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Electric fishes of the genus *Sternarchorhynchus* (Teleostei, Ostariophysi, Gymnotiformes); phylogenetic and revisionary studies

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Analysis of 88 characters of external and internal body systems yielded a phylogenetic reconstruction of the Neotropical electric knifefish genus *Sternarchorhynchus* (Apteronotidae; Gymnotiformes). The results support a hypothesis of *Sternarchorhynchus* as the sister group to *Platyurosternarchus*. A series of synapomorphies, many involving major innovations of the neurocranium, jaws, suspensorium, and associated systems that permit an unusual mode of grasp-suction feeding, support the monophyly of both genera. Synapomorphies largely resolve relationships within *Sternarchorhynchus* with basal nodes strongly supported by characters pertinent to prey capture and initial processing of food items. These possible key innovations may provide *Sternarchorhynchus* with a competitive advantage over other clades of the Apteronotidae and account for the species diversity of the genus in Neotropical rivers. Adaptive radiation in *Sternarchorhynchus* was analysed. Habitat preference transitions repeatedly occurred in the genus between deep-river channel dwelling species and rheophilic species with preferences for higher energy setting including rapids and swift-flowing fluviatile settings. Twenty-two species of *Sternarchorhynchus* are described as new based on samples that originated in the smaller rivers draining into the Golfo de Paria, the Marowijne and Essequibo River basins, the Río Orinoco and in particular the Amazon River basin. The 32 species in *Sternarchorhynchus* make it the most speciose genus in the Apteronotidae.

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INTRODUCTION

Electric knifefishes of the genus *Sternarchorhynchus* are tube-snouted, elongate, distinctly laterally compressed fishes with a broad range in many Atlantic drainages of South America. *Sternarchorhynchus* ranges from the Río Orinoco basin in Venezuela and Colombia (Mojica, 1999; Lasso *et al.*, 2004a, b) south through the rivers of the Guianas (Planquette, Keith & Le Bail, 1996; Meunier, 2004) and the Amazon basin (Goulding, Leal Carvalho & Ferreira, 1988; Cox-Fernandes, 1999) to the upper Rio Paraná in the Río de La Plata basin (Britski, Silimon & Lopes, 1999; Campos-da-Paz, 2000). The genus is unknown from the trans-Andean and Caribbean versant portions of South America, the rivers of north-eastern and south-eastern Brazil that drain directly into the Atlantic Ocean, all portions of the Río de La Plata basin exclusive of the upper Rio Paraná system, and the entirety of the southern reaches of the continent.

Sternarchorhynchus species are moderate-sized predators (150 to 540 mm maximum total length) of benthic invertebrates (Goulding *et al.*, 1988; Marrero & Taphorn, 1991). Their electrogenic abilities

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facilitate the location and capture of prey in soft mud and within the interstices between leaf litter and other detritus (Marrero & Winemiller, 1993; Crampton & Albert, 2006). Similarly they hunt for and capture aquatic insects, especially of the Chironomidae, Ephemeroptera, and Trichpotera, in small spaces in the river bottom and the tunnels and spaces in compacted clay nodules (Marrero, 1987; Marrero, Castillo & Machado-Allison, 1987; Marrero & Winemiller, 1993). Correlated modifications of the bones, musculature, and other soft tissues of the jaws, and suspensorium in the highly restructured, tube-like snouts, and anterior portions of the neurocranium allow extraction of prey items from these constricted refuges (Aguilera, 1986). These restructurings permit what has been termed 'grasp-suction' or 'suction assisted by mechanical grasping'. Morphological adaptations permitting this highly specialized feeding mode are unique to *Sternarchorhynchus* and the African mormyriform genus *Campylomormyrus* amongst orders of fishes entirely restricted to freshwaters (Marrero & Winemiller, 1993; Winemiller & Adite, 1997).

A diversity of secondary sexually dimorphic features characterize genera in the Apteronotidae, with these modifications most prominent in the morphology of the snout and jaws (Cox-Fernandes, 1998). Amongst these are the hypermorphic growth of the snout in males of some species of *Apteronotus* (Cox-Fernandes, Lundberg & Riginos, 2002; Albert & Crampton, 2009) and the elaboration of the anterior portion of the jaws and dentition in *Sternarchogiton* (de Santana & Crampton, 2007). Many species of *Sternarchorhynchus* are characterized by secondary sexual dimorphism of multiple body systems. Non-cephalic sexually dimorphic features of some species of *Sternarchorhynchus* involve pigmentation and more often the location of the anus and urogenital pore. More dramatic are the sexually dimorphic attributes involving the snout and jaws. Mature males of *Sternarchorhynchus mormyrus* have a wider snout than conspecific females of comparable body sizes, whereas the distinct fleshy dorsomedian ridge on the snout is limited to the males of *Sternarchorhynchus kokraimoro*. Some species in the genus demonstrate sexually dimorphic differences in the degree of curvature of the elongate snout. Most striking of the sexually dimorphic features in *Sternarchorhynchus* are the lengthened and transversely widened anterior portions of the dentaries in some larger males of ten species. This expanded region is rounded in the transverse plane and dorsally forms a bulbous structure crowned with a patch of variably enlarged teeth. Such enlarged dentition may be brought into play by males in confrontations during breeding contests (Marrero & Taphorn, 1991; Kirschbaum, 1995; Cox-Fernandes *et al.*, 2002). Although these elaborations of the lower jaw and associated dentition occur only in mature males, they are absent in some conspecific males of comparable body sizes with well-developed testes. Presence versus absence of these modifications potentially reflects a social hierarchy wherein the jaw and dentition elaborations are limited to alpha males. Alternatively, variability in the expression of these features may reflect seasonality in the manifestation of the modifications of the lower jaw and associated dentition.

As in other gymnotiforms, the species of *Sternarchorhynchus* generate and receive weak electrical signals that function in electrocommunication and electrolocation. Electrocommunication serves to signal species identity and aspects of behaviour, whereas electrolocation permits the detection of organisms and objects in the surrounding aquatic system via distortions of the electric field generated by the individual [see Carr & Maler, 1986 and Albert & Crampton (2005) for discussions of the adaptations associated with these functions]. Members of *Sternarchorhynchus* generate at least four types of electric organ discharges (EODs). These periodic (wave-type) signals are interspecifically variable with discharges ranging between 944 and 1922 Hz and considerable overlap in distance ranges between congeners (Crampton & Albert, 2006: 688–689, figs 23.10–11). Some *Sternarchorhynchus* species have a unique EOD modulation pattern (active phase coupling) possibly associated with information exchange between potential mates (Langner & Scheich, 1978; Gottschalk & Scheich, 1979); however, the degree to which these unusual EOD patterns are universal across the genus is unknown.

Species of *Sternarchorhynchus* dwell in diverse habitats, with many members of the genus resident in the deep-water benthos of the larger rivers. In these habitats, the species of *Sternarchorhynchus* constitute a significant portion of the fish biomass (Lopez-Rojas, Lundberg & Marsh, 1984; Lundberg *et al.*, 1987; Marrero & Taphorn, 1991). Jointly with other deep-water species of the Apteronotidae, they are preyed upon extensively by several catfish species of large body sizes (Marrero & Taphorn, 1991; Barbarino Duque & Winemiller, 2003). Some species of *Sternarchorhynchus* are adapted for life in smaller rivers and tributary streams where they often inhabit high-energy settings such as rapids and/or pools at the base of waterfalls (e.g. *Sternarchorhynchus severii*, *Sternarchorhynchus caboclo*; de Santana & Nogueira, 2006: 90).

Impoundments across the range of *Sternarchorhynchus* drowned many of the rapids and waterfalls that are preferred habitats for many species of the genus (Ferreira, 1995: 34–35; Campos-da-Paz, 2005: 399).

Proposed development projects furthermore threaten other sites occupied or likely to be occupied by members of the genus. Habitat loss of this scale renders species of *Sternarchorhynchus* vulnerable to extinction at least at the local level (e.g. *Sternarchorhynchus britskii* in the upper Rio Paraná; Campos-da-Paz, 2005: 399; Triques, 2007: 125). Indeed, some species described as new herein are possibly either extinct or face imminent extinction.

Deep main river channels, rapids, pools at the bases of waterfalls and large rapids, and subterranean waters potentially inhabited by species of *Sternarchorhynchus* (Campos-da-Paz, 2000; Bichuette & Trajano, 2003) remain unsampled ichthyologically in many regions. When surveyed, the ichthyofauna in these difficult-to-collect habitats is nearly always incompletely sampled because of resource limitations and/or restrictions on the use of the collecting methods (e.g. rotenone) often prerequisite for exhaustive collections of such faunas. Consequently, nearly all species of *Sternarchorhynchus* described to date are based on one to relatively few specimens. One notable exception (*Sternarchorhynchus roseni*) was described from a locality that was the subject of long-term sampling efforts. Limited samples of many species of *Sternarchorhynchus* continue to bedevil systematic, ecological, and behavioural studies of the genus; problems typified by the restricted samples of some of the species described herein. Rectifying the problem of limited sample size is unlikely in the short term, if ever, because of resource limitations; a problem compounded by the accelerating anthropogenic modifications of many of the habitats occupied by species of *Sternarchorhynchus*.

Müller & Troschel (1848) described the first species now placed in *Sternarchorhynchus* as *Sternarchus oxyrhynchus*. The next three decades saw the proposal of *Sternarchorhynchus* by Castelnau (1855), the description of *S. mormyrus* by Steindachner (1868a), the proposal of the subgenus *Rhamphosternarchus* within *Sternarchus* by Günther (1870) for species now assigned to *Sternarchorhynchus*, and the description of *Sternarchorhynchus curvirostris* by Boulenger (1887). In a dramatic reversal of the practice of progressive description of additional species, Ellis (1913) placed *S. mormyrus* and *S. curvirostris* as junior synonyms of *Sternarchorhynchus oxyrhynchus* and recognized a monotypic *Sternarchorhynchus.* Ellis' concept of *S. oxyrhynchus* was of a geographically broadly distributed species characterized by pronounced variation in external head morphology and anal-fin ray counts.

This broadly inclusive *S. oxyrhynchus* held sway for over a half a century (e.g. Eigenmann & Allen, 1942: 318; Fowler, 1951: 431) until Fernández-Yépez (1967) resurrected *S. curvirostris* and *S. mormyrus* from the synonymy of *S. oxyrhynchus* based on differences between what he identified as samples of those nominal forms. Fernández-Yépez failed to specify the localities where his samples originated, but the illustrations in that publication make it clear that the material considered *S. curvirostris* was misidentified and that the purported specimens of *S. mormyrus* were probably another species. Notwithstanding these misidentifications, Fernández-Yépez correctly surmised that *Sternarchorhynchus* encompassed more than one species. Subsequent authors followed Fernández-Yépez and recognized *S. oxyrhynchus*, *S. mormyrus*, and *S. curvirostris*.

The century-plus hiatus in the description of nominal species of *Sternarchorhynchus* ended with Mago-Leccia's (1994) description of *S. roseni* from the Río Orinoco system. Soon thereafter, Campos-da-Paz (2000) summarized the state of knowledge of the taxonomy of *Sternarchorhynchus*, addressed the questions of the monophyly of, and intrarelationships within, the genus, and described two new species (*S. britskii*, *Sternarchorhynchus mesensis*). de Santana & Taphorn (2006; *Sternarchorhynchus gnomus*), de Santana & Crampton (2006; *Sternarchorhynchus curumim*), and de Santana & Nogueira (2006; *S. severii*, *S. caboclo*) described four additional species of *Sternarchorhynchus*.

Notwithstanding the recent flurry of species descriptions, Albert & Crampton (2005) and de Santana & Nogueira (2006) proposed that thorough analyses of *Sternarchorhynchus* across its range would reveal additional undescribed species. Results reported on herein confirm those predications; indeed those forecasts as to the number of undescribed species proved quite conservative. In addition to the ten previously recognized *Sternarchorhynchus* species, we describe 22 new species of the genus. Populations of *Sternarchorhynchus* that probably represent additional yet-to-be described species are identified, but formal descriptions of those forms deferred for various reasons. Nonetheless, the 32 species of *Sternarchorhynchus* account for 40% of the species in the Apteronotidae, the ghost electric knifefishes (de Santana, Castillo & Taphorn, 2006; this study).

Campos-da-Paz (2000) and Albert (2001) delved into the question of the relationships of and within *Sternarchorhynchus* and proposed *Platyurosternarchus* as a potential sister group to that genus. Those analyses encompassed solely the limited number of species then recognized within the genus. The numerous species described as new in *Sternarchorhynchus* since the phylogenetic analysis by Campos-da-Paz (2000), along with the continued description of phylogenetically informative characters within the Gymnotiformes, necessitate a re-evaluation of the evidence for the monophyly of the genus. More importantly it is appropriate to develop an intrageneric phylogenetic hypothesis incorporating the dramatically higher number of species now recognized within *Sternarchorhynchus*.

This study had four primary goals:

1. To evaluate the hypothesis of the monophyly of *Sternarchorhynchus* and its sister-group relationship with *Platyurosternarchus*;
2. To generate a hypothesis of the phylogenetic relationships within *Sternarchorhynchus*;
3. To examine the correlations amongst major shifts in the jaws and associated structures, major transitions in body sizes, and shifts in habitat preferences in the species of *Sternarchorhynchus* within the context of the reconstructed phylogeny; and
4. To provide a comprehensive revision of species of *Sternarchorhynchus* with associated keys, species accounts, and distribution maps.

MATERIAL AND METHODS

Hypotheses of phylogenetic relationships are based on cladistic methods first proposed by Hennig (1966) and subsequently elaborated by a series of authors (e.g. Nelson & Platnick, 1981; Wiley, 1981; Wiley *et al.*, 1991; Forey *et al.*, 1996). The method used in the search for the hypothesis best supported by the incorporated data was Wagner parsimony under which reversals of, and convergencies in, characters are permissible and quantified equally (Swofford & Maddison, 1987). The analysis was carried out using PAUP*4.0B10 (Swofford, 2003). A parallel analysis was undertaken in NONA (Goloboff, 1999) in its shell WINCLADA (Nixon, 1999–2002). The matrix of 88 characters and 34 terminal taxa was built in MacClade (Maddison & Maddison, 2005) with tree manipulations and character diagnoses generated through the same program. Characters were coded as unordered in the analysis of the data matrix. Outgroup comparisons served as the basis for polarity inferences of character. Rooting was a posteriori at the clade formed by *Orthosternarchus* and *Sternarchorhamphus*, which is hypothesized as a basal group in the Apteronotidae (Albert, 2001; Triques, 2005; Hilton *et al.*, 2007). Ambiguous character distributions were resolved using the accelerated transformation optimization [ACCTRAN (Farris optimization)], which maximizes reversals over parallelism (de Pinna, 1991). Delayed transformation optimization (DELTRAN) optimizations are also discussed in Appendix 2.

MERISTICS AND MORPHOMETRICS

Many specimens of gymnotiforms suffer damage to or loss of their tails, most likely from predation, in some instances by other knifefishes (Lundberg *et al.*, 1996: 666). Caudal region damage is often followed by a partial regeneration, with most so-damaged individuals recognizable by the clearly 'truncated, or abruptly narrowed and/or abruptly depigmented tails.' (Mago-Leccia, Lundberg & Baskin, 1985: 1); however, some damaged individuals lack these external indictors. We excluded specimens with apparently regenerated posterior regions of the body from counts of anal- and caudal-fin rays and from morphometrics involving total length, tail length, and tail depth.

Counts

Vertebral counts were obtained from radiographs and cleared and stained specimens. The Weberian apparatus in gymnotiforms incorporates the four anteriormost centra with the second and third elements very closely applied, or sometimes fused, to each other, but still apparent (Hopkins, 1991: 152; Campos-da-Paz, 2000: 524). Abdominal vertebrae are the anterior components of the series that bear a pair of ribs extending over and along the sides of the abdominal cavity and include the vertebrae of the Weberian complex. Transitional vertebrae lack both ribs and neural spines.

Counts of anal-, pectoral-, and caudal-fin rays were most often taken under a microscope using transmitted light with those data supplemented by counts taken from digital radiographs. In the count of the pectoral-fin rays, unbranched anterior rays are represented by lower case Roman numerals and branched rays by Arabic numbers. The count of branched rays includes all rays posterior to the anterior unbranched rays including the posteriormost ray in the series that is apparently sometimes unbranched. Anal-fin ray counts are presented in terms of anterior unbranched and total rays. Caudal-fin rays are the total number of those rays. Observations on the number and form of the branchiostegal rays are from cleared and stained specimens and radiographs.

Measurements

Morphological measurements are point-to-point distances utilizing digital callipers to 0.1 mm total length (TL) with data for each species presented in tabular form in each species account. Measurements were as follows: anal-fin base – the distance between the bases of the first and last rays of the anal fin; anus to anal-fin insertion – the distance from the posterior margin of the anus to the base of the first anal-fin ray; branchial opening – the height of the opening measured along the vertical; caudal length – the distance from the base of the posteriormost ray of the anal fin to the posteriormost point on the body; caudal-fin length – the distance from the hypural joint to the distalmost point along the posterior margin of the caudal fin; eye diameter – the horizontal width of the eye; greatest body depth – the greatest vertical extent of the body, usually situated slightly anterior to the dorsal-fin origin; head depth at eye – the head depth measured at the eye; head depth at nape – the head depth measured at the nape; head width – the head width measured at the opercular region; head length – the distance from the tip of the snout to the posterodorsal angle of the branchial opening; internarial distance – the distance between the posterior of the base of the tubular anterior naris and the anterior margin of the opening of the posterior naris; interocular width (interorbital width of some previous authors) – the minimum width between the dorsal margins of the orbits; length to end of anal-fin (the LEA of Mago-Leccia *et al.*, 1985) – the distance from the tip of the snout to the end of the base of the anal fin; mouth length – the distance from the tip of the snout to the rictus of the mouth; pectoral-fin length – the distance between the base of the dorsalmost ray of the pectoral fin and the distalmost point on the margin of the fin; posterior naris to snout – the distance from the anterior border of the naris to the tip of snout; posterior naris to eye – the distance from the posterior border of the naris to the anterior margin of the eye; postocular distance – the distance from the posterior margin of the eye to the posterodorsal angle of the branchial opening; preanal-fin distance – the distance from the tip of the snout to the base of the first anal-fin ray; prepectoral-fin distance – the distance from the tip of the snout to the base of the dorsalmost pectoral-fin ray; snout length – the distance from the tip of the snout to the anterior margin of the eye; snout to anus – the distance from the tip of the snout to the anterior margin of the anus; tail depth – the depth of the tail measured immediately posterior of the base of the last anal-fin ray; and total length – distance from the tip of the snout to the end of the tip of the caudal fin.

Whenever possible, the sex of specimens was assessed via dissections in order to evaluate possible secondary sexual dimorphism. Ovaries of mature females are packed with yellow or cream-coloured eggs. Testes in mature males are, in contrast, white and smooth.

ABBREVIATIONS

Abbreviations used in text are: CS, cleared and stained; HL, head length; LEA, length from tip of snout to end of anal fin; and TL, total length.

Abbreviations for institutions and collections are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; AUM, Auburn University Museum, Auburn; BMNH, The Natural History Museum, London [formerly British Museum (Natural History)]; CAS, California Academy of Sciences, San Francisco; CAS-SU, former Stanford University collections, now deposited in CAS; CM, Carnegie Museum, Pittsburg, fish collections now deposited at various depositories; CU, Cornell University, Ithaca; FMNH, Field Museum of Natural History, Chicago; IAVHP, Instituto Alexander von Humboldt, Colleción de Peces, Villa de Leyva, Colombia; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; IRScNB, Institute Royal de Sciences Naturelles de Belgique, Brussels; IDSM, Instituto de Desenvolvimento Sustenavel, Mamiraua, Tefé, Brazil; IU, Indiana University, Bloomington, fish collections now at various depositories; LACM, Los Angeles County Museum, Los Angeles; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas; MCNG, Museum de Ciencias Naturales, Guanare; MCP, Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande de Sul, Porto Alegre; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNRJ, Museu National, Rio de Janeiro; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia da Universidade de São Paulo; NMW, Naturhistorisches Museum Wien, Vienna; ROM, Royal Ontario Museum, Toronto; UF, Florida Museum of Natural History, Gainesville; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoologisch Museum, Amsterdam; and ZMB, Museum für Naturkunde der Humboldt Universität, Zoologisches Museum, Berlin.

