

Two New Species of Thicklip Thornycats, Genus *Rhinodoras* (Teleostei: Siluriformes: Doradidae)

Mark H. Sabaj¹, Donald C. Taphorn², and Otto E. Castillo G.²

Rhinodoras is newly diagnosed within Doradidae by its unique combination of coloration (sides darkly mottled, usually with wide dark bars, light midlateral stripe absent) and lip morphology (labial tissue thick, fleshy, considerably expanded at corners of mouth forming rounded flap-like extensions with entire margins, all surfaces rugose with low, rounded and tightly spaced papillae, and distal margin of lower lip draped over bases of outer and inner jaw barbels, at times nearly encircling the latter). Three previously described species are considered valid, *R. thomersoni* (Lake Maracaibo basin), *R. boehlkei* (Amazonas), and *R. dorbignyi* (Paraguay–Paraná), and two new species are described. *Rhinodoras armbrusteri* from the Branco/Essequibo basins is diagnosed by having ventral surfaces with dark pigment, anterior midlateral plates moderately deep with dorsal and ventral wings subequal in depth, sum of midlateral plates 57–60, midlateral plates anterior to vertical through pelvic-fin origin usually five, tympanal portion of lateral-line canal moderately ossified with three distinct plates, postcleithral process moderately short and broad, adipose eyelid moderate to large, pectoral-fin rays usually eight, and one-part gas bladder. *Rhinodoras gallagheri* from the Orinoco basin is diagnosed by having ventral surfaces pale, anterior midlateral plates shallow to moderately deep with dorsal and ventral wings about equal in depth, midlateral plates anterior to vertical through pelvic-fin origin usually five, tympanal portion of lateral-line canal weakly ossified with two to three emergent plates, postcleithral process moderately long and narrow, adipose eyelid moderate to large, pectoral-fin rays usually eight, and one-part gas bladder. *Rhinodoras* is the only doradid genus with extant species in both trans- and cis-Andean drainages.

Se actualiza el diagnóstico del género *Rhinodoras* dentro de la familia Doradidae en base a su patrón de coloración; éste que consiste en lo siguiente: costados oscuramente moteados, carencia de una franja media lateral clara, y generalmente posee tres franjas verticales oscuras; estos caracteres en combinación con una morfología labial especial que en tener el tejido labial grueso, carnoso, y expandido considerablemente en las esquinas de la boca para formar una solapa redondeada sin borde aserrados; la superficie de este tejido es rugosa, con papilas bajas, redondas y casi tocándose entre sí; el margen distal del labio inferior pasa por encima de las bases de las barbillas mentonianas externas e internas, a veces casi encierran a éstas últimas. Se consideran válidas tres especies previamente descritas: *R. thomersoni* (cuenca del Lago de Maracaibo), *R. boehlkei* (Amazonas), and *R. dorbignyi* (Paraguay–Paraná), y se describen dos especies como nuevas. *Rhinodoras armbrusteri* del cuencas del Branco/Essequibo se distingue en poseer las superficies ventrales con pigmento oscuro, las placas laterales medias anteriores son moderadamente profundas y con las alas dorsales y ventrales desiguales en altura; la suma de los conteos de las placas medias laterales de ambos lados oscila entre 57 y 60; presenta cinco placas medias laterales anteriores hasta llegar al nivel del origen de las aletas pélvicas; la porción encima del tímpano del canal de la línea lateral está bien osificada y consiste de tres placas distintas; el proceso postcleitral es moderadamente corto y ancho; el ojo es de moderado a grande, los radios pectorales generalmente son ocho, y la vejiga natatoria presenta una sola cámara. *Rhinodoras gallagheri* del cuenca del Orinoco se distingue de las otras especies del género porque tiene las superficies ventrales claras, las placas medias laterales anteriores son de poca profundidad o de profundidad moderada y con las alas dorsales y ventrales más o menos iguales en altura, cinco placas medias laterales anteriores hasta el nivel de las aletas pélvicas, la porción encima del tímpano del canal de la línea lateral es pobremente osificada, con dos o tres placas emergentes; el proceso postcleitral es moderadamente largo y estrecho, el ojo es de moderado a grande, los radios pectorales usualmente son ocho, y la vejiga natatoria y tiene una sola cámara. *Rhinodoras* es el único género de doradidos existente que habita cuencas en ambos lados de los Andes.

THE Doradidae is a monophyletic assemblage of catfishes (Higuchi, 1992) endemic to South America and comprised of about 80 modern species (Sabaj, 2005; Sousa and Rapp Py-Daniel, 2005; Higuchi et al., 2007)

and one fossil species (Sabaj Pérez et al., 2007) in 31 modern genera (Sabaj and Ferraris, 2003; Higuchi et al., 2007). Commonly known as thorny catfishes, doradids are particularly abundant and species-rich in neotropical lowlands

¹Department of Ichthyology, Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103; E-mail: (MHS) sabaj@acnatsci.org; (DCT) taphorn@cantv.net; and (OEC) ottocastillo@cantv.net. Send reprint requests to MHS.

²Museo de Zoología, Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora, Mesa de Cavacas, Estado Portuguesa, Guanare 3310, Venezuela.

Submitted: 26 June 2005. Accepted: 6 September 2007. Section Editor: D. Buth.

© 2008 by the American Society of Ichthyologists and Herpetologists  Doi:

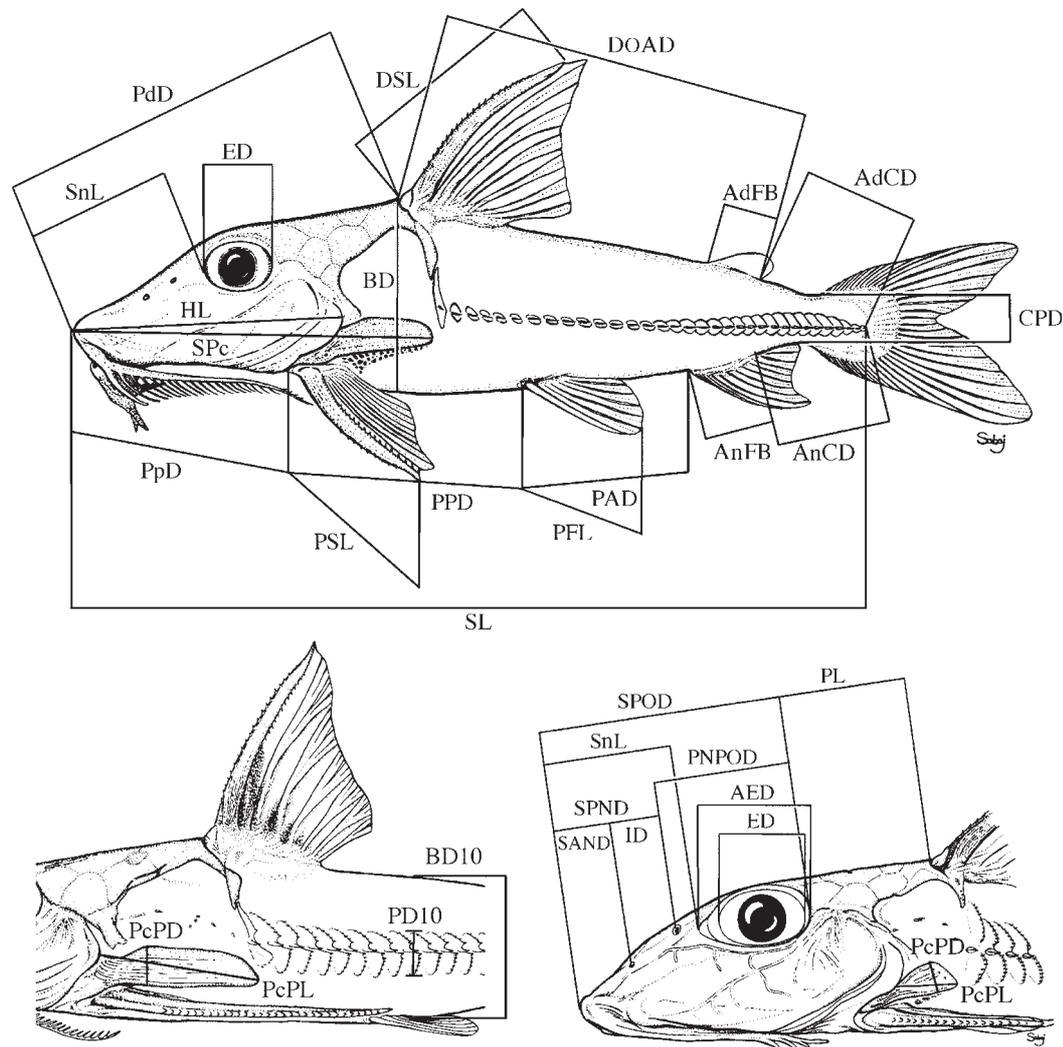


Fig. 1. Landmarks and measurements used for morphometric analysis (plotted on generalized doradids). See Materials and Methods for explanations of abbreviations.

(below 200 m) and large river systems with floodplains that experience prolonged seasonal inundation. The taxonomy of this family has been largely neglected until recently with only four new species having been described in the 30 years prior to 2005 (Glodek, 1976; Glodek et al., 1976; Taphorn and Lilyestrom, 1984; Higuchi et al., 1990). Progress in the taxonomy and systematics of the group has remained tenuous by the uncertain placement and identity of many nominal species. As Reis (2004) noted, modern-day revisions facilitate the discovery of new species in groups with long and unattended taxonomic histories.

The genus *Rhinodoras*, named by Bleeker (1862–63), contains three currently recognized valid species (Higuchi, 1992; Sabaj and Ferraris, 2003): *R. dorbignyi* from the Paraguay–Paraná basin described by Kner (1855), *R. boehlkei* from the Amazonas basin described by Glodek et al. (1976), and *R. thomersoni* from the Lake Maracaibo basin described by Taphorn and Lilyestrom (1984). *Doras nebulosus*, described by Eigenmann and Kennedy (1903), is considered a junior synonym of *R. dorbignyi* (Sabaj and Ferraris, 2003). In his revision of the family, Eigenmann (1925) suggested a close relationship between *Rhinodoras* and doradid taxa having long snouts, relatively narrow pectoral girdles, and fimbriate maxillary and mental barbels. However, *Rhinodoras* has simple barbels and its superficial similarity to other

long-snouted taxa is attributable to convergence (Higuchi, 1992). Herein we newly diagnose *Rhinodoras* and describe two new species, *R. armbrusteri* and *R. gallagheri*, from the Branco/Essequibo and Orinoco River basins, respectively.

MATERIALS AND METHODS

Institutional abbreviations follow Leviton et al. (1985) with the addition of IAvHP for Instituto Alexander von Humboldt, Bogotá, Colombia, UG/CSBD for University of Guyana, Center for the Study of Biological Diversity, Georgetown, and UNT for Universidade do Tocantins, Porto Nacional, Brazil. Measurements were made to the nearest 0.1 mm using digital calipers (<150 mm), dial calipers (150 to 180 mm), or a beam compass (>180 mm). Measurements and corresponding landmarks (Fig. 1) coincide in part with those of Böhlke (1970) and Higuchi et al. (1990). Some measurements were changed to improve repeatability (via better landmarks) or to link the terminus of one with that of another. Poorly defined landmarks (e.g., those requiring physical manipulation of specimen to visualize) were marked with insect pins prior to measurement.

Point-to-point straight-line measurements (Fig. 1) are defined as follows, with first set reported as percentages of standard length (SL): head length (HL), snout tip to

posterior-most extremity of fleshy opercular flap; snout–postcleithral process tip (SPc), snout tip to posterior end of postcleithral process; predorsal distance (PdD), snout tip to posterior margin of second nuchal plate coinciding with median sagittal plane; dorsal origin–posterior adipose distance (DOAD), from groove between posterior margin of second nuchal plate (anterior to base of dorsal-locking spine) to posterior base of adipose fin; adipose–caudal distance (AdCD), posterior base of adipose fin to flexion point of hypural plate coinciding with posterior terminus of SL; prepectoral distance (PpD), snout tip to point between notch formed by margin of cleithrum and anterior base of erected (30–45°) pectoral spine; pectoral–pelvic distance (PPD), from base of pectoral spine (terminus of PpD) to base of first (anterior-most) pelvic-fin ray (best measured by abducting pelvic fin); pelvic–anal distance (PAD), from base of first pelvic-fin ray to base of first anal-fin ray; anal–caudal distance (AnCD), from base of posterior-most anal-fin ray to flexion point of hypural plate coinciding with posterior terminus of SL; dorsal spine length (DSL), from groove between posterior margin of second nuchal plate and base of dorsal locking spine to bony tip of erected (30–45°) dorsal spine excluding soft break-away tip if present; pectoral spine length (PSL), from base of erected (30–45°) pectoral spine to bony tip, excluding soft break-away tip if present; pelvic fin length (PFL), from anterior-most base of first ray to distal-most tip of fin (not the measurement of an individual ray); anal-fin base (AnFB), distance between anterior-most and posterior-most bases of anal-fin insertion; adipose-fin base (AdFB), from origin (point at which anterior margin of adipose fin diverges most conspicuously from dorsal contour of body) to posterior insertion; body depth (BD), greatest distance in median sagittal plane between shallow crest of posterior margin of second nuchal plate and midventral contour of body; caudal peduncle depth (CPD), least depth of caudal peduncle; head width (HW), greatest transverse distance between lateral contours of head (opercula compressed to normal position if flared) anterior to cleithra (also expressed as percentage of HL); cleithral width (CW), greatest transverse distance between lateral contours of cleithra (also expressed as percentage of HL).

