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Three New Species of the Neotropical Electric Fish *Rhabdolichops* (Gymnotiformes: Sternopygidae) from the Central Amazon, with a New Diagnosis of the Genus

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Three new species of the Neotropical electric fish *Rhabdolichops* are described from the lowland Central Amazon Basin of Brazil. These taxa are described using features of color pattern, morphometric and meristic traits, squamation, and osteology. *Rhabdolichops nigrimans* and *R. navalha* are known only from low-conductivity blackwater systems whereas *R. lundbergi* occurs almost exclusively in the main channel of high-conductivity whitewater rivers and adjacent floodplain channels. *Rhabdolichops nigrimans* and *R. lundbergi* are sister species, forming a sister clade to all other *Rhabdolichops* species, and retaining transitional phenotypes between the genera *Eigenmannia* and *Rhabdolichops*. *Rhabdolichops nigrimans*, but not *R. lundbergi*, displays a striking sexual dimorphism in caudal appendage length. *Rhabdolichops navalha* and *R. stewarti* are sister species nested within a clade comprising *R. eastwardi* and *R. caviceps* + *R. troscheli*. *Rhabdolichops navalha* exhibits a unique morphology of the electric organ where the posterior margin ends abruptly and is replaced posteriorly by rigid and transparent non-electrogenic tissue.

Três espécies novas de peixes elétricos neotropicais, *Rhabdolichops*, são descritas da bacia Amazônica, Brasil. Estas espécies são descritas com base em características de pigmentação, morfologia, osteologia e dados merísticos. *Rhabdolichops nigrimans* e *R. navalha* são conhecidos exclusivamente de sistemas de águas pretas com condutividade baixa. *Rhabdolichops lundbergi* ocorre quase exclusivamente nas calhas principais dos rios de águas brancas e em canais de várzea (paranás) com condutividade alta. *Rhabdolichops nigrimans* e *R. lundbergi* formam um clado monofilético que representa um grupo irmão das demais espécies de *Rhabdolichops*. Estas duas espécies apresentam fenótipos transicionais entre os gêneros *Eigenmannia* e *Rhabdolichops*. *Rhabdolichops nigrimans* apresenta um dimorfismo sexual acentuado no comprimento do filamento caudal. Contudo, *R. lundbergi* não possui esta característica. *Rhabdolichops navalha* e *R. stewarti* são espécies irmãs dentro de um grupo monofilético constituido por *R. eastwardi* e *R. caviceps* + *R. troscheli*. *Rhabdolichops navalha* apresenta uma morfologia única do órgão elétrico onde a sua margem posterior finda-se abruptamente e é substituída, posteriormente, por um tecido rígido e não-eletrogênico.

THE weakly electric Neotropical fish *Rhabdolichops* Eigenmann and Allen 1942 inhabits rivers in lowland tropical South America, and is distributed throughout the lowland Amazon and Orinoco basins and the coastal rivers of the Guyanas (Albert, 2003; Table 1). *Rhabdolichops* species forage on small aquatic animals, and some species are zooplanktivores (Lundberg and Mago-Leccia, 1986; Crampton, 1998a). The genus *Rhabdolichops* was established by Eigenmann and Allen (1942) to separate *R. longicaudatus* from *Eigenmannia* Jordan and Evermann 1896 on the basis of four characteristics: absence of dorsal scalation, large mouth, equal jaws, and a concave dorsal head profile. In the most recent revision of the group Lundberg and Mago-Leccia (1986) recognized six species: *R. electrogrammus, R. zareti, R. eastwardi, R. stewarti, R. caviceps,* and *R. troscheli* (Table 1). Lundberg and Mago-Leccia (1986) diagnosed the genus *Rhabdolichops* based on eight characteristics: two prootic foraminae for facial nerve rami; extrascapular small and remote from posttemporal and pterotic bones; infraorbitals five and six are large trough-like ossicles; mouth terminal, gape quadrangular, premaxilla transversely elongate, and maxilla broad; two (or three) displaced hemal spines at posterior margin of body cavity; cleithrum with narrow posterior process; scales absent from anterior portion of dorsum; and ossified gill rakers. Since the revision by Lundberg and Mago-Leccia (1986) a single species of *Rhabdolichops* has been published, *Rhabdolichops jegui*, from French Guiana (Keith and Meunier, 2000). Here we describe three new species of *Rhabdolichops* from the central Amazon of Brazil, propose a hypothesis of their interrelationships within the phylogenetic framework of Lundberg

TABLE 1. VALID SPECIES OF *Rhabdolichops*. Arranged chronologically by year of description. See Lundberg and Mago-Leccia (1986) for comments on type locality of *R. troscheli*.

Species	Author(s)	Year	Country	Type locality
R. troscheli	Kaup	1856	''Guyana''	Unknown
R. caviceps	Fernández-Yépez	1968	Venezuela	Río Apure Seco
R. electrogrammus	Lundberg and Mago-Leccia	1986	Venezuela	Río Orinoco
R. zareti	Lundberg and Mago-Leccia	1986	Venezuela	Río Orinoco
R. eastwardi	Lundberg and Mago-Leccia	1986	Venezuela	Río Orinoco
R. stewarti	Lundberg and Mago-Leccia	1986	Brazil	Río Tapajós
R. jegui	Keith and Meunier	2000	French Guiana	Rivière Litany
R. lundbergi, new species	Correa, Crampton, and Albert	2005	Brazil	Rio Solimões
R. navalha, new species	Correa, Crampton, and Albert	2005	Brazil	Rio Tefé
R. nigrimans, new species	Correa, Crampton, and Albert	2005	Brazil	Rio Tefé

and Mago-Leccia (1986), and provide a new diagnosis of the genus using six unique and unreversed character states among Sternopygidae.

MATERIALS AND METHODS

Specimens of the new species described here were captured as part of a long-term (1993–2003) multi-habitat sampling program undertaken by one of us (WGRC) near the town of Tefé, Amazonas, Brazil. Specimens were captured using seine nets (30–50 × 4–8 m, 5-mm mesh) in beaches and shallow waters, fyke-net traps (10 m long, 10-mm mesh with 5-mm cod-end) in flooded forests and shore scrub, and with otter trawl nets (10-mm cod end mesh, 3-m mouth) employed at the bottom of rivers at depths from 5–25 m. Additional materials were examined from museum collections, for which abbreviations presented here follow Leviton et al. (1985) and Reis et al. (2003).

Measurements reported include: (1) length from snout to end of caudal appendage with lateral line horizontal (TL); (2) length to the end of the anal fin (LEA), measured from the tip of snout (anterior margin of upper jaw at mid-axis of body) to end of anal fin (where membrane posterior to last ray contacts the ventral surface of body); (3) anal-fin length (AF), from origin of anal fin to posterior end of anal fin; (4) caudal appendage (CA), measured as the distance from the last anal-fin ray to the distal end of the caudal appendage, which is often damaged and not fully regenerated, so was selectively excluded from the analysis; (5) pre-anal fin distance (PAF), from origin of anal fin to posterior margin of anus; (6) pre-pectoral length (PP) from snout to dorsal border of pectoral-fin base where it contacts cleithrum; (7) pre-anus distance (PA) from snout to anterior margin of anus; (8) head length (HL), measured from posterior margin of the bony opercle to tip of snout (anterior margin of upper jaw at mid-axis of body); (9) postorbital head length (PO), from posterior margin of the bony opercle to posterior margin of eye (at edge of the free orbital margin); (10) distance from snout to occiput (SO); (11) body depth (BD), vertical distance from origin of anal fin to dorsal body border; (12) head depth at occiput (HD-1), vertical distance at nape to ventral body border with lateral line held horizontal; (13) preorbital head length (PR), from anterior margin of eye (at edge of the free orbital margin) to tip of snout (anterior margin of upper jaw at mid-axis of body); (14) tail depth (TD) measured vertically at end of anal fin (with lateral line held horizontal); (15) pectoral-fin length (P1), from dorsal border of fin base where it contacts cleithrum to tip of the longest ray. Measurements of TL and AF were taken with a ruler to the nearest millimeter. All other measurements were taken with a digital caliper to the nearest 0.01 mm.

Meristic protocols follow Albert and Fink (1996). Skeletal counts obtained from radiographs include: precaudal vertebrae (PCV), which include those of the Weberian apparatus and is a proxy for body cavity length (Albert, 2001); caudal vertebrae to end of anal fin (CVA); total caudal vertebrae (CVT); anal-fin rays (AFR); and pleural rib pairs (PRP). Additional meristic measurements include: gill-rakers on anterior face of first arch (GR1); pectoral-fin rays (P1R); caudal electroplates rows (CEP), counted as the number of horizontally aligned rows of electroplates in the electric organ below the vertebral column and at the end of the anal fin (with the fish's tail placed under a stereoscopic microscope against strong backlighting and the scales above the electric organ removed); pored lateral-line scales (PLS1), from posterior edge of opercle to above of end of anal fin; pored lateral-line scales (PLS2), from posterior edge of opercle to end of

TABLE 2. MATRIX OF 42 CHARACTER-STATES USED IN CLADISTIC PHYLOGENETIC RECONSTRUCTION OF *Rhabdolichops* USING MAXIMUM PARSIMONY. ? = no information available, and - = not applicable. Character descriptions are listed with literature citations where relevant in Appendix 1.

