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Taxonomic revision of extant *Doras* Lacepède, 1803 (Siluriformes: Doradidae) with descriptions of three new species

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ABSTRACT.—Extant *Doras* are newly diagnosed among Doradidae by the unique combination of maxillary barbels long and fimbriate; mesethmoid with anterior lateral margins converging towards narrow tip; single anterior cranial fontanel contained largely within frontals and anteriorly by mesethmoid (posterior cranial fontanel occluded); anterior nuchal plate wide, pentaganol or roughly hexagonal, sharing distinct lateral suture with epioccipital and isolating supraoccipital from middle nuchal plate; nuchal foramina absent; coracoid process short, posterior tip falling well short of that of postcleithral process; dentary with acicular teeth; and skin immediately ventral to postcleithral process perforated with conspicuous pores. One fossil species, †*D. dioneae*, and two nominal extant species, *D. carinatus* and *D. micropoeus*, are recognized as valid and the latter two redescribed. Three additional extant species, *D. phlyzakion*, *D. higuchii* and *D. zuanoni*, are newly described from the middle Amazon and tributaries, lower Amazon tributaries and rio Araguaia (Tocantins drainage), respectively. *Doras phlyzakion* and *D. zuanoni* form a monophyletic group that is found in lowland, lentic habitats, and is characterized by multiple conspicuous pores in skin on breast and abdomen, a trait unique among doradids and rare if not unique among all catfishes. The remaining extant species, *D. carinatus*, *D. higuchii* and *D. micropoeus*, with uncertain relationships, are found in upland, lotic habitats. The occurrence of *D. carinatus* in the Orinoco basin suggests a historical link between right-bank tributaries of the lower Orinoco (e.g., Caroní) draining the western Guiana Shield and more eastern rivers (e.g., Cuyuní-Essequibo) that drain the Shield directly into the Atlantic Ocean. A key to extant species is provided, a neotype is designated for *Silurus carinatus* Linnaeus 1766, and *Mormyropsis* Miranda Ribeiro, 1911, is placed in the synonymy of *Doras* Lacepède, 1803.

RESUMO.—As espécies recentes de *Doras* são diagnosticas, no presente estudo, entre os Doradidae pela exclusiva combinação de barbilhão maxilar longos e fimbriados; mesetmóide com margens anteriores convergindo em uma ponta afilada; fontanela craniana única, contida entre os frontais e anteriormente no mesetmóide (fontanela posterior fechada); placa nucal anterior larga, pentagonal ou quase hexagonal, suturada lateralmente ao epioccipital, e isolando o supraoccipital da placa nucal mediana; forame nucal ausente; processo posterior do coracóide curto, extremidade posterior anterior à extremidade do processo pós-cleitral; dentário com dentes aciculares. Uma espécie fóssil, †*D. dioneae*, e duas espécies nominais recentes, *D. carinatus* e *D. micropoeus*, são reconhecidas como válidas e redescritas. Além destas, três espécies recentes, *D. phlyzakion*, *D. higuchii* e *D. zuanoni*, são descritas como novas do médio rio Amazonas e tributários, baixo rio Amazonas e tributários e do rio Araguaia (drenagem do rio Tocantins), respectivamente. *Doras phlyzakion* e *D. zuanoni* formam um grupo monofilético encontrado em terras baixas, ambientes lênticos, e caracterizado pelos múltiplos poros na pele do peito e abdômen, um caráter exclusivo entre doradídeos e raro, se não único entre todos os siluriformes. As demais espécies recentes, *D. carinatus*, *D. higuchii* e *D. micropoeus*, de relações incertas, são encontradas em terras altas, e ambientes lóticos. A ocorrência de *D. carinatus* na bacia do rio Orinoco sugere uma ligação histórica entre os tributários da margem direita do baixo rio Orinoco (e.g., Caroni) que drenam o oeste do Escudo Guianense e rios mais a leste (e.g., Cuyuni-Essequibo) que drenam os Escudo diretamente para o oceano Atlânico. Uma chave de identificação para as espécies recentes de *Doras* é fornecida, um neótipo para *Silurus cariantus* Linnaeus, 1766 é designado, e *Mormyopsis* Miranda Ribeiro, 1911 é considerado sinônimo júnior de *Doras* Lacepède, 1803.

New taxa: *Doras higuchii* Sabaj Pérez and Birindelli, *Doras phlyzakion* Sabaj Pérez and Birindelli, *Doras zuanoni* Sabaj Pérez and Birindelli

INTRODUCTION

Repeated expansion and contraction summarize the circumscription of genus *Doras* Lacepède throughout its long taxonomic history. Lacepède (1803:116) created *Doras* (his Genus 164) for two Linnaean species: *Silurus costatus* Linnaeus 1758 and *Silurus carinatus* Linnaeus 1766. Bleeker (1858:53–54) expanded *Doras* to include 19 valid species, plus one as questionable. In the same work, Bleeker (1858:48) was first to recognize a higher-level taxon, "Phalanx Doradini" ("Subfamilia Callichthyoidei"), for species currently placed in Doradidae and within this

group he recognized three genera: *Doras*, *Pseudodoras* (4 species) and *Hemidoras* (1 species). Bleeker (1862:5) later designated *Doras carinatus* the type species of the genus and subsequently restricted *Doras* to seven species in his early revision of doradids (Bleeker, 1863a:13). Eigenmann and Eigenmann (1888:158), evidently overlooking Bleeker's designation, transferred *Doras carinatus* to the genus *Hemidoras* Bleeker and re-expanded *Doras* to include 24 species in seven subgenera. Later Eigenmann and Eigenmann (1890) similarly recognized 24 species in *Doras* and designated *Silurus costatus* Linnaeus the type species of the genus while maintaining Linnaeus' *S. carinatus* in *Hemidoras*. Miranda Ribeiro (1911) restricted *Doras* to 14 species and unnecessarily created two new monotypic genera, *Mormyrostoma* and *Mormyropsis*, the latter in his "Bibliographia", for the Linnaean *S. carinatus*. Eigenmann (1925), in his remarkable monograph on the family Doradidae, recognized Bleeker's (1862) earlier designation of *Silurus carinatus* as the type species of *Doras* and restricted the genus to seven species: *D. carinatus, D. micropoeus, D. punctatus, D. fimbriatus, D. lipophthalmus, D. microstomus* and *D. brevis*. Eigenmann also noted in a footnote that two species, *Doras microstomus* and *D. brevis*, might belong in *Trachydoras*. Gosline (1945:23) removed *D. lipophthalmus* to *Hassar*, and Fernández-Yépez (1968:32) removed *D. microstomus* to *Anduzedoras*. Sabaj and Ferraris (2003) further restricted *Doras* to include but two valid species, *D. carinatus* and *D. micropoeus*, transferred *D. brevis* to *Trachydoras*, and treated *D. punctatus* and *D. fimbriatus* with *Oxydoras eigenmanni* as valid species *incertae sedis* in Doradidae. Finally, Sabaj Pérez et al. (2007) described a new fossil species, †*Doras dioneae*, from the Late Miocene (ca. 8 Ma) Urumaco Formation, Falcón State, Venezuela.

Prior to this study, the two extant species of *Doras* were considered inhabitants of Atlantic coast drainages from the Essequibo River, Guyana, to Amapá State in northeastern Brazil, with possible records from the lower Amazon and lower Orinoco representing one or more undescribed species (Le Bail et al., 2000; Sabaj and Ferraris, 2003; Sabaj Pérez et al., 2007). Examination of additional museum specimens and recent expeditions to the upper rio Xingu funded by the All Catfish Species Inventory (http://silurus.acnatsci.org) confirmed the existence of three new species of *Doras* in the middle Amazon (Solimões/Negro) basin, lower Amazon basin, and rio Araguaia (Tocantins basin), respectively. Furthermore, specimens previously identified as *Doras carinatus* from the upper Caroní system (lower Orinoco basin) were confirmed as such.

In this paper we rediagnose and redescribe *Doras*, *D. carinatus* and *D. micropoeus*, and designate a neotype for *Silurus carinatus* Linnaeus 1766. We describe three new extant species, provide a key to extant species, define two species groups within extant *Doras*, and discuss the biogeography of the genus.

MATERIALS AND METHODS

Measurements were made to the nearest 0.01 mm using digital calipers; methodology follows Sabaj (2005) and Sabaj Pérez et al. (2007) with the following additions and exceptions: oblique head length = distance from snout tip to dorsal terminus of gill aperture; caudal peduncle length = horizontal midlateral distance from vertical through base of last anal-fin ray to posterior margin of hypural plates; dorsal spine length = distance from point on midlateral base of spine even with dorsal margin of body to distal bony tip; snout length = from tip of snout to anteriormost margin of eye; head width = distance between dorsal termini of gill apertures; nuchal shield width = minimum transverse width of nuchal shield (across middle nuchal plate); maxillary barbel length = from inferior base of barbel (where it meets labial tissue) to distal tip; outer mental barbel length = from base of outer mental barbel to distal tip. Standard length (SL) expressed in mm; other measurements expressed as percentages of standard length or, for subunits of head, oblique head length.

Fin-ray formulae reported with spines in upper case Roman numerals (dorsal-locking spinelet included), unbranched rays in lower case Roman numerals, and branched rays in Arabic numerals. Vertebral counts include all elements (1–6) of Weberian complex; compound preural + ural centra counted as one. Midlateral scute counts were taken on the left side of body (when possible) and begin with the infranuchal scute, connected dorsally to posterior nuchal plate and medially to first rib, borne on sixth vertebra (see Fig. 5). The nuchal shield is considered herein to be composed of the anterior, middle, and paired posterior nuchal plates (dermal bones) which are superficial expansions associated with the supraneural, and first and second pterygiophores (endochondral bones). Primitively in actinopterygians each pterygiophore has three separate radials: proximal, middle and distal. In most catfishes each pterygiophore is composed of fused bony proximal and middle radials, otherwise referred to as "proximal-middle radial" (Johnson and Patterson, 1993; Mooi, 1993), and the distal radial remains separate and cartilaginous. Descriptions of first gill arch use the following terms accordingly: preaxial face = side of arch facing laterally when relaxed *in situ*, postaxial face = side of arch facing medially, inner row = row on postaxial face closer to rakers, outer row = row on postaxial face closer to filaments.

Specimens are designated as alc (alcohol), sk (dry skeleton) and cs (cleared and stained) prepared according

to Taylor and Van Dyke (1985). Measurements recorded as standard length (SL) unless specified as total length (TL). Museum abbreviations follow Ferraris (2007); collection dates for 1908 expedition to Guyana led by Carl H. Eigenmann follow Hardman et al. (2002). See Sabaj Pérez et al. (2007) for doradid comparative material examined. Only extant species of *Doras* are described and redescribed herein; for complete description of fossil †*D. dioneae* see Sabaj Pérez et al. (2007). Species description is most thorough for *D. carinatus*; subsequent species descriptions refer to *D. carinatus* when morphology is similar.

Doras Lacepède, 1803

Doras Lacepède, 1803:116 [type species: *Silurus carinatus* Linnaeus, 1766, by subsequent designation of Bleeker, 1862:5]. Gender masculine.

Mormyrostoma Miranda Ribeiro, 1911:192 [type species: *Silurus carinatus* Linnaeus, 1766, by original designation and monotypy]. Gender neuter.

Mormyropsis Miranda Ribeiro, 1911:436 [type species: *Silurus carinatus* Linnaeus, 1766, by monotypy]. Gender feminine.

Diagnosis.—Doras are distinguished among Doradidae by a unique combination of three characteristics exhibited by the postcleithral process (from Sabaj Pérez et al., 2007:164): 1) process blade-like, subrectangular (truncated) with dorsal and ventral margins nearly parallel, posterior margin straight, weakly oblique (tilted anteriorly), and dorsal posterior corner distinct; 2) surface ornamentation separable into three longitudinal fields (dorsal, middle, ventral) with dorsal and middle fields nearly planar; and 3) middle field narrowly triangular with fine, elongate ridges and shallow grooves diverging gradually from point posterior to shoulder bulge to posterior margin of process (see Fig. 2). This diagnosis holds true for the three new species added here, although it is noted that, on rare occasion, the dorsal posterior corner of the postcleithral process is indistinct, broadly rounded in one, *D. phlyzakion*.

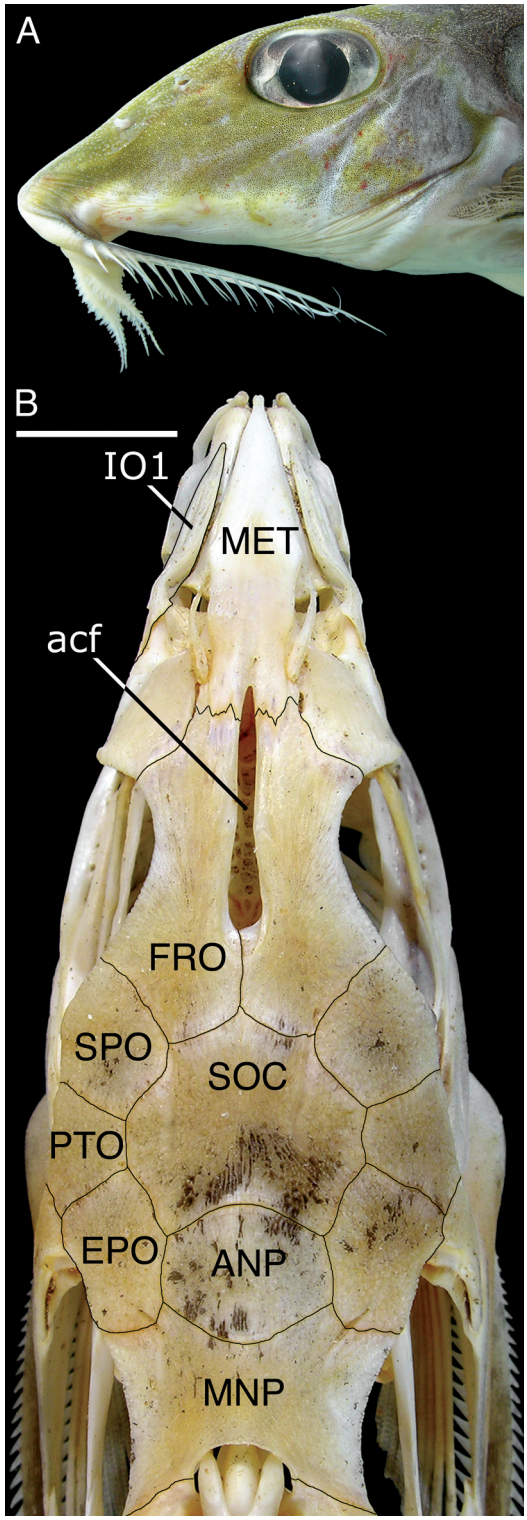

Fig. 1. Diagnostic features of extant *Doras*. A. Fimbriate maxillary barbels, exemplified by *D. carinatus*, ANSP 187114 (Neotype, 155 mm SL), Lawa River, Suriname, B. Dorsal view of head showing anteriorly pointed mesethmoid (MET), single anterior cranial fontanel (acf) contained within mesethmoid and frontals (FRO), anterior nuchal plate (ANP) wide, sharing suture with epioccipital (EPO) and nuchal foramina absent, exemplified by *D. micropoeus*, ANSP 187110 (205 mm SL), Lawa River, Suriname. IO1 first infraorbital (lacrimal), MNP middle nuchal plate, PTO pterotic, SOC supraoccipital, SPO sphenotic. Scale bar equals 1 cm. Photographs by M. Sabaj Pérez.

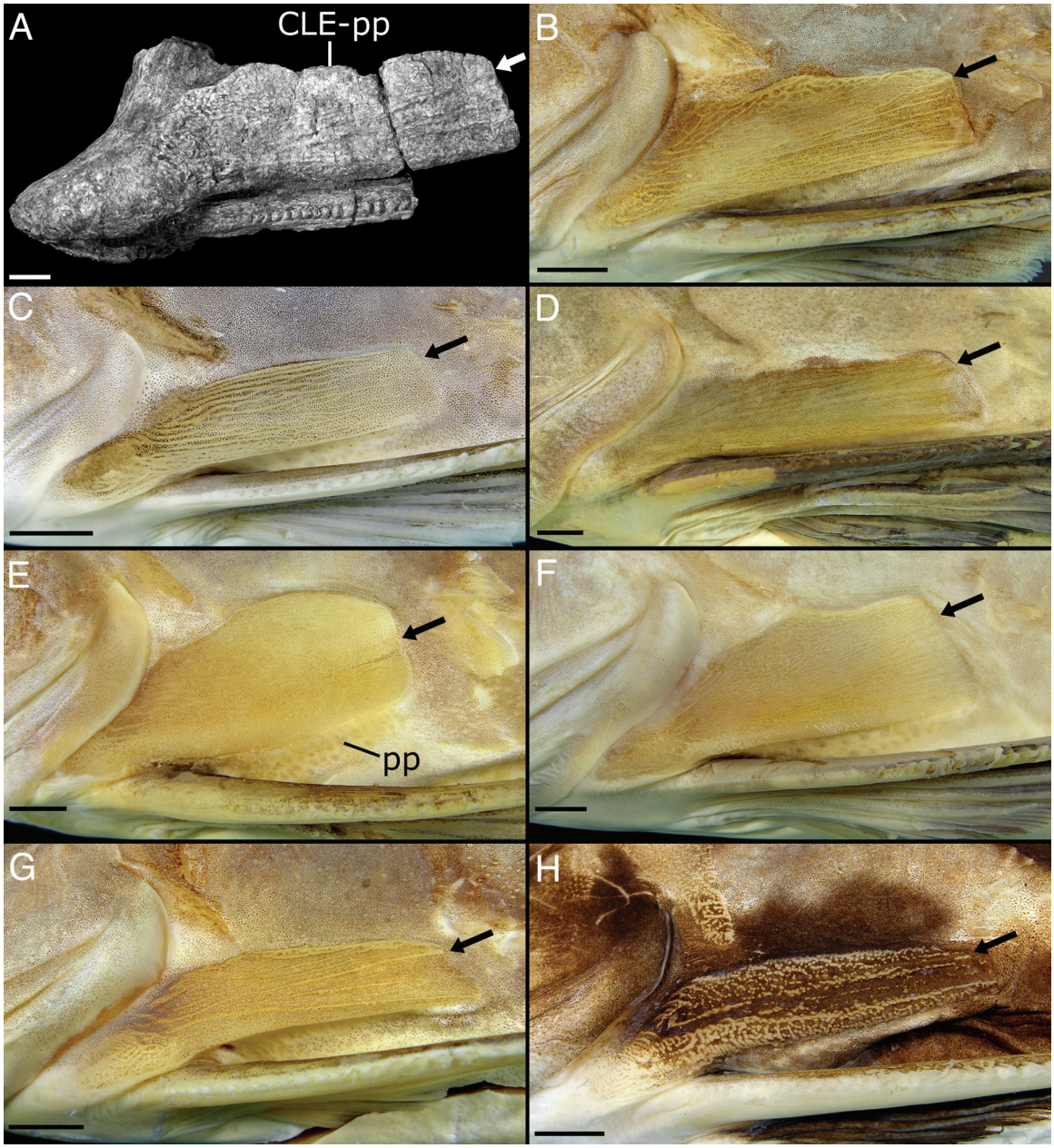

Fig. 2. Postcleithral processes (CLE-pp) and pectoral pores (pp) in *Doras*. A. †*D. dioneae*, UNEFM-PF-0411 (Holotype, TL 125.6 mm), Urumaco Formation, Venezuela, B. *D. carinatus*, ANSP 177275 (188 mm SL), Siparuni River, Guyana, C. *D. carinatus*, MHNG 2681.006 (154 mm SL), Oyapock River, French Guiana, D. *D. carinatus*, AMNH 96798 (302 mm SL), río Carapo, Venezuela, E. *D. higuchii*, ANSP 187491 (240 mm SL), rio Xingu, Brazil, F. *D. micropoeus*, ANSP 177880 (274 mm SL), Essequibo River, Guyana, G. *D. phlyzakion*, ANSP 181055 (148 mm SL), rio Tefé, Brazil, H. *D. zuanoni*, INPA 18628 (162.5 mm SL), rio Araguaia, Brazil. Arrows mark approximate boundary between dorsal and middle fields of ornamentation along posterior margin of process. Scale bars equal 5 mm. Photographs by K. Luckenbill (A) and M. Sabaj Pérez (B–H).

Table 1. Comparisons of postcleithral processes in adult *Doras*.

			Postcleithral process oblique length/depth		
Species	n	Range SL (mm)	Mean	Range	SD
D. higuchii (all)	8	153 - 240	2.22	1.80 - 2.49	0.22
Xingu	6	153 - 240	2.14	1.80 - 2.38	0.20
Trombetas	2	202 - 211	2.45	2.40 - 2.49	0.07
D. micropoeus	11	170 - 274	2.42	2.12 - 2.65	0.20
†*D. dioneae*	1	-	2.75	-	-
D. carinatus (all)	21	143.2 - 550	2.81	2.28 - 3.93	0.42
Corantijn/Essequibo	11	143.7 - 237	2.53	2.28 - 2.84	0.19
Maroni	4	143.2 - 170	2.80	2.61 - 3.00	0.16
Orinoco	3	302 - 550	3.29	2.85 - 3.93	0.57
Oyapock	3	154 - 196	3.36	3.21 - 3.48	0.14
D. phlyzakion	18	96 - 162.5	3.42	3.05 - 3.84	0.24
D. zuanoni	5	145.5 - 189.3	3.57	3.31 - 3.78	0.19

			Dorsal field ornamentation	
Species	Subrectangular shape	Free dorsal margin [“ ” = straight to weakly]	area relative to that of middle field	approx. participation in posterior margin
D. higuchii (all)	deep	“ ” convex	equal or slightly greater	one third to half
Xingu	deep	“ ” convex	equal or slightly greater	one third to half
Trombetas	deep	“ ” convex	about equal	one third to half
D. micropoeus	deep to moderate	“ ” concave	equal or slightly less	zero to one third
†*D. dioneae*	moderate	weakly concave	about equal	minimal (one tenth)
D. carinatus (all)	deep to shallow	“ ” concave	slightly less to slightly greater	zero to one third
Corantijn/ Essequibo	deep to moderate	“ ” concave	equal or slightly greater	zero to one third
Maroni	moderate	“ ” concave	about equal	zero to one third
Orinoco	moderate to shallow	“ ” concave	equal or slightly less	zero to one third
Oyapock	shallow	straight	about equal	zero to one third
D. phlyzakion	shallow	“ ” convex	equal or slightly less	zero to one third
D. zuanoni	shallow	“ ” concave	about equal	zero to one third

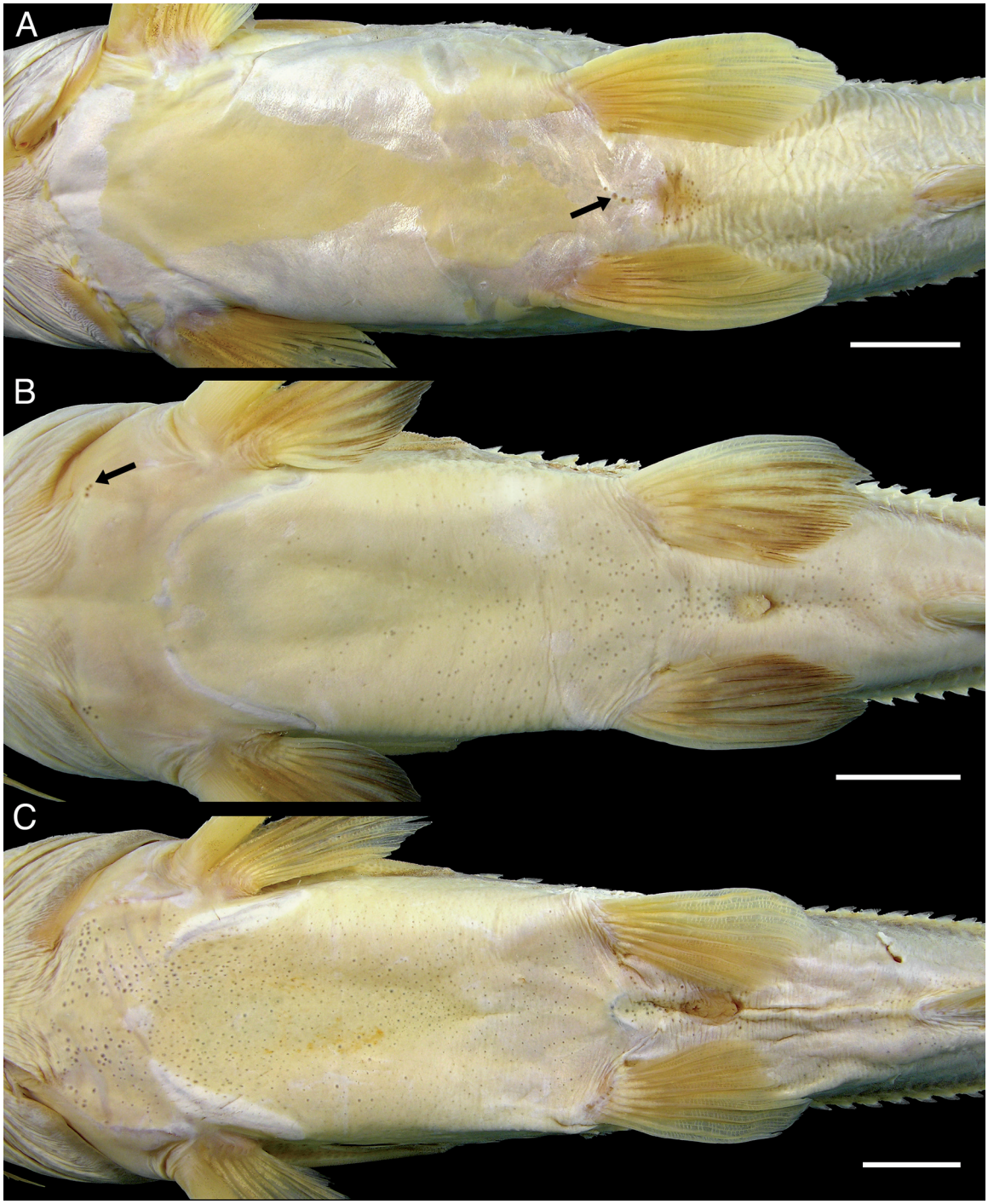

Fig. 3. Pore distribution on ventral surfaces in *Doras*. A. *D. higuchii*, INPA 4052 (153 mm SL), rio Xingu, Brazil, B. *D. zuanoni*, INPA 5244 (Holotype, 124 mm SL), rio Araguaia, Brazil, C. *D. phlyzakion*, ANSP 181055 (169 mm SL), rio Tefé, Brazil. Arrows mark individual pores. Scale bar equals 1 cm. Photographs by M. Sabaj Pérez.

