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Systematics and biogeography of New World sea catfishes (Siluriformes: Ariidae) as inferred from mitochondrial, nuclear, and morphological evidence

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Abstract

Ariid or sea catfishes include around 150 species that inhabit marine, brackish, and freshwater environments along world's tropical and subtropical continental shelves. Phylogenetic relationships for 46 New World and three Old World species of ariids were hypothesized using maximum parsimony and Bayesian inference reconstruction criteria on 2842 mitochondrial (cytochrome *b*, ATP synthase 8 and 6, ribosomal 12S and 16S) and 978 nuclear (*rag2*) nucleotide sites. The molecular topologies were compared to a previously compiled morphological dataset that was expanded herein to a total of 25 ariid species and 55 characters. Mitochondrial data yielded clades highly resolved at subfamilial, generic, and intrageneric levels. Nuclear *rag2* reconstructions showed poor resolution at supra- and intrageneric levels, but provided support for the monophyly of most genera (except *Ariopsis* and *Cathorops*) as well as for the subfamilial clades. The hypothesized phylogeny derived from the morphological data was congruent with the molecular topologies at infrafamilial and generic levels. As indicated by the statistical tests of topological congruence, Kailola's phylogenetic hypothesis of ariids based on anatomical data is significantly different from our molecular trees. All reconstructions agree in the division of the Ariidae into two subfamilies, the Ariinae and the monogeneric Galeichthyinae. Basal ariine resolution was negligible suggesting that early diversification events occurred rapidly. The three Indo-Pacific taxa were grouped into a clade, but New World ariines were never recovered as monophyletic. We provide a revised classification for New World ariines examined, which is consistent with the molecular and the morphological evidence. Our classification scheme includes the genera *Ariopsis*, *Bagre*, *Cathorops*, *Notarius*, *Potamarius*, and *Sciades*, and the description of two new genus-level taxa (*Occidentarius* n. gen and *Precathorops* n. subgen.). We also hypothesize plausible biogeographic scenarios that explain distributional patterns of major ariid lineages. Diversification of the predominantly circumtropical ariines likely occurred throughout the Tethys Sea, whereas speciation events in the subtropical galeichthyines were probably tied to the southern coast of Gondwana.

Keywords: Sea catfishes; Ariidae; Phylogeny; Systematics; Biogeography; Molecular evidence; Morphological evidence

1. Introduction

The order Siluriformes includes 37 recognized families of catfishes widely distributed and diverse in freshwaters (Sullivan et al., 2006). Only two families are predominantly marine: the Plotosidae, from the Indo-west Pacific, and the Ariidae. The ariids, or sea catfishes, include about 150 species occurring in warm-temperate to tropical continental shelves around the world. The species mainly inhabit marine and brackish waters but some are confined to freshwaters.

Monophyly of the Ariidae is well-supported on morphological (Kailola, 2004; Diogo, 2005) and molecular (Betancur-R., 2003; Hardman, 2005; Sullivan et al., 2006) grounds (see also Acero P. and Betancur-R., 2007). A number of works have attempted to resolve relationships among

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catfish families. Most recent studies using anatomical (Diogo, 2005) and molecular (Sullivan et al., 2006) data suggest that the Ariidae is the sister group to the Malagasy family Anchariidae. Ariids and anchariids have been placed in the superfamily Arioidea within the suborder Siluroidei (Sullivan et al., 2006), but there is still no consensus regarding the relationships of the arioid clade to other siluroid groups (see also Acero P. and Betancur-R., 2007). Kailola (2004) has made a pioneering contribution to the reconstruction of intrafamilial relationships of ariids. Kailola's phylogenetic analysis focused mainly on Old World ariids (46 species), but also included seven Neotropical species (Fig. 1). Kailola (2004) also provided a revised classification for ariids, recognizing 23 valid genera. Other studies have included preliminary phylogenetic reconstructions of New World lineages based on morphological features (Betancur-R. et al., 2004; 16 species), and genus-level phylogenies derived from mitochondrial data (*Notarius* and *Cathorops*: Betancur-R. and Acero P., 2004, 2005, 2006). On a broader scale, Acero P. and Betancur-R. (2007) presented a revision of major ariid clades, including descriptions of the subfamilies Galeichthyinae (one genus and four species) and Ariinae (remaining taxa). These subfamilial clades, however, are incongruent with Kailola's topology that places *Galeichthys* nested within the ariines (Fig. 1). Marceniuk and Ferraris (2003) presented a taxonomic classification of nominal ariids from South and Central America as a checklist that recognized 46 valid species in nine genera plus seven nominals as *species inquirendae* (i.e. validity and/or generic assignment uncertain). Their taxonomy followed conclusions derived from morphological phylogenies of ariid genera in Marceniuk's (2003) unpublished dissertation that will not be discussed here.

The primary purpose of this study is to resolve phylogenetic relationships of a wide spectrum of New World ariid

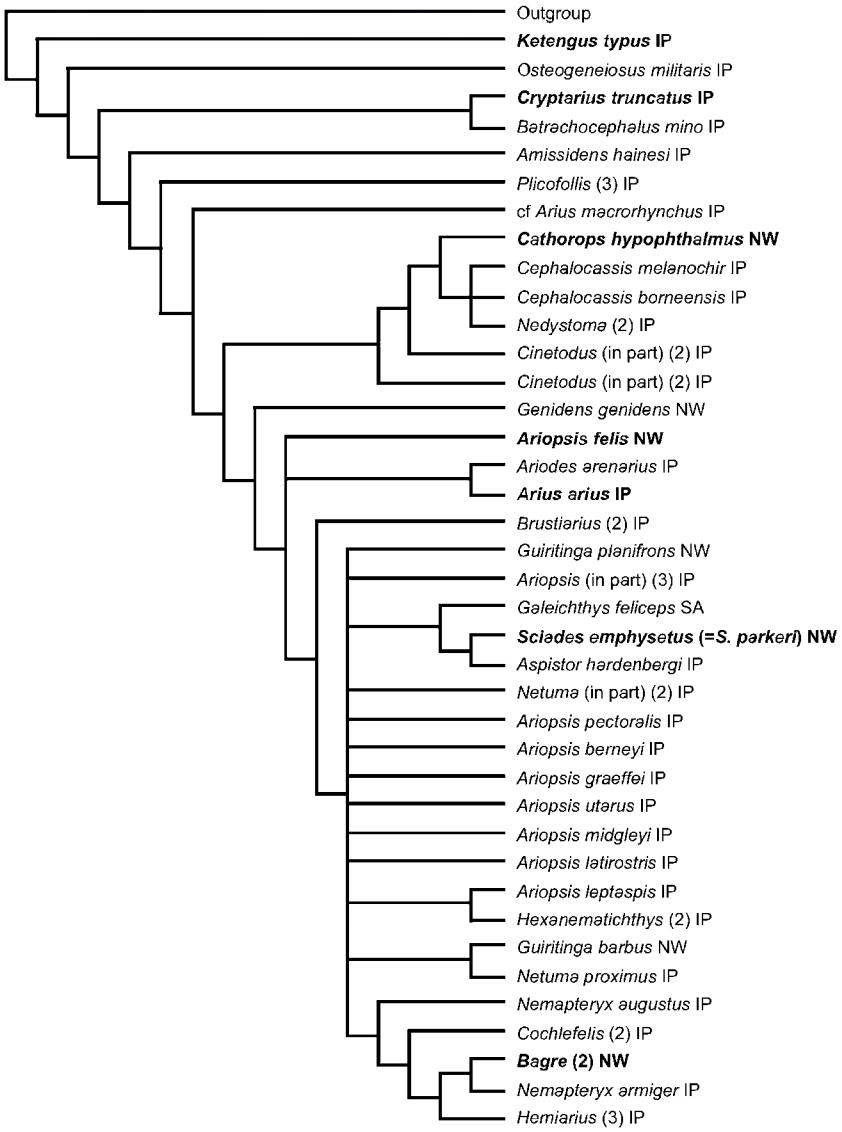

Fig. 1. Kailola's (2004) phylogenetic hypothesis of 53 ariid taxa based on 57 characters derived from anatomical examination. Figures in parentheses indicate number of terminals included in each genus-level clade. Taxa examined in this study are given in bold. IP, Indo-Pacific; NW, New World; SA, southern Africa.

taxa by using mitochondrial and nuclear sequence data from the partial cytochrome *b* (cyt *b*), complete ATP synthase 6 and 8 (ATPase 8/6), partial 12S and 16S, and partial recombination activating gene 2 (*rag2*), as well as morphological characters (modified from Betancur-R. et al., 2004). Based on the phylogenetic reconstructions obtained we also present a revised classification of New World ariids examined and provide hypotheses to explain biogeographical patterns of major clades. This paper provides the most complete treatment of New World ariid taxa to date using both molecular and morphological approaches. The results presented here are based on the findings obtained in the unpublished dissertations of the first two authors (Betancur-R., 2003; Acero P., 2004).

2. Materials and methods

2.1. Taxon sampling

Molecular data were obtained for a total of 49 ariid species, of which 46 are from the New World (including three putative cryptic species) and three from the Indo-Pacific (*Arius arius*, *Ketengus typus*, and *Cryptarius truncatus*). Such species are representatives of two subfamilies (Ariinae and Galeichthyinae) and eight New World genera. The ingroup also included a GenBank sequence from the sister family Anchariidae (*Gogo arcuatus*) (*rag2* only). Three species of non-closely related families of catfishes (Ictaluridae, Heptapteridae, and Auchenipteridae) were used as outgroups for the molecular component. The morphological dataset included 25 ariid species representing the same phylogenetic diversity sequenced (*A. arius* was the only Indo-Pacific representative included). The families Doradidae, Heptapteridae, and Auchenipteridae (one species each) were used as outgroups for the morphological component. Due to unavailability of tissue and anatomical material, the New World taxa *Arius grandoculis* Steindachner (from Brazil), *Arius labiatus* Boulenger (from Ecuador), and *Hexanematichthys henni* Eigenmann (from Ecuador), all with unclear generic status, as well as *Genidens sensu* Marceniuk and Ferraris (2003) (four species from Brazil to Argentina) were not included in the analysis.

Institutional catalog numbers of vouchers and tissues are listed in Appendix A (molecular data only). Morphological material examined is listed in Appendix B. Institutional abbreviations are as in Leviton et al. (1985) with the modification of INVEMAR to INVEMAR-PEC. Additionally, STRI (fish collection in Appendix A, archaeology collection of skulls in Appendix B) and stri (tissue collection) are abbreviations for Smithsonian Tropical Research Institute, Balboa, Panamá (PA); ECO-SC is the abbreviation for the fish collection of El Colegio de la Frontera Sur (ECOSUR), San Cristobal de las Casas, Chiapas, México.