LOCALITY DATA

Material examined for each species is geographically sorted by country and then, when available, major political divisions within countries, followed by specific localities within those divisions with the localities grouped to the degree possible by proximity. In the case of new species, the locality information is supplemented by data on collectors and date collected. Locality information (and collectors where appropriate) is followed by institutional abbreviation, catalogue number, and number of specimens in lot. Parenthetical information includes the range of total lengths of the specimens and when appropriate information about type status (for previously described species), type of preparation if not whole alcohol specimens, the sex of the specimens when determinable, and other pertinent information.

NOMENCLATURE

Family level names for outgroups are those utilized in Checklist of the Freshwater Fishes of South and Central America [CLOFFSCA (Reis, Kullander & Ferraris, 2003)]. The narrow, posteriorly tapering, fleshy structure that arises from the mid-dorsal line of the posterior half of the body and runs along and is attached to the mid-dorsal groove on the body is termed the electroreceptive filament. This structure was equated with the adipose fin by Ellis (1913) and termed the dorsal thong by Mago-Leccia (1994). The homology of this structure remains uncertain but as indicated by the name it serves an electroreceptive function (see discussion by Franchina & Hopkins, 1996).

Osteological terminology is that of Weitzman (1962) with the following modifications. The use of epioccipital rather than epiotic corresponds to the practice proposed by Patterson (1975). Following Nelson (1969), the ossification traditionally termed the epihyal is referred to as the posterior ceratohyal, and the ceratohyal of many previous authors as the anterior ceratohyal. The ethmoid of Weitzman (1962) is termed the mesethmoid following Fink & Fink (1981, 1996). Vomer is used instead of prevomer, but with the vomer considered to be fused to the ventral ethmoid as is the case in various groups of fishes (Johnson & Patterson, 1996). The anterior portion of that combined bone is identified as the ventral ethmoid as is the practice in recent analyses involving gymnotiforms (Albert, 2001; Hilton *et al.*, 2007). Intercalar is used instead of opisthotic as per the practice in recent studies (Albert, 2001). Following recent authors publishing on gymnotiforms we utilize endopterygoid rather than mesopterygoid (Fink & Fink, 1996). Recent literature on gymnotiform phylogeny includes alternative numbering systems for the gill arches (e.g., Albert, 2001). We follow Hilton *et al.* (2007) in using the number system for gill arches typical for studies of actinopterygian fishes. Nomenclature for muscles and associated tendons is that of Winterbottom (1974).

OSTEOLOGICAL PREPARATIONS

Samples were cleared and counterstained (CS) for cartilage and bone using the method outlined by Taylor & Van Dyke (1985). Removal of the pectoral girdle, suspensorium, and components of the head followed procedures outlined by Weitzman (1974). In order to identify anomalous features, two or more individuals of each species were prepared when specimens were of appropriate size and samples sufficiently large. The osteology of 23 of the 32 species of *Sternarchorhynchus* was examined via cleared and stained specimens. Cleared and counterstained specimens of these species are listed in Supporting Information Appendix S1. Specimens of *Sternarchorhynchus axelrodi*, *Sternarchorhynchus freemani*, *Sternarchorhynchus galibi*, *Sternarchorhynchus kokraimoro*, *Sternarchorhynchus marreroi*, *Sternarchorhynchus taphorni*, *Sternarchorhynchus yepezi*, and *Sternarchorhynchus villasboasi* could not be prepared in that fashion because of small sample sizes or because available specimens were of large body sizes. Radiographs served as supplementary sources of data for these species.

Available specimens of *S. axelrodi* are too large to clear and stain, but we were able to code the species for many osteological characters via radiographs of the type series (see Material examined under species account). That information and the external features allowed us to code the species for 73 of the 88 characters in the matrix. The question of missing data is problematic in phylogenetic analyses and has been discussed in various contexts (Novaceck, 1992; Wiens, 2003, 2005 and references therein). Wiens (2003, 2005) pointed out that even in instances of incomplete data, the available information will be phylogenetically informative when sufficient characters are coded. That has proved to be the case in this study, with the hypothesis of the phylogenetic relationships of *S. axelrodi* well supported.

FRAMEWORK FOR OUTGROUP COMPARISONS

The phylogenetic analysis centres on relationships within *Sternarchorhynchus* rather than suprageneric relationships in the Apteronotidae, a problem that Hilton *et al.* (2007) concluded is 'still the subject of debate' and whose resolution extends beyond the scope of this project. For the purposes of the phylogenetic analysis herein, we focus on *Platyurosternarchus* as the sister group to *Sternarchorhynchus* according to results of the more encompassing phylogenetic hypothesis based on multiple character systems examined herein and in some previous analyses [Albert & Campos-da-Paz (1998: 429, fig. 2 – clade H), Campos-da-Paz (2000: 527 – clade C), Albert (2001: 72, fig. 43 – clade V)].

The question of the appropriate second outgroup to *Sternarchorhynchus* is less straightforward. Campos-da-Paz (1995) identified a series of similarities between *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri*, a relationship reiterated by Alves-Gomes *et al.* (1995) based on genetic, morphologic and electrophysiologic data. Albert (2001), in turn, proposed that *O. tamandua* plus *Sternarchorhamphus muelleri* formed the sister group to the clade formed by *Platyurosternarchus* plus *Sternarchorhynchus* (Albert, 2001: 72, fig. 43 – clades U and V, respectively). Subsequent authors (Triques, 2005; Hilton *et al.*, 2007) advanced additional evidence for the monophyly of the clade formed by *O. tamandua* and *Sternarchorhamphus muelleri* based on morphological data, but questioned the placement of the lineage formed by those two species as the sister group to the clade formed by *Platyurosternarchus* plus *Sternarchorhynchus*. In particular, Hilton *et al.* (2007) highlighted problematic homology assumptions underpinning that phylogenetic hypothesis (see comments under Convergence in elongation of snout in Discussion). That issue notwithstanding, Hilton *et al.* noted that all four genera (*Orthosternarchus*, *Platyurosternarchus*, *Sternarchorhamphus*, and *Sternarchorhynchus*) were relatively basal to 'other apteronotid taxa.' A lack of resolution in the phylogenetic scheme proposed by Triques (2005) renders it uninformative on this issue, but the pattern of relationships does not run counter to that proposal. As such the *Orthosternarchus-Sternarchorhamphus* clade serves as an appropriate secondary outgroup to *Sternarchorhynchus* for the purposes of our analysis.

Concepts of relationships within the rest of the Apteronotidae remain incompletely resolved (Crampton & Albert, 2006: fig. 23.11). Representative taxa from the remaining major clades across the rest of the Apteronotidae (Albert, 2001) were included as more distant outgroups for the purposes of the phylogenetic analysis (*Apteronotus cuchillo*, *Apteronotus rostratus*, *Apteronotus albifrons*, '*Apteronotus*' *apurensis*, *Sternarchella orthos*, and *Sternarchogiton labiatus*). '*Apteronotus' apurensis* is a member of a small clade that Albert & Campos-da-Paz (1998) hypothesized failed to form a monophyletic group with *Apteronotus sensu stricto*. These authors used the convention of '*Apteronotus*' to highlight the uncertainty concerning the appropriate generic assignment for '*A.*' *apurensis* and the three other species in that clade.

Phylogenetic position of Ubidia

Divergent placements of the monotypic genus *Ubidia* necessitate comment. Triques (2005) concluded that *Platyurosternarchus* was the sister clade to *Ubidia magdalenensis*. Under the hypothesis advanced by that author, the *Platyurosternarchus–Ubidia* clade formed the sister group to *Sternarchorhynchus*. A sister-group relationship between *Ubidia* and *Platyurosternarchus* was supported by one proposed synapomorphy – 'the marmorated pigmentation pattern of the body with large dark blotches formed of dense aggregations of chromatophores' (Triques, 2005: 142; our translation). Marmoration was alternatively cited by Albert (2001) as synapomorphic for the members of the *Apteronotus magdalenensis* group [*A. magdalenensis* (= *Ubidia magdalenensis*) and *A. cuchillo*], which share several other hypothesized synapomorphies. In that analysis these species were deeply embedded within *Apteronotus*, with that genus separated from *Platyurosternarchus* and *Sternarchorhynchus* by several nodes supported by a series of characters (Albert, 2001: fig. 43). Both coding and homology questions pertain to the preferability of one of these alternative hypotheses as to the relationships of *Ubidia* with *Apteronotus* versus *Platyurosternarchus*.

Triques (2005) coded *A. cuchillo* as lacking marmoration. Examination of the types of *A. cuchillo* revealed marmoration formed of small scale, irregular, dark and light patterning over the entire head and body other than for the lightly coloured mid-dorsal region. Comparable patterning occurs in *U. magdalenensis*, albeit with the contrast between light and dark regions somewhat muted. Similar marmoration also occurs in the more recently described *Apteronotus eschmeyeri* (de Santana & Maldonado-Ocampo, 2005: fig. 5a).

One could broadly characterize the coloration of *Platyurosternarchus* as marmorated; however, the pigmentation scheme of that genus differs notably from that of *A. cuchillo*, *A. eschmeyeri*, and *U. magdalenensis* and was characterized by Mago-Leccia (1994) as 'highly diagnostic' within the Gymnotiformes. The species of *Platyurosternarchus* have intense dark pigmentation on the ventral portions of the body with the darker patches in that region nearly contiguous and interrupted by some expansive more lightly pigmented regions (Ferreira *et al.*, 2007: 164; de Santana & Vari, 2009: figs 1, 5). This pattern of expansive dark versus light pigmentation patches differs dramatically from the finer marmoration characteristic of *A. cuchillo*, *A. eschmeyeri*, and *U. magdalenensis*. *Platyurosternarchus* has more lightly coloured dorsolateral and dorsal regions of the body with some irregular large patches of somewhat darker pigmentation within the ground coloration; again a pattern absent in *A. cuchillo*, *A. eschmeyeri*, and *U. magdalenensis*. In light of these differences, we judge the marmoration in *A. cuchillo*, *A. eschmeyeri*, and *U. magdalenensis* as nonhomologous with the pigmentation pattern of *Platyurosternarchus.* This nonhomology eliminates support for the *Ubidia–Platyurosternarchus* clade proposed by Triques (2005) with those two genera plus *Sternarchorhynchus* thereby forming a trichotomy under that scheme of relationships. This, nonetheless, leaves *Ubidia* as potentially closely related to *Sternarchorhynchus*.

As noted, Albert (2001: fig. 43) proposed that a series of characters support the hypothesis that the relationships of *Ubidia* lie with a component of *Apteronotus* rather than *Platyurosternarchus* and *Sternarchorhynchus*. *Apteronotus cuchillo* and *U. magdalenensis* share distinctive juvenile coloration patterns, most notably lightly coloured bands proximate to the rear of the anal fin and the base of the caudal fin. These bands encircle the body within the dark background coloration (Schultz, 1949: 71, pl. 3, fig. A). Comparable ontogenetically vanishing contrasting coloration characterizes various *Apteronotus* species including *A. eschmeyeri* (de Santana *et al.*, 2004). Neither species of *Platyurosternarchus* demonstrates a comparable pigmentation pattern. The common possession of this distinctive pigmentation pattern provides further support for the hypothesis that the relationships of *U. magdalenensis* lie with a component of the genus *Apteronotus*.

Coding of internal features of *U. magdalenensis* by Albert (2001) and Triques (2005) apparently was limited to characters shown in the partial illustrations of head osteology in the original description by Miles (1945: fig. 11). This impediment resulted in numerous uncoded characters and was encumbered by apparent errors in those illustrations. Of note is the lateral ethmoid which, although present in specimens of *Ubidia* examined in this study, was absent from the illustration with its absence versus presence coded as unknown by Triques (2005). A lateral ethmoid is always present in the species of *Apteronotus* contrary to the derived absence of that element in *Platyurosternarchus* and *Sternarchorhynchus*. Triques (2005) proposed other features uniting *Ubidia* to *Platyurosternarchus* plus *Sternarchorhynchus*. Two of the characters optimized at that clade rather than being universal for the three genera. Comments on the other proposed synapomorphies are provided under the discussion of the features in the analysis (characters 2, 23, 26, 68, 87) and 'Convergence in the elongation of the snout'. The evidence from coloration and the lateral ethmoid, complemented by the information presented by Albert (2001: 76, 77, fig. 43, see synapomorphies for nodes Z, AA, AB, AC), support the hypothesis that the relationships of *Ubidia* lie with a subunit of *Apteronotus* rather than with *Platyurosternarchus* and *Sternarchorhynchus*. *Ubidia* is consequently not included as a proximate outgroup to *Sternarchorhynchus* in the phylogenetic analysis.

PHYLOGENETIC RESULTS

Eighty-eight characters that vary within *Platyurosternarchus* and *Sternarchorhynchus*, diagnose one of those genera as monophyletic, or are informative for resolution of structure in the outgroup phylogeny were examined in the cleared and stained specimens (Supporting Information Appendix S1) and whole specimens listed under the taxonomic accounts. Characters were divided into two or more discrete character states, with multistate characters present for three characters. Characters were coded as unordered in the analysis of the data matrix (Appendix 1). A heuristic search with stepwise addition, simple additional sequence, branch-swapping tree bisection–reconnection, and 'max' trees saved in PAUP* 4.0b10 (Swofford, 2003) included all outgroups with branches of zero maximum length collapsed and yielded eight most parsimonious trees each with a length of 190, consistency index (CI) = 0.484, and retention index (RI) = 0.820. The analysis using minimum tree length of zero resulted in four trees of the same topology and scores. A parallel analysis in NONA (Goloboff, 1999) in its shell WINCLADA (Nixon, 1999–2002) using the same conditions as in PAUP* and a search strategy of Mult* yielded four trees with the same topology as in the PAUP* analysis with a length of 190, CI = 0.480, and RI = 0.810. The strict consensus tree generated in both of the two software packages was identical, with a length of 193, CI = 0.477, and RI = 0.814 and is presented in Figure 23. Only two of these trees were pertinent to alternative hypotheses of relationships within the lineage formed by *Platyurosternarchus* and *Sternarchorhynchus* and involved the highly imbedded clade 24 within the latter genus (Fig. 24). The other alternative trees pertain to differing patterns of relationships amongst more distant outgroup taxa and as such are not germane to the foci of this study.

CHARACTER DESCRIPTION AND ANALYSIS

The following discussion is arranged by discrete body systems ordered in an approximately anterior to posterior sequence. Characters involving multiple portions of an individual (e.g. coloration) are last. The description of each of the characters first includes a brief descriptor of the character followed by summaries of the alternative character states, the consistency and retention indices under the final phylogenetic hypothesis (Fig. 23), and finally a discussion of the distribution of character states amongst the examined species and members of the examined outgroups. Additional comments on the characters follow where appropriate.

MOUTH

1. *Extent of gape*: (0) posterior terminus of gape not extending posteriorly to beyond vertical through posterior nares; (1) posterior terminus of gape extending posteriorly to beyond vertical through posterior nares (CI = 1.000; RI = 1.000).

Members of the proximate outgroups (*Orthosternarchus*, *Sternarchorhamphus*), along with *Sternarchella orthos* and all species of *Sternarchorhynchus* with the exception of *S. goeldii* and *S. oxyrhynchus*, have notably short mouths with the posterior limit of the gape falling short of the vertical through the posterior nares (state 0; Fig. 1B). Although the mouths in *S. goeldii* and *S. oxyrhynchus* are quite short along the snout axis compared to those in most fishes including many gymnotiforms (e.g. *Magosternarchus*, Lundberg *et al.*, 1996: fig. 2) they are, nonetheless, distinctly

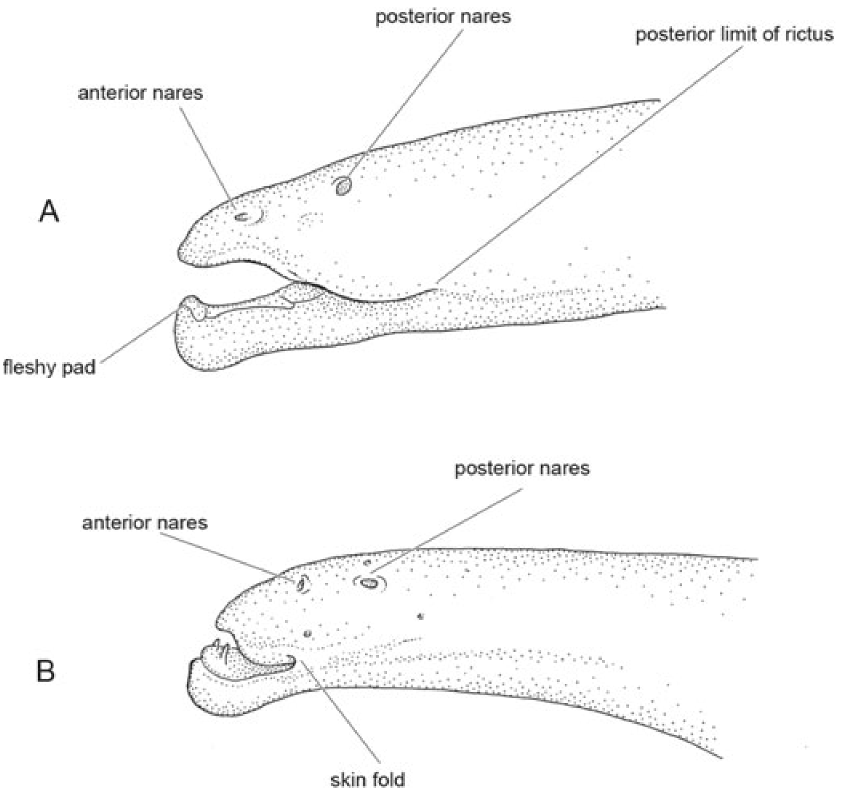

Figure 1. Lateral view of anterior portion of snout of A, *Sternarchorhynchus oxyrhynchus*, ANSP 162670; and B, *Sternarchorhynchus caboclo*, INPA 10594, showing differing degree of development of mouth and fold of skin at rear of rictus.

longer than the form of the mouth present in all remaining species of *Sternarchorhynchus*. As a consequence, the gape in *S. goeldii* and *S. oxyrhynchus* extends posteriorly distinctly beyond the vertical running through the posterior nares (state 1; Fig. 1A) rather than terminating short of that landmark. This character could not be coded for the species of *Platyurosternarchus* or the outgroups other than *Orthosternarchus*, *Sternarchorhamphus*, and *Sternarchella orthos*. In those taxa the proportionally distinctly posterior location of the nares relative to the location of the apertures in *Orthosternarchus tamandua*, *Sternarchorhamphus muelleri*, and the species of *Sternarchorhynchus* means that that those openings cannot serve as homologous landmarks, thereby rendering coding impossible.

2. *Presence or absence of small fold of skin on anterolateral surface of upper lip*: (0) skin of upper lip flat and without fold; (1) skin of upper lip with distinct fold (CI = 0.500; RI = 0.900).

Variation in the morphology of the skin overlying the anterolateral surface of the upper lip was reported by Triques (2005: 26) for apteronotids. Triques (2005) reported the fold as present in *S. oxyrhynchus*. His material originated in the Amazon basin, a region outside the known range of the species and is likely to represent another species. Our analysis found that the upper lip lacks a skin fold in the species of *Orthosternarchus*, *Platyurosternarchus*, and *Sternarchorhamphus*. Within *Sternarchorhynchus* the fold is similarly absent in *S. goeldii* and *S. oxyrhynchus* (Fig. 1A). Both of those species of *Sternarchorhynchus* also share a mouth form unique in the genus (see character 1). All other species of *Sternarchorhynchus* have a distinct fold within the skin of the upper lip (Fig. 1B) with that feature also present in *Sternarchella orthos* amongst the more distant outgroups.