The following unique combination of eight characteristics, indeterminate for the fossil species †*D. dioneae*, distinguish extant *Doras* among Doradidae: 1) maxillary barbels long and fimbriate, usually reaching ventralmost end of gill slit (Fig. 1A); 2) mesethmoid with anterolateral margins converging towards narrow tip (Fig. 1B); 3) single anterior cranial fontanel contained largely within frontals and anteriorly by mesethmoid (Fig. 1B); 4) anterior nuchal plate wide, pentaganol or roughly hexagonal, pointed posteriorly, and sharing broad lateral suture with epioccipital thereby isolating supraoccipital from middle nuchal plate (Fig. 1B); 5) nuchal foramina absent; 6) coracoid process short, not extending much beyond posterior insertion of pectoral fin with tip falling well short of tip of postcleithral process; 7) dentary typically with acicular teeth (edentate in one specimen of *D. zuanoni*); and 8) skin immediately ventral to postcleithral process perforated with many conspicuous pores (Figs. 2B–H).

Comparisons.—Fimbriate maxillary barbels (Fig. 1A) distinguish *Doras* from all other doradid genera except *Anduzedoras, Hassar, Hemidoras, Leptodoras, Nemadoras, Opsodoras* and *Trachydoras*. The wide anterior nuchal plate sharing suture with epioccipital and absence of nuchal foramina in *Doras* (Fig. 1B) distinguish it from *Anduzedoras, Hassar, Hemidoras, Nemadoras*, *Opsodoras*, and *Leptodoras* (except *L. copei* and *L. hasemani*, from which *Doras* is distinguished by lacking modifications of the oral hood; see Sabaj, 2005). The short coracoid process and presence of many conspicuous pores in skin immediately ventral to postcleithral process (Figs. 2B–H) distinguish *Doras* from three fimbriate-barbel species (*Doras fimbriatus, D. punctatus, Oxydoras eigenmanni*) that are *incertae sedis* in Doradidae (Sabaj and Ferraris, 2003). Porous skin ventral to the postcleithral process in *Doras* is a condition similarly found only in *Hassar, Nemadoras* (except *N. elongatus*), *Opsodoras ternetzi* and most *Trachydoras*.

Doras is clearly distinguished from *Trachydoras* by the shape of the mesethmoid. In *Doras* the anterolateral margins of the mesethmoid converge to a narrow and finely notched point that terminates well beyond the first infraorbitals (lacrimals; Fig. 1B). In *Trachydoras* the mesethmoid is broadly rounded and expanded by lateral cornua anteriorly, and its anteriormost margin is continuous with those of the first infraorbitals.

Description.—Extant species are medium-sized doradids (to about 550 mm SL) with moderately deep and weakly compressed head and body, relatively small and subterminal mouth, large dorsolateral eye, and conical snout that ranges from short and broad (*D. zuanoni*) to extremely long and tapered (*D. micropoeus*, sometimes *D. carinatus*). Ventral surface of head and body flattened from mouth to vent. Small pores often in skin surrounding vent and in some species (*D. phlyzakion*, *D. zuanoni*) also present on abdomen and breast (Fig. 3). First infraorbital (= lacrimal) variable (Fig. 4), either short, not extended anteriorly beyond concavity in medial margin for anterior naris (*D. phlyzakion*, *D. zuanoni*) or extended anteriorly well beyond concavity as long attenuate wing alongside autopalatine (*D. carinatus*, *D. higuchii*, *D. micropoeus*). Side of body with 30–36 midlateral scutes (hypertrophied lateral line ossicles beginning with infranuchal), except in specimens of *D. micropoeus* from Maroni basin wherein first 6-10 postinfranuchal scutes are lacking. Infranuchal scute (Fig. 5) tall; dorsal wing with long slender dorsal extension broadly contacting slender ventral extension of posterior nuchal plate; ventral wing shorter, lamellar, and broadly expanded anteriorly where it contacts or closely underlies distal margin of medial face of postcleithral process; medial thorn usually present and flanked by subtriangular, posteriorly pointed lamellar extensions (Figs. 5A–B) except in *D. micropoeus* medial thorn is absent or rudimentary and posterior expansions are lacking (Fig. 5C). All postinfranuchal scutes usually with medial thorn and subtriangular dorsal and ventral wings (Figs. 5A–B) except scutes progressively more reduced and sometimes lacking anteriorly in *D. micropoeus*. Total vertebrae 35–39. Centra 1–6 fused or deeply sutured into the Weberian complex with superficial ossification completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal. Fifth vertebra with or without parapophyses. Vertebrae 6–13 or 6–14 bearing 8 or 9 pairs of simple ribs, respectively; anterior ribs broadly overlapping posterior or posterodorsal side of parapophysis with head wrapping ventrally to ventral or ventroposterior attachment site. Caudal skeleton with hypural fusion pattern PH; HY 1+2; HY 3+4; HY 5 (see description of *D. carinatus* for more details on caudal skeleton). Gas bladder (Fig. 6) cordiform with broad anterior chamber contacting Müllerian rami of elastic-spring apparatus and slightly longer, narrower posterior chambers divided internally by T-shaped septum (Fig. 6A); posteriorly with singular terminal diverticulum (*D. carinatus*, *D. higuchii*, *D. micropoeus*; Figs. 6A–F) or paired diverticulae separate and subterminal (*D. phlyzakion*; Fig. 6G) or conjoined at their bases and terminal (*D. zuanoni*; Fig. 6H).

Distribution and habitat.—Extant species of *Doras* are known from major drainages along the Atlantic coast of the Guianas from the Essequibo to the Oyapock, middle Amazon drainages in northwestern Brazil (Solimões, Negro, Branco) and Colombia (Apaporis), lower Amazon drainages in northcentral Brazil (Trombetas, Jari, Xingu, Araguaia), and a right-bank tributary of the lower Orinoco

(Paragua–Caroní) in southeastern Venezuela (Fig. 7). *Doras* are notable for inhabiting both lowland floodplain lakes and waterways along the Solimões-Amazon River and its tributaries (e.g., *D. phlyzakion* and *D. zuanoni*) and sizeable upland rivers on the Guiana and Brazilian Shields (*D. carinatus*, *D. higuchii*, and *D. micropoeus*). *Doras* are conspicuously absent from deepwater trawls (i.e., Calhamazon Project collections) in both the main channels of the Amazon and lower courses of its major tributaries.

Etymology.—The origin of generic name *Doras* and henceforth the family Doradidae is oddly ambiguous. Lacepède's (1803:116) descriptions of *Doras* and its two nominal species, *D. carinatus* and *D. costatus*, did not specify a source. An etymology for "*doras*" is found, however, in Lacepède's treatment of *Corydoras*, a callichthyid genus that he newly proposed later in the same work. Lacepède (1803:148) explicitly noted the Greek "*Corys*" and "*doras*" to signify "casque" (helmet) and "cuirasse" (armor, with stem "cuir" meaning leather), respectively, in reference to the hard bony plates described separately for the head and body.

Transliterated Greek words that resemble *doras* and pertain specifically to armor are lacking. As a result subsequent ichthyologists have ventured to new meanings via quasi-*doras* transliterations of implicit Greek stems. Valenciennes (in Cuvier and Valenciennes, 1840:199 Strausbourg edition), for instance, stated without doubt that Lacepède's *Doras* was derived from the Greek "*dory*" meaning "lance". Miranda-Ribeiro (1911:199) later agreed. Jardine (in Schomburgk 1841:155–156) similarly speculated *Doras* to be from the Greek "*dorat*", a small spear, and commented on the spear-shaped postcleithral process in *P. costatus*, a structure noted by Lacepède (1803:118). Another possibility is the Greek *doris*, a sacrificial knife (Jaeger 1950:85). Alternatively, Ringuelet et al. (1967:283) interpreted *Doras* as "piel, pellejo [skin, hide]" from the Greek "*dora*" (Jaeger 1950:84).

Lacepède (1803:118–119) certainly appreciated the well-armed and armored nature his two species of *Doras*. He discussed at length the dangers that the serrated dorsal and pectoral-fin spines posed to fishermen as they removed this fish (presumably *costatus*, now in *Platydoras*) from their nets. He noted observations by Dutch naturalist Willem Pison that Brazilian fishermen believed the fin spines to be highly venomous, causing death in 24 hours unless treated with large quantities of its liver oil. Lacepède referred to the fin spines both as "dards" (meaning dart, sting or harpoon) and as "armes" (weapons) whose "dentelures" (serrations) were capable of making deep cuts in those who mishandled it.

One might consider the origin of *Doras* to be inspired by the catfishes' injurous armor, technically derived from the Greek *dora* for animal hide, and serendipitously akin to transliterated Greek words for spear (*dorat*, *doris*, *dory*) in reference to the so-shaped postcleithral process and serrated fin spines.

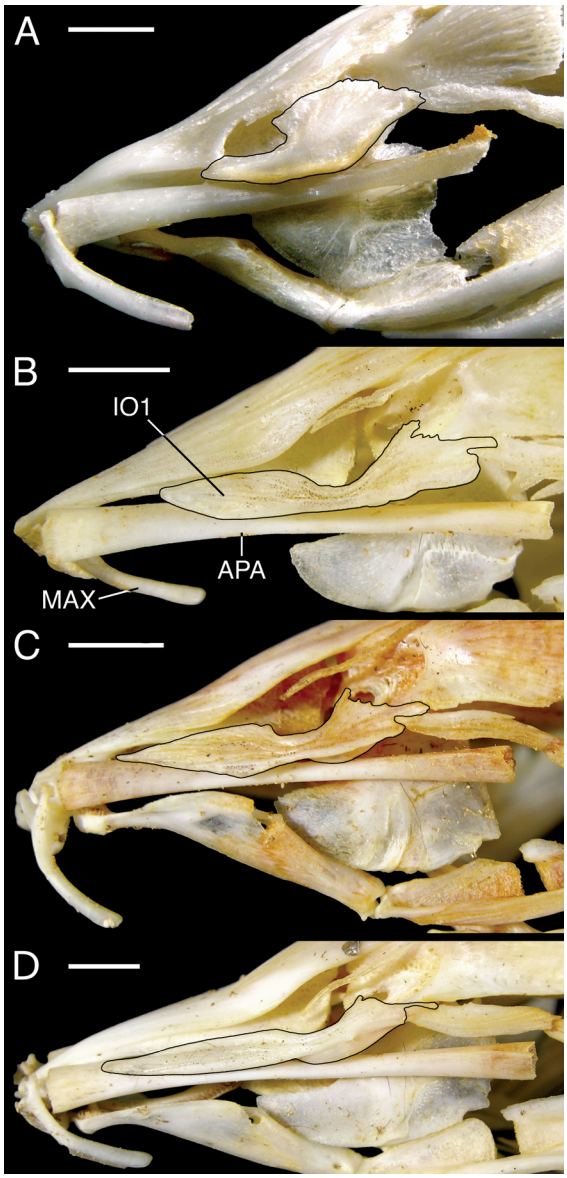

Fig. 4. First infraorbital (IO1) in *Doras* (sublateral views, scale bar equals 5 mm). A. *D. phlyzakion*, MZUSP 82294 (162 mm SL), rio Tefé, Brazil, B. *D. carinatus*, ANSP 180986 (170 mm SL), Essequibo River, Guyana, C. *D. carinatus*, ANSP 187399 (170 mm SL), Lawa River, Suriname, D. *D. micropoeus*, ANSP 187110 (205 mm SL), Lawa River, Suriname. APA autopalatine, MAX maxilla. Photos by J. Birindelli (A) and M. Sabaj Pérez (B–D).

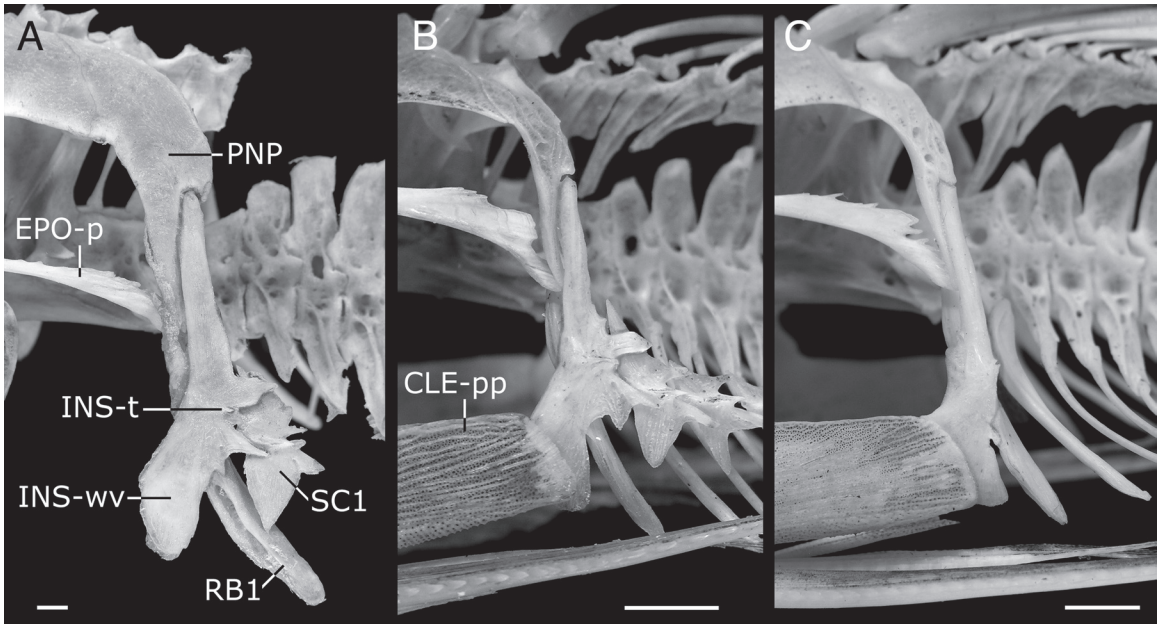

Fig. 5. Infranuchal scute (INS) in *Doras*. A. *D. carinatus*, ANSP 187157, río Carapo, Venezuela, B. *D. carinatus*, ANSP 187399 (170 mm SL), Lawa River, Suriname, C. *D. micropoeus*, ANSP 187110 (205 mm SL), Lawa River, Suriname. CLE-pp postcleithral process, EPO-p epioccipital posterior process, INS-t midlateral thorn on infranuchal scute, INS-wv ventral wing of infranuchal scute, PNP posterior nuchal plate, RB1 first rib, SC1 first postinfranuchal scute. Scale bar equals 5 mm. Photos by M. Sabaj Pérez.

***Doras carinatus* (Linnaeus, 1766)**
Figs. 1A, 2B–D, 4B–C, 5A–B, 6A–B, 7, 8, 9, 10A, 11
Tables 1 & 2

Silurus carinatus Linnaeus, 1766:504 [type locality: Surinami (= Suriname)].—Gmelin, 1789:1357 [Suriname].—Shaw, 1804:26 [Suriname].

Cataphractus carinatus.—Bloch and Schneider, 1801:108 [new generic assignment; Suriname].

Doras carinatus.—Lacepède, 1803:116 [assignment to new genus; common name; Suriname].—Cuvier and Valenciennes, 1840:214–216 [in part, description based on specimen from Cayenne and larger specimen from "Cabinet de Leyde", both assumed here not to be *Doras micropoeus*; not specimen figured in Pl. 442 as *Doras carinatus* and previously described as *Doras oxyrhynchus* Valenciennes in Humboldt and Valenciennes, 1821:184 (= *Anduzedoras oxyrhynchus*)].—? Müller and Troschel, 1849:629 [may include or alternatively be *Doras micropoeus*; Essequibo River, Guyana].—Bleeker, 1858:54 [in part, not *D. oxyrhynchus* in synonymy; Guiana].—Bleeker, 1862:5 [designation as type species of *Doras* Lacepède].—Bleeker, 1863a:11–13 [in part, not *D. oxyrhynchus* in synonymy].—Bleeker, 1863b:84 [identical to treatment in Bleeker 1862:5].—Bleeker, 1864:4, 31 [literature compilation, in part; not *D. oxyrhynchus* and *Doras* à carène in synonymy; description based on single Leiden specimen assumed here not to be *D. micropoeus*; Suriname].—Eigenmann, 1925:345, Pls. 1 (figs. 8, 9, 10), 2 (6), 20 (1, 2), 23 (4), 27 (8) [literature compilation, in part; not *D. oxyrhynchus* and *Oxydoras carinatus* Vaillant in synonymy; distinguished from *D. micropoeus* in key; annotated figures of gas bladder *in*/*ex situ* and bones of head and pectoral girdle; illustration of whole fish, lateral view].—Gosline, 1945:19 [checklist, in part; not *D. oxyrhynchus* in synonymy and not cited occurrence from Amazonas].—Van der Stigchel, 1947:94 [literature compilation, in part; not *D. oxyrhynchus* and *Oxydoras cariantus* Vaillant in synonymy; description of specimens from Suriname and Essequibo].—Fowler, 1951:487–488, fig. 508 [literature compilation, in part; not cited occurrence from Amazônia].—Burgess, 1989: 215, 223, 772 [checklist with figure reproduced from Fowler, 1951; Suriname].—Eschmeyer, 1990:130 [type species of *Doras* Lacepède].—Eschmeyer, 1998:330, 1922 [type catalog, type species of *Doras* Lacepède].—Le Bail, et al., 2000:36, 42–43 [compared to *D.* cf.

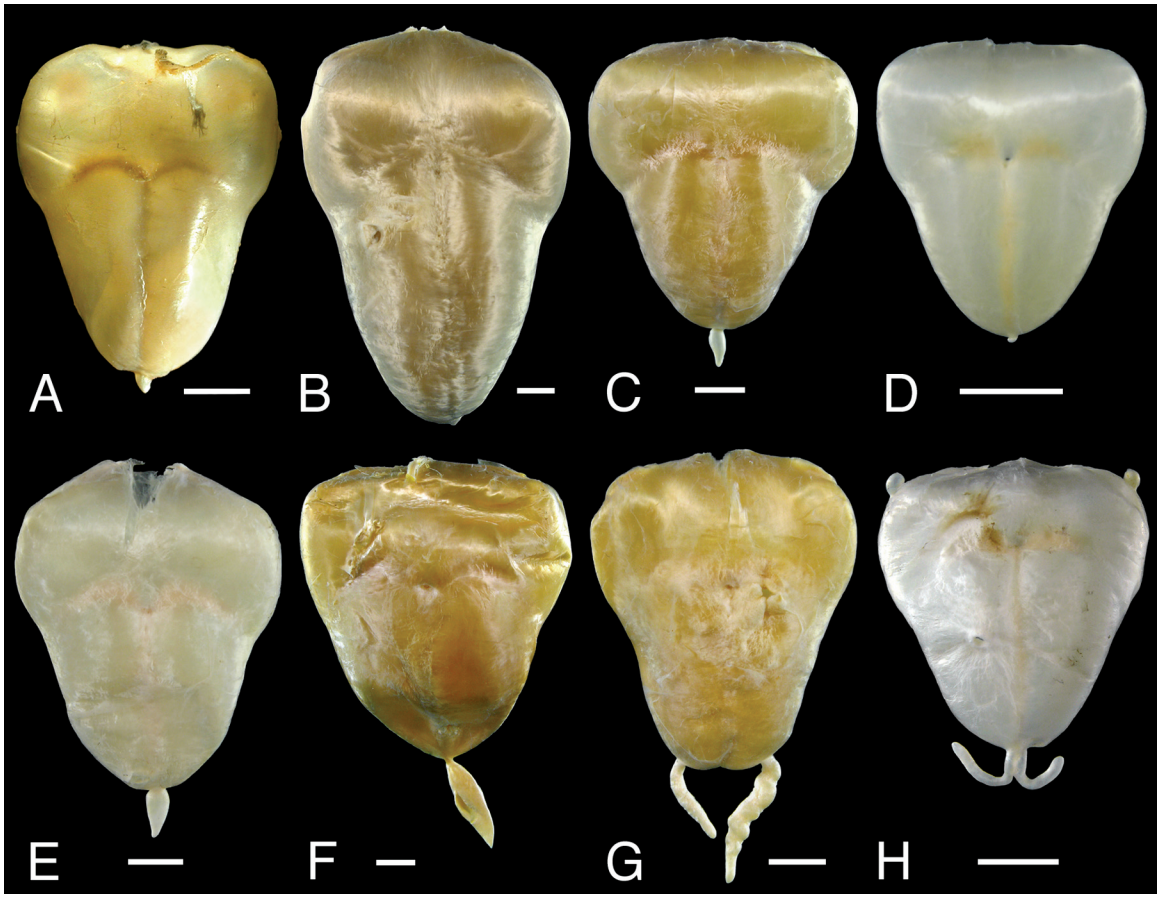

Fig. 6. Gas bladders in *Doras* (ventral views). A. *D. carinatus*, ANSP 177276 (124.5 mm SL), Yurrie Creek, Guyana, B. *D. carinatus*, AMNH 96798 (302 mm SL), río Carapo, Venezuela, C. *D. higuchii*, ANSP 181057 (160 mm SL), rio Xingu, Brazil, D. *D. higuchii*, INPA 5568 (83.8 mm SL), rio Trombetas, Brazil, E. *D. micropoeus*, ANSP 187110 (174 mm SL), Lawa River, Suriname, F. *D. micropoeus*, ANSP 178703 (222 mm SL), Essequibo River, Guyana, G. *D. phlyzakion*, ANSP 181055 (148 mm SL), rio Tefé, Brazil, H. *D. zuanoni*, MZUSP 96328 (96 mm SL), rio Araguaia, Brazil. Scale bar equals 5 mm. Photos by M. Sabaj Pérez (A–E,G–H) and T. Jones (F).

micropoeus in key; common names; description with figure of live specimen; distribution plotted in French Guiana; pectoral-fin spines emit sounds lasting 40–70 milliseconds at frequency 60–90 Hertz].—Hardman, et al., 2002:235 [distributional checklist, Essequibo and lower Potaro, Guyana].—Sabaj and Ferraris, 2003:460 [catalog; distribution in part; not cited form from lower Amazon; common names].—Akama in Buckup, et al., 2007:114 [checklist; distribution in part; not cited occurrence in lower Amazonas].—Ferraris, 2007:171 [type catalog].—Sabaj Pérez, et al., 2007:166, 186, 189, Figs. 3A,B [annotated figures of pectoral girdle; comparisons within *Doras*; coastal drainages of Guianas; material examined].—[Not of Valenciennes in Humboldt and Valenciennes, 1821:183–184 (= *Lithodoras dorsalis*)].

