



Taxonomic revision of the New World genus *Ariopsis* Gill (Siluriformes: Ariidae), with description of two new species

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Abstract

The taxonomy of sea catfishes (Ariidae) has had a complex history. A recent checklist of catfish species recognized Ariidae as having by far the highest number of species with uncertain status among siluriform families. One of the main problems concerns the classification and species delimitation of the amphiamerican genus *Ariopsis* Gill. Some recent studies have listed *Ariopsis* under the synonymy of other genera (e.g., *Sciades* Müller & Troschel), while other systematic revisions recognize *Ariopsis* as valid but have pointed out the need for clarification of the species composition of the genus. Based on morphological and molecular evidence, the systematic status and taxonomic limits of the genus *Ariopsis* are herein redefined. Two new species of *Ariopsis* are described, one only known from the Archipiélago de las Perlas, Pacific coast of Panama and another endemic to the Colombian Caribbean. Additionally, *Ariopsis gilberti* from the Pacific coast of Mexico and *Ariopsis simonsi* from Peru to Colombia (Eastern Pacific), previously listed as synonyms of *Ariopsis seemanni*, are herein resurrected. Finally, a molecular phylogeny is provided together with an identification key to the eight species in *Ariopsis*.

Key words: Sea catfishes, New Granada Sea Catfish, Eastern Pacific, Pearl Islands, Western Atlantic

Introduction

The classification and delineation of species in the sea catfish family Ariidae has been recognized as the most problematic of all siluriform groups (Ferraris, 2007), and many taxonomic revisions for ariids during the past century were until recently treated as provisional (e.g., Taylor & Menezes, 1978; Kailola & Bussing, 1995). A great degree of nomenclatural confusion is attributed to the strong similarity in external appearance of many ariid species, a problem that is further exacerbated by ontogenetic variation and sexual dimorphism (Marceniuk, 2005, 2007; Betancur-R. *et al.*, 2008). In recent years, morphological and molecular phylogenetic studies have improved our understanding of ariid relationships, leading to more objective classification schemes (Betancur-R. *et al.*, 2007; Marceniuk & Menezes, 2007). A concerted effort has also been made to better document the alpha taxonomy of the family, particularly in the Neotropics (Acero & Betancur-R., 2002; Betancur-R. & Acero, 2004, 2006; Betancur-R. *et al.*, 2008; Marceniuk & Betancur-R., 2008; Marceniuk *et al.*, 2009, 2012a).

One of the issues that remains contentious about ariid systematics is the taxonomic status of the amphiamerican genus *Ariopsis* Gill, 1861. While *Ariopsis sensu* Taylor & Menezes (1978) was validated by Betancur-R. *et al.* (2007), the classification proposed by Marceniuk & Menezes (2007) treated *Ariopsis* as a junior synonym of *Sciades* Müller & Troschel, 1849. In addition to the lack of stability concerning its generic status, the alpha taxonomy of *Ariopsis* needs revision. A total of 18 nominal species exists, but current checklists validate four or five species only (Kailola & Bussing, 1995; Acero P., 2003; Marceniuk & Ferraris, 2003). One of the main problems concerns the status of the New Granada Sea Catfish, an estuarine species endemic to the Colombian Caribbean in the Western Atlantic (WA) that is currently listed as endangered (Acero P. *et al.*, 2002, 2017). This species has been erroneously recognized by previous studies as *Ariopsis bonillai* (e.g., Taylor & Menezes, 1978), *Hexanemichthys bonillai* (Marceniuk & Ferraris, 2003), or *Sciades bonillai* (Marceniuk & Menezes, 2007). According to Acero P. & Betancur-R. (2006), however, *Galeichthys bonillai* Miles, 1945 (as originally described) is a freshwater ariid in the genus *Notarius* Gill, 1863 that is restricted to the Magdalena and Atrato rivers basins in Colombia. An important implication of the nomenclatural change made by Acero P. & Betancur-R. (2006) has been the lack of an appropriate scientific name for the New Granada Sea Catfish. Consequently, recent studies refer to this species as *Ariopsis* sp. (Betancur-R. *et al.*, 2007, 2012; Betancur-R., 2009; Acero P. *et al.*, 2017).

This paper provides a taxonomic revision of the genus *Ariopsis* based on molecular and morphological evidence. Two new species are described, including the New Granada Sea Catfish and another (previously unidentified) species known only from Panama in the Eastern Pacific (EP). Six other species are also redescribed. These include two nominal species previously listed under the synonymy of *Arius seemanni* Günther, 1864: *Galeichthys gilberti* Jordan & Williams, 1895 (EP of Mexico) and *G. simonsi* Starks, 1906 (Peru to Colombia in the EP). Finally, this study provides a molecular phylogenetic analysis that elucidates the relationships among most species in the genus together with a taxonomic key to identify the eight species herein validated.

Materials and methods

Morphological analyses. Following Marceniuk (2007), measurements were taken with either a ruler and recorded to the nearest millimeter or with dial caliper and recorded to the nearest 0.1 mm. Measurements are given as percentages of standard length (SL) unless stated otherwise. Individual measurements are given for primary types in tables and meristic values for the type specimens are indicated in bold in tables. Sex of specimens was either determined by examination of gonad morphology under magnification or based on the presence/absence of pelvic-fin pads (only present in mature females).

Three anatomical features require definition given their frequent use in diagnoses and descriptions. The dorsomedial groove of the neurocranium is formed in the fleshy portion that adheres (apposed) to the anterior cranial fontanel and is defined by the posterior branches of the mesethmoid and frontals (Marceniuk *et al.*, 2012). The posterior bony portion is formed by the mesial depression of the frontals and the anterior portion of the parieto-supraoccipital (Marceniuk *et al.*, 2012). The nuchal plate refers to the fusion of the anterior and medial nuchal plates (Royero, 1987).

Molecular analyses. To test whether the delimitation of species based on morphology is supported by molecular data, mitochondrial DNA (mtDNA) sequences from two gene fragments (cytochrome *b* or Cyt *b*, and

ATP synthase 6 and 8 or ATPase 8/6) were examined for all but two species of *Ariopsis* (*A. assimilis* and *A. gilberti*). Most sequences are from previous studies (Betancur-R. *et al.*, 2007, 2012; Betancur-R., 2009); newly generated sequences for this study have been deposited in GenBank (Table 1). All sequences were aligned using MAFFT (Katoh & Standley, 2013), and mtDNA trees were estimated under maximum likelihood in RAxML v7.2.8 (Stamatakis, 2006) and under Bayesian Inference in MrBayes v3.2.2 (Ronquist *et al.*, 2012) using by-codon partitions. The RAxML analyses were run under the GTR model with a 25-category gamma distribution and invariant sites. Edge support was assessed using bootstrapping with 1000 pseudoreplicates. For MrBayes, three independent replicates of the Markov Chain Monte Carlo (MCMC) runs were conducted for 30 million generations using four chains and sampling trees every thousandth generation. Ten percent of the initial trees sampled were discarded as burn-in. Convergence of the MCMC was verified using the ESS criterion for each parameter in Tracer v1.7 (Drummond & Rambaut, 2007); all ESS values were greater than 200 suggesting convergence. The mtDNA trees were rooted with *Sciades couma* and compared to a previously estimated time-calibrated, multi-locus tree for the family Ariidae using fossil calibrations in a Bayesian framework (Betancur-R. *et al.*, 2012). This latter tree also provides evidence for the monophyly of *Ariopsis* and illustrates its intergeneric relationships.

TABLE 1. Genbank number of sequences used and added in the present study. The abbreviations for the sampling locations correspond to ISO-3166 country codes.

Specie	Tissue	Country	Catalog	ATP synthase 8/6	cytochrome b
<i>Sciades couma</i>	x3560	GY	ANSP 178745	DQ990674	
<i>Ariopsis canteri</i>	x3602	CO	INV PEC5332/5340	DQ990663	DQ990487
<i>Ariopsis canteri</i>	x3603	CO	INV PEC5332/5340	DQ990664	DQ990488
<i>Ariopsis canteri</i>	.0604	CO	INV PEC5332/5340	FJ625865	
<i>Ariopsis felis</i>	x3609	US	AUM 5233-02	DQ990659	DQ119355
<i>Ariopsis guatemalensis</i>	stri15941	SV	STRI 5732	DQ990660	DQ990484
<i>Ariopsis jimenezi</i>	stri27707	PA	STRI 8566	KY944575	KY944573
<i>Ariopsis jimenezi</i>	stri27713	PA		KY944578	
<i>Ariopsis jimenezi</i>	stri27710	PA	STRI 8127	KY944576	KY944574
<i>Ariopsis jimenezi</i>	stri27704	PA		KY944577	
<i>Ariopsis seemani</i>	12668	PA	STRI 5730	DQ990661	DQ990485
<i>Ariopsis seemani</i>	15948	SV	STRI 5731	DQ990662	DQ990486
<i>Ariopsis simonsi</i>	AAP002	PE		KY944579	
<i>Ariopsis simonsi</i>	509	CO	INV PEC (NCA)	FJ625863	FJ626160
<i>Ariopsis simonsi</i>	ID182	PE	AUM 50249	FJ625864	

Results

Ariopsis Gill, 1861

Type species: *Arius milberti* Valenciennes, 1840, a junior synonym of *Silurus felis* Linnaeus, 1766 (Gill, 1861).

Taxonomic status and monophyly of *Ariopsis*. Two recent phylogenetic studies have proposed different treatments for the taxonomic status of *Ariopsis*. Based on morphological evidence, Marceniuk & Menezes (2007) and Marceniuk *et al.* (2012) listed *Ariopsis* as junior synonym of *Sciades* Müller & Troschel, 1849. Betancur-R. *et al.* (2007) and Betancur-R (2009), using multi-locus sequence data (up to five mitochondrial and six nuclear gene fragments) in conjunction with morphological evidence (Betancur *et al.*, 2007), found support for the monophyly of *Ariopsis* and a close relationship with *Potamarius* and *Sciades*.

The present study reconciles incongruent classification schemes and recognizes *Ariopsis* as a valid genus based on combined evidence from both molecular and morphological data (Marceniuk & Betancur-R, *in*

preparation), that supports the monophyly of *Ariopsis*, *Potamarius* and *Sciades*, representing independent lineages. The monophyly of *Ariopsis* is supported by synapomorphies with ambiguous optimization and derived conditions acquired independently in other ariid genera: 1) posterior cranial fontanel absent (also in *Batrachocephalus* and *Sciades*); 2) epiphyseal bar indistinct (also in *Batrachocephalus* and *Sciades*); 3) temporal fossa absent (also in *Occidentarius* and *Sciades*); 4) subvertebral process indistinct or weakly developed (also in *Occidentarius* and *Sciades*); and 5) posterolateral processes of urohyal of subequal length relative to the distal portion of the bone (also in *Occidentarius* and *Sciades*). Other diagnostic characteristics allow the separation of *Ariopsis* from other Neotropical ariid genera: (1) distinct fenestra delimited by the lateral ethmoid and frontal (*vs.* indistinct in *Sciades*, except in *Ariopsis jimenezi* n. sp.), (2) indistinct temporal fossa (*vs.* distinct in all other genera, except *Sciades*), (3) rakers present on the posterior margin of first and second gill arches (*vs.* absent in other genera, except for *Potamarius* and *Cathorops*), and (4) females with conspicuous pads on the pelvics (*vs.* pads inconspicuous in all other New World ariids, except for *Sciades herzbergii*).

***Ariopsis assimilis* (Günther, 1864)**

Mayan Sea Catfish (English), Bagre maya (Spanish).

Figures 1 and 2, Tables 2–5

Arius assimilis Günther, 1864:146. Type locality: Lake Izabal [Yzabal], Guatemala. Holotype: BMNH 1864.1.26.98.

Galeichthys assimilis, Regan, 1906–1908: 122.

Ariopsis assimilis, Taylor & Menezes, 1978; Castro Aguirre *et al.*, 1999: 156–157; Acero P., 2003: 838; Robertson *et al.*, 2015.

Material examined. *Type-specimen:* BMNH 1864.1.26.98 (female, 290 mm SL), Guatemala, Izabal. *Non-type specimens:* USNM 212131 (1, 207 mm SL), Mexico, Quintana Roo; UMMZ 196479 (4, 252–233 mm SL), Mexico, Quintana Roo, Laguna Bacalar; UMMZ 213491 (2, 168–225 mm SL), Mexico, Quintana Roo, Laguna Bacalar; FMNH 103770 (2, 243–254 mm SL), Belize, Belizean Beach, 4.5 miles on western highway; AMNH 35070 (7, 147–236 mm SL), Guatemala, Izabal, Río Nimblaja, 1 km above mouth into Río Sarstún; USNM 114587 (1, 196 mm SL), Guatemala, Río Sarstún, +/- 20 mi. above mouth; UMMZ 197214 (5, 144–200 mm SL), Guatemala, Izabal, Río Nimblaja, 1 km above mouth in Río Sarstún; AMNH 32941 (2, 194–245 mm SL), Guatemala, Izabal, Río Dulce, inside channel ca. 400 m, below Castillo San Felipe; UA 69–91 (1), Mexico, Quintana Roo, Isla Cozumel.

Diagnosis. *Ariopsis assimilis* is distinguished from its congeners as follows: from *A. canteri*, from Colombian Caribbean, by 31–36 gill rakers on the first and second gill arches, rarely 37 (*vs.* 38–44, rarely 36 or 37); from *A. felis*, from Massachusetts (US) to Yucatán in Mexico (Caribbean), by 34–37 gill rakers on the first and second gill arches (*vs.* 29–32), osseous medial groove absent (*vs.* present; Figs. 2 and 3), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, surpassing the posterior margin of eyes, Figs. 2 and 4), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 2 and 3), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 2 and 3); from *A. gilberti*, from Mexico (EP), by the presence of 14–18 gill rakers on the first gill arch (*vs.* 19–20, Table 3), osseous medial groove absent (*vs.* present; Figs. 2 and 3), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, surpassing the posterior margin of eyes, Figs. 2 and 4), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 2 and 3); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by its narrower mouth 10.5–13.2% SL (*vs.* 13.0–15.2% SL, rarely less than 13.2%), narrower cephalic shield at frontals area 8.8–10.1% SL (*vs.* 10.0–11.5% SL, rarely less than 10.1%), narrow mesethmoid median portion (*vs.* wide, Fig. 3), mesethmoid medial notch narrow and deep (*vs.* large and shallow, Fig. 3); from *A. jimenezi*, from Archipiélago de las Perlas in Panama (EP), by longer pectoral-fin spine 18.2–22.6% SL (*vs.* 14.6–18.1% SL), osseous medial groove absent (*vs.* present; Figs. 2 and 3), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, surpassing the posterior margin of eyes, Figs. 2 and 4), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 2 and 3), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 2 and 3), external posterior branch of lateral ethmoid columnar and thin (*vs.* depressed and thick, Fig. 3), fenestra

delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3); from *A. seemanni*, from El Salvador to Panama (EP), by the absence of osseous medial groove (*vs.* present; Figs. 2 and 3), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 2 and 3); from *A. simonsi*, from Colombia to Peru (EP), by the absence of osseous medial groove (*vs.* present; Figs. 2 and 3).



FIGURE 1. Body in lateral view. *Ariopsis assimilis*, Holotype, BMNH 1864.1.26.98.



FIGURE 2. Head in dorsal view. *Ariopsis assimilis*, Holotype, BMNH 1864.1.26.98.

Description. Morphometrics and meristics summarized in Tables 2–5. Head moderately long, wide and relatively low, notably depressed at lateral ethmoid and frontal area, profile elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostrils rounded, with fleshy edge, posterior nostril covered by flap of skin; nostrils moderately separated and moderately distant from orbit, not connected by fleshy furrow. Eye lateral, relatively large. Eyes widely spaced. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and wide on supracleithrum area, and relatively narrow on lateral ethmoid and frontal areas, with thick granulation forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, without reaching eyes, posterior osseous medial groove

inconspicuous or absent. Lateral margin of sphenotic straight, as wide medially as anteriorly. Pterotic lateral margin markedly convex, sometimes angled. Parietosupraoccipital process keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and relatively narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, moderately long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Fourteen to 18 acicular gill rakers on first arch, 17–20 spike-shaped gill rakers on second arch and some rudiments at the end; rakers present on posterior margin of all gill arches.