The following set is reported as percentages of head length: horizontal adipose eyelid diameter (AED), from anterior-most margin (usually level with weakly defined posterior lateral corner of lateral ethmoid marking anterior end of bony orbit) to posterior-most margin of adipose eyelid (adipose eyelid often becomes opaque during preservation and its anterior margin is usually distinguishable from pigmented skin on snout); snout length (SnL), snout tip to anterior-most margin of adipose eyelid (anterior terminus of AED); snout–anterior nares distance (SAND), snout tip to center of opening of anterior nares; snout–posterior nares distance (SPND), snout tip to center of opening of posterior nares; snout–posterior orbit distance (SPOD), snout tip to posterior bony margin of orbit coinciding with anterior lateral corner of sphenotic; anterior nares–posterior orbit distance (ANPOD), from center of opening of anterior nares to posterior bony margin of orbit coinciding with anterior lateral corner of sphenotic; posterior nares–posterior orbit distance (PNPOD), from center of opening of posterior nares to posterior bony margin of orbit coinciding with anterior lateral corner of sphenotic; internares distance (ID), between centers of openings of anterior and posterior nares; postorbital length (PL), from posterior

bony margin of orbit coinciding with anterior lateral corner of sphenotic to posterior margin of second nuchal plate coinciding with median sagittal plane; postcleithral (humeral) process length (PcPL), from posterior tip of process to point along anterodorsal margin of exposed process where cleithral bone is deflected medially (exposed surface of process appears textured compared to smooth face of medially deflected portion of cleithrum and this deflection often coincides with or lies just beneath posterior-most margin of fleshy opercular flap); postcleithral (humeral) process depth (PcPD), greatest depth orthogonal to straight line formed by long axis of process (also expressed as percentage of PcPL); interorbital width (IW), shortest transverse distance between orbital (lateral) margins of bony frontals. Two measurements are reported as percentages of body depth taken in same transverse plane (adapted from Böhlke, 1970): depth of fifth midlateral plate and of tenth midlateral plate, vertical depth orthogonal to horizontal line formed by medial thorns of plates, from dorsal-most exposed margin of fifth (or tenth) plate to ventral-most margin of corresponding plate.

Counts of fin rays follow Hubbs and Lagler (1958), Böhlke (1970), and Higuchi et al. (1990). Counts in dorsal, anal, and paired fins are separated into anterior spine (capital roman numeral) or unbranched soft ray (lower-case roman numeral) and posterior branched soft rays (arabic numerals). The small locking spine anterior to dorsal-fin spine was not counted. The last (posterior-most) pectoral-fin ray may appear unbranched, particularly in juveniles; it was counted if clearly segmented with base separate from penultimate ray. In rare instances the last pectoral-fin ray may be followed by a much smaller and rather inconspicuous sliver-like element that is clearly unsegmented; this bony element was not included in the count. The anterior-most anal-fin ray may be extremely small and closely adhered to the second ray. The last anal ray may be simple or composed of two branches with bases joined or in very close proximity (counted as one). Counts of midlateral plates begin with the vertically expanded infranuchal plate that dorsally contacts the posterior nuchal plate and ventrally contacts or approaches the distal tip of postcleithral process. Though conspicuous and sometimes bearing medial thorn, the small plate immediately anterior to the infranuchal plate (in tympanal region) was not included in counts of midlateral plates.

Principal component analysis (PCA) was used to investigate morphometric variation within *Rhinodoras*. Principal component analyses were performed separately on the covariance matrices of 30 log-transformed measurements (Table 1) for four sets of specimens (Fig. 2): inclusive of all species, *R. thomersoni* removed, *R. thomersoni* and *R. dorbignyi* removed, and *R. thomersoni*, *R. dorbignyi*, and *R. cf. dorbignyi* removed.

RESULTS

Morphometric analysis.—In all analyses, the resulting first principal component (PC I) explained a large proportion of the total variance (93–95%), and all variable loadings were positive and varied little in magnitude. Therefore PC I was interpreted as a general size factor (Jolicoeur and Mosimann, 1960; Jolicoeur, 1963; McElroy and Douglas, 1995). Scores were plotted for PC II and III, interpreted to represent “general-size-allometry-free shape” (Bookstein, 1989).

Table 1. Morphometric Data for Species of *Rhinodoras*. * indicates measurements used in principal components analyses; ** indicate morphometric based on single specimen.

	(A) <i>R. boehlkei</i> n = 10		(B) <i>R. armbrusteri</i> n.sp. n = 8		(C) <i>R. gallagheri</i> n.sp. n = 10	
	range	mean ± SD	range	mean ± SD	range	mean ± SD
Standard length* (SL) in millimeters percent SL	79.1–136.3	107.7 ± 17.3	63.2–96.2	76.5 ± 10.6	53–117.4	87 ± 23.2
Head length (HL)*	26.2–28.1	27.2 ± 0.6	27.6–29.2	28.6 ± 0.5	26.6–28.5	27.3 ± 0.6
Snout–postcleithral process tip (SPc)*	37.7–40.3	39.1 ± 0.7	41–43.8	42.2 ± 1	39–41.8	40.6 ± 0.8
Predorsal distance (PdD)*	34–35.9	34.9 ± 0.6	36–39.5	37.7 ± 1.3	34.6–37.2	36.2 ± 0.8
Dorsal origin–post. adipose (DOAD)*	53.4–56.6	55.3 ± 1.1	53.3–55.4	54.1 ± 0.9	53.6–55.7	54.7 ± 0.8
Adipose–caudal distance (AdCD)*	13.9–16.4	14.8 ± 0.8	13.6–15.1	14.4 ± 0.5	12.8–15.8	13.9 ± 0.9
Prepectoral distance (PpD)*	22.7–23.9	23.3 ± 0.4	23.9–26.4	24.9 ± 0.9	23.5–25.8	24.3 ± 0.8
Pectoral–pelvic distance (PPD)*	27.9–31.9	29.6 ± 1.3	27.2–32.5	30.6 ± 1.7	28.8–31.2	29.9 ± 0.8
Pelvic–anal distance (PAD)*	18.3–20.6	19.3 ± 0.7	18.1–20	18.9 ± 0.6	17.7–20.1	19.1 ± 0.9
Anal–caudal distance (AnCD)*	17.4–19.6	18.6 ± 0.6	16.7–18.6	17.6 ± 0.7	16.7–18.7	17.8 ± 0.6
Dorsal spine length (DSL)	20.2–26	24 ± 1.8	23.5–26.3	24.7 ± 0.9	22.3–27.4	25.5 ± 1.7
Pectoral spine length (PSL)*	21.7–25.4	23.5 ± 1.1	24.6–27.2	26.1 ± 0.9	24.3–27.1	25.9 ± 0.8
Pelvic fin length (PFL)*	13.6–16.2	15.3 ± 0.8	14.5–17.5	15.6 ± 1	14.9–16.6	15.5 ± 0.5
Anal-fin base (AnFB)*	11.8–13.7	12.9 ± 0.6	10.7–13.4	12.3 ± 0.8	12.3–14.4	13.5 ± 0.6
Adipose-fin base (AdFB)*	23.7–29.7	26.4 ± 1.7	25.5–27.9	26.2 ± 0.8	24.3–30.5	27.4 ± 2.1
Body depth (BD)*	19.7–22.6	21 ± 0.9	20–23.4	22.4 ± 1.1	20.6–22.4	21.5 ± 0.7
Caudal peduncle depth (CPD)*	6.7–7.8	7.2 ± 0.3	7.5–8.3	7.9 ± 0.3	7.2–7.8	7.4 ± 0.2
Head width (HW)	19.4–20.8	20 ± 0.5	20.6–22	21.4 ± 0.4	19.3–21	20.4 ± 0.5
Cleithral width (CW)* percent HL	20.9–23.1	21.7 ± 0.8	21.8–25.4	23.9 ± 1.2	21.6–24.1	22.8 ± 0.8
Horiz. adipose eyelid diameter (AED)*	9.3–11.5	10.3 ± 0.9	11.4–14.2	12.9 ± 0.9	10.9–14.6	12.7 ± 1.1
Snout length (SnL)*	44.2–47.9	46.5 ± 1	46.2–50.4	48.1 ± 1.3	44.8–49.8	47.5 ± 1.7
Snout–anterior nares (SAND)*	17.6–20.8	19.1 ± 1.1	19–21.4	19.8 ± 0.7	17.4–21.2	19.5 ± 1.4
Snout–posterior nares (SPND)*	35–40.5	37.6 ± 1.7	38.3–40.5	39.3 ± 0.7	34.9–38.8	37.1 ± 1.3
Snout–posterior orbit (SPOD)*	53.7–58.1	55.5 ± 1.3	57.4–60.7	59 ± 1.3	56.7–59.6	58.5 ± 1
Ant. nares–posterior orbit (ANPOD)*	36–40.5	38.2 ± 1.6	39.2–43.7	40.5 ± 1.4	38.3–40.2	39.3 ± 0.7
Post. nares–posterior orbit (PNPOD)*	17.9–20	19.2 ± 0.8	20.8–22.3	21.6 ± 0.5	20.2–23.3	21.8 ± 1.1
Internares distance (ID)*	16.8–21.6	19.3 ± 1.6	18.5–23	19.6 ± 1.5	16.5–19.9	18.3 ± 1.2
Postorbital length (PL)*	71.2–79.2	74.8 ± 2.5	66.2–76.3	73.5 ± 3.3	68.3–80.8	75.3 ± 3.9
Postcleithral process length (PcPL)*	39.2–50.4	45.3 ± 3.5	43–52.2	48.4 ± 3	43.8–52.9	48.5 ± 3.4
Postcleithral process depth (PcPD)*	17.9–22.9	19.8 ± 1.5	17–21.6	19.2 ± 1.6	12.5–16.5	14.7 ± 1.2
Interorbital width (IW)*	18–21.8	19.5 ± 1.1	18.8–21.2	19.9 ± 0.8	18.9–22.3	20.2 ± 1.2
Head width (HW)	70.3–77.5	73.7 ± 2	70.7–77.8	74.9 ± 2.4	72.5–78.2	74.6 ± 1.9
Cleithral width (CW)* percent body depth at 5th plate	77–86.3	80 ± 2.8	74.7–87.2	83.5 ± 3.9	79.4–88.5	83.6 ± 3.1
5th midlateral plate depth percent body depth at 10th plate	24.4–34	28.8 ± 2.7	26.3–29	27.4 ± 1	16.6–26.2	20.2 ± 3.6
10th midlateral plate depth percent postcleithral process length	27.7–39	34.2 ± 3.4	30.8–36.6	33.2 ± 2.3	20.1–35.6	26.5 ± 4.1
Postcleithral process depth	37.5–53.6	44.1 ± 5.8	36.8–44.3	39.6 ± 2.4	23.9–34.5	30.6 ± 3.5
	(D) <i>R. cf. dorbignyi</i> (Tocantins) n = 4		(E) <i>R. dorbignyi</i> n = 8		(F) <i>R. thomersoni</i> n = 6	
	range	mean ± SD	range	mean ± SD	range	mean ± SD
Standard length* (SL) in millimeters percent SL	86.5–110.4	97.3 ± 9.9	127.4–177.5	140.1 ± 16.6	66.1–84.5	76 ± 7.8
Head length (HL)*	26.8–27.4	27.2 ± 0.2	27–32.1	29.5 ± 1.6	27.4–28.6	28.1 ± 0.5
Snout–postcleithral process tip (SPc)*	38.5–42.2	40.2 ± 1.9	41.7–46.6	43.9 ± 1.6	44.8–47.4	46.1 ± 0.9
Predorsal distance (PdD)*	34–37.5	35.6 ± 1.6	34.6–40.4	37.2 ± 1.7	37.4–39.5	38.3 ± 0.8
Dorsal origin–post. adipose (DOAD)*	51.4–55.1	53.1 ± 1.5	50.3–55.5	53.6 ± 1.7	51.5–55	53.4 ± 1.2
Adipose–caudal distance (AdCD)*	14.3–15.6	14.9 ± 0.7	12.9–15.3	13.9 ± 0.9	13–15.4	14.3 ± 0.9
Prepectoral distance (PpD)*	22.8–25.7	24.2 ± 1.3	24.2–29.2	26.7 ± 1.7	24.1–27.3	25.4 ± 1.1
Pectoral–pelvic distance (PPD)*	29.8–34	31.9 ± 1.9	31–34.6	32.6 ± 1.6	29.5–32.7	30.8 ± 1
Pelvic–anal distance (PAD)*	17.8–19.2	18.5 ± 0.6	16.4–20.6	17.9 ± 1.3	14.6–16.6	15.9 ± 0.8
Anal–caudal distance (AnCD)*	16–18.1	17.1 ± 1.1	14.6–17.2	15.5 ± 0.9	16.3–19.3	17.8 ± 1.1

Table 1. Continued.