	1–10	11–20	21–30	31–40	41–42
Sternopygus branco	0000000010	0100000000	0000000000	0100000000	00
Archolaemus blax	0000000110	0100001000	0101001000	1011010000	00
Distocyclus conirostris	0000110110	0100001000	0111001000	1012111000	00
Eigenmania limbata	0000010110	0100001000	0111001000	1022111000	00
E. virescens	0000110110	0100001000	0111001000	1022111110	10
Rhabdolichops caviceps	1001112111	1111111111	1?01001010	1021111011	20
R. eastwardi	0001111111	1111111111	1?01001010	1021111111	20
R. electrogrammus	1001110111	1111101111	1?01001010	1021111111	00
R. lundbergi, new species*	0011110111	0101001101	1101101111	1021111010	10
R. navalha, new species*	1001111101	1111111111	-11001000	1021211111	21
R. nigrimans, new species*	0111110111	0101001101	1101111111	1021111010	10
R. stewarti	0001111111	1111111111	-11001010	1021111111	20
R. troscheli	0001112111	1111111111	1?01001010	1021111011	20
R. zareti	0001111111	1111111111	1001001010	1011111111	10

tail. Morphometric measurements and meristic counts were taken from the left side of specimens. Dietary preferences were characterized by the qualitative visual analysis of stomach contents placed in a glass dish under a stereo microscope.

Osteological data were taken from cleared-and-stained specimens using the techniques of Taylor and Van Dyke (1985). We used standardized micro-dissection methods of small teleosts (Weitzman 1974) and follow Fink and Fink (1981) and Albert (2001) for morphological nomenclature. Drawings of cleared-and-stained specimens were made with the aid of a drawing tube and subsequently scanned and edited with Macrosoft Flash 6.0.

A data matrix (Table 2) of comparative information on external morphology and osteology was compiled using MacClade 4.0 (vers. 4.0, D. R. Maddison and W. P. Maddison, Sinauer Associates, Inc., Sunderland, MA, 2000) for the *Rhabdolichops* species listed in Table 1 (excluding *R. jegui* due to unavailability of specimens) and on the sternopygid outgroup taxa: *Sternopygus branco, Archolaemus blax, Distocyclus conirostris, Eigenmannia limbata,* and *E. virescens.* Additional data for Table 2 was taken from characters described in Lundberg and Mago-Leccia (1986), Albert (2001), and Crampton et al. (2004). Descriptions of character states are summarized in Appendix 1. All character states apply to morphologically (as opposed to reproductively) mature specimens unless otherwise stated. Diagnoses were generated using the export branchlist option in MacClade 4.0, with all characters optimized unambiguously on a strict consensus of the equally most parsimonious tree topologies using the hard polytomy option. All multistate characters were treated as unordered (i.e., 7, 33, 34, and 41). Maximum parsimony analyses were conducted using the branch and bound search option in PAUP* (vers. 4.0b10, D. L. Swofford, PAUP*: phylogenetic analysis using parsimony [*and other methods], Sinauer, Sunderland, MA, 2003). Three support indices are reported for each internal node including branch lengths as character state changes (steps) of unambiguous optimization. Bremer decay values (Bremer, 1994) were calculated using TreeRot (Sorenson, University of Michigan, Ann Arbor, MI, 1996) to generate constraint files for PAUP. Bootstrap values were calculated using the heuristic search option in PAUP and 100 replicates.

Rhabdolichops Eigenmann and Allen 1942

Diagnosis.—Rhabdolichops is diagnosed by six unique and unreversed character states among Sternopygidae (*sensu* Albert 2001; Albert and Crampton, 2005): scales absent above lateral line on anterior portion of body (character 4) vs. scales present over entire postcranial portion of body; premaxilla trapezoidal and elongate (character 10) vs. triangular and broad; two prootic foraminae (character 18) vs. one foramen; extrascapular fused with neurocranium (character 20) vs. present as an independent ossification; gill rakers long and bony (character 21) vs. short, fleshy with fibrous cores; and gill rakers ossified (character 23) vs. not ossified. *Rhabdolichops* may also be differentiated from other sternopygids (except *Archolaemus*) by a body cavity of moderate length, with 12–15 precaudal vertebrae (PCV; character 34) vs. short, with 10–11 PCV (Albert, 2001; Hulen et al., 2005).

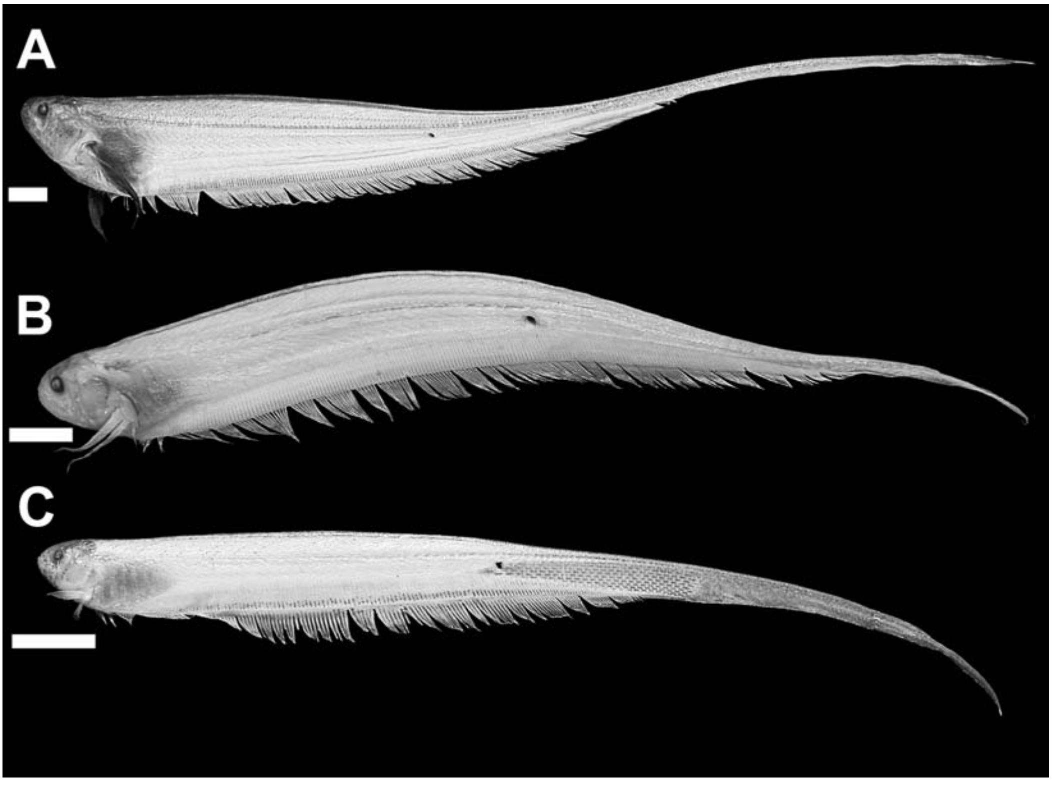

Fig. 1. Photographs of preserved specimens of the holotypes of three new species of *Rhabdolichops*. (A) *R. nigrimans* (female, MCP 36048). (B) *R. lundbergi* (male, MCP 36037). (C) *R. navalha* (immature, MCP 36046). Scale bar = 10 mm.

***Rhabdolichops nigrimans*, new species**
Figures 1–2, Tables 3–4

Holotype.—MCP 36048, female, 273 mm, Brazil, Amazonas, Rio Tefé, Municipality of Tefé, 03°43.41′S, 64°59.93′W, 22 Jan. 1999, W. Crampton.

Paratypes.—BMNH 1998.3.12.244, 1, 128 mm, Municipality of Maraã, Lago Amanã, Boca do Igarape Baré, 02°28.9′S, 64°42.8′W, 1 May 1995. INPA 25255, 5 (female, 272 mm; female, 261 mm; female, 230 mm; male, 431 mm; female, 305 mm), Rio Tefé, 03°43.41′S, 64°59.93′W, 22 January 1999. MCP 36047, 5 (male, 354 mm; male, 336 mm; male, 360 mm; female, 165 mm; female, 290 mm), collected with INPA 25255. MCP 36049, 7 (female, 288 mm; 243 mm; 126 mm; female, 285 mm; 314 mm; 225 mm; female, 212 mm), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W, 25 Oct. 1999. MCP 36050, 2 (male, 302 mm; 247 mm), Rio Tefé, 03°42.54′S, 65°00.43′W, 20 March 2000. MCP 36052, 1 (273 mm), Rio Tefé, 03°46.58′S, 64°59.78′W, 16 Feb. 2001. MCP 36053, 1 (male, 317 mm), Upper Lago Tefé, 03°34.59′S, 64°59.32′W, 5 May 1994. MCP 36054, 2 (female, 251 mm; female, 218 mm), Lago Tefé, Beach at Noguera, 03°34.59′S, 64°59.32′W, 13 Oct. 1997. All paratypes collected by W. Crampton from Municipality of Tefé, Amazonas, Brazil, and sexually immature otherwise stated.