TABLE 2. Meristic frequencies of anal-fin rays for species of *Ariopsis*. Bolded numbers indicate counts for primary types.

	16	17	18	19	20	21	22
<i>Ariopsis assimilis</i>		1	2	1	1		
<i>Ariopsis canteri</i>			1	5	19	8	3
<i>Ariopsis felis</i>		1	7	2			
<i>Ariopsis gilberti</i>		1	2	1			
<i>Ariopsis guatemalensis</i>		1	1	1			
<i>Ariopsis jimenezi</i>	1	2	5	2			
<i>Ariopsis seemanni</i>			1	3	1		
<i>Ariopsis simonsi</i>			4	4	2		

TABLE 3. Meristic frequencies of gill rakers on first arch for species of *Ariopsis*. Bolded numbers indicate counts for primary types.

	13	14	15	16	17	18	19	20
<i>Ariopsis assimilis</i>		1	2	8	2	1		
<i>Ariopsis canteri</i>					3	7	15	11
<i>Ariopsis felis</i>	2	4	3	1				
<i>Ariopsis gilberti</i>							2	3
<i>Ariopsis guatemalensis</i>			1		1	1		
<i>Ariopsis jimenezi</i>			3	8	1			
<i>Ariopsis seemanni</i>			2	6	1	1		
<i>Ariopsis simonsi</i>		1	4	7	3	2		

TABLE 4. Meristic frequencies of gill rakers on second arch for species of *Ariopsis*. Bolded numbers indicate counts for primary types.

	14	15	16	17	18	19	20	21	22	23	24
<i>Ariopsis assimilis</i>				1	4	3	4				
<i>Ariopsis canteri</i>						2	5	9	11	5	4
<i>Ariopsis felis</i>		2	5	3							
<i>Ariopsis gilberti</i>						1	3	3	1		
<i>Ariopsis guatemalensis</i>			1					1			
<i>Ariopsis jimenezi</i>	1	1	6	4							
<i>Ariopsis seemanni</i>		3	1		3						
<i>Ariopsis simonsi</i>	3	1	2	3	3	2	1	1			

TABLE 5. Morphometric data for *Ariopsis assimilis*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	N	Mean	Range
Standard length (mm)	24		144.0–333.0
Head length	24	26.6	24.4–28.8
Snout length	24	7.5	5.6–8.9
Distance between anterior nostrils	24	6.7	5.9–7.7
Distance between posterior nostrils	24	6.9	5.4–7.9
Orbital diameter	24	4.9	3.9–5.9
Interorbital distance	24	13.0	11.3–15.9
Maxillary barbel length	24	24.5	15.6–33.8
Lateral mental barbel length	24	16.4	11.7–20.4
Mesial mental barbel length	23	10.4	7.3–12.4
Mouth width	23	12.0	10.5–13.2
Width of cephalic shield at lateral ethmoid area	10	13.2	12.6–14.6
Width of cephalic shield at frontals area	10	9.4	8.8–10.1
Width of cephalic shield at supracleithrum area	10	18.5	17.5–19.2
Parietosupraoccipital process length	8	14.3	11.7–16.3
Parietosupraoccipital process width	10	3.9	3.5–4.4
Nuchal-plate length	10	6.8	6.4–7.1
Nuchal-plate width	10	6.7	6.3–7.2
Body depth	12	16.8	16.1–17.6
Body width	24	21.4	20.0–22.6
Distance from snout to pectoral fin	12	23.2	20.9–25.4
Distance from snout to dorsal fin	12	34.8	32.3–36.2
Distance from snout to pelvic fin	12	52.8	50.6–55.5
Distance from snout to adipose fin	12	74.2	71.9–76.0
Distance from snout to anal fin	12	69.9	67.3–72.1
Caudal-peduncle height	24	78.4	74.2–85.4
Pectoral-fin spine length	24	20.1	18.2–22.6
Dorsal-fin spine length	21	17.6	14.7–20.8
Pelvic-fin base length	24	5.1	4.3–6.7
Pelvic-fin height	24	16.4	13.8–19.0
Adipose-fin base length	24	9.5	7.6–11.5
Adipose-fin height	12	5.9	3.5–12.3
Anal-fin base length	24	14.3	12.6–15.4
Anal-fin height	12	15.5	14.2–19.1
Caudal-fin upper lobe length	10	34.4	29.8–36.3
Caudal-fin lower lobe length	10	30.8	18.2–33.6

Body significantly wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral-fin spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal

soft rays. Pectoral-fin spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with conspicuous serrations. Nine to 11 pectoral-fin soft rays. Posterior process of cleithrum triangular, slightly visible, smooth to rugose. Pelvic-fin deep and large at base, with six rays, well-developed fleshy protuberances in adult females. Adipose-fin low, with base moderately long, shorter than anal base. Anal fin moderately high and long at base, with 17–20 rays and ventral profile concave. Caudal peduncle moderately high. Caudal-fin forked, dorsal and ventral lobes moderately long, dorsal lobe somewhat longer than ventral lobe, posteriorly slightly pointed.

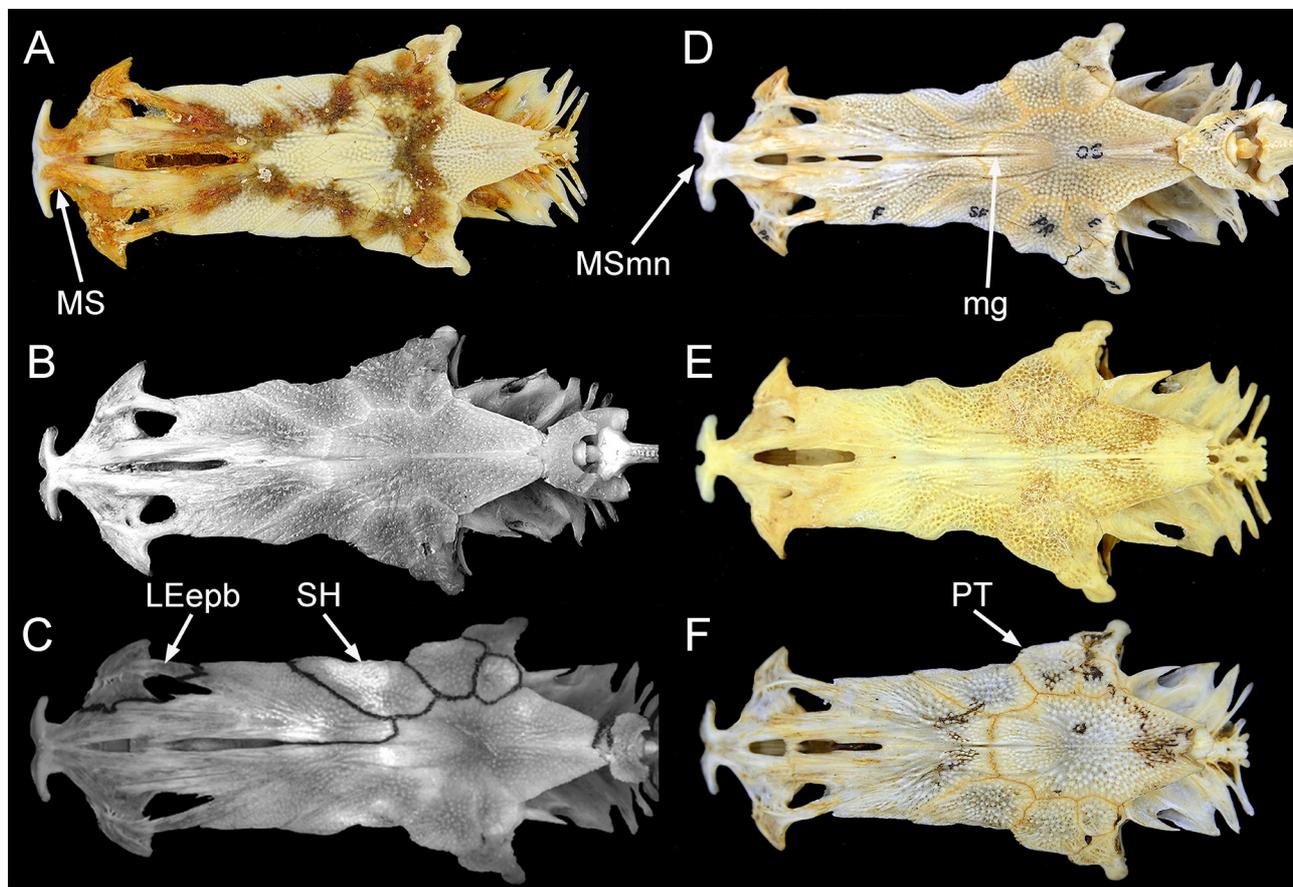


FIGURE 3. Neurocranium, dorsal view. A. *Ariopsis guatemalensis*, STRI 5.2.13.3.; B. *A. felis*, catfishesbone.acnatsci.org; C. *A. canteri*, uncataloged; D. *A. seemanni*, STRI 5.1.1.19.; E. *A. jimenezi*, STRI no registry; F. *A. simonsi*, STRI 5.1.1.10. Abbreviation: LEepb, external posterior branch of Lateral Ethmoid; PT, Pterotic; MS, Mesethmoid; MSmn, Mesethmoid medial notch; mg, medial groove of cranium; SH, Sphenotic.

Maximum length: Grows to 350 mm TL.

Coloration in alcohol. Head and body counter-shaded, dorsum brown to blackish, venter light beige; dorsal surfaces of pelvic and pectorals proximally black, distally lighter; anal dark, distal tips lighter; caudal grayish to blackish (Fig. 1).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. The WA *Ariopsis assimilis* occurs in fresh and estuarine waters, from Quintana Roo on the Caribbean coast of Mexico to Honduras (Fig. 5).

Remarks. *Ariopsis assimilis* was described by Günther (1864) based on a single specimen collected at Lake Izabal, Guatemala (Figs. 1 and 2). The original description used characters that are shared with congeneric species. Thus, the recognition of *A. assimilis* relies on a combination of morphometric, meristic, and osteological features observed on the type specimen and non-type specimens. Posteriorly, Jordan & Gilbert (1882) assigned *A. assimilis* to both coasts of tropical America, including Magdalena Bay, Mazatlán, and Altata in Mexico, and the Magdalena

River, Colombia. The Colombian Magdalena record is in error, since Jordan & Gilbert (1882) described a fontanel prolonged backward as a narrow groove. After Gunther “*median longitudinal fonticulus on the upper side of the head does not extend to the base of occipital process*”, a condition that is verified in the type specimen (Fig. 2).

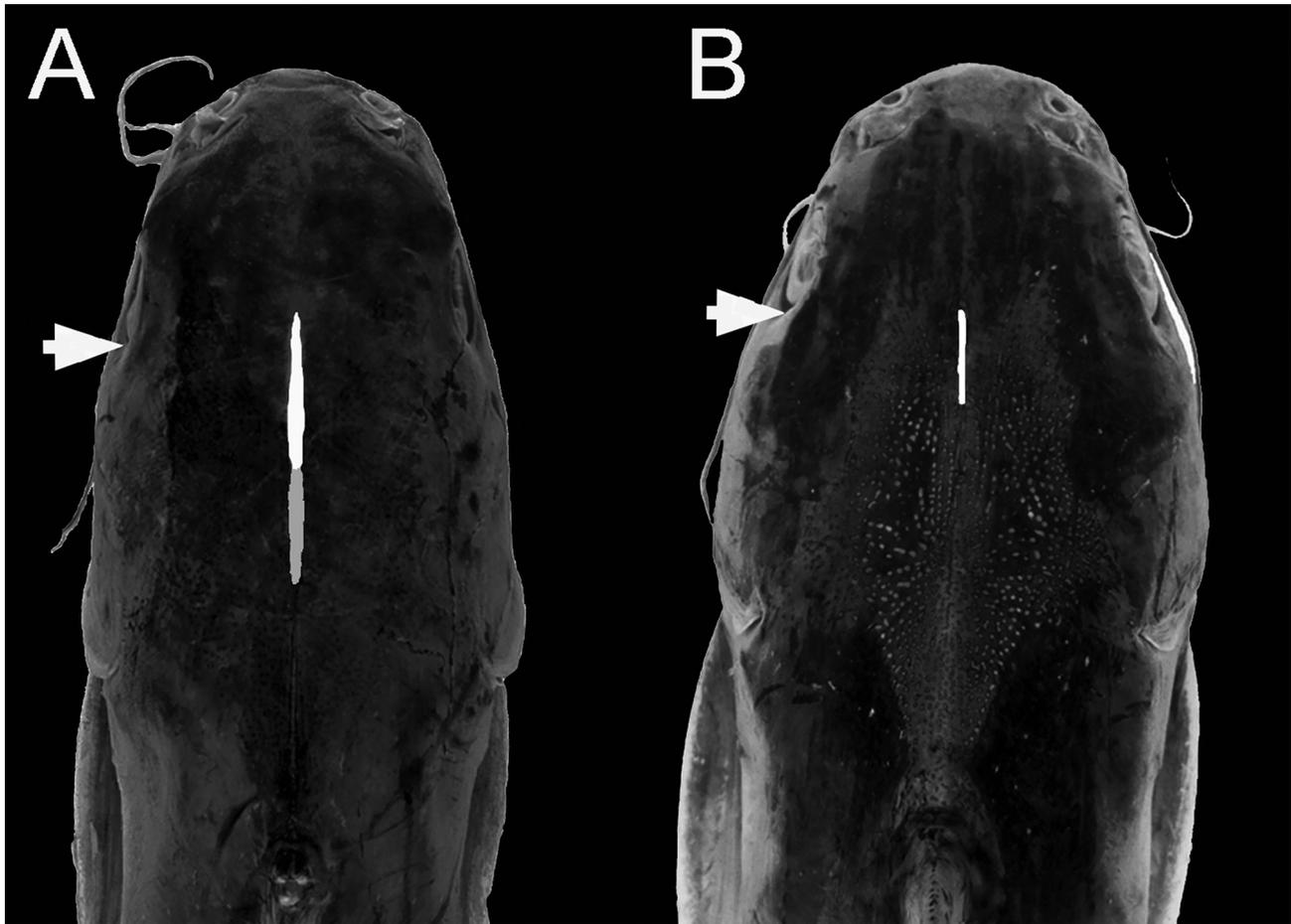


FIGURE 4. Medial groove of neurocranium. A. *Ariopsis felis* and B. *A. assimilis*. White, anterior fleshy portion (apposed to the anterior cranial fontanel); gray, posterior bony portion (formed by the mesial depression of the frontals and the anterior portion of parietosupraoccipital).

***Ariopsis canteri*, new species Acero P., Betancur-R. & Marceniuk**

New Granada Sea Catfish (English)

Chivo cabezón (Spanish)

Figures 6 and 7, Tables 2–4 and 6.

Ariopsis bonillai (non Miles), Dahl, 1971: 48–49; Taylor & Menezes, 1978; Acero P. *et al.*, 2002: 60–63; Acero P., 2003: 839.

Hexanematchthys bonillai (non Miles), Marceniuk & Ferraris, 2003.

Sciades bonillai (non Miles), Marceniuk & Menezes, 2007.

Ariopsis sp. Betancur-R *et al.*, 2012; Robertson *et al.*, 2015; Acero P. *et al.* 2017: 73–76.

