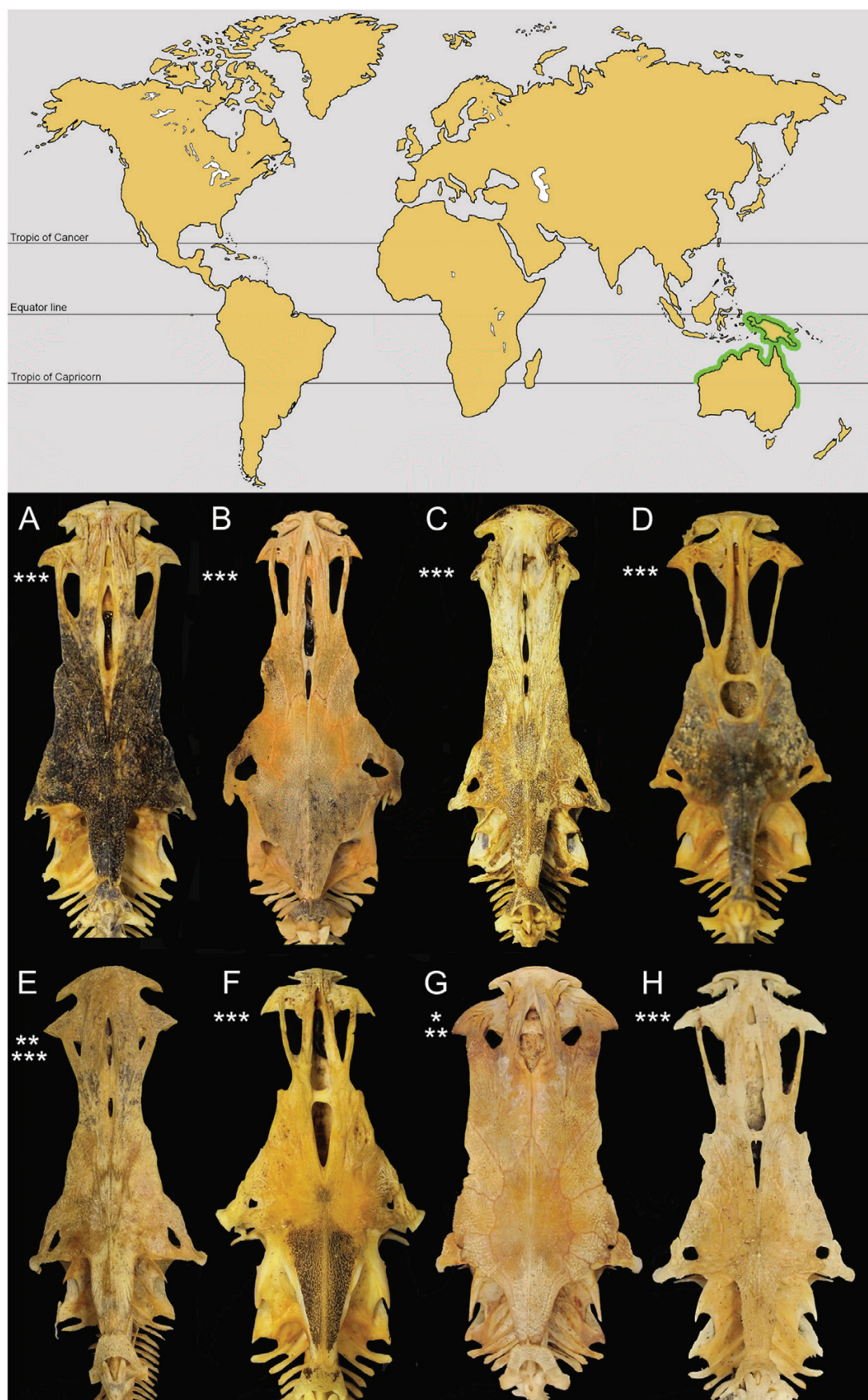


Figure 38. Representative skulls, in dorsal view, and distribution of the subtribe Doiichthyina. A, *Brustiarius nox*, AUM 47488. B, *Paracinetodus carinatus*, AUM 47550. C, *Cochlefelis spatula*, AUM 50296. D, *Nedystoma dayi*, AUM 47500. E, *Acerioichthys dioctes*, AUM 47507. F, *Pachyula crassilabris*, AUM 47509. G, *Pararius proximus*, AUM 47486. H, *Potamosilurus velutinus*, AUM 47489. * marine, ** brackish waters, *** freshwater.