UPPER JAW

3. *Form of premaxilla*: (0) somewhat to distinctly elongate from ventral view; (1) compact with longitudinal length approximately equal to transverse width (CI = 0.500; RI = 0.857).

As would be expected given the diversity of head forms across the Apteronotidae, the members of the family also demonstrate variation in the form of the premaxilla. In *Platyurosternarchus crypticus* and *Platyurosternarchus macrostoma* the premaxilla is

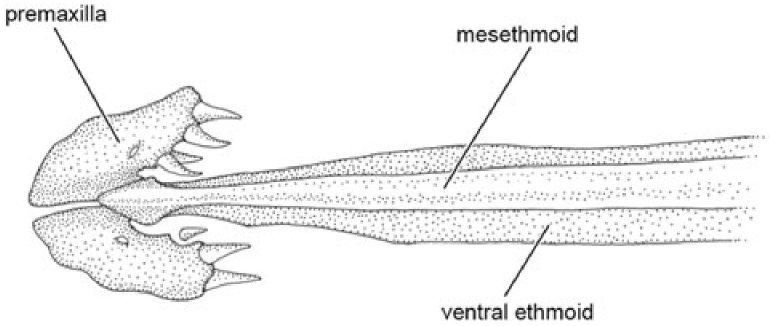

Figure 2. Premaxilla and anterior portion of neurocranium of *Sternarchorhynchus goeldii*, MCZ 46887; dorsal view, anterior to left.

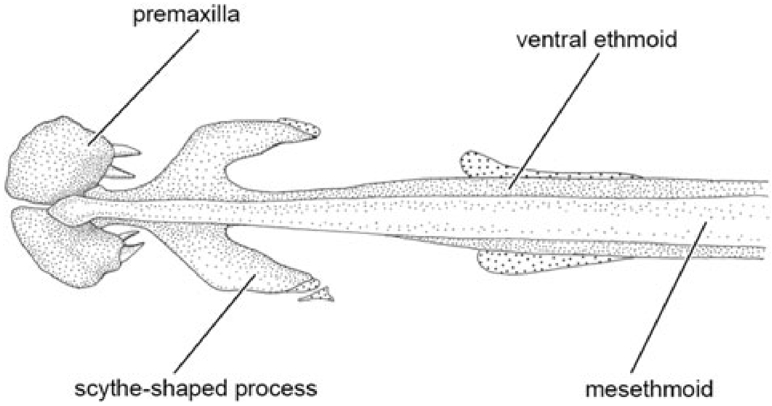

Figure 3. Premaxilla and anterior portion of neurocranium of *Sternarchorhynchus roseni*, MCNG 52591; dorsal view, anterior to left.

anteroposteriorly variably elongate, a condition found in the other proximate outgroups to *Sternarchorhynchus* (*Sternarchorhamphus muelleri*, Campos-da-Paz, 1995: fig. 4; *Orthosternarchus tamandua*, Hilton *et al.*, 2007: fig. 10) and various more distantly related gymnotiforms (Albert, 2001: fig. 6). An anteroposteriorly elongate premaxilla similarly characterizes a minority of the species of *Sternarchorhynchus* (*S. axelrodi*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus*; Fig. 2). The remaining species of *Sternarchorhynchus* have a compact form of the premaxilla in which the longitudinal length of the bone approximately equals its transverse width (Fig. 3). Looking beyond the immediate outgroups to *Sternarchorhynchus*, we find that comparable compact premaxillae are also present amongst examined apteronotids in the species of *Apteronotus* included in this study along with *Sternarchella orthos* (Lundberg *et al.*, 1996: fig. 4c) and *Sternarchogiton labiatus*.

4. *Presence or absence of teeth on premaxilla*: (0) teeth absent; (1) teeth present (CI = 0.500; RI = 0.500).

Presence of premaxillary teeth is the common condition across the Gymnotiformes. The species of *Orthosternarchus* (Hilton *et al.*, 2007: fig. 12), *Sternarchorhynchus* (Figs 2, 3), and *Sternarchorhamphus* (Campos-da-Paz, 1995: fig. 4) have premaxillary teeth present, albeit with the form of the dentition on the bone varying amongst those taxa. Premaxillary dentition is, in contrast, lacking in *P. crypticus* and *P. macrostoma*. Amongst the more distant outgroups included in the analysis, an edentulous premaxilla similarly occurs in *Sternarchogiton labiatus*. Other apteronotids not included in the outgroups that without premaxillary dentition are *Apteronotus cuchillejo* and the species of *Adontosternarchus*.

5. *Degree of development of anterior portion of maxilla*: (0) with distinct anteriorly pointed process; (1) without distinct anterior process (CI = 1.000; RI = 1.000).

Immediate outgroups to *Sternarchorhynchus* [*Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), *P. crypticus*, *P. macrostoma*, *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 4)] have a distinct, somewhat to distinctly anteriorly pointed process of the maxilla from lateral view (state 0). That condition is also present in the more distant outgroup genera *Apteronotus*, *Sternarchella*, and

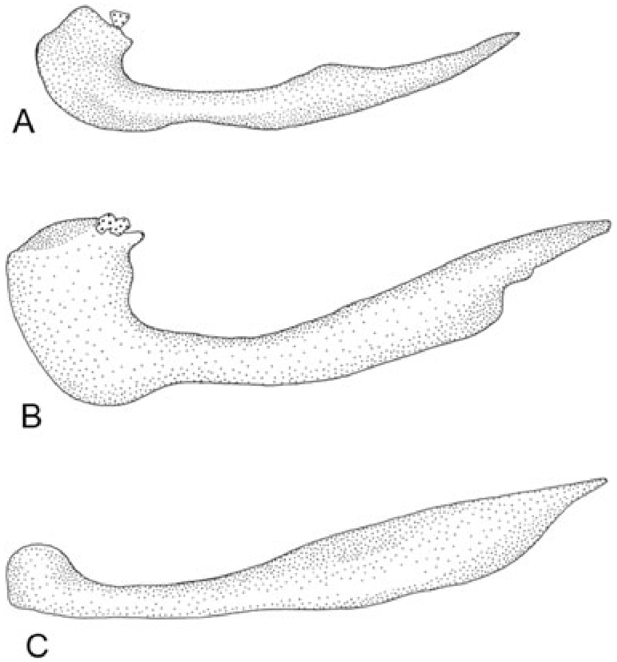

Figure 4. Maxilla of A, *Sternarchorhynchus roseni*, MCNG 52591; B, *Sternarchorhynchus mormyrus*, USNM 306843, and C, *Sternarchorhynchus goeldii*, MCZ 46887; left side, lateral view; larger stippling represents cartilage.

Sternarchogiton. All species of *Sternarchorhynchus* alternatively have an anterior portion of the maxilla that lacks an anterior extension and have instead a rounded to square margin to that portion of the bone (state 1; Fig. 4).

6. *Form of anterior portion of maxilla*: (0) moderately expanded; (1) reduced and only slightly wider than main portion of bone; (2) distinctly expanded into somewhat square plate with irregular margins (CI = 1.000; RI = 1.000).

The anterior portion of the maxilla in most species of *Sternarchorhynchus* is moderately expanded into a plate-like region (state 0; Fig. 4A) with a similar condition also present amongst the examined outgroup species in the included species of *Apteronotus*, along with *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), *Sternarchorhamphus muelleri* and *Sternarchogiton labiatus*. *Sternarchorhynchus axelrodi* and *S. mormyrus* have that portion of the maxilla proportionally further expanded into an approximately square plate with irregular margins (state 2; Fig. 4B). Two other species of *Sternarchorhynchus* (*S. goeldii*, *S. oxyrhynchus*) alternatively have the anterior portion of the maxilla reduced in size relative to the conditions present in most congeners, with that region of the bone only slightly higher vertically than are the proximate posterior portions of the maxilla (state 1; Fig. 4C).

Platyurosternarchus has a highly expanded maxilla (Mago-Leccia, 1994: fig. 23d) of a form unique within the Apteronotidae (see discussion in de Santana & Vari, 2009). This renders it impossible to code *Platyurosternarchus* for the form of the anterior portion of the maxilla. The maxilla in *Sternarchorhamphus muelleri* is anteriorly distinctly expanded (Mago-Leccia, 1994: fig. 23h; Campos-da-Paz, 1995: fig. 4), similarly rendering it impossible to code that species for this character.

7. *Form of ventral margin of maxilla*: (0) relatively smooth; (1) with distinct concavity (CI = 0.500; RI = 0.900).

Although there occurs a pronounced diversity in the overall forms of the maxilla across the Apteronotidae (Mago-Leccia, 1994: fig. 23), most species in the family (e.g. *Sternarchorhamphus muelleri*, Campos-da-Paz, 1995: fig. 4), along with *S. goeldii* and *S. oxyrhynchus*, have a smooth, variably convex ventral margin of the main body of the bone (state 0; Fig. 4C). Other examined *Sternarchorhynchus* species alternatively, have distinct concavities along the main body of the maxilla (state 1; Fig. 4A, B). Such a concavity of the maxilla is also present in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12) amongst the examined outgroups.

LOWER JAW

8. *Extent of fleshy pad at anterior of dentary*: (0) absent or only slightly developed; when present not overlapping tip of snout in closed mouth; (1) well-developed, dorsally directed, and overlapping tip of snout in closed mouth (CI = 1.000; RI = 1.000).

The anterior portion of the fleshy covering of the dentary is slightly to moderately developed in outgroups to *Sternarchorhynchus* along with most members of the genus (state 0; Fig. 1B). *Sternarchorhynchus goeldii* and *S. oxyrhynchus*, in contrast, have a very well-developed, somewhat distally pointed, fleshy pad at the anterodorsal limit of the dentary (state 1; Fig. 1A). This dorsally directed pad overlaps the anterior portion of the snout when the mouth is closed.

9. *Coronomeckelian bone*: (0) present in juveniles and adults; (1) present as small rounded ossification in smaller specimens but absent in adults (CI = 1.000; RI = 1.000).

The coronomeckelian bone is typically present in most gymnotiforms and indeed most fishes. In *P. crypticus* and *P. macrostoma* the coronomeckelian is an anteroposteriorly elongate ossification running along the dorsal margin of the anguloarticular and the posterior portion of the well-developed Meckel's cartilage (Fig. 5). Comparable overall morphologies of the bone occur in the other outgroup taxa in this

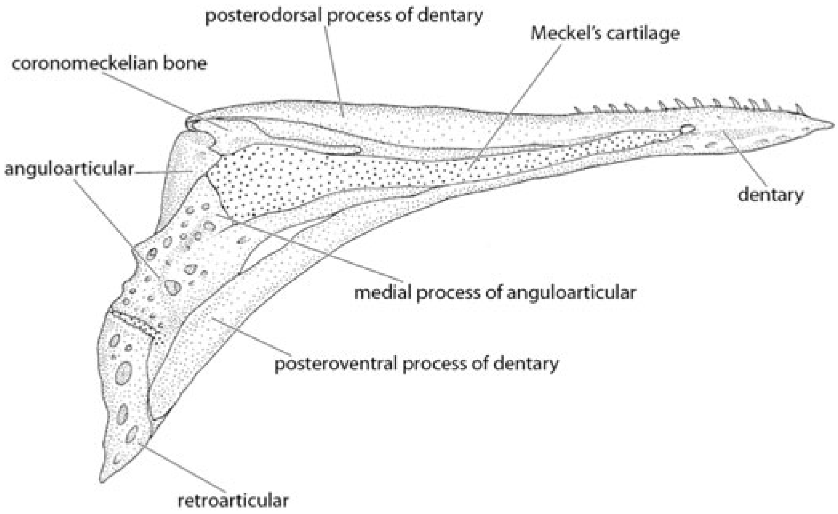

Figure 5. Lower jaw of *Platyurosternarchus macrostoma*, FMNH 100730; left side, medial view, anterior to right; larger stippling represents cartilage.

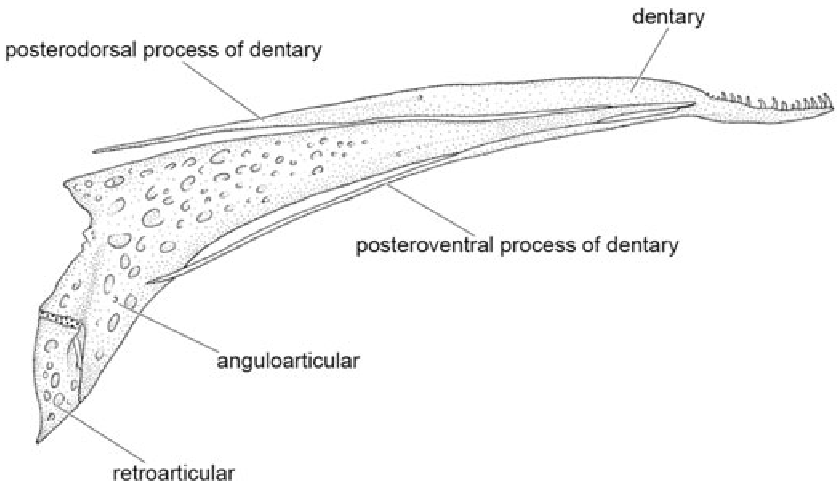

Figure 6. Lower jaw of *Sternarchorhynchus goeldii*, MCZ 46887; left side, medial view, anterior to right.

analysis [*A. albifrons*, *A. cuchillo*, *A. rostratus*, *'A.' apurensis*, *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12b), *Sternarchella orthos*, and *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5)]. A small, round ossification positionally comparable to the coronomeckelian bone of other gymnotiforms is present in an approximately 40 mm TL specimen of an unidentified species of *Sternarchorhynchus stewarti*. That element is comparable to the form of that bone in adults of some genera of the Apteronotidae (e.g. *Sternarchogiton labiatus*).

Adults of all species of *Sternarchorhynchus* examined osteologically neither have any indication of the coronomeckelian bone (state 1; Figs 6, 7), nor do they retain a residual cartilage mass in the area primitively occupied by that ossification. The space occupied in outgroups by the coronomeckelian bone and Meckel's cartilage is filled in *Sternarchorhynchus* by the dramatically anteriorly expanded anguloarticular characteristic of that genus (Figs 6, 7; see character 16).

Although the coronomeckelian bone was present in all non-*Sternarchorhynchus* gymnotiforms examined in this study, Mago-Leccia (1978: 36) reported that the element was of small size and 'not ossified in some specimens' [our translation] of *Eigenmannia virescens* of the family Sternopygidae. It is uncertain whether that statement indicates that the coronomeckelian is present as a cartilaginous precursor to the bone or that the element is completely absent in the individu-

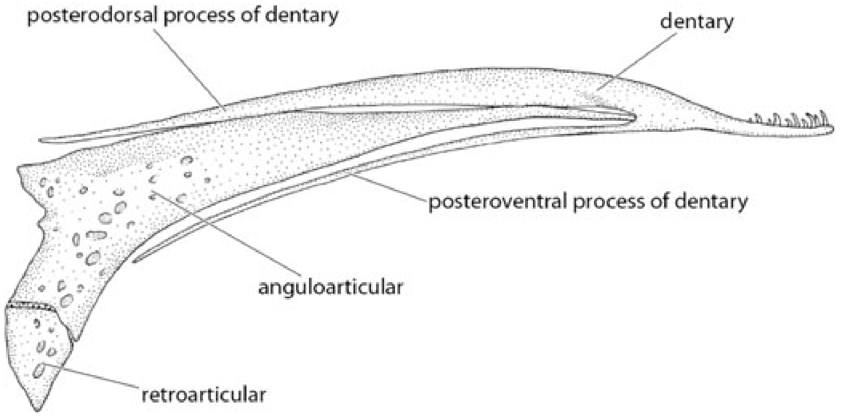

Figure 7. Lower jaw of *Sternarchorhynchus mareikeae*, INPA 22901; left side, medial view, anterior to right.

als in question. Regardless, the Sternopygidae is not phylogenetically proximate to *Sternarchorhynchus* and the absence of the ossification in a species of *Eigenmannia* is homoplastic relative to the condition in *Sternarchorhynchus*.

10. *Meckel's cartilage*: (0) present and well developed; (1) well developed in smaller individuals, but ontogenetically reduced and distinctly smaller in adults (CI = 1.000; RI = 1.000).

Meckel's cartilage is well developed across gymnotiforms and immediate outgroups to *Sternarchorhynchus* [*Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12b), *Platyurosternarchus* (Fig. 5), *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5)]; a condition comparable to that in most fishes. Within the Gymnotiformes, Meckel's cartilage most often has the form of an anteriorly attenuating body arising posteriorly from a distinct process on the medial wall of the anteromedial process of the anguloarticular and terminating anteriorly along the medial surfaces of that bone and the dentary (Fig. 5; Chardon & De La Hoz, 1974: fig. 6). Meckel's cartilage undergoes a progressive ontogenetic reduction in the species of *Sternarchorhynchus*. The cartilage is present and relatively well developed in small cleared and stained specimens of approximately 30 mm TL. At that body size, the cartilage arises from a distinct process that projects from the medial wall of the anguloarticular and then extends anteriorly to terminate a short distance posterior of the dentary symphysis. The notable difference in the form of Meckel's cartilage at that body size relative to the condition in outgroups is that in *Sternarchorhynchus* the cartilage is distinctly narrower vertically even at its highest portion proximate to its contact with the process on the medial wall of the anguloarticular. At approximately 110 mm TL, the cartilage in cleared and stained preparations of *Sternarchorhynchus* is reduced vertically to a very narrow band that arises posteriorly at the bony process of the medial wall of the anguloarticular. However, larger examined cleared and stained specimens of the genus (approximately 115 mm TL) have the cartilage reduced to a small, very narrow band limited to the anterior quarter of the anguloarticular and falling far short posteriorly of the position of the process on the medial wall of the anguloarticular in smaller specimens (state 1). Individuals of 225 mm TL show no indication of that process on the anguloarticular. This ontogenetic reduction of Meckel's cartilage in the species of *Sternarchorhynchus* parallels the pronounced anterior development of the anguloarticular in the genus, which in adults fills the space occupied by Meckel's cartilage in outgroups (Figs 6, 7).

11. *Relative lengths of posterodorsal and posteroventral processes of dentary*: (0) posterodorsal process shorter than ventrolateral process; (1) posterodorsal and posteroventral processes of approximately same length (CI = 0.500; RI = 0.875).

Proximate outgroups to *Sternarchorhynchus* [*Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), *P. crypticus*, *P. macrostoma* (Fig. 5), *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5)] along with other gymnotiforms have a posterodorsal process of the dentary extending dorsal of the anguloarticular that is, in turn, distinctly shorter than the posteroventral process of the dentary. The latter process runs ventral to the anguloarticular and sometimes along at least a portion of the ventral margin of the retroarticular (state 0; Fig. 5) (for conditions in some more distantly related gymnotiform taxa see Mago-Leccia, 1978: fig. 8; Mago-Leccia *et al.*, 1985: fig. 3; Albert, 2001: fig. 10). The species of *Sternarchorhynchus* alternatively have posterodorsal and posteroventral processes of the dentary of approximately identical lengths or in some instances with the dorsal process slightly longer (Figs 6, 7). This condition is approximated in *Sternarchella orthos* (Lundberg *et al.*, 1996: fig. 3c) amongst the outgroup taxa of this analysis. That species is, however, not closely related to *Sternarchorhynchus* (Albert, 2001) and the presence of this similar condition in these taxa is homoplastic.

12. *Form of posteroventral process of dentary*: (0) posteroventral process of dentary relatively robust and triangular overall; (1) posteroventral process of dentary very narrow and in form of elongate narrow strut of bone (CI = 1.000; RI = 1.000).

The posteroventral process of the dentary that extends ventral of the anterior portion of the anguloarticular is typically a relatively robust process in gymnotiforms including proximate outgroups such as *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), both species of *Platyurosternarchus* (Fig. 5), and *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 4). That morphology also occurs in the other outgroup apteronotids included in this study. Amongst all of those taxa, the process is either relatively broad vertically along most of its anteroposterior extent or gradually tapers to a point distally with a resultant overall triangular morphology (Mago-Leccia, 1978: fig. 8; Mago-Leccia *et al.*, 1985: fig. 3; Albert, 2001: fig. 10). The species of *Sternarchorhynchus* have the posteroventral process of the dentary dramatically restructured into a very narrow strut of bone that borders a major portion of the ventral margin of the anteroposteriorly elongate anguloarticular (Figs 6, 7).