Material examined. *Holotype*. INV PEC5332 (male, 225 mm SL), Colombia, Magdalena, Ciénaga Grande de Santa Marta, Pueblo Viejo, fisherfolk (10° 47' 8.7" N, 74° 24' 58.3" W). *Paratypes*. INV PEC276 (5, 185–259 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Boca Río Sevilla, hook (10° 52' 30.2" N, 74° 24' 53.6" W); INV PEC529 (1, 41 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Pueblo Viejo (10° 47' 8.7" N, 74° 24' 58.3" W); INV PEC782 (4, 125–306 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Boca Río Sevilla (10° 52' 30.2" N, 74° 24' 53.6" W); INV PEC895 (5, 45–82 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Cabaña Palmira (10° 52' 30.2" N, 74° 24' 53.6" W); INV PEC1356 (2, 45–48 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Boca de la Barra, west shore (10° 52'

30.2" N, 74° 24' 53.6" W); INV PEC1756 (2, 104–261 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, Caño Grande and Río Fundación (10° 52' 30.2" N, 74° 24' 53.6" W); INV PEC2294 (2, 68–73 mm SL), Colombia, Magdalena, Ciénaga Grande de Santa Marta, Boca Río Fundación (10° 43' 54.2" N, 74° 25' 44.7" W); INV PEC3651 (1, 155 mm SL) Colombia, Córdoba, close to Bahía Cispata (9° 24' 36.4" N, 75° 46' 41.3" W); INV PEC5945 (1, 117 mm SL) Colombia, La Guajira, Uribia, Bahía Portete (12° 8' 53.3" N, 71° 58' 1.1" W); INV PEC8169 (1, 149 mm SL), Colombia, Córdoba, San Antero, Ciénaga Ostional (9° 24' 18" N, 75° 52' 53" W); INV PEC9010 (1, 227 mm SL) Colombia, Magdalena, Ciénaga Grande de Santa Marta, collected with the Holotype, Pueblo Viejo, fisherfolk (10° 47' 8.7" N, 74° 24' 58.3" W); INV PEC9086 (23, 142–357 mm SL), Colombia, Magdalena, Ciénaga Grande de Santa Marta, Pueblo Viejo (10° 47' 8.7" N, 74° 24' 58.3" W); USNM 286488 (2, 220–248 mm SL), Colombia, Bolívar, Cartagena, among mangroves at La Boquilla; USNM 292999 (3, 207–215 mm SL), Colombia, Magdalena, Ciénaga Grande de Santa Marta, east side near SE end of highway bridge.

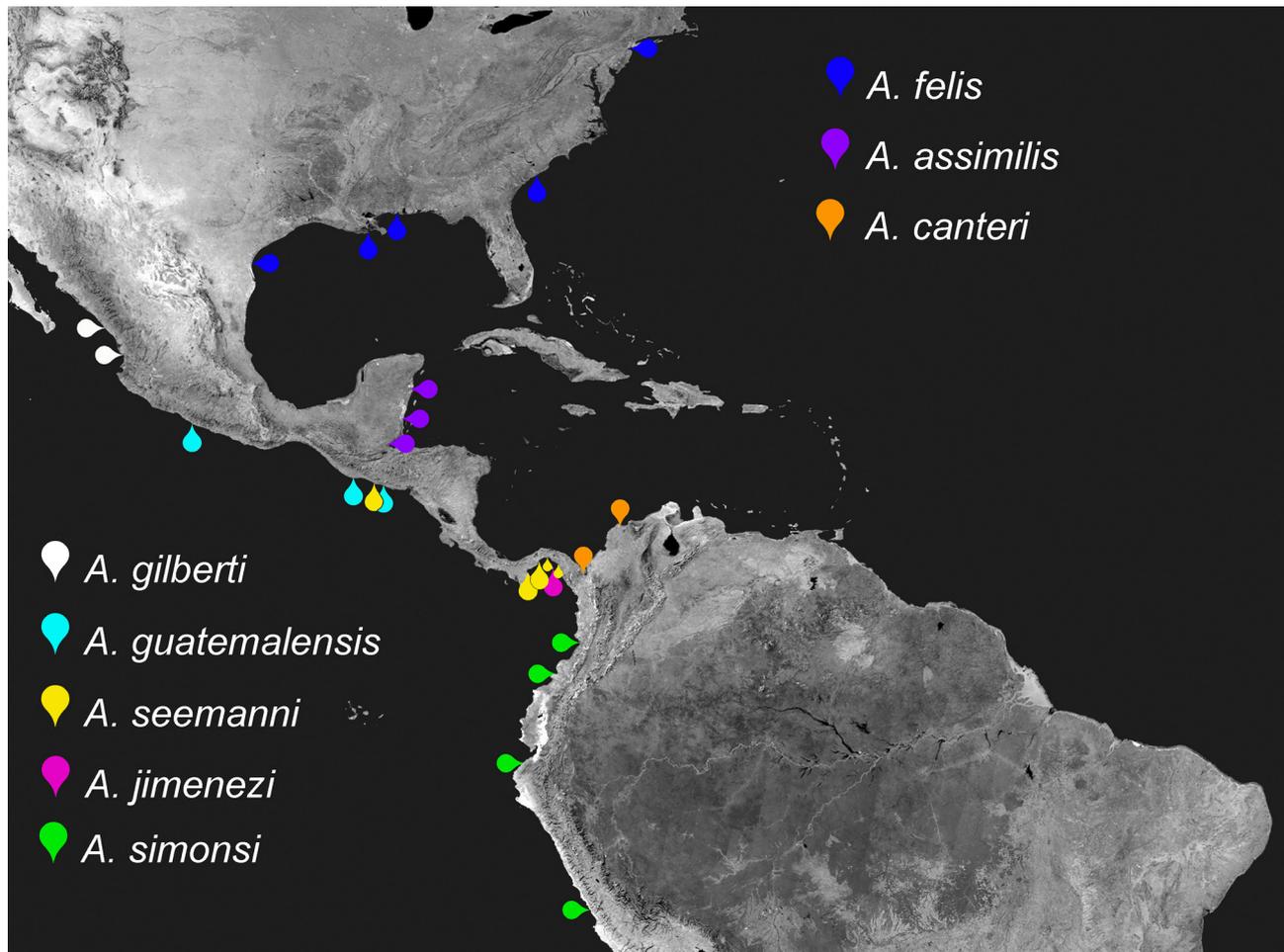


FIGURE 5. Sampling localities of examined material.

Diagnosis. *Ariopsis canteri* can be differentiated from its congeners as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by having 36–44 gill rakers on the first and second gill arches, rarely 37 or 36 (*vs.* 31–36, rarely 37); from *A. felis*, from Massachusetts (US) to Yucatán (Caribbean), by the presence of 36–44 gill rakers on the first and second gill arches (*vs.* 29–32), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 3 and 7), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 7); from *A. gilberti*, from Mexico (EP), by the absence of an osseous medial groove (*vs.* present; Figs. 3 and 7), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 3 and 7); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by its narrower median portion of mesethmoid (*vs.* wide, Fig. 3), mesethmoid medial notch narrow and deep (*vs.* large and shallow, Fig. 3); from *A. jimenezi*, from Archipiélago de las Perlas in Panama (EP), by the absence of an osseous medial groove (*vs.* present; Figs. 3 and 7), fleshy medial

groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 7), lateral margin of sphenotic straight, as wide anteriorly as medially (*vs.* notched laterally, narrower medially than anteriorly, Figs. 3 and 7), external posterior branch of lateral ethmoid columnar and thin (*vs.* depressed and thick, Fig. 3), fenestra delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3), lateral margin of pterotic markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 7); from *A. seemanni*, from El Salvador to Panama (EP), by the absence of an osseous medial groove (*vs.* present; Figs. 3 and 7); from *A. simonsi*, from Colombia to Peru (EP), by the absence of an osseous medial groove (*vs.* present; Figs. 3 and 7), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 7).



FIGURE 6. Body in lateral view. *Ariopsis canteri*, Holotype INV PEC5332.

Description. Morphometrics and meristics summarized in Tables 2–4, 6. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile elevated posteriorly, convex from mesethmoid to frontal and straight on parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, moderately distant to one another and moderately distant to orbit, not connected by fleshy furrow. Eye lateral, relatively large. Eyes widely separated. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and wide on supracleithrum, lateral ethmoid and frontal areas, with thick granulation forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, evident, reaching or not reaching eyes. Sphenotic straight laterally, as wide medially as anteriorly. Pterotic lateral margin markedly convex, sometimes angled. Parietosupraoccipital slightly keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide posteriorly, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, moderately long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Sixteen to 20 acicular gill rakers on first arch, 17–24 spike-shaped gill rakers on second arch, rakers present on posterior margin of all gill arches.

Body significantly wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal-fin soft rays. Pectoral spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with conspicuous

serrations. Nine to 11 pectoral soft rays. Posterior process of cleithrum triangular, smooth to rugose, slightly visible. Pelvic-fin deep and large at base, with six rays and well-developed fleshy protuberances in adult females. Adipose fin low; its base moderately long but shorter than the anal-fin base. Anal fin short and moderately long at base, with 18 to 22 rays and ventral profile almost straight. Caudal peduncle moderately high. Caudal fin forked, dorsal and ventral lobes relatively short; dorsal lobe somewhat longer than ventral lobe, posteriorly pointed.

TABLE 6. Morphometric data for *Ariopsis canteri*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Holotype	Paratypes			Mean Male / Female
		N	Mean	Range	
Standard length (mm)	225.0	41		117.0–357.0	(12) 183–284 (18) 117–357
Head length	26.7	41	26.0	22.8–31.4	27.9 / 24.6
Snout length	6.2	39	6.3	4.9–7.9	6.7 / 5.9
Distance between anterior nostrils	6.8	41	6.6	5.4–8.5	7.0 / 6.4
Distance between posterior nostrils	7.5	41	7.0	5.9–8.4	7.4 / 6.8
Orbital diameter	4.3	41	4.6	3.5–5.6	4.5 / 4.5
Interorbital distance	14.2	41	13.2	11.3–15.4	13.9 / 12.7
Maxillary barbel length	24.0	39	25.1	20.1–32.2	23.7 / 26.1
Lateral mental barbel length	13.7	39	15.9	12.3–21.6	14.8 / 16.8
Mesial mental barbel length	8.7	40	9.6	7.5–13.0	9.5 / 9.8
Mouth width	11.7	41	11.9	10.2–13.7	12.3 / 11.6
Width of cephalic shield at lateral ethmoid area	14.4	40	13.9	9.4–15.3	14.6 / 13.6
Width of cephalic shield at frontals area	9.9	40	9.7	8.8–11.7	10.2 / 9.5
Width of cephalic shield at supracleithrum area	18.2	40	18.3	17.3–19.9	18.5 / 18.1
Parietosupraoccipital process length		5	12.0	11.1–13.7	
Parietosupraoccipital process width		5	3.6	3.3–3.8	
Nuchal-plate length		5	7.1	6.8–7.4	
Nuchal-plate width		5	7.3	6.8–7.7	
Body depth	17.4	41	16.6	14.9–23.0	16.7 / 16.6
Body width	20.0	41	22.2	20.8–23.9	22.6 / 21.7
Distance from snout to pectoral fin	22.2	41	21.3	17.9–26.3	22.6 / 20.1
Distance from snout to dorsal fin	35.1	41	34.0	31.7–37.2	34.8 / 33.2
Distance from snout to pelvic fin	52.9	41	52.6	49.6–56.8	53.6 / 51.9
Distance from snout to adipose fin	75.1	41	74.5	71.1–78.6	74.9 / 74.2
Distance from snout to anal fin	69.3	41	69.6	66.2–74.6	70.6 / 68.7
Caudal-peduncle height	7.8	41	7.7	6.6–8.8	7.5 / 7.8
Pectoral-fin spine length		12	19.3	16.6–21.1	16.6 / 19.8
Dorsal-fin spine length		13	17.4	14.4–21.3	14.4 / 18.8
Pelvic-fin base length	3.8	41	4.6	3.0–7.2	3.8 / 5.3
Pelvic-fin height	15.6	41	16.5	12.7–21.9	14.4 / 18.5
Adipose-fin base length	9.1	41	9.8	7.4–13.3	9.3 / 10.1
Adipose-fin height		5	4.3	3.8–4.8	
Anal-fin base length	14.8	41	14.8	12.4–17.6	14.0 / 15.1
Anal-fin height		5	14.4	13.8–15.1	
Caudal-fin upper lobe length		4	31.8	29.9–33.3	
Caudal-fin lower lobe length		5	29.2	28.3–29.8	



FIGURE 7. Head in dorsal view. *Ariopsis canteri*, Holotype INV PEC5332.

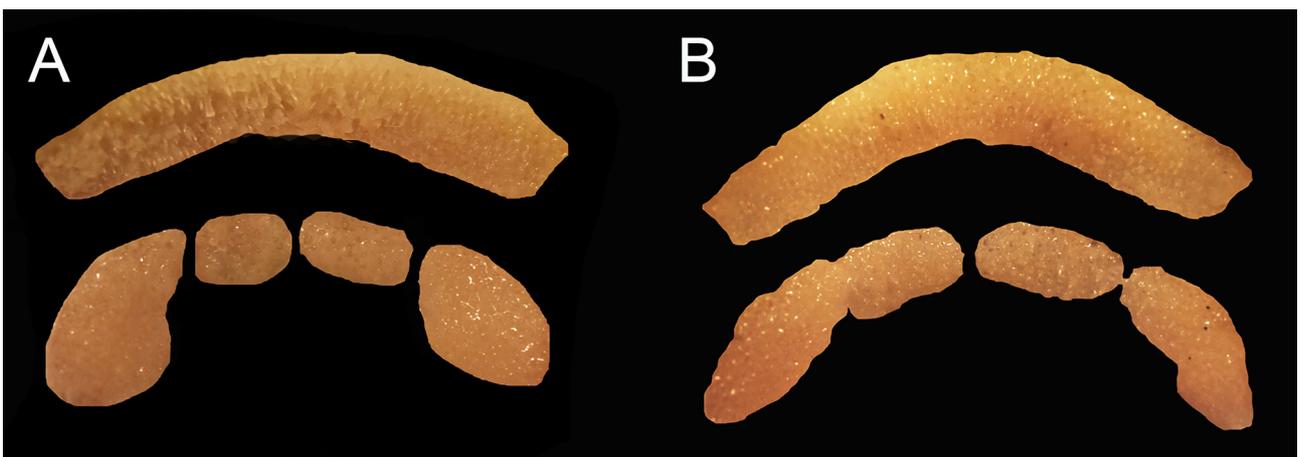


FIGURE 8. Premaxilla, vomerine and accessory tooth plates in female (A) and male (B), INV PEC, uncataloged specimens.

Maximum length: Grows to 460 mm TL.

Coloration in alcohol. Head and body dark brown to bluish above, whitish below; dorsal surfaces of pelvic fin proximally black, distally lighter; anal fin dark, distal tips lighter; caudal grayish to blackish (Figs. 6).

Sexual dimorphism. Only females have well developed fleshy protuberances or pads in basal portion of the pelvic fins, especially during the reproductive season. Vomerine tooth patches ovate to square in females, and reduced and transversally elongated in males. In females, accessory tooth patches larger and ovate, while relatively smaller and elongated in males (Fig. 8).

Distribution and habitat. Endemic to the Caribbean coast of Colombia in the WA (Fig. 5). Found in costal marine and brackish waters; sometimes entering freshwaters (e.g., Atrato, Sinú, Magdalena, and Ranchería rivers).

Molecular evidence and phylogenetic relationships. The Caribbean endemic *Ariopsis canteri* is the sister species of the EP *A. seemanni* (Fig. 9). This biogeographic pattern suggests that divergence of these species involved a transisthmian vicariant event (Betancur-R. *et al.*, 2007, 2012; Betancur-R., 2009).