	(D) <i>R. cf. dorbignyi</i> (Tocantins) <i>n</i> = 4		(E) <i>R. dorbignyi</i> <i>n</i> = 8		(F) <i>R. thomersoni</i> <i>n</i> = 6	
	range	mean ± SD	range	mean ± SD	range	mean ± SD
Dorsal spine length (DSL)	24.4–26.2	25.1 ± 0.7	22.3–25.2	24 ± 1.1	25.3–30	27.5 ± 1.8
Pectoral spine length (PSL)*	26.1–26.5	26.3 ± 0.2	23.2–26.8	24.6 ± 1.3	27.3–29.3	28.3 ± 0.8
Pelvic fin length (PFL)*	14.9–16.4	15.6 ± 0.8	12.7–14.1	13.5 ± 0.5	13.7–15.1	14.2 ± 0.5
Anal-fin base (AnFB)*	11.3–14.4	13 ± 1.3	11.2–14.5	13 ± 0.9	12.6–14.9	13.8 ± 0.9
Adipose-fin base (AdFB)*	25.4–28	26.4 ± 1.1	21.9–29.4	25.4 ± 2.6	24.6–26.3	25.3 ± 0.7
Body depth (BD)*	18.4–22.5	20.4 ± 2.1	21.3–23.9	22.4 ± 0.9	22.5–23.9	23.4 ± 0.5
Caudal peduncle depth (CPD)*	7.2–7.7	7.4 ± 0.2	7–8.1	7.6 ± 0.4	6.6–7	6.8 ± 0.2
Head width (HW)	19.4–20.9	20.1 ± 0.6	19.7–22.8	21.2 ± 1	20.3–22.4	21.2 ± 0.7
Cleithral width (CW)* percent HL	21.8–23.9	22.7 ± 1	23.3–26.1	24.6 ± 1	24.9–25.7	25.3 ± 0.3
Horiz. adipose eyelid diameter (AED)*	12.7–14.9	13.9 ± 0.9	10.4–13.9	11.8 ± 1.2	12.1–15.6	13.5 ± 1.3
Snout length (SnL)*	44.8–50.4	47.4 ± 2.6	43.2–47.5	45.2 ± 1.6	38.6–42.4	40.6 ± 1.6
Snout–anterior nares (SAND)*	17.6–21.4	19.6 ± 2	16.3–20.1	17.7 ± 1.1	11.8–14.1	12.9 ± 0.8
Snout–posterior nares (SPND)*	35.7–39.9	37.1 ± 1.9	32.8–38.4	35.7 ± 1.8	28.7–32.4	30.3 ± 1.4
Snout–posterior orbit (SPOD)*	58.2–61.5	59.5 ± 1.4	54.3–59.9	56.6 ± 1.8	51.6–58.6	54.3 ± 2.7
Ant. nares–posterior orbit (ANPOD)*	41.3–43.5	42.2 ± 1	39–41.5	40.2 ± 0.8	41.3–49.1	44.1 ± 3.5
Post. nares–posterior orbit (PNPOD)*	23.7–25.3	24.4 ± 0.7	20.1–24.2	22.4 ± 1.6	24.8–31.3	27.1 ± 2.6
Internares distance (ID)*	17.5–19.3	18.1 ± 0.8	15.5–20.9	18 ± 1.6	16.2–19.6	18 ± 1.1
Postorbital length (PL)*	68.9–76.6	71.9 ± 3.3	65.6–76.5	70.5 ± 4.5	81.2–87	84.9 ± 2.3
Postcleithral process length (PcPL)*	45.9–55.8	50.9 ± 4.2	42.3–57	51 ± 5.2	63.4–69.3	66.6 ± 2.1
Postcleithral process depth (PcPD)*	16.8–19	17.8 ± 0.9	14.5–18.8	16.9 ± 1.5	14.5–18.8	16.3 ± 1.9
Interorbital width (IW)*	17.9–20.1	19 ± 0.9	16.5–20	18.1 ± 1.1	20.6–23.5	21.8 ± 1.2
Head width (HW)	71.5–76.7	74 ± 2.5	68.5–76.3	71.8 ± 3.1	73.2–78.4	75.5 ± 2.3
Cleithral width (CW)* percent body depth at 5th plate	80.6–87.9	83.5 ± 3.3	79.1–90.3	83.4 ± 4	88.2–93.3	90.3 ± 1.7
5th midlateral plate depth percent body depth at 10th plate	20.4**	—	15.4–22.1	18.3 ± 2.2	17.7–24.5	20.7 ± 2.3
10th midlateral plate depth percent postcleithral process length	26.4–37.6	30.3 ± 5.1	21.1–29.9	26.5 ± 2.9	21–27.9	24.9 ± 3.5
Postcleithral process depth	32.2–38.2	35 ± 2.5	30.2–37.9	33.2 ± 2.9	21.7–29	24.4 ± 3

Scatterplot of PC II and III scores of 30 log-transformed morphometric characters (Table 1) resolved 46 specimens of *Rhinodoras* into three non-overlapping clusters on PC II corresponding to *R. thomersoni*, *R. dorbignyi*, and *R. boehlkei* + *R. armbrusteri* + *R. gallagheri* + *R. cf. dorbignyi* (Fig. 2A). Principal component II explained 3.1% of the total variance (Table 2A) and loaded most heavily for postcleithral process length (0.053) and distances snout–anterior nares (0.052) and posterior nares–posterior orbit (0.045). *Rhinodoras boehlkei* clustered apart from *R. armbrusteri*, *R. gallagheri*, and *R. cf. dorbignyi* on PC III (1.3% of total variance). Principal component III loaded most heavily for horizontal diameter of adipose eyelid (0.032), snout–anterior nares distance (0.031), and postcleithral process depth (0.026). Notably, the two specimens of *R. boehlkei* from the Rio Trombetas plotted between clusters formed by the remaining *R. boehlkei* and *R. armbrusteri*.

Scatterplot of PCII and III scores for 40 specimens of *Rhinodoras* (minus *R. thomersoni*) maintained separate clusters for *R. boehlkei* and *R. armbrusteri* (Fig. 2B). Specimens of *R. cf. dorbignyi* (Tocantins basin) grouped most closely with those of *R. dorbignyi* (Paraguay–Paraná basin), and together these specimens occupied a minimum space slightly overlapping that of *R. gallagheri*. Principal components II and III explained 1.8 and 0.8% of the total variance, respectively. Measurements loading most heavily on PC II (Table 2B) were horizontal adipose eyelid diameter (0.043),

posterior nares–posterior orbit distance (0.036), and postcleithral process depth (0.032). Measurements loading most heavily on PC III were postcleithral process depth (0.042), anal-fin base (0.024), and adipose-fin base (0.021).

Scatterplot of PC II and III scores for 32 specimens (minus *R. thomersoni* and *R. dorbignyi*) distributed specimens into four non-overlapping spaces corresponding to the remaining species: *R. boehlkei*, *R. armbrusteri*, *R. gallagheri*, and specimens treated as *R. cf. dorbignyi* (Fig. 2C). Principal components II and III explained 1.8 and 1.3% of the total variance, respectively. Measurements loading most heavily on PC II (Table 2C) were postcleithral process depth (0.048), horizontal adipose eyelid diameter (0.035), and posterior nares–posterior orbit distance (0.024). Measurements loading most heavily on PC III were postcleithral process depth (0.029), horizontal adipose eyelid diameter (0.027), and anal-fin base (0.024).

The fourth scatterplot of PC II and III scores (Fig. 2D) largely maintained separation of 28 specimens into three spaces corresponding to *R. boehlkei*, *R. armbrusteri*, and *R. gallagheri*. Principal components II and III explained 1.7 and 1.1% of the total variance, respectively. Measurements loading most heavily on PC II (Table 2D) were postcleithral process depth (0.06), anal-fin base (0.021), and horizontal adipose eyelid diameter and internares distance (0.016). Measurements loading most heavily on PC III were adipose eyelid diameter (0.031), anal–caudal distance (0.019), and anal-fin base (0.017).

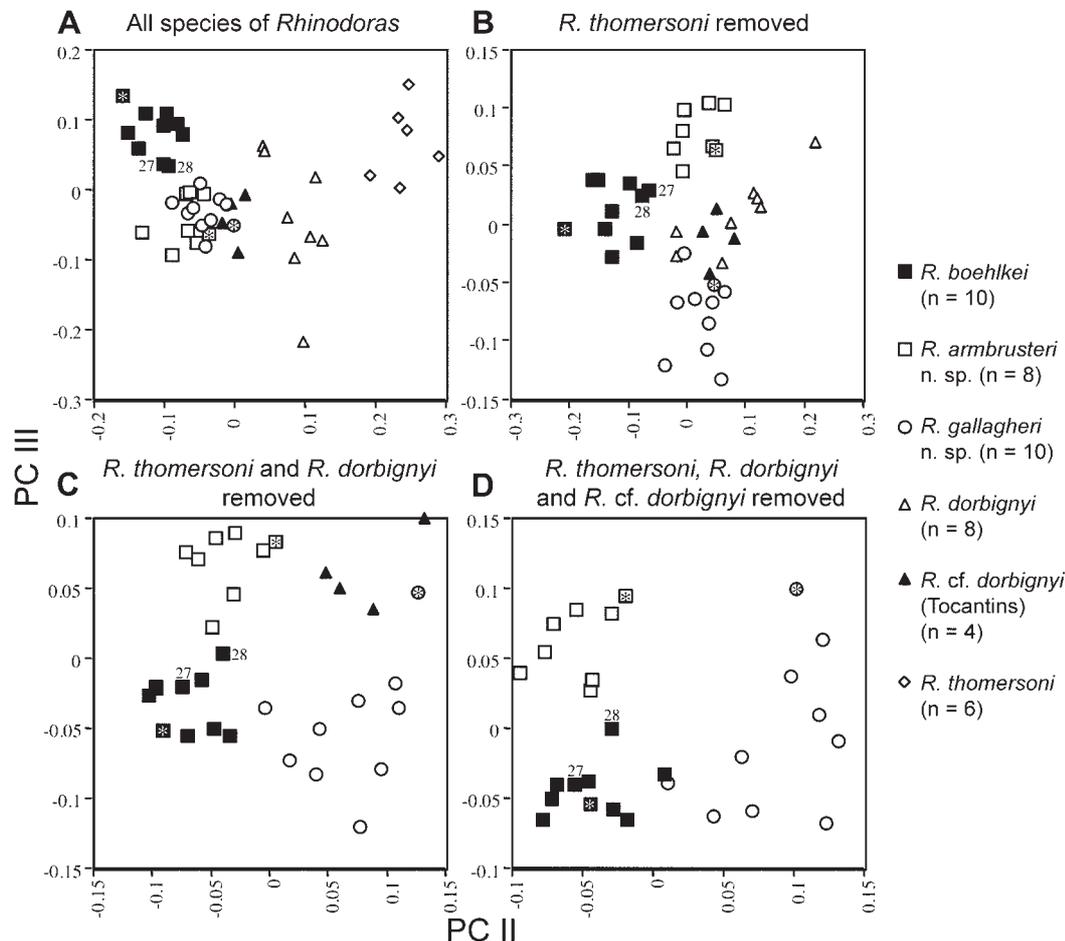


Fig. 2. Plot of scores factored from covariance matrix of 30 log-transformed morphometric variables on principal component axes II and III. Asterisks denote holotypes; numbers denote specimens from the Rio Trombetas.

Rhinodoras Bleeker, 1862

Thicklip thornycats

Rhinodoras Bleeker, 1862:5 [type species: *Doras* (*Oxydoras*) *dorbignyi* Kner, 1855, by original designation]. Gender masculine.

Diagnosis.—*Rhinodoras* is diagnosed within Doradidae by the unique combination of sides darkly mottled, usually with wide dark bars, light midlateral stripe absent; and labial tissue well-developed, fleshy, considerably expanded at corners of mouth forming relatively thick and rounded flap-like extensions with entire margins, labial surfaces rugose with low, rounded and tightly spaced papillae, distal margin of lower lip curves around and appears draped over bases of outer and inner mental barbels, in some specimens nearly encircling the latter (Fig. 3).