13. *Posterior limit of posteroventral process of dentary*: (0) posteroventral process of dentary reaching margin of posteroventral process of anguloarticular; (1) posteroventral process of dentary not reaching margin of posteroventral process of anguloarticular (CI = 0.200; RI = 0.200).

As mentioned under character 12, the posteroventral portion of the dentary of *Sternarchorhynchus* is a narrow, elongate process bordering the ventral margin of the anguloarticular (Fig. 6). The posterior extent of this process of the dentary varies within *Sternarchorhynchus*, with some species having the posterior terminus of the process falling short of the point where the posteroventral process of the anguloarticular arises from the main body of that ossification (state 1; Fig. 7). All other species in *Sternarchorhynchus* (Campos-da-Paz, 2000: fig. 6, for condition in *S. mesensis*) have the posteroventral process of the dentary extending further posteriorly (state 0; Fig. 6), with resultant contact of the posteroventral process of the dentary with the posteroventral process of the anguloarticular. A comparable contact between those elements occurs in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 4), the species of *Platyurosternarchus*, and the more distant outgroups of this analysis (state 0).

14. *Position of articulation between quadrate and dorsal surface of lower jaw*: (0) located in region of articulation of anguloarticular and retroarticular, with anterodorsal portion of retroarticular contributing to joint of lower law with quadrate; (1) located distinctly anterior to region of articulation of anguloarticular and retroarticular, with anterodorsal portion of retroarticular well separated from joint of lower law with quadrate (CI = 1.000; RI = 1.000).

In *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12) and *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: figs 4, 5) the articulation of the articular condyle of the quadrate with the lower jaw is via an articular socket positioned along the posterodorsal margin of the jaw. In these species, the socket is situated along the dorsal portion of the joint between the anguloarticular and the retroarticular. Such a form of the articular socket occurs in other gymnotiforms (e.g. *Rhabdolichops*, Mago-Leccia, 1978: fig. 8) and is apparently the primitive condition for the Apteronotidae. In both *Sternarchorhynchus* and *Platyurosternarchus*, the area of quadrate–lower jaw articulation is shifted anteriorly relative to the joint between the anguloarticular and retroarticular. As a result, the articular socket on the lower jaw is formed solely by a portion of the posterodorsal region of the anguloarticular (Figs 5–7) with a distinct separation of the anterodorsal corner of the retroarticular and the quadrate–lower jaw articulation.

The degree of separation of the retroarticular from the joint between the lower jaw and quadrate increases ontogenetically in both *Platyurosternarchus* and *Sternarchorhynchus*. Smaller specimens of both *Platyurosternarchus* (*P. crypticus*, approximately 90 mm TL) and *Sternarchorhynchus* (*Sternarchorhynchus* cf. *stewarti*, approximately 40 mm TL) have the quadrate–lower jaw articulation proportionally closer to the anguloarticular–quadrate joint than in larger individuals of each species or adults of congeners.

An articulation of the quadrate solely with the anguloarticular resolves as a synapomorphy for *Platyurosternarchus* and *Sternarchorhynchus* under the results of this study (see also character 15). This condition is also present in *A. albifrons*, *A. cuchillo*, *A. rostratus*, *'A.' apurensis*, *Sternarchella orthos*, and *Sternarchogiton labiatus* amongst the outgroups included in this analysis. The presence of this feature in these outgroup taxa is homoplastic to the condition in *Platyurosternarchus* and *Sternarchorhynchus* under present hypotheses of relationships within the Gymnotiformes (Albert, 2001).

15. *Degree of separation along dorsal margin of anguloarticular between joint for articulation with quadrate and anguloarticular-retroarticular joint:* (0)

distance approximately equal to width of articular facet on anguloarticular that contacts quadrate; (1) distance approximately about 4–4.5 times width of articular facet on anguloarticular that contacts quadrate (CI = 1.000; RI = 1.000).

The site of articulation of the lower jaw with the quadrate is restricted to the anguloarticular in both *Platyurosternarchus* and *Sternarchorhynchus* (character 14), albeit differing in relative positions in the genera. *Platyurosternarchus crypticus* and *P. macrostoma* have a shorter, albeit, distinct separation of the condyle from the joint between the anguloarticular and retroarticular (state 0; Fig. 5). In contrast, the species of *Sternarchorhynchus* along with the outgroups *A. albifrons*, *A. cuchillo*, *A. rostratus*, *'A.' apurensis*, *Sternarchella orthos*, and *Sternarchogiton labiatus* have a pronounced separation between these two landmarks (state 1; Figs 6, 7). This character could not be coded for *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri*, in which the articular condyle on the lower jaw is formed jointly by the anguloarticular and retroarticular rather than being restricted to the dorsal margin of the anguloarticular.

16. *Form of anterior portion and medial surface of anguloarticular*: (0) anterior portion of anguloarticular broad with medial surface of bone having distinct process at posterior terminus of Meckel's cartilage; (1) anterior portion of anguloarticular distinctly pointed with medial surface of bone unelaborated (CI = 1.000; RI = 1.000).

The anterior portion of the anguloarticular that articulates with the posterior region of the dentary is relatively broad in most gymnotiforms (e.g. Albert, 2001: fig. 10) including the proximate outgroups to *Sternarchorhynchus* in this study [*Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 13), the species of *Platyurosternarchus*, and *Sternarchorhamphus muelleri*]. All of the outgroups also have a distinct process that arises from the medial surface of the anguloarticular and serves as the posterior limit of Meckel's cartilage (Fig. 5). Amongst the species of *Sternarchorhynchus*, the anterior portion of the anguloarticular has instead a distinctly anteriorly tapering overall triangular form (Figs 6, 7). Although a triangular anterior portion of the anguloarticular also occurs in some members of the Sternopygidae (e.g. *Rhabdolichops*; Mago-Leccia, 1978: fig. 8), the form of region is not distinctly anteriorly attenuate in those species. Those members of the Sternopygidae are, furthermore, distantly related to *Sternarchorhynchus* (Albert, 2001) and the similarities between these taxa and *Sternarchorhynchus* in this character are clearly homoplastic. As discussed under character 16, larger individuals of the species of *Sternarchorhynchus* have an unelaborated medial surface of the anguloarticular. The ontogenetic loss in *Sternarchorhynchus* of the process present in that region of the anguloarticular in other gymnotiforms correlates with the pronounced reduction of Meckel's cartilage in adults of all species of the genus (character 10).

17. *Location of posterior terminus and form of posteroventral portion of the anguloarticular*: (0) anguloarticular terminating posteriorly approximately at vertical through dorsal portion of joint between anguloarticular and retroarticular and without distinct posteriorly attenuating process extending under retroarticular; (1) anguloarticular terminating posteriorly at, to distinctly posterior of, vertical through dorsal portion of joint between anguloarticular and retroarticular and with distinct, posteriorly attenuating process extending along anterior margin of retroarticular (CI = 1.000; RI = 1.000).

Two highly divergent forms of the posteroventral portion of the anguloarticular are found in *Sternarchorhynchus* and the other gymnotiforms incorporated into this study. In *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5) and *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12b) the posteriormost portion of the anguloarticular is situated within the dorsal portion of the joint between the anguloarticular and retroarticular. This portion of the anguloarticular is incorporated into the socket receiving the articular condyle of the quadrate. The retroarticular in these two species has an anteriorly directed process extending under the posterior portion of the anguloarticular (state 0) with this condition also present in the other outgroups. The process is moderately developed in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12) and extends further anteriorly in *Sternarchorhamphus muelleri.* The species of *Platyurosternarchus* and *Sternarchorhynchus* have the posteroventral portion of the anguloarticular extending further posteriorly, forming a distinct posteriorly attenuating process that extends under the anterior portion of the retroarticular (state 1; Figs 5–7). As such, the posterior terminus of the posteroventral portion of the anguloarticular in those genera is situated posterior of the vertical through the dorsal portion of the joint between the anguloarticular and the retroarticular.

18. *Position of posterior limit of dentary*: (0) posterior limit of dentary located distinctly anterior of vertical through vertical component of orbitosphenoid; (1) posterior limit of dentary located along vertical through vertical component of orbitosphenoid (CI = 0.500; RI = 0.800).

As discussed under characters 14 and 15, considerable variation occurs amongst the genera of interest in diverse aspects of the articulation of the lower jaw with the suspensorium. An additional difference reflective of the broader details of the arrangement of the bones of the head in these taxa involves the location of the position of the posteriormost point on the dentary with respect to the neurocranium. In *S. goeldii* and *S. oxyrhynchus*, along with the outgroups *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, and *Sternarchorhamphus muelleri*, the posterior limit of the dentary lies considerably anterior of the vertical running through the vertically aligned section of the orbitosphenoid (state 0). In the remaining species of *Sternarchorhynchus* the posterior termination of the dentary is more posteriorly positioned relative to the orbitosphenoid, being situated along, or posterior of, the vertical through the vertically orientated anterior portion of the orbitosphenoid (state 1). State 1 is also present amongst the outgroups in *Sternarchella orthos* and *Sternarchogiton labiatus*.

DENTITION

19. *Form of teeth in upper and lower jaws*: (0) teeth proportionally elongate with relatively little change in width other than distally and with slight posterior curvature distally; (1) teeth distinctly wider basally and tapering progressively to distinctly posteriorly recurved distal portion (CI = 1.000; RI = 1.000).

Species of *Sternarchorhynchus* and its immediate outgroup species, *P. crypticus* and *P. macrostoma*, along with the basal apteronotids *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12) and *Sternarchorhamphus muelleri* have teeth arranged in one or more rows along the dorsal portion of the dentary. These taxa also bear a patch of comparable dentition on the ventral surface of the premaxilla other than for the species of *Platyurosternarchus*, which lack upper jaw dentition. The tooth form differs amongst these taxa, with *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri* having relatively elongate teeth on each jaw (state 0). The teeth in these genera become only slightly narrower along most of their length and terminate in a slightly posteriorly recurved point [tooth form termed villiform by Albert (2001: 16) and some other authors). *Sternarchorhynchus* alternatively has the teeth in both jaws tapering to a pronounced degree from proportionally wider bases with the distal curvature more developed (state 1). A similar form of distally tapering dentition occurs in the lower jaw of the species of *Platyurosternarchus*. However, this genus has an edentulous premaxilla. Such a form of dentition is also present in both jaws of the other outgroups included in the analysis except *Orthosternarchus* and *Sternarchorhamphus*.

20. *Location of area of attachment of teeth on dentary*: (0) teeth attaching to exterior surface of dentary; (1) teeth attaching to interior surface of dentary (CI = 1.000; RI = 1.000).

Attachment of the teeth on the dentary is consistently on the inner surface of the dentary in the species of *Sternarchorhynchus*, *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5), *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12), and the other apteronotid outgroups in this study other than *P. crypticus* and *P. macrostoma.* The dentition in *Platyurosternarchus* instead attaches to the outer surface of the dentary. *Megadontognathus*, an apteronotid genus not amongst the outgroup taxa of this study, has teeth arising from the outer surface of the dentary. Dentary dentition in this genus is limited to the posterior portion of the dorsal margin of the dentary (Mago-Leccia, 1994: fig. 58), whereas *Platyurosternarchus* has the dentition restricted to the anterior one-third of the dorsal margin of the bone. These positional differences indicate nonhomology of the dentition on the outer margin of the dentary in the two genera; a hypothesis supported by the pronounced phylogenetic separation of *Megadontognathus* and *Platyurosternarchus* (Albert, 2001).

PALATINE ARCH

21. *Degree of development of anterior portion of palatoquadrate cartilage*: (0) moderately to well developed; (1) poorly developed and reduced to narrow, somewhat thread-like process (CI = 1.000; RI = 1.000).

The anterior portion of the palatoquadrate cartilage (the pars autopalatine of Hilton *et al.*, 2007: fig. 11) ranges from moderately to well developed in most of the apteronotids incorporated into this study. Although the palatoquadrate cartilage is somewhat reduced in *Platyurosternarchus* relative to the condition in some other apteronotids, the cartilage remains an overall moderately well-developed, triangular structure (Fig. 8). *Sternarchorhynchus* species have the palatoquadrate cartilage much further reduced, resulting in a small structure (Figs 9, 10) sometimes having an almost thread-like form. Such a reduction is unique to *Sternarchorhynchus* amongst the taxa in this analysis.

22. *Position of endopterygoid*: (0) endopterygoid positioned along dorsomedial margin of lower jaw with no, or limited, overlap by ventral portion of endopterygoid of posterodorsal process of dentary and posterodorsal region of anguloarticular; endopterygoid largely positioned above dorsal margins of dentary and anguloarticular; (1) endopterygoid positioned along medial surface of dentary and anguloarticular with dorsal margin of endopterygoid located distinctly ventral of dorsal margins of dentary and anguloarticular (CI = 1.000; RI = 1.000).

Most members of the Gymnotiformes have the endopterygoid (the mesopterygoid or entopterygoid of some previous authors) positioned distinctly dorsal of the dorsal margin of the bones of the lower jaw (e.g. *A. albifrons*, Chardon & De La Hoz, 1974: fig. 20;

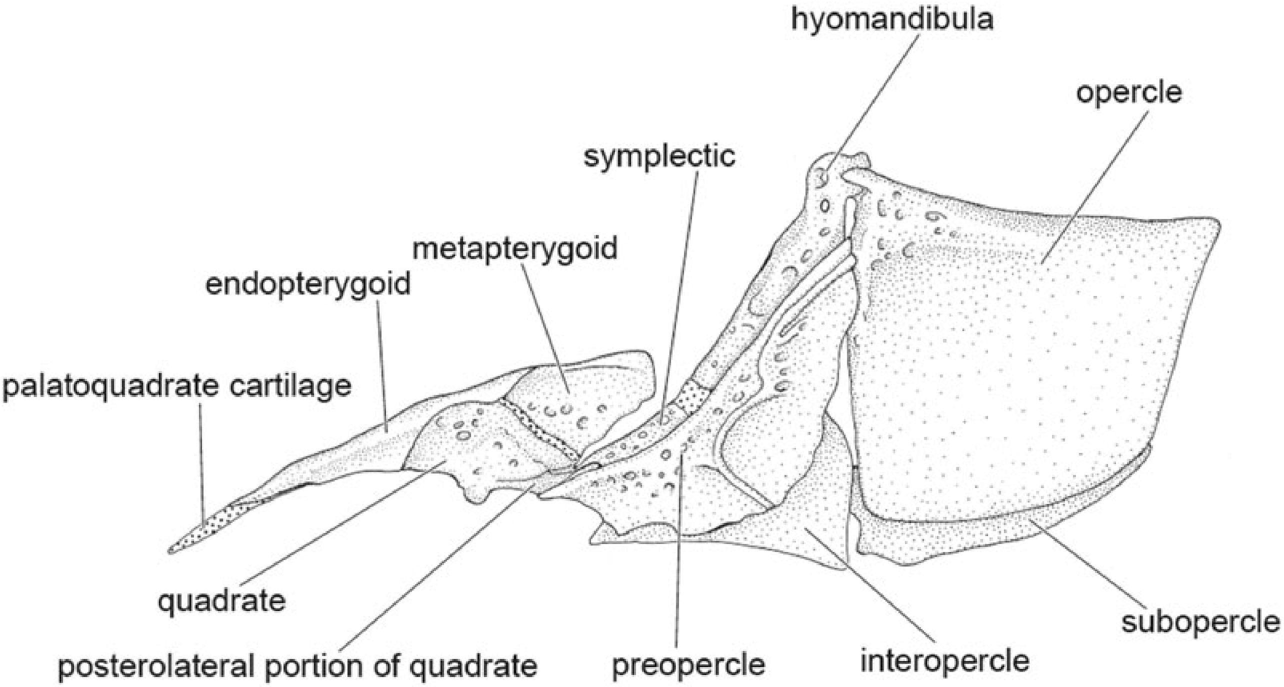

Figure 8. Suspensorium and opercular series of *Platyurosternarchus macrostoma*, FMNH 100730; left side, lateral view, anterior to left; larger stippling represents cartilage.

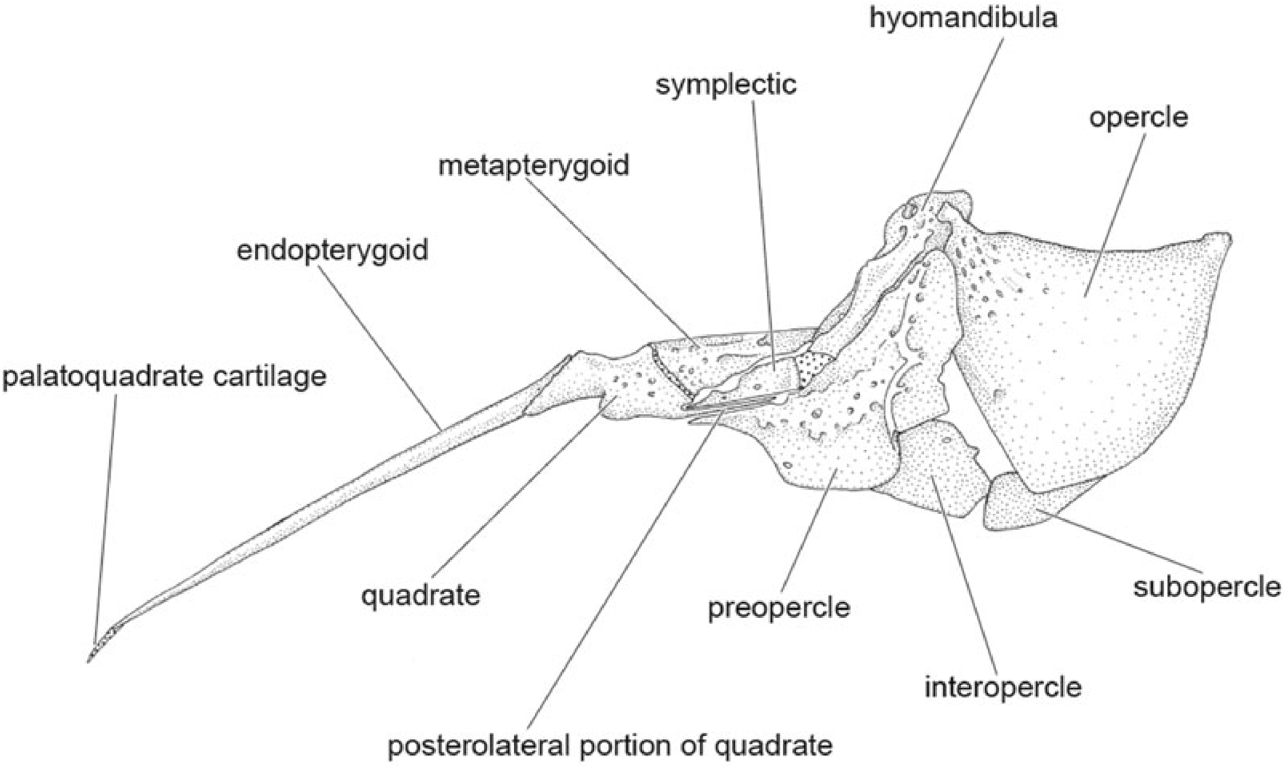

Figure 9. Suspensorium and opercular series of *Sternarchorhynchus chaoi*, INPA 20851; left side, lateral view, anterior to left; larger stippling represents cartilage.