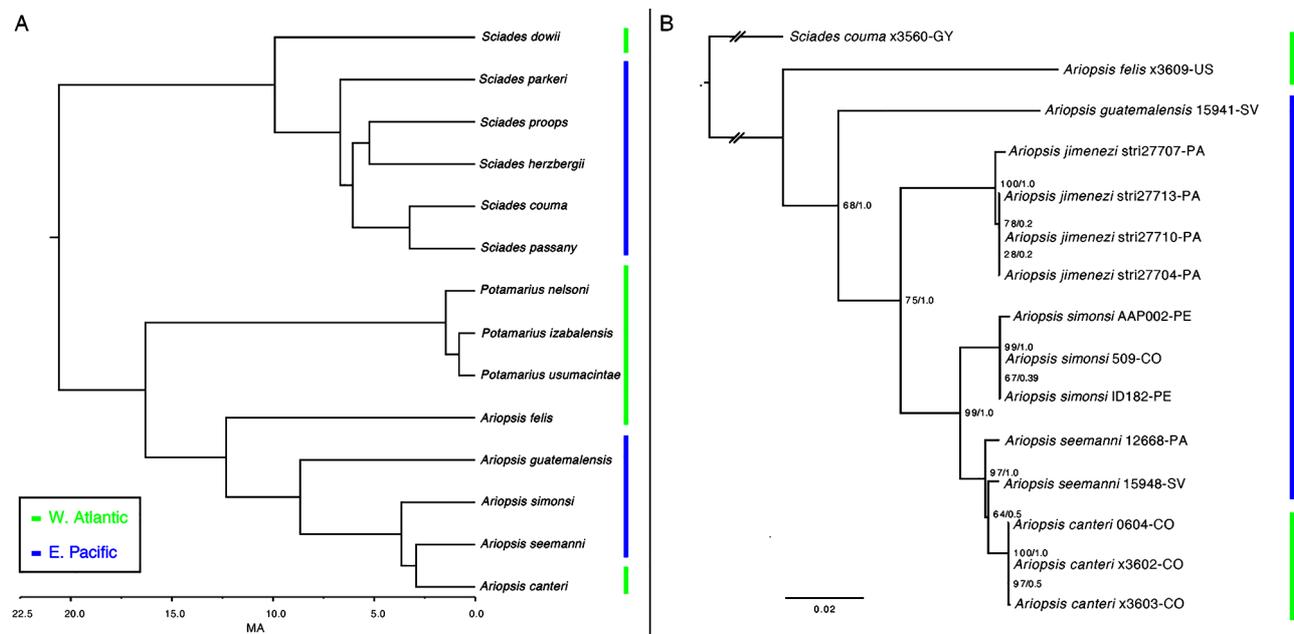


FIGURE 9. A, Clade including the genera *Sciades* + *Potamarius* + *Ariopsis*, extracted from the Ariidae tree of Betancur-R. *et al.* (2012), including five of the eight species of *Ariopsis* validated herein. The complete time tree was estimated using a Bayesian analysis of five mitochondrial and six nuclear gene fragments and 19 calibration points (both inside and outside Ariidae). B, Rooted RAxML phylogram with expanded specimen sampling for six species of *Ariopsis*, but based on the analysis of only two mitochondrial genes (Cyt b and ATPase 8/6; 1937 bp). Nodal numbers indicate RAxML bootstrap support values and posterior probability values (MrBayes tree), respectively. The RAxML and MrBayes trees are identical with respect to topology and highly similar with respect to branch lengths. Two letter country codes follow ISO-3166.

Etymology. Named after Diego Canter Ríos (1984–2007), a young and talented Colombian ichthyologist who died in a car accident near Santa Marta, along with three other biologists. Species delimitation in *Ariopsis* was part of Diego's B.Sc. thesis in Marine Biology, which he could not complete due to his untimely death. Diego collected most of the morphometric and meristic data for the new species and for *Ariopsis simonsi*.

Remarks. Description of *Ariopsis canteri* n. sp. contributes to the alpha taxonomy of New World Ariidae, providing formal scientific recognition of a species endemic to the Colombian Caribbean, which has been recognized as endangered (see Acero P. *et al.*, 2016, 2017). See Introduction about misidentification of the New Granada Sea Catfish with *Galeichthys bonillai* Miles, 1945, a freshwater ariid in the genus *Notarius* Gill, 1863 (Acero P. & Betancur-R., 2006).

Ariopsis felis (Linnaeus, 1766)

Hardhead sea catfish (English)

Mâchoiron chat (French),

Bagre boca chica or Bagre gato (Spanish).

Figure 10 and 11, Tables 2–4 and 7.

Silurus felis Linnaeus, 1766:503. Type locality: Charleston Harbor, South Carolina, US. Neotype: BMNH 1985.11.11.1.

Arius milberti Valenciennes, 1840:74. Type locality: New York; Charleston, South Carolina, US. Syntypes: MNHN B-0593 (3) New York.

Arius equestris Baird & Girard, 1854:26. Type locality: Matagorda Bay, at Indianola, Calhoun County, Texas, US, Gulf of Mexico. Holotype: USNM 836.

Galeichthys guentheri Regan, 1906–1908:124, Pl. 16 (fig. 1), 19 (fig. 3). Type locality: Gulf of Mexico. Syntypes: BMNH 1855.9.19.1105–1106 (2), BMNH (1) New Orleans, Louisiana.

Arius felis, Taylor & Menezes, 1978; McEachran & Fechhelm, 1998: 361.

Ariopsis felis, Castro-Aguirre *et al.*, 1999: 152–154; Acero P., 2003: 840.

Material Examined. *Type specimens:* MNHN B-0593 (3, 159–189 mm SL), New York. *Non-type specimens:* FMNH 37916 (2, 155–163 mm SL), US, South Carolina, Charleston Harbor; AMNH 52073 (5, 189–235 mm SL), US, Alabama, Mobile, Dauphin Island and Vicinity; AMNH 85099 (2, 63–67 mm SL) US, Alabama, Gulf of Mexico, Theodore Ship Channel; USNM 206742 (1, 128 mm SL), US, Louisiana, Grande Isle; USNM 120058 (1, 107 mm SL), US, Texas, off Aransas Pass.



FIGURE 10. Body in lateral view. (A) *Arius equestris*, Holotype USNM 836; (B) *Galeichthys guentheri*, Syntypes: BMNH 1855.9.19.1105–1106; (C) *Arius milberti*, Syntype: MNHN B-0593.

Diagnosis. *Ariopsis felis* differs from its congeners as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by the presence of 34–37 gill rakers on the first and second gill arches (*vs.* 29–32), osseous medial groove present (*vs.* absent; Figs. 3 and 11), fleshy medial groove of neurocranium conspicuous and long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 11), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 11), pterotic lateral margin smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 11); from *A. canteri*, from Colombia (Caribbean), by the presence of 29–32

rakers on the first and second gill arches (vs. 36–44), osseous medial groove present (vs. absent; Figs. 3 and 11), lateral margin of sphenotic notched, narrower medially than anteriorly (vs. straight, as wide medially as anteriorly, Figs. 3 and 11), pterotic lateral margin smoothly convex (vs. markedly convex, sometimes angled, Figs. 3 and 11); from *A. gilberti*, from Mexico (EP), by the presence of 29–32 gill rakers on the first and second gill arches (vs. 40–42), lateral margin of pterotic smoothly convex (vs. markedly convex, sometimes angled, Figs. 3 and 11); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by its smaller mouth 9.1–11.5% SL (vs. 13.0–15.2% SL), closer anterior nostrils 4.6–6.4% SL (vs. 7.1–8.6% SL), closer posterior nostrils 4.2–7.1% SL (vs. 7.2–8.7% SL), osseous medial groove present (vs. absent; Figs. 3 and 11), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (vs. conspicuous or inconspicuous, but never surpassing eyes, Figs. 4 and 11), mesethmoid median portion narrow (vs. wide, Fig. 3), mesethmoid medial notch narrow and deep (vs. large and shallow, Fig. 3), lateral margin of sphenotic notched, narrower medially than anteriorly (vs. straight, as wide medially as anteriorly, Figs. 3 and 11), pterotic lateral margin smoothly convex (vs. markedly convex, sometimes angled, Figs. 3 and 11); from *A. jimenezi*, from Archipiélago de Las Perlas in Panama (EP), by the presence of 13–15 gill rakers on the first gill arch, rarely 16 (vs. 16–17, rarely 15, Table 3), external posterior branch of lateral ethmoid columnar and thin (vs. depressed and thick, Figs. 3 and 11), fenestra delimited by mesethmoid and lateral ethmoid conspicuous (vs. inconspicuous, Figs. 3 and 11); from *A. seemanni*, from El Salvador to Panama (EP), by its fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (vs. conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 11), pterotic lateral margin smoothly convex (vs. markedly convex, sometimes angled, Figs. 3 and 11); from *A. simonsi*, from Colombia to Peru (EP), by its fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (vs. conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 11), lateral margin of sphenotic notched, narrower medially than anteriorly (vs. straight, as wide medially as anteriorly, Figs. 3 and 11), pterotic lateral margin smoothly convex (vs. markedly convex, sometimes angled, Figs. 3 and 11).

Description. Morphometrics and meristics summarized in Tables 2–4, 7. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, relatively close to one another and distant from orbit, not connected by fleshy furrow. Eye lateral, relatively large and moderately separated. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and relatively narrow on supracleithrum, lateral ethmoid and frontal areas, with thick granulation (rather conspicuous), forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium affixed to anterior cranial fontanel, long and conspicuous, reaching eyes. Lateral margin of sphenotic notched, narrower medially than anteriorly. Pterotic lateral margin smoothly convex. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, moderately granulated dorsally, moderately long and narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, moderately long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Thirteen to 16 acicular gill rakers on first arch, 13–17 spike-shaped gill rakers on second arch, rakers present on posterior margin of all gill arches.

Body significantly wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal soft rays. Pectoral spine relatively short and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with little conspicuous serrations. Nine to 11 pectoral soft rays. Posterior process of cleithrum triangular, smooth to rugose, slightly visible. Pelvic fin deep and large at base, with six rays, and well-developed fleshy protuberances in adult females.

Adipose fin low, with base moderately long, shorter than anal base. Anal fin moderately high and relatively long at base, with 17–19 rays and ventral profile convex. Caudal peduncle moderately high. Caudal fin forked, dorsal and ventral lobes relatively long, dorsal lobe somewhat longer than ventral lobe, posteriorly pointed.

TABLE 7. Morphometric data for *Ariopsis felis*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Paratypes			
	<i>A. milberti</i>	N	Mean	Range
Standard length (mm)	159.0–189.0	13		63.0–235.0
Head length	23.9–26.1	13	24.5	22.3–29.9
Snout length	7.9–8.5	13	7.3	5.2–9.3
Distance between anterior nostrils	4.6–5.2	13	5.6	4.6–6.4
Distance between posterior nostrils	4.6–5.4	13	5.9	4.2–7.1
Orbital diameter	4.7–5.0	13	5.4	4.5–6.2
Interorbital distance	10.4–11.4	13	12.3	10.1–14.8
Maxillary barbel length	20.4–23.3	13	26.1	20.0–35.7
Lateral mental barbel length	14.2–15.4	13	16.2	12.1–21.6
Mesial mental barbel length	8.8–10.1	13	10.2	7.7–13.4
Mouth width	10.1–10.8	13	10.5	9.1–11.5
Width of cephalic shield at lateral ethmoid area	11.7–12.7	9	13.6	12.7–15.1
Width of cephalic shield at frontals area	8.9–10.4	9	9.6	7.8–11.4
Width of cephalic shield at supracleithrum area	15.5–16.1	9	18.1	17.0–19.2
Parietosupraoccipital process length		9	10.6	9.8–11.5
Parietosupraoccipital process width		9	3.5	3.0–3.9
Nuchal-plate length		9	6.3	5.9–7.5
Nuchal-plate width		9	7.1	6.2–7.8
Body depth	14.7–15.5	13	17.3	16.4–20.3
Body width	17.2–18.7	13	20.4	19.2–22.1
Distance from snout to pectoral fin	18.5–19.7	13	21.6	19.2–25.1
Distance from snout to dorsal fin	32.1–34.0	13	33.6	30.1–39.0
Distance from snout to pelvic fin	51.6–53.7	13	52.0	50.0–54.3
Distance from snout to adipose fin	72.0–73.0	13	71.6	68.7–74.7
Distance from snout to anal fin	68.3–70.2	13	69.3	66.4–72.9
Caudal-peduncle height	6.6–7.4	13	7.8	7.2–9.3
Pectoral-fin spine length	15.5–17.3	13	18.8	17.7–19.7
Dorsal-fin spine length	14.9–17.0	13	18.4	15.9–20.6
Pelvic-fin base length	3.0–3.3	13	4.1	3.5–4.9
Pelvic-fin height	12.3–13.4	13	14.1	11.9–17.9
Adipose-fin base length	7.2–7.7	13	10.3	8.1–12.5
Adipose-fin height		9	3.8	3.2–4.8
Anal-fin base length	13.6–13.7	13	15.9	13.7–18.0
Anal-fin height		9	14.0	12.7–16.3
Caudal-fin upper lobe length		7	36.2	34.5–39.9
Caudal-fin lower lobe length		9	31.0	28.7–34.6

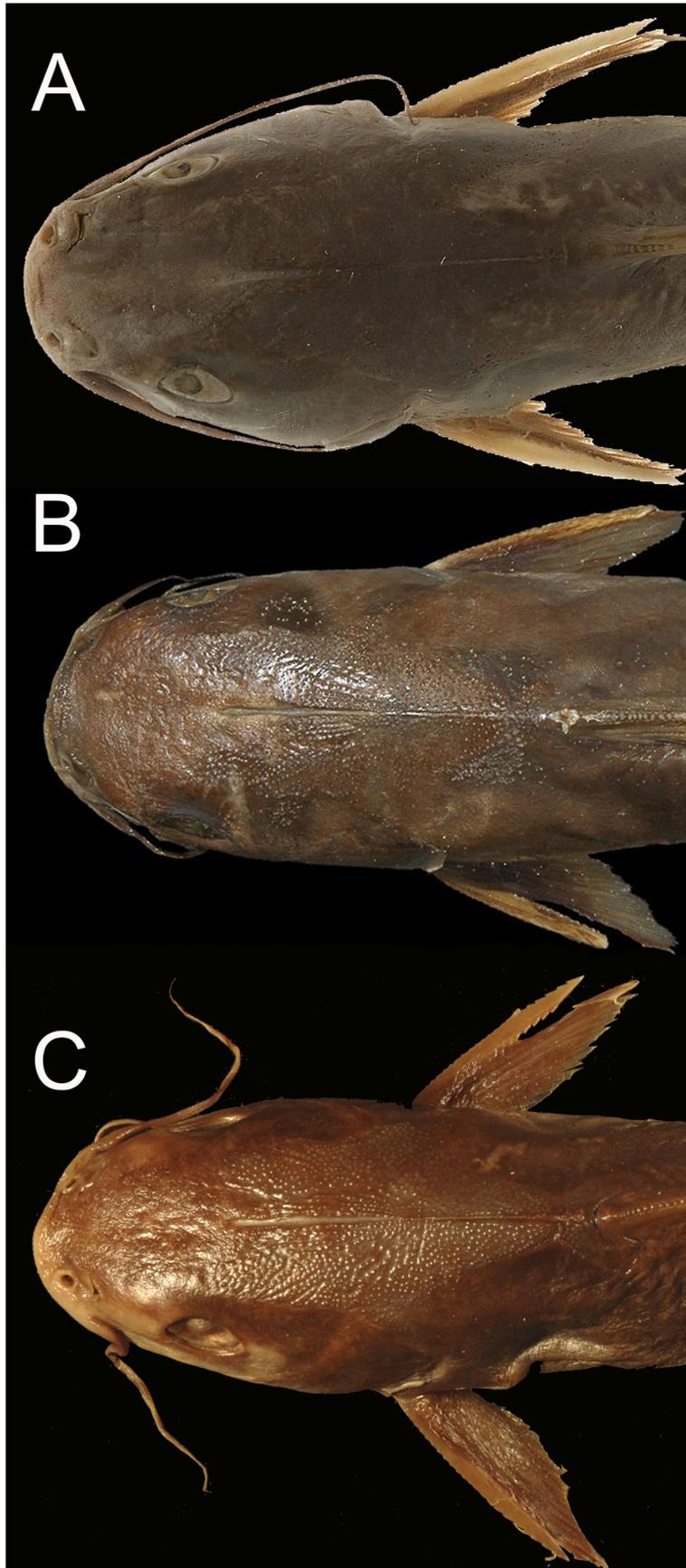


FIGURE 11. Head in dorsal view. (A) *Arius equestris*, Holotype USNM 836; (B) *Galeichthys guentheri*, Syntypes: BMNH 1855.9.19.1105–1106; (C) *Arius milberti*, Syntype: MNHN B-0593.