Mystus carinatus.—Swainson, 1839:305 [new generic assignment].

Doras (*Oxydoras*) *carinatus*.—Kner, 1855:144–146 [in part; not *D. oxyrhynchus* in synonymy; description in new subgenus based on specimen from Suriname; oral morphology compared to *Mormyrus*].

Oxydoras carinatus.—Günther, 1864:206 [literature compilation, in part; not *D. oxyrhynchus* in synonymy; new generic assignment, description based on specimens from Suriname and Essequibo assumed here not to include *D. micropoeus*].—[Not of Vaillant, 1880:154, based on specimens from Caldéron]

Hemidoras (*Hemidoras*) *carinatus*.—Eigenmann and Eigenmann, 1888:158 [in part; not *D. oxyrhynchus*

in synonymy; new generic and subgeneric assignment].—Eigenmann and Eigenmann, 1891:33 [in part; not cited occurrence from Caldéron and not *D. oxyrhynchus* in synonymy; Suriname, Cayenne, Essequibo].

Hemidoras carinatus.—Eigenmann and Eigenmann, 1890:252, 258 [key; literature compilation, in part; not *D. oxyrhynchus* and *Oxydoras carinatus* of Vaillant in synonymy; not cited occurrence from Caldéron; Guianas].—Eigenmann, 1910:394 [in part; not cited occurrence from Caldéron, not *D. oxyrhynchus* in synonymy; checklist, Guianas].—Eigenmann, 1912:194–195 [literature compilation, in part; not *Oxydoras carinatus* of Vaillant and *D. oxyrhynchus* in synonymy; description based on specimens from Essequibo and Potaro rivers and Georgetown market].—[Not of Steindachner, 1915:69–70, based on specimen from rio Negro likely to be *Anduzedoras oxyrhynchus*].

Mormyrostoma carinatum.—Miranda Ribeiro, 1911:192 [designation as type species of new genus *Mormyrostoma* Miranda Ribeiro; species description is translated quote from Kner, 1855].

Mormyropsis carinatum.—Miranda Ribeiro, 1911:436 [assignment to new genus; literature compilation, in part; not *D. oxyrhynchus* in synonymy].

Doras cariu.—Burgess, 1989: Pl. 99 (unnumbered fig.) [misspelling; figure of live specimen]

? *Anduzedoras microstomas*.—Ouboter and Mol, 1993:149 [distributional checklist, lower Corantijn and Kaburi Creek, Suriname; may include or alternatively be *D. micropoeus*].

Neotype.—ANSP 187114 (alc, 155 mm), Suriname: Sipalawini: Lawa River (Maroni Dr.), base camp ca. 8 km south-southwest of Anapaike/Kawemhakan (airstrip), 03°19'31"N, 054°03'48"W (SUR 07-01), M.H. Sabaj et al., 18 Apr 2007.

Non-type material.—**French Guiana:** Maroni Dr.: MHNG 2622.071 (3 alc, 114–142 mm), Inini River at confluence of small and large Inini rivers, Nov 1993; MHNG 2628.075 (4 alc, 41.4–68.8 mm), Tampoc River, Saut Pièrkuru, M. Jégu et al., 13 Oct 2000; MNHN 1998-1775 (1 alc, 184 mm), Tampoc River, St. Laurent du Maroni State, P.-Y. Le Bail & P. Keith, Nov 1998; MNHN 2000-4468 (3 alc, SL not recorded), Maroni River, Maripasoula, 15 Jun 1999; MNHN 2000-5863 (1 of 2 alc, SL not recorded), Tampoc River, Saut Pièrkuru (station niv1mar4), 02°49'N, 053°32'W, M. Jégu et al., 2000; Sinnamary Dr.: MNHN 1998-1820 (3 alc, 181-218 mm) Sinnamary River, 10 km in front of Sinnamary, Cayenne State, P.-Y. Le Bail, 25 May 1981; Oyapock Dr.: MNHN 1998-1693 (1 alc, 196 mm), Oyapock basin (station d), Cayenne State, P.-Y. Le Bail & P. Keith, 19 Oct 1986; MNHN 1981-0247 (2 alc, SL not recorded), Crique Pakoti, Cayenne State, Mr. Grenand, 11 Sep 1976; MNHN 1981-0257 (1 alc, SL not recorded), Oyapock River, Trois sauts, D'Aubenton et al., 3 Oct 1976; MHNG 2681.006 (1 alc, 154 mm), Oyapock River (main channel), downstream of Moulou Koulou creek, Camopi, Alicoto, 03°06'750"N, 052°20'463"W, R. Covain et al., 2006; MHNG 2681.071 (1 alc, 168 mm), Oyapock River (main channel), upstream of Fifine creek at Wacarayou rapids, 03°13'672"N, 052°17'577"W, R. Covain et al., 2006. **Guyana:** Essequibo Dr.: AMNH 7069 (3 alc, 72-136.5 mm), Essequibo River, Crabb Falls, C.H. Eigenmann, S.E. Shideler et al., 4–7 Nov 1908; AMNH 17632 (1 alc, 188 mm), upper Essequibo River, on or above cataract, Terry-Holden Expedition, 28 Dec 1937; AMNH 214981 (12 alc, 49.5-99.2 mm), Essequibo River, A.S. Pinkus, 1935; ANSP 175870 (1 alc, 65.9 mm), Essequibo River, sandbars in vicinity of Maipuri campsite, 04°34'17"N, 058°35'17"W (WGS97-28), W.G. Saul et al., 31 Jan 1997; ANSP 175871 (1 alc, 55.3 mm), Essequibo River at Essequibo campsite, 04°45'41"N, 058°45'53"W (WGS97-19), D. Torres et al., 26 Jan 1997; ANSP 175872 (4 alc, 42.9–52.3 mm), Essequibo River, sandbars in vicinity of Maipuri campsite, 04°34'17"N, 058°35'17"W (WGS97-31), W.G. Saul et al., 2 Feb 1997; ANSP 175873 (2 alc, 46–47.9 mm), Isolated stagnant pool/pond some 40 minutes from main Essequibo River channel, 04°32'43"N, 058°35'02"W (WGS97-27), W.G. Saul et al., 31 Jan 1997; ANSP 177272 (1 alc, 120.2 mm), Burro Burro River, creek tributary downstream from Burro Burro camp-between Lunch Spot and Water Dog Camp, 04°41'N, 058°51'W (GGW97-10), G. Watkins et al., 20 Nov 1997; ANSP 177273 (6 alc, 107.3–153.6 mm), Essequibo River, extensive sandbar 2.0 km upstream from Paddle Rock campsite, 04°42'20"N, 058°42'26"W (GGW97-23), C. Watson et al., 25 Nov 1997; ANSP 177274 (2 alc, 89.6–95.7 mm), Essequibo River, extensive sandbar 500m downstream from Paddle Rock campsite, 04°44'N, 058°43'W (GGW97-17), C. Watson et al., 23 Nov 1997; ANSP 177275 (1 alc, 188.0 mm), Siparuni River, Blackwater camp and blackwater creek, 04°44'21"N, 058°57'54"W (GGW97-27), G. Watkins et al., 4 Dec 1997; ANSP 177276 (17 alc, 82.1–196 mm), Essequibo River, Yurrie Creek approx. 2.0 km upstream from Paddle Rock campsite, 04°42'03"N, 058°42'44"W (GGW97-24A), C. Watson et al., 26 Nov 1997; ANSP 178704 (1 alc, 97.4 mm), Essequibo River, 180 yd. upstream from Essequibo campsite (Maipuri), 04°45'43"N, 058°45'52"W (WGS97-23), D. Allicock, 27 Jan 1997; ANSP 179619 (3 alc, 33.6–47.4 mm), Essequibo River (east bank) at Kurukupari, 04°39'41"N, 058°40'31"W (GUY 02-01), M.H. Sabaj et

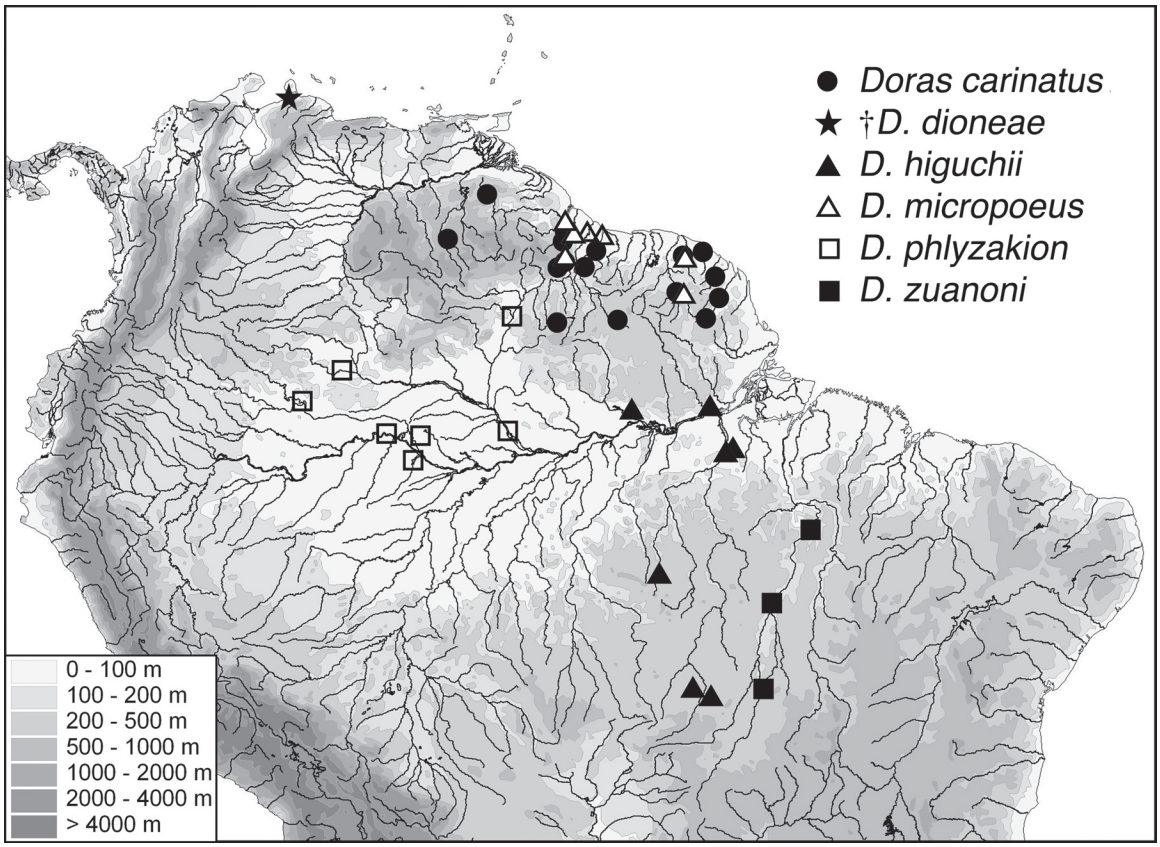

Fig. 7. Distribution of *Doras*. Base map provided by Conservation Science Program, World Wildlife Fund, US.

al., 24 Oct 2002; ANSP 180986 (1 sk, 170 mm), Essequibo River, Yukanopito Falls, 44.5 km SW of mouth of Kuyuwini River, 01°54'53"N, 058°31'14"W (GUY 03-19), M.H. Sabaj et al., 9 Nov 2003; ANSP 182334 (2 alc, 34.2–47.3 mm), Essequibo River, Kassi-Attae Rapids, 5.5 km SE of mouth of Kuyuwini River, 02°13'36"N, 058°17'38"W (GUY 03-15), M.H. Sabaj et al., 8 Nov 2003; ANSP 185199 (1 alc, 108.5 mm), Kuyuwini River, 60.6 km ENE of Kuyuwini Landing, 179 km SE of Lethem, 02°11'35"N, 058°42'15"W (GUY 03-11), M.H. Sabaj et al., 6 Nov 2003; ANSP 185200 (1 alc, 36.2 mm), Kuyuwini River, main channel and backwater 19.5 km W of confluence with Essequibo River, 02°14'28"N, 058°30'03"W (GUY 03-22), M.H. Sabaj et al., 11 Nov 2003; AUM 27845 (1 alc, 125.5 mm), Essequibo River, Rockstone, 05°59'07.5"N, 058°33'02.9"W (Guy 98-14), M.H. Sabaj et al., 19–20 Oct 1998; AUM 28013 (1 alc, 47.4 mm), Essequibo River, large sandbar & small cataract, 31.9 mi SSW Rockstone, bearing 204°, 05°31'39.5"N, 058°37'43.6"W (Guy 98-17), J.W. Armbruster et al., 21 Oct 1998; FMNH 53189 (1 alc, 74.7 mm), Bartica, C.H. Eigenmann et al., 1908; FMNH 53190 (10 alc, 57.5–194 mm), Rockstone, C.H. Eigenmann et al., 1908; FMNH 53191 (1 alc, 36.5 mm), 53734 (1 alc, 207.5 mm), Georgetown Market, C.H. Eigenmann et al., 1908; FMNH 53711 (72 alc), Potaro River at Tumatumari, C.H. Eigenmann et al., 1908; INHS 49235 (1 alc), Essequibo River, 0.72 mi SW Rockstone at sandbar, bearing 221°, 05°58'34.0"N, 58°33'19.3"W (Guy 98-11), M.H. Sabaj et al., 19 Oct 1998; INHS 49321 (2 alc, 141–152 mm), same data as AUM 27845; INHS 49359 (2 alc, 40.3–131.7 mm), same data as AUM 28013; INHS 49445 (43 alc, 31–43.2 mm), Potaro River, beach on N bank, downstream of Tumatumari Cataract, 05°21'48.4"N, 059°00'04.4"W (Guy 98-20), M.H. Sabaj et al., 22 Oct 1998; MZUSP 88605 (4 alc, 77.2–157.7 mm), same data as ANSP 177276; ROM 62641 (13 alc, 31.5–50.6 mm), Essequibo River, inlet and beach downstream from Kurupukari, 04°42'57"N, 058°42'40"W (H90-43), E. Holm et al., 10 Oct 1990; USNM 66201 (4 alc, 47.9–83.8 mm), same data as FMNH 53711; USNM 66202 (6 alc, 36.8–134.9 mm), Essequibo River at Crab Falls, C.H. Eigenmann et al., 1908. **Suriname:** Maroni Dr.: ANSP

187138 (1 alc, 100.5 mm), Litanie River at mouth and confluence with Marowini River, just upstream from settlement of Konya Kondre, 03°17'24"N, 054°04'38"W (SUR 07-05), M.H. Sabaj, J.G. Lundberg et al., 21 Apr 2007; ANSP 187139 (5 alc, 77.5–143.2 mm), Lawa River, large cataract complex in side channel west of base camp, ca. 8km SSW Anapaike, 03°19'52"N, 054°04'20"W (SUR 07-06), M.H. Sabaj et al., 21 Apr 2007; ANSP 187399 (1 alc, 147.5 mm; 1 sk 170 mm), same data as neotype; Corantijn Dr.: MHNG 2671.071 (2 alc, 143.7–198 mm), Corantijn River, downstream of Wonotobo Falls camp, J.I. Montoya-Burgos et al., 8 Nov 2005; MHNG 2672.075 (3 alc, 173–203 mm) Corantijn River, Wonotobo Falls near camp, J.I. Montoya-Burgos et al., 5 Nov 2005; MHNG 2699.048 (3 alc, 168–237 mm), Sipaliwini River, J. Mol et al., 2007; MZUSP 97654 (1 alc, 178 mm) same data as MHNG 2672.075; USNM 226185, 226187 (2 alc, 109.6–113.6 mm) Matappi Creek 05°01'N, 57°17'30"W, H.M. Madarie, 17 May 1980. **Venezuela:** Bolivar: Essequibo Dr.: INHS 31676 (1 alc, 194 mm), río Yuruari (rio Cuyuní Dr.), near La Pastora, W of Guasipati, (DCT 94-25), D.C. Taphorn et al., 10 Jan 1994; Caroní–Orinoco Dr.: AMNH 91129 (1 alc, 139.7 mm), río Lima, trib río Carapo, south face of Cerro Guaiquinima, 05°30'40"N, 63°30'40"W (CJF-90-02), C.J. Ferraris et al., 16 Feb 1990; AMNH 96798 (1 of 4 alc, 302 mm), río Carapo, trib. río Paragua, base camp, 05°30'40"N, 063°30'40"W (CJF-90-17), C.J. Ferraris & A. Machado-Allison, 24 Feb 1990; AMNH 91330SD (1 sk, ca. 550 mm), same data as AMNH 96798; ANSP 187157 (1 sk), río Carapo, trib. río Paragua, below closest set of rapids to mouth, a large caño on left bank (CJF-90-13), C.J. Ferraris & A. Machado-Allison, 24 Feb 1990.

Diagnosis.—Doras carinatus is diagnosed among extant congeners by the following combination of characteristics: midlateral scutes 33–36; total vertebrae 37–39; gas bladder with single posterior (terminal) diverticulum (Figs. 6A–B); teeth present on premaxilla; first infraorbital with elongate anterior wing extending well beyond medial concavity for anterior naris (Figs. 4B–C); ventral surface without conspicuous pores or with few small pores restricted to skin around vent; symphyseal limb of cleithrum with concave lateral margin; pectoral girdle truncated anteriorly with concave margin across symphysis; distal anterior margin of pectoral spine smooth; postinfranuchal midlateral scutes overlapping and of approximately uniform depth anterior to anal fin; infranuchal scute with medial thorn flanked by subtriangular wings (Figs. 5A–B); postcleithral process depth variable (2.28–3.93 times into oblique length) with straight to weakly concave free dorsal margin and dorsal field ornamentation moderately expanded, excluded from or forming less than one-third of posterior margin of process (Figs. 2B–D); skin covering dorsal-locking spinelet and base of dorsal spine moderately darkened by weak concentration of pigment with dorsal spine dusky or becoming gradually lighter distally (Figs. 8, 9); caudal fin uniformly dusky with scattered pigment (Figs. 8, 9).

Distinguished from fossil species †*D. dioneae* by combination of characteristics of pectoral girdle (see Figs. 2, 3B in Sabaj Pérez et al., 2007). Triangular ventral posterior process of cleithrum well developed with broad base and distal tip extending beyond articulation of anterior process of pectoral spine; thin anterior keel on ventral surface of coracoid strongly oblique, forming about 45° angle with transverse line through body; transition between medial margin of posterior coracoid keel (process) and transverse vertical wall of coracoid gradual and remote (displaced anteriorly and medially) from articulation with anterior process of pectoral spine; trench between anterior and posterior coracoid keels broad, width about equal to that of notch for pectoral-spine insertion.

Comparisons.—Doras phlyzakion and *D. zuanoni* have 30–32 midlateral scutes; 35 total vertebrae; gas bladder with two posterior diverticula (Figs. 6G–H); premaxilla edentate; first infraorbital relatively short, anterior tip extended short distance beyond medial concavity for anterior naris (Fig. 4A); ventral surface with many small pores in skin particularly on abdomen and near ventral insertion of gill flap (Figs. 3B–C); symphyseal limb of cleithrum with straight lateral margin; pectoral girdle truncated anteriorly with rounded (convex) margin across symphysis; and distal anterior margin of pectoral spine serrated. *Doras micropoeus* has postinfranuchal midlateral scutes distinct-ly increasing in separation and decreasing in depth anteriorly from above anal-fin origin; infranuchal scute lacking posteriorly pointed wings and with medial thorn absent or rudimentary (Fig. 5C). *Doras higuchii* has a deep post-cleithral process (depth 1.8–2.49 times into oblique length) with free dorsal margin straight to weakly convex, and dorsal field ornamentation broadly expanded, forming one-third to half of posterior margin (Fig. 2E); skin covering dorsal-locking spinelet and sometimes base of dorsal spine blackened by strong concentration of pigment and distal dorsal spine markedly lighter, pale (see Fig. 13); caudal fin with two dusky longitudinal stripes, one on ventral half of dorsal lobe and second on dorsal half of ventral lobe, particularly in juveniles (see Fig. 13A).

The fossil †*D. dioneae* has triangular ventral posterior process of cleithrum small, tip falling short of articulation of anterior process of pectoral spine; thin anterior keel on ventral surface of coracoid more transversely aligned, forming less than 45° angle with transverse line through body; medial margin of posterior coracoid keel distinctly arched and more proximal to articulation of anterior process of

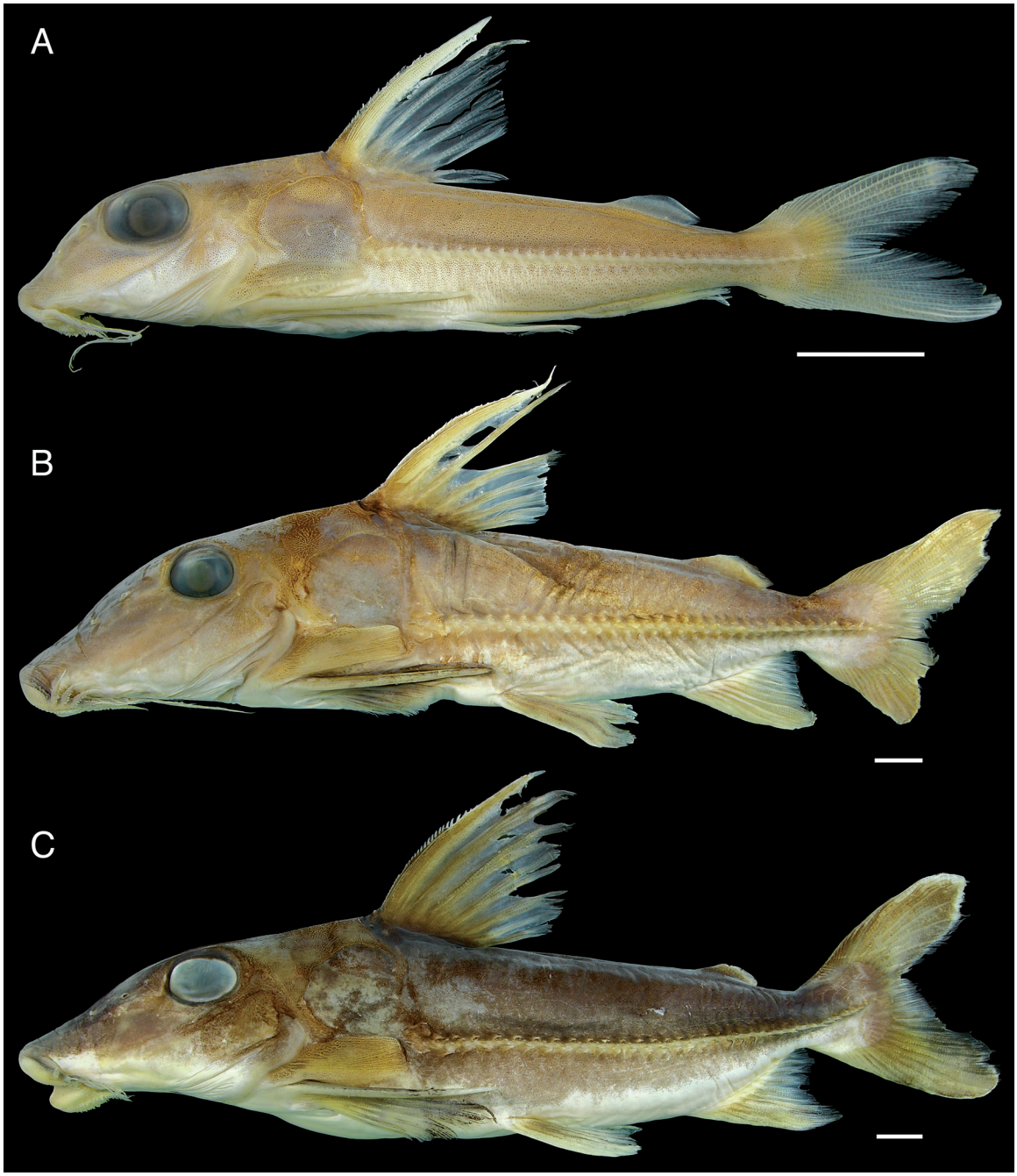

Fig. 8. *Doras carinatus*. A. ANSP 175870 (65.9 mm SL), Essequibo River, Guyana, B. ANSP 177275 (188 mm SL), Siparuni River, Guyana, C. MHNG 2671.071 (198 mm SL), Corantijn River, Suriname. Scale bar equals 1 cm. Photos by M. Sabaj Pérez.