2.2. DNA sequence data

DNA was extracted from a small piece of tissue (10–20 mg) using standard CTAB/phenol/chloroform techniques (Sambrook et al., 1989) or the DNeasy Tissue Kit (Qiagen) according to the manufacturer's protocol. Primers used for amplification are listed in Table 1. Double-stranded DNA was PCR synthesized using different sets of primers in 25 μl reactions (50 μl for *rag2*), consisting of 2.5 μl 10 mM Tris–HCl buffer, 2 μl 2.0 mM $MgCl_2$, 1.25 μl 10 mM of each primer, 2.5 μl at 200 nM of each dNTP, 13.25 μl ddH_2O, 0.25 μl (1 U) Amplitaq polymerase (Perkin-Elmer), and 2 μl template DNA. Amplification conditions consisted of an initial 94 °C denaturation step for 120–180 s, 30–34 cycles of 94 °C for 30–45 s, annealing for 30–45 s (52 °C for cyt *b*, 53–58 °C for ATPase 8/6, 50 °C for 12S and 16S fragments and 56 °C for *rag2*), extension at 72 °C for 60–90 s, followed by a final extension at 72 °C for 300 s. The PCR products

Table 1
List of primers used for amplification and sequencing

Primer	Gene	Sequence	Use	Reference
Glu-2	Cyt *b*	5′-AACCACCGTTGTTATTCAACTA-3′	PCR/sequencing	[a]
Pro-R1	Cyt *b*	5′-TAGTTTAGTTTAGAATTCTGGCTTTGG-3′	PCR/sequencing	[a]
OsCytb-F1	Cyt *b*	5′-CACCCATACTTCTCMTAYAAAGA-3′	sequencing	[b]
OsCytb-R1	Cyt *b*	5′-TCTTTRTAKGAGAAGTATGGGTG-3′	sequ encing	[b]
ACytb-F1	Cyt *b*	5′-GACYTMCCYGCCCCMTCYAAYATYTCT-3′	sequencing	[b]
ACytb-R1	Cyt *b*	5′-TCCGGATTACAAGACCGGYGCTTT-3′	sequencing	[b]
A-int	Cyt *b*	5′-TCTTACATGAAACAGGSTCCA-3′	sequencing	[c]
8.2 L8331	ATPase 8/6	5′-AAAGCRTYRGCCTTTTAAGC-3′	PCR/sequencing	[d]
3.2 H9236	ATPase 8/6	5′-GTTAGTGGTCAKGGGCTTGGRTC-3′	PCR/sequencing	[d]
8.3 L8524	ATPase 8/6	5′-AAYCCTGARACTGACCATG-3′	sequencing	[d]
12Sa	12S	5′-AAACTGGGATTAGATACCCCACTAT-3′	PCR/sequencing	[d]
12Sb	12S	5′-GAGGGTGACGGGCGGTGTGT-3′	PCR/sequencing	[d]
16Sar1	16S	5′-CCCGCCTGTTTATCAAAAACAT-3′	PCR/sequencing	[d]
16Sbr	16S	5′-CCGGTCTGAACTCAGATCACGT-3′	PCR/sequencing	[d]
MHRAG2-F1	*rag2*	5′-TGYTATCTCCCACCTCTGCGYTACC-3′	PCR/sequencing	[a]
MHRAG2-R1	*rag2*	5′-TCATCCTCCTCATCKTCCTCWTTGTA-3′	PCR/sequencing	[a]

[a] Hardman and Page (2003).
[b] Hardman (2005).
[c] This study.
[d] http://striweb.si.edu/bermingham/research/primers/index.html.

were electrophoresed in 1.5% low melting point agarose gels using a Tris–acetate buffer (pH 7.8) containing 1 μg/ml of ethidium bromide. The single amplification product was visualized with UV light, cut from the gel, and digested with 1 μl Gelase (Epicentre Technologies) at 70 °C for 120 s, followed by overnight incubation at 45 °C. Three microliters of a purified PCR product was used as a template in a 10-μl cycle sequencing reaction using dRhodamine terminator cycle sequencing kit (PE Applied Biosystems). Each PCR product was sequenced using the two amplification primers and in some cases additional internal primers (Table 1). Cycle sequencing conditions were 96 °C pre-heat, and 25 cycles at 96 °C for 15 s, 50 °C for 1 s, and 60 °C for 240 s. Sequencing products were purified by passing the reactions through 700 μl Sephadex columns and sequenced on an ABI prism 377 DNA sequencer (PE Applied Biosystems) following the manufacturer's instructions. Contig assembly was performed in Sequencher 4.1 (Gene Codes Corp., Inc.).

Sequences of protein-coding genes were aligned manually and translated in MacClade version 4.06 (Maddison and Maddison, 2000). Ribosomal 12S and 16S sequences were aligned using CLUSTAL X (Thompson et al., 1997) with the default parameter settings (gap opening/gap extension: 15/6.66) and then refined manually by visual inspection. Sites with dubious positional homology were excluded from the analyses. Homogeneity of nucleotide frequencies across taxa was examined for each gene region using the χ^2 test implemented in PAUP* version 4.0b10 (Swofford, 2002). Comparisons of divergence rates among different data partitions were approximated by calculating the mean and the standard deviation (SD) of all possible pairwise distance ratios among two regions. Genetic distances were calculated under the Kimura two-parameter model.

2.3. Morphological data

The previously compiled morphological dataset of Betancur-R. et al. (2004) was expanded to include a total of 25 ariid species and 55 characters. Ten characters and nine terminals (*Ariopsis felis*, *A. arius*, *Bagre bagre*, *Cathorops dasycephalus*, *Galeichthys peruvianus*, *Notarius neogranatensis*, *Potamarius* sp., *Potamarius nelsoni*, *Sciades parkeri*) were added to the previous study. Additional material from other species was also examined and five characters (Nos. 3, 15, 33, 34, and 49) were redefined and/or recoded. All characters were parsimony-informative. Polymorphic taxa were coded as missing data. Names for skeletal structures follow Mo (1991) and Arratia (2003a,b).

2.4. Phylogenetic reconstructions

Congruence among different mitochondrial data partitions was assessed using 100 replicates of the partition homogeneity test in PAUP* (=incongruence length difference test of Farris et al., 1994). Phylogenetic reconstructions were performed using maximum parsimony (MP) and Bayesian inference (BI) criteria. MP reconstructions were conducted in PAUP* using either branch-and-bound (morphological dataset) or heuristic (molecular datasets) searches. Heuristic searches were performed using 1000 replicates with random addition of sequences and tree-bisection–reconnection (TBR) branch-swapping algorithm. All characters were assigned equal weights and states treated as unordered. Clade support was evaluated with 10,000 pseudoreplicates of non-parametric bootstrapping using random addition of sequences (10 replicates) and TBR. Clades with boostrap values lower than 70% were considered poorly supported. For the morphological dataset, nodal support was also evaluated using decay indices (Bremer, 1988) with TreeRot version 2 (Sorenson, 1999) and PAUP*.

The best-fit models of sequence evolution for different data partitions were estimated using the Akaike information criterion (AIC) in ModelTest version 3.7 (Posada and Crandall, 1998). BI analyses were performed in MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003) using four chains, one cold and three incrementally heated (molecular data only). Markov chain Monte Carlo (MCMC) analyses were conducted in triplicate and each was run for 6.0×10^6 generations, sampling trees every 100 generations. Conservatively, 25% of the first trees (15,000 trees) sampled in each MCMC run were discarded as burn-in. Marginal probabilities of summary parameters, consensus phylograms, and posterior probabilities of nodes were estimated from the post-burn-in samples of the three independent runs combined (total 135,003 trees). The MCMC runs were set based on the number of substitution parameters (1, 2 or 6), gamma-shape parameter (constraint or unconstraint), and proportion of invariable sites (constraint or unconstraint), according to the models selected with the AIC for each partition. Partitions were defined by gene and codon positions (for protein coding genes) and were set as unlinked. Nodes with posterior probabilities lower than 0.95 were considered poorly supported. Amino acid and morphological transformations were reconstructed in MacClade.

A unique phylogenetic hypothesis representing robust clades above the generic level was estimated based on the topologies obtained from different datasets and reconstruction criteria. The summarized phylogeny was computed using matrix representation with parsimony (MRP) supertree method (Baum, 1992). Clades from input trees were coded in r8s version 1.70 (Sanderson, 2003) using default options (Baum method, equal weights). The coded matrix was subsequently analyzed using MP heuristic searches in PAUP*. In order to provide a highly conservative hypothesis, the matrix was bootstrapped and intergeneric clades with support values lower than 90% in the strict consensus cladogram were collapsed.

2.5. Tests of morphological phylogenetic hypotheses

The morphological phylogenetic hypotheses available for ariid catfishes (Kailola, 2004; this study) were compared to the mitochondrial and the nuclear topologies. Molecular datasets were assembled including only taxa in

common with the morphological studies [Kailola, 2004: nine taxa in common (*Galeichthys feliceps* was replaced by *G. peruvianus* in order to include a representative of the subfamily Galeichthyinae), see Fig. 1; this study: 24 taxa in common with the mitochondrial dataset, 17 taxa in common with the *rag2* dataset]. A MP molecular tree that represented a particular morphological topology was estimated using constrained tree searches in PAUP*. The constrained trees were compared to the unconstrained MP topologies using the nonparametric Templeton test as implemented in PAUP*. Likewise, constrained and unconstrained topologies were estimated under the maximum likelihood (ML) criterion and compared using the Shimodaira and Hasegawa (1999) (SH) test in PAUP* (1000 replicates and the RELL sampling). ML reconstructions on the mitochondrial and the *rag2* datasets were performed under the best-fit models estimated with the AIC in ModelTest.

3. Results

3.1. Dataset attributes

All sequences obtained are available from GenBank. Accession numbers of sequences and voucher specimens are listed in Appendix A. The morphological data matrix and character definitions are summarized in Appendices C and D, respectively. For 20 species, cyt *b* and/or ATPase 8/6 sequences of two or more individuals were obtained. In many cases intraspecific variation was observed (<1.3%), but preliminary neighbor-joining analyses (not shown) suggested no evidence of paraphyly or polyphyly of any species; thus, only one haplotype for each species was included as terminals in the final datasets. *Bagre marinus* and *Notarius planiceps* revealed high intraspecific variation among different localities (3.6% and 3.5%, respectively), suggesting the existence of putative cryptic species. In those cases different haplotypes were analyzed as separate terminals, referring the haplotypes collected close to the type locality as the nominal species and the allopatric entities as *affinis* (*aff.*). The same criterion was applied for *Cathorops fuerthii*, which showed intermediate intraspecific variation (1.7%) plus morphological differentiation.

The alignment of partial cyt *b* sequences included 1095 bp, beginning 34 bases downstream of the start codon (as compared to *Ictalurus punctatus*, GenBank Accession No. AF482987). The entire ATPase 8/6 overlapped genes were sequenced (ATPase 8: 168 bp; ATPase 6: 684 bp; overlap: 10 bp; total region: 842 bp). The alignments of cyt *b* and ATPase 8/6 contained no indels, except for eight species of *Notarius* (*Notarius cookei*, *Notarius bonillai*, *Notarius kessleri*, *N. neogranatensis*, *N. planiceps*, *N.* aff. *planiceps*, *Notarius quadriscutis*, and *Notarius rugispinis*) that lacked a codon 111 bases downstream of the start codon of ATPase 8, as compared to the rest of catfishes analyzed. For ATPase 6, three initiation codons were observed: UUG present in most species of *Cathorops* (not in *C. dasycephalus*), GUG present in *N. planiceps* and *N. aff. planiceps*, and the typical AUG in the remaining taxa. The former two codons have been shown to be weaker variants of the latter in some genes (Stenstrom et al., 2001). Partial ribosomal 12S and 16S sequences ranged in size from 385 to 392 bp and 556 to 571 bp, with final alignment lengths of 396 and 586 bp, respectively. In the final alignments 17 sites of 12S and 60 sites of 16S were excluded due to ambiguous positional homology. The partition homogeneity test suggested no conflicting phylogenetic signal among different mitochondrial regions ($P = 0.64$). Therefore, all mitochondrial sequences were concatenated into a single dataset containing 2842 aligned sites.

Preliminary neighbor-joining trees (not shown) and genetic-distance analyses (see below) based on nuclear *rag2* data, demonstrated poor intrageneric variation and low divergence rates. Thus, *rag2* sequences were obtained only for 25 ariid species representing major lineages. In the nuclear *rag2* dataset not all ingroup taxa had the same sequence length, which ranged from 861 to 978. All outgroup taxa had 720 bp. The longest sequences began 226 bp downstream of the start codon, as compared to *Danio rerio* (GenBank Accession No. NM 131385). No indels were observed in the final *rag2* alignment.

The χ^2 test of base frequency homogeneity across taxa suggested no departures from stationarity for any of the six gene regions ($P = 1.0$). Cyt *b* and ATPase 8/6 have similar divergence rates as suggested by estimations of pairwise genetic distance ratios (means ± SD ATPase 8/6/cyt *b* = 1.1 ± 0.1, $n = 1326$). Likewise, pairwise divergence values of these two mitochondrial protein coding regions combined are roughly three times higher than those in their ribosomal counterparts (ATPase 8/6 + cyt *b*/12S + 16S = 3.2 ± 1.1, $n = 1326$) and more than one order of magnitude higher than those in the nuclear *rag2* (ATPase 8/6 + cyt *b*/*rag2* = 11.8 ± 9.7, $n = 379$). High standard deviations in the latter two comparisons suggest a differential of saturation rates among different gene regions. Considering only ariid taxa, mitochondrial and nuclear alignments contain 1047 (36.8%) and 82 (8.4%) variable sites, and 954 (30.7%) and 36 (3.7%) parsimony-informative sites, respectively. These data suggest that different markers used have different levels of phylogenetic signal.