Maximum length: Grows to 70 cm TL, commonly to 250 mm TL.

Coloration in alcohol. Head and body dark brown above, whitish below; dorsal surfaces of pelvic proximally black, distally lighter; anal lighter; caudal grayish to blackish (Fig. 10).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. The WA *Ariopsis felis* occurs in estuarine and marine waters, from Massachusetts (US) to Yucatán, Mexico (Caribbean) (Fig. 5).

Molecular evidence and phylogenetic relationships. *Ariopsis felis* is the earliest-branching species in *Ariopsis* (Fig. 9).

Remarks. *Ariopsis felis* was described based on a type specimen collected in North/South Carolina, US (Figs. 10a and 11a). Original description was based on features common to other species of *Ariopsis*. In the present study, the identification of *A. felis* is based on a combination of external and internal characters. *Arius milberti*, *A. equestres* and *Galeichthys guentheri* are accepted as synonyms of *A. felis* following Taylor & Menezes (1978). The fossil *Felichthys stauroforus* (Miocene of Maryland; Lynn & Melland, 1939) appears to be very close to this species.

***Ariopsis gilberti* (Jordan & Williams, 1895)**

Tete Sea Catfish (English)

Figure 12 and 13, Tables 2–4 and 8.

Galeichthys gilberti Jordan & Williams, 1895:395, Pl. 26. Type locality: Upper part of Astillero at Mazatlán, Sinaloa, western Mexico. Holotype: USNM 29213; Paratypes: BMNH 1895.5.27.244–246 (3); CAS-SU 1667 (2), 11666–68 (1, 1, 1); USNM 28161 (1, missing), 28189 (1), 28210 (1, missing), 28213 (1, missing), 28221 (2, missing), 28232 (1), 28276 (1), 28304 (1); ZMB 14043 (1).

Ariopsis seemanni (non Günther, 1864), Kailola & Bussing, 1995; Castro Aguirre *et al.*, 1999: 155–156.

Material examined. *Type specimens:* Holotype, USNM 29213 (1, 291 mm SL), Mexico, Sinaloa, upper part of Astillero at Mazatlán; Paratype, USNM 28232 (1, 152, mm SL), USNM 28276 (1, 215 mm SL), USNM 28304 (1, 161 mm SL), all collected with the Holotype. *Non-type specimens:* LACM W58–32 (9, 211–247 mm SL), Mexico, Nayarit, San Blas; UA 68–124 (1), Mexico, Nayarit, Punta Novillero; UA 69–49–3 (3), Mexico, Nayarit, San Blas, beach in front of village; UA 71–64–1 (11), Mexico, Nayarit, Ensenada Jaltemba, Rincón de La Guayabita (=just south of La Peñita).

Diagnosis. *Ariopsis gilberti* can be differentiated from its congeners as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by the presence of 19–20 gill rakers on the first gill arch (*vs.* 14–18, Table 3), osseous medial groove present (*vs.* absent; Figs. 3 and 13), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 13), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 13); from *A. canteri*, from Colombian Caribbean, by the presence of an osseous medial groove (*vs.* absent; Figs. 3 and 13), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 13); from *A. felis*, from Massachusetts (US) to Yucatán in Mexico (Caribbean), by the presence of 40–42 gill rakers on the first and second gill arches (*vs.* 29–32), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 13); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by the presence of 40–42 rakers on the first and second gill arches (*vs.* 31–39), its smaller mouth 10.7–12.3% SL (*vs.* 13.0–15.2% SL), closer anterior nostrils 5.5–6.5% SL (*vs.* 7.1–8.6% SL), closer posterior nostrils 4.9–6.7% SL (*vs.* 7.2–8.7% SL), cephalic shield narrower in the frontal area 8.3–9.8% SL (*vs.* 10.0–11.5% SL), cephalic shield narrower in the lateral ethmoid area 12.5–14.0% SL (*vs.* 14.3–15.3% SL), mesethmoid median portion narrow (*vs.* wide, Fig. 3), mesethmoid medial notch narrow and deep (*vs.* large and shallow, Fig. 3), osseous medial groove present (*vs.* absent; Figs. 3 and 13), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 13), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as

anteriorly, Figs. 3 and 13); from *A. jimenezi*, from Archipiélago de Las Perlas in Panama (EP), by the presence of 40–42 gill rakers on the first and second gill arches (*vs.* 29–34), external posterior branch of lateral ethmoid columnar and thin (*vs.* depressed and thick, Fig. 3) fenestra delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 13); from *A. seemanni*, from El Salvador to Panama (EP), by the presence of 40–42 gill rakers on the first and second gill arches (*vs.* 30–36), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 13); from *A. simonsi*, from Colombia to Peru (EP), by the presence of 40–42 gill rakers on the first and second gill arches (*vs.* 28–37), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 13), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 13).



FIGURE 12. Body in lateral view. *Ariopsis gilberti*, Holotype, USNM 29213.

Description. Morphometrics and meristics summarized in Tables 2–4, 8. Head relatively short, wide and high, especially depressed at lateral ethmoid and frontal area, profile slightly elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, nostrils moderately separated and distant from orbit, not connected by fleshy furrow. Eye lateral, relatively large. Eyes moderately separated. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and relatively narrow on supracleithrum, lateral ethmoid and frontal areas, with thick granulation, forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, long and conspicuous, reaching eyes. Lateral margin of sphenotic notched, narrower medially than anteriorly. Pterotic lateral margin markedly convex, sometimes angled. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, moderately long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Nineteen to 20 acicular gill rakers on first arch, 21–22 spike-shaped gill rakers on second arch and rakers present on posterior margin of all gill arches.

Body wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral spine; anterior margin granulated on basal two thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal soft rays. Pectoral spine relatively short and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with serrations. Nine to ten pectoral soft rays. Posterior process of cleithrum triangular smooth to rugose, slightly visible. Pelvic fin deep and large at base, with six rays, and well-developed fleshy protuberances in adult females. Adipose fin low, with base moderately long,

shorter than anal base. Anal fin moderately high and long at base, with 17–19 rays and ventral profile convex. Caudal peduncle moderately high. Caudal fin forked, dorsal and ventral lobes relatively long, dorsal lobe somewhat longer than ventral lobe, slightly pointed.

Maximum length: Maximum size unknown; largest specimen examined 291 mm SL.

TABLE 8. Morphometric data for *Ariopsis gilberti*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Holotype	Paratypes	N	Mean	Range
Standard length (mm)	291.2	152.7–215.9	9		211–247
Head length	25.9	24.2–26.7	9	24.8	23.6–25.6
Snout length	8.0	7.7–7.9	9	6.5	5.9–6.9
Distance between anterior nostrils	6.0	5.6–5.8	9	6.0	5.5–6.5
Distance between posterior nostrils	6.4	4.9–5.6	9	6.3	5.6–6.7
Orbital diameter	5.0	4.6–5.6	9	4.9	4.5–5.1
Interorbital distance	12.1	10.3–11.7	9	13.6	12.7–14.5
Maxillary barbel length	19.2	22.5–30.0	9	25.4	23.1–27.8
Lateral mental barbel length	11.0	16.2–20.8	9	18.0	15.4–19.6
Mesial mental barbel length	8.7	10.3–11.6	9	11.2	10.3–12.1
Mouth width	11.4	10.7–11.0	9	11.6	10.9–12.3
Width of cephalic shield at lateral ethmoid area	12.9	12.6–12.7	9	13.2	12.5–14.0
Width of cephalic shield at frontals area	8.3	8.6–9.0	9	9.2	8.5–9.8
Width of cephalic shield at supracleithrum area	17.8	17.7–18.2	9	19.0	18.1–19.4
Parietosupraoccipital process length	6.8	7.1–7.3	9	8.4	7.5–9.5
Parietosupraoccipital process width			9	3.7	3.2–4.3
Nuchal-plate length			9	7.0	6.3–7.6
Nuchal-plate width			9	7.4	7.1–7.7
Body depth			9	18.7	17.7–19.8
Body width			9	20.9	19.9–21.5
Distance from snout to pectoral fin			9	20.5	19.6–21.3
Distance from snout to dorsal fin			9	32.1	30.5–34.7
Distance from snout to pelvic fin			9	50.5	48.8–51.8
Distance from snout to adipose fin			9	74.1	72.6–75.7
Distance from snout to anal fin			9	69.7	66.9–73.0
Caudal-peduncle height	7.7	8.4–9.2	9	8.7	8.2–9.2
Pectoral-fin spine length	16.2	18.8–19.8	9	17.4	15.9–19.4
Dorsal-fin spine length	16.0	18.8–19.5	8	17.6	15.5–18.6
Pelvic-fin base length	6.5	4.4–6.1	9	6.8	6.2–7.5
Pelvic-fin height	19.2	14.0–18.4	9	17.7	15.8–19.2
Adipose-fin base length			9	9.2	7.8–10.2
Adipose-fin height			9	4.8	4.3–5.0
Anal-fin base length			9	14.8	14.2–15.8
Anal-fin height			9	13.5	12.4–15.2
Caudal-fin upper lobe length			8	36.4	35.5–38.0
Caudal-fin lower lobe length			8	32.8	31.1–35.3



FIGURE 13. Head in dorsal view. *Ariopsis gilberti*, Holotype, USNM 29213.

Coloration in alcohol. Head and body bluish above, whitish below; dorsal surfaces of pelvic proximally black, distally lighter; anal dark, distal tips lighter; caudal grayish to blackish (Fig. 12).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. The EP *Ariopsis gilberti* occurs in estuarine and marine waters of Mexico, from Laguna de San Juan (Sonora) to Mar Muerto (Chiapas, Gulf of Tehuantepec; Fig. 5).

Remarks. *Ariopsis gilberti* was described from a well represented type series collected at the upper part of Astillero in Mazatlán (Sinaloa, Mexico; Figs. 12 and 13) (Jordan & Williams, in Jordan 1895). Jordan & Evermann (1896) mentioned the species as being common in Sinaloa, and by far the most abundant species in Mazatlán. Apparently Boulenger (1898) was the first to propose that the species is a junior synonym of *A. seemanni*. Regan (1906–1908) examined the type series of *A. gilberti* and backed its synonymization, a condition accepted by Kailola & Bussing (1995). No other authors questioned the clear differences in gill-raker counts (most congeners have less than 40 gill-rakers on the first and second gill arches combined, except for *A. canteri* and *A. simonsi*) or any other morphological feature differentiating the species (see diagnosis).

***Ariopsis guatemalensis* (Günther, 1864)**

Blue sea catfish (English)

Cominata azulada, Bagre cuatete (Spanish)

Figure 14 and 15, Tables 2–4 and 9.

Arius guatemalensis Günther, 1864:145. Type locality: Guatemala. Syntypes: BMNH 1853.1.11.6 (1).

Arius caeruleus Günther, 1864:149. Type locality: Huamuchal, Guatemala. Syntypes: BMNH 1864.1.26.208–209 (2).

Galeichthys azureus Jordan & Williams, 1895:398, Pl. 27. Type locality: Estuary at Mazatlán, Sinaloa, western Mexico. Holotype: CAS–SU 11575.

Galeichthys guatemalensis, Regan, 1906–1908: 123; Meek & Hildebrand, 1923: 110.

Arius guatemalensis, Kailola & Bussing, 1995;

Ariopsis guatemalensis, Castro-Aguirre, 1999.

Material examined. *Type specimen:* BMNH 1853.1.11.6 (1 male, 249 mm SL), Guatemala. Syntypes of *Arius caerulescens*: BMNH 1864.1.26.208–209 (2, 218 and 258 mm SL), Guatemala, Huamuchal (=Guamuchal). *Non-type specimens:* STRI 15941 (1, 255 mm SL), El Salvador, fish market; UMMZ 178475 (2, 152–212 mm SL), Mexico, Guerrero, Laguna de Coyuca, ca 10 mi NW of Acapulco, 3 mi NW of military airport on SW side of the Laguna; UA 67–138–1 (1), Mexico, Nayarit, beach at San Blas; UA 70–24–4 (1), Mexico, Oaxaca, Laguna Pto Escondido.

Diagnosis. *Ariopsis guatemalensis* is distinguished from all other congeners by mesethmoid median portion wide (*vs.* narrow, Fig. 3), medial notch of mesethmoid large and shallow (*vs.* narrow and deep, Fig. 3). The species can be further differentiated as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by its wider mouth, 13.0–15.2% SL (*vs.* 10.5–12.9% SL), wider cephalic shield at frontal area, 10.0–11.5% SL (*vs.* 8.8–10.1% SL); from *A. felis*, from Massachusetts (US) to Yucatán in Mexico (Caribbean), by its wider distance between anterior nostrils, 7.1–8.6% SL (*vs.* 4.6–6.4% SL), wider distance between posterior nostrils 7.2–8.7% SL (*vs.* 4.2–7.1% SL), osseous medial groove absent (*vs.* present; Figs. 3 and 15), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 15), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notching, at middle portion narrower than anterior portion, Figs. 3 and 15), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 15); from *A. gilberti*, from Mexico (EP), by 31–39 gill rakers on the first and second gill arches (*vs.* 40–42), wider distance between anterior nostrils 7.1–8.6% SL (*vs.* 5.5–6.5% SL), wider distance between posterior nostrils 7.2–8.7% SL (*vs.* 4.9–6.7% SL), wider cephalic shield at frontal area 10.0–11.5% SL (*vs.* 8.3–9.8% SL), wider cephalic shield at lateral ethmoid area 14.3–15.3% SL (*vs.* 12.5–14.0% SL), osseous medial groove absent (*vs.* present; Figs. 3 and 15), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 15), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 15); from *A. jimenezi*, from Archipiélago de Las Perlas in Panama (EP), by its wider distance between anterior nostrils 7.1–8.6% SL (*vs.* 5.6–6.5% SL), longer pectoral spine 18.2–20.5% SL (*vs.* 14.6–18.1% SL), osseous medial groove absent (*vs.* present; Figs. 3 and 15), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 15), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 15), external posterior branch of lateral ethmoid colunar and thin (*vs.* depressed and thick, Fig. 3), fenestra delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3); from *A. seemanni*, from El Salvador to Panama (EP), by the absence of osseous medial groove delete (*vs.* present; Figs. 3 and 15), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 15); from *A. simonsi*, from Colombia to Peru (EP), by the absence of an osseous medial groove (*vs.* present; Figs. 3 and 15).

Description. Morphometrics and meristics summarized in Tables 2–4, 9. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile slightly elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin; nostrils moderately separated relatively near to orbit, not connected by fleshy furrow. Eye lateral, relatively small; eyes well separated. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and relatively narrow on supracleithrum area, and wider on lateral ethmoid and frontal areas, with thick granulation, forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, short, conspicuous or inconspicuous, and not reaching eyes. Lateral margin of sphenotic straight, as wide medially as anteriorly. Pterotic lateral margin markedly convex, sometimes angled. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively long and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and narrow. Mouth subterminal, very large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth,

separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Fourteen to 18 acicular gill rakers on first arch, 16–21 spike-shaped gill rakers on second arch and rakers present on posterior margin of all gill arches.