Comparisons.—The striking lip morphology of *Rhinodoras* is shared by the monotypic *Orinocodoras eigenmanni* and to a lesser degree by *Oxydoras*. In *Orinocodoras*, however, the sides of the body are dark with a distinct white midlateral stripe running along the midlateral plates and converging dorsally with its pair on the head (vs. sides liberally mottled, often with three wide dark bars and never with white midlateral stripe in *Rhinodoras*). In *Oxydoras* the lips are generally thinner, the papillae are smaller and less conspicuous, the flap-like extensions are shorter, and the lower margin of the lower lip is less closely associated with the bases of the mental barbels. Furthermore in *Oxydoras* the sides are more

uniformly dark above the midlateral plates and either white or mottled below (wide dark bars absent).

Other doradids (e.g., *Anduzedoras*, *Doras*, *Hassar*, *Leptodoras*) may have well-developed labial tissues with flap-like extensions at the corners of the mouth. In these taxa, however, the labial extensions are relatively thin and the bases of the mental barbels are continuous with the lower lip. Furthermore, these taxa have fimbriate maxillary and mental barbels (vs. simple in *Rhinodoras*).

Description.—Morphometric data for each species presented in Table 1. Morphology of head, body, and fins generally similar among all species of *Rhinodoras* (see Descriptions for *R. armbrusteri* and *R. gallagheri*) with diagnostic differences summarized in Table 3. Salient differences relate to head shape and gas bladder morphology. In all *Rhinodoras* except *R. thomersoni* snout elongated (43.2–50.4% HL) and dorsal profile of head and nuchal shield moderately oblique, sometimes becoming gradually level posteriorly and effecting appearance of low rounded hump between the middle pitline of supraoccipital and dorsal-fin origin vs. in *R. thomersoni* snout short (38.6–42.4% HL) and dorsal profile strongly oblique, becoming gradually steeper posteriorly (particularly at middle pitline) before leveling off near suture between anterior and middle nuchal plates (i.e., dorsal profile with distinct, rounded, convex hump from middle pitline to dorsal-fin origin). In *R. armbrusteri*, *R. boehlkei*, and *R. gallagheri* each posterior chamber of gas bladder termi-

Table 2. Highest Loadings for Principal Components II and III Compared for Four Separate Analyses of Body Shape in *Rhinodoras*. Percentages in parentheses refer to total variance explained for corresponding component and analysis.

(A) All species		(B) <i>R. thomersoni</i> removed	
PCII (3.12%)	PCIII (1.26%)	PCII (1.8%)	PCIII (0.81%)
0.053 Postcleithral process length	0.032 Horizontal adipose eyelid diameter	0.043 Horizontal adipose eyelid diameter	0.042 Postcleithral process depth
0.052 Snout–anterior nares distance	0.031 Snout–anterior nares distance	0.036 Posterior nares–posterior orbit distance	0.024 Anal-fin base
0.045 Posterior nares–posterior orbit distance	0.026 Postcleithral process depth	0.032 Postcleithral process depth	0.021 Adipose-fin base
(C) <i>R. thomersoni, R. dorbignyi</i> removed		(D) <i>R. thomersoni, R. dorbignyi, R. cf. dorbignyi</i> removed	
PCII (1.84%)	PCIII (1.29%)	PCII (1.69%)	PCIII (1.06%)
0.048 Postcleithral process depth	0.029 Postcleithral process depth	0.06 Postcleithral process depth	0.031 Horizontal adipose eyelid diameter
0.035 Horizontal adipose eyelid diameter	0.027 Horizontal adipose eyelid diameter	0.021 Anal-fin base	0.019 Anal–caudal distance
0.024 Posterior nares–posterior orbit distance	0.024 Anal-fin base	0.016 Horizontal adipose eyelid diameter and Internares distance	0.017 Anal-fin base

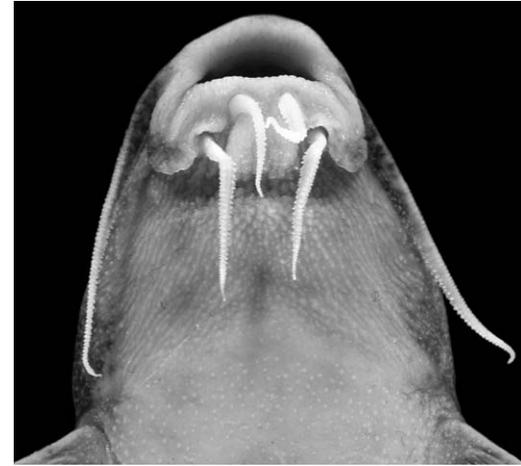


Fig. 3. Lip morphology of *Rhinodoras* exemplified by *R. boehlkei*, ANSP 179562, 116.3 mm SL.

nates with small, horn-like diverticulum medially fused (Fig. 4A). In *R. thomersoni* and *R. dorbignyi* the fused terminal diverticula expand to form second distinct, yet smaller, more elongated bladder with internal longitudinal septum and transverse struts effecting partial honeycomb appearance (Fig. 4B).

Distribution and ecology.—*Rhinodoras* is distributed in the trans-Andean Lake Maracaibo basin and the cis-Andean Amazonas/Tocantins, Essequibo, Orinoco, and Paraguay–Paraná river basins (Fig. 5). The Amazonas, Essequibo, and Orinoco species of *Rhinodoras* are secretive fishes that hide in hollow logs or cavities in lateritic boulders during the day and forage at night. *Rhinodoras dorbignyi* migrates seasonally and spawns by the end of spring (October and November) in the Paraguay–Paraná basin where it feeds on fish, crustaceans, and a variety of other animal and vegetable matter (Ringuélet et al., 1967). Carvajal (2005) reported gut contents of Trichoptera (Helicopsychidae) for *R. gallagheri* and vegetable matter and colonial bryozoans for *R. thomersoni*. Gut contents of *R. armbrusteri* examined in this study included small bivalves (two to three mm long, swallowed whole) and aquatic insects. Guts of *R. armbrusteri* (UG/CSBD 11046) and *R. gallagheri* (FMNH 116466) harbored nematode parasites that appear to represent the fourth larval stage (L4) of an indeterminate species of Camallanoidea (group with sclerotized, jaw-like buccal apparatus; S. Bullard, pers. comm.).

***Rhinodoras armbrusteri*, new species Sabaj**

Dirty Thicklip Thornycat
 Figures 5, 6, 7; Tables 1B, 3B

Holotype.—UG/CSBD 11046 (ex. ANSP 180411), 83 mm SL, Guyana, Rupununi, Takutu River, Branco drainage, St. Ignatius, 1.9 km NNE of Lethem, 03°21'21½N, 059°48'19½W, 2 Nov. 2003, J. Armbruster et al.

Paratypes.—Guyana, Rupununi: ANSP 179095, 1, 81.2 mm SL, Ireng River, Takutu drainage, 6.9 km WSW of village of Karasabai, 04°01'10"N, 059°36'06"W, 1 Nov. 2002, M. Sabaj et al.; ANSP 179096, 2, 51.5, 66.1 mm SL, Takutu River, Branco drainage, ca. 2.8 km W of Saint Ignatius, 03°21'18"N, 059°49'51"W, 5 Nov. 2002, M. Sabaj et al.; ANSP 179097, 2,

Table 3. Summary of Diagnostic Differences between Species of *Rhinodoras*.

	(A) <i>R. boehlkei</i>	(B) <i>R. armbrusteri</i> , new species	(C) <i>R. gallagheri</i> , new species	(D) <i>R. cf. dorbignyi</i> (Tocantins)	(E) <i>R. dorbignyi</i>	(F) <i>R. thomersoni</i>
pigmentation on dorsal and lateral surfaces	moderate to heavy, dark saddles/bars usu. well contrasted with lighter interspaces	heavy, dark saddles/bars evident but poorly contrasted with lighter interspaces	moderate, dark saddles/bars usu. well contrasted with lighter interspaces	heavy, dark saddles/bars usu. evident but poorly contrasted with lighter interspaces	moderate to heavy, dark irregular scattered blotches and/or saddles/bars usu. poorly contrasted with lighter interspaces	weak to moderate, dark saddles/bars usu. poorly contrasted with lighter interspaces and obscured by scattered blotches
pigmentation on ventral surface between mouth and pelvic-fin insertions	weak, pale with few dark speckles on belly (Amazon) or heavy with many large dark speckles (Trombetas)	heavy with many small to large dark speckles on belly and often gular region	weak, pale and largely without dark speckles	heavy with many small to large dark speckles on belly and gular region	weak to heavy with few to many dark speckles on belly usu. not continuing anteriorly beyond pectoral fin	weak, pale and largely without dark speckles
anterior midlateral plates	moderate to deep, depth of 5th plate 24.4–34% of corresponding body depth	moderate, depth of 5th plate 26.3–29% of corresponding body depth	shallow to moderate, depth of 5th plate 16.6–26.2% of corresponding body depth	moderate, depth of 5th plate 20.4% of corresponding body depth	shallow to moderate, depth of 5th plate 15.4–22.1% of corresponding body depth	shallow to moderate, depth of 5th plate 17.7–24.5% of corresponding body depth
dorsal and ventral wings of anterior midlateral plates	subequal, depth of dorsal wing \geq twice that of ventral	subequal, depth of dorsal wing < twice that of ventral	equal depth or nearly so	equal depth or nearly so	equal depth or nearly so	equal depth or nearly so
sum of midlateral plates beginning with infranuchal to pelvic-fin origin	61–64	57–60	59–62	59–61	55–60	58–61
midlateral plates anterior degree of ossification in tympanal portion of lateral-line canal (small juveniles excluded)	usually 5 (range 5–6)	usually 5 (range 4–5.5)	usually 5 (range 5–5.5)	6	usually 6 (range 5–7)	usually 5 (range 5–5.5)
dorsal profile of head and nuchal shield	strong with 3 separate ossifications evident as plates; posteriormost largest with low medial ridge/thorn and well-developed wings with serrated margins	moderate with 2 or 3 separate ossifications evident as plates; posteriormost largest with low medial ridge/thorn and moderately-developed wings with serrated margins	weak with 2 or 3 separate ossifications evident as small plates; posteriormost largest with a low medial ridge/thorn	weak with 1 or 2 separate ossifications evident posteriorly as small plates or emergent thorns	weak with 1 or 2 separate ossifications evident posteriorly as small plates or emergent thorns	moderate with 3 separate ossifications usu. evident as plates; posteriormost largest with strong medial thorn and moderately developed wings
snout	moderately oblique; nuchal hump absent or weak	moderately oblique; nuchal hump absent or weak	moderately oblique; nuchal hump absent or weak	moderately oblique; nuchal hump absent or weak	moderately oblique; nuchal hump absent or weak	strongly oblique; nuchal hump prominent
adipose eyelid	long, 44.2–47.9% of HL	long, 46.2–50.4% of HL	long, 44.8–49.8% of HL	long, 44.8–50.4% of HL	long, 43.2–47.5% of HL	short, 38.6–42.4% of HL
	small to moderate, horizontal diameter 9.3–11.5% of HL	moderate to large, horizontal diameter 10.8–14.2% of HL	moderate to large, horizontal diameter 10.9–14.6% of HL	moderate to large, horizontal diameter 12.7–14.9% of HL	small to moderate, horizontal diameter 10.4–13.9% of HL	moderate to large, horizontal diameter 12.1–15.6% of HL

Table 3. Continued.

	(A) <i>R. boehlkei</i>	(B) <i>R. armbrusteri</i> , new species	(C) <i>R. gallagheri</i> , new species	(D) <i>R. cf. dorbignyi</i> (Tocantins)	(E) <i>R. dorbignyi</i>	(F) <i>R. thomersoni</i>
postcleithral process	extremely short and broad, depth 39.5–53.6% of length	moderately short and broad, depth 36.8–44.3% of length	moderately long and narrow, depth 23.9–34.5% of length	moderately long and narrow to moderately short and broad, depth 32.2–38.2% of length	moderately long and narrow to moderately short and broad, depth 30.2–37.9% of length	extremely long and narrow, depth 21.7–29% of length
pectoral fin	1, 8	usually 1, 8; sometimes 1, 7	1, 8; rarely 1, 7	1, 8	usually 1, 8 (range 1, 7–9)	usually 1, 9 (range 1, 8–10)
gas bladder	one-part with small fused terminal diverticula	one-part with small fused terminal diverticula	one-part with small fused terminal diverticula	one-part with small fused terminal diverticula	two-part with fused terminal diverticula expanded into second bladder	two-part with fused terminal diverticula expanded into second bladder