Non-type material.—INPA 9579, 2, Rio Negro, Lago Janema, near mouth of Rio Jaú, 7 Oct. 1994, M. Garcia and J. Zuanon.

Diagnosis.—Distinguished from all other species of *Rhabdolichops* by the presence of black pectoral and anal fins, with dark chromatophores extending to the distal tips of the fin rays, and from all congeners (except *R. lundbergi*) by long pectoral fins (P1/HL = 127.7 ± 13.4 vs. 60–100). Also unique among congeners (except *R. lundbergi*) in that the anterodorsal margin of the opercle forms a sharp right (vs. sloping obtuse) angle (Fig. 3A). *Rhabdolichops nigrimans* can further be distinguished from all other congeners, except *R. lundbergi*, by the following characters: sickle-shaped maxilla with concave dorsal margin (vs.

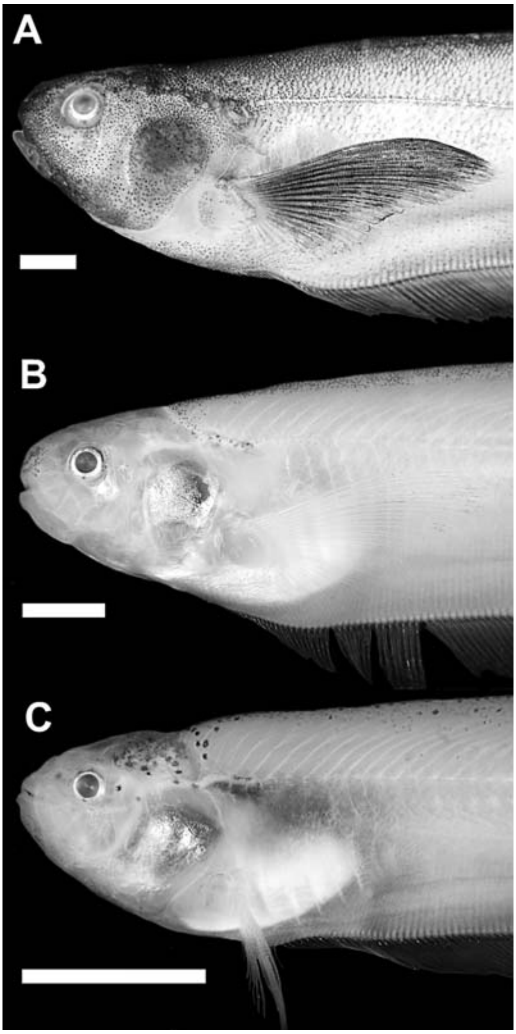

Fig. 2. Photographs of heads of live specimens of three new species of *Rhabdolichops*. (A) *R. nigrimans* (female, MCP 36052). (B) *R. lundbergi* (immature, MCP 36044). (C) *R. navalha* (immature, INPA 15782). Scale bar = 5.0 mm.

broad maxilla with straight dorsal margin); infraorbital canal bones five and six ossified as complete slender tubes (vs. broad partial cylinders with bony arches); sphenotic spine ventral to infraorbital portion on frontal (vs. posterior to infraorbital portion on frontal); posttemporal fossa absent (vs. present); opercle with anterodorsal facet (Fig. 3A); cleithral process narrow (vs. broad); cleithrum with a semi-lunar margin against the base of the pectoral-fin radials, a long pectoral-fin (longer than head length vs. shorter); displaced hemal spines 3–4 (vs. 2; Fig. 4A); and pectoral-fin with black chromatophores on rays (vs. hyaline rays). *Rhabdolichops nigrimans* can further be distinguished from *R. lundbergi* by having: a longer body (maximum total length 419 vs. 233 mm TL; n = 15 for each species); an exaggeratedly scaly appearance of anterior epaxial body surface due to chromatophores concentrated along outer scale margins; larger teeth on premaxilla, mesopterygoid and dentary; and more numerous teeth on premaxilla (20–25 vs. 18–20), mesopterygoid (11–13 vs. 8), and dentary (25–34 vs. 12–13; n = 2 adults for each species); and sexual dimorphism of the caudal appendage (tail) length in which mature males possess a longer caudal appendage than mature females (mean CA 44 ± 2.9% vs. 38 ± 3.2%; n = 5 each).

Description.—Head and body are illustrated in Figures 1A and 2A. Morphological and meristic data of *R. nigrimans* are summarized in Tables 3 and 4, respectively. Body slender (BD < 14% LEA) of moderate size, up to 419 mm TL (222 mm LEA). Scales absent from dorsum for approximately one head length's distance posterior to nape. Dorsal surface of head covered by thick skin. Eye subcutaneous. Mouth subterminal. Gape about equal to preorbital distance, quadrangular when fully open in medial, frontal aspect. Rictus at a vertical with posterior margin of posterior nares. Lips smooth, continuous with head integument; a shallow labial groove medial to maxilla. Premaxilla trapezoidal, elongate with 20 to 25 small, recurved, villiform teeth. Maxilla sickle-shaped, with dorsal margin concave. Anterior process of maxilla narrow. Maxilla and palate toothless. Dentary broad and robust, with 25 to 34 villiform teeth. Infraorbital and opercular series bones partially externally visible. Infraorbital canal bones one to four partial cylinders with slender osseous arches. Infraorbital canal bones five and six slender tubes. Sphenotic process (spine) present below infraorbital portion of frontal. Two prootic foraminae. Posttemporal fossa absent. Extrascapular fused with neurocranium. Ascending process of mesopterygoid very robust and incompletely attached to frontal, extending dorsal to orbitosphenoid, and with broad distal margin. Mesopterygoid with 11–13 small conical teeth. Twelve–15 (mode 14) gill rakers on first branchial arch (n = 13), long, ossified, not attached to branchial arches (Table 4).

Posttemporal fused to supracleithrum. Scapular foramen present. Cleithral posterior process narrow. Postcleithrae thin and discoid. Parapophyses of second vertebrae near os suspensorium. Anterior intermuscular bones within epaxial muscles highly branched in region behind head. Body cavity of moderate length with 12–13 PCV. Five to seven pairs of pleural ribs. Anterior five

TABLE 3. MORPHOMETRIC DATA FOR THREE NEW SPECIES OF *Rhabdolichops*. Percentage measurements in LEA, HL, or TL. Abbreviations: *n*, number of specimens (these vary because measurements were excluded from specimens with damage or unusual preservation artifacts); TL, total length; LEA, length to end of anal fin base; HL, head length; AF, anal fin length; CA, caudal appendage length; PAF, pre-anal fin length; PP, pre-pectoral fin length; PA, pre-anus distance; PO, postorbital length; SO, snout to occiput length; BD, body depth; HD-1, head depth at occiput; PR, preorbital length; TD, tail depth; P1, pectoral fin length.

	R. nigrimans, new species			*R. lundbergi*, new species			*R. navalha*, new species		
	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*
TL	222.0–419.0	289.9	15	109.0–233.0	161.3	15	95.0–178.0	124.2	15
LEA	128.0–222.0	175.0	15	100.0–171.0	129.3	15	71.0–115.0	81.8	15
LEA/TL	53.0–75.3	60.7	15	56.5–97.8	82.5	13	59.2–84.9	66.1	15
AF/LEA	86.1–91.4	88.6	15	84.4–91.0	87.3	13	87.3–95.8	89.7	15
CA/LEA	48.1–88.7	68.4	14	11.9–77.1	26.1	13	51.0–69.0	58.1	13
PAF/LEA	8.1–10.9	9.4	14	6.2–10.1	7.5	13	5.5–11.8	8.4	13
PP/LEA	10.5–13.6	11.6	15	10.9–13.4	11.8	13	8.7–10.5	9.8	15
PA/LEA	1.2–5.2	3.4	15	2.3–4.2	3.4	13	3.4–6.6	5.0	14
HL/LEA	10.1–12.8	11.1	15	10.2–12.2	10.8	13	9.4–11.6	10.5	15
PO/HL	50.8–60.0	56.3	15	51.3–56.7	54.3	15	48.7–65.3	57.6	15
SO/HL	69.7–94.0	79.2	15	86.1–104.9	93.1	15	76.9–97.4	83.4	15
BD/LEA	10.7–13.9	12,4	15	10.7–12.9	11.8	13	9.7–13.2	11.6	15
HD-1/HL	82.4–111.6	94.3	15	87.6–106.2	98.0	15	93.8–116.9	102.3	15
PR/HL	23.1–32.2	28.5	15	20.7–28.8	26.1	15	22.1–29.4	26.4	15
TD/LEA	1.4–3.0	2.1	15	1.2–3.0	2.0	13	5.0–6.3	5.7	15
TD/CA	1.8–5.7	3.1	14	2.3–15.4	8.7	14	8.3–12.3	10.0	13
P1/HL	101.3–147.3	127.7	15	103.9–142.7	124.0	15	66.7–97.4	85.6	15

pairs of ribs long, extending almost to ventral margin of body cavity. Proximal pectoral radials three and four fused. Anal-fin rays 163–243 (mode 215; $n = 13$; Table 4). Anal-fin pterygiophores longer than hemal spines at midbody. Three or four displaced hemal spines at posterior margin of body cavity (Fig. 4). Anus enclosed within folds of branchial membranes, located at a vertical with anterior margin of eye. Anal-fin origin below pectoral-fin base. Anal fin reaches its greatest height (about one-third body length) posterior to greatest body depth, its distal margin straight. Pectoral-fin pointed, long, second and third branched rays longest.