TABLE 9. Morphometric data for *Ariopsis guatemalensis*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Holotype <i>A. guatemalensis</i>	Paratypes <i>A. azureus</i>	Mean	Range
Standard length (mm)	229	389		152–212
Head length	31.7	31.3	26.4	25.9–27.5
Snout length	9.2	8.2	7.0	5.7–8.6
Distance between anterior nostrils	7.1	8.4	8.3	8.1–8.6
Distance between posterior nostrils	7.2	7.6	8.3	8.2–8.7
Orbital diameter	5.3		4.2	3.9–4.5
Interorbital distance	14.0		14.1	13.2–15.1
Maxillary barbel length	23.6		25.8	22.9–28.4
Lateral mental barbel length	14.3		18.1	16.4–19.9
Mesial mental barbel length	9.0		11.2	8.9–12.5
Mouth width	15.2	13.7	13.7	13.0–14.5
Width of cephalic shield at lateral ethmoid area	15.3		14.6	14.3–15.0
Width of cephalic shield at frontals area	11.5		10.3	10.0–10.5
Width of cephalic shield at supracleithrum area	19.9		18.6	18.3–18.9
Parietosupraoccipital process length			13.8	13.6–13.9
Parietosupraoccipital process width			3.5	3.5–3.6
Nuchal-plate length			6.7	6.6–6.7
Nuchal-plate width			6.8	6.8–6.8
Body depth	16.2	16.2	18.0	17.1–18.8
Body width	21.0	22.2	21.9	20.3–22.9
Distance from snout to pectoral fin	26.7		22.7	22.4–22.8
Distance from snout to dorsal fin	37.7		34.6	33.6–36.1
Distance from snout to pelvic fin	59.9		53.8	52.2–55.3
Distance from snout to adipose fin	80.4		74.2	71.3–76.1
Distance from snout to anal fin	78.2		71.4	70.1–72.2
Caudal-peduncle height	6.8	7.7	8.0	7.3–8.6
Pectoral-fin spine length	18.5		19.3	18.2–20.5
Dorsal-fin spine length	16.0		18.3	17.5–19.2
Pelvic-fin base length	4.1		4.1	3.5–4.5
Pelvic-fin height	13.9		13.7	13.4–14.4
Adipose-fin base length	7.2		10.4	7.2–13.5
Adipose-fin height				5.8–5.7
Anal-fin base length	14.0		13.6	11.6–16.0
Anal-fin height				11.3–12.7
Caudal-fin upper lobe length				38.3–39.5
Caudal-fin lower lobe length				32.6–34.0



FIGURE 14. Body in lateral view. (A) *Ariopsis guatemalensis*, 260 mm SL, Syntypes, BMNH 1853.1.11.6; (B) *Arius caerulescens*, Syntypes, BMNH 1864.1.26.208–209; (C) *Galeichthys azureus*, Holotype, CAS-SU 11575.

Body wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal soft rays. Pectoral spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with weak serrations. Nine to eleven pectoral soft rays. Posterior process of cleithrum triangular smooth to rugose, slightly visible. Pelvic fin deep and large at base, with six rays, and well-developed fleshy protuberances in adult females. Adipose fin low, with base moderately long, shorter than anal base. Anal fin moderately high and long at base, with 16–19 rays and ventral profile convex. Caudal peduncle moderately high. Caudal-fin forked, dorsal and ventral lobes relatively long, dorsal lobe somewhat longer than ventral lobe, slightly pointed.

Maximum length: Grows to 450 mm TL.

Coloration in alcohol. Head and body dark brown to bluish above, whitish below; dorsal surfaces of pelvic proximally black, distally lighter; anal dark, distal tips lighter; caudal grayish to blackish (Fig. 14).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. The EP *Ariopsis guatemalensis* occurs in estuarine and marine waters, from the mouth of Colorado River (Sonora), Pacific Mexico, to Costa Rica (Fig. 5).

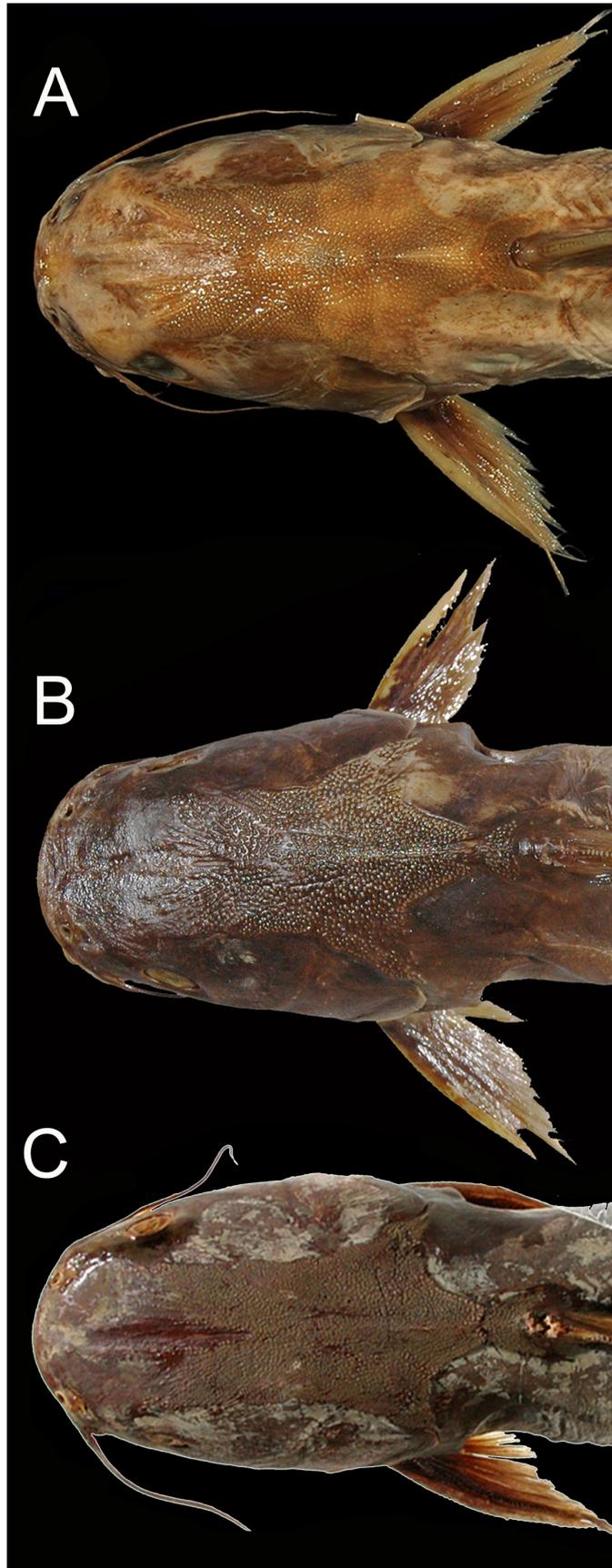


FIGURE 15. Head in dorsal view. (A) *Ariopsis guatemalensis*, Syntypes, BMNH 1853.1.11.6; (B) *Arius caerulescens*, Syntypes, BMNH 1864.1.26.208–209; (C) *Galeichthys azureus*, Holotype, CAS-SU 11575.

Molecular evidence and phylogenetic relationships. *Ariopsis guatemalensis* is the sister species of a clade including *A. jimenezi*, *A. simonsi*, *A. seemanni* and *A. canteri* (Fig. 9).

Remarks. Günther (1864) described *Arius guatemalensis* based on specimens collected on the Pacific side of Guatemala (Figs. 14 and 15). In recent literature (Kailola & Bussing, 1995; Ferraris, 2007), two nominal species have been considered junior synonyms of *Ariopsis guatemalensis*. *Arius caeruleus*, described by Günther (1864) based on two specimens from Guamuchal (=Huamuchal) in Guatemala, and *Galeichthys azureus*, described by Jordan & Williams (1895) based on a unique specimen from an estuary at Mazatlán (Sinaloa), western Mexico. There is little conflict in the literature about the taxonomic status of *Galeichthys azureus*, as junior synonym of *A. guatemalensis*. *Arius caeruleus* (*sensu* Jordan & Gilbert, 1882; Jordan & Evermann, 1896; Eigenmann & Eigenmann, 1890; Regan, 1906, 1908) is accepted as a synonym of *A. guatemalensis* based on characters recognized in present study as sexually dimorphic (e.g., the vomerine tooth plates continuous with larger club-shaped palatine, *vs.* oblong or oval, continuous or not, with palatine patches a little larger than vomerine in *A. guatemalensis*) or show ontogenetic variation (e.g., maxillary barbel extending to the opercle or near to base of pectoral; *vs.* extending beyond the base of pectoral in *A. guatemalensis*).

***Ariopsis jimenezi*, new species.**

Jimenez's sea catfish (English)

Figure 16 and 17, Tables 2–4 and 10.

Material examined. *Holotype*, STRI 8660 (female, 260 mm SL), Panama, Casaya Island, Archipiélago de las Perlas; *Paratypes*, STRI 8661 (14, 240–302 mm SL), Panama, Casaya Island, Archipiélago de las Perlas; STRI 8662 (2, 240–258 mm SL) Panama, Casaya Island, Archipiélago de las Perlas; STRI 8127 (2, tissue 27110–27711) Panama, Casaya Island, Archipiélago de las Perlas; STRI 8566 (1, tissue 27707) Panama, Casaya Island, Archipiélago de las Perlas.

Diagnosis. *Ariopsis jimenezi* differs from its congeners by external posterior branch of the lateral ethmoid thick and depressed (*vs.* columnar and thin, Fig. 3), and an inconspicuous fenestra delimited by the mesethmoid and lateral ethmoid (*vs.* a conspicuous fenestra, Fig. 3). The species can be further differentiated as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by shorter pectoral spine 14.6–18.1% SL (*vs.* 18.2–22.6% SL), osseous medial groove present (*vs.* absent; Figs. 3 and 17), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 17), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 17); margin of pterotic smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 17); from *A. canteri*, from Colombian Caribbean, osseous medial groove present (*vs.* absent; Figs. 3 and 17), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 17), pterotic lateral margin smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 17); from *A. felis*, from Massachusetts (US) to Yucatán in Mexico (Caribbean), by the presence of 16–17 gill rakers on the first gill arch, rarely 15 (*vs.* 13–15, rarely 16, Table 3); from *A. gilberti*, from Mexico (EP), by 29–34 gill rakers on the first and second gill arches (*vs.* 40–42), pterotic lateral margin smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 17); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by its narrower mouth 9.0–11.4% SL (*vs.* 13.0–15.2% SL); narrower distance between anterior nostrils 5.6–6.5% SL (*vs.* 7.1–8.6% SL); shorter pectoral spine 14.6–18.1% SL (*vs.* 18.2–20.5% SL), osseous medial groove present (*vs.* absent; Figs. 3 and 17), fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 17), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 17), median portion of mesethmoid narrow (*vs.* wide, Figs. 3 and 17), medial notch of mesethmoid narrow and deep (*vs.* large and shallow, Figs. 3 and 17); from *A. seemanni*, from El Salvador to Panama (EP), by fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but never surpassing posterior margin of eyes, Figs. 4 and 17), pterotic lateral margin smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 17); from *A. simonsi*, from Colombia to Peru (EP), by fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (*vs.* conspicuous or inconspicuous, but

never surpassing posterior margin of eyes, Figs. 4 and 17), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 17), pterotic lateral margin smoothly convex (*vs.* markedly convex, sometimes angled, Figs. 3 and 17).



FIGURE 16. Body in lateral view. *Ariopsis jimenezi*, Holotype, STRI 8660.

Description. Morphometrics and meristics summarized in Tables 2–4, 10. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile slightly elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, moderately distant to one another and moderately distant to orbit, not connected by fleshy furrow. Eye lateral, relatively small. Eyes well separated. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of opercle, lateral and mesial mental barbel not reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid very short and very thick, delimiting a fenestra not evident under the skin. Cephalic shield exposed, moderately long and relatively narrow on supracleithrum area, and wider on lateral ethmoid and frontal areas, with thick granulation, sparse and especially visible on sphenotic and parietosupraoccipital. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, long and conspicuous, reaching eyes. Lateral margin of sphenotic notched, narrower medially than anteriorly. Pterotic lateral margin smoothly convex. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively long and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, relatively long and wide. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Fifteen to 17 acicular gill rakers on first arch, 14–17 spike-shaped gill rakers on second arch and rakers present on posterior margin of all gill arches.

Body wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal spine relatively short and thick, shorter than pectoral spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal-fin soft rays. Pectoral-fin spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with serrations. Nine to ten pectoral-fin soft rays. Posterior process of cleithrum triangular smooth to rugose, slightly visible. Pelvic-fin deep and large at base, with six rays, and well-developed fleshy protuberances in females. Adipose-fin low, with base moderately long, shorter than anal base. Anal fin moderately high and long at base, with 16–19 rays and ventral profile convex. Caudal peduncle moderately high. Caudal-fin forked, dorsal and ventral lobes relatively long, dorsal lobe somewhat longer than ventral lobe, slightly pointed.

Maximum length: Grows to about 350 mm TL.

TABLE 10. Morphometric data for *Ariopsis jimenezi*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Holotype	Paratype		
		N	Mean	Range
Standard length (mm)	260	14		240.0–302.0
Head length	24.2	13	25.6	24.2–28.1
Snout length	6.1	14	7.1	6.0–8.1
Distance between anterior nostrils	5.7	14	6.0	5.6–6.5
Distance between posterior nostrils	6.4	13	6.4	5.8–7.2
Orbital diameter	5.0	14	4.6	4.0–5.0
Interorbital distance	14.0	14	13.6	12.6–14.8
Maxillary barbel length	2.3	14	22.5	19.0–26.0
Lateral mental barbel length	1.5	14	15.7	13.2–18.4
Mesial mental barbel length	9.4	14	9.1	7.6–10.5
Mouth width	9.8	14	9.8	9.0–11.4
Width of cephalic shield at lateral ethmoid area	14.2	13	13.7	12.9–14.4
Width of cephalic shield at frontals area	10.0	14	10.3	9.6–11.8
Width of cephalic shield at supracleithrum area	19.4	14	18.9	18.1–19.5
Parietosupraoccipital process length	10.5	13	9.3	7.7–10.5
Parietosupraoccipital process width	4.0	14	3.6	3.1–4.3
Nuchal-plate length	6.7	8	6.9	6.4–7.3
Nuchal-plate width	7.4	9	7.3	6.8–8.0
Body depth	18.7	12	18.5	17.2–20.0
Body width	21.0	12	20.8	19.9–21.7
Distance from snout to pectoral fin	21.3	13	21.2	19.2–22.8
Distance from snout to dorsal fin	32.0	14	32.7	30.1–34.8
Distance from snout to pelvic fin	50.1	14	51.3	46.2–53.4
Distance from snout to adipose fin	76.1	9	76.3	73.7–78.3
Distance from snout to anal fin	72.2	6	71.0	69.8–72.1
Caudal-peduncle height	8.5	14	8.2	7.3–8.8
Pectoral-fin spine length	17.7	14	16.7	14.6–18.1
Dorsal-fin spine length	13.0	9	16.6	13.0–18.9
Pelvic-fin base length	6.7	14	6.9	5.8–8.1
Pelvic-fin height	16.6	14	16.9	15.1–18.3
Adipose-fin base length	8.9	14	8.6	7.8–9.7
Adipose-fin height	3.3	14	4.0	3.0–4.6
Anal-fin base length	14.6	13	14.3	13.0–15.6
Anal-fin height	11.8	14	10.9	9.0–12.7
Caudal-fin upper lobe length	37.2	13	33.4	29.0–37.1
Caudal-fin lower lobe length	29.2	13	29.3	26.5–31.3

Coloration in alcohol. Head and body dark brown above, whitish below; dorsal surfaces of pelvic proximally black, distally lighter; anal dark, distal tips lighter; caudal grayish to blackish (Fig. 16).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads, in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches ovate to square in females, and reduced and transversally elongated in males. In females, accessory tooth patches larger and ovate (relatively smaller and elongated in males).

Distribution and habitat. *Ariopsis jimenezi* is only known from Archipiélago de Las Perlas in Panama (EP). It occurs in shallow inshore marine waters (Fig. 5).

Molecular evidence and phylogenetic relationships. *Ariopsis jimenezi* is the sister species of a clade including *A. simonsi*, *A. seemanni* and *A. canteri* (Fig. 9).

Etymology. The species is named after Máximo Jiménez Acosta, zooarchaeology technician at the Smithsonian Tropical Research Institute, Panama, who drew attention to the possible existence of a new species based on the examination of osteological characters in specimens formerly missidentified as *A. seemanni*.



FIGURE 17. Head in dorsal view, *Ariopsis jimenezi*, Holotype STRI 8660.