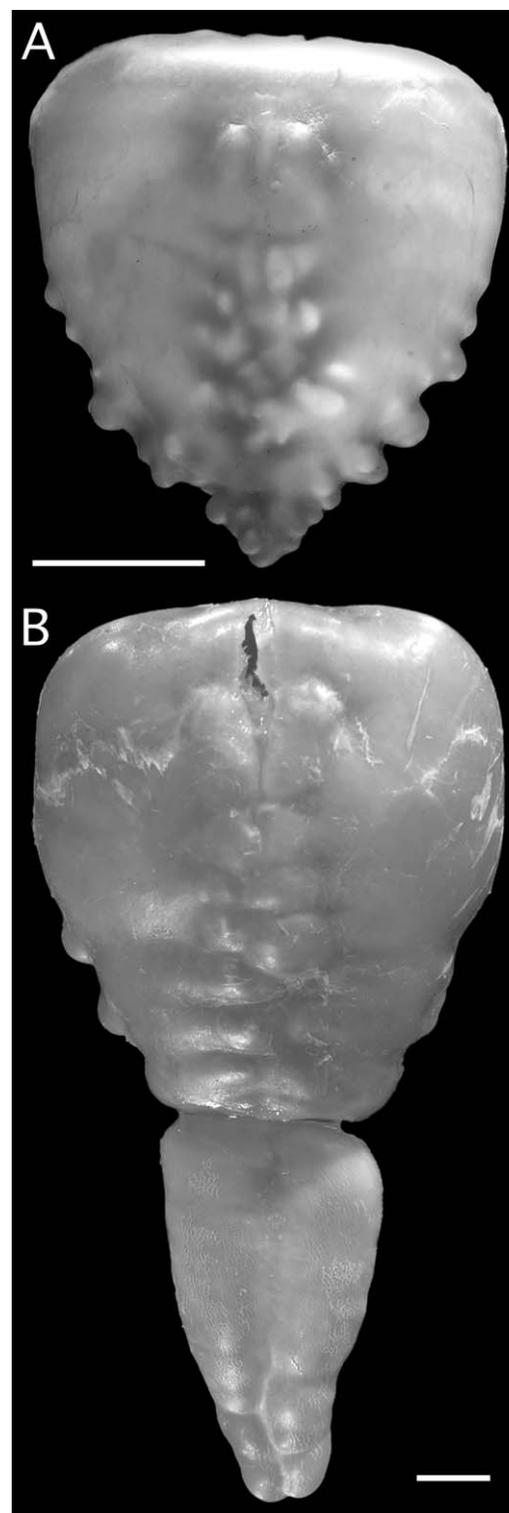


Fig. 4. Ventral views of disarticulated gas bladders (scale bars equal 1 cm). (A) *Rhinodoras gallagheri*, paratype FMNH 116466, SL 90.2 mm; (B) *R. dorbignyi*, ANSP 179535, 194 mm SL.

33.5, 63.8 mm SL, Rupununi River, Essequibo drainage, 4.6 km NW of village of Massara, 03°55'34"N, 059°16'49"W, 26 Oct. 2002, M. Sabaj et al.; ANSP 179694, 1, 96.2 mm SL, Rupununi River, Essequibo drainage, Dadanawa cattle ranch, 02°49'53"N, 059°31'39"W, 15 Nov. 2003, M. Sabaj et al.; ANSP 180411, 1, 63.2 mm SL, same data as holotype; AUM 35756, 1, 34.2 mm SL, same data as ANSP 179097; AUM 35757, 2, 24.6, 36.4 mm SL, same data as ANSP



Fig. 5. Distributions of species of *Rhinodoras* based on specimens examined. Base map by M. J. Weitzman.

179096; AUM 38684, 1, 70.2 mm SL, same data as holotype; INHS 97814, 1, 53.8 mm SL, same data as ANSP 179096; MCNG 49698, 1, 73.8 mm SL, same data as ANSP 179096; MZUSP 83765, 1, 77.9 mm SL, same data as holotype.

Diagnosis.—*Rhinodoras armbrusteri* is distinguished from all other nominal species of *Rhinodoras* by the following combination of characters: ventral surfaces heavily pigmented with many dark speckles or larger spots on belly usually extending onto gular region (vs. ventral surface usually pale in *R. gallagheri* and *R. thomersoni*); anterior midlateral plates moderately deep, depth of fifth plate 26.3–29% of corresponding body depth (vs. 15.4–26.2% in *R. gallagheri*, *R. dorbignyi*, and *R. thomersoni*); depths of dorsal and ventral wings of anterior plates subequal, depth of dorsal wing slightly less than twice that of ventral (vs. depth of dorsal wing slightly greater than or equal to twice that of ventral in *R. boehlkei* and depths of dorsal and ventral wings about equal in *R. gallagheri*, *R. dorbignyi*, and *R. thomersoni*); sum of midlateral plates 57–60 (vs. 61–64 in *R. boehlkei*), midlateral plates anterior to vertical through pelvic-fin origin usually five (vs. usually six in *R. dorbignyi*); tympanal portion of lateral-line canal moderately ossified with two or three distinct plates, posterior-most largest with low medial ridge or thorn and moderately developed wings with serrated margins (vs. weakly ossified with one to three small plates or emergent thorns in *R. gallagheri* and *R. dorbignyi* and moderately ossified with three plates, posterior-most with strong medial thorn in *R. thomersoni*); postcleithral process moderately short and broad, depth 36.8–44.3% of length (vs. moderately to extremely long and narrow, depth 21.7–34.5% of length in *R. gallagheri* and *R. thomersoni*); adipose eyelid moderate to large, horizontal diameter 10.8–14.2% of head length (vs. small to moderate, horizontal diameter 9.3–11.5% of head length in *R. boehlkei*); pectoral fin usually I,8 (vs. usually I,9 in *R. thomersoni*); and gas

bladder one-part with terminal diverticula small and fused (vs. two-part with terminal diverticula expanded to form second distinct bladder in *R. dorbignyi* and *R. thomersoni*).

Rhinodoras armbrusteri most closely resembles *R. boehlkei* (Amazonas basin). It differs primarily from this species in having ventral surfaces heavily pigmented with many dark speckles or spots (vs. usually pale to weakly pigmented in *R. boehlkei* except for specimens from Rio Trombetas), more elongated postcleithral process, depth 36.8–44.3% (vs. 39.5–53.6% of length), larger adipose eyelid, horizontal diameter 10.8–14.2% (vs. 9.3–11.5% of head length), and fewer midlateral plates, sum 57–60 (vs. 61–64).

Description.—Morphometric data presented in Table 1B; diagnostic features summarized in Table 3B. Body elongate, slightly compressed overall with ventral surface moderately flattened from snout to vent (Fig. 6). Cross-section at dorsal-fin origin triangular, becoming vertically elliptical posterior to vent. Body depth greatest at dorsal-spine origin (20–23.4% SL), tapering slightly to anal-fin origin, then more sharply to caudal peduncle imparting gentle hourglass-shape profile to posterior body, peduncle, and anterior caudal fin. Caudal peduncle long and relatively narrow (depth 7.5–8.3% SL). Snout elongated (46.2–50.4% HL), smoothly rounded. Dorsal profile of head nearly straight and oblique from posterior nares to suture between anterior and middle nuchal plates, becoming slightly more level just before dorsal-spine origin. Skin, especially on head and upper sides (including adipose fin), often textured with numerous pale, minute mounds (i.e., tubercles), some aligned and weakly joined to form elongated ridges.

Eyes relatively small, covered with thin layer of adipose tissue (horizontal diameter of adipose eyelid 11.4–14.2% HL), and placed dorsolaterally on head closer to snout tip than to dorsal-fin origin. Anterior and posterior nares well separated (internares distance 18.5–23% HL), openings surrounded by short tube of thin skin. Anterior nares with posterior wall of tube slightly elongated to form weakly defined flap; posterior nares with similar condition imparted by anterior wall.

Mouth subterminal to ventral. Upper and lower jaws with oval patch of thin acicular teeth weakly curved inward (appearance obscured by surrounding oral tissue). One pair of maxillary barbels, somewhat thickened and weakly flattened, tips usually reaching ventral-most terminus of gill slit, occasionally to pectoral spine or slightly beyond in juveniles. Two pairs of mental barbels, somewhat thickened and rounded to weakly compressed, origins staggered (inner pair more anterior); outer pair longer with tips finishing just short of line between ventral-most termini of gill slits; inner pair finishing below eye. Maxillary and mental barbels simple (without true fimbriae), but scabrous with enlarged papillae. Leading edges of barbels with transversely elongated papillae often scale-like in appearance and arrangement; trailing edges with similar papillae more subdivided and loosely arranged. Lips thick, fleshy, well expanded at corners of mouth to form rounded flap-like extensions; surfaces rugose with low, rounded and closely spaced papillae. Branchiostegal membrane broadly attached to isthmus; ventral margin of gill opening extending to point just anterior and medial to base of pectoral fin.

Outermost gill arch with 10–12 moderate rakers (two to four upper and eight or nine lower, length of longest about four to five times width). Sides and lateral edge of rakers smooth, medial edge rugose with minute papillae. Slightly



Fig. 6. *Rhinodoras armbrusteri*, new species, holotype UG/CSBD 11046 (ex. ANSP 180411), 83 mm SL.

larger papillae scattered on inner surface of outermost arch (medial to bases of rakers) and sometimes grouped into small broccoli-like clusters on inner surface of upper arch.

Nuchal shield well developed, distinctly arched in transverse plane; medial furrow indistinct to distinct but shallow; lateral margins of shield weakly concave to nearly straight. Nuchal foramina absent. Anterior nuchal plate present,

roughly pentagonal (pointed posteriorly), moderately widened and sharing lateral suture with epioccipital. Postcleithral process relatively short and broad (depth 36.8–44.3% of length), lanceolate with acute tip; surface weakly ornamented with granulations and fine ridges above and below low subventral carina; margins entire or with minute dentitions.



Fig. 7. *Rhinodoras armbrusteri*, new species, paratype ANSP 179096, 66.1 mm SL, photographed live.

Midlateral plates (including infranuchal) 28–30 per side (sum 57–60), last of which occasionally posterior to flexion point of hypural plate. Each plate with well-developed lamina (or wings) above and below sturdy thorn curved posteriorly; depth of dorsal wing slightly less than twice that of ventral. Plates weakly overlapping; posterior margins of lamina usually exposed and finely serrate, anterior margins shallowly embedded in skin. Lateral line in tympanal region (bounded posteriorly by infranuchal plate) with two or three separate ossifications clearly evident as plates, posterior-most largest with low medial ridge or weak procumbent thorn and moderately developed wings with serrated margins adjacent to anterior margin of infranuchal plate.

Dorsal fin I,6; pectoral fin I,7–8; pelvic fin i,6; anal fin iii–iv,8–10; caudal fin i,7+8,i. Dorsal spine sturdy, gently curved over entire length, laterally compressed and relatively smooth sided with well-developed antrorse teeth along anterior margin and larger retrorse teeth along posterior margin (teeth larger in distal half of spine, largest subterminal). Pectoral spines also sturdy and gently curved, dorso-ventrally compressed with relatively smooth surfaces; and likewise with well-developed antrorse teeth along leading margin and larger retrorse teeth along trailing margin (teeth larger in distal half of spine, largest subterminal). Soft break-away tips sometimes present on dorsal and pectoral spines. Pelvic fins weakly rounded with relatively straight distal margin when extended. Anal fin triangular with distal margin nearly vertical to body and straight or gently rounded (convex) when extended. Caudal fin distinctly forked with moderately pointed lobes; lower lobe slightly broader and more rounded than upper. Upper and lower procurrent caudal-fin rays grading into series of seven to ten flat, laterally expanded and weakly overlapping plates (total count of procurrent rays and plates 14–17 upper, 15–18 lower). Procurrent plates finish at or near bases of adipose and anal fins, thereby framing caudal peduncle dorsally and ventrally. Adipose fin prominent, tapering anteriorly as long, slightly thickened ridge; distal free margin thinner and rounded.

Gas bladder roughly cordiform, anterior ventral surfaces and margins smooth, posterior ventral surfaces and margins sometimes with tuberos swellings or very short, rounded diverticula. Gas bladder with internal T-shaped septum; transverse portion incomplete; longitudinal portion divides posterior gas bladder into right and left chambers and gives

rise to transverse struts that extend outwards along internal surface of central portion of ventral wall, sometimes imparting partial honeycomb-like appearance. Each posterior chamber terminates with small horn-like diverticulum; terminal diverticula completely fused medially.

Coloration in alcohol.—Head, body, and fins profusely mottled with dark brown to black pigmentation on light yellowish to white background (Fig. 6). Mottling non-uniform, particularly on sides, forming three dark saddles that continue ventrally as bars separated by relatively depigmented interspaces. Contrast between dark bars and lighter interspaces greater in small specimens (<70 mm SL). Two anteriormost saddles/bars wide, broadly joined across back and to lesser degree along midlateral plates; bars wider and more densely mottled above midlateral plates, tapering and fading ventrally. Bar one largely situated between vertical planes through dorsal-spine origin and pelvic-fin origin; bar two above anal-fin insertion and continuing dorsally onto adipose fin; bar three relatively narrow, on narrowest part of caudal peduncle. Smaller specimens (<70 mm SL) with posterior margin of nuchal shield (including posterior nuchal plate) relatively depigmented, forming light chevron-shaped saddle with apex anterior to dorsal-spine origin (light saddle lacking in specimens >80 mm SL). Ventral surfaces peppered with melanophores often forming dense pattern of speckles and diffuse spots, especially between insertions of paired fins in specimens >50 mm SL. Region between pectoral-fin insertions (coracoid bridge) usually with more diffuse speckling or sometimes relatively depigmented. Gular region sometimes depigmented or with light diffuse speckles (condition apparently independent of pigmentation in coracoid region).