Electric organ visible between hypaxial and pterygiophore muscles posterior to about one-

TABLE 4. MERISTIC DATA FOR THREE NEW SPECIES OF *Rhabdolichops*. Abbreviations: *n*, number of specimens (these vary because counts were excluded from specimens with damage or unusual preservation artifacts); Med, Median value; GR1, gill rakers on first arch; P1R, pectoral-fin rays (unbranched rays in roman numbers followed by number of branched rays); AFR, anal-fin rays; CEP, caudal electroplate rows; PCV, precaudal vertebrae; CVA, caudal vertebrae to end of anal fin; CVT, total number of caudal vertebrae; PLS1, pored lateral line scales from posterior edge of opercle to above of end of anal fin; PLS2, pored lateral-line scales from posterior edge of opercle to end of tail; PRP, pleural rib pairs.

	R. nigrimans, new species			*R. lundbergi*, new species			*R. navalha*, new species		
	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*
GR1	12–15	14	13	12–15	15	15	7–9	9	12
P1R	ii18–ii20	ii20	14	ii18–ii20	ii18	15	ii9–ii12	ii9	12
AFR	163–243	215 (Med)	13	217–247	232 (Med)	8	123–160	140 (Med)	12
CEP	4–5	4	10	4–6	5	9	8–10	10	12
PCV	12–13	13	13	12–13	13	8	12–13	12	12
CVA	49–56	54	11	46–55	49	6	42–48	44	12
CVT	58–92	69	9	66	66	1	50–72	50	12
PLS1	119–141	131 (Med)	14	111–146	129 (Med)	15	71–92	81 (Med)	12
PLS2	187–252	225 (Med)	14	118–252	170 (Med)	15	95–137	124 (Med)	12
PRP	5–7	6	13	4–5	5	8	5	5	12

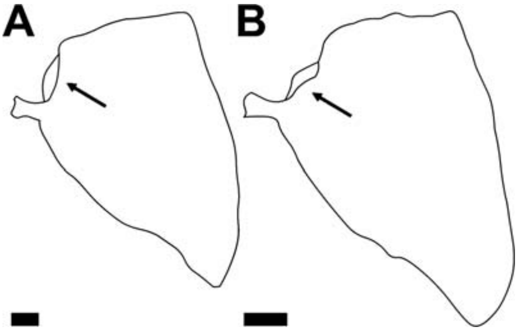

Fig. 3. Camera lucida tracing of opercle (left side in lateral view). (A) *Rhabdolichops nigrimans.* (B) *R. lundbergi.* Scale bar = 1.0 mm.

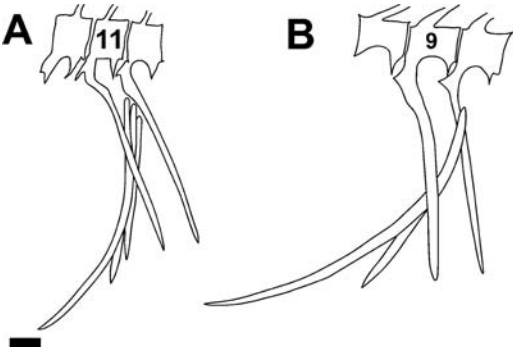

Fig. 4. Camera lucida tracing of displaced hemal spines (left side in lateral view). (A) *Rhabdolichops nigrimans.* (B) *R. navalha.* Labeled vertebrae number are counted in an anterior to posterior direction and include those of Weberian apparatus. Scale bar = 1.0 mm.

third LEA, becoming deeper posteriorly, with five rows visible at posterior end of anal fin, and with three rows extending along majority of length of caudal appendage. Electrocytes at last anal-fin ray arranged in irregular rows, and of unequal sizes, ranging from 0.8–1.4 mm in length (mean 1.1 $\pm$ 0.19, n = 10) and 0.6–1.9 mm in depth (mean 1.6 $\pm$ 0.38). Electrocytes usually hexagonal (sometimes pentagonal) in lateral aspect. Caudal appendage of sexually mature males much longer than in females, extending approximately one LEA beyond last anal-fin ray. Electric organ with 4–5 (mode 4) rows of electrocytes at last anal-fin ray.

Coloration in ethanol.—Background color pale yellow or light tan. Concentration of chromatophores along the middorsum and over lateral line. Chromatophores concentrated along outer scale margins over anterior epaxial portion of body giving surface a distinct ''scaly'' appearance. Humeral region grading to charcoal color without sharp margins. Area over anal-fin pterygiophores immaculate except for a concentration of chromatophores between the distal portions of the anal-fin radial muscles. Head ground color similar to body with more dense chromatophore speckling and a slight counter-shading. Dense chromatophore aggregations variably present in patches over cheeks, infraorbital series, snout, and chin. Pectoral-fin rays black to distal tip, with chromatophore intensity increasing distally. Anal-fin rays and membranes translucent, with black chromatophores along distal margin.

Coloration in life.—Similar to color in ethanol except chromatophores are often more expanded giving body a dusky or pale gray appearance.

Ecology.—*Rhabdolichops nigrimans* is known only from low-conductivity blackwater systems of the Tefé region, including the mouthbay lakes Lago Tefé and Lago Amanã and also the Rio Tefé. The waters of these systems are typical of blackwater systems of the Central Amazon, with electrical conductivity in the range 8–30 μScm^{-1} and pH in the range 4–6. During the low water period *R. nigrimans* was encountered in trawl samples taken at depths of from five to 15 m in the Rio Tefé. At this time of the year the Rio Tefé is swiftly flowing and well oxygenated from surface to bottom. During the low water period *R. nigrimans* was also captured with fyke-net traps in flooded shore scrub thickets growing on low-lying sand bars. During the high water period the floodplain of the Rio Tefé is swollen with flood waters which inundate extensive floodplain forests (igapós). At this time of the year the main channel of the Rio Tefé no longer serves as a major conduit for flow and instead contains almost static water, which is completely anoxic near the bottom. All benthic gymnotiform fishes disappear from this deep water habitat at this time of the year–some into adjacent floodplain forests and others possibly downstream to the mouthbay lake, Lago Tefé, whose shallow waters are usually well-oxygenated and well mixed. During the high water period *R. nigrimans* moves into the igapó forests where it can be detected with portable electric fish detectors. Like all other *Rhabdolichops* species *R. nigrimans* is absent in terra firme rainforest streams. *Rhabdolichops nigrimans* breeds during the rising-water phase and spawning males and females are common in newly flooded igapó forests–often appearing in fyke nets. Males develop elongated tails and also generate EODs at a much lower repetition rate than females during the breeding season (Crampton and Albert, 2005). Adult *R. nigrimans* feed on a variety of aquatic invertebrates including the larvae of Odonata, Coleoptera, Ephemeroptera, and Trichoptera, in addition to smaller food items such as chironomid larvae (Diptera). Very small fishes are also eaten. Within flooded forests diverse allochthonous invertebrate food items were found including ants, termites, and Lepidoptera larvae.

Distribution.—Known only from the type locality (Rio Tefé, Brazil) and from the lower Rio Negro, Brazil.

Etymology.—From the Latin noun *manus* (hand) and adjective *nigrum* (black), in reference to the diagnostic black pectoral fin.

Rhabdolichops lundbergi, new species
Figures 1–2, Tables 3–4

Holotype.—MCP 36037, 1, male, 151 mm, Brazil, Amazonas, Rio Japurá, near Boca do Lago Mamirauá (0.2 km offshore of lowest water mark), Municipality Alvarães, 03°07.67′S, 64°46.43′W, 7 Dec. 1999, W. Crampton.

Paratypes.—INPA 25254, 20 (3 males, 2 females, 102–170 mm), Rio Japurá, near Boca do Lago Mamirauá (0.2 km offshore of lowest water mark), 03°07.67′S, 64°46.43′W, 7 Dec. 1999. MCP 36031, 1, female, 175 mm, Rio Japurá, between Boca do Lago Mamirauá and Boca do Paraná do Jaquiri, 03°07.58′S, 64°47.30′W, 19 Jan. 1999. MCP 36032, 1, male, 241 mm, Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W, 26 Jan. 1999. MCP 36033, 1, female, 162 mm, Rio Japurá at mouth of Lago Caxinguba, 03°06.17′S, 64°45.84′W, 3 Feb. 1999. MCP 36034, 1, male, 201 mm, Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W, 4 Feb. 1999. MCP 36035, 1, female, 175 mm, Mamirauá Lake System, Paraná Maiana, 03°04.10S, 64°47.52′W, 5 Feb. 1999. MCP 36036, 18, 116–149 mm, collected with INPA 25254. MCP 36038, 1, 151 mm, Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W, 12 Jan. 2000. MCP 36039, 15 (1 male, 1 female, 120–180 mm), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W, 24 Feb. 2000. MCP 36040, 1, 119 mm, Lago Juruazinho, flooded forest, fyke nets, 03°01.85′S, 64°51.12′W, 9 Oct. 1994. MCP 36041, 1, 187 mm, Lake Tefé at Noguera, 03°17.97′S, 64°46.35′W, 13 Oct. 1997. MCP 36042, 1, 132 mm, Rio Solimões, near Alvarães, 03°12.63′S, 64°47.38′W, 7 Feb. 2001. MCP 36043, 1, 217 mm, Parana-Apará, 03°17.97′S, 64°46.35′W, 7 July 1994. MCP 36044, 7 (multi, 133–229 mm), Brazil, Municipality of Tefé, Rio Japurá-Solimões Confluence, Praia Caborini, 03°07.13′S, 64°47.30′W, 10 Feb. 2001. MCP 36051, 1, 132 mm, Rio Solimões, South bank, ca. 5 km downstream of mouth of Lago Alvarães, 03°14.72′S, 64°46.08′W, 15 Jan. 2001. UF 146880, 42 (multi, 118–190 mm), Brazil, Municipality of Tefé, Rio Japurá-Solimões Confluence, Praia Caborini, 03°07.13′S, 64°47.30′W, 10 Feb. 2001. All paratypes collected in the municipality of Alvarães, Brazil by W. Crampton and sexually immature unless otherwise stated.