3.2. Phylogenetic inference

The MP analysis of the mitochondrial dataset resulted in two optimal trees of 5516 steps, consistency index (CI) of 0.31, retention index (RI) of 0.62 (Fig. 2A). The best-fit models selected with the AIC for each data partition are listed in Table 2. The majority rule consensus of the BI search of 135,003 post-burn-in trees based on mixed models is shown in Fig. 2B. Both MP and BI topologies are identical and have highly supported nodes at subfamilial and generic levels, but often reveal incongruence and low support values at inter- and intrageneric levels. *G. peruvianus*, the only representative of the subfamily Galeich-

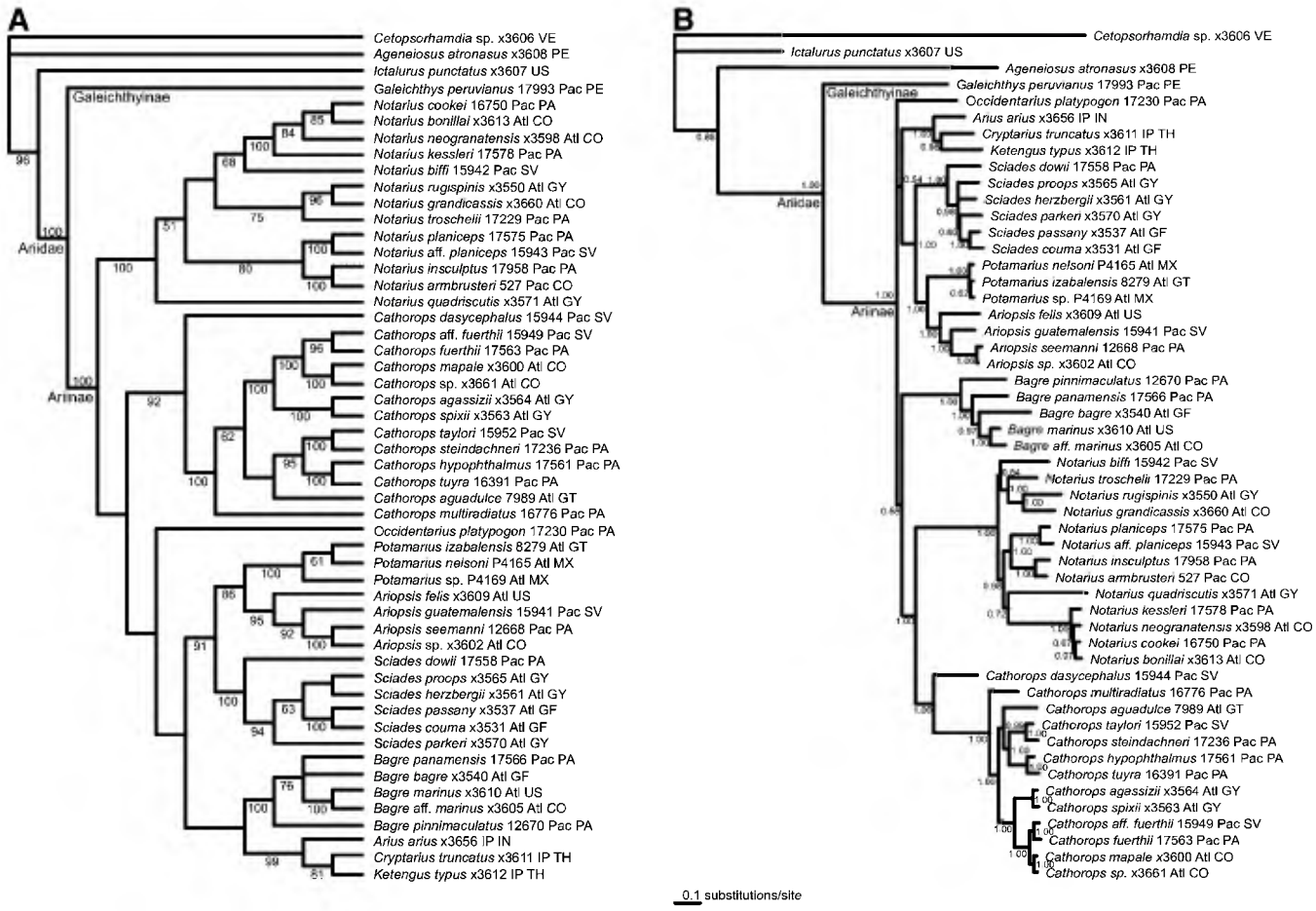

Fig. 2. Phylogenetic reconstructions based on 2842 aligned sites of the mitochondrial dataset (cyt *b*, ATPase 8/6, 12S, and 16S). (A) Strict consensus cladogram of the two most parsimonious topologies of 5516 steps (CI = 0.31, RI = 0.62); numbers on nodes indicate bootstrap support values. (B) 50% majority rule consensus phylogram resulting from the Bayesian analysis of 135,003 post-burn-in trees; numbers on nodes indicate posterior probabilities. Specimen tags indicate specimen tissue numbers (see details on Appendix A). Atl, Atlantic; Pac, Eastern Pacific; IP, Indo-Pacific. Country codes follow ISO-3166.

thyinae examined, was recovered sister to the Ariinae. The monophyly of the Ariinae and its New World genera (based on current placements) is highly supported. Except for the well-supported node including *Sciades* + (*Ariopsis* + *Potamarius*), other intergeneric clades within the Ariinae have low support values and are incongruent among both reconstruction criteria. The monotypic *Occidentarius* n. gen. was recovered as an isolated lineage within the ariines. New World ariines were rendered paraphyletic due to the nested position of a clade including the three Indo-Pacific species. The position of *A. arius* within the Indo-Pacific clade confirms recent classification schemes that reject the placement of New World species in *Arius* (Betancur-R. and Acero P., 2004; Kailola, 2004). *Cathorops dasycephalus*, previously included in *Arius*, was recovered as the most basal *Cathorops* lineage. BI and MP topologies of *Cathorops* and *Ariopsis* clades are identical and include highly supported nodes. The only instances of congruent and well-supported reconstructions within *Sciades* are the basal position of *Sciades dowii* and the sister-taxa relationship of *Sciades couma* and *Sciades passany*. Relationships of the species of *Notarius* are generally poorly supported at basal nodes and well-supported at internal nodes. Both reconstruction criteria often reveal incongruence within *Notarius* and *Potamarius*, but nodal support is low. Resolution and

Table 2
Best-fit models selected with the Akaike information criterion for each data partition

Partition	Model	# subs. parameters
1st position ATPase 8	TVM+I+Γ	6
2nd position ATPase 8	GTR+Γ	6
3rd position ATPase 8	HKY+Γ	2
1st position ATPase 6	GTR+Γ	6
2nd position ATPase 6	TrN+I+Γ	6
3rd position ATPase 6	GTR+Γ	6
1st position cyt *b*	TVM+I+Γ	6
2nd position cyt *b*	TVM+I+Γ	6
3rd position cyt *b*	GTR+Γ	6
12S	GTR+I+Γ	6
16S	GTR+I+Γ	6
Combined mitochodrial	GTR+I+Γ	6
1st position *rag2*	HKY+Γ	2
2nd position *rag2*	TrN+I	6
3rd position *rag2*	HKY+Γ	2
rag2	K80+I	2

clade support within *Bagre* is high in the BI tree, but includes a polytomy in the MP tree.

Reconstructions based on MP (786 trees of 257 steps, CI = 0.83, RI = 0.74) and BI (majority rule consensus of 135,003 post-burn-in trees) analyses of the nuclear *rag2* dataset are shown in Fig. 3. The *rag2* gene is highly conserved among ariids, resulting in poorly resolved clades. As was expected from previous studies (Diogo, 2005; Sullivan et al., 2006), the anchariid genus *Gogo* was recovered sister to the Ariidae. MP and BI reconstructions confirm the subfamilial divisions as well as the monophyly of most New World genera and the Indo-Pacific group. Both topologies, however, failed to support the monophyly of *Ariopsis* and *Cathorops*. The poorly supported assignment of *C. dasycephalus* sister to *Potamarius* in the BI topology is likely erroneous as it contradicts both mitochondrial and morphological (see below) topologies that strongly place *C. dasycephalus* as a basal *Cathorops*. Basal resolution within the ariine clade as well as intrageneric resolution was negligible.

The MP analysis based on the morphological dataset yielded 24 optimal trees with 90 steps (CI = 0.70, RI = 0.89) (Fig. 4). Considering only common taxa, the topology recovered is identical to that previous reported (Betancur-R. et al., 2004). *Galeichthys ater* from South Africa was recovered sister to *G. peruvianus* from the Eastern Pacific, demonstrating the monophyly of the subfamily Galeichthyinae, although statistical support is low. The monophyly of the Ariinae is strongly supported. All ariine genera with more than one species are monophyletic but only *Cathorops*, *Sciades*, and *Bagre* are highly supported. *Occidentarius platypogon* was recovered as the sister species of *Bagre*. Other instances of intergeneric relationships are poorly supported. The Indo-Pacific *A. arius* is nested within the ariine clade, confirming the non-monophyly of New World sea catfishes. Except for the basal placement of *C. dasycephalus* within *Cathorops*, other intrageneric clades are either resolved with low support or non-resolved. The topology obtained within the *Bagre* clade [*B.* aff. *marinus* (*Bagre panamensis* (*B. bagre* + *Bagre pinnimaculatus*))] is identical to that of Acero P. et al. (2005) using multivariate methods on morphometric data. Both morphological hypotheses are in conflict with the molecular topologies that place *B. pinnimaculatus* as the sister taxon of the remaining species of *Bagre*, but internal node support values are often low.

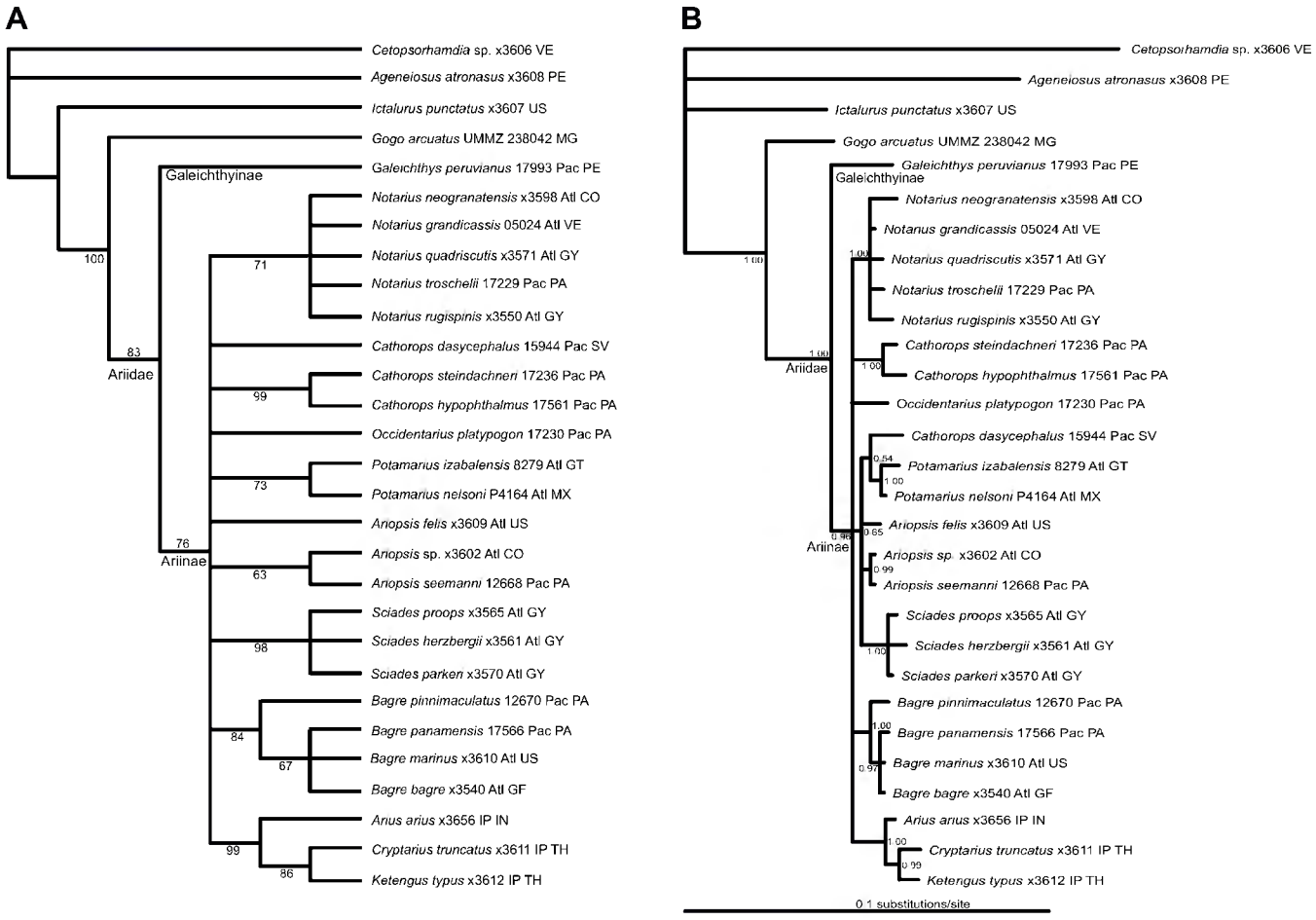

Fig. 3. Phylogenetic reconstructions based on 978 aligned sites of the nuclear *rag2* dataset. (A) Strict consensus cladogram of 786 most parsimonious topologies of 257 steps (CI = 0.83, RI = 0.74); numbers on nodes indicate bootstrap support values. (B) 50% majority rule consensus phylogram resulting from the Bayesian analysis of 135,003 post- burn-in trees; numbers on nodes indicate posterior probabilities. Specimen tags indicate specimen tissue or catalog numbers (see details on Appendix A). Atl, Atlantic; Pac, Eastern Pacific; IP, Indo-Pacific. Country codes follow ISO-3166.