Dorsal fin with dark wedge-shaped band along base (broadest anteriorly), distal portion with dark speckles or larger spots. Pectoral, pelvic, anal, and caudal fins also with dark speckles or spots. Speckles and/or spots sometimes loosely arranged into irregular bands in dorsal, anal, and caudal fins. Caudal fin also with dark crescent-shaped vertical band on bases of procurrent and primary fin rays. Adipose fin with two depigmented regions, one at anterior insertion and second on free posterior lobe (both aligned with depigmented interspaces on body); intervening portion darkly mottled.

Coloration in life.—Ground color on sides and dorsum reddish-orange to salmon. Pelvic, anal, and caudal rays with lighter touch of reddish-orange along bases (Fig. 7).

Distribution and habitat.—*Rhinodoras armbrusteri* is known from the Takutu River (and its tributary the Ireng) that drains into the upper Rio Branco (Amazonas basin), Guyana and Roraima State, Brazil, and the Rupununi River (Essequibo basin), southwestern Guyana. In the Takutu River specimens were found during the day hiding in cavities in lateritic boulders submerged in less than three meters of water. In the Rupununi River a single adult was collected at night in a swift shallow run over bedrock.

Etymology.—Named in honor of Jonathan William Armbruster, for his sterling contributions to the collection and study of neotropical fishes and for deftly leading the expedition to Guyana that resulted in the discovery of this species.

***Rhinodoras gallagheri*, new species**

Orinoco Thicklip Thornycat

Figures 4A, 5, 8; Tables 1C, 3C

Holotype.—ANSP 165233, 113.1 mm SL, Venezuela, Apure State, Río Apure, Orinoco drainage, between Río Portuguesa mouth and San Fernando de Apure airport, 07°54'N, 067°32'W, 4 Nov. 1989, W. Saul et al.

Paratypes.—Orinoco Drainage, Colombia, Arauca Department, Arauquita Municipality: IAvHP 3208, 4, Río Aguas de Limón, 7 Nov. 1989. Venezuela, Apure State: ANSP 179102, 2, 53, 66.3 mm SL, Río Apure, upriver of San Fernando de Apure and downriver of mouth of Río Portuguesa, 19 July 1984, J. Baskin et al.; AUM 42735, 1, 62.5 mm SL, Río Apure, Isla del Medio, near mouth of Río Manglar, 19 Dec. 1983, O. Castillo et al.; FMNH 116466, 1, 90.2 mm SL, Río Apure, 10 km downriver of San Fernando de Apure, 07°51'50½N, 067°23'30½W, 15 May 1985, D. Taphorn et al.; INPA 24643, 1, 77.9 mm SL, same data as AUM 42735; MBUCV-V-14505, 4, Río Apure, Cueva del Sapo, 20 Nov. 1983, O. Castillo et al.; MBUCV-V-32700, 1, 75.8 mm SL, Río Apure, Isla del Medio, 7 Aug. 1984, O. Castillo et al.; MCNG 13873, 1, 91.2 mm SL, same data as FMNH 116466; MCNG 20079, 1, Río Capanaparo, 6 km downriver of Macanilla, 07°2'40½N, 067°30'10½W, 2 May 1989, A. Miranda et al.; MCNG 32701, 3, same data as AUM 42735; MCNG 32702, 1, Río Apure, opposite Laguna Jarina, 27 July 1983, F. Provenzano et al.; MCNG 32703, 1, Río Apure, in front of Isla Apurito, 23 Jan. 1984, O. Castillo et al.; MCNG 32704, 2, same data as MBUCV-V-32700; MCNG 32705, 1, Río Apure, in front of Isla Apurito, 15 May 1985, O. Castillo et al.; MCNG 37361, 1, 120.8 mm SL, Río Arauca, 100 m from mouth of Cañafistola, 07°32'50½N, 067°32'W, 6 Nov. 1997, local fishermen; MCNG 37415, 1, Río Arauca, 30 Oct. 1997, A. Barbarino et al.; MCNG 38928, 1, 142.5 mm SL, 8 km from El Picacho de Caujarito, 15 Dec. 1997, D. Arana et al.; MCP 37702, 1, same data as MCNG 32703; MZUSP 87692, 1, same data as MCNG 37415; MZUSP 83766, 103.0 mm SL, same data as holotype; Barinas State: MCNG 5927, 1, 149.5 mm SL, Río Bocono at La Veguita, 08°50'10½N, 069°59'30½W, 21 July 1980, D. Taphorn et al.

Diagnosis.—*Rhinodoras gallagheri* is distinguished from all other nominal species of *Rhinodoras* by the following

combination of characters: ventral surfaces pale, largely without dark pigmentation (vs. ventral surfaces pigmented with dark speckles and/or spots in *R. armbrusteri*, *R. dorbignyi*, and sometimes *R. boehlkei*); anterior midlateral plates shallow to moderately deep, depth of fifth plate 16.6–26.2% of corresponding body depth (vs. 26.3–29% in *R. armbrusteri*); depths of dorsal and ventral wings of anterior plates about equal, (vs. depth of dorsal wing slightly greater than or equal to twice that of ventral in *R. boehlkei* and depth of dorsal wing slightly less than twice that of ventral in *R. armbrusteri*); midlateral plates anterior to vertical through pelvic-fin origin usually five (vs. usually six in *R. dorbignyi*); tympanal portion of lateral-line canal weakly ossified with two to three plates, posterior-most largest with low medial ridge or procumbent thorn (vs. moderately to well ossified with two or three distinct plates, posterior-most largest with low medial ridge or procumbent thorn and moderately to well developed wings with serrated margins in *R. boehlkei* and *R. armbrusteri*, and moderately ossified with three plates, posterior-most with strong medial thorn and moderately developed wings in *R. thomersoni*); postcleithral process moderately long and narrow, depth 23.9–34.5% of length (vs. extremely long and narrow, depth 21.7–29% in *R. thomersoni*, and moderately to extremely short and broad, depth 36.8–53.6% of length in *R. boehlkei* and *R. armbrusteri*); adipose eyelid moderate to large, horizontal diameter 10.9–14.6% of head length (vs. small to moderate, horizontal diameter 9.3–11.5% of head length in *R. boehlkei*); pectoral fin usually 1,8 (vs. usually 1,9 in *R. thomersoni*); and gas bladder one-part with terminal diverticula small and fused (vs. two-part with terminal diverticula expanded to form second distinct bladder in *R. dorbignyi* and *R. thomersoni*).

Rhinodoras gallagheri most closely resembles *R. boehlkei* (Amazonas basin) and *R. armbrusteri* (Branco/Essequibo basins). It differs primarily from the former in having moderately long and narrow postcleithral process, depth 23.9–34.5 (vs. 39.5–53.6% of length in *R. boehlkei*), tympanal region of lateral line weakly ossified with two to three small plates (vs. strongly ossified with three distinct plates), and anteriormost midlateral plates with dorsal and ventral wings of about equal depth (vs. subequal wings, depth of dorsal wing about twice that of ventral). *Rhinodoras gallagheri* differs primarily from *R. armbrusteri* in having ventral surfaces largely pale and unpigmented (vs. darkly speckled and/or spotted in *R. armbrusteri*), moderately long and narrow postcleithral process, depth 23.9–34.5 (vs. 36.8–44.3% of length), and dorsal and ventral wings of about equal depth (vs. subequal wings, depth of dorsal wing slightly less than twice that of ventral).

Description.—Morphometric data presented in Table 1C; diagnostic features summarized in Table 3C. Body elongate, slightly compressed with ventral surface moderately flattened from snout to vent (Fig. 8). Cross-section at dorsal-fin origin triangular, becoming vertically elliptical posterior to vent. Body depth greatest at dorsal-spine origin (20.6–22.4% SL), tapering slightly to anal-fin origin, then more sharply to caudal peduncle imparting gentle hourglass-shape profile to posterior body, peduncle, and anterior caudal fin. Caudal peduncle long and relatively narrow (depth 7.2–7.8% SL). Snout elongated (44.8–49.8% HL), smoothly rounded. Dorsal profile of head nearly straight and oblique from posterior nares to suture between anterior and middle nuchal plates, becoming slightly more level just before

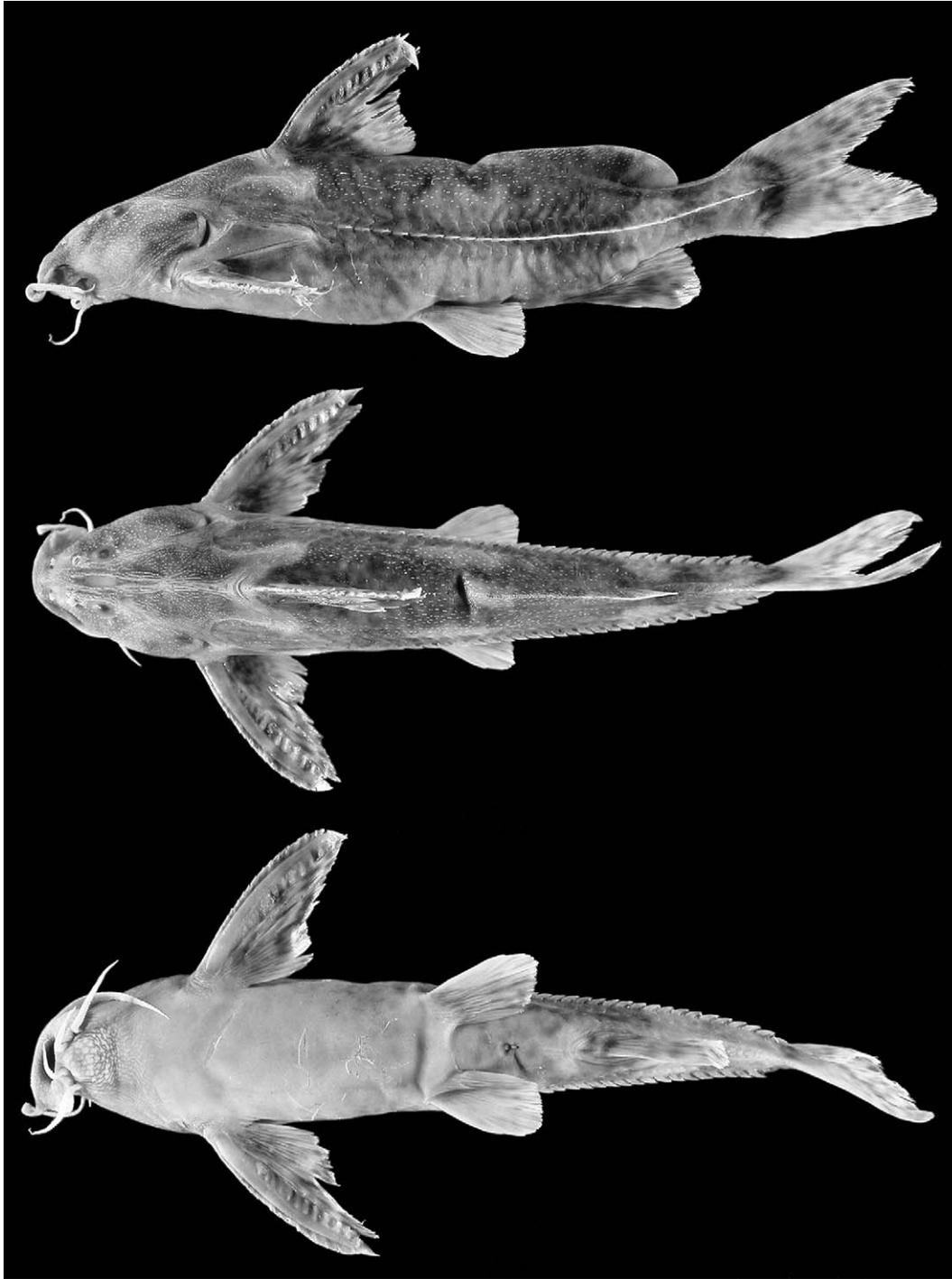


Fig. 8. *Rhinodoras gallagheri*, new species, holotype ANSP 165233, 113.1 mm SL.

dorsal-spine origin. Skin, especially on head and upper sides (including adipose fin), often textured with numerous pale, minute tubercles, some aligned and weakly joined to form elongated ridges.

Eyes relatively small, covered with thin layer of adipose tissue (horizontal diameter of adipose eyelid 10.9–14.6% HL), and placed dorsolaterally on head closer to snout tip than to dorsal-fin origin. Anterior and posterior nares well separated (internares distance 16.5–19.9% HL), openings surrounded by short tube of thin skin. Anterior nares with posterior wall of tube slightly elongated to form weakly defined flap; posterior nares with similar condition imparted by anterior wall.