Diagnosis.—Distinguished from all other species of *Rhabdolichops* (except *R. nigrimans*) by the presence of long pectoral fins (P1/HL = 124.0 ± 9.7 vs. 60–100), with chromatophores generally restricted to the distal portions of the fin rays, creating a dark tip. Further distinguished from other species of *Rhabdolichops* (except *R. nigrimans*) by characters used in the diagnosis of *R. nigrimans* (above). Further distinguished from *R. nigrimans* by smaller adult body size; shorter caudal appendage with absence of sexual length dimorphism; smaller teeth on premaxilla, mesopterygoid, and dentary; and less numerous teeth on the premaxilla (18–20 vs. 20–25), mesopterygoid (8 vs. 11–13), and dentary (12–13 vs. 25–34; $n = 2$ adults for each species).

Description.—Head and body are illustrated in Figures 1B and 2B. Morphological and meristic data of *R. lundbergi* are summarized in Tables 3 and 4, respectively. Body slender (BD < 13% LEA) of moderate size, up to 233 mm TL (171 mm LEA). Scales absent above the lateral line on anterior portion of body. Dorsal surface of head covered by thick skin. Eye subcutaneous. Mouth subterminal. Gape about equal to preorbital distance, quadrangular when fully open in medial, frontal aspect. Rictus at a vertical with posterior margin of posterior nares. Lips smooth, continues with head integument; a shallow labial groove medial to maxilla. Premaxilla trapezoidal, elongate with 18–20 small, recurved, villiform teeth. Dentary broad and robust, with 12–13 villiform teeth. Anterior process of maxilla narrow. Maxilla sickle-shaped, with dorsal margin concave. Maxilla and palate toothless. Infraorbital series bones partially visible. Infraorbital canal bones one and two partial cylinders with osseous arches. Infraorbital canal bones five and six slender tubes. Sphenotic process (spine) present below infraorbital portion of frontal. Two prootic foraminae. Posttemporal fossa absent. Extrascapular fused with neurocranium. Ascending process of mesopterygoid very robust and incompletely attached to frontal, extending dorsal to orbitosphenoid, and with a broad distal margin. Mesopterygoid with 7–10 small conical teeth. Twelve–15 (mode 15) gill rakers on first branchial arch (n = 15), long, ossified, not attached to branchial arches (Table 4).

Posttemporal fused to supracleithrum. Scapular foramen present. Cleithral posterior process narrow. Postcleithra thin and discoid. Parapophyses of second vertebrae near *os suspensorium*. Anterior intermuscular bones within epaxial muscles highly branched in region behind head. Body cavity of moderate length with 12–13 PCV. Four or five pairs of pleural ribs. Anterior pairs of ribs long, extending almost to ventral margin of body cavity. Proximal pectoral radials three and four fused. Anal-fin rays 217–247 (mode 232; n = 8; Table 4). Anal-fin pterygiophores longer than hemal spines at midbody. Three or four displaced hemal spines at posterior margin of body cavity. Anus enclosed within folds of branchial membranes, located at a vertical with anterior margin of eye. Anal-fin origin below pectoral-fin base. Anal fin reaches its greatest height (about one third body length) posterior to greatest body depth, its distal margin straight. Pectoral-fin pointed, long, second and third branched rays longest.

Electric organ visible between hypaxial and pterygiophore muscles posterior to about one-third LEA, becoming deeper posteriorly, with five rows visible at posterior end of anal fin, and with three rows extending along majority of length of caudal appendage. Electric organ with 4–6 (mode 5; n = 9) rows of electrocytes at last anal-fin ray. Electrocytes at last anal-fin ray arranged in irregular rows usually hexagonal (sometimes pentagonal) in lateral aspect.

Coloration in ethanol.—Background color very pale yellow or light tan. Diffuse chromatophores along the middorsum, and over lateral line. Areas over the axial muscles with scattered chromatophores. Area over anal-fin pterygiophores immaculate except for a concentration of chromatophores between the distal portions of the anal-fin radial muscles. Head ground color similar to body with more dense chromatophore speckling and slightly counter shaded. Dense chromatophore aggregations in patches over infraorbital series and chin. Proximal portion of pectoral-fin rays hyaline, distal portion sometimes dark. Anal-fin rays and membranes translucent.

Coloration in life.—Similar to color in ethanol except body translucent or pale pinkish white contrasting to charcoal gray pigmentation of *R. nigrimans.*

Ecology.—*Rhabdolichops lundbergi* is common in the main channel of the whitewater rivers of the Tefé region. Here it was found both in trawl-net samples at depths of 10–18 m and also, very abundantly, on sandy and muddy beaches sampled with seine nets. Here, *R. lundbergi* occurs in syntopy with *R. eastwardi*, *R. caviceps*, and *R. electrogrammus* (but not *R. nigrimans* or *R. navalha*). The species evidently moves from deeper water into shallow beaches at night when seine nets intercept much larger numbers of this species. *Rhabdolichops lundbergi* is also found in the well oxygenated paraná channels that wind through the whitewater várzea floodplain flanking major whitewater rivers such as the Rio Solimões. However, at high water paraná channels fill with hypoxic water emanating from adjacent flooded forests, and all species of *Rhabdolichops*, along with other riverine gymnotiforms, migrate out into the main river channels (Crampton, 1998b). Small numbers of *R. lundbergi* were found in the lower reaches of Lago Tefé, a blackwater lake containing low-conductivity water (e.g., MCP 36041). However, the preferred habitat of this species is turbid river water with electrical conductivity in the range of 80–150 μScm^{-1}. Nothing is known about the breeding habits of this species. Mature males and females were found during the rising water phase of the Amazon River and were encountered among many other immature specimens on beaches. *Rhabdolichops lundbergi* feeds on aquatic invertebrates–mainly Trichoptera and Ephemeroptera larvae, but also the larvae of Coleoptera and Chironomidae. Some specimens had also ingested large amounts of adult Conchostraca.

Distribution.—Known only from the type localities near the confluence of the Rio Japurá and Rio Solimões (Amazon), Amazonas, Brazil.

Etymology.—Patronym in honor of John G. Lundberg for his contributions to the study of gymnotiform and other Neotropical fishes.

***Rhabdolichops navalha*, new species**

Figures 1–2, Tables 3–4

Holotype.—MCP 36046, 161 mm, Brazil, Amazonas, Rio Tefé, Toco Preto, Municipality Tefé, 03°47.31′S, 64°59.91′W, 26 Oct. 1999, W. Crampton.

Paratypes.—INPA 15782, 20 (94–128 mm), Brazil, Rio Tefé, Toco Preto, Municipality Tefé, 03°47.31′S, 64°59.91′W, 26 Oct. 1999, W. Crampton. MCP 36045, 22 (95–179 mm), Brazil, Rio

Tefé, Toco Preto, Municipality Tefé, 03°47.31′S, 64°59.91′W, 26 Oct. 1999, W. Crampton.

Diagnosis.—Distinguished from all other species of *Rhabdolichops* by the following unique characters: an unusual electric organ (EO) morphology in which the posterior EO margin ends abruptly and is replaced by rigid and transparent non-electrogenic tissue in the posterior approximate one-half of the caudal appendage (Fig. 1C); the readily visible presence of hemal spines in the posterior half of the caudal appendage; the presence of five (vs. six or seven) pairs of pleural ribs; oral teeth conical, with diameter at base more than at midlength (vs. villiform, about as wide at base as at midlength in all congeners; cleithral posterior process broad (vs. narrow in all congeners). *Rhabdolichops navalha* can also be distinguished from all congeners except *R. stewarti* in possessing non-ossified gill rakers and from all congeners except *R. electrogrammus* and *R. caviceps* in possessing a distinct ''black cap'' (dense region of dark chromatophores in the parietal region).