Figure 39. *Aceroichthys dioctes*, Australia and New Guinea, photograph by Ricardo Betancur-R., type species of the genus.



Figure 40. *Bleekeriella leptaspis*, northern Australia and New Guinea, photograph by Ricardo Betancur-R., type species of the genus.

but results of the total-evidence analysis indicate that it is not closely related to species of either genus, but is related closely to an unnamed species from Indonesia. These findings corroborate a previous molecular study (Betancur-R. 2009).

Brustiarius Herre, 1935

MP 100, BI 1, ML 100

(Figs 1–3, 38A, 41)

Type species: *Arius nox* Herre, 1935.

Diagnosis

Accessory tooth plates small, oval to rounded (60, 0 > 1); lateral and mesial portions of premaxilla of different sizes (121, 0 > 1); metapterygoid anterior process acute (138, 1 > 0).

Ambiguous optimization: Posterior cranial fontanel small (27, 1 > 0); vomer lateral processes very narrow (53, 0 > 1); maxilla lateral and mesial margins considerably closer to each other

proximally, distally narrow and pointed (102, 2 > 3); articulation of autopalatine with lateral ethmoid in middle of bone (111, 2 > 1); first external branchiostegal ray narrow proximally and broad distally (147, 1 > 0); posterior ceratohyal long (153, 0 > 1).

Included species

Brustiarius nox Herre, 1935

Brustiarius solidus Herre, 1935

Brustiarius utarus Kailola, 1990.

Habitat and distribution: Freshwater, northern New Guinea (Fig. 38).

Remarks

As indicated by the total-evidence analysis, *Brustiarius* follows the definition and species composition proposed in previous morphological studies (Kailola 2004, Marceniuk and Menezes 2007, Marceniuk et al. 2012), with the inclusion of *Brustiarius utarus* sensu Betancur-R. (2009). The species in *Brustiarius* were treated as a species flock, based on the shallow genetic divergences found by Betancur-R. (2009).

Cinetodus Ogilby, 1898

(Figs 1–3, 42)

Type species: Arius froggatti Ramsay & Ogilby, 1886.*Diagnosis*

Mesethmoid median portion very narrow (2, 2 > 0); extrascapular subtriangular (37, 1 > 2); epioccipital contacting a small narrow area of diagonal crest associated with neural spine of fourth vertebra (44, 1 > 0); vomer anterior margin very pronounced and acute (50, 0 > 1); basioccipital lateral process absent with anterior and posterior portions equally developed (83, 1 > 0); anteroventral portion of opercle subtrapezoidal, very long (127, 1 > 0); metapterygoid one and one-half times longer than deep in perpendicular section (135, 1 > 2); posterolateral processes of urohyal short (160, 1 > 0); third basibranchial chalice shaped (168, 0 > 1); upper (pharyngeal) tooth plate round, as wide as long (195, 1 > 0); dorsal processes of upper

(pharyngeal) tooth plate very short or absent (197, 1 > 0); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1); Müllerian ramus robust (207, 0 > 1); ventral surfaces of parapophyses of fifth and sixth vertebrae conspicuously concave (212, 0 > 1); adipose fin long (222, 2 > 1).

Ambiguous optimization: Mesethmoid medial notch narrow and deep (1, 0 > 1); lateral horn of lateral ethmoid compressed and spatulate (11, 0 > 1); premaxilla very wide and short, as long as wide (120, 1 > 3); posterior process of cleithrum very long (224, 0 > 2).

Included species

Cinetodus froggatti Ramsay & Ogilby, 1886.

Habitat and distribution: Fresh and brackish waters, southern New Guinea and northern Australia (Fig. 38).

Remarks

The results of the total-evidence analysis support the recognition of *Cinetodus* as previously defined by morphological and



Figure 41. *Brustiarius nox*, New Guinea, photograph by Ricardo Betancur-R., type species of the genus.