Remarks. The new species is recognized based on a combination of meristic and morphometric features as well as on unique osteological characters. Notably, the depressed and thick external posterior branch of the lateral ethmoid and the inconspicuous fenestra (delimited by mesethmoid and lateral ethmoid) are recognized as derived states (autapomorphies) within a phylogenetic framework of *Ariopsis* (see Marceniuk, *et al.* 2012b; Marceniuk & Betancur-R, *in preparation*).

***Ariopsis seemanni* (Günther, 1864)**

Congo Prieto or Musengue (Spanish, Panama)

Figures 18 and 19, Tables 2–4 and 11.

Arius seemanni Günther, 1864:147. Type locality: Central America (Pacific). Holotype (unique): BMNH 1855.9.19.1107.

Tachisurus jordani Eigenmann & Eigenmann, 1888:142. Type locality: Panama (Pacific). Syntypes: MCZ 4945 (2).

Galeichthys eigenmanni Gilbert & Starks, 1904:21, Pl. 4, fig. 8. Type locality: Panama. Holotype: CAS-SU 6986. Paratypes: (11) BMNH 1903.5.15.319–320; CAS-SU 12878–80 (1, 1, 1); USNM 50379 (1); ZMB 15858 [ex USNM] (2).

Arius seemanni, Kailola & Bussing, 1995: 874.

Ariopsis seemanni, Robertson & Allen, 2015.

Material examined. *Holotype*: BMNH 1855.9.19.1107 (1, 227 mm SL). *Non-type specimens*: MCZ 4945 (2, 198–201 mm SL), Panama; STRI 15948 (1, 178 mm SL), El Salvador, Acajutla; STRI 12668 (1, 171 mm SL), Panama, bahía de Parita; STRI 12667 (1, 177 mm SL), Panama, Bahía de Parita; STRI 17240 (1, 314 mm SL), Panama, isla Majagual; STRI 17241 (2, 155–219 mm SL), Panama, Isla Majagual; STRI 9297 (1, 204 mm SL), Panama, Punta Chame outer beach and inside lagoon; STRI 16754 (1, 153 mm SL), Panama, Bahía de Panama, isla Naos; STRI 3071 (1, 145 mm SL), Panama, Veracruz Beach; FMNH 19791 (2, 226–285 mm SL), Panama, Chame Point.

Diagnosis. *Ariopsis seemanni* can be differentiated from its congeners as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), by the presence of an osseous medial groove (*vs.* absent; Figs. 3 and 19), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 19); from *A. canteri*, from the Colombian Caribbean, by the presence of an osseous medial groove (*vs.* absent; Figs. 3 and 19), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 19); from *A. felis*, from Massachusetts (US) to Yucatán in Mexico (Caribbean), by its fleshy medial groove of neurocranium, never surpassing posterior margin of eyes (*vs.* very long, always surpassing the posterior margin of eyes, Figs. 4 and 19), pterotic lateral margin convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 19); from *A. gilberti*, from Mexico (EP), by the presence of 30–36 gill rakers on the first and second gill arches (combined counts; *vs.* 40–42), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 3 and 19); from *A. guatemalensis*, from Mexico to Costa Rica (EP), by its narrower mouth 9.7–12.7% SL (*vs.* 13.0–15.2% SL), osseous medial groove present (*vs.* absent; Figs. 3 and 19), lateral margin of sphenotic notched, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 19), median portion of mesethmoid narrow (*vs.* wide, Fig. 3), medial notch of mesethmoid narrow and deep (*vs.* large and shallow, Fig. 3); from *A. jimenezi*, from Archipiélago de Las Perlas in Panama (EP), by its fleshy medial groove of neurocranium, conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 19), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 19), external posterior branch of lateral ethmoid columnar and thin (*vs.* depressed and thick, Fig. 3), fenestra delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3); from *A. simonsi*, from Colombia to Peru (EP), by its notched lateral margin of sphenotic, narrower medially than anteriorly (*vs.* straight, as wide medially as anteriorly, Figs. 3 and 19).

Description. Morphometrics and meristics summarized in Table 2–4, 11. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile slightly elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, moderately separated and moderately distant from orbit, not connected by fleshy furrow. Eye lateral, moderately large and distant to one another. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel not

reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and moderately wide on supracleithrum, lateral ethmoid and frontal areas, with thick granulation, forming distinct patterns from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, moderately long and conspicuous, not surpassing eyes. Lateral margin of sphenotic notched, narrower medially than anteriorly. Pterotic lateral margin convex, sometimes angled. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Fifteen to 18 acicular gill rakers on first arch, 15–18 spike-shaped gill rakers on second arch and rakers present on posterior margin of all gill arches.



FIGURE 18. Body in lateral view. (A) *Ariopsis seemanni*, 300 mm TL, Holotype, BMNH 1855.9.19.1107; (B) *Tachisurus jordani*, Syntype, MCZ 4945; (C) *Galeichthys eigenmanni*, Holotype, CAS-SU 6986.

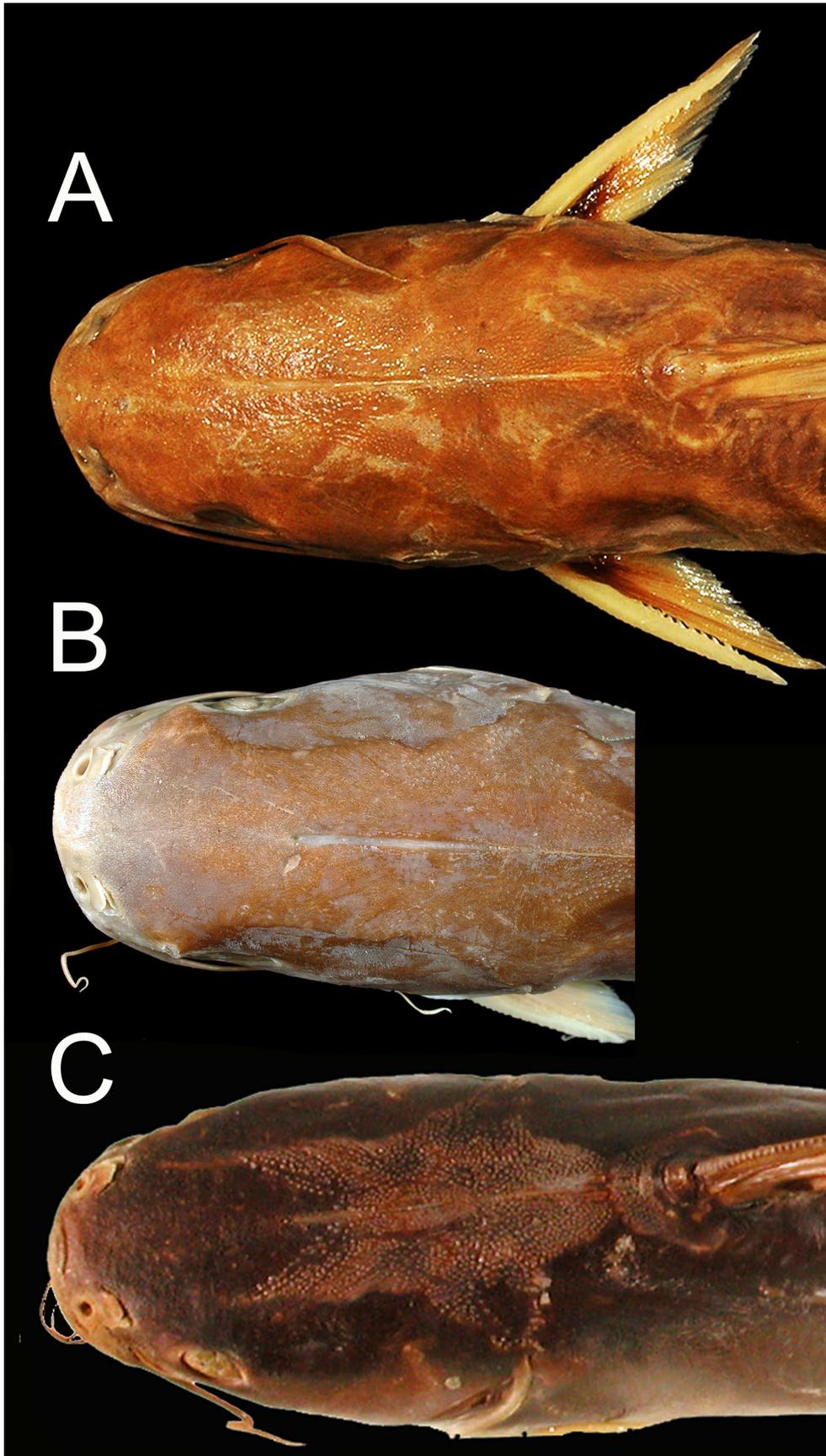


FIGURE 19. Head in dorsal view. (A) *Ariopsis seemanni*, Holotype, BMNH 1855.9.19.1107; (B) *Tachisurus jordani*, Syntype, MCZ 4945; (C) *Galeichthys eigenmanni*, Holotype, CAS-SU 6986.

TABLE 11. Morphometric data for *Ariopsis seemanni*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Syntypes		Holotype		
	<i>A. jordani</i>	<i>A. eigenmanni</i>	N	Mean	Range
Standard length (mm)	198.4–201.5		11		145–314
Head length	28.7–29.2	26.7	11	26.6	23.5–30.7
Snout length	8.1–8.2	7.5	11	7.1	5.9–8.0
Distance between anterior nostrils	5.7–5.8	6.5	11	6.1	4.7–7.4
Distance between posterior nostrils	5.4–5.5	5.3	11	6.5	5.3–8.0
Orbital diameter	5.3–5.8		11	4.5	3.7–5.1
Interorbital distance	13.3–13.7		11	13.3	11.4–16.5
Maxillary barbel length	26.9–24.5		11	25.5	13.9–32.7
Lateral mental barbel length	16.1–18.8		11	16.9	11.3–20.3
Mesial mental barbel length	10.1–11.6		11	9.9	5.9–13.3
Mouth width	11.7–11.9	11.4	11	11.3	9.7–12.7
Width of cephalic shield at lateral ethmoid area	14.2–14.4		11	13.4	12.5–15.2
Width of cephalic shield at frontals area	9.8–10.0		11	9.6	8.9–10.4
Width of cephalic shield at supracleithrum area	18.5–18.8		11	18.3	16.8–19.9
Parietosupraoccipital process length			2	8.0	6.2–9.9
Parietosupraoccipital process width			2	4.2	3.5–4.8
Nuchal-plate length			2	7.3	7.1–7.4
Nuchal-plate width	7.1–7.6		2	7.2	7.1–7.3
Body depth		18.4	11	20.7	19.3–24.3
Body width		22.1	11	20.4	18.9–23.4
Distance from snout to pectoral fin			11	22.7	19.3–27.1
Distance from snout to dorsal fin			11	34.3	31.3–37.6
Distance from snout to pelvic fin			11	53.1	49.7–58.1
Distance from snout to adipose fin			11	74.6	69.6–78.6
Distance from snout to anal fin			11	70.6	68.0–73.6
Caudal-peduncle height		8.3	11	7.6	7.2–9.1
Pectoral-fin spine length	19.0–19.4		11	19.5	17.3–20.8
Dorsal-fin spine length	18.7		11	19.2	16.6–21.0
Pelvic-fin base length	4.2–5.2		11	4.6	3.8–6.1
Pelvic-fin height	14.1–15.0		11	14.6	12.1–17.9
Adipose-fin base length			11	8.9	7.8–10.3
Adipose-fin height			2	4.3	4.0–4.5
Anal-fin base length			11	14.1	12.9–15.3
Anal-fin height			2	13.2	12.9–13.5
Caudal-fin upper lobe length			1	31.5	
Caudal-fin lower lobe length			2	29.4	29.1–29.7

Body wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal fin spine relatively short and thick, almost as long as pectoral-fin spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal fin soft rays.

Pectoral fin spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with serrations. Nine to ten pectoral fin soft rays. Posterior process of cleithrum triangular, smooth to rugose, slightly visible. Pelvic fin deep and large at base, with six rays, and well-developed fleshy protuberances in adult females. Adipose fin low, with base moderately long, shorter than anal base. Anal fin moderately high and long at base, with 18–20 rays and ventral profile convex. Caudal peduncle moderately high. Caudal-fin forked, dorsal and ventral lobes moderately long, dorsal lobe somewhat longer than ventral lobe and pointed.

Maximum length: May exceed 350 mm TL.

Coloration in alcohol. Head and body dark brown to bluish above, whitish below; dorsal surfaces of pelvic proximally black, distally lighter; anal dark, distal tips lighter; caudal grayish to blackish (Fig. 18).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvics, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. *Ariopsis seemanni* occurs in estuarine and marine waters, from El Salvador to Panama (EP) (Fig. 5). In Panama, it is abundant in tidal rivers and high salinity salt pans, but has not been recorded from freshwaters.

Molecular evidence and phylogenetic relationships. Our phylogenetic analyses failed to support the monophyly *Ariopsis seemanni*, suggesting the existence of a species complex segregated by geography (Fig. 9). Examined specimens from Panama and El Salvador are not each other's closest relatives. Instead, the specimen from El Salvador appears to be closer to the new Caribbean species, *A. canteri*.

Remarks. *Arius seemanni* was described by Günther (1864), based on a single specimen collected in Pacific coast of Central America (Figs. 18 and 19). The original description recognizes *Ariopsis seemanni* based on morphometric, meristic and osteological characteristics that are clearly also present in other species in the genus (i.e., are not diagnostic). Here, *A. seemanni* is tentatively delimited based on a combination of morphometric, meristic, and osteological characters. The molecular evidence, however, failed to resolve the species as monophyletic (see above). The apparent absence of conspicuous or unique features in *A. seemanni* may also explain the difficulties faced by previous ichthyologists in delimiting this species. In fact, most nominal species in the tropical EP (except for *Ariopsis guatemalensis*) have at times been subsumed in synonymy under *A. seemanni*. *Galeichthys eigenmanni* from Panama, described by Gilbert & Starks (1904), is confirmed as a junior synonym of *A. seemanni* (*sensu* Regan, 1906–1908; Meek & Hildebrand, 1923; Kailola & Bussing, 1995), while *Ariopsis gilberti* and *Ariopsis simonsi* have been taxonomically redefined herein. *Tachisurus jordani* Eigenmann & Eigenmann (1888), described from the EP of Panama, is recognized as valid by Eigenmann & Eigenmann (1889), Jordan & Everman (1896), Meek & Hildebrand (1923), and Hildebrand (1946). *Galeichthys jordani* (*sensu* Meek & Hildebrand, 1923) was differentiated from *Ariopsis seemanni* based on qualitative degrees of granulation on the cephalic shield, i.e., “roughly granular vs. smooth” or “slightly granular”, “median keel of the occipital process low and blunt vs. sharp”, “snout very low, and the eye small vs. larger” (see Meek & Hildebrand, 1923: 105). Because our perusal of these characters reveal intraspecific variation and ontogenetic variation, they cannot be used as diagnostic. For these reasons, we follow the opinion of Regan (1906–08) and Kailola & Bussing (1995) that *T. jordani* is a junior synonym of *Ariopsis seemanni*, but acknowledge that the species, as delimited herein, possibly represents a species complex.

***Ariopsis simonsi* (Starks, 1906)**

Canchimala Sea Catfish (English)

Canchimala blanca (Spanish)

Figures 20 and 21, Tables 2–4 and 12.

Galeichthys simonsi Starks, 1906:764, Figs. 1–2. Type locality: Callao, Peru. Holotype: USNM 53466.

Ariopsis seemanni (non Günther), Chirichigno & Cornejo, 2001: 18.

Material Examined. *Type-specimens.* USNM 53466 (1, 215 mm SL), Peru, Callao. USNM 284549 (3, 88–117 mm SL) Peru, Tumbes, Lower Rio Tumbes, NE Ar Las Paralles. *Non type-specimens.* AUM 57436 (1, 92 mm SL),

Peru, Lima; INV PEC6718 (2, 183–210 mm SL), Colombia, Valle del Cauca, Buenaventura, La Barra-Juanchaco-Ladrilleros (4° 1' 0" N, 77° 28' 0" W), trawl, 3.4 m, Biomálaga. INV PEC9087 (3, 183–245 mm SL), Valle del Cauca, Mercado de Buenaventura, A. Acero P., 1999. Discarded Material: (7, 185–274 mm SL), Valle del Cauca, Mercado de Buenaventura, 1998–2006.