Description.—Head and body are illustrated in Figures 1C and 2C. Morphological and meristic data of *R. navalha* are summarized in Tables 3 and 4, respectively. Scales absent above lateral line on anterior portion of body. Body elongate, slender (BD $<$ 14% LEA), of small size, up to 178 mm TL (115 mm LEA). Dorsal surface of head covered by thin skin. Eye subcutaneous. Mouth large, slightly superior. Rictus anterior to a vertical with posterior margin of posterior nares. Gape width more than preorbital head length, mouth ovoid when fully open. Lips smooth, continuous with head integument; a shallow labial groove medial to maxilla. Premaxilla trapezoidal, elongate, with 8–9 recurved, conical teeth arranged in two rows along the oral margin. Maxilla broad, not sickle-shaped, with a narrow anterior process and a straight dorsal margin. Maxilla and mesopterygoid toothless. Dentary with 12–13 recurved, conical teeth arranged in two rows along the oral margin. Infraorbital canal bones one to four partial cylinders with slender osseous arches. Infraorbital canal bones five and six partial cylinders, osseous arches. Sphenotic process (spine) present below infraorbital portion of frontal. Two prootic foraminae. Posttemporal fossa present. Extrascapular fused with neurocranium. Ascending process of mesopterygoid long, robust and abutting frontal medially dorsal to orbitosphenoid. Gill rakers not ossified; 7–9 (mode 9) long gill rakers on first branchial arch (n = 12; Table 4).

Posttemporal fused to supracleithrum. Scapular foramen present. Cleithral posterior process broad. Postcleithrae thin and discoid. Parapophyses of second vertebrae near os suspensorium. Anterior intermuscular bones within epaxial muscles highly branched in region behind head. Body cavity of moderate length with 12–13 (mode 12) PCV. Five pairs of pleural ribs, all long, extending almost to ventral margin of body cavity. Proximal pectoral radials three and four fused. Anal-fin rays 123–160 (median 140; n = 12). Anal-fin pterygiophores longer than hemal spines at midbody. Two displaced hemal spines at posterior margin of body cavity (Fig. 4B). Anus enclosed within folds of branchial membranes, located at a vertical with anterior margin of eye. Anal-fin origin posterior to pectoral-fin base. Anal fin reaches its greatest height (about one-third body length) at about greatest body depth, its distal margin strongly convex. Pectoral fin short, less than head length, its second and third branched rays longest. The electric organ visible from about two thirds LEA (with strong back-illumination) between hypaxial and pterygiophore muscles becoming deeper posteriorly with 8–10 rows at posterior limit of anal fin. Caudal appendage extending approximately one-half (0.51–0.69) LEA beyond last anal-fin ray. Electrocytes uniformly hexagonal in lateral view. Electrocytes arranged in regular rows, and of similar sizes, at 80% LEA ranging from 1.4–1.5 mm in length (mean 1.5 $\pm$ 0.07, n = 10) and 0.4–0.5 mm in depth (mean 0.5 $\pm$ 0.03).

Coloration in ethanol.—Background color pale yellow or light tan. Middorsum pale yellow, with a few scattered chromatophores. Areas over the lateral line, axial muscles and pterygiophore muscles immaculate, except for a faint concentration of chromatophores between the distal portions of the anal-fin radial muscles. Head ground color similar to body with dense chromatophore concentration over neurocranium and around orbit and speckling on rostrum, mental, and gular regions. No pigments over opercular bones, except for over laterosensory canals. Pectoral and anal-fin rays and membranes translucent.

Coloration in life.—Pigmentation patterns similar to color in ethanol, but body highly translucent, with color restricted to region of body cavity and head, with a pinkish hue in opercular region from underlying gills, a silvery sheen to surface of opercle, and viscera enclosed within a white membrane.

Ecology.—*Rhabdolichops navalha* is known only from the main channel of the low-nutrient

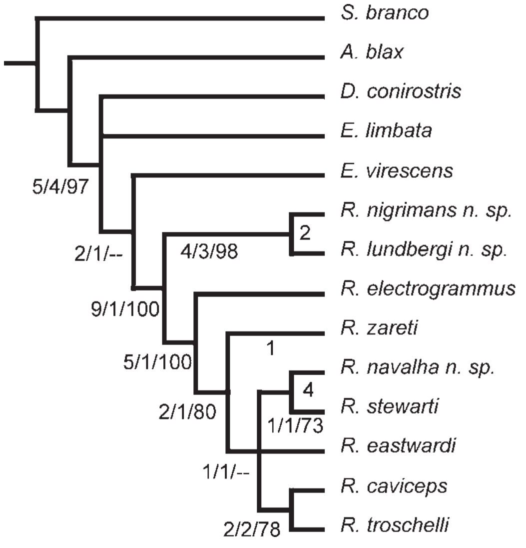

Fig. 5. Phylogenetic relationships of *Rhabdolichops* species and representative species of all other sternopygid genera (S = *Sternopygus*, A = *Archolaemus*, D = *Distocyclus*, E = *Eigenmannia*). Topology is a strict consensus of six equally parsimonious trees consistent with the data matrix of Table 2, with all characters weighted equally. Each tree: length = 55, consistency index (CI) = 0.80, retention index (RI) = 0.90, rescaled consistency index (RC) = 0.72. Numbers on nodes: unambiguous branch length/Bremer decay index/bootstrap values. Bootstrap values <70% are indicated with "–".

blackwater Rio Tefé. Here it is abundant in trawl samples taken at depths from 5–10 m in mid channel during the low water period. Both day and night trawls intercepted this species. Seine-net samples conducted both by day and night on sandy beaches along the same stretch of river and taken at the same time of the year did not intercept *R. navalha*, suggesting that this species is a benthic specialist. *Rhabdolichops navalha* was captured in trawl nets in syntopy with *R. eastwardi, R. troscheli, R. caviceps, R. nigrimans*, and *R. electrogrammus* (all congeners known from the Tefé region except *R. lundbergi*). *Rhabdolichops navalha*, in contrast to *R. nigrimans* (and *R. eastwardi*) was never encountered from fyke-net samples set in flooded igapó forests along the margins of the Rio Tefé. *Rhabdolichops nigrimans* was also never encountered at high water in Lago Tefé in contrast with all other congeners with which *R. nigrimans* is sympatric during the low water period. No sexually mature specimens of this species were encountered, although the osteology of the larger specimens was characteristic of adult specimens, including complete ossification of elements of the neurocranium that are normally cartilaginous in immature specimens. The diet of *R. navalha* comprises small planktonic crustaceans–primarily Cladocera and Copepoda but also small Conchostraca and Ostracoda. Plankton net samples of the benthos of the Rio Tefé revealed a rich community of planktonic crustaceans.

Distribution.—Known only from the type locality in the Rio Tefé, Amazonas, Brazil.

Etymology.—From the Portuguese *navalha* (razor) in reference to the highly laterally compressed body. A noun in apposition.

Discussion

Phylogenetic positions of the new species.—The phylogenetic positions of the three new *Rhabdolichops* species described in this report were estimated within the context of the comparative analysis of Lundberg and Mago-Leccia (1986). Maximum parsimony analysis of the 42 morphological characters provided in Table 2 supports the topology and polarity of the phylogeny presented by Lundberg and Mago-Leccia (1986), resolves several of the polytomies resulting from that study, and further includes the positions of *R. nigrimans, R. lundbergi*, and *R. navalha*.

This hypothesis of relationships based on the strict consensus tree of six trees (L = 55; CI = 0.80, RI = 0.90, and RC = 0.72) is summarized in Figure 5. In this phylogeny *R. nigrimans* and *R. lundbergi* are sister species and together form the sister taxon to a clade comprising seven other *Rhabdolichops* species, including *R. navalha*. Information on the osteology of *R. jegui* from French Guiana was not available for this study, and this species was excluded from the phylogenetic analysis. *Rhabdolichops nigrimans* and *R. lundbergi* share four uniquely derived character states: pectoral-fins with black chromatophores on rays (character 3); opercle anterodorsal facet present (character 25); pectoral-fin longer than head length (character 28); cleithral pectoral margin semi-lunar (vs. forming an obtuse angle; character 30). The other *Rhabdolichops* species (*R. electrogrammus, R. zareti, R. eastwardi, R. navalha, R. stewarti, R. caviceps*, and *R. troscheli*) share five uniquely derived character states: maxilla broad with a straight dorsal margin (vs. sickle-shaped with a curved dorsal margin; character 11); infraorbital canal bones five and six forming broad partial cylinders with open osseous arches (vs. slender tubes; character 13); sphenotic spine located posterior to infraorbital portion of frontal (vs. below infraorbital portion of frontal; character 15); posttemporal fossa present (vs.

absent; character 19); two displaced hemal spines (vs. three or four spines; character 40). *Rhabdolichops navalha* is nested high within the tree as a member of a clade including *R. stewarti*, *R. caviceps*, and *R. troscheli*. *Rhabdolichops navalha* and *R. stewarti* share one uniquely derived character state: gill rakers not ossified (character 23).

Comment on the diagnosis of Rhabdolichops.—The clade consisting of *Rhabdolichops nigrimans* and *R. lundbergi* exhibits a transitional suite of phenotypes between the genera *Eigenmannia* and *Rhabdolichops* as recognized in the previous literature (Lundberg and Mago-Leccia, 1986; Albert, 2001). In particular these species possess several primitive features (i.e., characters 11, 13, 15, 19, and 40) thought previously to be characters excluded from *Rhabdolichops* (Albert, 2001). Notable among these characters is the absence of a prootic foramen (character 19). The diagnosis of *Rhabdolichops* presented in this paper therefore differs from that of previous studies (Mago-Leccia, 1978; Lundberg and Mago-Leccia, 1986; Albert and Campos-da-Paz, 1998; Albert, 2001).