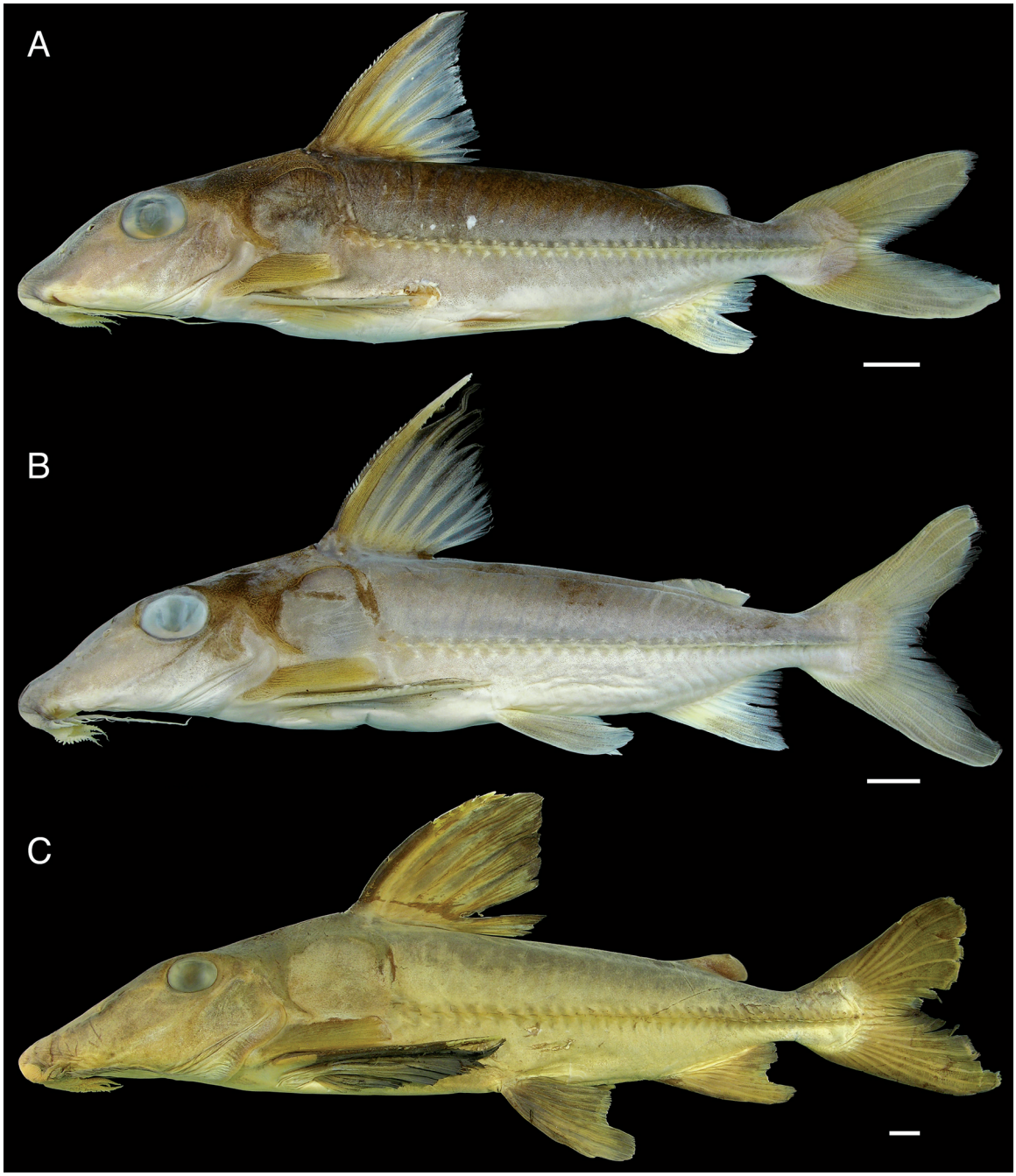

Fig. 9. *Doras carinatus*. A. ANSP 187114 (Neotype, 155 mm SL), Lawa River, Suriname, B. MHNG 2681.071 (168 mm SL), Oyapock River, French Guiana, C. AMNH 96798 (302 mm SL), río Carapo, Venezuela. Scale bar equals 1 cm. Photos by M. Sabaj Pérez.

Table 2. Morphometrics and meristics in *Doras carinatus*.

	Essequibo				Maroni
Measurements	n	Mean	Range	SD	Neotype
Standard Length (mm)	18	132.78	91.30 - 195.00		155
% in SL					
Predorsal distance	18	43.22	41.14 - 51.38	2.26	40.06
Prepectoral distance	18	29.64	27.53 - 31.90	1.22	28.19
Oblique head length	18	33.06	31.67 - 34.91	1.00	31.61
Body depth at dorsal-fin origin	18	23.23	22.08 - 24.89	0.69	21.42
Depth of caudal peduncle	18	6.21	5.57 - 6.97	0.38	6.06
Length of caudal peduncle	18	12.27	10.70 - 13.18	0.74	11.42
Length of postcleithral process	18	12.17	10.95 - 13.04	0.61	10.19
Dorsal-fin spine length	18	24.93	20.81 - 27.87	1.81	22.13
Pectoral-fin spine length	17	25.74	23.27 - 27.51	1.17	22.58
Anal-fin base length	18	12.91	11.67 - 13.94	0.76	12.52
Adipose-fin base length	18	10.63	8.98 - 12.37	0.98	9.42
Depth of tenth midlateral scute	18	4.20	3.37 - 4.92	0.45	1.94
% in Oblique Head Length					
Snout length	18	57.42	52.46 - 65.63	3.72	55.31
Horizontal eye diameter	18	27.78	22.19 - 31.06	2.54	26.53
Interorbital minimum width	18	15.09	12.46 - 18.28	1.53	16.33
Head width	18	51.32	47.44 - 55.81	2.07	47.76
Nuchal shield minimum width	18	22.84	16.92 - 25.78	1.96	22.24
Cleithral width	18	65.18	61.65 - 70.54	2.45	60.41
Maxillary barbel length	18	63.83	51.11 - 74.53	7.95	65.10
Outer mental barbel length	18	23.36	18.63 - 31.69	3.24	18.57
	Corantijn/Essequibo/Maroni/Orinoco				Maroni
Counts	n	Range	Mode		Neotype
Dorsal fin	30	II,6-7	II,6		II,6
Pectoral fin	30	I,8-11	I,9		I,9
Pelvic fin	30	i,6	-		i,6
Anal fin	30	iv-vi,8-11	v,10		iv,10
Caudal fin (dorsal/ventral)	30	i,7/8,i	-		i,7/8,i
Dorsal/ventral procurrent rays	29	13-16/12-16	15/14		14/14
Midlateral scutes	33	33-36	34		34

pectoral spine; and trench between anterior and posterior coracoid keels narrow, width less than 3/4 maximum width of notch.

Description.—Morphometrics and meristics summarized in Table 2; aspects of postcleithral process summarized in Table 1. Largest specimen examined ca. 550 mm SL. Head large, deep, weakly compressed with prominent conical snout. Body elongate, slightly compressed, deepest at dorsal-fin origin, gently tapering to short, slender caudal peduncle. Ventral surface flattened from snout to anal-fin origin. Dorsal profile straight to weakly concave from snout tip to between anterior and posterior nares, then curving gently (convex) to interorbital region and finishing straight, weakly oblique to dorsal-fin origin except in the two largest specimens examined (AMNH 91330SD, ca. 550 mm SL and ANSP 187157, ca. 500 mm SL), both as skeletons. In these large specimens the skull begins to rise more steeply at the middle pitline of the supraoccipital, elevating the nuchal region and imparting a shallow concavity to the dorsal profile from the interorbital region to the dorsal-fin origin. Eye large (22.19–31.06% of oblique head length), covered by thin skin (adipose eyelid not distinct), positioned high on head; dorsal margin of orbit concave in dorsal view (Fig. 1B); interorbital width relatively narrow (12.46–18.28% of oblique head length).

Mouth small, subterminal; gape with rounded anterior (premaxillary) margin, straight to weakly concave posterior (dentary) margin. Teeth present on dentary and usually premaxilla (only one in 19 specimens examined with premaxilla edentate). Premaxilla with 1–8 strong acicular teeth set close in one or two irregular rows (n = 18, 143.2–302 mm SL). Dentary with about 10–50 strong acicular teeth in a few rows or small patch.

First gill arch with 18–24 rakers (3–4 upper, 15–20 lower; n = 6, 128–302 mm SL), length of longest raker 5 to 8 times lateralmost width; medial edge of raker extended by soft fleshy flap fringed with 1–5 small papillae. Postaxial face and in most specimens preaxial face of first arch with soft fleshy lamellae and papillae (Fig. 10A); lamellae/papillae becoming more abundant and elaborate in larger individuals, and part of larger system of similar structures associated with remaining arches that carpets inner surfaces of pharyngeal cavity. Lamellae/papillae on postaxial face of first arch largely arranged into two rows between which a few solitary papillae may occur (Fig. 10A, right); inner row wide, occupying much of surface; outer row narrow, arising from skin along bases of filaments; both rows following entire length of arch or nearly so. Inner row with 11–14 wide lamellae oriented almost perpendicular to long axis of arch (appearing as distinctly spaced oblique columns); lamellar margin deeply lobed and/or fringed with papillae. Outer row with 22–29 smaller papillae either short, elongate (fingerlike or leaf-like), or distally expanded and multi-lobed. Prominent lamellae/papillae in inner and outer rows loosely aligned, but not regularly aligned with rakers. Preaxial face of first arch smooth (Fig. 10A, left) or with single row of 3–20 small, short to elongate papillae arising from skin along bases of filaments, particularly those along lower arch near axil.

Anterior and posterior nares separate, each surrounded by short tubular skin; posterior naris larger than anterior one, located approximately at midpoint between anterior naris and anterior margin of eye; anterior naris closer to posterior naris than snout tip. Cephalic shield weakly ornamented, usually with distinct middorsal groove extending from middle pitline of supraoccipital to about suture between anterior and middle nuchal plates, sometimes extending onto middle nuchal plate. Cranial fontanel with single opening anterior to epiphyseal bar (posterior cranial fontanel occluded). Fontanel elongate, narrow, widest with rounded margin posteriorly, attenuate anteriorly; enclosed posteriorly and laterally by frontals, anteriorly by mesethmoid. Nuchal foramina absent. Nuchal shield roof-shaped, forming transverse angle. Anterior nuchal plate well-developed, pentagonal to hexagonal, wider than long and usually sharing broad lateral suture with epioccipital. Mesethmoid elongate, shaped like a fountain pen nib, attenuate anteriorly with acutely pointed tip. First infraorbital elongate with long tapered anterior wing extending well beyond medial concavity for anterior naris (Figs. 4B–C). Epioccipital posterior process long, contacting posterior nuchal plate; ribbon-like, twisted from horizontal plane (anteriorly) to vertical plane (posteriorly); vertically expanded, often weakly bifid posteriorly (Figs. 5A–B).

Three pairs of barbels (Fig. 1A). Maxillary barbel long, tip often reaching beyond medialmost end of gill opening; fimbriate with about 15-18 fimbriae along lateral margin; proximal fimbriae rugose with papillae and secondary fimbriae along trailing margin. Mental barbels nearly equal in size, reaching to about halfway between anterior margin of lower jaw and medialmost extent of gill opening; bases thick, profusely ornamented with fleshy papillae. Lips fleshy, surfaces with low rounded papillae near insertion of maxillary barbels.

Pectoral girdle in ventral view subtriangular, elongated with medially convergent lateral margins of symphyseal (horizontal) limbs of cleithrum long, concave; truncated anteriorly with with concave margin across symphysis. Transverse limb of coracoid with distinct posterior process (keel) relatively short, extending slightly beyond posterior insertion of pectoral fin and falling well short of posterior tip of postcleithral process. Ventral surfaces of pectoral girdle (including posterior processes of coracoid) covered with skin (not externally visible).

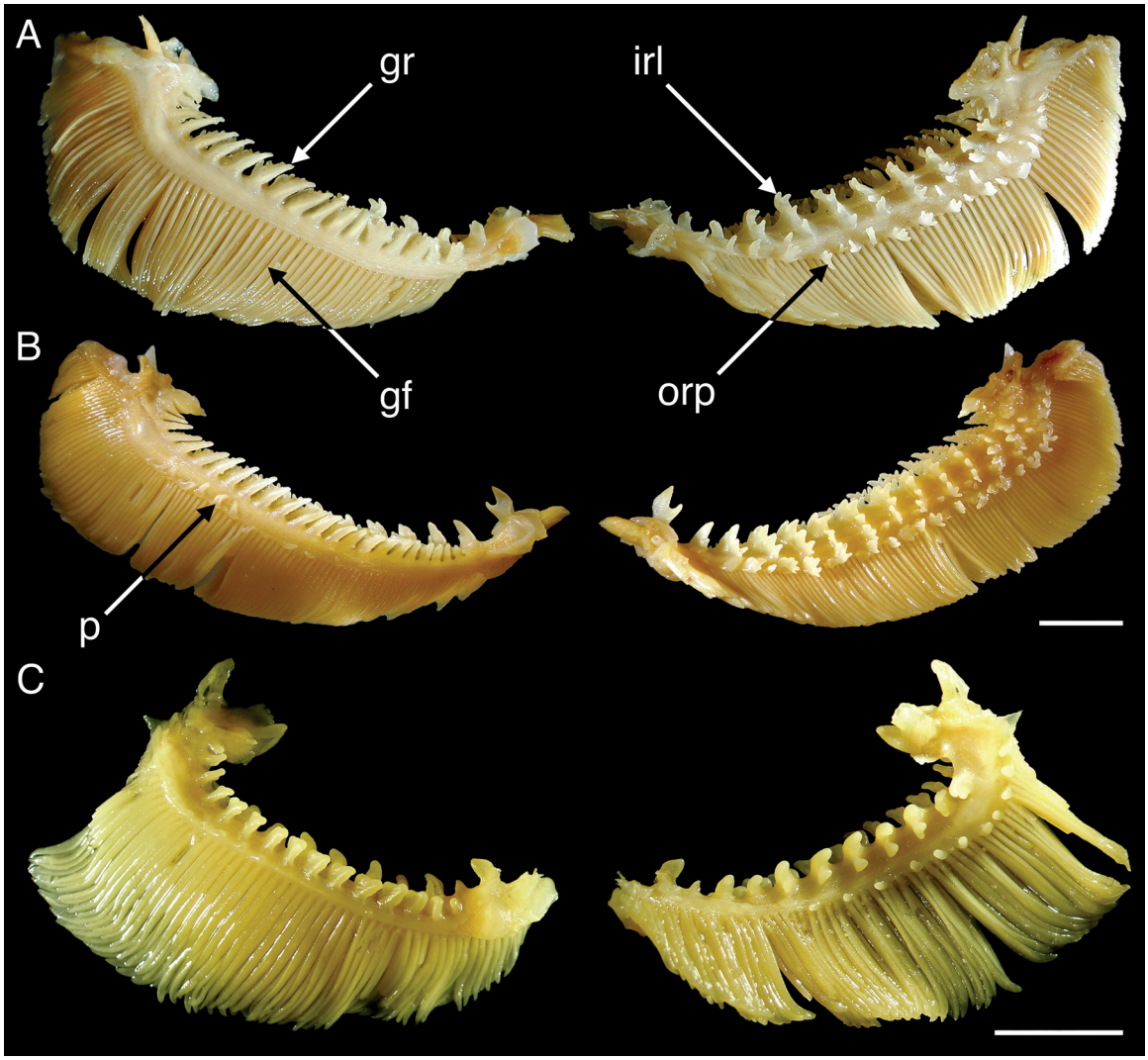

Fig. 10. Preaxial (left) and postaxial (right) faces of first gill arch in *Doras*. A. *D. carinatus*, ANSP 177276 (197 mm SL), Yurrie Creek, Guyana, B. *D. micropoeus*, INPA 28898 (194 mm SL), Essequibo River, Guyana, C. *D. zuanoni*, INPA 5244 (Holotype, 124 mm SL), rio Araguaia, Brazil. gf gill filament, gr gill raker, irl inner row lamellae, orp outer row papillae, p papillae. Scale bar equals 5 mm (same for A and B). Photos by M. Sabaj Pérez.

Postcleithral process variable in shape (Figs. 2B–D), moderately to deeply subrectangular (depth 2.28–3 times into oblique length) in adult specimens from Essequibo, Corantijn and Maroni basins vs. moderately to shallowly subrectangular (depth 2.85–3.93 times into oblique length) in adults from Orinoco and Oyapock basins (Table 1); all margins entire, without conspicuous dentations; free dorsal margin (posterior to posttemporal-supracleithrum) always straight (Oyapock specimens) or straight to weakly concave (remaining specimens); ventral margin nearly straight from shoulder to ventral posterior corner of process; posterior margin straight, weakly oblique, tilted anteriorly. Entire postcleithral process laterally compressed, thickness nearly uniform (i.e., blade-like), without distinct longitudinal swelling or thickening along medial face.

Lateral surface of postcleithral process ornamented with low, narrow ridges and shallow grooves; pattern of ornamentation separable into three longitudinal fields (dorsal, middle, and ventral) with the dorsal and middle fields occupying approximately equal areas (Figs. 2B–D). Dorsal

field widest anteriorly, tapering posteriorly to dorsal posterior corner, excluded from or forming less than one third of posterior margin of process; surface with network of fine ridges best developed on dorsal anterior portion. Middle field narrowly triangular (expanded posteriorly); surface with elongate longitudinal ridges and grooves, all of which diverge gradually from point posterior to shoulder bulge to posterior margin of process; dorsalmost ridge finishes at or slightly below dorsal posterior corner of process and ventralmost ridge finishes at ventral posterior corner. Ventral field very narrow, tapering posteriorly to ventral posterior corner; surface with network of fine ridges. Dorsal and middle fields planar; ventral field sloping medially.

Skin relatively smooth except for extremely minute punctate tubercles scattered on head, body and fins, particularly on gill covers and dorsal surfaces of head. Elongate slit-like pore in axilla of pectoral fin. Skin immediately ventral to entire length of postcleithral process perforated with numerous small round pores imparting sponge-like appearance (Figs. 2B–C). Smaller pores also present in skin surrounding anteriormost scutes, usually just posterior to medial thorn. Conspicuous pores absent from skin on ventral surfaces or restricted to skin immediately surrounding vent.

Dorsal fin II,6 (n = 27), rarely II,7 (3); pectoral fin modally I,9, range I,8–11 (30); pelvic fin i,6 (30), anal fin modally v,10, range iv–vi,8–11 (30); caudal fin i,7/8,i (30) with dorsal procurrent rays modally 15, range 13–16 (29) and ventral procurrent rays modally 14, range 12–16 (29). Dorsal-fin origin located about one-third SL from snout tip. Dorsal-fin spine long, compressed, gently curved basally, becoming straight distally; ossified tip sharply pointed. Dorsal spine with distinct antrorse serrations along basal four-fifths of anterior margin, distal one-fifth smooth; serrations small and crowded basally, becoming slightly larger and more separated towards middle of spine; posterior margin with serrations along distal half nearly to tip, serrations smaller and more separated than those along anterior margin, proximal serrations weakly antrorse, distal serrations erect to weakly retrorse. Adipose fin teardrop shaped with distal free margin rounded; base not continued anteriorly as fleshy keel; origin approximately at vertical through anal-fin origin. Pectoral-fin spine strong, dorsoventrally flattened, gently curved and tapering to sharp point; length about equal to that of dorsal spine. Anterior margin of pectoral spine with moderate antrorse serrations; serrations small and crowded basally, becoming larger and more separated towards middle, typically absent from distalmost tip; posterior margin with moderate retrorse serrations along entire margin; serrations slightly larger and more separated than those along anterior margin and becoming gradually more separated and larger towards middle. Pelvic fin subtriangular, tip rounded and distal margin relatively straight when extended; origin near vertical through adpressed tip of pectoral spine and posterior to midpoint of standard length. Anal fin large, triangular with extended distal margin straight to weakly concave. Caudal fin distinctly forked with somewhat rounded lobes; ventral lobe slightly larger and more broadly rounded than dorsal. Dorsal and ventral procurrent caudal-fin rays like those of caudal fin, not modified into plates.

Neural and hemal arches on penultimate centrum (PU2) with paired triangular prezygopophyses (Fig. 11). Last hemal spine singular; proximal portion with central thickening expanded anteroventrally and posterodorsally by thinner, blade-like keels, the former longer and wider, sometimes continuing for entire length of spine; anteroventral margin of spine contacting hemal spine on antepenultimate centrum (PU3) in larger specimens (SL ≥ 170 mm); posterodorsal margin of spine free from parhypural (97 mm SL) or contacting parhypural proximally and distally

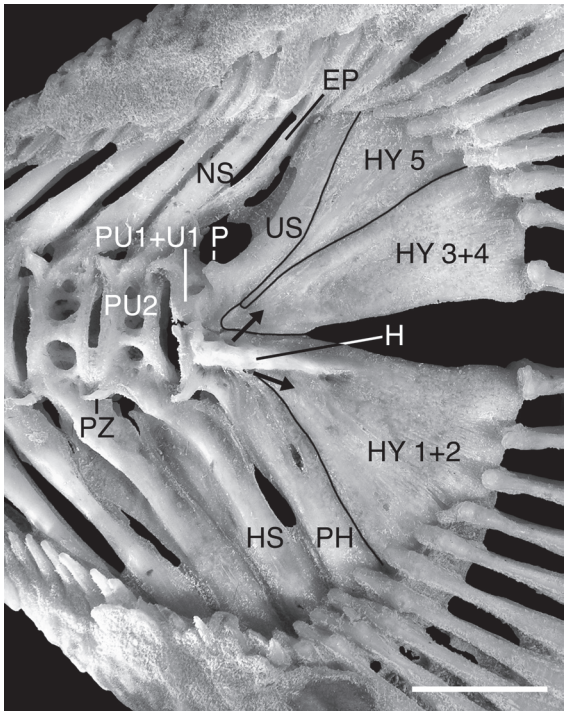

Fig. 11. Caudal skeleton (left side) in *Doras carinatus*, AMNH 91330 (ca. 550 mm SL), río Carapo, Venezuela. EP epural, H hypurapophysis, HS last hemal spine, HY hypural, NS last neural spine, P prezygopophysis-like process, PH parhypural, PU1+U1 fused first preural and first ural centra, PU2 second preural centra, PZ ventral prezygopophysis on penultimate hemal arch, US urostyle. Arrows mark exits for dorsal and ventral branches of caudal blood vessels. Scale bar equals 1 cm. Photos by M. Sabaj Pérez.

aside lenticular gap. First Preural (PU1) and first ural (U1) centra presumably fused into compound centrum, no evidence of second ural centrum (completely fused with base of hypural 3+4). PU1 portion of compound centrum fused to nearly complete neural arch; base of each side of arch square with distal posterior corner drawn out into narrower rectangular extension directed dorsoposteriorly towards, and weakly contacting base of single epural, and distal anterior corner drawn out into small triangular prezygopophysis directed dorsoanteriorly in larger specimens (SL ≥ 170 mm). Last hemal arch formed by base of parhypural and fused to PU1 portion of compound centrum; ventral anterior margin of arch drawn out into small triangular prezygopophysis pointed anteriorly or ventroanteriorly.