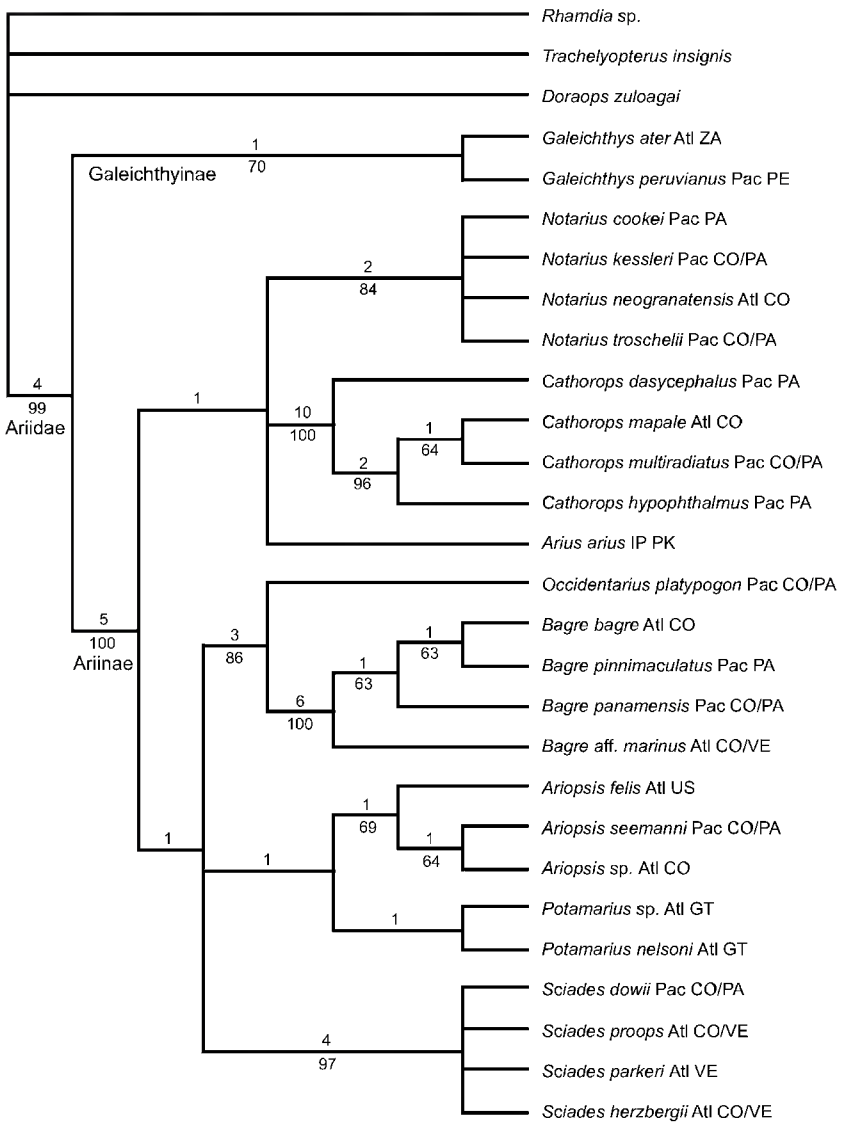

Fig. 4. Phylogentic reconstruction based on 55 morphological characters. The topology corresponds to the strict consensus of 24 optimal trees with 90 steps (CI = 0.70, RI = 0.89). Numbers above and below nodes indicate decay indices and bootstrap values, respectively. Atl, Atlantic; Pac, Eastern Pacific; IP, Indo-Pacific. Country codes follow ISO-3166.

3.3. Tests of morphological phylogenetic hypotheses

The results obtained with Templeton and SH tests are summarized in Table 3. In all comparisons performed, trees constrained under the morphological hypothesis of Kailola (2004) yielded scores significantly worse than those obtained with the unconstrained searches. Both Templeton and SH tests also evidenced significant departure from congruence between the mitochondrial trees constrained under our morphological hypothesis and the unconstrained trees. However, the *rag2* dataset under the same constraint did not reveal any conflicts.

4. Discussion

4.1. Congruence, conflicts, and phylogenetic signal

The results obtained using different reconstruction criteria and molecular datasets were often incongruent with low support for supra- and infrageneric levels. The subfamilial divisions and the monophyly of the New World genera examined, however, were highly congruent among different topologies. Mitochondrial data contained strong phylogenetic signal, yielding (in most cases) well-resolved and well-supported nodes. Our nuclear *rag2* dataset, containing only 36 (3.7%) parsimony-informative sites within the Ariidae, provided low inter- and intrageneric resolution. Similarly, Hardman and Page (2003) found that phylogenetic analyses of *rag2* yielded less resolved topologies than cyt *b* in ictalurid catfishes. The main drawbacks associated with *rag2* reconstructions in this study include the non-monophyly of *Ariopsis* and *Cathorops* and the placement of *C. dasycephalus* sister to *Potamarius* in the BI topology. Such problems are likely caused by insufficient data due to the low variability of *rag2*, which may lead to random errors. At deeper phylogenetic levels in fishes, including suprafamilial categories within siluriforms, *rag2* has been

Table 3
Summary of results obtained with Templeton and Shimodaira–Hasegawa (SH) tests of topology congruence between trees constrained under the morphological hypotheses and unconstrained trees

	Mitochondrial Templeton	Mitochondrial SH	*rag2* Templeton	*rag2* SH
Kailola (2004)				
Unconstraint tree score	1363 steps	−ln L 9685.3	54 steps	−ln L 1715.0
Constraint tree score	1414 steps	−ln L 9723.7	61 steps	−ln L 1740.9
Score difference	51 steps	−ln L 38.38	7 steps	−ln L 25.9
P value	**0.0001**	**0.002**	**0.0391**	**0.007**
This study				
Unconstraint tree score	2810 steps	−ln L 1518.6	80 steps	−ln L 1899.3
Constraint tree score	2854 steps	−ln L 1539.4	82 steps	−ln L 1910.8
Score difference	44 steps	−ln L 20.8	2 steps	−ln L 11.5
P value	**0.0017**	**0.030**	0.6875	0.11

shown to be more variable and contain stronger signal (e.g. Lavoué and Sullivan, 2004; Calcagnotto et al., 2005; Sullivan et al., 2006). The lack of resolution or poorly supported nodes among basal ariines is consistent with MP and BI reconstructions derived from both mitochondrial and nuclear datasets. Given that different markers used have different levels of phylogenetic signal, this pattern might be explained by a rapid radiation of early ariines.

Sequence data was incongruent with Kailola's (2004) topology when considering only common taxa. The main inconsistencies of Kailola's phylogenetic hypothesis, as compared to the molecular topologies, are (1) the nested position of *Galeichthys*, (2) the basal placement of *K. typus* and *C. truncatus*, and (3) the non-monophyly of the Indo-Pacific group composed by *A. arius* + (*K. typus* + *C. truncatus*). With regard to our morphological hypothesis, only mitochondrial data detected significant topological incongruence between constrained and unconstrained searches. The conflicting nodes are at supra- and infrageneric levels. As was mentioned before, however, both our mitochondrial and morphological topologies support the monophyly or the status of all New World genera examined as well as the subfamilial divisions.

4.2. Revised classification of New World ariines

A conservative scheme summarizing generic and suprageneric clades from the five trees in Figs. 2–4 is shown in Fig. 5. The MRP supertree matrix included 53 terminals and 137 characters (i.e. coded clades), and the heuristic search yielded 64 optimal trees with 154 steps. Two intergeneric clades with relatively low support values were collapsed in the strict consensus, one grouping *Notarius* + *Cathorops* (69%) and the other grouping the remaining ariine lineages (68%). Supertree methods have been criticized because their resulting hypotheses may reveal unsupported novel clades (i.e. clades not specified in any of the inputs trees) (Bininda-Emonds and Bryant, 1998; Bininda-Emonds, 2003); however, no instances of unsupported novel clades were observed in our supertree topology.

The subfamilial status of the monogeneric Galeichthyinae and the Ariinae was revised in Acero P. and Betancur-R. (2007), and thus the classification scheme presented herein is restricted to New World ariine taxa. The revision is at generic and suprageneric categories according to Fig. 5, and includes the description of new genus-level names. Due to the unavailability of material of *A. labiatus*, *H. henni*, *A. grandoculis*, and *Genidens* spp., these taxa are not revised herein. Diagnostic morphological transformations are as listed in Appendix D, unambiguous synapomorphies are given in bold. Genera lacking unambiguous morphological synapomorphies (e.g. *Ariopsis*, *Potamarius*, and *Notarius*) are also diagnosed by a combination of features. Positions for unambiguous amino acid synapomorphies are referenced from the start codon as specified in the Section 3.

Our classification scheme differs in part from that of Marceniuk and Ferraris (2003) and Kailola (2004). The disagreements are either because the specific composition of genera is largely dissimilar and/or because species are placed in different genera. Different generic names used by Marceniuk and Ferraris (2003) and Kailola (2004) are listed in the description of each genus.

4.2.1. *Informal clade* Sciades + Ariopsis + Potamarius

Diagnosis (amino acid). Cyt *b*, 291: leucine → methionine.

4.2.2. *Genus* Sciades *Müller and Troschel (1849)*

Type species. Bagrus (*Sciades*) *emphysetus* Müller & Troschel (1849) (synonym of *S. parkeri* Traill).

Synonyms. Sciadeichthys Bleeker (1858), *Selenaspis* Bleeker (1858), *Leptarius* Gill (1863).

Diagnosis (morphological). **5:0 → 1,** 48: 0 → 1, **50:0 → 1, 51:1 → 2.**

Taxa and distribution. The genus includes six species, one from México to northern Perú in the Eastern Pacific (EP) (*S. dowii*) and five from Colombia to Brazil in the Western Atlantic (WA) (*S. couma*, *S. herzbergii*, *S. parkeri*, *S. passany*, and *S. proops*). Habitat: brackish, freshwater, and marine.

Comments. Kailola (2004) also placed *Notarius troschelii* and *Potamarius* sp. (as '*usumacinctae* MS of Bailey') in *Sciades*. Marceniuk and Ferraris (2003) included the species of *Sciades* in the Old World genus *Hexanematichthys*.

4.2.3. *Informal clade* Ariopsis + Potamarius

Diagnosis. Morphological: 55: 0 → 1 [this feature is also known in other Indo-Pacific taxa not examined herein

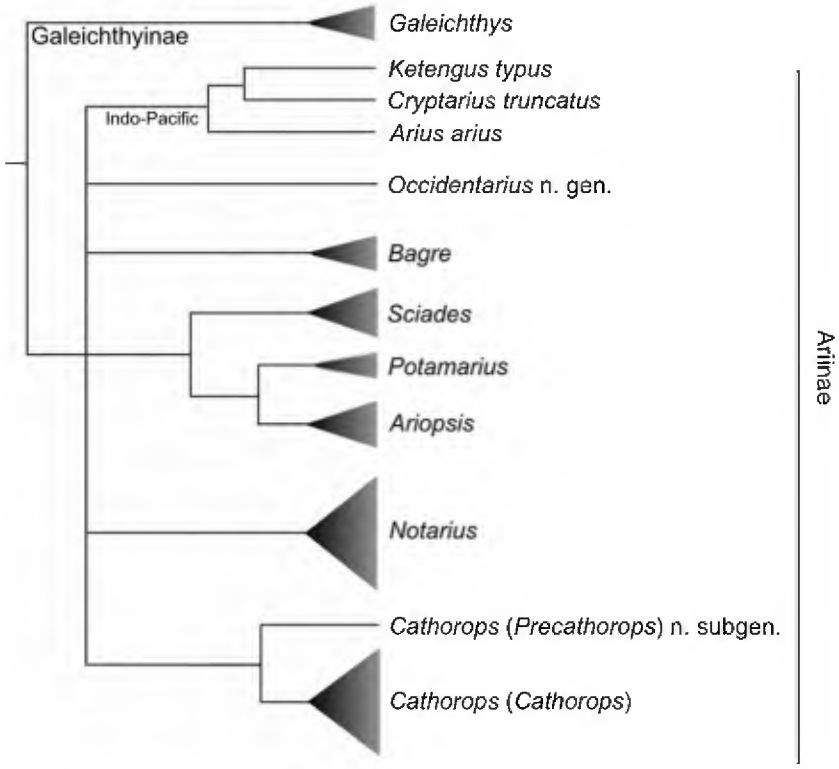

Fig. 5. Conservative scheme summarizing generic and suprageneric relationships of most New World ariids and some Old World taxa. The topology was estimated using MRP supertree approach based on the trees shown on Figs. 2–4 (strict consensus of 64 optimal trees with 154 steps; two weakly supported intergeneric nodes were collapsed). Area of triangles is proportional to the number of species included in each New World genus.