Material Examined

Data are arranged alphabetically by species, then by country, state, museum acronym, and number. Catalog numbers are followed in parentheses by number of specimens, size range in mm TL, type-status (HT = holotype, PT = paratype, ST = syntype), summary locality, and geographical coordinates. Additional specimens examined are reported in Albert (2001), Crampton et al. (2004), and Hulen et al. (2005).

Rhabdolichops caviceps. Brazil: Amazonas: INPA 15790 (3, 252–340), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. INPA 15791 (2, 131–150), Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W. INPA 18162 (2, 170–253), Rio Japurá at mouth of Lago Caxinguba, 03°06.17′S, 64°45.84′W. INPA 18163 (1, 165), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. INPA 18209 (1, 250), Rio Japurá, near Boca do Lago Mamirauá, 0.2 km offshore of lowest water mark, 03°07.67′S, 64°46.43′W. MCP 35999 (1, 219), Mamirauá Lake System, Paraná Maiana, 03°03.15′S, 64°48.03′W. MCP 36000 (2, 225–250), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36001 (1, 286), Rio Japurá at mouth of Lago Caxinguba, 03°06.17′S, 64°45.84′W. MCP 36002 (1, 263), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. MCP 36003 (8, 155–376), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. MCP 36004 (6, 146–188), Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W. MCP 36005 (2, 316–374), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36006 (1, 279), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36007 (3, 163–261), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. MCP 36008 (1, 208), Rio Solimões, Ilha do Prego, 03°12.63′S, 64°47.38′W. MCP 36009 (1, 91), Rio Solimões, Ilha Paramin, 03°17.29′S, 64°41.49′W. MCP 36010 (1, 291), Paraná-Maiana, 03°06.74′S, 64°47.53′W. MCP 36011 (1, 176), Rio Solimões, Ilha Içé, 03°16.08′S, 64°41.35′W. Venezuela: Amazonas: UMMZ 230812 (3, 151–165), mouth of Río Guaviare, San Fernando de Atabapo. Delta Amacuro: BMNH 1988.3.7.38–42 (3, 133–216), Río Orinoco delta region. UMMZ 214592 (2, 203–208), Río Orinoco, above Barrancas. UMMZ 214593 (12, 90–222), Río Orinoco, Isla Tres Caños. UMMZ 214594 (3, 183–213), Río Orinoco, Brazo Imataca. UMMZ 214597 (2, 160–273), Río Orinoco, at Paula.

Rhabdolichops eastwardi. Brazil: Amazonas: BMNH 1998.3.17.24 (1, 134), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. INPA 15789 (3, 138–236), Mamirauá Lake System, Paraná Maiana, 03°04.10′S, 64°47.52′W. INPA 15793 (14, 95–160), Mamirauá Lake System, Paraná Maiana, 03°04.83′S, 64°47.30′W. INPA 18211 (4, 103–124), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. INPA 18212 (7, 111–195), Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W. INPA 18213 (22, 151–270), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. INPA 18214 (4, 104–183), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. INPA 18215 (1, 128), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. INPA 18216 (2, 148–190), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. INPA 18217 (1, 181), Rio Japurá, between Boca do Lago Mamirauá and Boca do Paraná do Jaquiri, 03°07.58′S, 64°47.30′W. INPA 18218 (1, 180), Rio Japurá at mouth of Lago Caxinguba, 03°06.17′S, 64°45.84′W. INPA 18219 (3, 187–194), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. INPA 18220 (1, 158), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36012 (1, 170), Rio Japurá, between Boca do Lago Mamirauá and Boca do Paraná do Jaquiri, 03°07.58′S, 64°47.30′W. MCP 36013 (2, 170–184), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36014 (2, 154–216), Rio Japurá at mouth of Lago Caxinguba, 03°06.17′S, 64°45.84′W. MCP 36015 (3, 234–276), Rio

Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. MCP 36016 (16, 122–246), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. MCP 36017 (1, 118), Rio Tefé, Ilha do Martelo, 03°46.82′S, 64°59.48′W. MCP 36018 (25, 86–177), Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W. MCP 36019 (8, 101–177), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36020 (2, 142–162), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36021 (1, 174), Rio Tefé, 03°46.58′S, 64°59.78′W. MCP 36022 (2, 212–219), Rio Solimões, Ilha do Prego, 03°12.63′S, 64°47.38′W. MCP 36023 (2, 135–297), Parana-Apará, 03°17.97′S, 64°46.35′W. MCP 36024 (2, 165–260), Rio Solimões, 03°12.63′S, 64°47.38′W. MCP 36025 (33, 72–261), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. UF 146878 (40, 78–175), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. Rondonia: UF 100651 (1, 325), Madeira River, Jaciparana River. Venezuela: BMNH 1988.3.7.33–37 (4, 122–207), Río Orinoco delta across from Palma, 8°23.00′N, 62°11.00′W. Amazonas: UMMZ 228968 (23, 170–276), mouth of Río Guaviare, San Fernando de Atabapo. UMMZ 230813 (30, 125–256), mouth of Río Guaviare, San Fernando de Atabapo. Apure: UF 37027 (22, 79–159), Río Apure, Hato El Frio, near Río Guaritico. Barinas: FMNH 100748 (14, 118–256), Río Suripa, mouth of Río Anaro. Delta Amacuro: UMMZ 214598 (12, 114–213), Lagoon of Río Orinoco.

Rhabdolichops electrogrammus. Brazil: Amazonas: INPA 15792 (3, 101–127), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36026 (1, 260), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. MCP 36027 (1, 109), Rio Japurá, near Boca do Lago Mamirauá, 03°07.67′S, 64°46.43′W. MCP 36028 (1, 120), Rio Solimões, Ilha Içé, 03°16.08′S, 64°41.35′W. MCP 36029 (3, 128–189), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. MCP 36030 (1, 172), Rio Solimões; North bank, near Boca do Paraná Coxiu Muni, 03°17.16′S, 64°37.84′W. UF 146879 (20, 84–135), Rio Japurá-Solimões Confluence, Praia Caborini, 03°09.14′S, 64°47.06′W. Guyana: Potaro-Siparuni: INHS 49451 (1, 215), near Tumatumari cataract, 05°21.48′N, 59°00.04′W. Venezuela: Amazonas: MBUCV 14666 (1, 292), Río Cataniapo, near Puerto Ayacucho. Delta Amacuro: BMNH 1988.3.7.43–44 (2, 164–229), Río Orinoco delta, Isla Portuguesa, 08°37.00′N, 61°48.36′W. FMNH 97070 (3, 125–142), Isla Portuguesa. MBUCV 10489 (1, 225.7, HT), Isla Tres Caños, near Caño Aragüaito. UMMZ 214599 (1, 212), Río Orinoco, downstream of Isla Portuguesa.

Rhabdolichops stewarti. Brazil: Pará: ANSP 158678 (1, 98, HT), 26 km E Jacaréacanga, Rio Tapajós. Venezuela: Amazonas: MBUCV 7541 (1, PT, 110), Quiritare, near mouth Río Cuncunuma, Río Orinoco.

Rhabdolichops troscheli. Brazil: Amazonas: BMNH 1927.6.7.26 (1, 411), Rio Solimões, Upper Rio Amazonas. INPA 4827 (46, 100–490), Rio Uatumá, Balbina, Barquem. INPA 18210 (3, 335–470), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. MBUCV 9772 (6), Rio Amazonas, near Manaus. MCZ 54336 (4), Rio Solimões, near Paraná de Janauaca. MCP 36055 (1, 320), Mamirauá Lake System, Paraná Maiana, 03°04.10′S, 64°47.52′W. MCP 36056 (8, 317–580), Rio Tefé, Toco Preto, 03°47.31′S, 64°59.91′W. MCP 36057 (1, 381), Mamirauá Lake System, Paraná Maiana, 03°06.74′S, 64°47.53′W. MCP 36058 (1, 224), Parana-Apará, 03°17.97′S, 64°46.35′W. MCP 36059 (1, 238), Lago Tefé, 03°34.59′S, 64°59.32′W. Pará: BMNH 1849.11.8.31 (1, HT, 382) Rio Capim. Bolivia: Beni Department: UMMZ 204707 (3, 93–152), Río Itenez, Costa Marques. UMMZ 205078 (1, 85), Río Mamore at Cachuela, just below Guayaramerin. Venezuela: Delta Amacuro: MBUCV 10625 (1).

Rhabdolichops zareti. Venezuela: Delta Amacuro: BMNH 1988.3.7.29–32 (4, 90–141), Rio Orinoco delta main channel, north of Isla Tres Caños. UMMZ 214569 (94, 85–225), Lagoon of Río Orinoco, naut. mi. 210, on south side of Isla Isabela, between Paula and Ciudad Bolivar.