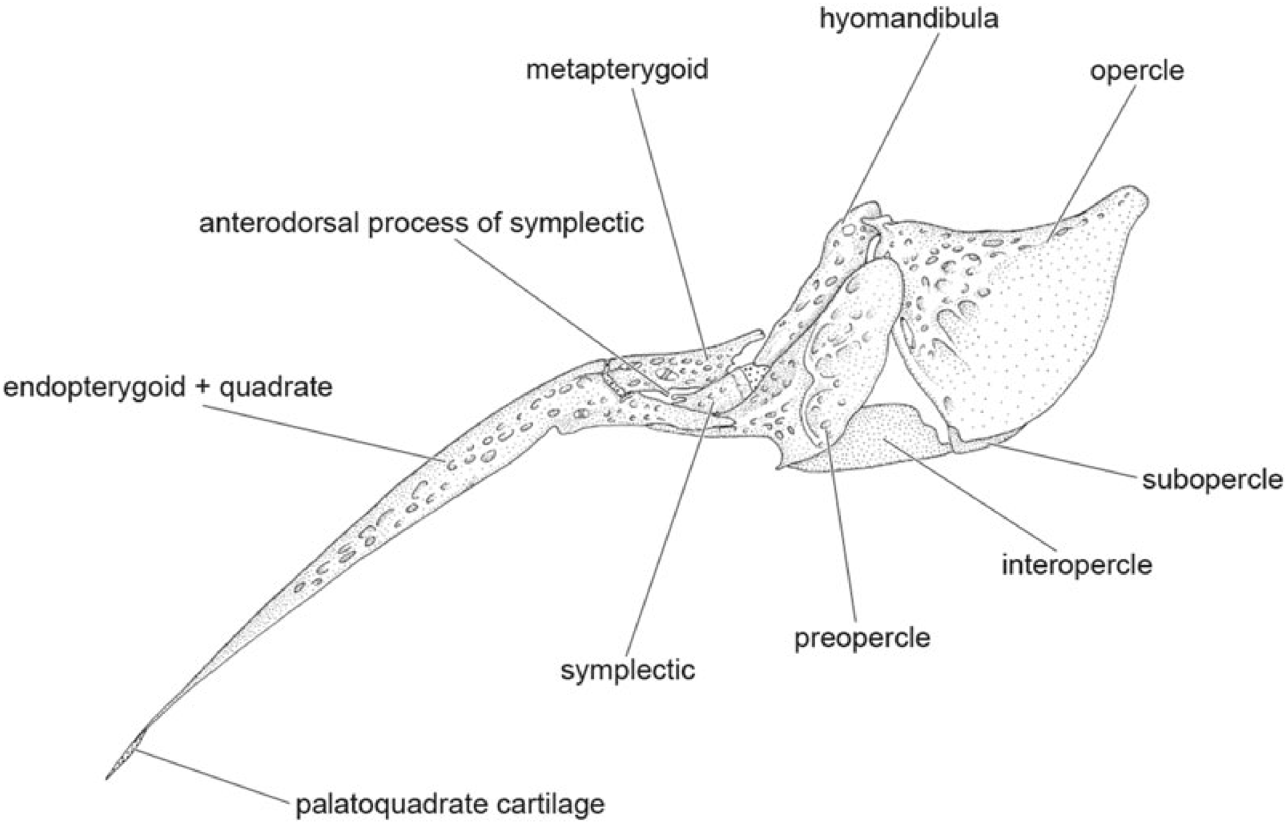

Figure 10. Suspensorium and opercular series of *Sternarchorhynchus goeldii*, MCZ 46887; right side, lateral view, anterior to left; larger stippling represents cartilage.

state 0) or demonstrate limited overlap of the endopterygoid and the dorsal portions of the dentary and anguloarticular (e.g. species of *Platyurosternarchus*, *Sternarchorhamphus muelleri*, and more distant outgroups in the analysis; also state 0). The palatine arch is shifted ventrally relative to the lower jaw in the species of *Sternarchorhynchus* as part of the revamping necessitated by space restrictions along the vertical axis in the elongate tubular snout characteristic of the genus. One of the changes required to accommodate a dorsoventrally narrow snout is the shift dorsally of the lower jaw relative to the endopterygoid. This repositioning results in the endopterygoid being situated medial to the dentary and anguloarticular in *Sternarchorhynchus* (state 1). The dorsal margin of the endopterygoid is consequently positioned ventral of the dorsal border of the dorsal portions of the dentary and anguloarticular; a unique arrangement of these elements amongst examined gymnotiforms.

23. *Form of anterior portion of endopterygoid*: (0) anterior portion of bone attenuating, but with anterior region approximately as wide transversely as high; (1) anterior portion of bone very narrow and compressed transversely and distinctly higher than wide (CI = 1.000; RI = 1.000).

All examined outgroup gymnotiforms have a dorsoventrally higher anterior portion of the endopterygoid, which, nonetheless, extends medially to an extent such that it is approximately as wide transversely as it is high (state 0; Fig. 8). *Sternarchorhynchus* species have an unusual endopterygoid that is very narrow along the anteroposterior axis and reduced along the transverse plane. As a consequence, the endopterygoid is proportionally higher vertically than wide transversely state 1; (Figs 9, 10).

An endopterygoid with the anterior portion larger than the posterior section of the bone was proposed as a synapomorphy for *Platyurosternarchus*, *Sternarchorhynchus*, and *Ubidia* by Triques (2005; ossification termed the mesopterygoid therein). The landmark delimiting those portions of the bone was not identified. That issue aside, although the endopterygoid is distinctly elongate in *Sternarchorhynchus* (Fig. 9), the proportional length of the bone in *Platyurosternarchus* (Fig. 8; Albert, 2001: fig. 31a) is comparable to that not only in *Ubidia* (Miles, 1945: fig. 11) but also species of *Apteronotus* (e.g. *A. albifrons*, Chardon & De La Hoz, 1974: fig. 6; *Apteronotus bonapartii*, Hilton & Cox-Fernandes, 2006: fig. 5). Elongation of the element is thus of broader occurrence and a more encompassing analysis is necessary to determine the phylogenetic level at which it is applicable.

24. *Form of posterior portion of endopterygoid*: (0) relatively high vertically and broadly overlapping dorsal portion of quadrate and anterodorsal region of metapterygoid; not fused to quadrate or metapterygoid; (1) vertically reduced to very elongate, somewhat horizontally aligned process extending along and either tightly attached to lateral surface of quadrate and metapterygoid or fused to quadrate (CI = 1.000; RI = 1.000).

The typical form of the posterior portion of the endopterygoid in gymnotiforms including *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11), the species of *Platyurosternarchus* (Albert, 2001: fig. 31a), *Sternarchorhamphus muelleri* (Albert, 2001: fig. 31b), and examined outgroups is a vertically relatively expansive ossification closely applied and tightly attached to the lateral surface of portions of the quadrate and metapterygoid (state 0; Fig. 8). *Sternarchorhynchus* has the vertical extent of the posterior region of the endopterygoid dramatically reduced to an elongate process extending along the middle of the lateral portions of the quadrate and metapterygoid (state 1; Figs 9, 10). The reduction of the primitively broad contact between the overlapping endopterygoid, quadrate, and metapterygoid and the consequent decrease in the area of contact of the entopterygoid with the posterior elements of the palatine arch is offset by the very tight association of the reduced posterior portion of the endopterygoid with the lateral surface of the quadrate in the species of *Sternarchorhynchus*. Maximal connectivity of the endopterygoid and quadrate is achieved in *S. goeldii* and *S. oxyrhynchus* where these bones are fused into a single ossification without trace in adults of the original line of contact (Fig. 10; see character 25).

25. *Association of quadrate and endopterygoid*: (0) bones closely applied but separate; (1) bones fused (CI = 1.000; RI = 1.000).

The quadrate and endopterygoid are closely applied to each other but separate in examined outgroup gymnotiforms and in all species of *Sternarchorhynchus* other than *S. goeldii* and *S. oxyrhynchus* (state 0; Fig. 9). These two species have the quadrate and endopterygoid fused into a single anteroposteriorly elongate ossification without any indication of the original joint between those elements (state 1; Fig. 10).

26. *Ascending process of endopterygoid*: (0) absent; (1) present (CI = 0.250; RI = 0.500).

Diverse gymnotiforms have a variably elongate, dorsally directed ascending process of the endopterygoid arising from the dorsal surface of that bone (e.g. *Sternarchella sima*, Albert, 2001: fig. 31c). Such a process is present in *S. mormyrus* but absent across all of the other members of the genus examined osteologically (state 1). The feature was, nonetheless, included in the analysis because it may serve to define a small assemblage of species once the remaining recognized members of the genus are examined osteologically or further species of *Sternarchorhynchus* are described and evaluated as to their phylogenetic relationships. Within proximate outgroups such an endopterygoid process is encountered in *P. crypticus* but is absent in *P. macrostoma*. A comparable process is also present in smaller individuals of *Sternarchorhamphus muelleri* but is lost ontogenetically. We were unable to code *S. axelrodi* for this feature.

Possession of the process optimized as a synapomorphy for the clade consisting of *Platyurosternarchus*, *Sternarchorhynchus*, and *Ubidia* in the analysis by Triques (2005) that included a limited number of *Sternarchorhynchus* species. The process is only present in one species in the genus and one of the two species of *Platyurosternarchus* and as such does not serve to unit those three genera.

27. *Attachment area of pterygocranial ligament*: (0) limited to dorsal surface of endopterygoid; (1) involving both endopterygoid and quadrate (CI = 0.250; RI = 0.727).

The pterygocranial ligament extends posterodorsally from the suspensorium to an attachment on the orbitosphenoid. In examined outgroups along with *S. caboclo*, *Sternarchorhynchus chaoi*, *S. curvirostris*, *S. curumim*, *S. goeldii*, *Sternarchorhynchus higuchii*, *Sternarchorhynchus mendesi*, *S. mesensis*, *S. mormyrus*, *S. oxyrhynchus*, and *S. roseni*, the ligament attaches onto the suspensorium solely via a small dorsal process extending from the endopterygoid (state 0; Fig. 11A) that is best viewed from an oblique dorsoventral angle. *Sternarchorhynchus britskii*, *Sternarchorhynchus cramptoni*, *S. gnomus*, *Sternarchorhynchus hagedornae*, *Sternarchorhynchus inpai*, *Sternarchorhynchus jaimei*, *Sternarchorhynchus mareikeae*, *Sternarchorhynchus montanus*, *Sternarchorhynchus retzeri*, *Sternarchorhynchus starksi*, *S. stewarti*, and *S. severii* instead have the quadrate also contributing the attachment of the pterygocranial ligament on the suspensorium. This attachment site most often has the form of a dorsal process extending along the surface of the dorsal process of the entopterygoid and often completely overlapping the corresponding portion of the entopterygoid from medial view (state 1; Fig. 11B). We were unable to code *S. axelrodi* for this feature from radiographs of the type series.

28. *Overall form of dorsal portion of quadrate*: (0) with relatively broad, anterodorsal plate-like process; (1) without broad, anterodorsal plate-like process (CI = 1.000; RI = 1.000).

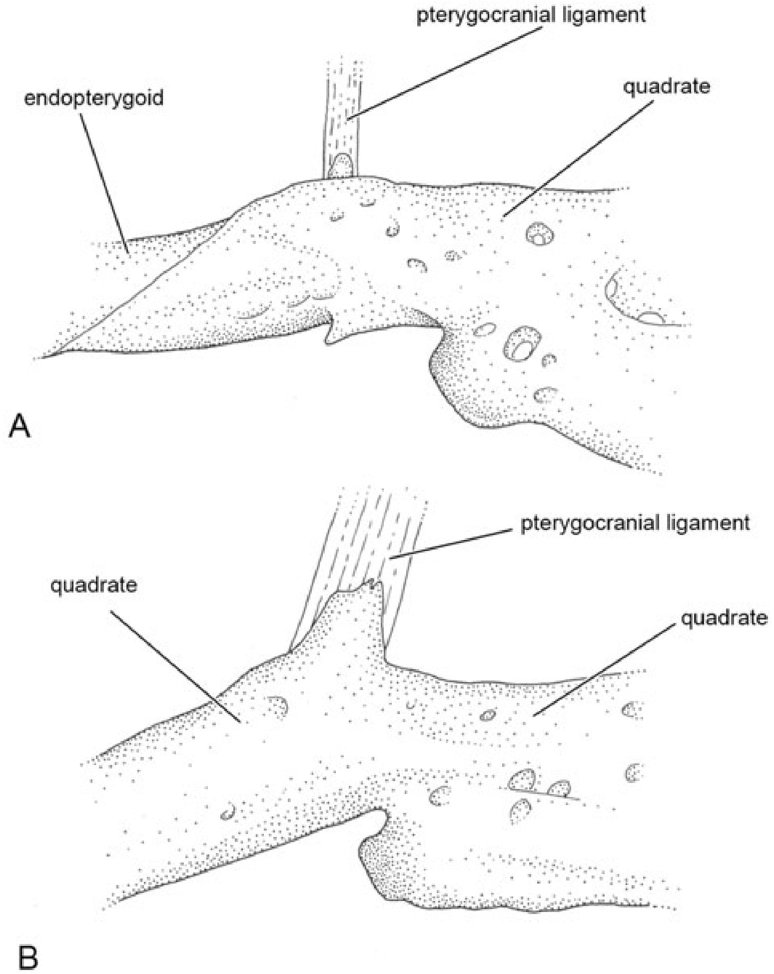

Figure 11. Anterior portion of quadrate and associated structures of A, *Sternarchorhynchus mormyrus*, USNM 306843 (note: small bony process at base of pterygocranial ligament is part of endopterygoid), and B, *Sternarchorhynchus retzeri*, FMNH 11515; showing differing contributions of bones to attachment areas for pterygocranial ligament; process of endopterygoid shown in (A) is hidden by process of quadrate in (B); right side, medial view, anterior to left.

Outgroup gymnotiforms in this study including the immediate outgroups in this analysis (e.g. *P. macrostoma*, *Sternarchorhamphus muelleri*; Albert, 2001: fig. 31a, b) have a variably well-developed plate-like process of the quadrate that extends dorsal of the articular condyle that contacts the lower jaw (state 0; Fig. 8). In the species of *Sternarchorhynchus*, the quadrate is dorsoventrally shallower and lacks this dorsal process on the bone (state 1; Figs 9, 10).

29. *Form of dorsal margin of quadrate*: (0) straight to slightly convex; (1) concave (CI = 1.000; RI = 1.000).

A straight or convex dorsal margin along the plate-like dorsal process of the quadrate typifies most gymnotiforms including all proximate outgroups for *Sternarchorhynchus* in this analysis [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11); *Sternarchorhamphus muelleri* (Albert, 2001: fig. 31a, b)]. As described under character 28, *Sternarchorhynchus* species have the quadrate reduced vertically. *Sternarchorhynchus axelrodi*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus*, nonetheless, retain a straight to slightly convex dorsal margin of the reduced quadrate comparable to the form of that portion of the ossification in outgroups (state 0; Fig. 10). All other members of *Sternarchorhynchus* have a distinctly concave dorsal margin to the quadrate (state 1; Fig. 9).

30. *Form of posterolateral portion of quadrate*: (0) without lateral expansion; (1) with lateral expansion into rounded ridge terminating posteriorly in articular facet (CI = 1.000; RI = 1.000).

Outgroups have the lateral surface of the quadrate unelaborated (state 0), with the posterolateral region of this bone overlapped laterally by the endopterygoid [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11)]. The posterolateral portion of the quadrate is

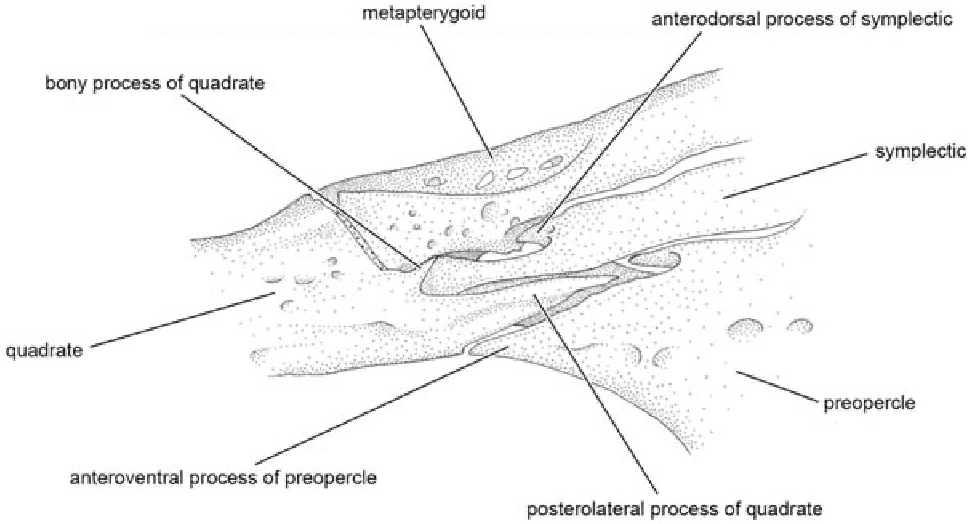

Figure 12. Posterior portion of quadrate, anterior portion of metapterygoid and symplectic, and adjoining bones in *Sternarchorhynchus curvirostris*, USNM 163887; left side, lateral view, anterior to left; larger stippling represents cartilage.

exposed laterally but unelaborated in all *Sternarchorhynchus* species other than *S. goeldii* and *S. oxyrhynchus* and is consequently coded as state 0 for these taxa (Fig. 9). *Sternarchorhynchus goeldii* and *S. oxyrhynchus* bear a lateral expansion of the lateral surface of the posterodorsal portion of the quadrate, with the expanded region having the form of a raised, laterally rounded, longitudinally aligned ridge terminating in a distinct posterior facet (state 1; Fig. 10) that articulates with a corresponding facet on the anterior surface of the metapterygoid (see character 39).

31. *Form of posteroventral margin of main body of quadrate that receives anterior tip of symplectic*: (0) with distinct notch; notch open laterally and most often also medially; (1) notch very small or absent and when present enclosed laterally and medially by vertical sheet of bone (CI = 0.333; RI = 0.500).

The narrow anterior portion of the symplectic fits into a distinct concavity in the posteroventral margin of the main body of the quadrate in proximate outgroups to *Sternarchorhynchus* together with all examined members of the genus other than *S. mormyrus* and perhaps *S. axelrodi* (state 0). In *S. mormyrus* the anteriormost portion of the symplectic fits into a dorsally open pocket bordered medially and laterally by vertical bony processes arising from the quadrate (state 1). Such a modification of the quadrate also appears to be present in *S. axelrodi* based on radiographs of several specimens of this species. Looking to more distant outgroups, we find that state 1 is present in *A. albifrons*, *'A.' apurensis*, and *Sternarchogiton labiatus*. The character was included in the analysis as a potential synapomorphy for *S. axelrodi* and *S. mormyrus* that are herein proposed as sister taxa and perhaps for other species not examined osteologically in this study.

32. *Position of area of articulation of symplectic with quadrate*: (0) anterior portion of symplectic fitting into notch or bony pocket along posteroventral margin of quadrate located anterior of ventral limit of joint between quadrate and metapterygoid; (1) anterior portion of symplectic fitting into notch or pocket along posteroventral margin of quadrate located distinctly posterior of ventral limit of joint between quadrate and metapterygoid (CI = 0.500; RI = 0.500).

The notch or pocket in the posteroventral portion of the quadrate that accommodates the anterior tip of the symplectic is located anterior to, distinctly anterior of, the ventral terminus of the quadrate–metapterygoid joint in examined outgroups to *Sternarchorhynchus* and in all species in the genus other than *S. curvirostris*, *S. goeldii*, and *S. oxyrhynchus* (state 0; Fig. 9). These three species have the articulation of these ossifications shifted distinctly posteriorly relative to that landmark and situated ventral of the metapterygoid (state 1; Fig. 12).

33. Lateral closure of notch along posteroventral margin of quadrate that receives symplectic: (0) present; (1) absent (CI = 0.250; RI = 0.500).

Outgroup taxa in the analysis along with *S. axelrodi*, *S. britskii*, *S. curvirostris*, *S. curumim*, *S. gnomus*, *S. goeldii*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. mareikeae*, *S. mendesi*, *S. montanus*, *S. mormyrus*, *S. oxyrhynchus*, *S. severii*, *S. starksi*, and *S. stewarti* have the lateral portion of the notch in the quadrate that receives the anterior tip of the symplectic covered, or largely covered, by a thin sheet of bone arising from the main body of the quadrate (state 0; Figs 10, 12). This thin bony sheet is absent in *S. caboclo*, *S. chaoi*, *S. cramptoni*, *S. jaimei*, *S. mesensis*, *S. retzeri*, and *S. roseni* (state 1; Fig. 9). A comparable bony sheet appears to be present in *S. axelrodi* based on radiographs.