(Kailola, 2004: character 34)]. *Amino acid*: ATPase 8, 42: threonine → proline.

4.2.4. Genus Ariopsis *Gill (1861)*

Type species. Arius milberti Valenciennes (1840) [synonym of *Silurus felis* Linnaeus (1766)].

Diagnosis (morphological). 46: 0 → 1. The following combination of features also distinguish the species of *Ariopsis* from other New World ariines: three pair of barbels present; gill rakers on posterior surfaces of first two gill arches absent or rudimentary; medial groove on head present; broad granulations or spinulations on anterior surface of head shield absent; lapillus otolith rounded; and tooth patches in the roof of mouth often arranged in two pairs (vomerine tooth patches in *A. felis* often missing on one or both sides), the external pair (palatal) rounded to ovate. Apparently, the species of *Ariopsis* are also characterized by having five (vs. six) branchiostegal rays (W.R. Taylor, unpublished data).

Taxa and distribution. Ariopsis includes five species, three from the Gulf of Mexico to western Venezuela in the WA (*A. assimilis*, *A. felis*, and *Ariopsis* sp.) and two from México to Perú in the EP (*A. guatemalensis* and *A. seemanni*). Habitat: brackish, freshwater, and marine.

Comments. Ariopsis sensu Kailola (2004), including 19 species from the New World and the Old World, is not monophyletic (see Fig. 1). Preliminary analyses based on mitochondrial sequences suggest no affinity between two Indo-Pacific species placed in *Ariopsis* by Kailola (2004) (*Arius graeffei* and *A. midgleyi*) and the Neotropical taxa (unpublished data). Marceniuk and Ferraris (2003) placed the species of *Ariopsis* in *Hexanematichthys*.

4.2.5. Genus Potamarius *Hubbs and Miller (1960)*

Type species. Conorhynchos nelsoni Evermann and Goldsborough (1902).

Diagnosis. Morphological: 9: 0 → 1, 24: 0 → 1. Other putative diagnostic features (not coded into the data matrix): lateral cornu of lateral ethmoid long and paddle-shaped, directed posteriorly and forming a very-acute angle with the posterolateral process of the bone; posterior cranial fontanelle developed and lanceolate; supraoccipital process long and narrow. The following combination of features also distinguish the species of *Potamarius* from other New World ariines: posterior gill rakers on rear surfaces of first two gill arches well developed, dorsomedian head groove absent, lapillus otolith rounded in shape. Amino acid: *rag2*, 239: glutamic acid → aspartic acid.

Taxa and distribution. Three species occurring in rivers draining into the WA in Mesoamerica (México and Guatemala) (*Potamarius* sp., *P. izabalensis*, and *P. nelsoni*). Habitat: freshwater.

Comments. It has been suggested that *A. grandoculis* (from freshwaters in Brazil), and *A. labiatus* and *H. henni* (from freshwaters in Ecuador) belong to *Potamarius* (Marceniuk and Ferraris, 2003; Betancur-R. and Acero P., 2004). Given that such generic placement would imply that *Potamarius* has a wide disjunct distribution, a more defin-

itive phylogenetic assessment of these species is required to clarify whether the genus is endemic to Mesoamerica.

4.2.6. Genus Bagre *Cloquet (1816)*

Type species. Silurus bagre Linnaeus (1766).

Synonyms. Bagre Oken (1817), *Glanis* Agassiz (1829), *Breviceps* Swainson (1838), *Stearopterus* Minding (18320, *Felichthys* Swainson (1839), *Ailurichthys* Baird and Girard (18540, *Mystus* Gray (1854), *Anemanotus* Fowler (1944).

Diagnosis. Morphological: **2:0 → 1,** 9:0 → 1, **23:0 → 1,** 27: 0 → 1, 33: 0 → 1, **35:0 → 1, 43:0 → 1.** Amino acid: ATPase 6, 4: asparagine → serine, 7: aspartic acid → asparagine; *rag2*, 252: leucine → phenylalanine.

Taxa and distribution. Four recognized species, two from Cape Cod (USA) to Brazil in the WA (*B. bagre* and *B. marinus*) and two from California to northern Perú in the EP (*B. panamensis* and *B. pinnimaculatus*). High mitochondrial distances (combined cyt *b* and ATPase 8/6 = 3.6%) between haplotypes of *B. marinus* from the Gulf of Mexico and Colombia suggest that the southern entity (*B.* aff. *marinus*) is a putative cryptic species. Habitat: brackish and marine.

4.2.7. Genus Cathorops *Jordan and Gilbert (1883)*

Type species. Arius hypophthalmus Steindachner (1877).

Diagnosis. Morphological: **1:0 → 1, 8:0 → 1, 15:0 → 1, 16:0 → 1,** 17: 0 → 1, **18:1 → 2, 21:0 → 1,** 24: 0 → 1, **30:0 → 1, 34:0 → 1.** Amino acid: ATPase 6, 29: isoleucine → methionine; *rag2*, 219: leucine → methionine.

4.2.8. Subgenus Precathorops *n. subgen. Betancur-R. and Acero P.*

Type species. Arius dasycephalus Günther (1864).

Diagnosis. This monotypic subgenus is diagnosed by the following autapomorphies of *Cathorops dasycephalus*. Morphological: presence of bony spinulations on posterior limbs of mesethmoid, posterolateral process of lateral ethmoids, and anterior portion of frontals (more developed in mature females). Amino acid: ATPase 6, 40: asparagine → aspartic acid; *rag2*, 296: valine → isoleucine.

Etymology. From the latin *pre* meaning before, and the genus name *Cathorops*. The noun *Precathorops* can be interpreted as 'primitive *Cathorops*', in reference to the basal position of *C. dasycephalus*.

Taxa and distribution. The subgenus is monotypic, including only *Cathorops* (*Precathorops*) *dasycephalus* from México to Colombia in the EP. Habitat: brackish and marine.

4.2.9. Subgenus Cathorops *Jordan and Gilbert (1883)*

Diagnosis. Morphological: **10:0 → 1,** 26: 0 → 1, **32:0 → 1.** Amino acid: ATPase 8, 11: alanine → isoleucine; ATPase 6, 1: methionine → leucine, 71: methionine → threonine; *rag2*, 100: asparagine → serine, 292: threonine → isoleucine.

Taxa and distribution. The subgenus has at least 14 species, including two undescribed (*Cathorops* sp. from Colombia to Venezuela in the WA, *C.* aff. *fuerthii* from El Salvador in the EP). Six recognized species are distributed from México to Brazil in the WA (*C. agassizii*, *C. aguadulce*, *C. arenatus*, *C. mapale*, *C. melanopus*, *C. spixii*) and six from México to northern Perú in the EP (*C. fuerthii*, *C. hypophthalnus*, *C. multiradiatus*, *C. steindachneri*, *C. taylori*, and *C. tuyra*). Habitat: brackish, freshwater, and marine.

Comments. Genetic divergence data corroborate subgeneric differentiation in *Cathorops*. Combined cyt *b* + ATPase 8/6 distances between the subgenera *Precathorops* and *Cathorops* are 12.3–13.82%, whereas the distances among the species of the subgenus *Cathorops* are 0.94–9.51% (see also Fig. 2B).

4.2.10. Genus Notarius *Gill (1863)*

Type. Arius grandicassis Valenciennes (1840).

Synonyms. Aspistor Jordan and Evermann (1898), *Sciadeops* Fowler (1944).

Diagnosis. Morphological: 6: 0 → 1 (this feature is absent in *N. grandicassis* not examined here), 12: 0 → 1, 13: 0 → 1. The following combination of features also distinguish the species of *Notarius* from other New World arines: three pair of barbels present; posterior gill rakers on rear surfaces of first two gill arches absent; narrow groove on median depression of head absent; lapillus otolith square; broad granulations or spinulations on anterior surface of head shield absent; and except for *Notarius phrygiatus* and *Notarius rugispinins*, vomerine tooth patches present. Amino acid: ATPase 8, 53: proline → leucine; ATPase 6, 39: leucine → valine, 62: leucine → methionine, 227: valine → isoleucine; cyt *b* 257: proline → serine, 329: alanine → methionine; *rag2*, 280: serine → proline.

Taxa and distribution. Notarius has at least sixteen species, including one cryptic (*N.* aff. *planiceps* from El Salvador in the EP). Seven species are distributed from Colombia to Brazil in the WA (*N. bonillai*, *N. grandicassis*, *N. luniscutis*, *N. neogranatensis*, *N. phrygiatus*, *N. quadriscutis*, and *N. rugispinins*) and eight from México to Ecuador in the EP (*N. armbrusteri*, *N. biffi*, *N. cookei*, *N. insculptus*, *N. kessleri*, *N. lentiginosus*, *N. planiceps*, *N. troschelii*). Habitat: brackish, freshwater, and marine.

Comments. Kailola (2004) placed the species of *Notarius* in the genera *Ariopsis*, *Aspistor*, *Hemiarius* (from the Indo-Pacific), and *Sciades*, but none of such species were included in her phylogenetic analysis (see Fig. 1). Marceniuk and Ferraris (2003) used *Notarius* (only four species), *Aspistor*, *Arius*, and *Hexanematichthys*. The usage of other generic names (e.g. *Aspistor* and *Sciadeops*) may be acceptable at the subgeneric level, once the relationships among basal *Notarius* lineages are clarified.

4.2.11. Genus Occidentarius *n. gen. Betancur-R. and Acero P.*

Type species. Arius platypogon Günther (1864).

Diagnosis. This monotypic genus is diagnosed from other New World genera by the following autapomorphies of *O. platypogon*. Morphological: Anterior cavities of lateral ethmoids (where the olfactory bulb is housed) greatly developed; bony excrescence of posterolateral process of lateral ethmoids prominent, completely closing the lateral fenestrae; basioccipital with a laminar bony crest bordering

the anterior foramen of aortic tunnel. Amino acid: cyt *b*, 93: isoleucine → leucine; *rag2*, 299: arginine → glutamine, 309: serine → cysteine.

Etymology. From the latin *occidens* meaning west, and the genus name *Arius*. The name is in reference to the restriction of the species to the EP, the western-most region occupied by ariids.

Taxa and distribution. The genus is monotypic, including only *O. platypogon* from México to Perú in the EP. Habitat: marine.

Comments. Although *Genidens* was not examined here, it is distinguished from the new genus by lacking the bony excrescence of lateral ethmoids (see Marceniuk, 2005, Fig. 2). Marceniuk and Ferraris (2003) and Kailola (2004) placed *O. platypogon* in the genera *Hexanematichthys* and *Aspistor*, respectively.

4.3. Biogeography of major ariid lineages

Sea catfishes are the only siluriform family distributed on all continents in tropical and temperate regions (Fig. 6). They occur in three main biogeographic provinces: New World, western and southern Africa, and Indo-West Pacific (also divided into Madagascar, India–Southeast Asia or Sunda shelf, and Papua New Guinea–Australia or Sahul shelf). Compared to most tropical marine fish groups, ariids have a rather limited dispersal capability. They are restricted to continental shelves, not only as adults because of their non-pelagic behavior, but also in early stages due to their specialized reproductive habits (i.e. male mouthbrooding). This inability to disperse through oceanic waters suggests that ancient ariid diversification was driven by plate tectonic events. Although a more complete taxon sampling is still required to provide comprehensive phylogenetic and biogeographic hypotheses for ariids, we infer here plausible scenarios that explain distributional patterns of major clades recovered.