Figure 42. *Cinetodus froggatti*, USNM 217080, Papua New Guinea and northern Australia, type species of the genus.

molecular data (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk *et al.* 2012), with a new hypothesis of relationships.

Cochlefelis Whitley, 1941

MP 100, BI 1, ML 100

(Figs 1–3, 38C, 43)

Type species: *Arius spatula* Ramsay & Ogilby, 1886.

Diagnosis

Posterior branch of lateral ethmoid depressed (13, 0 > 1); vomer lateral processes very narrow (53, 0 > 1); parasphenoid very wide in ventral view (66, 0 > 1); exoccipital posterior process not supporting Müllerian ramus (94, 1 > 0); maxilla lateral and mesial margins slender proximally, narrow and pointed distally (102, 2 > 3); articulation of autopalatine with lateral ethmoid in middle of bone (111, 2 > 1); premaxilla wide and short, its length more than four times in width (120, 1 > 0); dorsal crest on premaxilla beginning between lateral one-third or one-half of anterior margin (124, 0 > 1); anteroventral portion of opercle subtriangular (127, 1 > 4); one-half or less of interopercle posterior part contacting ventral margin of opercle (131, 1 > 0); first external branchiostegal ray narrow proximally and broad distally (147, 1 > 0); posterior ceratohyal long (153, 0 > 1); third basibranchial long and narrow (169, 1 > 2); mesial one-fourth of fourth epibranchial robust, almost as wide as long (186, 1 > 0); 39 or more caudal vertebrae (216, 1 > 0).

Ambiguous optimization: Posterior cranial fontanel formed exclusively frontals (25, 0 > 1); lateral margin of third pharyngobranchial weakly developed and rounded (193, 1 > 0); 15 or more ribs (213, 0 > 1).

Included species

Cochlefelis danielsi Regan, 1908

Cochlefelis insidiator Kailola, 2000 * *sedis mutabilis*
Cochlefelis spatula Ramsay & Ogilby, 1886.

Habitat and distribution: Fresh and brackish water, southern New Guinea (Fig. 38).

Remarks

The monophyly and species composition of *Cochlefelis*, *sensu* Kailola 2004, Betancur-R. 2009, and Marceniuk *et al.* 2012, are supported by the total-evidence analysis.

Doiichthys Weber, 1913

(Figs 1–3, 44)

Type species: *Doiichthys novaeguineae* Weber, 1913.

Diagnosis

Lateral horn of lateral ethmoid long and posteriorly oriented (12, 1 > 2); nasal not well defined (19, 0 > 1); ventral crest of parieto-supraoccipital process weakly developed, restricted to base of process (48, 1 > 0); three infraorbitals (95, 3 > 1); articulation of autopalatine with lateral ethmoid slightly anterior to middle of bone (111, 2 > 0); metapterygoid twice as deep as long in perpendicular section (135, 1 > 0); first external branchiostegal ray proximally narrow and distally broad (147, 1 > 0); posterior ceratohyal very long (153, 0 > 2); urohyal very long (157, 1 > 2); posterior end of urohyal bifurcate (158, 0 > 1); urohyal posterolateral processes one-third as long as distal portion of bone (162, 2 > 4); first and second epibranchials straight for entire length (178, 0 > 1); mesial portion of first epibranchial very large and depressed (180, 0 > 2); first pharyngobranchial on mesial end of first epibranchial (191, 1 > 0); third pharyngobranchial funnel shaped (192, 1 > 0); upper (pharyngeal) tooth plate long and narrow, its length three times its width (195, ? > 2); transverse crest associated with neural spine of fourth vertebra low



Figure 43. *Cochlefelis spatula* Regan, 1908, New Guinea, photograph by Ricardo Betancur-R., type species of the genus.

(200, 1 > 0); median crest associated with neural spine of third vertebra low or absent (201, 1 > 0).

Ambiguous optimization: Accessory tooth plates present (58, 0 > 1).

Included species

Doiichthys novaeguineae Weber, 1913.

Habitat and distribution: Brackish waters, southern New Guinea (Fig. 38).