34. Overlap laterally of anteroventral corner of metapterygoid by bony process of quadrate: (0) absent; (1) present (CI = 0.333; RI = 0.600).

The anteroventral corner of the metapterygoid proximate to the joint between this ossification and the quadrate is laterally exposed in most gymnotiforms including all examined outgroups to *Sternarchorhynchus* (state 0). *Sternarchorhynchus curvirostris*, *S. gnomus*, *S. hagedornae*, *S. higuchii*, *S. mareikeae*, and *S. starksi* have a further development dorsally of the bony sheet such that it overlaps the lateral surface of the notch in the posteroventral portion of the quadrate. This expansion results in the lateral overlap of the anteroventral corner of the metapterygoid by the dorsal process of the quadrate in these species (state 1; Fig. 12).

35. *Location of posterior limit of posteroventral process of quadrate*: (0) when present, process terminates approximately at, or slightly posterior of, vertical through ventral portion of joint between quadrate and metapterygoid; (1) process terminates approximately at vertical through two-thirds of length of metapterygoid or posterior of that point (CI = 1.000; RI = 1.000).

Most gymnotiforms either lack a posteroventral process of the quadrate that extends ventral of the symplectic and over the anteroventral process of the preopercle (e.g. *Gymnotus carapo*, Chardon & De La Hoz, 1974: fig. 4) or have a relatively short process that terminates approximately at, or slightly posterior of, the vertical through the ventral portion of the area of contact of the metapterygoid and quadrate (state 0). The latter condition is present in all examined outgroups to *Sternarchorhynchus* [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11); *Platyurosternarchus* (Albert, 2001: fig. 31a); *Sternarchorhamphus muelleri* (Albert, 2001: fig. 31b)]. *Sternarchorhynchus* species have a much more elongate posteroventral process of the quadrate. This process extends from the body of the ossification as a narrow flange of bone running ventral of the symplectic to a point at least as far posterior as the vertical located two-thirds of the distance along the length of the metapterygoid (state 1; Figs 9, 10, 12).

36. *Overall form of symplectic*: (0) symplectic relatively slender, with height of posteriormost portion of bone approximately one-fifth length of bone; (1) symplectic proportionally vertically higher, with height of posteriormost portion of bone approximately one-third length of bone (CI = 0.250; RI = 0.625).

Species of *Sternarchorhynchus* other than *S. axelrodi*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus* have a relatively slender symplectic that from a lateral view gradually increases posteriorly in its vertical extent. As a consequence, the height of the posteriormost portion of the symplectic is approximately one-fifth of its length (state 0). This symplectic form also occurs in *A. cuchillo*, *A. rostratus*, *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11), *P. crypticus*, and *Sternarchorhamphus muelleri* in the outgroups (state 0). *Sternarchorhynchus axelrodi*, *S. chaoi*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus* have instead a distinctly more posterodorsally angled dorsal margin of the symplectic with a resultant greater disparity in the height of the anterior versus posterior portions of the bone (state 1). State 1 is present amongst the examined outgroups in *A. albifrons*, *'A.' apurensis*, *P. macrostoma*, *Sternarchella orthos*, and *Sternarchogiton labiatus*.

37. *Anterodorsally directed process on dorsal margin of symplectic:* (0) absent; (1) present (CI = 0.250; RI = 0.667).

The dorsal margin of the symplectic is straight to variably irregular in outgroups to *Sternarchorhynchus* (Hilton *et al.*, 2007: fig. 11, for condition in *Orthosternarchus tamandua*) and nearly all species of the genus (state 0; Fig. 9). *Sternarchorhynchus cramptoni*, *S. curumim*, *S. curvirostris*, *S. goeldii*, *S. hagedornae*, *S*, *mareikeae*, *S. oxyrhynchus*, *S. retzeri*, *S. starksi*, and *S. stewarti* rather have the dorsal portion of the symplectic elaborated into an anteriorly and slightly medially directed process (state 1; Figs 10, 12).

38. *Form of metapterygoid*: (0) approximately triangular overall; (1) somewhat to distinctly horizontally elongate and approximately quadrilateral (CI = 1.000; RI = 1.000).

The metapterygoid in outgroups to *Sternarchorhynchus* is approximately triangular [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11); *Platyurosternarchus* (Albert, 2001: fig. 31a); *Sternarchorhamphus* (Albert, 2001: fig. 31b)] with the posterior portion tapering to a variably distinct point (state 0; Fig. 8). Species of *Sternarchorhynchus*, in contrast, have a more elongate metapterygoid with an overall quadrilateral form (state 1; Figs 9, 10).

39. *Form of lateral surface of dorsal portion of metapterygoid*: (0) overall flat or gently convex with minimal thickening; (1) with distinct rounded lateral ridge terminating anteriorly in well-developed articular surface (CI = 1.000; RI = 1.000).

Outgroups to *Sternarchorhynchus* have the posterior portion of the endopterygoid overlapping the anterodorsal region of the metapterygoid, with the latter ossification having a smooth lateral surface [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007:

fig. 11a)]. The dorsal portion of the metapterygoid in *Sternarchorhynchus* is not overlapped by the endopterygoid; however, all members of the genus other than *S. goeldii* and *S. oxyrhynchus* have the exposed portion of the metapterygoid unelaborated laterally or bearing at most some minor ridges and/or expansions on that surface (state 0; Fig. 9). Both *S. goeldii* and *S. oxyrhynchus* have a lateral elaboration of the dorsolateral portion of the metapterygoid expanded into a thickened, laterally rounded, anteroposteriorly aligned ridge. This metapterygoid expansion is particularly well developed anteriorly, where it forms a broad facet that articulates with a corresponding process of the quadrate (state 1, Fig. 10; see also character 30).

40. *Association of posterior tip of posteroventral process of quadrate and dorsal margin of horizontal arm of preopercle*: (0) tip of posteroventral process of quadrate positioned above dorsal margin of preopercle; (1) tip of posteroventral process of quadrate fitting into variably developed notch along dorsal margin of preopercle (CI = 1.000; RI = 1.000).

Outgroups to *Sternarchorhynchus* and *S. goeldii*, *S. oxyrhynchus*, and *S. mormyrus* have the elongate posteroventral process of the quadrate running along and closely applied to the dorsal margin of the horizontal arm of the preopercle. In that condition the tip of the quadrate process is neither enveloped posteriorly nor dorsally by the preopercle (state 0; Fig. 10). We were unable to code this feature for *S. axelrodi*. All remaining species of *Sternarchorhynchus* have the dorsal margin of the preopercle expanded dorsally in the region posterior to the tip of the posteroventral process of the quadrate. Consequently, the posteriormost portion of the quadrate lies within a depression along the dorsal margin of the preopercle (state 1; Figs 9, 12). Species with this expansion often, but not always, have the dorsally expanded portion of the preopercle elaborated into an anterodorsally directed process extending towards or over the tip of the quadrate process, sometimes encompassing the tip.

41. *Anterior extent of preopercle*: (0) terminating variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; (1) extending to location anterior of vertical through ventral portion of joint between quadrate and metapterygoid (CI = 0.143; RI = 0.625).

Examined apteronotid outgroups and *S. axelrodi*, *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. montanus*, *S. mormyrus*, and *S. starksi* have the horizontal arm of the preopercle extending anteriorly to a point situated distinctly posterior of the ventral portion of the quadrate–metapterygoid joint (state 0; Figs 8, 9). *Sternarchorhynchus britskii*, *S. caboclo*, *S. curumim*, *S. curvirostris*, *S. gnomus*, *S. goeldii*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. oxyrhynchus*, *S. retzeri*, *S. roseni*, *S. severii*, and *S. stewarti* instead possess an anteroposteriorly longer horizontal arm of the preopercle terminating anteriorly somewhat, to distinctly, anterior of the vertical through the ventral portion of this joint (state 1; Fig. 10).

42. *Form of laterosensory canal segment in vertical arm of preopercle*: (0) in form of two shallowly anteriorly concave segments; (1) in form of two deeply anteriorly concave segments (CI = 0.167; RI = 0.545).

The portion of the laterosensory canal system in the vertical arm of the preopercle in *Sternarchorhynchus* has the form of two anteriorly concave segments that join, or nearly meet, approximately midway along the vertical length of the bone. Two major alternative morphologies of this system occur in the genus. In *S. axelrodi*, *S. caboclo*, *S. chaoi*, *S. cramptoni*, *S. curumim*, *S. goeldii*, *S. mormyrus*, *S. oxyrhynchus*, *S. retzeri*, and *S. severii*, the canals form deeply anteriorly convex arcs (state 1; Figs 9, 10, 13A). State 1 is also present in *'A.' apurensis* and *P. macrostoma* in the outgroups. *Sternarchorhynchus britskii*, *S. curvirostris*, *S. gnomus*, *S. higuchii*, *S. hagedornae*, *S. inpai*, *S. jaimei*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. roseni*, *S. starksi*, and *S. stewarti* also have concave canal segments such as those in congeners, but with the convexity of the laterosensory canal segments much less pronounced and in the form of distinctly shallow arcs (state 0; Fig. 13B). State 0 is also present in the outgroups in the three examined species of *Apteronotus*, *Orthosternarchus tamandua*, *P. crypticus*, *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri*.

43. *Form of dorsal margin of opercle*: (0) very slightly concave to distinctly convex; (1) distinctly concave (CI = 0.250; RI = 0.500).

Outgroups to *Sternarchorhynchus* have the dorsal margin of the opercle ranging from very slightly concave to distinctly convex, with the species of *Platyurosternarchus* plus *Sternarchorhamphus muelleri* having slightly concave margins to the bone (state 0; Fig. 8). That condition also occurs amongst more distant outgroups in *A. albifrons*, *A. cuchillo*, *'A.' apurensis*, and *Sternarchogiton labiatus*. *Sternarchorhynchus*, in contrast, has the opercular margin distinctly concave (Figs 9, 10) with this condition (state 1) also present amongst outgroups in *A. rostratus*, *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11), and *Sternarchella orthos* (Lundberg *et al.*, 1996: fig. 5c).

44. *Form of posterodorsal corner of opercle*: (0) rounded to pointed, but not forming distinct process; (1) extended in form of distinct 'ear-like' process (CI = 0.500; RI = 0.875).

The posterodorsal corner of the opercle varies in form across the Gymnotiformes, ranging most often

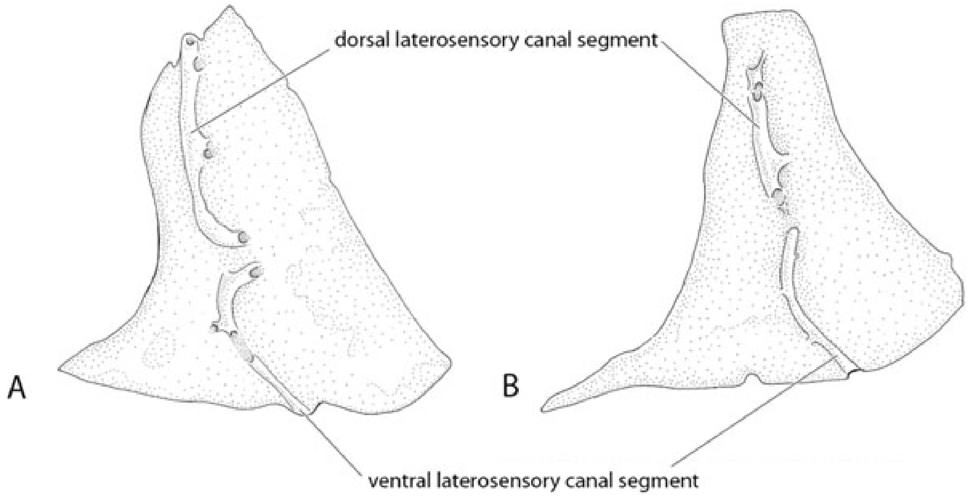

Figure 13. Preopercle of A, *Sternarchorhynchus severii*, INPA 22898; and B, *Sternarchorhynchus gnomus*, INPA 25636; showing differing forms of laterosensory canals in bone; left side, lateral view, anterior to left.

from being gently rounded [e.g. *Sternarchorhamphus* (Albert, 2001: fig. 31b); *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11)] to somewhat concave [e.g. *Electrophorus electricus* (Albert *et al.*, 2005: fig. 7)]. Species of *Sternarchorhynchus*, in contrast, have a distally rounded 'ear-like' posterior extension of this region of the opercle (state 1; Figs 9, 10). This process is present solely in *Sternarchella orthos* amongst outgroups in this study.

45. *Association of posterodorsal corner of opercle and supracleithrum*: (0) rounded posterior extension of opercle lying ventral of, or very slightly overlapping, ventralmost portion of supracleithrum; (1) rounded posterior extension of opercle extending over ventralmost portion of supracleithrum (CI = 0.250; RI = 0.625).

Sternarchorhynchus species other than *S. axelrodi* and *S. mormyrus* share state 0 in which the opercle demonstrates no or at most minimal overlap of the ventral portion of the supracleithrum. State 0 is present amongst outgroups in *P. crypticus*, *Sternarchella orthos*, and *Sternarchorhamphus*. Cleared and stained specimens of *S. mormyrus* have an extensive overlap of the ventralmost region of the supracleithrum by the posterodorsal portion of the opercle. Radiographs of specimens of its sister species, *S. axelrodi*, revealed a comparable degree of overlap of the two bones in that species (state 1). A similar degree of extensive overlap (state 1) occurs in outgroups in *A. albifrons*, *A. cuchillo*, *A. rostratus*, *'A.' apurensis*, *Orthosternarchus tamandua*, *P. macrostoma*, and *Sternarchogiton labiatus.*

HYOID ARCH

The number of branchiostegal rays within the Gymnotiformes ranges from two to five (Albert, 2001). Variation in the number of elements involves differences in the number of rays associated with the anterior and occasionally posterior ceratohyals. One to three ceratohyals can attach to the ventral margin of the anterior ceratohyal. The fourth element has a variable area of attachment ranging from the lateral surface of the posterior portion of the anterior ceratohyal to the lateral surface of the anterior region of the posterior ceratohyal. A fifth ray, when present, attaches to the area of the joint of the anterior and posterior ceratohyals (see Mago-Leccia, 1978: fig. 13 for illustration of this arrangement of five rays in *Eigenmannia virescens*) or to the lateral surface of the posterior ceratohyal (see de Santana & Nogueira, 2006: fig. 3 for illustration of this condition in *S. caboclo*). Various authors have used total ray counts to advance hypotheses of phylogenetic relationships (e.g. McAllister, 1968). Such data, albeit informative at a general level, fail to specify the presence versus absence of individual rays. Phylogenetically useful information can be better expressed in terms of individual elements; a procedure we use herein.

46. *Presence or absence of anterior most branchiostegal ray attaching to ventral margin of anterior ceratohyal:* (0) absent; (1) present (CI = 0.500; RI = 0.900).

One to three branchiostegal rays attach to the ventral margin of the anterior ceratohyal; however, in the absence of landmarks that allow us to homologize elements unambiguously we only coded the number of rays attaching to this bone when fewer than three rays are present. Nonetheless, based on positional information it appears that loss of branchiostegal rays proceeds in an anterior posterior sequence that leads us to cast the discussion within that framework.

The first ray is absent in *Orthosternarchus tamandua*, which also lacks the apparent second ray, retaining only a single branchiostegal ray attaching to the anterior ceratohyal (Hilton *et al.*, 2007: fig. 13). The first ray is missing in all species of *Platyurosternarchus*, the examined species of *Apteronotus*, and *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* amongst the outgroup taxa (state 0) and uniquely in *S. caboclo* within *Sternarchorhynchus*. Although this condition is autapomorphic for *S. caboclo* amongst osteologically examined species of *Sternarchorhynchus*, we retained it in the analysis because it may prove to be synapomorphic for a small clade once additional species of the genus are examined osteologically.

47. *Presence or absence of posteriormost branchiostegal ray attaching either to lateral surface of area of articulation of anterior and posterior ceratohyals or to anterior region of lateral surface of posterior ceratohyal:* (0) present; (1) absent (CI = 1.000; RI = 1.000).

The posteriormost, typically larger, branchiostegal ray in gymnotiforms attaches to the lateral surface of the hyoid arch within the area delimited by the area of joint between the anterior and posterior ceratohyals and the anterior region of the posterior ceratohyal. Variation in the area of attachment forms a continuum across the examined taxa and we coded only presence versus absence of the ray in this analysis. This posteriormost branchiostegal ray is absent (state 1) in both *Sternarchorhamphus muelleri* and *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 13), but present in *Platyurosternarchus* and *Sternarchorhynchus* (state 0). This ray is similarly present in the examined species of *Apteronotus* and *Sternarchella orthos* and *Sternarchogiton labiatus*.

Sternarchorhamphus muelleri and *S. caboclo* each have four branchiostegal rays. That number is an equivalent character state under previous coding schemes focused on total numbers of rays rather than presence versus absence of individual elements. The reduced number of branchiostegal rays is achieved in different fashions in the two taxa, being a consequence of the loss of the anteriormost ray in *S. caboclo* versus the absence of the posteriormost ray in *Sternarchorhamphus muelleri*.

48. *Relative size of first and second branchiostegal rays*: (0) rays of approximately same length; (1) first ray approximately one-third length of second ray (CI = 1.000; RI = 0.000).

Variation occurs in both the relative overall size and length of the first and second branchiostegal rays, but we focus in this character on the length of the rays as this is a more readily quantifiable attribute. With the single exception of *S. inpai* all species of *Sternarchorhynchus* have the first and second rays of more or less comparable lengths (state 0). In *S. inpai* the first ray is shortened to approximately one-third of the length of the second ray (state 1). Although this condition is autapomorphic for *S. inpai* within *Sternarchorhynchus* in the present analysis, we included it herein because it may define a small clade within the genus in future studies that incorporate species not examined osteologically in this study. This character could not be coded in outgroups to *Sternarchorhynchus* or in the genus for *S. caboclo*, all of which lack the anteriormost ray.

49. *Form of anterodorsal margin of third branchiostegal ray*: (0) smoothly convex; (1) with distinct angular process (CI = 1.000; RI = 1.000).

The third branchiostegal ray has an overall smoothly convex margin along its anterodorsal region in both proximate outgroups to *Sternarchorhynchus* [e.g. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 13); the br1 of those authors] and the more distantly related apteronotids in the analysis (state 0). Species of *Sternarchorhynchus* other than *S. goeldii* and *S. oxyrhynchus* similarly share state 0. Both *S. goeldii* and *S. oxyrhynchus* have the anterodorsal portion of the third branchiostegal ray expanded into a broadly angular pointed process (state 1).

50. *Length of anterior branchiostegal ray attaching to lateral surface of the anterior ceratohyal*: (0) 1.5 times or less of distance from anterior limit of ventral hypohyal to posterior limit of posterior ceratohyal; (1) approximately three times distance from anterior limit of ventral hypohyal to posterior limit of posterior ceratohyal (CI = 1.000; RI = 1.000).