During the Cretaceous and the Paleogene, the Tethys Sea was the dominant tropical seaway connecting the Atlantic and Indian Oceans (Adams and Ager, 1967). Many tropical marine groups presently distributed world-wide have been hypothesized to represent Tethyan relicts (Adams and Ager, 1967; Bellwood and Wainwright, 2002). The distribution of modern ariines (Fig. 6), a predominantly circumtropical group comprising about 97% of ariid diversity, might therefore be the result of an ancient diversification through the Tethys Sea before its final closure in the Early to Middle Miocene (Steininger and Rögl, 1984). The lack of resolution or poorly supported nodes among basal ariine lineages suggests that early diversification events took place in relatively short periods of time. This may explain the failure of different topologies to support the monophyly of New World ariines (see Figs. 2–5). With the exception of a few punctual records (e.g. Golani and Sonin, 1996), ariines are absent from the Mediterranean Sea, the remnant of the Tethys Sea. This is probably due to the Messinian salinity crisis of the Mediterranean (5–6 Mya), which caused local extirpation of several marine taxa (Duggen et al., 2003).

Unlike ariines, galeichthyines are absent from the tropics and have a disjunct distributional pattern: one species occurs in the Eastern Pacific in Perú and three are restricted to southern Africa (Fig. 6). In order to explain the biogeography of galeichthyines based on the hypothesis presented for ariines, a more complex scenario is required. Such a scenario implies (1) that the galeichthyine ancestor was tropical and subsequently both African and South American lineages became independently subtropical and (2) that the galeichthyines became extinct along the eastern coast of tropical America. Although fossil ariids have been widely recorded in the Neotropics, currently available data offer no support for this scenario (e.g. Nolf and Aguilera, 1998; Gayet and Meunier, 2003; Aguilera and Rodríguez de Aguilera, 2004). Alternatively, galeichthyines may have

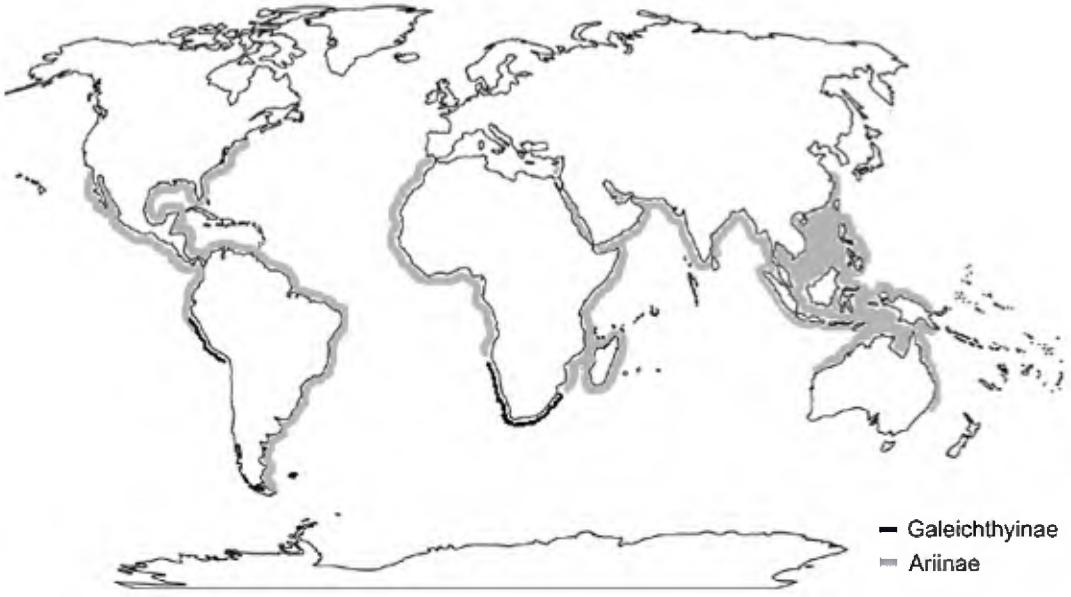

Fig. 6. Approximate distribution of major ariid lineages.

originated as a subtropical lineage in the embayment formed at southern Gondwanaland after the separation of Australia before the Early Cretaceous (Fig. 7A). It is remarkable that before the Eocene Antarctica had a temperate climate and included fish fauna found at lower latitudes today (Bellwood and Wainwright, 2002). After the final separation of the supercontinent 90 Mya (Barron et al., 1981), galeichthyines may have remained in the southern tips of both South America and Africa and perhaps in northern Antarctica (Fig. 7B). The complete separation of Antarctica and South America and the opening of the Drake Passage permitted the formation of the circum-Antarctic current that caused a significant decrease in water temperature 37 mya (Veevers and Ettriem, 1988). After that period, habitat conditions in southern South America were suboptimal for galeichthyines, which probably caused their progressive migration to lower latitudes through the western coast of the continent (Fig. 7C), finally reaching today's subtropical waters of Perú (Fig. 6).

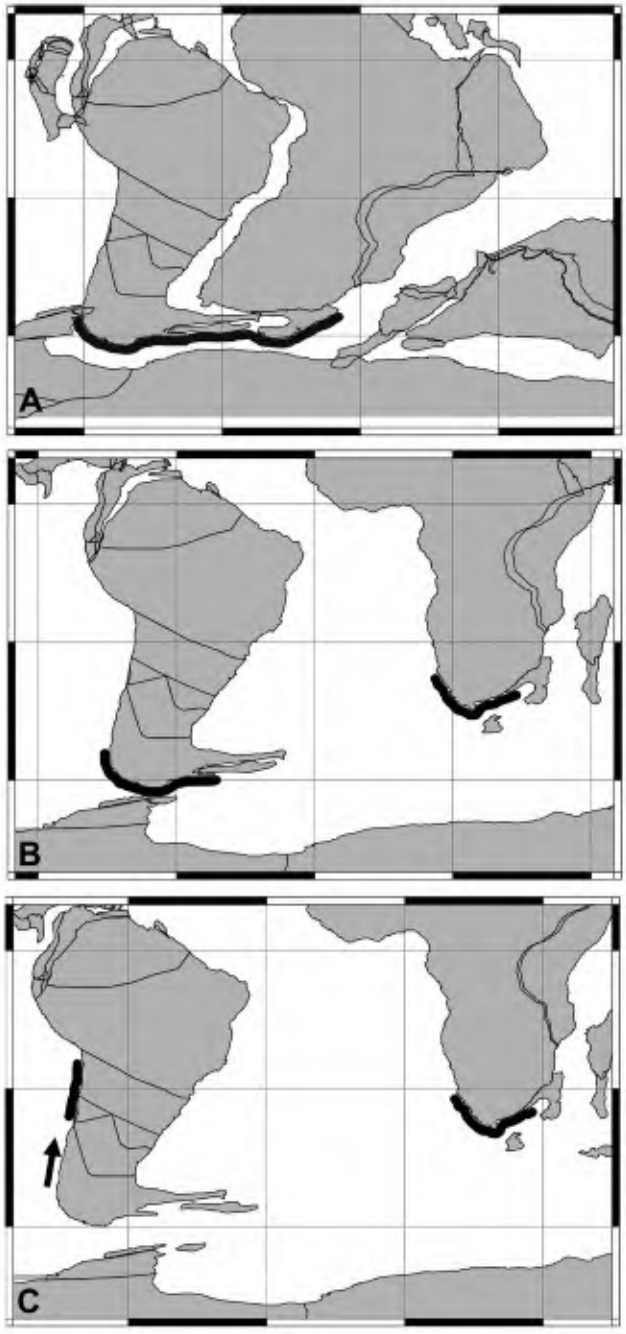

Fig. 7. Inferred distribution of galeichthyines during the plate tectonic progression of Gondwanaland. Reconstructions are based on the following events: (A) Gondwana after the separation of Australia (before Early Cretaceous), (B) final separation of the supercontinent before the opening of Drake Passage (between Early Cretaceous to Late Eocene), and (C) opening of Drake Passage and cooling of Antarctica (after Late Eocene) (Reconstructions from: http://www.odsn.de/).

The earliest fossil specimens of catfishes date from Late Campanian to Early Maastrichtian (ca. 72–75 mya) (Gayet and Meunier, 2003). Interestingly, ariids are one of the most abundant and oldest groups of catfishes in the fossil record. Ariid fragments are widespread and the earliest representatives are known from South and North America 75–68 Mya (Cione, 1987; Nolf and Stringer, 1996). The record also includes fossils from Europe, Africa, and Asia (Gayet and Meunier, 2003). Fragments found on every continent pre-date the Early Eocene, suggesting that the hypothesis of Tethyan ariine diversification is not in disagreement with the fossil record. The same is not true, however, for the southern Gondwanan origin of galeichthyines, which should date back at least to the Early Cretaceous. Recent works have argued that the origin of catfishes occurred much before than suggested by the fossil record. Molecular clock estimations indicate that the divergence time of siluriforms took place between 150 and 170 Mya (Briggs, 2005; Peng et al., 2006). Furthermore, Diogo (2004) pointed out that (1) although the oldest catfish fossil dates to the Late Cretaceous, by that period the group was already distributed on various continents; and (2) despite the fact that ariids have an apomorphic position in the catfish tree (see Diogo, 2005; Sullivan et al., 2006), the family includes the oldest fossil records within the order. Such scenarios imply a much older origin of siluriforms. It has been suggested that the lack of older otophysian fossils (including catfishes) may be due to a failure of preservation or detection (Lundberg, 1998).

Sea catfish species richness is greatest in the Western Atlantic between the Southern Caribbean and northern Brazilian coasts from Golfo de Urabá (Colombia) to the mouth of the Amazon; in the Eastern Pacific, it is greatest in the Panamic province (Hastings, 2000), between southern Golfo de Fonseca (Honduras) and southern Golfo de Guayaquil (northern Perú). Given that both provinces were united until 3.2 mya, before the Pliocenic rising of the isthmus of Panamá, it would be expected that there are amphiamerican clades. Five of the seven Neotropical ariine genera examined occur in both provinces (*Ariopsis*, *Bagre*, *Cathorops*, *Notarius*, and *Sciades*). As suggested by terminal relationships (Fig. 2) and by genetic distances, the genera *Notarius*, *Cathorops*, and *Ariopsis* all include taxa involved in recent trans-isthmian speciation events, but this is not the focus of this article and will be discussed elsewhere.

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Appendix A. List of molecular material and GenBank Accession numbers