Remarks

The total-evidence analysis supports a sister group relationship of *Doiichthys* plus *Nedystoma*, which was uncovered previously in independent molecular and morphological studies (Kailola 2004, Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk *et al.* 2012). The synonymy of *Doiichthys* with *Nedystoma* proposed by Kailola (2004) is rejected and *Doiichthys* is recognized as a valid genus following Marceniuk and Menezes (2007) and Betancur-R. (2009).

Megalosciades gen. nov.

(Figs 1–3, 45)

ZooBank registration: [urn:lsid:zoobank.org:act:1DF58A15-AE63-4686-BEE0-9511F9971FFF](https://zoobank.org/act:1DF58A15-AE63-4686-BEE0-9511F9971FFF).

Type species: *Arius augustus* Roberts, 1978.

Diagnosis

The genus *Megalosciades* is defined based on unique characters of external morphology reported by Roberts (1978) in the species description: extremely short maxillary barbel; very small eye; broad head and broad mouth.

Etymology

Named for the disproportionally large head of the type species in comparison to those observed in *Sciades* and close relatives. Gender: masculine.

Included species

Megalosciades augustus Roberts, 1978.



Figure 44. *Doiichthys novaeguineae*, New Guinea, photograph by Ricardo Betancur-R., type species of the genus.



Figure 45. *Megalosciades augustus* Roberts, 1978, Papua New Guinea, photograph by Ricardo Betancur-R., type species of the genus.

Habitat and distribution: Freshwater, southern New Guinea (Fig. 38).

Remarks

Over that past two decades, *Megalosciades augustus* has been treated by different authors as a valid species in three different genera: *Arius*, *Nemapteryx*, and *Neoarius*. Molecular data (Betancur-R. 2009) does not support the inclusion of that species within any of those genera, nor does it appear to be the sister group of any of them. Although BI and ML analyses support the inclusion of *Megalosciades augustus* in *Cochlefelis*, the two genera are externally very distinct (Figs 45, 53) and the absence of internal morphological data makes it impossible to establish a diagnosis. This is an unstable situation, which may be resolved by assigning that enigmatic species to its own genus, within which it can remain until a discovery that its phylogenetic position is actually embedded within another genus.

Nedystoma Ogilby, 1898

(Figs 1–3, 38D, 46)

Type species: *Hemipimelodus dayi* Ramsay & Ogilby, 1886.

Diagnosis

Mesethmoid median portion very narrow ($2, 2 > 1$); premaxilla wide and moderately long, its length more than three times in width ($120, 3 > 1$); premaxilla lateral and mesial portions of different sizes ($121, 0 > 1$); anterior margin of premaxilla fringed ($122, 0 > 1$); anteroventral portion of opercle subtrapezoidal, very long ($127, 1 > 0$); dorsal crest of hyomandibula short and high ($141, 0 > 1$); second external branchiostegal ray almost as wide as first ray ($148, 0 > 1$); distal portion of third external branchiostegal ray spatulate ($149, 0 > 1$); contact face between first epibranchial and first pharyngobranchial very conspicuous ($177, 0 > 1$).

Ambiguous optimization: Upper (pharyngeal) tooth plate very long and narrow, its length more than four times its width ($195, ? > 3$).

Included species

Nedystoma dayi Ramsay & Ogilby, 1886.

Habitat and distribution: Predominantly freshwaters, but also in brackish waters, southern New Guinea (Fig. 38).

Remarks

See Remarks of *Doiichthys*.

Nemapteryx Ogilby, 1908

MP 100, BI 1, ML 100

(Figs 1–3, 47)

Type species: *Arius stirlingi* Ogilby, 1898.