Species of *Sternarchorhynchus* and *Platyurosternarchus* plus most examined outgroup apteronotids have the anterior branchiostegal ray attaching to the lateral surface of the anterior ceratohyal (the fourth branchiostegal ray under the scheme of five total rays detailed above) of a length equal to, or shorter than, 1.5 times the distance from anterior limit of the ventral hypohyal to posterior limit of posterior ceratohyal. Fourth branchiostegal rays of comparable relative lengths also occur in more distantly related outgroups [e.g. *Eigenmannia virescens* (Mago-Leccia, 1978: fig. 15)]. *Sternarchorhamphus muelleri* and *Orthosternarchus tamandua* have significantly longer fourth rays of lengths approximately three or more times the distance from the anterior limit of the ventral hypohyal to the posterior limit of the posterior ceratohyal (see Hilton *et al.*, 2007: fig. 13 for *Orthosternarchus tamandua*). Although the derived elongation of the fourth branchiostegal ray is not pertinent to the question of relationships within *Sternarchorhynchus*, we included the character to provide structure to the outgroup phylogeny. A comparable elongation of the second branchiostegal ray attaching to the lateral surface of the posterior portion of the

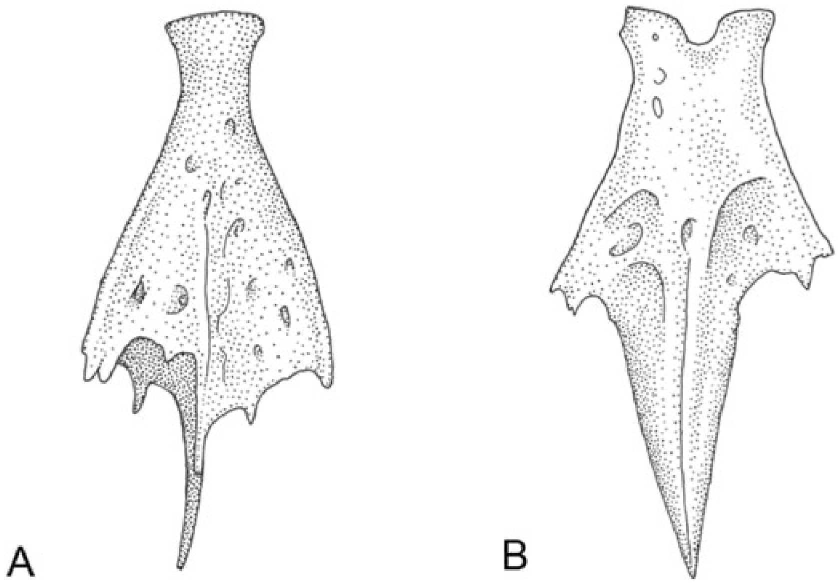

Figure 14. Urohyal of A, *Sternarchorhynchus oxyrhynchus*, USNM 228787, and B, *Sternarchorhynchus hagedornae*, USNM 391574; dorsal view, anterior at top.

hyoid arch (the fifth ray under the numbering scheme herein) characterizes *Sternarchorhamphus muelleri* and is apparently autapomorphic for that species.

51. *Form of dorsal margin of proximate portion of anterior branchiostegal ray attaching to lateral surface of the anterior ceratohyal:* (0) dorsally pointed or rounded; (1) dorsally concave with angled margins (CI = 1.000; RI = 0.000).

The dorsal portion of the anterior ray attaching to the lateral surface of the anterior ceratohyal (the fourth ray under the system described above) is either dorsally rounded or pointed in outgroups to *Sternarchorhynchus* in the Apteronotidae. *Sternarchorhynchus caboclo*, in contrast, has a strongly concave dorsal margin to the ossification demarked by distinct angled areas both anteriorly and posteriorly. This character (state 1) is autapomorphic in the present study, but was retained in the analysis as a potential synapomorphy once additional species of *Sternarchorhynchus* are examined osteologically.

52. *Relative size of anterior portion of urohyal*: (0) relatively narrow and one-fifth or less of length of main body of bone; (1) relatively wide and one-third or more of length of main body of bone (CI = 0.333; RI = 0.500).

In *Orthosternarchus tamandua*, *Sternarchorhamphus muelleri*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus*, the anterior portion of the urohyal is narrow relative to the overall size of the bone with its transverse width approximately one-fifth or less of the length of the main body (state 0; Fig. 14A). Because of the reduction of the overall proportional length of the urohyal, the anterior portion of the urohyal is relatively wide relative to the overall size of the bone in species of *Sternarchorhynchus* other than *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus*. This is reflected in a transverse width of the urohyal that is approximately one-third or more of the length of the main body of the ossification (state 1; Fig. 14B). The urohyal is dramatically reduced in size and modified in form in the outgroup apteronotids other than *P. crypticus*, *P. macrostoma*, and *Sternarchella orthos* but, nonetheless, fits the definition of state 1 and was coded accordingly. This character was not coded for *Sternarchogiton labiatus* and the three examined species of *Apteronotus*, all of which have highly modified urohyals. It was impossible to code *S. axelrodi* for this character solely from radiographs of the types.

53. *Form of anterior margin of urohyal*: (0) straight or slightly irregular, but without distinct medial notch; (1) with distinct medial notch (CI = 0.200; RI = 0.556).

The anterior margin of the urohyal is transversely nearly straight or at most slightly irregular in *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchorhamphus muelleri*, and most *Sternarchorhynchus* species (state 0; Fig. 14A). *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. curumim*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. mesensis*, *S. montanus*, *S. roseni*, and *S. stewarti* alternatively have a distinct medial notch along the anterior margin of the urohyal (state 1; Fig. 14B). This character could neither be coded for the other outgroup apteronotids in which the urohyals are dramatically reduced in relative size and also modified in form, nor for *S. starksi*, which had a deformed urohyal in the single available cleared and stained specimen of the species and *S. axelrodi* in the absence of cleaned and stained specimens.

GILL ARCHES

54. *Form of basihyal*: (0) without lateral processes; (1) with lateral processes (CI = 0.250; RI = 0.773).

The anteriormost component of the median ossifications of the lower half of the gill arches in all examined apteronotids is an elongate ossification identified by Hilton *et al.* (2007) as a fused basihyal plus first basibranchial. Underlying this assumption was the fact that the ossification occupies the area encompassed by those elements in some other gymnotiform families (e.g. Sternopygidae, see Mago-Leccia, 1978: fig. 7) or by the ossified basihyal plus cartilaginous first basibranchial in some taxa (e.g. *Eigenmannia*, Mago-Leccia, 1978: fig. 17). In *Sternarchorhynchus* the posterior limit of the anterior element terminates between the anterior portions of the first hypobranchials, the typical position for the end of the basihyal and as such it appears that basibranchial 1 is absent. We consequently identify the elongate anterior ossification as the basihyal. *Apteronotus albifrons*, *A. cuchillo*, *A. rostratus*, *'A.' apurensis*, *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 14), *P. crypticus*, *P. macrostoma*, *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* have this ossification ranging from rod-like to slightly expanded transversely anteriorly, but without distinct lateral processes (state 0; Fig. 15). Within *Sternarchorhynchus* an unelaborated form of the basihyal (state 0) is restricted to *S. britskii*, *S. goeldii*, *S. higuchii*, *S. jaimei*, *S. oxyrhynchus*, and *S. roseni*. Other species of *Sternarchorhynchus* have definite lateral processes along at least the posterior half of the bone (state 1; Figs 16, 17).

55. *Presence or absence of medial ridge on posterior portion of dorsal surface of basihyal:* (0) present; (1) absent (CI = 1.000; RI = 1.000).

Various gymnotiforms have a medial ridge on the dorsal surface of the posterior portion of the basihyal (Triques, 1993: figs 12, 13). Such a process (state 0; Figs 15–17) is present in all outgroups in this study other than *A. rostratus*, *Orthosternarchus tamandua*, and *Sternarchella orthos* and all species of *Sternarchorhynchus* other than *S. inpai* and *S. montanus* (state 0). This ridge is absent in those two species (state 1). This character could not be coded for in *S. axelrodi* from radiographs.

56. *Degree of separation between basihyal and second basibranchial*: (0) ossifications in close proximity with posterior limit of basihyal extending posteriorly nearly to transverse to posterior limit of ossified portions of first hypobranchial; (1) ossifications distinctly separated with posterior limit of basihyal extending posteriorly only to, or proximate to, anterior region of ossified portion of first hypobranchial (CI = 1.000; RI = 1.000).

One notable variable amongst examined taxa involves the degree of the extension posteriorly of the basihyal. The condition typical for most apteronotids including the outgroups to *Sternarchorhynchus* in this study has a relatively small gap between the posterior limit of the basihyal and the anterior margin of the second basibranchial (state 0). This posterior position of the terminus of the basihyal is reflected in the location of the end of the ossification approximately at the transverse to the posterior limit of the ossified portion of the first hypobranchial (Hilton *et al.*, 2007: fig. 14 for an illustration of this condition in *Orthosternarchus tamandua*). The examined species of *Sternarchorhynchus*, in contrast, have the posterior limit of the basihyal situated between the anterior portions of the contralateral first hypobranchials or anterior of that position (state 1; Figs 15–17). This anterior position of the terminus of the basihyal results in a major gap between that ossification and the anterior limit of the first hypobranchial.

57. *Form of first hypobranchial*: (0) triangular overall with transverse dimension of ossified portion slightly less than one-half length of that region; (1) elongate with transverse dimension of ossified portion approximately one-quarter to one-fifth length of that region (CI = 1.000; RI = 1.000).

An overall triangular first hypobranchial (state 0; Figs 15–17) is broadly distributed across all examined taxa in the Apteronotidae and indeed elsewhere in the Gymnotiformes (Mago-Leccia, 1978: fig. 7 for condition in a representative of the Sternopygidae). Within the Apteronotidae, a distinct elongation of the first hypobranchial occurs in both *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri* (state 1) amongst the taxa examined in this study. Although not directly informative as to intrageneric relationships within *Sternarchorhynchus*, we retained the character in the analysis to provide structure within the outgroup phylogeny.

58. *Form of second basibranchial*: (0) with midlength constriction; (1) with lateral margins running approximately in parallel (CI = 0.250; RI = 0.700).

The majority of species of *Sternarchorhynchus* along with all of the examined outgroups have the second basibranchial constricted to a variable, but nonetheless pronounced, degree along its midlength (state 0). As a consequence, the element has a variable hour-glass shape from dorsal view (Figs 15, 16). In some outgroup taxa [e.g. *Orthosternarchus*

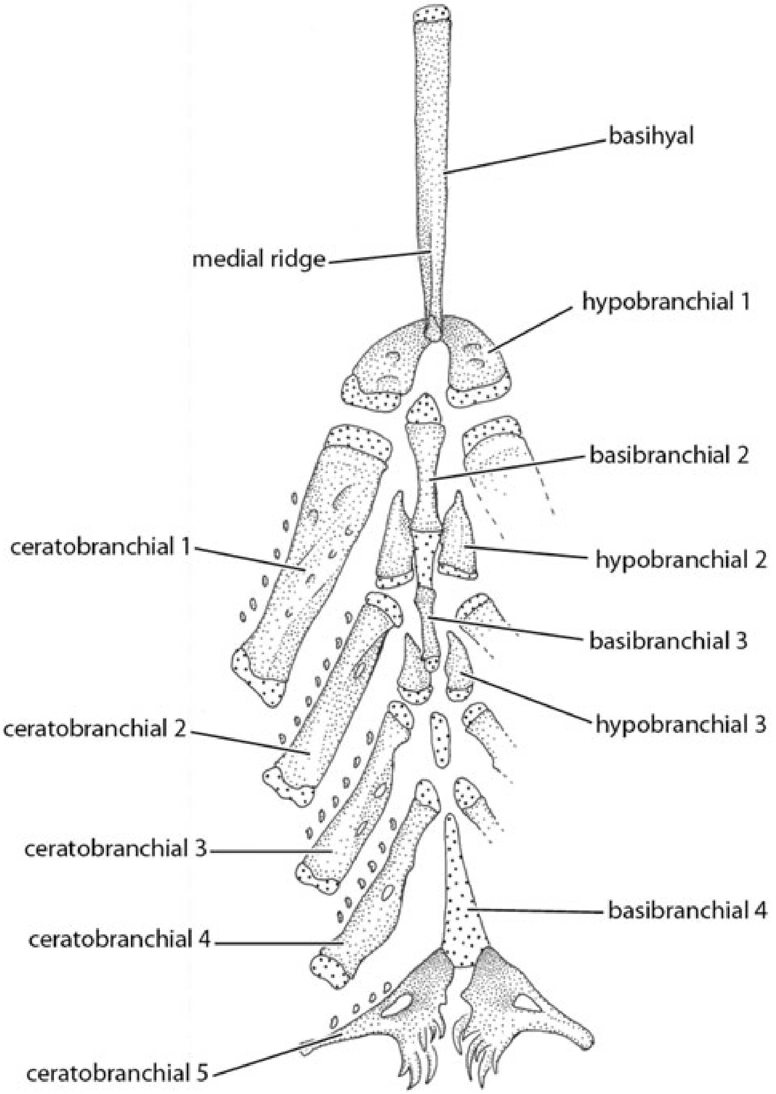

Figure 15. Ventral portion of gills arches of *Sternarchorhynchus goeldii*, MCZ 46887; dorsal view, anterior at top; larger stippling represents cartilage; small elements along anterior margins of ceratobranchials are highly reduced gill rakers.

tamandua (Hilton *et al.*, 2007: fig. 14)], the second basibranchial is proportionally more elongate with a relatively less pronounced but still obvious midlength constriction. A subset of the species of *Sternarchorhynchus* (*S. chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. jaimei*, *S. mesensis*, *S. mormyrus*, *S. retzeri*, *S. severii*, *S. starksi*, and *S. stewarti*) have a bony plate extending laterally from the lateral margins of the constricted portion of the main body of the second basibranchial (state 1; Fig. 17). These lateral extensions result in parallel lateral margins to the second basibranchial from a dorsal view, albeit with the constricted main body of the bone still obvious; more so, in transmitted light (state 1). This character could not be coded for *S. axelrodi* from radiographs.

59. *Form of anterior portion of second hypobranchial*: (0) without distinct anterior extension from main body; (1) with distinct anterior extension from main body (CI = 1.000; RI = 1.000).

The second hypobranchial is a variably anteroposteriorly elongate bone amongst gymnotiforms, typically with an progressively tapering anterior region that extends along the lateral margin of the second basibranchial. Although outgroups to *Sternarchorhynchus* along with *S. goeldii* and *S. oxyrhynchus* have the anterior portion of this ossification somewhat pointed overall, the region is not developed into a distinct narrow, often somewhat slightly medially curving process (state 0; Fig. 15). All *Sternarchorhynchus* species other than *S. goeldii* and *S. oxyrhynchus* have the anterior portion of the second hypobranchial

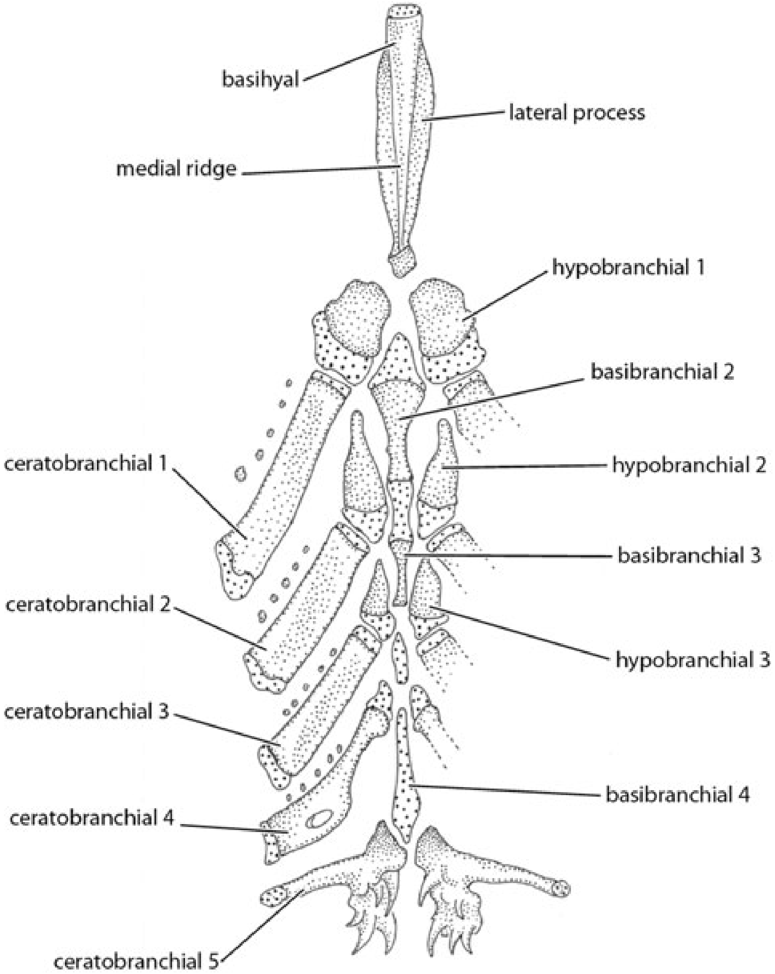

Figure 16. Ventral portion of gills arches of *Sternarchorhynchus caboclo*, INPA 10594; dorsal view, anterior at top; larger stippling represents cartilage; small elements along anterior margins of ceratobranchials are highly reduced gill rakers.

more attenuate, with this anterior extension often slightly medially curving anteriorly (state 1; Figs 16, 17).

60. *Degree of development of medial portion of second hypobranchial in adults*: (0) with distinct medial process extending ventral of second basibranchial and approaching contralateral second hypobranchial; (1) without distinct medial process and with contralateral second hypobranchials separated by second basibranchial (CI = 0.500; RI = 0.000).

The second hypobranchial in adults of nearly all outgroups and all species of *Sternarchorhynchus* has a medial extension directed towards its contralateral partner in the area ventral of the second basibranchial. Amongst species for which we had a size range of osteological preparations, the extension is less developed in smaller individuals but ontogenetically expands into a distinctly pointed process (state 0; Figs 15, 17). Uniquely amongst the species examined herein, *S. caboclo* and *S. higuchii* lack that medial process of the second hypobranchial. They instead have the contralateral ossifications completely separated by the second basibranchial and the cartilage that lies between that ossification and the third basibranchial (state 1; Fig. 16). This character could not be coded for in *S. axelrodi* from radiographs.

61. *Degree of constriction of medial portion of fourth ceratobranchial*: (0) constriction limited when present; (1) constriction very distinct (CI = 1.000; RI = 1.000).

When viewed from the dorsal view, the fourth ceratobranchial has nearly parallel lateral and medial margins, or tapers slightly anteriorly in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 14) and *Sternarchorhamphus muelleri* (state 0). Most examined apteronotids and more distantly related gymnotiform taxa either retain that morphology of the fourth ceratobranchial or have on occasion a lateral expansion of the anterior portion of that ossification (e.g. *Rhabdolichops troschelii*, Mago-Leccia, 1978: fig. 7). Species

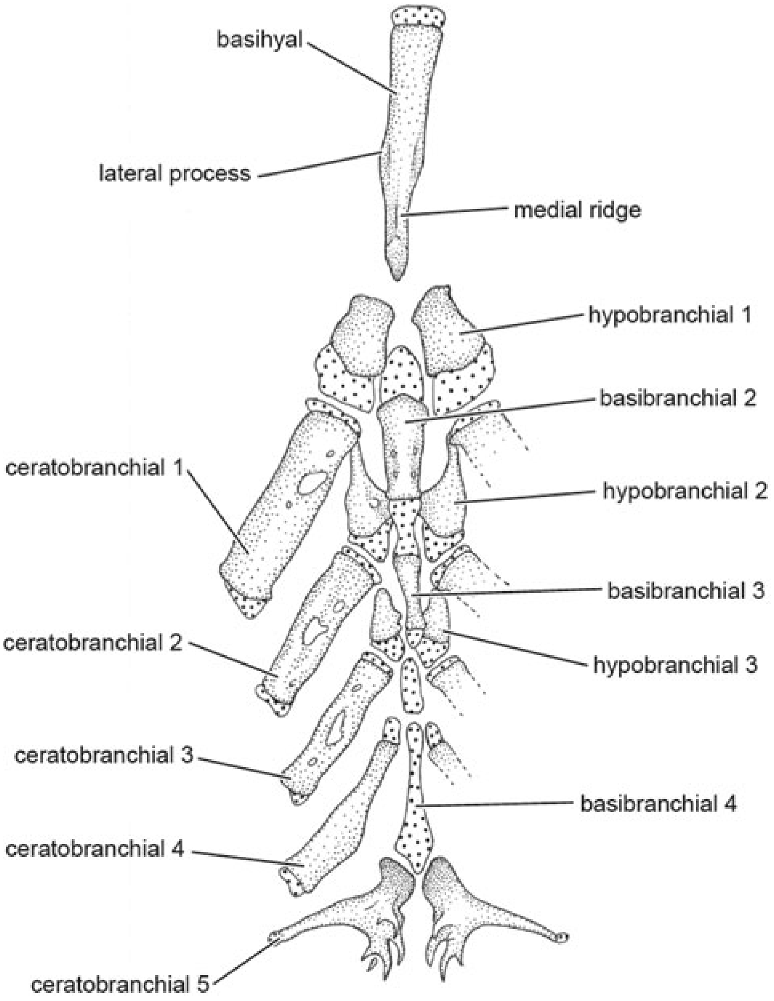

Figure 17. Ventral portion of gills arches of *Sternarchorhynchus hagedornae*, USNM 391574; dorsal view, anterior at top; larger stippling represents cartilage; highly reduced gill rakers along anterior margins of ceratobranchials not illustrated.

of *Platyurosternarchus* and *Sternarchorhynchus*, however, have the anterior portion of the fourth ceratobranchial transversely constricted along the portion of the bone somewhat distal of the region where the ossified portion of the ceratobranchial merges into the cartilage that caps the bone (state 1; Figs 15–17). Such constriction of the fourth ceratobranchial is particularly pronounced in *S. goeldii* amongst species of the genus represented by cleared and stained specimens in this analysis. That condition may serve to define a subunit of that genus once additional congeners are examined osteologically.