Rhabdolichops sp. (unidentified). Guyana: Potaro-Siparuni: BMNH 1934.9.12.361–363 (3, 276–294) River Mazaruni. Suriname: NRM 64 (ST), no locality on label, from King Adolf Fredrik's collection at Ulriksdal, probably from near Paramaribo. Venezuela: Amazonas: UMMZ 230832 (6, 56–122), mouth of Río Guaviare, across from San Fernando de Atabapo. UMMZ 228969 (1, 190), mouth of Río Guaviare, across from San Fernando de Atabapo. UMMZ 230833 (1, 89), mouth of Río Guaviare, across from San Fernando de Atabapo.

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APPENDIX 1. ABBREVIATED CHARACTER DESCRIPTIONS. Previously described characters followed by citation in parentheses.

1. Head color. 0: dorsal surface of head pale or slightly counter shaded. 1: black cap of large chromatophores speckling restricted to region over parietal bones.
2. Anal-fin color. 0: hyaline rays and membrane. 1: black chromatophores on distal tips of rays.
3. Pectoral-fin color. 0: hyaline. 1: black chromatophores on rays.
4. Postcranial body squamation. 0: scales over entire postcranial portion of body. 1: absent above lateral line on anterior portion of body (Lundberg and Mago-Leccia, 1986, character 23).
5. Body depth. 0: deep, BD less than 14% LEA. 1: elongate, slender, BD more than 14% LEA.
6. Eye subcutaneous. 0: surface of eye not covered by epidermis in adults; free orbital margin. 1: eye completely covered by epidermis in adults; orbital margin not free (Lundberg and Mago-Leccia, 1986, character 16; Albert, 2001, character 104).
7. Mouth position in specimens >80% max TL. 0: subterminal (subinferior). 1: terminal. 2: superior. (Figs. 1 and 2; Lundberg and Mago-Leccia, 1986, character 26).
8. Anterior maxillary process shape. 0: anterior process of maxilla broad and triangular, its ventral margin continuous with descending blade of maxilla, tapering evenly to anterior tip. 1: anterior process of maxilla extends as a narrow bar perpendicular to main axis of maxilla, its ventral margin not continuous with that of descending blade (Lundberg and Mago-Leccia, 1986, character 4; Albert, 2001, character 33).
9. Shape of teeth. 0: teeth in both jaws conical, with a broad base tapering toward the cusp. 1: teeth in both jaws villiform each tooth a long cylindrical shaft with a narrow base (Lundberg and Mago-Leccia, 1986, character 2; Albert, 2001, character 54).
10. Premaxilla shape. 0: triangular, broad. 1: trapezoidal, elongate (Lundberg and Mago-Leccia, 1986, character 20 in part).
11. Maxilla shape. 0: sickle-shaped, dorsal margin concave. 1: broad, dorsal margin straight. (Lundberg and Mago-Leccia, 1986, character 20 in part).
12. Infraorbital canal bones one to four. 0: canal bearing portion of infraorbital bones slender and tubular. 1: antorbital and infraorbitals 1–4 large, partial cylinders with slender osseous arches (Lundberg and Mago-Leccia, 1986, character 1; Albert, 2001, character 57).
13. Infraorbitals canal bones five and six. 0: fifth and sixth infraorbitals are slender tubes. 1: fifth and sixth infraorbitals are modified as enlarged, trough-like ossicles, similar in form to the anterior infraorbitals (Lundberg and Mago-Leccia, 1986, character 19 in part).
14. Neurocranial shape. 0: elongate: length (from posterior margin of basioccipital to anterior tip of mesethmoid)/depth (vertical distance at parasphenoid flexure) 2.0–4.0. 1: foreshortened: 1.6–1.9.
15. Sphenotic spine. 0: sphenotic spine below IO portion of the frontal bone. 1: sphenotic spine is posterior to IO portion of the frontal bone. (Lundberg and Mago-Leccia, 1986, character 19 in part).
16. Mesopterygoid dentition. 0: present. 1: absent (Lundberg and Mago-Leccia, 1986, character 25).
17. Sphenotic process. 0: dorsolateral margin of sphenotic straight, anterior margin underlies frontal. 1: dorsolateral margin of sphenotic bearing a transversely oriented crest or process exposed on dorsolateral edge, anterior margin not underlying frontal (Lundberg and Mago-Leccia, 1986, character 3; Albert, 2001, character 75).
18. Foraminae in prootic. 0: a single foramen in the prootic. 1: two foramina in the prootic (Lundberg and Mago-Leccia, 1986, character 17). The two foraminae in the prootic of *Rhabdolichops* allows the two main rami of the facial nerve to exit the skull separately.
19. Posttemporal fossa. 0: absent. 1: space between pterotic, exoccipital, and epioccipital open to neurocranial vault. Not equal to posttemporal fossa of Lundberg and Mago-Leccia (1986).
20. Extrascapular. 0: independent ossification. 1: fused with neurocranium (Lundberg and Mago-Leccia, 1986, character 18; Albert, 2001, character 170).
21. Gill raker shape. 0: short, fleshy, fibrous cores. 1: long, bony.
22. Gill raker attachment. 0: gill rakers directly attached to gill arches. 1: base of gill rakers not mineralized, rakers (when present) not attached to gill arches (Lundberg and Mago-Leccia, 1986, character 24 in part; Albert, 2001, character 146).

23. Gill raker ossification. 0: ossified. 1: not ossified.
24. Posttemporal. 0: posttemporal independent from supracleithrum. 1: posttemporal fused with supracleithrum (Lundberg and Mago-Leccia, 1986, character 10; Albert, 2001, character 169).
25. Opercle anterodorsal facet. 0: absent. 1: present (Fig. 3).
26. Opercle anterodorsal margin. 0: obtuse angle. 1: right angle (Fig. 3).
27. Scapular foramen. 0: unossified area along medial margin in scapulocoracoid cartilage separating coracoid and scapular ossifications. 1: unossified region of scapulocoracoid cartilage included entirely within the scapula, forming a large foramen (Lundberg and Mago-Leccia, 1986, character 9; Albert, 2001, character 173).
28. Pectoral-fin length. 0: shorter than head length. 1: longer than head length.
29. Cleithral posterior process. 0: cleithral process on the posterior margin above the axilla broad. 1: cleithral process on the posterior margin above the axilla narrow (Lundberg and Mago-Leccia, 1986, character 22).
30. Cleithral pectoral margin. 0: obtuse angle. 1: semi-lunar.
31. Shape of postcleithrae. 0: postcleithrae robust, posterior margins straight; main axes of postcleithrae aligned with that of supracleithrum. 1: postcleithrae thin and discoid, posterior margins curved; main axes of postcleithrae oblique with that of supracleithrum (Lundberg and Mago-Leccia, 1986, character 11 in part; Albert, 2001, character 171).
32. Anterior vertebrae. 0: close proximity between parapophyses of second vertebrae and os suspensorium. 1: parapophyses of second vertebrae separated by distinct gap from os suspensorium (modified from Lundberg and Mago-Leccia, 1986, character 8; Albert, 2001, character 181).
33. Anterior intermuscular bones. 0: simple or little branched. 1: anterior epipleurals branched, with 2–4 rami each. 2: anterior epipleurals highly branched, with 6–20 rami each at the level of the seventh to ninth precaudal vertebrae (Lundberg and Mago-Leccia, 1986, character 7; Albert, 2001, character 174).
34. Body cavity length. 0: body cavity associated with 16–18 precaudal vertebrae (PCV). 1: body cavity short; associated with 12–15 PCV. 2: Body cavity very short; associated with 10 to 11 PCV (Table 4; Lundberg and Mago-Leccia, 1986, character 5; Albert, 2001, character 206).
35. Number of pleural ribs. 0: eight (or more) pairs of pleural ribs. 1: six or seven pairs. 2: five pairs (Table 4; Lundberg and Mago-Leccia, 1986, characters 13; Albert, 2001, character 203).
36. Length of anterior ribs. 0: anterior two or three ribs relatively short, their lengths less than 80% body depth at pectoral girdle. 1: length of anterior two ribs greater than 80% body depth at pectoral girdle (Lundberg and Mago-Leccia, 1986, character 6; Albert, 2001, character 210).
37. Proximal pectoral radials. 0: proximal radials three and four separate. 1: proximal radials three and four co-ossified in adult specimens (Lundberg and Mago-Leccia, 1986, character 15; Albert, 2001, character 176).
38. Anal-fin rays. 0: mean 210–300 AFR. 1: mean 145–209 AFR (Table 4).
39. Anal-fin pterygiophore length at midbody. 0: shorter than hemal spines. 1: longer than hemal spines.
40. Number of displaced hemal spines (DHS). 0: three to four DHS (''rib-like bones'') in the ventral body wall, attached loosely to the first and second hemal spines. 1: two DHS in the ventral body wall, attached loosely to the first and second hemal spines (Fig. 4, Table 4; Lundberg and Mago-Leccia, 1986, character 21; Albert, 2001, character 191).
41. Visible electrocyte rows. 0: mode 0–3. 1: mode 4–7. 2: mode 8–10 (Fig. 1; Lundberg and Mago-Leccia, 1986, character 27, table 1).
42. Electric organ posterior margin. 0: Not truncate, obliquely continuous with ventral margin of anal fin. 1: vertically truncate, not continuous with ventral margin of anal fin (Fig. 1).