Diagnosis (all of ambiguous optimization)

Posterior branches of mesethmoid narrow ($6, 0 > 1$); posterior branches of mesethmoid parallel throughout ($7, 0 > 1$); posterior branches of mesethmoid moderately long, delimiting between one-fourth and one-half of length of anterior cranial fontanel ($8, 0 > 1$); fenestra delimited by lateral ethmoid and frontal very large ($17, 1 > 2$); frontal mesial laminar projection absent ($23, 1 > 0$); anterior portion of anterior cranial fontanel not delimited by dorsal expansion of orbitosphenoid ($24, 1 > 0$); posterior cranial fontanel very wide and long ($27, 1 > 3$); tooth plates associated with vomer present ($55, 0 > 1$); lateral expansions of orbitosphenoid and pterospheneid absent ($64, 1 > 0$); optic foramen very reduced ($67, 1 > 2$); ventral tip of subvertebral process spatulate ($80, 2 > 3$); contact face for articulation of transcapular process with basioccipital large and depressed ($85, 0 > 1$); transcapular process very short and thick ($87, 2 > 1$); articulation of autopalatine with lateral ethmoid in middle of bone ($111, 2 > 1$); premaxilla wide and moderately long, its length more than three times its width ($120, 2 > 1$); dorsal crest of premaxilla beginning between lateral one-third or one-half of anterior margin ($124, 0 > 1$); metapterygoid anterior process acute ($138, 1 > 0$); dorsal crest of hyomandibula short and high ($141, 0 > 1$); second basibranchial mushroom shaped ($166, 0 > 1$); distal portion of uncinat process of third epibranchial truncate ($183, 0 > 1$); Müllerian ramus bone blade inconspicuous ($206, 2 > 0$); dorsal-fin spine prolonged into a



Figure 46. *Nedystoma dayi*, New Guinea, photograph by Ricardo Betancur-R., type species of the genus.

filament (221, 0 > 1); cleithrum lateral face very narrow (227, 0 > 1).

Included species

Nemapteryx armiger De Vis, 1884.

Nemapteryx aff. *armiger*.

Habitat and distribution: Brackish and marine waters, southern New Guinea and northern Australia (Fig. 38).

Remarks

The total-evidence analysis supports the morphological and molecular distinctiveness of *Nemapteryx* (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012), with the addition of a currently unnamed species from New Guinea (Betancur-R. 2009).

Neoarius Castelnau, 1878

BI 0.74

(Figs 1–2, 48)

Type species: *Arius curtisii* Castelnau, 1878.

Diagnosis

Mesethmoid median portion moderately wide (2, 2 > 1); pterotic mesial border with parieto-supraoccipital longer than anterior border with sphenotic (36, 0 > 1); anterior process of first hypobranchial in middle of bone (174, 0 > 1).

Ambiguous optimization: Lateral horn of lateral ethmoid compressed and spatulate (11, 0 > 1); one-half or less of interopercle posterior part contacting ventral margin of opercle (131, 1 > 0); Müllerian ramus distal one-third markedly curved (208, 1 > 2).

Included species

Neoarius berneyi Whitley, 1941

Neoarius graeffei Kner & Steindachner, 1867

Neoarius aff. *graeffei* sp 1

Neoarius aff. *graeffei* sp 2

Neoarius hainesi Kailola, 2000

Neoarius midgleyi Kailola & Pierce, 1988

Neoarius pectoralis Kailola, 2000 * *sedis mutabilis*.



Figure 47. *Nemapteryx armiger* (senior synonym of *Arius stirlingi*), northern Australia and central-southern New Guinea, photograph by Ricardo Betancur-R., type species of the genus.



Figure 48. *Neoarius graeffei*, MNHN B-0693 (senior synonym of *Arius curtisii*), southern New Guinea and northern Australia, type species of the genus.



Figure 49. *Pachyula crassilabris*, AMS B 9961, New Guinea, type species of the genus.

Habitat and distribution: Fresh, brackish, and marine waters, southern New Guinea and Australia (Fig. 38).

Remarks

The MP and BI analyses support the monophyly of *Neoarius* in contrast to previous morphological studies, which treated the group as a synonym of *Ariopsis* (Kailola 2004) or as a valid genus (Marceniuk and Menezes 2007, Marceniuk *et al.* 2012). This study supports the inclusion of *Neoarius midgleyi* and two currently unnamed species into the genus (Betancur-R. 2009) and renders *Amissidens* (type species: *Arius hainesi* Kailola, 2000) into synonymy.

Pachyula Ogilby, 1898

(Figs 1–3, 38F, 49)

Type species: *Hemipimelodus crassilabris* Ramsay & Ogilby, 1886.