FIGURE 20. Body in lateral view. *Ariopsis simonsi*, Holotype, USNM 53466.



FIGURE 21. Head in dorsal view. *Ariopsis simonsi*, Holotype, USNM 53466.

Diagnosis. *Ariopsis simonsi* differs from its congeners as follows: from *A. assimilis*, from Mexico (Quintana Roo) to Honduras (Caribbean), the presence of an osseous medial groove (*vs.* absent; Figs. 3 and 21); from *A. canteri*, from Colombian Caribbean, the presence of an osseous medial groove (*vs.* absent; Figs. 3 and 21); from *A. felis*, from Massachusetts (US) to Yucatán, Mexico (Caribbean), by its fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 21), pterotic lateral margin convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 21), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 21); from *A. gilberti*, from Mexico (EP), by 28–37 gill rakers on the first and second gill arches (*vs.* 40–42), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 21), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.*

notched, narrower medially than anteriorly, Figs. 3 and 21); from *A. guatemalensis*, from Mexico (EP) to El Salvador, by the presence of an osseous medial groove (*vs.* absent, Figs. 3 and 21), median portion of mesethmoid narrow (*vs.* wide, Fig. 3), medial notch of mesethmoid narrow and deep (*vs.* large and shallow, Fig. 3); from *A. jimenezi*, from Archipiélago de Las Perlas in Panama (EP), by its longer pectoral spine, 18.7–22.5 (*vs.* 14.6–18.1), fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (*vs.* conspicuous and very long, always surpassing the posterior margin of eyes, Figs. 4 and 21), pterotic lateral margin markedly convex, sometimes angled (*vs.* smoothly convex, Figs. 3 and 21), lateral margin of sphenotic straight, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 21), external posterior branch of lateral ethmoid columnar and thin (*vs.* depressed and thick, Fig. 3), fenestra delimited by mesethmoid and lateral ethmoid conspicuous (*vs.* inconspicuous, Fig. 3); from *A. seemanni*, from El Salvador to Panama (EP), by its straight lateral margin of sphenotic, as wide medially as anteriorly (*vs.* notched, narrower medially than anteriorly, Figs. 3 and 21).

Description. Morphometrics and meristics summarized in Tables 2–4, 12. Head moderately long, wide and high, especially depressed at lateral ethmoid and frontal area, profile slightly elevated posteriorly, straight from mesethmoid to parietosupraoccipital. Snout rounded and moderately long. Anterior nostril rounded, with fleshy edge, posterior nostril covered by flap of skin, moderately separated and moderately distant from orbit, not connected by fleshy furrow. Eye lateral, relatively large and moderately distant to one another. Three pairs of long teretiform barbels; maxillary barbel surpassing or not membranous portion of operculum, lateral and mesial mental barbel reaching posterior margin of gill membrane. Osseous bridge formed by lateral ethmoid and frontal moderately long and slender, delimiting a fenestra little evident under the skin. Cephalic shield exposed, moderately long and moderately wide on supracleithrum, lateral ethmoid and frontal areas, with thick granulation, forming distinct patterns visible from eyes to parietosupraoccipital process. Fleshy portion of dorsomedial groove of neurocranium, affixed to anterior cranial fontanel, moderately long and conspicuous, not surpassing eyes. Lateral margin of sphenotic straight, as wide medially as anteriorly. Pterotic lateral margin convex, sometimes angled. Parietosupraoccipital keeled, triangular, with straight lateral margins converging posteriorly, relatively short and moderately wide at posterior portion, with posterior margin convex. Nuchal plate crescent-shaped, conspicuously granulated dorsally, moderately long and narrow. Mouth subterminal, moderately large, with lips moderately thick and lower jaw arched. Vomerine tooth plates rounded. One pair of accessory tooth plates ovate, with sharp teeth. Premaxilla rectangular transversally, long and wide, with sharp teeth. Dentary with eyebrow-shaped patch of teeth, separated at midline with sharp teeth. Gill membranes fused, attached to isthmus. Fourteen to 18 acicular gill rakers on first arch, 14–21 spike-shaped gill rakers on second arch and rakers present on posterior margin of all gill arches.

Body wider than its height at pectoral girdle area, progressively compressed from pectoral to caudal peduncle, ventrally flattened from pectoral girdle to anal origin. Lateral line sloping ventrally on anterior one-third, extending posteriorly to caudal peduncle, bending abruptly onto dorsal lobe of caudal. Dorsal-fin spine relatively short and thick, almost as long as pectoral-fin spine; anterior margin granulated on basal two-thirds, with weak serrations on distal third; posterior margin smooth on basal third, distal third with weak serrations. Seven dorsal-fin soft rays. Pectoral fin spine moderately long and thick; two-thirds of anterior margin weakly granulated, with weak serrations on distal third; posterior margin straight on basal one-fourth, distal three-fourths with serrations. Nine to ten pectoral-fin soft rays. Posterior process of cleithrum triangular smooth to rugose, slightly visible. Pelvic fin deep and large at base, with six rays, and well-developed fleshy protuberances in adult females. Adipose fin low, with base moderately long, shorter than anal base. Anal fin moderately high and long at base, with 18–20 rays and ventral profile convex. Caudal peduncle moderately high. Caudal-fin forked, dorsal and ventral lobes moderately long, dorsal lobe somewhat longer than ventral lobe and pointed.

Maximum length: The largest specimen examined is 330 mm TL.

Coloration in alcohol. Head and body dark brown above, whitish below; dorsal surfaces of pelvic fin proximally black, distally lighter; anal fin dark, distal tips lighter; caudal fin grayish to blackish (Fig. 20).

Sexual dimorphism. Only females have well-developed fleshy protuberances or pads in basal portion of pelvic fins, especially during reproductive season. Vomerine tooth patches and accessory tooth patches not observed directly, but possibly showing same variation described for *A. canteri* and *A. jimenezi*.

Distribution and habitat. The EP *Ariopsis simonsi* occurs in estuarine and marine waters, from Colombia to Peru (Talará) (Fig. 5).

TABLE 12. Morphometric data for *Ariopsis simonsi*. Standard length is expressed in millimeters and all other measurements are expressed in percents of standard length.

	Holotype			
		N	Mean	Range
Standard length (mm)	215.9	16		88–274
Head length	27.7	16	26.3	23.5–30.6
Snout length	7.8	15	6.4	5.4–7.0
Distance between anterior nostrils	7.2	16	5.8	5.1–6.6
Distance between posterior nostrils	6.5	16	6.1	5.1–6.6
Orbital diameter	5.3	16	5.3	4.2–6.7
Interorbital distance	15.2	16	12.5	11.3–13.7
Maxillary barbel length	24.6	14	26.2	21.6–34.0
Lateral mental barbel length	18.4	16	16.7	11.7–21.8
Mesial mental barbel length	10.3	16	10.0	8.0–12.5
Mouth width	13.1	16	10.3	8.9–11.2
Width of cephalic shield at lateral ethmoid area	14.9	16	13.4	11.6–14.8
Width of cephalic shield at frontals area	10.9	16	9.7	8.7–11.0
Width of cephalic shield at supracleithrum area	19.3	16	18.2	16.9–19.6
Parietosupraoccipital process length				
Parietosupraoccipital process width				
Nuchal-plate length	5.9			
Nuchal-plate width	7.6			
Body depth		16	18.7	15.4–21.9
Body width		16	20.0	18.4–21.1
Distance from snout to pectoral fin		16	21.2	19.6–24.2
Distance from snout to dorsal fin		16	34.1	30.7–36.0
Distance from snout to pelvic fin		16	52.5	50.4–55.1
Distance from snout to adipose fin		16	74.2	69.2–76.6
Distance from snout to anal fin		16	69.9	65.8–72.5
Caudal-peduncle height	7.7	16	7.3	6.5–8.6
Pectoral-fin spine length	18.7	4	21.5	20.1–22.5
Dorsal-fin spine length	18.2	4	22.1	20.6–22.9
Pelvic-fin base length	5.0	16	4.5	3.2–6.0
Pelvic-fin height	14.6	15	17.6	14.4–21.3
Adipose-fin base length		16	8.6	6.5–11.3
Adipose-fin height				
Anal-fin base length		16	14.2	12.3–16.3
Anal-fin height				
Caudal-fin upper lobe length				
Caudal-fin lower lobe length				

Molecular evidence and phylogenetic relationships. *Ariopsis simonsi* is the sister species of a clade including *A. seemanni* and *A. canteri* (Fig. 9).

Remarks. *Ariopsis simonsi* was described by Starks (1906) based on a single specimen collected at Callao, Peru (Figs. 20 and 21). Wilson (1916) validated *A. simonsi* based on specimens collected at Buenaventura and Tumaco, thus broadening the geographical range of this species. In several more recent treatments, however, *A.*

simonsi was synonymized with *A. seemanni* (Meek & Hildebrand, 1923) and *Galeichthys jordani* (Hildebrand, 1946). Hildebrand (1946) also compared two specimens collected at Cabo Blanco, Peru (290–340 mm TL), the type specimen of *A. simonsi*, and a specimen from Tumbes, Peru (335 mm TL), with specimens collected in Panama. The author inferred that the specimens from Peru are closer to *G. jordani*, than to *A. seemanni*, supporting his conclusions on a series of observations; e.g., “the large eye, the rather flat deep snout with nearly vertical edges, the mouth flat interorbital, which rises scarcely more than diameter of pupil above upper margin of eye, and the broad mouth, which is arched forward only slight” (see Hildebrand, 1946: 126).

The difficulty of identifying *A. simonsi* and differentiating it from *A. seemanni* results from the fact that the profile of the lateral margin of the sphenotic is the only character separating this species, which had hitherto been differentiated only by reference to combined morphometric, meristic and osteological features apparent on the type and non-type specimens. The taxonomic value of a specific osteological marker on the sphenotic has been confirmed by molecular analysis, which supports the presence of *A. simonsi* in Colombia and Ecuador and its differentiation from *A. seemanni* from Panama. (Fig. 9). A recent study of the genetic and morphological responses of ariid catfish to the transition from marine to fresh water likewise underlined the need to test seemingly slight, but constant, osteological details with molecular data (Stange *et al.*, 2016).

Key to the species of *Ariopsis*

- 1a. Osseous medial groove of neurocranium absent (Fig. 3a, c) 2
- 1b. Osseous medial groove of neurocranium present (Figs. 3b, d, e, f) 4
- 2a. Mesethmoid median portion wide (Fig. 1a), medial notch of mesethmoid large and shallow (Fig. 3a)
..... *A. guatemalensis* (Mexico to Costa Rica, EP)
- 2b. Mesethmoid median portion narrow (Figs. 3b–e), medial notch of mesethmoid narrow and deep (Figs. 3b–e) 3
- 3a. Total number of gill rakers on the first plus the second gill arches 31–36, rarely 37
..... *A. assimilis* (Quintana Roo, Mexico to Honduras in the Caribbean)
- 3b. Total number of gill rakers on the first plus the second gill arches 38–44, rarely 36 or 37 ... *A. canteri* (Colombia, Caribbean)
- 4a. Total number of gill rakers on the first plus the second gill arches 40–42 *A. gilberti* (Mexico, EP)
- 4b. Total number of gill rakers on the first plus the second gill arches 28–37 5
- 5a. Fleshy medial groove of neurocranium conspicuous and very long, always surpassing the posterior margin of eyes (Fig. 4); pterotic lateral margin smoothly convex (Fig. 3) 6
- 5b. Fleshy medial groove of neurocranium conspicuous or inconspicuous, but never surpassing posterior margin of eyes (Fig. 4); pterotic lateral margin markedly convex, sometimes angled (Fig. 3) 7
- 6a. 13–15 gill rakers on the first gill arch, rarely 16; fenestra delimited by mesethmoid and lateral ethmoid conspicuous (Fig. 3); external posterior branch of lateral ethmoid columnar and thin (Fig. 3)
..... *A. felis* (Massachusetts, US, to Yucatán, Mexican Caribbean)
- 6b. 15–17 gill rakers on the first gill arch; fenestra delimited by mesethmoid and lateral ethmoid inconspicuous (Fig. 3); external posterior branch of lateral ethmoid depressed and thick (Fig. 3) *A. jimenezi* (Archipiélago de las Perlas, Panama, EP)
- 7a. Lateral margin of sphenotic notched, narrower medially than anteriorly (Figs. 3 and 19)
..... *A. seemanni* (El Salvador to Panama, EP)
- 7b. Lateral margin of sphenotic straight, as wide medially as anteriorly (Figs. 3 and 21) *A. simonsi* (Colombia to Peru, EP)

Discussion

Our study makes progress towards the completion of ariid taxonomy, a group with a long history of systematic confusion, including by far the highest numbers of species inquirendae among siluriform families (Ferraris, 2007). Revalidation of the genus *Ariopsis* reconciles previous conflicts among ariid classification schemes (Betancur-R. *et al.*, 2007; Marceniuk and Menezes, 2007; Betancur-R., 2009; Marceniuk *et al.*, 2012). Given the striking similarity in external morphology among most species in *Ariopsis*, examination of internal anatomical features coupled with molecular phylogenetic analyses provided an important source of information for species delimitation. Our taxonomic revision expands the composition of species in this genus, including the resurrection of two nominal species previously listed under the synonymy of *A. seemanni* and description of two new species, one endemic to the Colombian Caribbean that was previously recognized but misidentified in the literature (*A. canteri*). Notably, formal description of *A. canteri* is significant from a conservation standpoint as the species has been included in the red list of endangered commercial fishes in Colombia (Acero *et al.*, 2002, 2017; Acero, 2003).

A major limitation of this study is the lack of support for the monophyly of *Ariopsis seemanni* (Fig. 9), which suggests the existence of a species complex. To address this problem, future studies implementing broader geographic and genetic sampling are needed.

From a biogeographic perspective, distributional patterns in *Ariopsis* are largely congruent with the recognition of subprovinces in the WA and the EP (Fig. 9). For instance, while *Ariopsis felis* and *A. assimilis* are restricted to Northern and Central Caribbean Provinces in the WA, respectively, *A. canteri* is a Southern Caribbean endemic (Robertson & Cramer, 2014). Likewise, in the EP, *A. gilberti* is endemic to the Mexican province in the north, whereas *A. seemanni*, *A. jimenezi* and *A. simonsi* are all found in the Panamic province (Hastings, 2000). Only *A. guatemalensis* appears to occur in both the Mexican and Panamic provinces. Finally, *Ariopsis canteri* from the Caribbean is the sister species *A. seemanni* in the EP, suggesting that divergence of these lineages took place as result of the formation of the Panama isthmus approximately three million years ago (O’Dea *et al.*, 2016).

Acknowledgements

The authors are extremely grateful to Wolmar Benjamin Wosiacki curator at the Museu Paraense Emílio Goeldi and Alessio Datovo curator at the Museu de Zoologia da Universidade de São Paulo for receiving the material examined of *A. jimenezi*. We are indebted to Jeff Clayon (National Museum of Natural History, Smithsonian Institution), and Maria Fernanda Castillo, Oris Sanjur and Juan Maté (Smithsonian Tropical Institute, Panama) for their assistance with matters relating to the storage and transferal of *Ariopsis* specimens. Andrea Polanco and Miguel Martelo (Invemar) were very help finding misplaced material. This study was supported by the National Science and Technology Council of the Brazilian Federal Government (CNPq grant no. 300462/2016–6 to APM), the Pará State Research Foundation (FAPESPA grant no. ICAAF 017/2016 to APM), and the National Science Foundation (NSF) grants (DEB-147184, DEB-1541491 to R.B.R.). Colciencias and the Universidad Nacional de Colombia funded AAP through proposal 1101-09-138-98. This paper is the contribution number 452 of CECIMAR.

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