Species	Tissue No.	Catalog No.	GenBank Accession Nos.
Outgroup			
Cetopsorhamdia sp. (Heptapteridae)	stri-x3606	INHS 56139	DQ119442[a], DQ990631, DQ990527, DQ990579, DQ990502
Ageneiosus atronasus (Auchenipteridae)	stri-x3608	INHS 54689	DQ119403[a], DQ990633, DQ990529, DQ990580, DQ990503
Ictalurus punctatus (Ictaluridae)	stri-x3607	INHS 47559	AY184253[a], DQ990632, DQ990528, DQ990581, AY184245[b]
Ingroup			
Gogo arcuatus (Anchariidae)	—	UMMZ 238042	DQ492415[b]
Ariopsis felis	stri-x3609	AUM 5233-02	DQ119355[a], DQ990659, DQ990564, DQ990599, DQ492410[b]
A. guatemalensis	stri-15941	STRI-5732	DQ990484, DQ990660, DQ990562, DQ990598
A. seemanni	stri-12668/15948	STRI-5730/5731	DQ990485, DQ990486, DQ990661, DQ990662, DQ990561, DQ990596, DQ990517
Ariopsis sp.	stri-x3602/x3603	INVEMAR-PEC 5332/5340	DQ990487, DQ990488, DQ990663, DQ990664, DQ990563, DQ990597, DQ990516
Arius arius	stri-x3656/3657	USNM 376608	AY688674, DQ990501, AY688661, AY688648, DQ990681, DQ990576, DQ990622, DQ990525
Bagre bagre	stri-x3540/x3545	MHNG 2608.096, ANSP 178751	AY688673, AY688660, AY688647, DQ990678, DQ990572, DQ990626, DQ990523
B. marinus	stri-x3610	AUM 5234-003	DQ119472[a], DQ990679, DQ990573, DQ990627, DQ990524
B. aff. *marinus*	stri-x3605	INVEMAR-PEC 5336	DQ990500, DQ990680, DQ990574, DQ990628
B. panamensis	stri-17566/12672	STRI-5735/5734	DQ990498, DQ990497, DQ990676, DQ990571, DQ990625, DQ990521
B. pinnimaculatus	stri-12670	STRI-5736	DQ990499, DQ990677, DQ990575, DQ990629, DQ990522
C. agassizii	stri-x3541/x3564	MHNG 2608.097, ANSP 178743	DQ990473, DQ990474, DQ990645, DQ990646, DQ990552, DQ990620
Cathorops aguadulce	stri-7989, P4172	STRI-5450, ECO-SC 4270	DQ990476, DQ990648, DQ990649, DQ990544, DQ990614
C. dasycephalus	stri-15944/17233	STRI-5718/5717	DQ990467, DQ990638, DQ990639, DQ990556, DQ990621, DQ990510
C. fuerthii	stri-17563	STRI-5720	DQ990469, DQ990641, DQ990554, DQ990617
C. aff. *fuerthii*	stri-15949	STRI-5726	DQ990468, DQ990640, DQ990555, DQ990618
C. hypophthalmus	stri-17561	STRI-5722	DQ990478, DQ990651, DQ990548, DQ990612, DQ990512
C. mapale	stri-x3600/x3601	INVEMAR-PEC 5333/5348	AY575016, AY575017, AY575018, AY575019, AY575021, AY575020, DQ990550, DQ990616
C. multiradiatus	stri-16776	STRI-5723	DQ990477, DQ990650, DQ990545, DQ990609
C. spixii	stri-x3563	ANSP 178744	DQ990475, DQ990647, DQ990551, DQ990619
C. steindachneri	stri-17236	STRI-5725	DQ990472, DQ990644, DQ990546, DQ990611, DQ990511
C. taylori	stri-15952	STRI-5727	DQ990471, DQ990643, DQ990547, DQ990610
C. tuyra	stri-16391	STRI-5724	DQ990479, DQ990652, DQ990549, DQ990613
Cathorops sp.	stri-x3661	INVEMAR-PEC 5734 (494)	DQ990470, DQ990642, DQ990553, DQ990615
Cryptarius truncatus	stri-x3611	INHS 93580	DQ119391[a], DQ990682, DQ990578, DQ990624, DQ990526
Galeichthys peruvianus	stri-17993	STRI-5781	DQ990462, DQ990634, DQ990530, DQ990582, DQ990504
Ketengus typus	stri-x3612	INHS 93581	DQ119485[a], DQ990683, DQ990577, DQ990623, DQ492413[b]
Notarius armbrusteri	527, 529	INVEMAR-PEC 6677/6678	DQ373045, DQ373046, DQ373041, DQ373042, DQ373043, DQ373044, DQ990542, DQ990585
N. biffi	stri-15942	STRI-5713	AY688667,AY688654, AY688641, DQ990538, DQ990589
N. bonillai	stri-x3613	INVEMAR-PEC 5342	AY582861, AY582863, AY582865, DQ990533, DQ990592
N. cookei	stri-16750/16752	STRI-5709	AY582860, DQ990463, AY582862, AY582864, DQ990534, DQ990594
N. grandicassis	stri-x3660, VEN05024	NV, AUM 44230	AY688671, AY688658, AY688645, DQ990637, DQ990540, DQ990587, DQ990509
N. insculptus	stri-17958	STRI-5715	AY688666, AY688653, AY688640, DQ990543, DQ990586

Appendix A (*continued*)

Species	Tissue No.	Catalog No.	GenBank Accession Nos.
N. kessleri	stri-17578/17231/17577	STRI-5711/5710	AY688663, DQ990465, DQ990466, AY688650, AY688637, DQ990532, DQ990591
N. neogranatensis	stri-x3598/x3599	INVEMAR-PEC 5337/5338	AY688662, DQ990464, AY688649, AY688636, DQ990531, DQ990593, DQ990505
N. planiceps	stri-17575	STRI-5712	AY688664, AY688651, AY688638, DQ990536, DQ990583
N. aff. planiceps	stri-15943	STRI-5714	AY688665, AY688652, AY688639, DQ990537, DQ990584
N. rugispinis	stri-x3550/x3538/x3532	ANSP 178749, MHNG 2595.70/2608.094	AY688668, AY688655, AY688642, DQ990635, DQ990636, DQ990539, DQ990588, DQ990506
N. quadriscutis	stri-x3571	ANSP 178740 (24J6)	AY688670, AY688657, AY688644, DQ990535, DQ990590, DQ990508
N. troschelii	stri-17229	STRI-5716	AY688669, AY688656, AY688643, DQ990541, DQ990595, DQ990507
Occidentarius platypogon	stri-12651/17230	STRI-5728/5729	AY688672, DQ990480, AY688659, AY688646, DQ990653, DQ990557, DQ990630, DQ990513
Potamarius sp.	P4169/4173	ECO-SC 4274, NV	DQ990483, DQ990657, DQ990658, DQ990560, DQ990600
P. izabalensis	stri-8279	STRI-5612	DQ990481, DQ990654, DQ990558, DQ990602, DQ990514
P. nelsoni	P4165/4164	ECO-SC 4266/4267	DQ990482, DQ990655, DQ990656, DQ990559, DQ990601, DQ990515
Sciades couma	stri-x3531/x3560/x3562/x3556	NV, ANSP 178745-747	DQ990495, DQ990494, DQ990672, DQ990671, DQ990674, DQ990673, DQ990569, DQ990604
S. dowii	stri-17558	STRI-5733	DQ990489, DQ990665, DQ990565, DQ990608
S. herzbergii	stri-x3561	ANSP 178746	DQ990496, DQ990675, DQ990568, DQ990603, DQ990520
S. parkeri	stri-x3570	ANSP 178741	DQ990492, DQ990669, DQ990567, DQ990606, DQ990519
S. passany	stri-x3537	NV	DQ990493, DQ990670, DQ990570, DQ990607
S. proops	stri-x3565, stri-x3539, stri-x3604	ANSP 178742, MHNG 2608.095, NV	DQ990491, DQ990490, DQ990667, DQ990668, DQ990666, DQ990566, DQ990605, DQ990518

NV, not vouchered.

[a] From Hardman (2005).

[b] From Sullivan et al. (2006).

Appendix B. List of morphological material examined

Ariopsis felis, USNM 206742, 128 mm standard length (SL), Grande Island, Louisiana, USA, UF 56867, 78 mm skull length (SkL), Florida, USA, WA. *A. seemanni*, STRI 5-1-1-9, 265 mm total length (TL), STRI 5-1-1-17, 260 mm TL, Panamá, EP. *Ariopsis* sp., INVEMAR-PEC 6781 (2), 274 mm ?SL, Ciénaga Grande de Santa Marta, Colombia, INVEMAR-PEC 6782, 128 mm SkL, Colombia, WA. *Ariopsis seemanni*, INVEMAR-PEC 6783, 88 mm SkL, Buenaventura, Colombia, EP. *Arius arius*, USNM 297279, 234 mm SL, Sind River, Hyderabad, Pakistan, Indo-Pacific, USNM 292812, 141 mm SL, Negombo, Ceylon, IP. *Notarius cookei*, INVEMAR-PEC 6784, 445 mm SL, STRI-5-2-10-2, 340 mm SL, STRI-5-2-10-4, 410 mm SL, Río Santa María, Herrera, Panamá, EP. *N. kessleri*, INVEMAR-PEC 6785 (4), 104–120 mm SkL, Buenaventura, Colombia, STRI 5-2-4-1, 205 mm SL, Bahía de Parita, Herrera, Panamá, EP. *N. neogranatensis*, INVEMAR-PEC 6786, 289 mm SL, Bahía de Cispatá, Córdoba, Colombia, WA. *N. troschelii*, INVEMAR-PEC 6787, male, 345 mm SL, Buenaventura, Colombia, EP; STRI 5-2-8-2, 320 mm TL, STRI 5-2-8-3, 290 mm SL, Panamá, EP. *Bagre bagre*, INVEMAR-PEC 6789, 68 mm SkL, Bahía de Cispatá, Córdoba, Colombia, WA. *B. aff. marinus*, INVEMAR-PEC 6790, female, 310 mm SL, La Guajira, Colombia, INVEMAR-PEC 6791 (3), 130–157 mm SkL, Venezuela, WA. *Bagre panamensis*, INVEMAR-PEC 6792, female, 239 mm SL, Buenaventura, Colombia, STRI 5-3-1-7, 350 mm SL, Aguadulce, Coclé, Panamá, EP, STRI 5-3-1-12, 295 mm SL, Panamá, EP. *B. pinnimaculatus*, INVEMAR-PEC 6793, female, 260 mm SL, Panamá, STRI 5-3-2-8, 510 mm SL, Nayarit, México, STRI 5-3-2-13, Punta Patiño, Panamá, EP. *Cathorops dasycephalus*, INVEMAR-PEC 6794, 197 mm SL, México, STRI 5-2-1-1, 200 mm TL, Aguadulce, Coclé, Panamá, STRI 5-2-1-5, 150 mm SL, Santa Catalina, Veraguas, Panamá, EP. *C. hypophthalmus*, INVEMAR-PEC 6795, male, 186 mm SL, Panamá, STRI 5-4-2-3, 305 mm SL, Bahía de Parita, Herrera, Panamá, EP. *Cathorops mapale*, INVEMAR-PEC 6796, male, 149 mm SL, Ciénaga Grande de Santa Marta, Colombia, WA. *C. multiradiatus*, INVEMAR-PEC 6798, female, 186 mm SL, Buenaventura, Colombia, STRI 439, 190 mm TL, Panamá, EP. *Galeichthys ater*, INVEMAR-PEC 6799, female, 239 mm SL, South Africa, Cape of Good Hope. *Galeichthys peruvianus*, INVEMAR-PEC 6800, 234 mm SL, STRI not cataloged, Perú, EP. *Occidentarius platypogon*, INVEMAR-PEC 6802, male, 261 mm SL, Buenaventura, Colombia, STRI 5-2-7-1, 230 mm SL, Panamá, EP. *Potamarius* sp., UMMZ 188048-S, 585 mm SL, 595 mm SL, UMMZ 198714-S, 460 mm SL, UMMZ 198715-S, 432 mm SL, Río de la Pasión, Petén, Guatemala, WA. *P. nelsoni*, UMMZ 198713-S, 540 mm SL, 480 mm SL, Río de la Pasión, Petén, Guatemala, WA. *Sciades dowii*, INVEMAR-PEC 6803, male, 296 mm SL, Buenaventura, Colombia, STRI 5-2-2-11, 470 mm SL, Aguadulce, Coclé, Panamá, EP. *S. herzbergii*, INVEMAR-PEC 6805, 93 mm SkL, 295 mm SL, San Lorenzo de Camarones, La Guajira, Colombia, INVEMAR-PEC 6806, 137 mm SkL, 158 mm SkL, Venezuela, WA. *S. parkeri*, INVEMAR-PEC 6811, 201 mm SkL, 300 mm SkL, Venezuela. *Sciades proops*, INVEMAR-PEC 6808, 120 mm SkL, INVEMAR-PEC 6809, 114 mm SkL, 377 mm SL, Ciénaga Grande de Santa Marta, Colombia, INVEMAR-PEC 6810 (3), 169–237 mm SkL, Venezuela, WA.