Mouth subterminal to ventral. Upper and lower jaws with oval patch of thin acicular teeth weakly curved inward. One pair of maxillary barbels, somewhat thickened and weakly flattened, tips usually reaching ventral-most terminus of gill slit, occasionally to pectoral spine or slightly beyond in juveniles. Two pairs of mental barbels, somewhat thickened and rounded to weakly compressed, origins staggered (inner pair more anterior); outer pair longer with tips finishing just short of line between ventral-most termini of gill slits; inner pair finishing below eye. Maxillary and mental barbels simple (without true fimbriae), but scabrous with enlarged papillae. Leading edges of barbels with transversely elongated papillae often scale-like in appearance and arrangement;

trailing edges with similar papillae more subdivided and loosely arranged. Lips thick, fleshy, well-expanded at corners of mouth to form rounded flap-like extensions; surfaces rugose with low, rounded and closely spaced papillae. Branchiostegal membrane broadly attached to isthmus; ventral margin of gill opening extending to point just anterior and medial to base of pectoral fin.

Outermost gill arch with 11–14 moderate rakers (three or four upper and eight to ten lower, length of longest about five times width). Sides and lateral edge of rakers smooth, medial edge rugose with minute papillae. Slightly larger papillae scattered on inner surface of outermost arch (medial to bases of rakers) and sometimes grouped into small broccoli-like clusters on inner surface of upper arch.

Nuchal shield well developed, distinctly arched in transverse plane; medial furrow indistinct to distinct but shallow; lateral margins of shield weakly concave to nearly straight. Nuchal foramina absent. Anterior nuchal plate present, roughly pentagonal (pointed posteriorly), moderately widened and sharing lateral suture with epioccipital. Postcleithral process relatively long and narrow (depth 23.9–34.5% of length), lanceolate with acute tip; surface weakly ornamented with granulations and fine ridges above and below low subventral carina; margins entire or with minute dentitions.

Midlateral plates (including infranuchal) 29–31 per side (sum 59–62), last of which occasionally posterior to flexion point of hypural plate. Each plate with well-developed lamina (or wings) above and below sturdy thorn curved posteriorly; depths of dorsal and ventral wings equal or nearly so. Plates weakly overlapping; posterior margins of lamina usually exposed and finely serrate, anterior margins shallowly embedded in skin. Lateral line in tympanal region (bounded posteriorly by infranuchal plate) with two or three separate ossifications clearly evident as small plates, posterior-most largest with low medial ridge or weak procumbent thorn and shallow wings.

Dorsal fin I,6; pectoral fin I,7–8; pelvic fin i,6; anal fin iii–iv,8–11; caudal fin i,7+8,i. Dorsal spine sturdy, gently curved over entire length, laterally compressed and relatively smooth sided with well-developed antrorse teeth along anterior margin and larger retrorse teeth along posterior margin (teeth larger in distal half of spine, largest subterminal). Pectoral spines also sturdy and gently curved, dorso-ventrally compressed with relatively smooth surfaces; and likewise with well-developed antrorse teeth along leading margin and larger retrorse teeth along trailing margin (teeth larger in distal half of spine, largest subterminal). Soft break-away tips sometimes present on dorsal and pectoral spines. Pelvic fins weakly rounded with relatively straight distal margin when extended. Anal fin triangular with distal margin nearly vertical to body and straight or gently rounded (convex) when extended. Caudal fin distinctly forked with moderately pointed lobes; lower lobe slightly broader and more rounded than upper. Upper and lower procurrent caudal-fin rays grading into series of nine to ten flat, laterally expanded and weakly overlapping plates (total count of procurrent rays and plates 16–17 upper and lower). Procurrent plates finish at or near bases of adipose and anal fins, thereby framing caudal peduncle dorsally and ventrally. Adipose fin prominent, tapering anteriorly as long, slightly thickened ridge; distal free margin thinner and rounded.

Gas bladder (Fig. 4A) roughly cordiform, anterior ventral surfaces and margins smooth, posterior ventral surfaces and

margins sometimes with tuberos swellings or short, rounded diverticula. Gas bladder with internal T-shaped septum; transverse portion incomplete; longitudinal portion divides posterior gas bladder into right and left chambers and gives rise to transverse struts that extend outwards along internal surface of central portion of ventral wall, sometimes imparting partial honeycomb-like appearance. Each posterior chamber terminates with small horn-like diverticulum; terminal diverticula completely fused medially.

Coloration in alcohol.—Dark mottling usually less profuse and its distribution less liberal than in *R. armbrusteri* (except among juveniles), yet overall pattern remains similar as three dark saddles/bars separated by depigmented interspaces on sides (Fig. 8). Contrast between dark bars and lighter interspaces usually more pronounced in adults of *R. gallagheri* than *R. armbrusteri*. Mottling on head less uniform, darkest in patches on lacrimal region (below eye), on skin covering opercle, on supraoccipital and nuchal shield, and on skin covering tympanal region and dorsal portion of postcleithral process. Light chevron-shaped saddle with apex anterior to dorsal-spine origin clearly evident in well preserved specimens. Ventral surfaces dull yellow, unpigmented from mouth to vent. Pigmentation on fins similar to that of *R. armbrusteri* except dark speckling less pronounced and sometimes completely lacking in pelvic, anal, and caudal fins in juveniles (SL < 65 mm).

Distribution.—*Rhinodoras gallagheri* is known from Río Apure, Río Capanaparo, and Río Arauca, all left bank tributaries of the middle Orinoco, in the llanos regions of Apure and Barinas States, Venezuela. It is also known from the Río Aguas de Limón, in Arauca Department, Colombia. This river is alternatively mapped in the headwaters of the Río Cinaruco and the Río Capanaparo (both left bank tributaries of the middle Orinoco).

Etymology.—Named in honor of Francis Richard Gallagher, mailroom supervisor at The Academy of Natural Sciences of Philadelphia from 1967 to 2003, for 37 years of dedicated service to the global community of taxonomists and systematists via the shipping and receiving of countless loans of biological specimens.

DISCUSSION

Morphometric analyses.—The four-part principal component analysis proved useful for distinguishing specimens of *Rhinodoras* and for identifying measurements that separate the species. The first analysis (all specimens included) separated into non-overlapping clusters specimens of *R. boehlkei* (Amazonas), *R. dorbignyi* (Paraguay–Paraná), and *R. thomersoni* (Maracaibo), yet left questionable the distinctiveness of specimens from the Orinoco, Branco/Rupununi, and Tocantins drainages and the identities of two specimens from the Trombetas drainage (Amazonas basin).

The second PCA (*R. thomersoni* removed) grouped the Tocantins specimens with *R. dorbignyi*, prompting their treatment as *R. cf. dorbignyi*. Although the Tocantins specimens are morphometrically similar to *R. dorbignyi*, their identification as such remains tentative because the Tocantins specimens lack the two-part gas bladder characteristic of *R. dorbignyi* (J. Birindelli, pers. comm.). The

Tocantins specimens are under study by José Birindelli and may represent an undescribed species. The second PCA separated into non-overlapping clusters specimens of *R. armbrusteri* (Branco/Essequibo) and *R. gallagheri* (Orinoco). The second PCA also plotted the two Trombetas specimens closer to *R. boehlkei* (Amazonas) than to *R. armbrusteri*, supporting their identification as the former. The midlateral plate count of the two Trombetas specimens (both 62) is higher than that in *R. armbrusteri* (57–60) and within the range of *R. boehlkei* (61–64). The ventral surfaces of the Trombetas specimens, however, are rather heavily pigmented with dark speckles and spots, a condition closer to *R. armbrusteri* than to *R. boehlkei*. Given that the Trombetas specimens are closer to other *R. boehlkei* morphometrically and meristically, they are referred to this species. The lability of pigmentation on ventral surfaces may be related to water clarity as individuals from sediment-poor rivers (e.g., *R. boehlkei* in the Trombetas, *R. armbrusteri* in the Ireng and upper Rupununi, *R. cf. dorbignyi* in the Tocantins) are more darkly pigmented than those from more sediment-rich waters (e.g., *R. boehlkei* in the Itaya and Amazonas channel and *R. gallagheri* in the Apure).

The third PCA (*R. thomersoni* and *R. dorbignyi* removed) resolved into non-overlapping clusters specimens of *R. armbrusteri*, *R. boehlkei*, *R. gallagheri*, and *R. cf. dorbignyi*, thereby corroborating their morphometric distinctiveness at a finer scale. The fourth PCA (*R. thomersoni*, *R. dorbignyi*, and *R. cf. dorbignyi* removed) maintained this distinctiveness for specimens assigned to *R. armbrusteri*, *R. boehlkei*, and *R. gallagheri*.

Postcleithral process length, snout–anterior nares distance and posterior nares–posterior orbit distance contributed most heavily to the separation of *R. thomersoni*, *R. dorbignyi*, and *R. armbrusteri* + *R. boehlkei* + *R. cf. dorbignyi* + *R. gallagheri* in the all-inclusive PCA (Table 3). In the more restricted PCAs, postcleithral process depth and horizontal adipose eyelid diameter contributed most heavily to the separation of *R. armbrusteri*, *R. boehlkei*, *R. cf. dorbignyi*, and *R. gallagheri*.

Biogeography.—*Rhinodoras* is notable in that it contains one of only three extant species of trans-Andean doradids: *R. thomersoni* and *Doraops zuloagai* (Maracaibo endemics) and *Centrochir crocodili* (Magdalena endemic). *Rhinodoras* is the only doradid genus represented by extant species in trans-Andean and cis-Andean (Amazonas/Tocantins, Essequibo, Orinoco, and Paraguay–Paraná) drainages. This distinction is somewhat lessened by the observation that *Pterodoras* occurs in cis-Andean drainages and its sister taxon, as proposed by Moyer et al. (2004), is the monotypic Maracaibo endemic *Doraops zuloagai*.

The vicariant isolation and origin of trans-Andean *Rhinodoras* may date to the late Miocene with the closing of the Maracaibo/Falcón outlet of the paleo-Orinoco (or paleo-Amazonas–Orinoco) basin by historic uplift and union of the central and western parts of the Mérida Andes, Sierra de Perijá, and Eastern Cordillera (Lundberg et al., 1998). This event isolated the Maracaibo basin from the putative paleo-Orinoco/Amazonas–Orinoco river basin that drained much of northwestern South America (Lundberg et al., 1998), and thus may indicate a minimum age of divergence for *R. thomersoni* as about 8 Ma. The occurrence of *Rhinodoras* in the paleo-Orinoco/Amazonas–Orinoco is evidenced by at least one fossil (i.e., cleithrum) identified as *R. cf. thomersoni* by Sabaj Pérez et al. (2007; same identifi-

cation for separate fossil neurocranium questionable) from the Miocene Urumaco Formation (ca. 9 Ma), Falcón State, Venezuela.

The occurrence of *Rhinodoras armbrusteri* in both the upper Branco (Negro–Amazonas drainage) and Rupununi (Essequibo drainage) may be the result of a seasonal conduit between the two basins. In wet years (between May and September) the north Rupununi savanna (between the Pakaraima and Kanuku mountains) becomes a vast flooded plain known as Lake Amaku (Lowe-McConnell, 1964). This inundation affords the opportunity for faunal exchanges between the upper Branco and Essequibo basins. It is uncertain, however, whether this largely shallow, lentic passage is suitable for movement of *Rhinodoras*. Alternatively, the current distribution of *R. armbrusteri* may be attributable to a putative stream piracy of the Takutu River by the Rio Branco in the late Tertiary. McConnell (1959) reported geological and fossil evidence for an old river system that began with the Takutu and Ireng Rivers, continued through present day channels of the Rupununi–Essequibo and emptied into the Atlantic via the present day lower Berbice River. Signatures specific to each alternative explanation for the current distribution of *R. armbrusteri*, as well as other species shared by the Branco and Essequibo basins, may be found via population genetic studies.

KEY TO THE SPECIES OF RHINODORAS

- 1a. Gas bladder one-part with small fused terminal diverticula (Fig. 4A) 2
- 1b. Gas bladder two-part with fused terminal diverticula expanded to form second bladder (Fig. 4B) 4
- 2a. Anterior midlateral plates moderate to deep (depth of 5th plate 24.4–34% of corresponding body depth) with subequal wings (depth of dorsal wing twice that of ventral wing or nearly so); postcleithral process short and broad (depth 36.8–53.6% of length); Amazonas/Essequibo basins 3
- 2b. Anterior midlateral plates shallow to moderate (depth of 5th plate 16.6–26.2% of corresponding body depth) with dorsal and ventral wings of equal depth (or nearly so); postcleithral process moderately long and narrow (depth 23.9–34.5% of length); Orinoco basin
Rhinodoras gallagheri, new species
- 3a. Sum of midlateral plates 61–64; postcleithral process extremely short and broad (depth 39.5–53.6% of length); adipose eyelid small to moderate (horizontal diameter 9.3–11.5% of head length); Amazonas basin (minus upper Branco)
Rhinodoras boehlkei
- 3b. Sum of midlateral plates 57–60; postcleithral process moderately short and broad (depth 36.8–44.3% of length); adipose eyelid moderate to large (horizontal diameter 10.8–14.2% of head length); Essequibo/Branco basins
Rhinodoras armbrusteri, new species
- 4a. Snout short (length 38.6–42.4% of head length); postcleithral process extremely long and narrow (depth 21.7–29% of length); tympanal plates moderately ossified, usually three evident, posterior-most largest with strong medial thorn and moderately developed wings; pectoral fin usually I,9 (range I,8–10); Maracaibo basin
Rhinodoras thomersoni

- 4b. Snout long (length 43.2–47.5% of head length); postcleithral process shorter and broader (depth 30.2–37.9% of length); tympanal plates weakly ossified, only one or two evident posteriorly as small plates or emergent thorns; pectoral fin usually I,8 (range I,7–9); Paraguay–Paraná basin *Rhinodoras dorbignyi*

MATERIAL EXAMINED

Measurements in parentheses refer to standard lengths.