Diagnosis

Mesethmoid median portion very narrow (2, 2 > 0); epioccipital visible dorsally (41, 0 > 1); vomer anterior margin pronounced and acute (50, 0 > 1); basioccipital lateral process absent with anterior and posterior portions equally developed (83, 1 > 0); anteroventral portion of opercle subtrapezoidal, very short (127, 1 > 2); metapterygoid one and a one-half times longer than deep in perpendicular section (135, 1 > 2); posterolateral processes of urohyal short (160, 1 > 0); third basibranchial chalice shaped (168, 0 > 1); posterior margin of first epibranchial straight (181, 1 > 0); first pharyngobranchial large and depressed (190, 0 > 1); median crest associated with neural spine of fourth vertebra very high (202, 0 > 1); Müllerian ramus robust (207, 0 > 1); ventral surfaces of parapophyses of fifth and sixth vertebrae conspicuously concave (212, 0 > 1); adipose fin-base long (222, 2 > 1).

Ambiguous optimization: Mesethmoid medial notch narrow and deep (1, 0 > 1); lateral horn of lateral ethmoid compressed and spatulate (11, 0 > 1); Müllerian ramus distal one-third gently curved (208, 2 > 1); posterior process of cleithrum very long (224, 0 > 2).

Included species

Pachyula crassilabris Ramsay & Ogilby, 1886

Pachyula conorhynchus Weber, 1913 * *sedis mutabilis*.

Habitat and distribution: Freshwater, southern New Guinea (Fig. 38).

Remarks

Total-evidence analysis confirms the validity of this genus, in agreement with previous morphological and molecular studies (Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk *et al.* 2012).

Paracinetodus gen. nov.

(Figs 1–3, 38B, 50)

ZooBank registration: [urn:lsid:zoobank.org:act:01D775F1-CA33-42B6-AE05-AC1D3E9DBE6C](https://zoobank.org/act:01D775F1-CA33-42B6-AE05-AC1D3E9DBE6C).

Type species: *Arius carinatus* Weber, 1913.

Diagnosis

Lateral horn of lateral ethmoid compressed and spatulate (11, 0 > 1); extrascapular subtriangular (37, 1 > 2); epioccipital contacting small narrow area of diagonal crest associated with neural spine of fourth vertebra (44, 2 > 0); ventral tip of subvertebral process acute (80, 0 > 2); basioccipital lateral process absent with anterior and posterior portions equally developed (83, 1 > 0); transcapular process at right angle to body axis (86, 0 > 1); transcapular process short and thick (87, 0 > 2); space between transcapular process and otic capsule small (89, 1 > 2); premaxilla narrow and long, length two to three times its width (120, 1 > 2); bony blade connecting posterolateral processes of urohyal absent (159, 0 > 1); posterolateral processes of urohyal two-thirds as long as distal portion of bone (162, 0 > 2); transverse crest associated with neural spine of fourth vertebra high (200, 0 > 1); median crest associated with neural spine of fourth vertebra high (202, 0 > 1); Müllerian ramus bony blade evident in more than one-half length (206, 0 > 2); ventral surfaces of parapophyses of fifth and sixth vertebrae conspicuously concave (212, 0 > 1); seventh vertebra free from ventral superficial ossification (214, 0 > 1); posterior process of cleithrum very long (224, 1 > 2); second dorsal cleithral process dorsally directed and parallel to first dorsal process (226, 0 > 1).

Etymology

Derived from the Greek ‘para’ for ‘near’, highlighting its morphological similarity with the genus *Cinetodus*. Gender: masculine.

Included species

Paracinetodus carinatus Weber, 1913.

Habitat and distribution: Freshwater, southern New Guinea (Fig. 38).

Remarks

Arius carinatus was included in *Cinetodus* in previous morphological studies (Kailola 2004, Marceniuk and Menezes 2007, Marceniuk et al. 2012). The results of the total-evidence analysis place the species in a lineage distinct from that of *Cinetodus*, corroborating a previous molecular result (Betancur-R. 2009), and requiring the establishment of the new genus.