Hypural fusion pattern PH; HY 1+2; HY 3+4; HY 5 (Fig. 11). Parhypural spine rectangular; proximal portion expanded by thin, narrow blade-like keel that is drawn out into small triangular point above arch in smaller cs specimen (97 mm SL); distal half of spine thicker, more plate-like. Hypural 1+2 fused to compound centrum, triangular, plate-like and relatively thick except for thinner ventral proximal portion contacting base of parhypural in smaller specimens (SL ≤ 170 mm). Hypural 3+4 slightly smaller and triangular, platelike, not fused to compound centrum. Hypural 5 smallest, narrowly triangular, platelike. Parhypural spine contacting hypural 1+2 for entire length (hairline gap separates ossified portions of bones in cs specimen); hypural 1+2 separated from 3+4 by relatively wide V-shaped notch except for proximal contact for 1/4 or less of length; ventroposterior margin of hypural 5 completely abuts hypural 3+4, dorsoanterior margin largely contained in shallow groove between fused paired elements of urostyle. Hypurapophyses Type C (sensu Lundberg and Baskin, 1969:15); primary hypurapophysis shifted dorsally onto PU1 portion of compound centrum and laterally continuous with secondary hypurapophyses forming distinct horizontal shelf that is widest anteriorly, attenuated posteriorly, and runs just ventral to dorsal margin of hypural 1+2, finishing near its midlength. Caudal blood vessels exiting parhypural hemal arch via two separate foramina on each side, larger one opening dorsally from anterior base of hypurapophyseal shelf and second smaller one opening ventrally below shelf near proximal contact between spinous portions of parhypural and hypural 1+2. Urostyle of largest specimen (ca. 550 mm SL) with pair of small processes, one on each side near its anterior base; processes similar in appearance to prezygopophyses on last neural arch.

Total vertebrae 37 (n = 2) or 39 (1). Centra 1–6 fused into Weberian complex with superficial ossification completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal. Vertebra five with pair of slender parapophyses directed posterolaterally. Vertebrae 6–13 bearing 8 pairs of simple ribs.

Lateral line surrounded by complete series of 33–36 midlateral bony scutes per side (modally 34; n = 33) beginning with infranuchal. Lateral line in tympanal region (from posttemporal-supracleithrum to infranuchal scute, between nuchal shield and postcleithral process) without emergent scutes but partially enclosed by three separate canal-like ossifications of decreasing length posteriorly and covered with thin skin. Infranuchal scute tall, contacting posterior nuchal plate dorsally and first rib (borne on sixth vertebra) medially; ventral anterior expansion strongly contacting medial surface of distal postcleithral process; retrorse medial thorn flanked by subtriangular, posteriorly pointed wing-like extensions (Figs. 5A–B). Postinfranuchal scutes oblique and weakly overlapping, depth uniform to anal-fin origin. Scute depth at pelvic-fin origin about one-fifth to one-eighth of corresponding body depth. Each postinfranuchal scute with distinct medial thorn, and subtriangular dorsal and ventral wings with posterior margin entire or with a few serrations; dorsal wing slightly smaller and drawn out into anterodorsal and posterior points; ventral wing drawn out into ventral and posterior points. First postinfranuchal midlateral scute with dorsal wing underlying that of infranuchal scute.

Gas bladder large, occupying most of dorsal portion of visceral cavity; shape cordiform with paired posterior chambers longer than single anterior chamber; walls smooth except for small (sometimes rudimentary), singular, posteriormost (= terminal) diverticulum. Terminal diverticulum asymmetric, formed by expansion of only one of the two posterior chambers and without internal septa (Figs. 6A–B).

Coloration.—In alcohol dorsal and dorsolateral surfaces of head and body uniform gray to tan ground color (tinted olive in life); side of body becoming gradually lighter ventrally from midlateral scutes; lowermost side and ventral surfaces pale, white (Figs. 8, 9). Maxillary barbel gray to tan; mental barbels pale, white. Fins without distinct marks, tinted yellow-olive in life. Skin around dorsal-locking spinelet and base of dorsal spine moderately darkened by weak concentration of pigment; remaining dorsal spine dusky or becoming gradually lighter distally; bases of rays and membranes dusky, becoming gradually clear distally. Paired, anal and caudal fins more or less uniformly dusky with pigment scattered on spines, rays and membranes. Live specimen figured in Le Bail et al. (2000:43).

Distribution and habitat.—*Doras carinatus* occurs in rivers draining the northern side of Guiana Shield in Brazil (Amapá State), French Guiana, Suriname, Guyana and

Venezuela (Fig. 7). From east to west it is known from the Oyapock, Approuague, Sinnamary, Mana, Maroni, Corantijn, Essequibo (including the Cuyuní), and Paragua (Caroní-Orinoco Dr.) basins (includes records reported by Le Bail et al., 2000:43). In the Essequibo basin, Guyana, *D. carinatus* was collected in the main channels of medium to large rivers over substrates of sand or gravel and often in moderately clear water and swift currents associated with cataracts. *Doras carinatus* is syntopic with *D. micropoeus* in the lower Essequibo and upper Maroni basins and likely elsewhere.

Reproduction.—Two females, ANSP 187399 (170 mm) and ANSP 187139 (143.5 mm), swollen with mature eggs, were collected in mid-April (highwater season) in the upper Lawa River, a large tributary of Maroni, Suriname. The larger female was collected in a gill net set in the main channel and the smaller one was collected closer to shore (depth <1.5 m) at night over sand in moderately swift water below a large cataract. *Doras carinatus* is likely a non-guarding open substrate spawner in the lithophilous guild of Kryzhanovsky (1949) and Balon (1975). Diameter of eggs about 1 mm after fixation in formalin and storage in 70% ethanol.

Etymology.—Species named for spines on midlateral scutes based on Linnaeus' (1766:504) reference to "*Linea lateralis subserrata & carinata spinis, ut in Scombris*". Evidently, the scutes in *D. carinatus* reminded Linnaeus of the longitudinal keels in "*Scombris*", presumably *Scomber scombrus* Linnaeus 1758, the Atlantic mackerel.

Remarks.—Linnaeus (1766:504) specified the habitat (= type locality) of *D. carinatus* as "Surinami" (Suriname) and in his brief description noted "*…linea laterali spinosa, cirris 6 pinnatis*", essentially diagnosing a doradid with fimbriate barbels. *Doras carinatus* and *D. micropoeus* are the only fimbriate-barbel doradids known from Suriname where they occur sympatrically in the Corantijn and Maroni basins (Le Bail et al., 2000; pers. obs.). Linnaeus' description of *Silurus carinatus* applies equally well to both species. Early references to the Linnaean species, often as "Silure", "Doras", or "carené", by Bonnaterre (1788:153), Bloch and Schneider (1801:108), and Lacepède (1803:117) provide no clues to its identity. Valenciennes (in Cuvier and Valenciennes, 1840) confused the issue as his description (at least in part) and certainly his illustration (Plate 442) of *D. carinatus* was based on the holotype of *Doras oxyrhynchus*, a valid species currently in *Anduzedoras* (Sabaj and Ferraris, 2003). Eigenmann (1912) effectively established the identity of the Linnaean species by providing an illustration and brief redescription of *S. carinatus* in the genus *Hemidoras*, and naming a new species *H. micropoeus* which he distinguished by having midlateral scutes "from ventrals forward rudimentary" vs. "nearly equally well-developed along entire length" in *H. carinatus*. Eigenmann did not examine types of *S. carinatus*; the basis for his assignment of the Linnaean name was unstated and presumably by convention or nonexistent.

The International Code of Zoological Nomenclature (ICZN, 4th Edition, on-line) permits the designation of a neotype under a number of qualifying conditions "when no name-bearing type specimen…is believed to be extant and an author considers that a name-bearing type is necessary to define the nominal taxon objectively". The exceptional need for a neotype designation for *S. carinatus* Linneaus 1766 with respect to the qualifying conditions (Articles 75.3.1–7) is expressed as follows. *Silurus carinatus* cannot be precisely identified from among two distinct nominal species of *Doras* that occur syntopically in Suriname, the stated type locality (satisfying Article 75.3.1). These two species, *D. carinatus* and *D. micropoeus*, are rediagnosed and redescribed herein (Article 75.3.2) with figure and complete collection, morphometric and meristic data provided for the proposed neotype of *D. carinatus* (Article 75.3.3). Multiple inventories of Linnaeus' types (Wheeler, 1958, 1985, 1989, 1991; Fernholm and Wheeler, 1983; Eschmeyer et al., 1998 and on-line version 29 Jan 2008; Ferraris, 2007; S. Kullander, pers. comm. 2008) have not located those pertaining to his *S. carinatus* (Article 75.3.4). The neotype is consistent with Linnaeus' original description of *S. carinatus* and subsequent treatment by other authors (Article 75.3.5); originates from Suriname, the stated type locality (75.3.6); and is deposited in The Academy of Natural Sciences, Philadelphia (ANSP 187114) where it is accessible for study (75.3.7).

***Doras micropoeus* (Eigenmann, 1912)**

Figs. 1B, 2F, 4D, 5C, 6E–F, 7, 10B & 12
Tables 1 & 3

? *Doras carinatus.*—Müller and Troschel, 1849:629 [may include or truly be *Doras carinatus*; Essequibo River, Guyana].

Hemidoras micropoeus Eigenmann MS.—Eigenmann, 1910 [name only in checklist; Demerara River, Guyana]

Hemidoras micropoeus Eigenmann, 1912:195 [type locality: Wismar (= upper Demerara River at Wismar, Guyana)].—Ibarra and Stewart, 1987:44 [type catalog; holotype (CM 1636) missing, paratype from Lama Stop-off, Guyana]

Doras micropoeus.—Eigenmann, 1925:346, Pls. 1 (fig. 17), 2 (1), 20 (3), 24 (1,2) 27 (5) [new generic assignment; Lama Stop-Off and Wismar, Demerara River; annotated figures of gas bladder *ex situ*, bones of head; illustration of whole fish, lateral view].—Henn,

1928:74 [type catalog; Carnegie Museum holotype no. 1636, 365 mm; Wismar, Guyana].—Gosline, 1945:19 [checklist, Guyana].—Burgess, 1989:223, 772, Pl. 99 (unnumbered fig.) [checklist, Guyana; figure of live specimen].—Eschmeyer, 1998:1086 [type catalog and depositories].—Hardman, et al., 2002:235 [distributional checklist, Demerara, Guyana].—Sabaj and Ferraris, 2003:460 [catalog; Essequibo, Demerara, Corantijn basins; common names].—Ferraris, 2007:171 [type catalog].—Sabaj Pérez, et al., 2007:166, 186, 189, Figs. 3C, 5 [annotated figures of pectoral girdle and bones of head; comparisons within *Doras*; coastal drainages of Guianas; material examined].

? *Anduzedoras microstomas*.—Ouboter and Mol, 1993:149 [distributional checklist, lower Corantijn and Kaburi Creek, Suriname; may include or alternatively be *D. carinatus*]

Doras cf. *micropoeus*.—Le Bail, et al., 2000:36, 44–45 [compared to *D. carinatus* in key; common names; description with figure of live specimen; distribution plotted in Maroni and Mana rivers, French Guiana].

Holotype.—CM 1636 (365 mm TL; missing, not found at FMNH by Ibarra and Stewart, 1987:44, although previously recorded at CM by Henn, 1928:74): Guyana: Demerara River at Wismar, C.H. Eigenmann et al., 24–29 Sep, Oct 3, 1908.

Paratypes (3).—Guyana: CAS 46959 (1 alc), FMNH 53193 (1 alc, 197 mm) [ex CM 1637, ex IU 12029], Lama Stop-Off; CAS 60712 (1 alc, 217 mm TL), same data as holotype.

Non-type material.—"**Guianas**": ANSP 78070 [ex. Hyrtl Coll.] (1 sk, 160 mm), pre-1870. **French Guiana**: St. Laurent du Maroni (Mana Dr.): MNHN 1998-1691 (1 alc), Mana River, Cayenne Market, P. Planquette, 13 Mar 1983; MNHN 1998-1773 (2 alc), Mana River, P.-Y. Le Bail & P. Keith, 1998; MNHN 1998-1774 (1 alc); (Maroni Dr.): Tampoc River, P.-Y. Le Bail & P. Keith, Nov 1998; MNHN 2000-5863 (1 of 2), Tampoc River, Saut Pièrkuru (station niv1mar4), 02°49'N, 053°32'W, M. Jégu et al., 2000. **Guyana:** Berbice Dr.: MHNG 2651.065 (1 alc, 140 mm), Berbice River, Dubulay Ranch, Station MCF04-29, J.I. Montoya-Burgos et al., 5 Nov 2004; Demerara Dr.: AMNH 12946 (3 alc, 42.7–149.6 mm) Demerara River, Wismar, A.S. Pinkus, 1934?; AMNH 214844 (9 alc, 37.6–94.4 mm) Demerara River, Malali, A.S. Pinkus 1934; AMNH 214896 (14 alc, 45–86.4 mm), Demerara river, Wismar, A.S. Pinkus, 20 Nov–9 Dec 1934; AMNH 214907 (1 alc, 73.2 mm), Demerara River, Malali, A.S. Pinkus, 26 Nov–1 Dec 1934; AMNH 214957 (3 alc, 43-57.6 mm), Demerara River, Malali, A.S. Pinkus, 1935; AMNH 215083 (1 alc, 64.6 mm), Demerara River, Malali, A.S. Pinkus, Aug 1935; AUM 27983 (11 alc, 27.5–156 mm), Demerara River, north bank near Linden, 06°01'14"N, 058°18'03"W (Guy 98-9), L.M. Page et al., 18 Oct 1998; INHS 49098 (49 alc), Demerara River, 5.05 mi SSW Linden, bearing 195°, 05°56'00"N, 058°18'22"W (Guy 98-6), L.M. Page et al., 17-18 Oct 1998; INHS 49162 (12 alc), same data as AUM 27983; Essequibo Dr.: AMNH 72897 (4 alc, 122.1–170 mm), Mazaruni and Cuyuni Rivers at confluence, about 100 m off Kartabo Point (RES-83-3), R.E. Schmidt & A. Pappantoniou, 10 Aug 1983; ANSP 175867 (1 alc, 175.4 mm), Essequibo River, approx. 3 hours upstream from Kurupukari field station, 04°34'17"N, 058°35'17"W (WGS97-26), W.G. Saul et al., 30 Jan 1997; ANSP 175868 (1 alc, 170 mm), Essequibo River, 180 yd. upstream from Essequibo campsite (Maipuri), 04°45'43"N, 058°45'52"W (WGS97-23), D. Allicock, 27 Jan 1997; ANSP 177426 (1 alc, 302.0 mm), Essequibo River, small blackwater creek opposite Paddle Rock campsite, 04°45'00"N, 058°42'00"W (GGW97-16), C. Watson et al., 23 Nov 1997; ANSP 177880 (4 alc, 181–274 mm), Essequibo River at Essequibo campsite, 04°45'41"N, 058°45'53"W (WGS97-19), D. Torres et al., 26 Jan 1997; ANSP 178703 (1 alc, 222 mm), Essequibo River, extensive sandbar 500 m downstream from Paddle Rock campsite, 04°44'00"N, 058°43'00"W (GGW97-17), C. Watson et al., 23 Nov 1997; INPA 28898 (1 alc, 194 mm), same data as ANSP 177880; MZUSP 88606 (1 alc, 164 mm), same data as ANSP 175868. **Suriname:** Maroni Dr.: Sipalawini: ANSP 187110 (2 alc, 174–225 mm; 2 sk, 205–210 mm), Lawa River, base camp ca. 8 km south-southwest of Anapaike/Kawemhakan (airstrip), 03°19'31"N, 054°03'48"W (SUR 07-01), J.G. Lundberg et al., 18 Apr 2007; Corantijn Dr.: Nickerie: USNM 226188 (1 alc, 136.2 mm), Corantijn River, between Baviian Island and Guyana border, 05°31'N, 57°12'W (RPV 80-10), R.P. Vari et al., 6 Sep 1980.

Diagnosis.—*Doras micropoeus* is diagnosed among extant congeners by two unique characteristics: 1) post-infranuchal midlateral scutes gradually but distinctly decreasing in depth anteriorly from above anal-fin origin, becoming either reduced and non-overlapping or absent entirely, and 2) infranuchal scute lacking posteriorly pointed wing-like expansions, and with medial thorn absent or rudimentary (Fig. 5C). *Doras micropoeus* differs from fossil species †*D. dioneae* by having a deeper postcleithral process, depth 2.12–2.65 (vs. 2.75) times into oblique length, and by sharing the same combination of characteristics of pectoral girdle described for *D. carinatus* (see Diagnosis of *D. carinatus*).

Comparisons.—*Doras micropoeus* is further distinguished from *D. phlyzakion* and *D. zuanoni* by having 38–39 total vertebrae (vs. 35); a deeper postcleithral process, depth 2.12–2.65 times into oblique length (vs. 3.05–3.84; see Fig. 2); gas bladder with one terminal diverticulum (vs. two posterior diverticula; see Fig. 6); premaxilla with teeth (vs. edentate); first infraorbital elongate, anterior wing well-developed with tip extending well beyond medial concavity for anterior naris (vs. first infraorbital relatively short, anterior tip extending short distance beyond concavity; see Fig. 4); ventral surface without conspicuous pores or with few small pores restricted to skin surrounding vent (vs. ventral surface with small pores in skin particularly on abdomen and near ventral insertion of gill flap; see Fig. 3); symphyseal limb of cleithrum with concave (vs. straight) lateral margin; pectoral girdle truncated anteriorly with concave margin across symphysis (vs. margin rounded, convex); and distal anterior margin of pectoral spine smooth (vs. serrated).

Description.—Morphometrics and meristics summarized in Table 3; aspects of postcleithral process summarized in Table 1. Largest specimen examined 302 mm SL, 337 mm TL. As reported by Eigenmann (1912) holotype (missing) is larger at 365 mm TL. Head large, deep, weakly compressed with elongate, conical snout (particularly in adults). Body elongate, slightly compressed, deepest at dorsal-fin origin, gently tapering to short, slender caudal peduncle. Ventral surface flattened from snout to anal-fin origin. Dorsal profile notably concave from snout tip to between anterior and posterior nares, then gently convex to above eye and finishing straight, weakly oblique to dorsal-fin origin. Eye large (19.81–26.42% oblique head length), covered by thin skin (adipose eyelid not distinct), positioned high on head; dorsal margin of orbit concave in dorsal view; interorbital width relatively narrow (13.73–17.77% oblique head length).

Mouth small, subterminal; gape with rounded anterior (premaxillary) margin, straight to weakly concave posterior (dentary) margin. Teeth present on dentary and premaxilla. Premaxilla with 4–9 strong acicular teeth set close in one or two irregular rows (n = 8, 170–274 mm SL). Dentary with many (ca. 20–60) strong acicular teeth in a subrectangular patch.

First gill arch with 23–26 rakers (4–5 upper, 19–21 lower; n = 5, 146–274 mm SL), length of longest raker 3 to 6 times lateralmost width; medial edge of raker extended by soft fleshy flap fringed with 1–4 small papillae. Postaxial face and in most specimens preaxial face of first arch with soft fleshy lamellae and papillae (Fig. 10B); lamellae/papillae becoming more abundant and elaborate in larger individuals, and part of larger system of similar structures associated with remaining arches that carpets inner surfaces of pharyngeal cavity. Lamellae/papillae on postaxial face of first arch largely arranged into two separate rows between which a few solitary papillae may occur (Fig. 10B, right); inner row wide, occupying much of surface; outer row narrow, arising from skin along bases of filaments; both rows following entire length of arch or nearly so. Inner row with 11–15 wide lamellae oriented almost perpendicular to long axis of arch (appearing as distinctly spaced oblique columns); lamellar margin deeply lobed and/or fringed with papillae. Outer row with 19–29 smaller papillae either short, elongate (fingerlike or leaflike), or distally expanded and multi-lobed; papillae often overhang bases of filaments, but do not appear attached to filaments. Prominent lamellae/papillae in inner and outer rows loosely aligned with each other, but not regularly so with rakers. Preaxial face of first arch rarely smooth, usually with single row of 9–20 small, thin, short to elongate papillae arising from skin along bases of filaments, particularly those along lower arch near axil (Fig. 10B, left).

Anterior and posterior nares separate, each surrounded by short tubular skin; posterior naris larger, located near midpoint between anterior naris and anterior margin of eye; anterior naris much closer to posterior naris than snout tip. Cephalic shield weakly ornamented, middorsal groove lacking or weak, extending from middle pitline of supraoccipital to suture between anterior and middle nuchal plates. Cranial fontanel with single opening anterior to epiphyseal bar (posterior cranial fontanel occluded). Fontanel elongate, narrow, widest with rounded margin posteriorly, attenuate anteriorly; enclosed posteriorly and laterally by frontals, anteriorly by mesethmoid (Fig. 1B). Nuchal foramina absent. Nuchal shield roof-shaped, forming transverse angle. Anterior nuchal plate well-developed, pentagonal to hexagonal, wider than long and usually sharing broad lateral suture with epioccipital (Fig. 1B). Mesethmoid elongate, attenuate anteriorly with acutely pointed tip (Fig. 1B). First infraorbital very elongate with long, narrow, tapered anterior wing extending well beyond medial concavity for anterior naris (Figs. 1B, 4D). Epioccipital posterior process long, weakly contacting posterior nuchal plate; ribbon-like, twisted from horizontal plane (anteriorly) to vertical plane (posteriorly); posterior end vertically expanded with irregular margin (Fig. 5C).

Three pairs of barbels. Maxillary barbel long, reaching medialmost end of gill opening; fimbriate with about 15-18 fimbriae along lateral margin, proximal fimbriae rugose with papillae and secondary fimbriae along trailing margin. Mental barbels nearly equal in size, reaching to about halfway between anterior margin of lower jaw and medialmost end of gill opening, bases thick, profusely ornamented with fleshy papillae. Lips fleshy, surfaces with low rounded papillae near insertion of maxillary barbels.

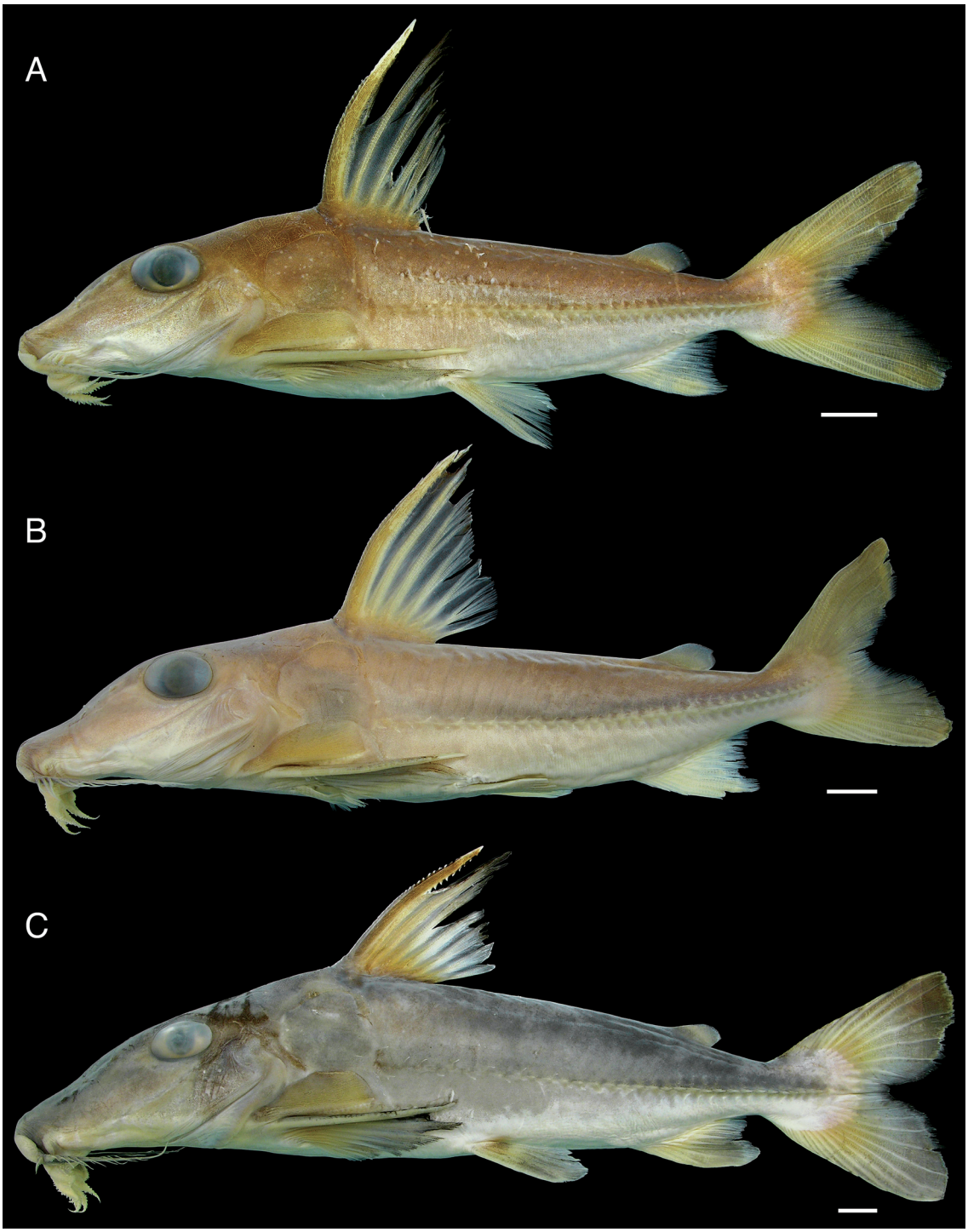

Fig. 12. *Doras micropoeus*. A. AUM 27983 (146.2 mm SL), Demerara River, Guyana, B. ANSP 175867 (175.4 mm SL), Essequibo River, Guyana, C. ANSP 187110 (225 mm SL), Lawa River, Suriname. Scale bar equals 1 cm. Photos by M. Sabaj Pérez.