Rhinodoras boehlkei. Brazil, Amazonas State: ANSP 178539, 1, 33.5 mm, Rio Solimões, 7 km upstream from Vila Careiro, 3°14'13½S, 59°54'15½W, 21 July 1996, M. Toledo-Piza et al.; ANSP 179121, 1, 38.3 mm, Rio Solimões, 9.5 km upriver of São Antonio do Iça, 3°08'48½S, 67°53'56½W, 22 Nov. 1993, J. Friel et al.; Pará State: INPA 20998, 2, 79.1, 104.7 mm, Rio Trombetas, montante da cachoeira Porteira, 19 April 1985, E. Ferreira. Ecuador: FMNH 79203 (holotype), 136.3 mm, Río Bobonaza, between Montalvo and Chicherato, Feb. 1958, G. Herrera; FMNH 88195, 111.8 mm, Río Bobonaza, March 1958, G. Herrera. Peru, Loreto Department: ANSP 179562, 1, 116.3 mm, INHS 52172, 2, 84.8, 118.0 mm, SIUC 39703, 3, 93.3–119 mm, purchased near Iquitos, reportedly from Río Itaya, 28 July 1999, M. Sabaj et al.

Rhinodoras dorbignyi. ANSP 78093, skeleton, 82.5 mm, Río de la Plata basin, Hyrtl Collection; CAS 31186 (ex IU 9837, holotype), 121 mm, either in Mato Grosso [at Descalvados, Brazil] or [in the Paraguay at] Asuncion [Paraguay], pre-1903, C. Ternetz. Argentina: MCP 11602, 1, 130 mm, Río de La Plata, Punta Atalaya, Pto. Magdalena, May 1981, M. Azpelicueta et al.; NMW 44555 (not 44551, holotype), 123 mm; Río de la Plata, probably near Buenos Aires, pre-1855. Bolivia, Tarija State: USNM 314286, 13, 97.3–127.8 mm, Río Pilcomayo at Villa Montes, 1 Oct. 1988, W. Starnes et al. Brazil, Rio Grande do Sul State: ANSP 179535, 2, 177.5, 194 mm, Rio Uruguai at Rancho da Amizade, São Borja, 28°38'S, 56°02'W, 12 Dec. 1987, E. Lerner et al.; ANSP 179536, 1, 140.2 mm, Rio Uruguai, Trojan family farm between arroios Salso and Itapitocai, Uruguaiana, 6 Oct. 1985, L. Pena; MCNG 33002, 1, Rio Uruguai, MCP Lab de Ictiologia; MCP 6957, 2, 137.5, 160 mm, same data as ANSP 179536; MCP 11974, 2, 158, 167 mm, same data as ANSP 179535; MCP 13067, 2, 147.8, 148 mm, Rio Uruguai, Porto de Sto. Izidro, São Nicolau, 3–4 Jan. 1989, R. Reis et al.; São Paulo State: AMNH 8588, 1, 127.9 mm, 1910, E. Garbe; FMNH 95541, 2, 128.5–132.1 mm, Rio Grande, Miguelopolis, dam of Volte Grande, CETESB, 6–7 Nov. 1975.

Rhinodoras cf. *dorbignyi*. Brazil: INPA 5248, 1, 86.5 mm, Rio Tocantins, Breu Branco, Eq. Ictiologia INPA, 10 July 1982; UNT 2972, 2, 94.9, 97.4 mm, Rio Santo Antonio, trib Rio Tocantins, at Peixe, 1995–2002, C. Agostinho et al.; UNT 317, 1, 110.4 mm, Rio Tocantins, at Paranã, 12°28'S, 48°13'W, 1995–2002, C. Agostinho et al.

Rhinodoras thomersoni. Venezuela, Zulia State, Lago Maracaibo drainage: FMNH 96003 (3 paratypes), 66.1–82.7 mm, Río Catatumbo, at mouth near El Congo, 6–7 Aug. 1977, D. Taphorn et al.; INHS 35391, 1, 70.1 mm, Caño La Yuca, at confluence with Río Escalante, 8°49'10½N, 72°00'57½W, 31 Jan. 1995, D. Taphorn et al.; INHS 55437, 1, 54.8 mm, Río Escalante, on road from Santa Barbara to La Solita, N of Las Casas, 9.08987°N, 71.89983°W, 20 Dec. 1999, J. Armbruster et al.; MCNG 368 (holotype), 79.8 mm, MCNG 11295 (12 paratypes), same data as FMNH 96003; MCNG

33458, 5, Río Santa Ana, at Lagunitas, 10 May 1977, D. Taphorn et al.; MCNG 33459, 2, Río Escalante, 11 May 1977, D. Taphorn et al.; UF 41970 (2 paratypes), 81.4, 84.5 mm, same data as FMNH 96003.

ACKNOWLEDGMENTS

For access to and loans of specimens in their care we thank: C. Agostinho, J. Albert, J. Armbruster, J. Birindelli, B. Brown, B. Burr, D. Catania, Z. de Lucena, W. Eschmeyer, T. Iwamoto, F. Lima, P. Lucinda, J. Maldonado, C. Mayer, N. Menezes, E. Mikschi, O. Oyakawa, L. Rapp Py-Daniel, S. Raredon, R. Reis, R. Robins, M. Rogers, S. Schaefer, L. Sousa, J. Stewart, K. Swagel, and H. Wellendorf. We are grateful to C. Allison, M. Arce, D. Arjoon, J. Armbruster, C. Chin, N. Flores, M. Hardman, E. Isern, N. Lujan, C. Pérez, M. Thomas, D. Werneke, and numerous others whose fieldwork and logistical support yielded the aforementioned vouchers. Special thanks to M. Thomas for photographs of NMW holotype, J. Birindelli for sharing his expertise on doradids, K. Ponader for assistance with German translations, J. Lundberg for reviewing biogeography discussion, and S. Bullard for identification of parasites. Guyana fieldwork supported by NSF grant DEB-0107751 to J. Armbruster; project funded by grant from U.S. National Science Foundation (DEB-0315963) to MHS (in part) entitled Planetary Biodiversity Inventory: All Catfish Species (Siluriformes)–Phase I of an Inventory of the Otophysi.

LITERATURE CITED

- Bleeker, P. 1862–63. Atlas Ichthyologique des Indes Orientales Néerlandaises, publié sous les auspices du gouvernement colonial Néerlandais. Tome II. Siluroïdes, Chacoïdes et Hétérobranchoïdes. Amsterdam.
- Böhlke, J. E. 1970. A new species of the doradid catfish genus *Leptodoras*, with comments on related forms. Proceedings of the California Academy of Sciences (Series 4) 38:53–61.
- Bookstein, F. L. 1989. "Size and shape": a comment on semantics. Systematic Zoology 38:173–180.
- Carvajal, V. A. 2005. Diversidad y dieta de los bagres de la familia Doradidae de Venezuela. Unpubl. bachelor diss., Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora," Guanare, Venezuela.
- Eigenmann, C. H. 1925. A review of the Doradidae, a family of South American Nematognathi, or catfishes. Transactions of the American Philosophical Society 22:280–365.
- Eigenmann, C. H., and C. H. Kennedy. 1903. On a collection of fishes from Paraguay, with a synopsis of the American genera of cichlids. Proceedings of the Academy of Natural Sciences, Philadelphia 55:497–537.
- Glodek, G. S. 1976. *Rhynchodoras woodsi*, a new catfish from Eastern Ecuador (Siluriformes: Doradidae) with a redefinition of *Rhynchodoras*. Copeia 1976:43–46.
- Glodek, G. S., G. L. Whitmire, and G. Orcés V. 1976. *Rhinodoras boehlkei*, a new catfish from eastern Ecuador (Osteichthyes, Siluroidei, Doradidae). Fieldiana, Zoology 70:1–11.
- Higuchi, H. 1992. A phylogeny of the South American thorny catfishes (Osteichthyes; Siluriformes, Doradidae). Unpubl. Ph.D. diss., Harvard University, Cambridge, Massachusetts.
- Higuchi, H., J. L. O. Birindelli, L. M. Sousa, and H. A. Britski. 2007. *Merodoras nheco*, new genus and species

- from Rio Paraguay basin, Brazil (Siluriformes, Doradidae), and nomination of the new subfamily Astrodoradinae. *Zootaxa* 1446:31–42.
- Higuchi, H., H. A. Britski, and J. C. Garavello.** 1990. *Kalyptodoras bahiensis*, a new genus and species of thorny catfish from northeastern Brazil (Siluriformes: Doradidae). *Ichthyological Exploration of Freshwaters* 1:219–225.
- Hubbs, C. L., and K. F. Lagler.** 1958. *Fishes of the Great Lakes Region*. Cranbrook Institute of Science Bulletin 26, Ann Arbor, Michigan.
- Jolicoeur, P.** 1963. The multivariate generalization of the allometry equation. *Biometrics* 19:497–499.
- Jolicoeur, P., and J. E. Mosimann.** 1960. Size and shape variation in the painted turtle, a principal component analysis. *Growth* 24:339–354.
- Kner, R.** 1855. *Ichthyologische Beiträge* [Subtitles I–III]. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch–Naturwissenschaftlichen Classe, Wien 17:92–162.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson.** 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- Lowe-McConnell, R. H.** 1964. The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of the Linnean Society (Zoology)* 45:103–144.
- Lundberg, J. G., L. G. Marshall, B. H. Guerrero, M. C. Malabarba, and F. Wesselingh.** 1998. The stage for neotropical fish diversification: a history of tropical South American Rivers, p. 13–48. *In: Phylogeny and Classification of Neotropical Fishes*. L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena, and C. A. S. Lucena (eds.). EDIPUCRS, Porto Alegre, Brazil.
- McConnell, R. B.** 1959. Fossils in the North savannas and their significance in the search for oil in British Guiana. *Timehri, Journal of the Royal Agricultural and Commercial Society of British Guiana* 38:65–85.
- McElroy, D. M., and M. E. Douglas.** 1995. Patterns of morphological variation among endangered populations of *Gila robusta* and *Gila cypha* (Teleostei: Cyprinidae) in the Upper Colorado River Basin. *Copeia* 1995:636–649.
- Moyer, G. R., B. M. Burr, and C. Krajewski.** 2004. Phylogenetic relationships of thorny catfishes (Siluriformes: Doradidae) inferred from molecular and morphological data. *Zoological Journal of the Linnean Society* 140:551–575.
- Reis, R. E.** 2004. *Otocinclus cocama*, a new uniquely colored loricariid catfish from Peru (Teleostei: Siluriformes), with comments on the impact of taxonomic revisions to the discovery of new taxa. *Neotropical Ichthyology* 2:109–115.
- Ringuelet, R. A., R. H. Arámburu, and A. A. de Arámburu.** 1967. *Los Peces Argentinos de Agua Dulce*. Comisión de Investigación Científica, La Plata, Argentina.
- Sabaj, M. H.** 2005. Taxonomic assessment of *Leptodoras* (Siluriformes: Doradidae) with descriptions of three new species. *Neotropical Ichthyology* 3:637–678.
- Sabaj, M. H., and C. J. Ferraris, Jr.** 2003. Doradidae (Thorny catfishes), p. 456–469. *In: Checklist of the Freshwater Fishes of South and Central America*. R. E. Reis, S. O. Kullander, and C. J. Ferraris, Jr. (eds.). EDIPUCRS, Porto Alegre, Brazil.
- Sabaj Pérez, M. H., O. A. Aguilera S., and J. G. Lundberg.** 2007. Fossil catfishes of the families Doradidae and Pimelodidae (Teleostei: Siluriformes) from the Miocene Urumaco Formation of Venezuela. *Proceedings of the Academy of Natural Sciences of Philadelphia* 156:157–194.
- Sousa, L. M., and L. H. Rapp Py-Daniel.** 2005. Description of two new species of *Physopyxis* and redescription of *P. lyra* (Siluriformes: Doradidae). *Neotropical Ichthyology* 3:625–636.
- Taphorn, D. C., and C. G. Lilyestrom.** 1984. *Rhinodoras thomersoni*: un bagre sierra, nuevo en Venezuela (Pisces, Doradidae). *Revista UNELLEZ de Ciencia y Tecnología* 2:87–92.