Pararius Whitley, 1940

BI 1, ML 75

(Figs 1–3, 38G and 51)

Type species: *Arius proximus* Ogilby, 1898.

Diagnosis

Lateral horn of lateral ethmoid variable in length and laterally oriented (12, 1 > 0); posterior cranial fontanel absent (26, 1 > 0); epiphyseal bar indistinct (28, 0 > 1); temporal fossa

very reduced (39, 1 > 0); accessory tooth plates small, oval to rounded (60, 0 > 1); lateral margins of orbitosphenoid progressively diverging anteriorly (63, 0 > 1); lateral and mesial portions of premaxilla of different sizes (121, 0 > 1).

Included species

Pararius mastersi Ogilby, 1898

Pararius proximus Ogilby, 1898.

Habitat and distribution: Brackish and marine waters, southern New Guinea and northern Australia (Fig. 38).

Remarks

The recognition of a close relationship between *Pararius proximus* and *Pararius mastersi* is a new result not found in previous studies (Kailola 2004, Marceniuk and Menezes 2007, Betancur-R. 2009, Marceniuk et al. 2012).



Figure 50. *Paracinetodus carinatus*, photograph by Ricardo Betancur-R., Papua New Guinea and northern Australia, type species of the genus.



Figure 51. *Pararius proximus*, Papua New Guinea and Australia, photograph by Ricardo Betancur-R., type species of the genus.

Papuarius gen. nov.

(Figs 1–3, 52)

ZooBank registration: [urn:lsid:zoobank.org:act:AD2D552B-DF0E-46F1-B9CD-B712C9703F4](https://zoobank.org/urn:lsid:zoobank.org:act:AD2D552B-DF0E-46F1-B9CD-B712C9703F4).

Type species: *Arius latirostris* Macleay, 1883.

Diagnosis

Mesethmoid median portion moderately wide (2, 2 > 1); lateral ethmoid main component of bony bridge formed by lateral ethmoid and frontal (15, 1 > 0); frontal mesial laminar projection absent (23, 1 > 0); posterior cranial fontanel relatively narrow and long (27, 1 > 2); epiphyseal bar transversely elongate and longitudinally narrow (29, 0 > 1); medial groove of cranium absent (30, 0 > 1); anterior opening of aortic canal at base of subvertebral process and anteroventrally oriented (77, 0 > 1); contact face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1); dorsal crest of hyomandibula short and high (141, 0 > 1); contact face between first epibranchial and first pharyngobranchial conspicuous (177, 0 > 1); distal portion of uncinat process of third epibranchial acute (183, 1 > 0).

Ambiguous optimization: Lateral horn of lateral ethmoid compressed and spatulate (11, 0 > 1); posterolateral processes of urohyal lateroposteriorly oriented, forming angle greater than 70° (161, 1 > 0).

Etymology

The first part of the generic name comes from Papua, a common element of the names of the six Indonesian provinces as well as the independent country that together compose the island group called New Guinea. The second part is from the frequently used ariid generic name *Arius*. Gender: masculine.

Included species

Papuarius latirostris Macleay, 1883.

Habitat and distribution: Freshwater, southern New Guinea (Fig. 38).

Remarks

The genus *Papuarius* is established to accommodate *Papuarius latirostris*, a species that has been assigned to a number of

different genera over time. In this study it is likewise assigned to different places within the Ariina, but without a clear association to any single genus.

Potamosilurus Marceniuk & Menezes, 2007

MP 99, BI 1, ML 99

(Figs 1–3, 38H and 53)

Type species: *Hemipimelodus macrorhynchus* Weber, 1913.

Diagnosis

Lateral ethmoid as main component of bony bridge formed by lateral ethmoid and frontal (15, 1 > 0); accessory tooth plates absent (58, 1 > 0); contact face for articulation of transcapular process with basioccipital large and depressed (85, 0 > 1).

Ambiguous optimization: Mesethmoid medial notch indistinct, obscured by bone deposition (1, 1 > 2); mesethmoid median portion moderately wide (2, 2 > 1); dorsal crest of hyomandibula short and high (141, 0 > 1); adipose-fin base moderately long (222, 1 > 2).