Table 3. Morphometrics and meristics in *Doras micropoeus*.

	Essequibo only			
Measurements	n	Mean	Range	SD
Standard Length (mm)	15	158.26	27 - 282.3	
% in SL				
Predorsal distance	11	42.2	40.52 - 45.16	1.49
Prepectoral distance	11	29.68	28.75 - 31.94	0.98
Oblique head length	11	33.64	32.26 - 36.65	1.39
Body depth in dorsal-fin origin	11	21.39	20.05 - 24.19	1.14
Depth of caudal peduncle	11	5.72	5.07 - 6.16	0.32
Length of caudal peduncle	11	12.65	10.92 - 13.66	0.85
Length of postcleithral process	11	10.63	9.83 - 11.04	0.43
Dorsal-fin spine length	10	23.64	21.8 - 26.03	1.43
Pectoral-fin spine length	10	24.03	21.96 - 26.8	1.78
Anal-fin base length	11	11.57	10.89 - 12.2	0.39
Adipose-fin base length	11	7.85	6.45 - 9.02	0.8
Depth of tenth midlateral scute	11	1.82	1.58 - 2.44	0.25
% in Oblique Head Length				
Snout length	11	59.47	56.6 - 65.1	2.48
Horizontal eye diameter	11	24.58	19.81 - 26.42	1.92
Interorbital minimum width	11	15.06	13.73 - 17.77	1.34
Head width	11	44.36	42.67 - 46.69	1.32
Nuchal shield minimum width	11	19.86	18.11 - 22.26	1.31
Cleithral width	11	54.18	51.18 - 57.06	1.72
Maxillary barbel length	11	57.04	47.94 - 67.25	5.94
Outer mental barbel length	11	19.58	17.63 - 21.65	1.33

	Berbice/Demerara/Essequibo			Maroni		
Counts	n	Range	Mode	n	Range	Mode
Dorsal fin	11	II,6	-	4	II,6	-
Pectoral fin	11	I,9-10	I,10	4	I,9-10	I,10
Pelvic fin	11	i,6	-	4	i,6	-
Anal fin	11	iv-vi,9-10	v,9	4	v-vi,8-9	v,8
Caudal fin (dorsal/ventral)	11	i,7/8,i	-	4	i,7/8,i	-
Dorsal/ventral procurrent rays	11	14-16/13-16	14/15	4	14-16/15	14/15
Midlateral scutes/pores*	11	33-36*	34*	2	32-34*	-

*includes placeholder postinfranuchal pores in anterior lateral line without evident scutes and /or spines

Pectoral girdle in ventral view subtriangular, elongated with medially convergent lateral margins of symphyseal (horizontal) limbs of cleithrum long, concave. Pectoral girdle truncated anteriorly with with deeply concave margin across symphysis. Transverse limb of coracoid with distinct posterior process (keel) relatively short, extending slightly beyond posterior insertion of pectoral fin and falling well short of posterior tip of postcleithral process. Ventral surfaces of pectoral girdle (including posterior processes of coracoid) covered with skin (not externally visible).

Postcleithral process blade-like, deeply to moderately subrectangular, depth 2.12–2.65 times into oblique length in adults (n = 11, 170–274 mm SL). Margins entire; free dorsal margin straight to weakly concave; ventral margin straight; posterior margin oblique, tilted anteriorly (Fig. 2F). Surface ornamentation of postcleithral process similar to *D. carinatus* except divisions between three longitudinal fields often less distinct and dorsal and middle fields more broadly expanded.

Skin relatively smooth except for extremely minute punctate tubercles scattered on head, body and fins, particularly on gill covers and dorsal surfaces of head. Elongate slit-like pore in axilla of pectoral fin. Skin immediately ventral to entire length of postcleithral process perforated with numerous small round pores imparting a sponge-like appearance (Fig. 2F). Smaller pores sometimes evident in skin surrounding anteriormost scutes, usually just posterior to medial thorn. Conspicuous pores absent from skin on ventral surfaces or restricted to skin immediately surrounding vent.

Dorsal fin II,6 (n = 15); pectoral fin modally I,10, range I,9–10 (15); pelvic fin i,6 (15), anal fin modally v,8 in Maroni specimens (4), v,9 in remaining specimens (11), overall range iv–vi,8–10 (15); caudal fin i,7/8,i (15) with dorsal procurrent rays modally 14, range 14–16 (15) and ventral procurrent rays modally 15, range 13–16 (15). Dorsal-fin origin located approximately two-fifths SL from snout tip. External morphology of fins as described for *D. carinatus*.

Penultimate centrum (PU2) and neural and hemal arches and spines similar to those of *D. carinatus*; last hemal spine with anteroventral margin proximally contacting hemal spine of antepenultimate centra, and posterodorsal margin contacting parhypural proximally and distally aside lenticular gap. Compound centrum (PU1+U1) similar to that of *D. carinatus*. Hypural fusion pattern as in *D. carinatus*: PH; HY 1+2; HY 3+4; HY 5. Parhypural spine similarly rectangular but ventroanterior half thicker, with marginal keel indistinct or restricted to base and dorsoposterior half relatively thin, keel-like. Hypural plates similar to *D. carinatus*. Contact between hypural plates similar to *D. carinatus* except V-shaped notch between hypural 1+2 and 3+4 slightly shallower, separating plates for one half to two-thirds of their lengths. Hypurapophyses Type C (sensu Lundberg and Baskin, 1969: 15); condition as in *D. carinatus*. Prezygopophyses-like process on urostyle absent in smaller specimens and scarcely evident in largest (210 mm SL, sk).

Total vertebrae 38 (n = 2) or 39 (1). Centra 1–6 fused or deeply sutured into Weberian complex with superficial ossification completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal; eighth centrum with superficial ventral ossifications sharing brief interdigitating sutures with that of seventh centrum on either side of aortic channel. Vertebra five with pair of slender parapophyses directed posterolaterally. Vertebrae 6–13 (1) or 6–14 (2) bearing 8 and 9 pairs of simple ribs, respectively.

Lateral line surrounded by complete or incomplete series of midlateral bony scutes; total count of scutes and scuteless pores (placeholders) 32–36 per side (modally 34; n = 13). Specimens from Maroni drainage with first 6–10 postinfranuchal scutes lacking; other specimens occasionally with one or two anteriormost postinfranuchal scutes lacking medial thorns or missing entirely. Infranuchal scute tall, narrow with anteroventral expansion strongly contacting internal surface of distal postcleithral process; usually without medial thorn (small emergent thorn or carina sometimes present) and without subtriangular, posteriorly pointed dorsal and ventral expansions (Fig. 5C). Postinfranuchal scutes oblique, shallow and (when present) non-overlapping anterior to vertical between pelvic- and anal-fin origins, becoming deeper and weakly overlapping posteriorly. Depth of scute above pelvic-fin origin approximately one-tenth of corresponding body depth. When present, each postinfranuchal scute usually with distinct medial thorn (thorns smallest anteriorly, gradually increasing in size posteriorly to caudal peduncle) and subtriangular dorsal and ventral wings lacking distinct serrations along posterior margin (wings best developed posteriorly); dorsal wing slightly smaller and drawn out into anterodorsal and posterior points; ventral wing drawn out into ventral and posterior points.

Gas bladder large, cordiform with paired posterior chambers longer than single anterior chamber; walls smooth except for single elongate terminal diverticulum (Figs. 6E–F).

Coloration.—Largely as described for *D. carinatus* except in some specimens of *D. micropoeus* dark pigment is more concentrated in distal portion of dorsal fin, particularly on membranes (Fig. 12). Live specimen figured in Le Bail et al. (2000:45).

Distribution and habitat.—*Doras micropoeus* occurs in Atlantic coast rivers draining the northern side of the Guiana Shield in French Guiana, Suriname and Guyana. From east to west it is known from the Mana, Maroni, Corantijn, Berbice, Demerara and Essequibo basins. In the Lawa River, Suriname, adults (ANSP 187110) were collected using gill nets set the main channel below a large cataract. *Doras micropoeus* is syntopic with *D. carinatus* in the lower Essequibo and upper Maroni basins and probably elsewhere.

Etymology.—Species name from the Greek words *mikros* (small) and *poieo* (to make) in reference to the reduced or "rudimentary" anterior midlateral scutes.

***Doras higuchii*, new species**

Figs. 2E, 3A, 6C–D, 7 & 13
Tables 1 & 4

Doras carinatus.—Sabaj and Ferraris, 2003:460 [in part, identification of putatively distinct form from lower Amazon].—Akama in Buckup, et al., 2007:114 [checklist; distribution in part, lower Amazonas].

Doras sp. (Xingu).—Sabaj Pérez, et al., 2007:166, 189 [comparisons within *Doras*; material examined; rios Curisevo and Xingu].

Holotype.—MZUSP 96333 (alc, 177.7 mm): Brazil: Pará: Altamira Municipality: rio Curuá, (Iriri-Xingu Dr.), near town of Castelo dos Sonhos, 08°19'07"S, 055°05'23"W (PIPE2007102203), J.L. Birindelli, M.H. Sabaj Pérez, L.M. Sousa, A.N. Ferreira, N.K. Lujan, 23 Oct 2007.

Paratypes (50).—**Brazil:** Xingu Dr.: Mato Grosso: ANSP 181056 (5 alc. 57.6–63 mm; 1 cs, 58 mm), rio Corisevo, Porto do Vitório, near Ribeirão Kevuaieli, 13°02'05"S, 053°25'10"W (AXE2004101904), C. Moreira et al., 19 Oct 2004; MZUSP 86887 (5 alc, 56.4–64.7 mm), rio Sete de Setembro, approx. 20 km west of Canarana by road MT-020 (Canarana-garapu), 13°30'19"S, 052°24'57"W, C. Moreira, et al. 19 Oct 2004; MZUSP 87025 (17 alc, 59.6–75 mm), same data as ANSP 181056; MZUSP 87055 (2 alc, 69.6–70.5 mm), rio Corisevo, rock-bed and beach under bridge of road to Sorriso, approx. 30 km west of Gaúcha do Norte, 13°12'58"S, 053°29'53"W (AXE2004101906), C. Moreira et al., 19 Oct 2004; Pará: ANSP 181057 (1 alc, 160 mm), rio Xingu, Belo Monte, 03°07'S, 051°42'W (MIG83070002), M. Goulding, Jul 1983; ANSP 187378 (1 alc, 184 mm), same data as holotype; ANSP 187491 (1 alc, 240 mm), rio Xingu, Ilha do Babaquara, Altamira, L. Rapp Py-Daniel & J.A. Zuanon, 5 Oct 1990; INPA 4051 (6 alc, 168–213.5 mm), rio Xingu, Altamira, L. Rapp Py-Daniel & J.A. Zuanon, 1 Oct 1990; INPA 4052 (6 alc), same data as ANSP 187491; MNHN 1999-0020 (1 alc, 206 mm), rio Xingu (lower), Cachoeira Kaituka, M. Jégu, 10 Oct 1992; MZUSP 82297 (3 alc, 164.6–183.8 mm), same data as ANSP 181057; MZUSP 96334 (1 sk), same data as holotype.

Non-type material.—**Brazil:** Pará: Jari Dr.: INPA 5250 (12 alc, 65.7-201 mm), rio Jari, north-northeast of Almeirim, approx. 00°52'S, 052°25'W (MJ87062314), M. Jégu & J.A. Zuanon, 23-24 Jun 1987; Trombetas Dr.: Oriximiñã Municipality: ANSP 187380 (1 alc, 202 mm), rio Trombetas, Igarapé Caxipacoré, E.G. Ferreira et al., 20 Apr 1985; INPA 3548 (1 alc, 202 mm) rio Trombetas, upstream of Vira Mundo (waterfall) 01°45'S, 055°52'W (EGF85100821), E.G. Ferreira & L. Rapp Py-Daniel, 8 Oct 1985; INPA 5065 (2, 190–197 mm), rio Trombetas, Cachoeira Porteira, E.G. Ferreira & M. Jégu, 15 Apr 1985; INPA 5068 (2 alc, 153.5–217 mm) rio Cachorro, E.G. Ferreira, 26 May 1988; INPA 5447 (5 alc), same data as ANSP 187380; INPA 5568 (5 alc, 60.9–132 mm); rio Trombetas, upstream of Cachoeira Vira-Mundo, E.G. Ferreira & J.A. Zuanon, 3 Sep 1990.

Diagnosis.—*Doras higuchii* is diagnosed among fossil and extant congeners by the following combination of characteristics. Midlateral scutes 33–36; total vertebrae 38; gas bladder with single terminal diverticulum (Figs. 6C–D); teeth typically present on premaxilla; first infraorbital with elongate anterior wing extending well beyond medial concavity for anterior naris; ventral surface without conspicuous pores or with few small pores restricted to skin around vent (Fig. 3A); symphyseal limb of cleithrum with concave lateral margin; pectoral girdle truncated anteriorly with concave margin across symphysis; distal anterior margin of pectoral spine smooth; postinfranuchal midlateral scutes overlapping and of approximately uniform depth anterior to anal fin; infranuchal scute with medial thorn flanked by subtriangular wings; postcleithral process always deep (depth 1.8–2.49 times into oblique length) with straight to weakly convex free dorsal margin and dorsal field ornamentation broadly expanded, forming one-third to half of posterior margin of process (Fig. 2E); skin covering dorsal-locking spinelet and sometimes base of dorsal spine blackened with strong concentration of pigment, distal dorsal spine markedly lighter, pale (Fig. 12); caudal fin with two dusky longitudinal stripes, one on ventral half of dorsal lobe and second on dorsal half of ventral lobe, particularly in juveniles (Fig. 13A).

Comparisons.—*Doras phlyzakion* and *D. zuanoni* have 30–32 midlateral scutes; 35 total vertebrae; gas bladder with two posterior diverticula (Figs. 6G–H); premax-

illa edentate; first infraorbital relatively short, anterior tip extended short distance beyond medial concavity for anterior naris (Fig. 4A); ventral surface with many small pores in skin particularly on abdomen and near ventral insertion of gill flap (Figs. 3B–C); symphyseal limb of cleithrum with straight lateral margin; pectoral girdle truncated anteriorly with rounded, convex margin across symphysis; and distal anterior margin of pectoral spine serrated. *Doras micropoeus* has postinfranuchal midlateral scutes distinctly increasing in separation and decreasing in depth anteriorly from above anal-fin origin; infranuchal scute lacking posteriorly pointed wings and with medial thorn absent or rudimentary (Fig. 5C). *Doras carinatus* has postcleithral process deep to shallow (depth 2.28–3.93 times into oblique length) with straight to weakly concave free dorsal margin and dorsal field ornamentation moderately expanded, excluded from or forming less than one-third of posterior margin of process (Figs. 2B–D); skin covering dorsal-locking spinelet and base of dorsal spine moderately darkened by weak concentration of pigment with dorsal spine dusky or becoming gradually lighter distally (Figs. 8, 9); caudal fin uniformly dusky with scattered pigment (Figs. 8, 9). †*Doras dioneae* has a shallower postcleithral process (depth 2.75 times into oblique length) with free dorsal margin weakly concave and dorsal field ornamentation moderately expanded, forming minimal portion of posterior margin (Fig. 2A). *Doras higuchii* is further distinguished from †*Doras dioneae* by sharing the same combination of characteristics of the pectoral girdle described for *D. carinatus* (see Diagnosis of *D. carinatus*).

Description.—Morphometrics and meristics summarized in Table 4; aspects of postcleithral process summarized in Table 1. Largest specimen examined 240 mm SL. Head large, deep, weakly compressed with prominent conical snout. Body elongate, slightly compressed, deepest at dorsal-fin origin, gently tapering to short, slender caudal peduncle. Ventral surface flattened from snout to anal-fin origin. Dorsal profile straight to concave from snout tip to between anterior and posterior nares, then either curving gently (convex) to above eye and finishing straight, weakly oblique to dorsal-fin origin or curving more continuously (shallowly convex) from posterior naris to dorsal-fin origin. Eye large (21.91–30.99% of oblique head length), covered by thin skin (adipose eyelid not distinct), positioned high on the head; dorsal margin of orbit concave in dorsal view; interorbital width narrow to moderate (13.89–22.92% of oblique head length).

Mouth small, subterminal; gape with rounded anterior (premaxillary) margin, straight to weakly concave posterior (dentary) margin. Teeth present on dentary and typically premaxilla. Premaxilla usually with 2–5 strong acicular teeth set close in one or two irregular rows (n = 7, 153–240 mm SL); rarely edentate. Dentary with 14–22 strong acicular teeth in a few rows or small patch.

First gill arch with 15–18 rakers (3 upper, 12–15 lower; n = 3, 160–211 mm SL), length of longest raker 5 to 6 times lateralmost width; medial edge of raker extended by soft fleshy flap fringed with small papillae. Postaxial face and in one specimen preaxial face of first arch with soft fleshy lamellae and papillae (morphology most similar to *D. carinatus*); lamellae/papillae becoming more abundant and elaborate in larger individuals, and part of larger system of similar structures associated with remaining arches that carpets inner surfaces of pharyngeal cavity. Lamellae/papillae on postaxial face of first arch largely arranged into two rows between which a few solitary papillae may occur; inner row wide, occupying much of surface; outer row narrow, arising from skin along bases of filaments; both rows following entire length of arch or nearly so. Inner row with 9 or 10 wide lamellae oriented almost perpendicular to long axis of arch (appearing as distinctly spaced oblique columns); lamellar margin deeply lobed and/or fringed with papillae. Outer row with 20 or more smaller papillae either short, elongate (fingerlike or leaf-like), or distally expanded and multi-lobed. Prominent lamellae/papillae in inner and outer rows loosely aligned, but not regularly aligned with rakers. Preaxial face of first arch smooth or with single row of small, short to elongate papillae arising from skin along bases of filaments, particularly those along lower arch near axil.

Anterior and posterior nares separate, each surrounded by short tubular skin; posterior naris larger than anterior one, located approximately at midpoint between anterior naris and anterior margin of eye; anterior naris closer to posterior naris than snout tip. Cephalic shield weakly ornamented, often with middorsal groove from middle pitline of supraoccipital usually to suture between anterior and middle nuchal plates, sometimes extending onto middle nuchal plate. Cranial fontanel with single opening anterior to epiphyseal bar (posterior cranial fontanel occluded). Fontanel elongate, narrow, widest with rounded margin posteriorly, attenuate anteriorly; enclosed posteriorly and laterally by frontals, anteriorly by mesethmoid (compare Fig. 1B). Nuchal foramina absent. Nuchal shield roof-shaped, forming transverse angle. Anterior nuchal plate well-developed, pentagonal to hexagonal, wider than long and sharing broad lateral suture with epioccipital. Mesethmoid elongate, attenuate anteriorly with acutely pointed tip. First infraorbital elongate with long tapered anterior wing extending well beyond medial concavity for anterior naris (most similar to *D. carinatus*).

Three pairs of barbels. Maxillary barbel long, tip approximately reaching medialmost end of gill opening; fimbriate with 15-18 fimbriae along lateral margin, proxi-

Fig. 13. *Doras higuchii*. A. ANSP 181056 (SL 61.8 mm), Rio Corisevo (Xingu Dr.), Brazil, B. INPA 5568 (SL 83.8 mm), Rio Trombetas, Brazil, C. MZUSP 96333 (Holotype, SL 177.7 mm), Rio Curuá (Xingu Dr.), Brazil, D.ANSP 187491 (SL 240 mm), Rio Xingu, Brazil. Scale bar equals 1 cm. Photos by M. Sabaj Pérez.

Table 4. Morphometrics and meristics in *Doras higuchii* n. sp.

Measurements	n	Mean	Range	SD	Holotype
Standard Length (mm)	22	176.74	92.9 - 241.0		177.7
% in SL					
Predorsal distance	22	41.52	37.94 - 44.65	1.81	41.70
Prepectoral distance	22	28.38	25.58 - 32.07	1.84	28.14
Oblique head length	22	31.71	29.14 - 34.90	1.64	31.74
Body depth at dorsal-fin origin	22	22.98	20.38 - 25.73	1.56	23.07
Depth of caudal peduncle	22	6.23	5.74 - 7.11	0.42	6.19
Length of caudal peduncle	22	12.28	10.66 - 13.56	0.81	12.38
Length of postcleithral process	22	10.86	9.26 - 12.19	0.74	12.16
Dorsal-fin spine length	22	21.45	16.67 - 25.46	1.86	22.34
Pectoral-fin spine length	22	23.26	20.79 - 27.00	1.73	24.20
Anal-fin base length	21	12.58	10.74 - 14.52	0.95	13.06
Adipose-fin base length	22	9.74	7.44 - 10.83	0.84	9.85
Depth of tenth midlateral scute	20	4.38	2.72 - 5.64	0.57	3.94
% in Oblique Head Length					
Snout length	22	58.73	52.16 - 63.62	3.38	57.80
Horizontal eye diameter	22	25.36	21.91 - 30.99	2.41	25.71
Interorbital minimum width	22	18.25	13.89 - 22.92	2.63	18.97
Head width	22	51.76	46.52 - 62.85	3.69	51.42
Nuchal shield minimum width	22	23.68	19.80 - 30.56	2.50	22.70
Cleithral width	22	65.42	56.93 - 77.26	5.74	65.96
Maxillary barbel length	22	55.26	39.72 - 76.39	9.23	55.67
Outer mental barbel length	22	23.61	19.21 - 26.06	1.95	24.82

Counts	n	Range	Mode	Holotype
Dorsal fin	32	II,6	-	II,6
Pectoral fin	32	I,8-10	I,9	I,9
Pelvic fin	32	i,6	-	i,6
Anal fin	12	iv-vi,8-10	v,9	vi,9
Caudal fin (dorsal/ventral)	32	i,7/7-8,i	i,7/8,i	i,7/7,i
Dorsal/ventral procurrent rays	22	12-14/12-14	13/14	14/14
Midlateral scutes	32	33-36	34	34

mal fimbriae with secondary fimbriae along trailing margin. Mental barbels nearly equal in size, reaching to about halfway between anterior margin of lower jaw and medialmost end of gill opening, bases thick, profusely ornamented with fleshy papillae. Lips fleshy, surfaces with low rounded papillae near insertion of maxillary barbels.

Pectoral girdle in ventral view subtriangular, similar in shape to *D. carinatus* with lateral margin of symphyseal limb of cleithrum concave and truncated anteriorly with concave margin across symphysis. Transverse limb of coracoid with distinct posterior process (keel) relatively short as in other *Doras*. Ventral surfaces of pectoral girdle, including posterior processes of coracoid, covered with skin (not externally visible).

Postcleithral process blade-like, deeply subrectangular in adults; depth greatest in Xingu specimens (1.8–2.38 times into oblique length), less so in Trombetas specimens (2.4–2.49 times into oblique length). Margins entire; free dorsal margin of process straight or more often weakly convex. Surface ornamentation similar to *D. carinatus* except dorsal field more broadly expanded, forming one third to half of posterior margin of process, and region near distal border between dorsal and middle fields often covered with short sliver of pigmented skin (Fig. 2E).

Skin relatively smooth except for extremely minute punctate tubercles. In Trombetas specimens tubercles densely scattered or in irregular rows on upper side, particularly in tympanic region. In Xingu specimens tubercles sparsely scattered on head, body and fins, particularly on gill covers and dorsal surfaces of head; specimens also with tubercles crowded in wide patch below infranuchal scute along posterior margin of postcleithral process, extending ventrally to lowermost side. Elongate slit-like pore in axilla of pectoral fin. Skin immediately ventral to entire length of postcleithral process perforated with numerous small round pores imparting a sponge-like appearance (Fig. 2E). Numerous pores crowded in skin surrounding vent (Fig. 3A); pores absent from abdomen and breast.