Appendix C. Morphological data matrix

TAXA	1–10	11–20	21–30	31–40	41–50	51–55
Outgroup						
Rhamdia sp. (Heptapteridae)	0 0 0 0 0 0 0 0 0 0	0 0 0 0 ? 0 0 ? 0 ?	? ? 0 0 ? ? ? 0 0 0	0 0 0 0 ? 0 0 0 ? ?	? 0 0 0 0 0 0 0 0 0	0 0 0 0 0
Doraops zuloagai (Doradidae)	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 ? 0 1 ? ? ? 0 0 0	0 0 0 0 0 0 0 0 ? ?	? 0 0 0 0 0 0 0 0 0	0 0 0 0 0
Trachelyopterus insignis (Auchenipteridae)	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 ? 0 0 ? ? ? 0 0 0	0 0 1 0 0 0 0 0 ? ?	? 0 0 0 1 1 0 0 0 0	0 0 0 0 0
Ingroup						
Ariopsis felis Atl US	0 0 0 1 0 0 0 0 0 0	1 1 0 1 0 0 0 1 1 0	0 0 0 0 0 0 0 0 1 0	2 0 0 0 0 0 0 1 1 ?	1 1 0 0 0 1 0 0 1 0	1 0 0 0 1
A. seemanni Pac CO/PA	0 0 0 1 0 0 0 0 0 0	1 1 0 1 0 0 0 1 1 0	0 0 0 0 0 0 0 0 1 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 1 0 0 1 0	1 0 0 0 1
Ariopsis sp. Atl CO	0 0 0 1 0 0 0 0 0 0	1 1 0 1 0 0 0 1 1 0	0 0 0 0 0 0 0 1 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 1 0 0 1 0	1 0 0 0 1
Arius arius IP PK	0 0 0 1 0 0 0 0 1 0	1 0 0 1 0 0 0 1 1 0	0 1 ? 0 0 1 2 0 1 0	2 0 0 0 0 0 1 1 0 ?	0 1 0 0 1 0 0 0 1 0	1 0 0 0 0
Bagre bagre Atl CO	0 1 0 1 0 0 0 0 1 0	1 0 0 1 2 0 0 1 1 0	0 0 1 0 0 0 1 0 1 2	2 0 1 0 1 2 1 1 1 0	1 1 1 0 1 0 0 0 1 0	1 0 0 0 0
B. aff. *marinus* Atl CO/VE	0 1 0 1 0 0 ? ? 1 0	1 0 0 1 2 0 0 1 1 0	0 0 1 0 0 0 1 0 1 2	2 0 1 0 1 2 1 1 1 0	1 1 1 0 1 0 0 0 1 0	1 1 0 1 0
B. panamensis Pac CO/PA	0 1 0 1 0 0 1 0 1 0	1 0 0 1 2 0 0 1 1 0	0 0 1 0 0 0 1 0 1 2	2 0 1 0 1 2 1 1 1 0	1 1 1 0 1 0 0 0 1 0	1 1 0 0 0
B. pinnimaculatus Pac PA	0 1 0 1 0 0 0 0 1 0	1 0 0 1 2 0 0 1 1 0	0 0 1 0 0 0 1 0 1 2	2 0 1 0 1 2 1 1 1 0	1 1 1 0 1 0 0 0 1 0	1 1 0 1 0
Cathorops dasycephalus Pac PA	1 0 1 1 0 0 1 1 1 0	1 0 0 1 1 1 1 2 1 1	1 1 0 1 0 0 2 0 1 1	2 0 0 1 0 2 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
C. hypophthalmus Pac PA	1 0 2 1 0 0 1 1 1 1	1 0 0 1 1 1 1 2 1 1	1 1 0 1 0 1 2 0 1 1	2 1 0 1 0 1 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
C. mapale Atl CO	1 0 2 1 0 0 1 1 1 1	1 0 0 1 1 1 1 2 1 1	1 1 0 1 1 1 2 0 1 1	2 1 0 1 0 1 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
C. multiradiatus Pac CO/PA	1 0 2 1 0 0 1 1 1 1	1 0 0 1 1 1 1 2 1 1	1 1 0 1 1 1 2 0 1 1	2 1 0 1 0 1 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
G. ater Atl ZA	0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0 0	0 0 ? 0 0 0 0 0 1 0	1 0 0 0 0 0 0 1 0 0	0 1 0 0 0 0 1 0 0 0	0 0 1 0 0
G. peruvianus Pac PE	0 0 0 1 0 0 0 0 0 0	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	1 0 0 0 0 0 0 1 0 0	0 1 0 0 0 0 1 0 0 0	0 0 1 0 0
Notarius cookei Pac PA	0 0 0 1 0 1 1 0 1 0	1 1 1 1 0 0 0 1 1 1	0 0 0 0 0 0 2 0 1 0	2 0 0 0 0 0 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
N. kessleri Pac CO/PA	0 0 0 1 0 1 1 0 1 0	1 1 1 1 0 0 0 1 1 1	0 0 0 0 0 0 2 0 1 0	2 0 0 0 0 0 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
N. neogranatensis Atl CO	0 0 0 1 0 1 1 0 1 0	1 1 1 1 0 0 0 1 1 1	0 0 0 0 0 0 2 0 1 0	2 0 0 0 0 0 0 1 0 1	0 1 0 0 0 0 0 0 1 0	1 0 0 0 0
N. troschelii Pac CO/PA	0 0 0 1 0 1 0 0 1 0	1 1 1 1 0 0 0 1 1 1	0 0 0 0 0 0 2 0 1 0	2 0 0 0 0 0 0 1 0 1	0 1 0 0 0 0 0 1 1 0	1 0 0 0 0
Occidentarius platypogon Pac CO/PA	0 0 0 1 0 0 0 0 0 0	1 1 0 1 2 0 0 1 1 0	0 0 0 0 0 0 0 0 1 2	2 0 0 0 0 2 1 1 1 0	1 1 0 0 1 0 0 0 1 0	1 0 0 0 0
Potamarius sp. Atl GT	0 0 0 1 0 1 0 0 1 0	1 1 0 1 0 0 0 1 1 0	0 ? 0 1 0 0 1 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 0 0 0 1 0	1 0 0 0 1
P. nelsoni Atl GT	0 0 0 1 0 ? 0 0 1 0	1 0 0 1 0 0 1 1 1 1	0 1 0 1 0 ? 0 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 0 0 0 1 0	1 0 0 0 1
Sciades dowii Pac CO/PA	0 0 0 1 1 0 0 0 0 0	1 1 1 1 0 0 0 1 1 0	0 0 0 0 0 0 0 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 1 0 0 0 1 1 1	2 0 0 0 0
S. herzbergii Atl CO/VE	0 0 0 1 1 0 0 0 0 0	1 1 0 1 0 0 0 1 1 0	0 0 0 0 0 0 0 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 1 0 0 0 1 1 1	2 0 0 0 0
S. parkeri Atl VE	0 0 0 1 1 0 0 0 0 0	1 1 1 1 0 0 0 1 1 0	0 0 0 0 0 0 1 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 0 0 1 1 1	2 0 0 0 0
S. proops Atl CO/VE	0 0 0 1 1 0 0 0 0 0	1 1 1 1 0 0 0 1 1 0	0 0 0 0 0 0 0 0 1 0	2 0 0 0 0 0 0 1 1 0	1 1 0 0 0 0 0 1 1 1	2 0 0 0 0

Atl, Atlantic; Pac, Eastern Pacific; IP, Indo-Pacific. Country codes follow ISO-3166.

Appendix D. Morphological character definitions and states [characters 1–45 modified from Betancur-R. et al. (2004), characters 46–55 added in this study]

(1) Constitution of lateral ethmoid: 0, robust; 1, thin.
(2) Anterior laminar expansion of lateral ethmoid: 0, absent or rudimentary; 1, developed.
(3) Fenestra between mesethmoid and lateral ethmoid: 0, absent; 1, reduced; 2, developed.
(4) Anterior elevation of mesethmoid: 0, absent; 1, present.
(5) Anterior laminar expansion of frontals covering lateral fenestrae: 0, absent; 1, present.
(6) Posterior edge of cranial fontanel posteriorly limited by: 0, only frontals; 1, frontals with participation of parieto-supraoccipital.
(7) Pterotic: 0, mesial border with parieto-supraoccipital shorter than anterior border with sphenotic; 1, mesial border with parieto-supraoccipital longer than anterior border with sphenotic.
(8) Mesial suture between extrascapular and parieto-supraoccipital: 0, forming an angle relative to longitudinal axis; 1, parallel to longitudinal axis.
(9) Fossa between dorsomedial limb of posttemporo-supracleithrum, extrascapular, and pterotic: 0, absent or reduced; 1, well developed.
(10) Participation of extrascapular in the aforementioned fossa: 0, less than 50%; 1, 50% or more.
(11) Otic capsules (=bulla acoustico utricularis): 0, flat; 1, swollen.
(12) Angular process of otic capsules (on pterotic): 0, absent; 1, present.
(13) Wing-like expansions of parasphenoid: 0, absent; 1, present.
(14) Articulation between posterior process of epioccipital and sustentaculum of Weberian apparatus: 0, absent; 1, present.
(15) Posterior projection of epioccipital: 0, relatively wide, with low mesial border; 1, relatively wide, mesial border elevated forming a crest; 2, narrow, mesial border elevated forming a crest.
(16) Strong medial limb of posttemporo-supracleithrum: 0, cylindrical; 1, dorsoventrally depressed.
(17) Inferomesial limb of posttemporo-supracleithrum compared to the inferolateral limb: 0, shorter; 1, equal or longer.
(18) Lateral expansions of basioccipital: 0, cylindrical; 1, stakelike and short; 2, stakelike and long.
(19) Ventral process of basioccipital: 0, absent or rudimentary; 1, well-developed, forming a cone-shaped structure.
(20) Ventral process of basioccipital: 0, low; 1, high.
(21) Anterior crest of ventral process of basioccipital: 0, absent; 1, present.
(22) Mesial palatal (=vomerine) tooth patches: 0, present; 1, absent.
(23) Lateral processes of parurohyal: 0, short, not reaching distal end of mesial process; 1, long, extending beyond mesial process.
(24) Posterior expansion of dentary: 0, absent or reduced. 1, well-developed.
(25) Molariform teeth on dentary: 0, absent; 1, present.
(26) Teeth on lateral palatal patches: 0, villiform; 1, molariform.
(27) Wing-like expansion of anterodorsal limb of lateral crest of hyomandibula: 0, moderate; 1, absent; 2, well-developed.
(28) Length of metapterygoid–hyomandibula suture compared to maximum length of metapterygoid: 0, less than 50%; 1, greater than 50%.
(29) Müllerian ramus of Weberian apparatus: 0, absent; 1, expanded and ventrally curved.
(30) Medial crest of sustentaculum of Weberian apparatus: 0, absent or reduced; 1, moderate; 2, well-developed.
(31) Ventral ossification of complex vertebrae: 0, absent or reduced; 1, extensive, mesially opened; 2, extensive, mesially continued forming the aortic tunnel.
(32) Canals for anterior cardinal veins located between the parapophysis of anterior vertebrae and adjacent superficial ossification: 0, dorsal to foramen of dorsal aorta; 1, lateral to foramen of dorsal aorta.
(33) Crest formed by the articulation of scapulo-coracoid and cleithrum: 0, well-developed; 1, rudimentary.
(34) Crest running on dorsal surface of horizontal lamina of cleithrum: 0, cylindrical; 1, flattened.
(35) Posterior dorsal process of cleithrum: 0, dorsally directed; 1, ventrally directed.
(36) Laminar expansion of fourth neural spine: 0, reduced; 1, moderate and anterolaterally directed; 2, wide and parallel to transverse axis.
(37) Fourth neural spine: 0, markedly inclined posteriorly; 1, slightly inclined posteriorly.
(38) Size of lapillus (=utricular otolith): 0, slightly larger than asteriscus and sagitta; 1, several times larger than asteriscus and sagitta.
(39) Shape of anterolateral upper margin of lapillus: 0, angular and produced (square shaped); 1, rounded.
(40) Lateral upper margin of lapillus: 0, flattened, groove reduced or absent; 1, markedly grooved.
(41) Anteromedial lower protuberance of lapillus: 0, moderate. 1, well-developed.
(42) Male mouthbrooding of eggs and embryos: 0, absent; 1, present.
(43) Barbels: 0, three pairs (maxillary, mental, and mandibular), maxillary pair transversally rounded; 1, two pairs (mandibular pair absent), maxillary pair flattened.
(44) Fleshy furrow between posterior nostrils: 0, absent; 1, present.
(45) Adipose fin base: 0, long; 1, short.
(46) Extrascapular: 0, elongated; 1, subrounded.
(47) Supraoccipital process: 0, flattened or keeled; 1, grooved.
(48) Posterior portion of supraoccipital process: 0, with dermal and endochondral components, middle nuchal plate not overlapping it; 1, only endochondral components, middle nuchal plate overlapping it.
(49) Anterior nuchal plate: 0, present; 1, absent.
(50) Granulations on cranial surface: 0, few or none, sharp if present; 1, numerous and blunt.
(51) Anterodorsal bony block of orbitosphenoid: 0, absent; 1, present and moderate in size: posterior limbs of mesethmoid surpassing its posterior end; 2, present and developed: posterior limbs of mesethmoid not surpassing its posterior end.
(52) Lateral portion of sphenotic: 0, developed; 1, reduced.
(53) Postcleithral (=humero-cubital) process: 0, produced and distinct from posterodorsal process of cleithrum; 1, fused to posterodorsal process, forming a fan-shaped lamina.
(54) Maxillary barbels: 0, relatively short, not reaching beyond pelvic fins; 1, relatively long, reaching at least to anal fin.
(55) Axial surface of pelvic fins in mature females with thick fleshy protuberances: 0, absent; 1, present.

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