Included species

Potamosilurus coatesi Kailola, 1990

Potamosilurus macrorhynchus Weber, 1913

Potamosilurus robertsi Kailola, 1990 * *sedis mutabilis*

Potamosilurus velutinus Weber, 1907.

Habitat and distribution: Freshwater, southern New Guinea (Fig. 38).

Remarks

Potamosilurus is recognized as a valid genus, as defined by Marceniuk and Menezes (2007) excluding *Papuarius latirostris*, which is assigned to a new genus based on the results of the total-evidence analysis.

CONCLUSIONS

Some recent studies of the phylogenetic relationships of various zoological groups suggested that the best approach to establishing a stable taxonomy is to combine as many types of evidence as possible to obtain the most complete picture



Figure 52. *Papuarius latirostris*, AMS I 9072, New Guinea, type species of the genus.



Figure 53. *Potamosilurus macrorhynchus*, ZMA 111086, New Guinea, type species of the genus.

of their evolutionary history (de Queiroz and Gatesy 2007, Lopardo *et al.* 2010, Assis *et al.* 2011). ‘Total evidence’ or ‘pooled evidence’ based phylogenetic analyses have been employed to resolve incongruities between independent morphological and molecular analyses in different animal groups (Giribet *et al.* 2001, Nylander *et al.* 2004, Bond and Hedin 2006, Sanders *et al.* 2006). Conflicts between molecular and morphological analyses and taxonomic problems within the Ariidae have been clarified in the present study. For example, the monophyly and composition of the genus *Notarius* Gill, 1863 was revised with the recognition of the synonymy of *Amphiarius* proposed based on morphological data (Marceniuk and Menezes 2007), while the genus *Aspistor*, with an uncertain position in previous molecular analyses (Betancur-R. *et al.* 2007, Betancur-R. 2009), was supported as a monophyletic genus sister to *Notarius*. The relationship of species restricted to freshwaters in the New World was also revised, with the redefinition of the genus *Potamarius* (*sensu* Marceniuk and Menezes 2007), composed of species found in the Usumacinta River Basin and Lake Izabal in Mexico and Guatemala. This result confirms the recognition of two other restricted freshwater genera, *Paragenidens* and *Chinchaysuyoa*, the first restricted to coastal drainages of south-eastern Brazil (western Atlantic) and the second restricted to coastal drainages of Ecuador and Peru (eastern Pacific).

The monophyly of the genera *Brustiarius*, *Cochlefelis*, *Neoarius*, and *Potamosilurus* (*sensu* Marceniuk and Menezes 2007) restricted to Papua New Guinea and Australia, was revised, with a redefinition of the species composition of these genera. The recognition of suprageneric taxa (tribes and subtribes) for New World and Old World genera, as well as distinct groups from Asia and Oceania, reflect vicariant events as noted by Betancur-R. (2009).

The total-evidence approach led to the recognition of morphological convergences in taxa with similar ecologies, found in different geographic areas that were previously thought to be phylogenetically closely related. These results support the revalidation of synonymized genera (e. g., *Hexanematichthys*) or description of a new genus (*Pseudosciades*, see Figs 24D, E) that is similar in appearance to *Sciades* (Fig. 16C), and occupy similar habitats (estuarine and marine waters). *Hemipimelodus* is also morphologically similar to *Cephalocassis* (Fig. 24B), as are *Paracinetodus* and *Cinetodus* (Fig. 38B), all restricted to freshwater habitats.

Our total-evidence analysis confirms the recognition of the subfamily Bagreinae (which includes the genus *Bagre*, sister group to all Ariidae except *Galeichthys*), previously supported only by morphological data (Marceniuk *et al.* 2012). The decision to propose new generic names was done to preserve, as much as possible, the already proposed description of several genera and to keep only monophyletic genera (Figs 1–3).

In summary, the results of the total-evidence analysis clarified taxonomic incongruences between morphological and molecular phylogenetic analyses, producing a consensus classification which improves our knowledge of the systematics and the evolution of the Ariidae and morphologically based diagnoses of all of the named taxa.

SUPPORTING INFORMATION

Supplementary data is available at *Zoological Journal of the Linnean Society* Journal online.

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