Dorsal fin II,6 (n = 32); pectoral fin modally I,9, range I,8–10 (32); pelvic fin i,6 (32), anal fin modally v,9, range iv–vi,8–10 (12), caudal fin typically i,7/8,i (31), rarely i,7/7,i (1) with dorsal procurrent rays modally 13, range 12–14 (22) and ventral procurrent rays modally 14, range 12–14 (22). Dorsal-fin origin located approximately two-fifths SL from snout tip. Morphology of fins as largely as described for *D. carinatus* except caudal fin more deeply forked, lobes bluntly pointed.

Caudal skeleton similar to that of *D. carinatus* with same hypural fusion pattern (PH; HY 1+2; HY 3+4; HY 5), relatively wide V-shaped notch between hypurals 1+2 and 3+4, and Type C hypurapophyses (sensu Lundberg and Baskin, 1969:15). Pair of small prezygopophysis-like processes on anterior base of urostyle in larger specimen (172 mm SL, sk), but absent from smaller specimen (58 mm SL, cs).

Total vertebrae 38 (n = 6). Centra 1–6 fused into the Weberian complex with superficial ossifications completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal. Vertebra five with pair of slender parapophyses directed posterolaterally. Vertebrae 6–13 (1) or 6–14 (1) bearing 8 and 9 pairs of simple ribs, respectively.

Lateral line surrounded by complete series of 33–36 midlateral bony scutes per side (modally 34; n = 32). Scute morphology as described for *D. carinatus* except range of scute depth at pelvic-fin origin one-fifth to one-seventh of corresponding body depth.

Gas bladder large, cordiform with paired posterior chambers longer than single anterior chamber; walls smooth except for single terminal diverticulum most similar to *D. carinatus* (Figs. 6C–D).

Coloration.—Preserved specimens with dorsal and dorsolateral surfaces of head and body uniform gray to tan ground color; side of body below medial thorns lighter gray or tan to pale; lowermost side and ventral surfaces pale, white. Maxillary barbel gray to tan; mental barbels pale. Skin covering base of dorsal-locking and dorsal spines blackened with strong concentration of pigment; distal portion of dorsal spine usually markedly lighter, pale; dark pigment scattered on rays and membranes along anterior margins of rays, remaining portions of membranes clear. Pectoral fins dusky with scattered pigment particularly on spine and anteriormost rays and membranes. Pelvic fin similarly dusky with scattered pigment, particularly on anterior membranes. Anal fin largely pale with sparsely scattered pigment. Caudal fin with two dusky longitudinal stripes, one on ventral half of dorsal lobe and second on dorsal half of ventral lobe (particularly evident in juveniles, Fig. 13A). In life dorsal head and side above midlateral scutes tinted olive; scutes and portions of snout and fins tinted yellowish-olive; lower side and undersurfaces white (Fig. 13C).

Distribution and habitat.—*Doras higuchii* occurs in the lower Jari, lower Trombetas and Xingu basins, all tributaries of the lower Amazon River, in the states of Mato Grosso and Pará, Brazil. Three adults taken at the type locality in the rio Curuá were collected at night using cast nets and bag seine over sand in swift clear water (depth <2 m) of a medium-size channel immediately below a large cataract.

Etymology.—Species named in honor of Horácio Higuchi in recognition of his groundbreaking contributions to the systematics of the thorny catfishes.

***Doras phlyzakion*, new species**
Figs. 2G, 3C, 4A, 6G, 7 & 14A
Tables 1 & 5

? *Oxydoras carinatus*.—Regan, 1905:190 [presumably pertains to identification of illustration no. 34 by Wallace; rio Negro, Brazil].

? *Doras carinatus*.—Wallace, 2002:325 (fig. 131) [illustration no. 34 by Wallace previously identified as *Oxydoras*/*Doras carinatus* and re-identified as *Doras carinatus* or *Hassar* (= *Leptodoras*) *praelongus*].

Doras sp. (Amazonas).—Sabaj Pérez, et al., 2007:166, 189 [comparisons within *Doras*; material examined; rio Tefé].

Holotype.—Brazil: Amazonas: MZUSP 88508 (alc, 160.8 mm), rio Tefé (Amazonas Dr.), beach, Vista Escura, 03°38'S, 064°59'W (MIG1979073001), M. Goulding, 30 Jul 1979.

Paratypes (46).—**Brazil**: Amazonas: Negro Dr.: MZUSP 91671 (1 alc, 87.5 mm), rio Uaupés, 00°09'N, 067°50'W, J.Chernela, no date; MZUSP 50836 (1 cs, 87.3 mm), Lagoa Central, lower rio Negro basin between rios Camanaú and Apuaú, approx. 100-180 km NW of Manaus (TYR68112001), T.R. Roberts, 20 Nov 1968; Solimões-Amazonas Dr.: ANSP 181055 (2 alc, 148–169 mm), AUM 47712 (1 alc, 170 mm), same data as holotype; INPA 19140 (4 alc, 86.4-136.8 mm), Lago Amanã, mouth of rio Baré, 02°23'S, 064°42'W, W. Crampton, 13-18 Dec 1997; INPA 19141 (1 alc, 76.8 mm), rio Tefé, Ilha do Martelo, 03°38'S, 064°59'W, W. Crampton, 16 Sep 1999; MCP 32947 (1 alc, 175 mm), Lago Amanã, mouth of rio Baré, 02°27'23"S, 064°43'35"W (WC1997121301), W. Crampton, 13 Dec 1997; MCP 32948 (1 alc, 73.2 mm), Lago Tefé, community of Nogueira, 03°17'58"S 064°46'21"W (WC1997101301), W. Crampton, 13 Oct 1997; MCP 32949 (5 alc, 90.7–113.8 mm), Lago Amanã, mouth of rio Baré, 02°27'S, 064°43'W (WC1997121801), W. Crampton, 18 Dec 1997; MCP 32950 (1 alc, 145.3 mm), Lago Tefé, community of Nogueira 03°17'58"S 064°46'21"W (WC1997101401), W. Crampton, 14 Oct 1997; MHNG 2699.05 (1 alc, 175 mm), same data as holotype; MZUSP 50837 (4 alc, 98.6–133.3 mm), rio Solimões, Fonte Boa, 02°31'S, 066°06'W (EPA68102502) Expedição Permanente à Amazônia, 25 Oct 1968; MZUSP 82294 (14 alc, 145.5–189.3 mm, 1 sk, 162 mm), same data as holotype; MZUSP 88466 (6 alc, 159–167.2 mm), rio Tefé [label indicates "Mucura", presumably in error], M. Goulding, 30 Jul 1979; Roraima: Negro Dr.: MZUSP 62583 (1 alc, 116.6 mm), rio Mucajaí, trib rio Branco, south of Boa Vista, 02°32'N, 060°54'W, E. Dente, Apr 1962; **Colombia:** Japurá Dr.: Vaupés: IAvH-P 2860 (1 alc), Laguna Taraira, río Apaporis, northeast of La Pedrera, H. Lopez, 13 Jun 1990.

Diagnosis.—*Doras phlyzakion* is diagnosed among extant congeners by a single unique characteristic: gas bladder with two elongate posterior (subterminal) diverticula with bases well separated (Fig. 6G). *Doras phlyzakion* is distinguished from fossil species †*Doras dioneae* by having a shallow postcleithral process, depth 3.05–3.84 (vs. 2.75) times into oblique length. Additional characteristics diagnostic in combination include: midlateral scutes 31–32; total vertebrae 35; premaxilla edentate; first infraorbital relatively short, anterior tip extended short distance beyond medial concavity for anterior naris (Fig. 4A); ventral surface with numerous pores in skin on breast (Fig. 3C); symphyseal limb of cleithrum with straight lateral margin; pectoral girdle truncated anteriorly with rounded, convex margin across symphysis; distal anterior margin of pectoral spine serrated; infranuchal scute with distinct medial thorn and posteriorly pointed dorsal and ventral wings; postinfranuchal scutes uniform in size and overlapping anteriorly from above anal fin; middorsum and side dusky, weakly contrasting pale midlateral stripe along scutes; fins without distinct dark marks; and interorbital width 17.07–24.03% of oblique head length.

Comparisons.—*Doras carinatus*, *D. higuchii* and *D. micropoeus* have 37–39 total vertebrae; gas bladder with single terminal diverticulum (Figs. 6A–F); premaxilla with acicular teeth; first infraorbital elongate, anterior wing well-developed with tip extending well beyond anterior naris (Figs. 4B–D); pores on ventral surfaces absent or restricted to skin surrounding vent (Fig. 3A); symphyseal limb of cleithrum with concave lateral margin; pectoral girdle truncated anteriorly with concave margin across symphysis; and distal anterior margin of pectoral spine smooth. *Doras carinatus* and *D. higuchii* are further distinguished by having more midlateral scutes, 33–36. *Doras micropoeus* is further distinguished by having infranuchal scute with medial thorn absent or rudimentary and without posteriorly pointed wings (Fig. 5C); and postinfranuchal scutes non-overlapping and decreasing in size or absent anteriorly. *Doras zuanoni* is distinguished by having two terminal diverticula conjoined at base with long divergent ends and short diverticulum present on each anterior lateral shoulder of anterior chamber (Fig. 6H); pores on breast few, restricted to small patch near ventral medial insertion of gill flap (Fig. 3B); side dusky to black, strongly contrasting pale midlateral stripe (Figs. 14B–C); fins with dark marks; and interorbital width 26.7–28.24% of oblique head length.

Description.—Morphometrics and meristics summarized in Table 5; aspects of postcleithral process summarized in Table 1. Largest specimen examined 189.3 mm

Table 5. Morphometrics and meristics in *Doras phlyzakion* n. sp.

Measurements	n	Mean	Range	SD	Holotype
Standard Length (mm)	33	153.65	89.1 - 189.3		160.8
% in SL					
Predorsal distance	33	44.09	42.52 - 45.56	0.7	43.91
Prepectoral distance	33	30.13	28.84 - 32.11	0.9	29.66
Oblique head length	33	33.43	32.35 - 34.57	0.5	33.27
Body depth at dorsal-fin origin	33	24.85	22.7 - 26.29	0.74	24.38
Depth of caudal peduncle	33	5.82	5.22 - 6.62	0.3	5.91
Length of caudal peduncle	33	12.09	10.05 - 14.23	0.93	10.95
Length of postcleithral process	33	13.54	12.12 - 14.42	0.49	12.94
Dorsal-fin spine length	28	23.11	18.63 - 26.76	1.98	23.01
Pectoral-fin spine length	33	27.91	16.94 - 31.39	2.3	26.68
Anal-fin base length	33	11.79	10.54 - 13.88	0.78	11.82
Adipose-fin base length	33	8.84	7.23 - 10.67	0.81	9.51
Depth of tenth midlateral scute	33	5.41	4.52 - 6.31	0.33	5.78
% in Oblique Head Length					
Snout length	33	59.53	51.79 - 63.24	2.11	59.07
Horizontal eye diameter	33	22.89	20.94 - 26.71	1.16	23.36
Interorbital minimum width	33	19.53	17.07 - 24.03	1.3	18.5
Head width	33	51.66	47.82 - 55.81	1.44	51.03
Nuchal shield minimum width	33	17.71	15.63 - 20.3	1.07	18.32
Cleithral width	33	69.65	65.26 - 73.9	2.04	68.22
Maxillary barbel length	32	54.2	37.57 - 71.33	7.35	57.01
Outer mental barbel length	32	23.82	18.87 - 28.48	2.08	20.56

Counts	n	Range	Mode	Holotype
Dorsal fin	34	II,6	-	II,6
Pectoral fin	34	I,8-10	I,9	I,9
Pelvic fin	34	i,6	-	i,6
Anal fin	12	iv-v,9-10	v,9	iv,10
Caudal fin (dorsal/ventral)	35	i,7/8,i	-	i,7/8,i
Dorsal/ventral procurrent rays	34	12-15/12-15	14/13	14/14
Midlateral scutes	34	31-32	32	32

SL. Head large, deep, weakly compressed with prominent conical snout. Body elongate, slightly compressed, deepest at dorsal-fin origin, gently tapering to short, slender caudal peduncle. Ventral surface flattened from snout to anal-fin origin. Dorsal profile straight to weakly concave from snout tip to between anterior and posterior nares, then curving gently (convex) to above eye, continuing straight, weakly oblique to middle pitline of supraoccipital and finishing with low rounded (convex) hump along nuchal shield. Eye very large, covered by thin skin (adipose eyelid not distinct), positioned high on head; dorsal margin of orbit concave in dorsal view; interorbital width narrow to moderate (17.07–24.03% of oblique head length).

Mouth small, subterminal; gape with rounded anterior (premaxillary) margin, straight to weakly concave posterior (dentary) margin. Teeth absent from premaxilla. Dentary typically with 4–15 acicular teeth in small patch.

First gill arch with 13–14 rakers (3 upper, 10–11 lower; n = 2, ANSP 181055, 148.6 and 169 mm SL), length of longest raker 4 to 5 times lateralmost width; medial edge of raker extended by soft fleshy flap usually with shallowly scalloped to deeply lobed margin. Preaxial face of first arch smooth; postaxial face with soft fleshy lamellae and papillae; lamellae/papillae part of larger system of similar structures associated with remaining arches that carpets inner surfaces of pharyngeal cavity. Lamellae/papillae on postaxial face of first arch arranged into two distinctly spaced rows; inner row wide, occupying about half the width of face; outer row narrow, arising from skin along bases of filaments; both rows following entire length of arch or nearly so. Inner row with 9–10 wide and thick lamellae oriented approximately perpendicular to long axis of arch; smaller lamellae triangular with entire margin, larger ones with lobed or scalloped margins, particularly in larger specimen. Outer row with 8–13 smaller papillae either short or elongate (fingerlike), but not lobed. Lamellae/papillae in inner and outer rows not regularly aligned with each other, nor with rakers.

Anterior and posterior nares separate, each surrounded by short tubular skin; posterior naris larger than anterior one, located approximately at midpoint between anterior naris and anterior margin of eye; anterior naris closer to posterior naris than snout tip. Cephalic shield weakly ornamented, typically without distinct middorsal groove posterior to middle pitline of supraoccipital. Cranial fontanel with single opening anterior to epiphyseal bar (posterior cranial fontanel occluded). Fontanel elongate, narrow, widest with rounded margin posteriorly, attenuate anteriorly; enclosed posteriorly and laterally by frontals, anteriorly by mesethmoid, and set in shallow bony furrow that continues posteriorly onto supraoccipital, finishing before middle pitline. Nuchal foramina absent. Nuchal portion of cephalic shield slightly elevated forming low rounded hump and roof-shaped, forming transverse angle. Anterior nuchal plate well-developed, pentagonal to hexagonal, wider than long and sharing broad lateral suture with epioccipital. Mesethmoid elongate, attenuate anteriorly with acutely pointed tip. First infraorbital comparatively short, anterior end evenly tapered and extending relatively short distance beyond medial concavity for anterior naris (Fig. 4A). Epioccipital posterior process long, ribbon-like, twisted from horizontal plane (anteriorly) to vertical plane (posteriorly), not expanded posteriorly, and weakly contacting posterior nuchal plate.

Three pairs of barbels. Maxillary barbel long, tip reaching approximately medialmost end of gill opening; fimbriate with 6-10 fimbriae along lateral margin; proximal fimbriae rugose with elongate papillae. Mental barbels nearly equal in size, reaching to about halfway between anterior margin of lower jaw and medialmost end of gill opening; bases thick, profusely ornamented with fleshy papillae. Lips fleshy, surfaces with low rounded papillae near insertion of maxillary barbels.

Pectoral girdle in ventral view subtriangular; elongated with medially convergent lateral margins of symphyseal (horizontal) limbs of cleithrum long, straight; truncated anteriorly with bluntly rounded (convex) margin across symphysis. Transverse limb of coracoid with distinct posterior process (keel) relatively short, extending slightly beyond posterior insertion of pectoral fin. Distal ends of posterior coracoid processes with weak ornamentation (ridges) visible beneath thin skin. Remaining ventral surfaces of pectoral girdle covered with slightly thicker skin.

Postcleithral process blade-like, long and shallowly subrectangular (depth 3.05–3.84 times into oblique length in adults); margins entire, without conspicuous dentations. Dorsal margin variable, usually lacking distinct hump below posterior margin of posttemporal-supracleithrum; dorsal free margin either straight, forming distinct dorsal posterior corner with oblique posterior margin (Fig. 2G), or weakly convex, curving continuously to ventral posterior corner. Ventral margin nearly straight from shoulder to ventral posterior corner of process. Lateral surface of postcleithral process with three longitudial fields of ornamentation usually evident, as described for *D. carinatus* except middle field longer and narrower.

Skin relatively smooth except for extremely minute punctate tubercles scattered on head, body and fins, particularly on skin in tympanal region above postcleithral process. Elongate slit-like pore in axilla of pectoral fin. Skin immediately ventral to entire length of postcleithral process perforated with numerous small round pores imparting a sponge-like appearance. Smaller pores present in skin above and below anterior midlateral scutes. Ventral

surfaces (including branchiostegal membranes) with many conspicuous pores, particularly in skin covering breast and abdomen and surrounding vent (Fig. 3C).

Dorsal fin II,6 (n = 34); pectoral fin modally I,9, range I,8–10 (34); pelvic fin i,6 (34), anal fin modally v,9, range iv–v,9–10 (12); caudal fin i,7/8,i (35) with dorsal procurrent rays modally 14, range 12–15 (34) and ventral procurrent rays modally 13, range 12–15 (34). Dorsal-fin origin located approximately two-fifths SL from snout tip. Morphology of fins as described for *D. carinatus* except pectoral-fin spines with serrations along entire anterior margin and caudal-fin lobes slightly more elongate with rounded tips.

Caudal skeleton similar to that of *D. carinatus* with same hypural fusion pattern (PH; HY 1+2; HY 3+4; HY 5), relatively wide V-shaped notch between hypurals 1+2 and 3+4, and Type C hypurapophyses (sensu Lundberg and Baskin, 1969:15). Prezygopophysis-like processes absent from urostyle in single specimen examined (162 mm SL, sk).

Total vertebrae 35 (n = 5). Centra 1–6 fused into Weberian complex with superficial ossification completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal. Vertebra five with pair of slender parapophyses directed posterolaterally in smaller specimen (87.3 mm SL, cs); parapophyses absent from larger specimen (162 mm SL, sk). Vertebrae 6–13 (2) bearing 8 pairs of simple ribs.

Lateral line surrounded by complete series of 31–32 midlateral bony scutes per side (modally 32; n = 34). Morphology largely as described for *D. carinatus* except range of scute depth at pelvic-fin origin one-fifth to one-sixth of corresponding body depth.

Gas bladder large, cordiform with paired posterior chambers longer than single anterior chamber (Fig. 6G). Each posterior chamber with a relatively long, finger-like posterior (subterminal) diverticulum with bases well separated.

Coloration.—Coloration in alcohol largely as described for *D. carinatus* except midlateral scutes lighter making pale midlateral stripe more conspicuous (Fig. 14A). Pelvic fin paler with less dark pigment on dorsal surface; anal fin similarly pale.

Distribution and habitat.—*Doras phlyzakion* is known from lowland drainages in the Solimões (Apaporis-Japurá, Tefé, Lago Amaña) and Negro (Uaupés, Branco) basins in Brazil and Colombia (Fig. 7). This species apparently prefers lentic habitats as it is often recorded from large permanent lakes on the floodplains of major rivers.

Etymology.—Species name from the Greek *phlyzakion*, meaning blister (Jaeger, 1950), alluding to the abundant pores on the ventral surface of body. A noun in apposition.

Remarks.—The ichthyological discovery of this species is likely attributable to the famous naturalist-explorer Alfred Russel Wallace. From 1850-1852 Wallace traveled up the rio Negro to the sources of this river and the río Orinoco during which he took notes on and prepared detailed drawings of fishes collected (Wallace, 2002). Wallace's drawing number 34 of a specimen labeled "*Doras carinatus* Val." (with "*Oxydoras*" written above *Doras*) from the rio Negro, Brazil, corresponds well with *D. phlyzakion*, the only species of *Doras* known from the Negro basin. This drawing's modern identification, by the senior author here in Wallace (2002:325), as alternatively pertaining to *Leptodoras praelongus* is less likely because this species has a distinct black wedge-shaped blotch along base of dorsal fin, a feature that Wallace would not have missed in a fresh specimen.

***Doras zuanoni*, new species**

Figs. 2H, 3B, 6H, 7 & 14B–C
Tables 1 & 6

Doras sp. (Tocantins).—Sabaj Pérez, et al., 2007:166, 189 [comparisons within *Doras*; material examined; rio Araguaia].

Holotype.—Brazil: Tocantins: Tocantins Dr.: INPA 5244 (alc, 124 mm), rio Araguaia, Laguinho Central, Xambioá (GMS82112404), G.M. Santos, 24 Nov 1982.

Paratypes (4).—**Brazil:** Tocantins Dr.: INPA 18628 (1 alc, 162.5 mm), rio Araguaia INPA ichthyological team, Feb 2000; Goiás: ANSP 185367 (1 alc, 139.0 mm), Lagos do rio Araguaia, near city of Luis Alves, 13°14'S, 050°35'W (FLG94-02), F.L.T. Garro, Sep 1994; MCP 18188 (1 alc, 141.0 mm), same data as ANSP 185367; Tocantins: MZUSP 96328 [ex INPA 20408] (1 alc, 96.0 mm), Caseara Lago Paredão, rio Araguaia, 09°17'S, 049°58'32"W, J.A. Zuanon et al., 14 Nov 2000.

Diagnosis.—*Doras zuanoni* is diagnosed among extant congeners by six unique characteristics: 1) gas bladder with two elongate posterior (terminal) diverticula with bases conjoined (Fig. 6H); 2) anterior lateral shoulders of anterior chamber of gas bladder each with a short rounded diverticulum (Fig. 6H); 3) interorbital region wide, 26.7–28.24% of oblique head length; 4) dorsal and ventral procurrent caudal fin rays few, 10; 5) pale midlateral stripe distinct, strongly contrasted with darker sides above and below, beginning near posterior margin of orbit, continuing across tympanal region and finishing along

midlateral scutes to caudal fin (Figs. 14B–C); and 6) pale middorsal stripe present from nuchal shield to caudal fin. *Doras zuanoni* is distinguished from fossil species †*Doras dioneae* by having a shallow postcleithral process, depth 3.31–3.78 (vs. 2.75) times into oblique length.

Comparisons.—Other species of extant *Doras* have gas bladder with two posterior diverticula subterminal with bases separate (*D. phlyzakion*; Fig. 6G) or with a single terminal diverticulum (*D. carinatus*, *D. micropoeus*, *D. higuchii*; Figs. 6A–F); shoulders of anterior chamber of gas bladder smooth, lacking diverticula; interorbital relatively narrow, width 12.46–24.03% of oblique head length; dorsal and ventral procurrent caudal fin rays more numerous, 12–16; pale midlateral stripe absent or weakly evident and restricted to midlateral scutes; and pale middorsal stripe absent.

Description.—Morphometrics and meristics summarized in Table 6; aspects of postcleithral process summarized in Table 1. Largest specimen examined 162.5 mm SL. Head large and deep with short conical snout. Body comparatively stout, deepest at dorsal-fin origin, gently tapering to short, slender caudal peduncle. Ventral surface flattened from snout to anal-fin origin. Dorsal profile straight to weakly concave from snout tip to between anterior and posterior nares, then curving gently (convex) to middle pitline of supraoccipital, usually finishing with low rounded (convex) hump along nuchal shield. Eye large (24.36–27.76% of oblique head length), covered by thin skin (adipose eyelid not distinct), positioned high on head and slightly anterior to midpoint between snout tip and dorsal-fin origin; dorsal margin of orbit concave in dorsal view; interorbital comparatively wide (26.7–28.24% of oblique head length).

Mouth small, subterminal; gape with rounded anterior (premaxillary) margin, straight to weakly concave posterior (dentary) margin. Teeth absent from premaxilla. Dentary edentate (one specimen, 162.5 mm SL) or with 3–5 acicular teeth in single row (holotype, 124 mm SL).

First gill arch with 15 short rakers (3 upper, 12 lower; n = 1, holotype, 124 mm SL), length of longest raker about 3 times lateralmost width; medial edge of raker extended by soft fleshy flap with entire margin (Fig. 10C). Medial and preaxial faces of first arch with soft fleshy lamellae and papillae; lamellae/papillae part of larger system of similar structures associated with remaining arches that carpets inner surfaces of pharyngeal cavity. Lamellae/papillae on postaxial face of first arch arranged into two distinctly spaced rows; inner row wide, occupying about half the width of face; outer row narrow, arising from skin along bases of filaments; both rows following entire length of arch or nearly so (Fig. 10C, right). Inner row with 10 wide and thick lamellae oriented approximately perpendicular to long axis of arch; lamellar margin entire or lobed in larger papillae. Outer row with 16 smaller papillae either short or elongate (fingerlike), but not lobed. Lamellae/papillae in inner and outer rows not regularly aligned with each other, nor with rakers. Preaxial face of first arch with single row of a few very small, short rounded papillae arising from skin along bases of filaments on lower arch (Fig. 10C, left).

Anterior and posterior nares separate, each surrounded by short tubular skin; posterior naris larger than anterior one, located approximately at midpoint between anterior naris and anterior margin of eye; anterior naris closer to posterior naris than snout tip. Cephalic shield weakly ornamented; middorsal groove on posterior supraoccipital and nuchal shield largely absent, but partially evident in one specimen (ANSP 185367, 139 mm SL), beginning at middle pitline of supraoccipital and finishing before suture between anterior and middle nuchal plates. Cranial fontanel with single opening anterior to epiphyseal bar (posterior cranial fontanel occluded). Fontanel elongate, narrow, widest with rounded margin posteriorly, attenuate anteriorly; enclosed posteriorly and laterally by frontals, anteriorly by mesethmoid, and set in shallow bony furrow that continues posteriorly onto anterior supraoccipital, finishing at or just before middle pitline. Nuchal foramina absent. Nuchal portion of cephalic shield slightly to sharply elevated forming rounded hump and roof-shaped, forming transverse angle. Anterior nuchal plate well-developed, pentagonal to hexagonal, wider than long and sharing broad lateral suture with epioccipital. Mesethmoid elongate, anterior end attenuate with acutely pointed tip. First infraorbital comparatively short, anterior end evenly tapered and extending relatively short distance beyond medial concavity for anterior naris (compare Fig. 4A). Epioccipital posterior process long, ribbon-like, twisted from horizontal plane (anteriorly) to vertical plane (posteriorly), weakly expanded posteriorly and contacting posterior nuchal plate.

Three pairs of barbels. Maxillary barbel long, tip reaching approximately medialmost end of gill opening; fimbriate along lateral margin; proximal fimbriae rugose with papillae. Mental barbels nearly equal in size, reaching to about halfway between anterior margin of lower jaw and medialmost end of gill opening, bases thick, moderately ornamented with fleshy papillae. Lips fleshy, surfaces with low rounded papillae near insertion of maxillary barbels.

Pectoral girdle in ventral view subtriangular; elongated with medially convergent lateral margins of symphyseal (horizontal) limbs of cleithrum long, straight; truncated anteriorly with bluntly rounded (convex) margin across symphysis. Transverse limb of coracoid with distinct posterior process (keel) relatively short, extending slightly

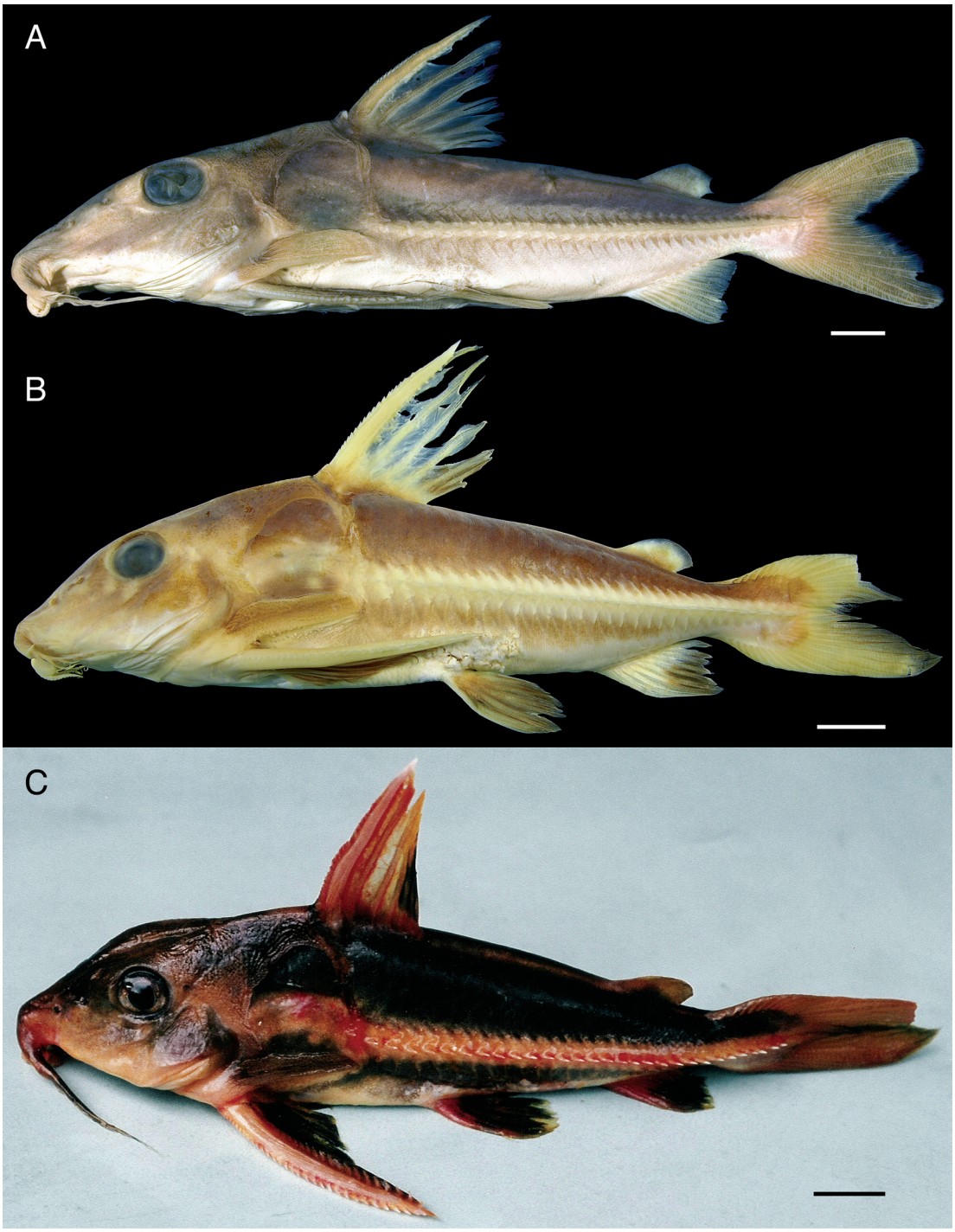

Fig. 14. A. *Doras phlyzakion*, MZUSP 88508 (Holotype, SL 160.8 mm), Rio Tefé, Brazil, B. *D. zuanoni*, INPA 5244 (Holotype, SL 124 mm), Rio Araguaia, Brazil, C. *D. zuanoni* (live), INPA uncataloged (SL ca. 110 mm), Rio Araguaia basin, Brazil. Scale bar equals 1 cm. Photos by E. Baena (A), M. Sabaj Pérez (B) and J. Zuanon (C).

Table 6. Morphometrics and meristics in *Doras zuanoni* n. sp.

Measurements	n	Mean	Range	SD	Holotype
Standard Length (mm)	5	132.5	96 - 162.5		124
% in SL					
Predorsal distance	5	44.15	42.77 - 45.94	1.28	43.71
Prepectoral distance	5	29.68	28.31 - 31.35	1.48	28.31
Oblique head length	5	31.36	29.85 - 33.19	1.38	30.81
Body depth at dorsal-fin origin	5	27.44	26.85 - 28.13	0.51	26.85
Depth of caudal peduncle	5	7.19	6.85 - 7.7	0.34	6.85
Length of caudal peduncle	5	14.08	12.81 - 15.57	1.03	14.52
Length of postcleithral process	5	14.69	14.15 - 15.32	0.46	14.44
Dorsal-fin spine length	5	23.47	21.94 - 24.18	0.88	23.63
Pectoral-fin spine length	5	30.39	29.17 - 31.37	0.93	31.37
Anal-fin base length	5	11.35	10.46 - 12.71	0.83	11.29
Adipose-fin base length	5	11.13	9.52 - 13.72	1.57	9.52
Depth of tenth midlateral scute	5	6.57	6.03 - 7.26	0.5	7.26
% in Oblique Head Length					
Snout length	5	55.18	53.18 - 56.81	1.62	56.81
Horizontal eye diameter	5	25.73	24.36 - 27.76	1.37	24.61
Interorbital minimum width	5	27.31	26.7 - 28.24	0.64	26.7
Head width	5	62.4	60.73 - 65.41	1.76	60.73
Nuchal shield minimum width	5	22.08	20.51 - 23.53	1.1	21.99
Cleithral width	5	86.17	83.77 - 89.65	2.43	83.77
Maxillary barbel length	4	59.03	49.65 - 65.45	7.52	65.45
Outer mental barbel length	4	24.18	20.9 - 30.31	4.37	24.35

Counts	n	Range	Mode	Holotype
Dorsal fin	5	II,6	-	II,6
Pectoral fin	5	I,8	-	I,8
Pelvic fin	5	i,6	-	i,6
Anal fin	4	iii-v,8	iv,8	v,8
Caudal fin (dorsal/ventral)	5	i,7/8,i	-	i,7/8,i
Dorsal/ventral procurrent rays	5	10/10	-	10/10
Midlateral scutes	5	30-32	31	31

beyond posterior insertion of pectoral fin. Distal ends of posterior coracoid processes with weak ornamentation (ridges) visible beneath thin skin. Remaining ventral surfaces of pectoral girdle covered with slightly thicker skin.

Postcleithral process blade-like, long and shallowly subrectangular (depth 3.31–3.78 times into oblique length); margins entire, without conspicuous dentations (Fig. 2H). Free dorsal margin straight to weakly concave; dorsal posterior corner usually distinct; ventral margin nearly straight from shoulder to ventral posterior corner of process. Lateral surface of postcleithral process with three longitudial fields of ornamentation usually evident, as described for *D. carinatus* except ornamentation more granular and middle field narrower.

Skin relatively smooth except for minute punctate tubercles scattered on head, body and fins. Elongate slit-like pore in axilla of pectoral fin. Skin immediately ventral to entire length of postcleithral process perforated with numerous smaller round pores imparting a sponge-like appearance. Smaller pores present in skin above and below anterior midlateral scutes. Ventral surfaces with conspicuous pores, a few in skin on breast in small patch near ventral medial insertion of gill flap, many scattered on abdomen becoming more abundant in pelvic region and around vent (Fig. 3B).

Dorsal fin II,6 (n = 5); pectoral fin I,8 (5); pelvic fin i,6 (5), anal fin modally iv,8, range iii–v,8 (4); caudal fin i,7/8,i (5) with dorsal and ventral procurrent rays 10 (5). Dorsal-fin origin located approximately two-fifths SL from snout tip. Morphology of fins as described for *D. carinatus* except pectoral-fin spine with serrations along entire anterior margin.

Caudal skeleton similar to that of *D. carinatus* with same hypural fusion pattern (PH; HY 1+2; HY 3+4; HY 5), relatively wide V-shaped notch between hypurals 1+2 and 3+4, and Type C hypurapophyses (sensu Lundberg and Baskin, 1969:15). Prezygopophysis-like processes absent from urostyle in single specimen examined (139 mm SL, alc, dissected).

Total vertebrae 35 (n = 3). Centra 1–6 fused into Weberian complex with superficial ossification completely enclosing aortic passage; seventh centrum firmly attached to Weberian complex via interdigitating suture and bearing exit of aortic canal. Parapophyses not observed on fifth vertebra in single dissected specimen (139 mm SL). Vertebrae 6–13 (1) or 6–14 bearing 8 or 9 pairs of simple ribs, respectively.

Lateral line surrounded by complete series of 30–32 midlateral bony scutes per side (modally 31; n = 5); morphology largely as described for *D. carinatus* except midlateral scutes with posterior margins more regularly serrated, and range of midlateral scute depth at pelvic-fin origin about one-fourth to one-sixth of corresponding body depth.

Gas bladder large, cordiform, with paired posterior chambers longer than single anterior chamber (Fig. 6H). Each posterior chamber with elongate, finger-like terminal diverticulum; bases of diverticula conjoined, distal ends separate, divergent. Anterior lateral shoulders of anterior chamber each with short rounded diverticulum.

Coloration.—Dorsal and lateral surfaces of head and body with dark gray-brown (preserved) to black (live) ground color; distinct pale stripe begins near posterior orbit, continues across tympanal region and along midlateral scutes to caudal fin; narrower pale middorsal stripe from nuchal shield to caudal fin (Fig. 14B–C). Ventral surfaces and ventralmost side of body and head completely pale, white. Maxillary barbels dark, gray-tan to black; jaw barbels pale, white. Dorsal fin pale along base and on dorsal spine; dark blotch on posterior half of fin. Pectoral-fin spine relatively pale; rays and membranes dark. Pelvic fin dusky with pigment more concentrated on membranes. Anal fin with base and anterior margin pale, remaining portion dusky with pigment more concentrated on membranes.

The contrasting black and white coloration of *D. zuanoni* closely resembles that of the distantly related doradid genus *Platydoras*. Carvalho et al. (2003) described daytime interactions wherein juvenile *Platydoras* were observed cleaning the piscivorous characin *Hoplias* in a tributary of the rio Araguaia. They hypothesized the strongly contrasting black and white coloration of *Platydoras* to signal its recognition as a cleaner. It is unknown whether such coloration similarly serves the sympatric *D. zuanoni*.

Distribution and habitat.—*Doras zuanoni* is known from the lower to middle rio Araguaia, the largest tributary of rio Tocantins in east-central Brazil (Fig. 7). This species, like *D. phlyzakion*, appears to prefer lentic habitats.

Etymology.—Species named in honor of Jansen Alfredo Sampaio Zuanon for his extensive and valuable contributions to the collection, taxonomy and natural history of neotropical fishes, including discovery of this species.

DISCUSSION

Species groups.—The five extant species of *Doras* are separated into two groups, the monophyletic *phlyzakion* group composed of *D. phlyzakion* (Solimões-Amazon tributaries) and *D. zuanoni* (Araguaia-Tocantins drainage), and the *carinatus* group composed of *D. carinatus*, *D. micropoeus* (both Atlantic coast drainages of the Guianas, the former also in a right-bank tributary of lower Orinoco), and *D. higuchii* (lower Amazon tributaries). The

two groups are defined by the following set of eight characteristics: 1) midlateral scutes 30-32 in *phlyzakion* group vs. typically 33-36 in *carinatus* group, 2) total vertebrae 35 in *phlyzakion* group vs. 37–39 in *carinatus* group, 3) many small conspicuous pores in skin surrounding vent and especially on abdomen in *phlyzakion* group vs. pores absent or restricted to skin surrounding vent in *carinatus* group, 4) first infraorbital short, not extending far beyond medial concavity for anterior naris in *phlyzakion* group vs. first infraorbital elongate, extended well beyond medial concavity as attenuate wing in *carinatus* group, 5) serrations along anterior margin of pectoral spine present to tip in *phlyzakion* group vs. serrations usually absent from distalmost tip in *carinatus* group, 6) symphyseal (horizontal) limb of cleithrum with lateral margin straight and pectoral girdle truncated anteriorly with bluntly rounded (convex) margin across symphysis in *phlyzakion* group vs. lateral margin of symphyseal limb and anterior margin of pectoral girdle across symphysis concave in *carinatus* group, 7) dentition reduced, premaxilla edentate and dentary with 15 or fewer acicular teeth in *phlyzakion* group vs. premaxilla typically with 1–9 acicular teeth and dentary with patch of 10–60 acicular teeth in *carinatus* group, 8) gas bladder with two posterior finger-like diverticula in *phlyzakion* group vs. posterior diverticula asymmetrical, one side absent or grossly reduced and fused, effecting single terminal diverticulum in *carinatus* group.

The occurrence of numerous pores in skin on undersurface of body in the *phlyzakion* group diagnoses it as monophyletic as this has not been observed in other species of doradids and is rare if not unique among catfishes. *Dinotopterus foveolatus*, a deepwater lake clariid, is reported to have "skin of the body covered with numerous flat-bottomed circular pits or depressions (Jackson, 1955:682)" which are of uncertain affinity to the pores herein described for *Doras*. Relationships among species of the *carinatus* group remain uncertain. Morphology aside the two groups also are found in different habitats. The *phlyzakion* group is most often recorded from lentic habitats associated with large low-lying rivers and lakes whereas the *carinatus* group is typical of lotic habitats in large, relatively upland rivers on the Guiana and Brazilian Shields.

Biogeography.—Sabaj Pérez et al. (2007) hypothesized extinction events for the genus *Doras* in the Maracaibo and Orinoco river basins based in part on their newly described fossil, †*D. dioneae*, from the Urumaco Formation, northwestern Venezuela, and presumed absence of *Doras* from the present-day Maracaibo and Orinoco. According to their scenario †*D. dioneae* inhabited the "Paleo-Amazon-Orinoco", a large and long-persistent river system that originated far south in western Amazonia and flowed north in the Andean foreland basin to empty into the Caribbean on the northern coast of South America near the present-day exposure of the Urumaco Formation. In the Late Miocene (ca. 8 Ma) the rising mountain divides of the Eastern Andes and Coastal Cordilleras isolated the Caribbean outlet, and the "Paleo-Amazon-Orinoco" river system fragmented into today's fluvial courses. The present Maracaibo basin represents the lowermost course and outlet (in part) of the "Paleo-Amazon-Orinoco" whereas the modern Orinoco receives waters formerly draining into its middle course. The Amazon and possibly extreme northern headwaters of the Paraná system now drain its upper course eastward and southward, respectively (Sabaj Pérez et al., 2007, and references therein).

Doras are absent from the present Maracaibo and their extinction from the Miocene precursor to this basin is paralleled by another fossil catfish described from the Urumaco Formation, †*Phractocephalus nassi* (Lundberg and Aguilera, 2003). Based on personal communications with P. Petry, F. Provenzano, and C. Ferraris adult specimens collected in the Paragua, a tributary of the Caroní, itself draining into the lower Orinoco, were examined here and their identifications confirmed as *D. carinatus* as diagnosed in this study. *Doras* remains unknown from the remainder of the Orinoco river system.

The fish fauna of upper Caroní shares common elements with those of the upper Caura (Orinoco drainage) to the west, and the Cuyuní (Essequibo drainage) to the east (Lasso et al., 1991; Machado-Allison et al., 2003). The upper Caroní fauna, however, appears to be relatively distinct from the mainstem Orinoco, its low-lying floodplain and left-bank tributaries (e.g., Meta, Apure) draining into the middle to lower Orinoco (Abell et al., 2008). Lasso et al. (1991) used faunal similarities and modern drainage patterns to hypothesize a historical connection between the Caroní and Cuyuní. Specifically, rivers of the Gran Sabana region of southeastern Bolivar State, Venezuela, are thought to have drained northeastward into the upper Cuyuní (Essequibo basin) prior to their capture by the upper Caroní and present incorporation into the Orinoco basin. The occurrence of *Doras carinatus* in both the upper Caroní and upper Cuyuní (i.e., Yuruari) basins provides further evidence for historical and sizeable connections between upland rivers currently draining the western Guiana Shield northward into the Orinoco and more eastern rivers (e.g., Cuyuní-Essequibo) draining the Shield into the Atlantic Ocean. Taken together the presumed absence of *Doras* in left-bank tributaries of the middle to lower Orinoco, the fossil †*D. dioneae*, and the putative course of the "paleo-Amazon-Orinoco" imply an extinction event in a portion of the modern-day Orinoco basin and further distinguish the fish faunas of its middle to lower left-bank (Andean) and right-bank (Shield) tributaries.

The distributions of the two species groups also imply interesting historical connections. The *carinatus* group is distributed both north and south of the Amazon channel in rivers draining the Guiana Shield northwards (*D. carinatus* and *D. micropoeus*) and southwards (*D. higuchii* in the Trombetas and Jari) and the Brazilian Shield northwards (*D. higuchii* in the Xingu). The *phlyzakion* group, on the other hand, occurs in lowland portions of the Solimões (*D. phlyzakion*) and Araguaia (*D. zuanoni*), two regions separated by the northcentral uplands of the Brazilian Shield centered on Serra do Cachimbo and currently inhabited by *D. higuchii*.

KEY TO EXTANT SPECIES OF *DORAS*

1A. Midlateral scutes (beginning with infranuchal) 30–32; first infraorbital relatively short, anterior tip extending short distance beyond medial concavity for anterior naris (Fig. 4A); many small conspicuous pores in skin surrounding vent and especially on abdomen (Figs. 3B–C); premaxilla edentate (toothless); gas bladder with two distinct posterior diverticula, their bases either separate or conjoined (Figs. 6G–H) ……..…….. **2**

1B. Midlateral scutes 33–36 or less than 30 with anteriormost postinfranuchal scutes absent; first infraorbital elongate, anterior wing well-developed with tip extending far beyond medial concavity for anterior naris (Figs. 4B–D); conspicuous pores absent from undersurfaces or few small pores restricted to skin surrounding vent (Fig. 3A); premaxilla typically with 1–9 strong acicular teeth (rarely edentate); gas bladder with one small posteriormost (= terminal) diverticulum (Figs. 6A–F) …..... **3**

2A. Side of body dark gray to black above and below white midlateral stripe along scutes; narrow white middorsal stripe evident; procurrent caudal fin rays 10; interorbital width 26.7–28.2% of oblique head length; pores on breast restricted to small patch near ventral medial insertion of gill flap (Fig. 3B); gas bladder with two long posteriormost (terminal) diverticula conjoined at base, and short rounded diverticulum on each anterior lateral shoulder of anterior chamber (Fig. 6H); Araguaia basin.....***Doras zuanoni* n.sp.**

2B. Side of body above midlateral scutes gray, only slightly darker along and above dorsal wings of midlateral scutes; white middorsal stripe absent; procurrent caudal fin rays 12–15; interorbital width 17.1–24% of oblique head length; numerous pores scattered on breast (Fig. 3C); gas bladder with two long posterior (= subterminal) diverticula with bases well separated, and lacking diverticulae on anterior chamber (Fig. 6G); middle Amazon basin.....***Doras phyzakion* n.sp.**

3A. Infranuchal scute typically covered with skin, lacking posteriorly pointed wings and with medial thorn weak or absent (Fig. 5C); postinfranuchal midlateral scutes gradually but distinctly decreasing in depth and increasing in separation anteriorly from above anal fin (anteriormost scutes sometimes lost entirely); coastal drainages of Guianas…..... ***Doras micropoeus***

3B. Infranuchal scute partially exposed with posteriorly pointed wings flanking distinct medial thorn (Figs. 5A–B); postinfranuchal midlateral scutes overlapping and of approximately uniform depth anterior to anal fin, not decreasing in depth anteriorly…….....…….....**4**

4A. Postcleithral process typically longer and shallower (depth 2.28–3.93 times into oblique length in adults) with free dorsal margin straight to weakly concave and dorsal field of ornamentation moderately expanded, excluded from or forming less than one third of posterior margin of process (Figs. 2B–D); skin covering dorsal-locking spinelet and base of dorsal spine moderately darkened by weak concentration of pigment, remaining dorsal spine dusky or becoming gradually lighter distally; caudal fin uniformly dusky with scattered pigment; lower Orinoco basin and coastal drainages of Guianas.....…….....……...***Doras carinatus***

4B. Postcleithral process typically shorter and deeper (depth 1.80–2.49 times into oblique length in adults) with free dorsal margin straight to weakly convex and dorsal field of ornamentation broadly expanded, forming one third to half of posterior margin of process (Figs. 2E); skin covering dorsal-locking spinelet and sometimes base of dorsal spine blackened with strong concentration of pigment, remaining dorsal spine relatively pale; caudal fin with two dusky longitudinal stripes, one on ventral half of dorsal lobe and second on dorsal half of ventral lobe, particularly in juveniles; lower Amazon basin.....***Doras higuchii* n.sp.**

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2007 Pipe Expedition (left to right: Nathan Lujan, José Birindelli, Leandro Sousa, André Netto-Ferreira) at rio Curuá, near town of Castelo dos Sonhos, Brazil, type locality of *Doras higuchii*. Photo by M. Sabaj Pérez.

Doras micropoeus, ANSP 187110, 225 mm SL, Suriname, Lawa River (Marowijne Dr.), base camp about 8 km south-southwest of Anapaike/Kawemhakan, 18 April 2007. Photo by M. Sabaj Pérez.