62. *Condition of fourth infrapharyngobranchial*: (0) totally cartilaginous; (1) ossified (CI = 1.000; RI = 1.000).

The fourth infrapharyngobranchial is an anteroposteriorly elongate, posteriorly wider cartilaginous body without ossification centres in both *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 14) and *Sternarchorhamphus muelleri*. An entirely cartilaginous fourth infrapharyngobranchial is, furthermore, general amongst other outgroups in the Apteronotidae (e.g. *Adontosternarchus*, Mago-Leccia *et al.*, 1985: fig. 5) and across the Gymnotiformes (e.g. the sternopygids *Eigenmannia* and *Rhabdolichops*, Mago-Leccia, 1978: figs 9, 17). It thus represents the primitive condition across the Gymnotiformes (state 0). The species of *Sternarchorhynchus* and *Platyurosternarchus* have a well-ossified fourth infrapharyngobranchial with an overall triangular, posteriorly widening form (state 1; Fig. 18). The ossified portion of the fourth infrapharyngobranchial is bordered anteriorly by a small cartilage cap that contacts the cartilages of the third epibranchial and third infrapharyngobranchial and terminates posteriorly along a transversely elongate cartilage that broadly articulates with the cartilage along the anterior margin of the fourth epibranchial.

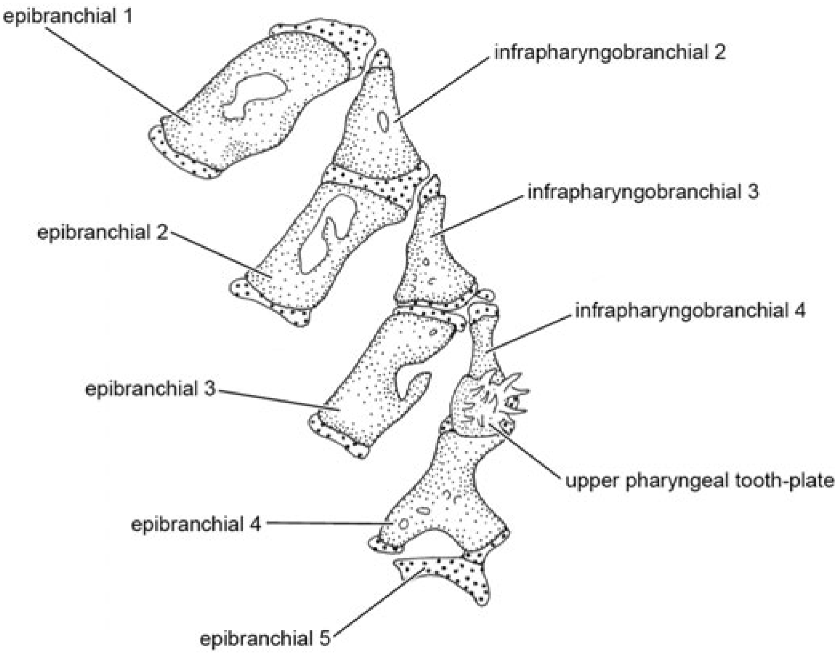

Figure 18. Dorsal portion of gills arches of *Sternarchorhynchus hagedornae*, USNM 391574; right side, ventral view, anterior at top; larger stippling represents cartilage.

63. *Degree of medial development of cartilage along anterior margin of first epibranchial*: (0) cartilage extending along lateral, but not anterior margin of cartilage at anterior of second infrapharyngobranchial; (1) cartilage expanded medially and extending along all, or nearly all, of anterior margin of cartilage along anterior margin of second infrapharyngobranchial (CI = 1.000; RI = 1.000).

Two primary conditions of the cartilages along the anterior limits of the first epibranchial and the second infrapharyngobranchial occur in *Sternarchorhynchus* and its proximate outgroups. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 14), *Sternarchorhamphus muelleri*, and other examined outgroup apteronotids have a moderately sized cartilage along the anterior margin of the first epibranchial. This cartilage extends solely along the lateral margin of the cartilage that caps the anterior limit of the ossified portion of the second infrapharyngobranchial. In this configuration, the cartilage that anteriorly caps the second infrapharyngobranchial retains a distinct transversely exposed margin anteriorly (state 0). *Platyurosternarchus* and *Sternarchorhynchus* have the cartilage along the anterior portion of the first epibranchial further expanded medially to a notable degree. Therefore that cartilage overlaps not only the lateral margin of the cartilage that caps the second infrapharyngobranchial anteriorly, but extends to varying degrees along the anterior margin of that cartilage. As a consequence of this expansion of the anterior cartilage of the first epibranchial, the cartilage at the anterior margin of the second infrapharyngobranchial in *Platyurosternarchus* and *Sternarchorhynchus* lacks a broadly exposed margin anteriorly; a derived condition (state 1; Fig. 1).

MYORHADOI

64. *Form of ventral myorhadoi in central portions of body*: (0) central portion of myorhadoi without ventral or dorsal elaborations; (1) central portion of myorhadoi with ventral elaboration; (2) central portion of myorhadoi with ventral and dorsal elaborations (CI = 0.667; RI = 0.900).

Myorhadoi are the superficial series of the intermuscular bones that extend along the length of the body in gymnotiforms and are variably present in other fishes. The most common form of the large series of these ossifications present across the Gymnotiformes is a bony rod that progressively subdivides distally at both ends with these terminal processes extending further into the musculature. Such an unelaborated bony rod along the central region of the myorhadoi occurs in *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchorhamphus muelleri*, *Sternarchella orthos*, and *Sternarchorhynchus goeldii* amongst the taxa in this study (state 0). All other examined taxa have elaborations of the central rod-like section of at least some of the myorhadoi;

with such extensions taking either of two forms (states 1 or 2). *Apteronotus albifrons*, *Sternarchogiton labiatus*, and all species of *Sternarchorhynchus* with the exception of *S. goeldii* have an elaboration of the portion of the central section of the portion of the myorhadoi series located in the region of the body approximately one-quarter the distance between the rear of the abdominal cavity and the end of the anal fin. The myorhadoi in that region have a relatively long, curving, anteromedially directed extension arising from the medial surface of the rod-like central portion of the bone (states 1 and 2; Fig. 19A, B). *Sternarchorhynchus chaoi* uniquely also has a shorter anterodorsally orientated process arising from the dorsal surface of the myorhadoi at a point approximately directly opposite to the base of the larger anteroventral extension of the ossification (state 2; Fig. 19B). This character could not be coded for *S. axelrodi* solely based on radiographs of the types.

POSITION OF ANUS AND UROGENITAL PAPILLA

65. *Ontogenetic shift in position of anus*: (0) position of anus relatively invariant in juveniles and adults with anus situated posterior to vertical through eye in adults; (1) position of anus distinctly ontogenetically variable and shifting anteriorly with growth to location anterior to vertical through eye in adults (CI = 0.125; RI = 0.500).

Orthosternarchus tamandua, *P. crypticus*, *P. macrostoma*, and *Sternarchorhamphus muelleri* lack an ontogenetic anterior migration of the anus and urogenital papilla. Positional transitions were absent in *A. cuchillo*, *A. rostratus*, *Sternarchella orthos*, and *Sternarchogiton labiatus* amongst the more distant outgroups in this analysis (state 0). Campos-da-Paz (2000) remarked that the position of the anus (and presumably the associated urogenital papilla) was ontogenetically variable in a subset of the few species of *Sternarchorhynchus* recognized at the time of his analysis. Our analysis, involving as it does a significantly greater number of now-recognized species, documents that many *Sternarchorhynchus* species demonstrate an ontogenetic shift anteriorly of the anus and urogenital papilla (state 1; see listing of species in Appendix 1). An anterior shift of the position of the anus and urogenital papilla occurs in *A. albifrons* and *'A.' apurensis'* amongst the more distantly related apteronotids incorporated into the analysis. This character was not coded for species of *Sternarchorhynchus* for which available ontogenetic series are too restricted to demonstrate potential shifts in the position of the anus and urogenital papilla.

NEUROCRANIUM

66. *Presence or absence of scythe-shaped process along lateral margin of ventral ethmoid*: (0) absent; (1) present (CI = 1.000; RI = 1.000).

The ventral ethmoid is fused to the anterior portion of the vomer to form a compound ossification (see discussion in Albert, 2001: 6–7). The lateral margin of the ventral ethmoid lacks any pronounced scythe-shaped elaborations in outgroups to *Sternarchorhynchus* (state 0). Species of *Sternarchorhynchus* with the exception of *S. goeldii* and *S. oxyrhynchus* (Fig. 2) have contralateral, well-developed, posteriorly directed, scythe-shaped processes arising from the lateral margins of what is considered positionally to be the ventral ethmoid (state 1; Fig. 3). Each scythe-shaped process has a very small distal cartilage in specimens of approximately 40 mm TL, but is completely ossified in adults and separate from any cartilage masses associated with the main body of the vomer and/or parasphenoid.

The positionally somewhat similar expansions on the lateral margin of the ventral ethmoid in examined

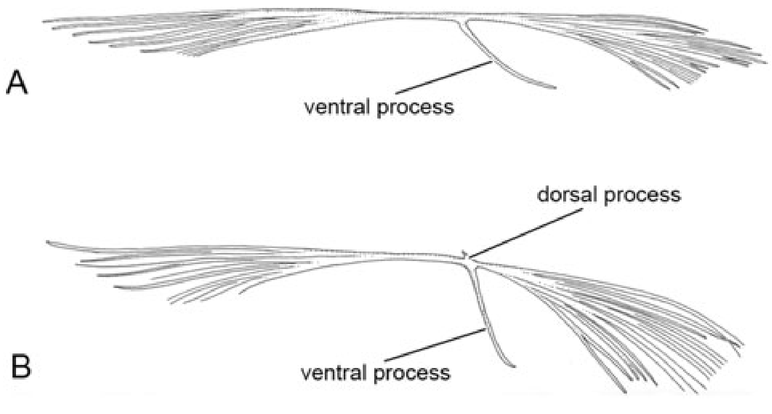

Figure 19. Myorhadoi from central portion of body of A, *Sternarchorhynchus higuchii*, INPA 20855; and B, *Sternarchorhynchus chaoi*, INPA 20851; lateral view, anterior to left.

species of *Apteronotus*, along with *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 10c), *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* lack the scythe-shaped process present in the vast majority of *Sternarchorhynchus* species. These outgroups have, in contrast, posterolaterally directed articular surfaces on the ventral ethmoid that form the anterior limit of anteroposteriorly elongate cartilage bodies that extend along the length of the vomer and sometimes parasphenoid. In light of their significantly different overall morphology and association with the vomerine cartilages, those processes of the ventral ethmoid in these outgroups are coded as state 0.

67. *Relative length of the mesethmoid in adults*: (0) distance from tip of mesethmoid to vertical through posteriormost limit of that bone less than, to distinctly less than, distance from anteriormost point on frontal to anterior margin of parietal; (1) distance from tip of mesethmoid to vertical through posteriormost limit of that bone equal to, or longer than, distance from anteriormost point on frontal to anterior margin of parietal (CI = 1.000; RI = 1.000).

One of the striking features of *Sternarchorhynchus* is the pronounced development of the snout into an elongate overall tubular structure. Elongation of the snout is achieved via diverse alterations within the Apteronotidae (see Convergence in elongation of snout under Discussion), but in *Sternarchorhynchus* the pronounced lengthening of the mesethmoid is one of the major contributing factors to the elongation of the dorsal portion of the neurocranium. The mesethmoid in adults of that genus spans approximately one-half the distance between the tip of the snout and the anterior margin of the opercle (state 1; Campos-da-Paz, 2000: fig. 6), with the extension reflected in the relative length of the mesethmoid versus the frontal. Juveniles of *Sternarchorhynchus* have a proportionally much shorter mesethmoid (compare Albert, 2001: fig. 17A, B) with that ossification progressively increasing in length ontogenetically. Although *Orthosternarchus tamandua* amongst the proximate outgroups also has an elongate overall head, the proportional elongation of the mesethmoid is much less pronounced in that species (Hilton *et al.*, 2007: fig. 10) than in *Sternarchorhynchus*. We also did not encounter dramatically elongated mesethmoids amongst outgroup apteronotids in this study (state 0).

68. *Presence or absence of lateral ethmoid*: (0) present; (1) absent (CI = 1.000; RI = 1.000).

A lack of the lateral ethmoid was ambiguously polarized as a possible synapomorphy for *Platyurosternarchus* plus *Sternarchorhynchus* by Albert & Campos-da-Paz (1998) and Albert (2001; cited therein as lateral ethmoid not ossified). Triques (2005) alternatively proposed that the lateral ethmoid was present in both genera as is the case in the vast majority of gymnotiforms, albeit sometimes represented as a cartilaginous element. The ambiguity in the earlier studies as to the applicability of the absence of a lateral ethmoid as a synapomorphy for *Platyurosternarchus* plus *Sternarchorhynchus* was a consequence of optimization resulting from the lack of an ossified lateral ethmoid in the examined specimens of *Orthosternarchus tamandua*. An ossified lateral ethmoid was, however, reported as present in *Orthosternarchus tamandua* by Hilton *et al.* (2007: 6, fig. 10), albeit reduced in size and shifted anteriorly relative to the typical condition in apteronotids. A lateral ethmoid is similarly present in the cleared and stained material of *Orthosternarchus tamandua* examined herein. In light of the consequent recoding of the condition in *Orthosternarchus* from lateral ethmoid absent to present, the absence of the lateral ethmoid in *Platyurosternarchus* and *Sternarchorhynchus* (state 1) resolves in this study as an unambiguous synapomorphy for those genera.

69. *Degree of development of the ventral portion of the orbitosphenoid*: (0) well developed and extensive along anteroposterior axis and extending anteriorly along dorsal margin of parasphenoid; (1) relatively narrow along anteroposterior axis and not extending anteriorly along dorsal margin of parasphenoid (CI = 1.000; RI = 1.000).

The orbitosphenoid extends ventrally from the frontal to contact the dorsal margin of the parasphenoid in gymnotiforms and many other ostariophysans. In the case of *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 10b), the species of *Platyurosternarchus crypticus*, and *Sternarchorhamphus muelleri* the ventral portion of the orbitosphenoid proximate to the parasphenoid is anteroposteriorly elongate with a definite anterior extension along the dorsal surface of the latter bone. This condition (state 0) occurs in the examined outgroup species of *Apteronotus* and *'Apteronotus'* along with *Sternarchella orthos* and *Sternarchogiton labiatus. Sternarchorhynchus*, in contrast, has a more pillar-like form of the ventral portion of the orbitosphenoid with either a limited anterior extension where it contacts the parasphenoid or a lack of such an elaboration. The orbitosphenoid in *Sternarchorhynchus* similarly has at most a limited posterior extension along the dorsal margin of the parasphenoid (state 1; Fig. 20).

70. *Form of posterior margin of orbitosphenoid*: (0) straight and abutting anterior margin of pterosphenoid along its entire length; (1) concave and contacting pterosphenoid only at dorsal and ventral limits of areas of contact of orbitosphenoid and pterosphenoid (CI = 1.000; RI = 1.000).

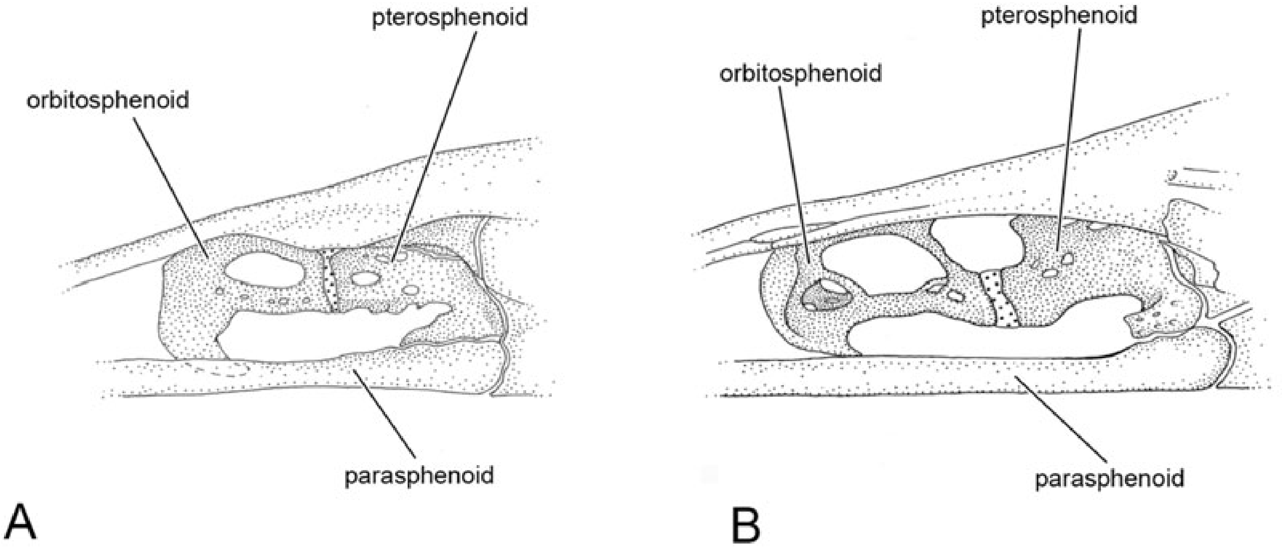

Figure 20. Anterior portion of braincase and proximate bones of A, *Sternarchorhynchus hagedornae*, USNM 391574; and B, *Sternarchorhynchus mormyrus*, USNM 306843; left side, lateral view, anterior to left; larger stippling represents cartilage.

Examined outgroups to *Sternarchorhynchus* and all species of that genus other than *S. axelrodi* and *S. mormyrus* have a continuous vertical cartilaginous joint between the orbitosphenoid and pterosphenoid [state 0; Fig. 20A; see also Hilton *et al.* (2007: fig. 10b), for illustration of ventral portion of joint]. Cleared and stained and radiographed individuals of *S. mormyrus* instead have a distinctly anteriorly concave posterior margin of that portion of the orbitosphenoid. Contact between the orbitosphenoid and the pterosphenoid is thus limited to separate areas of articulation situated ventral and dorsal to concavity (state 1; Fig. 20B). Although we lacked cleared and stained specimens of *S. axelrodi*, the anterior concavity of the posterior margin of the orbitosphenoid is obvious in radiographs of the large specimens and the species was coded as having state 1.

71. *Form of anterior margin of pterosphenoid*: (0) straight and abutting anterior margin of orbitosphenoid along its entire length; (1) concave and contacting orbitosphenoid only at dorsal and ventral limits of areas of contact of pterosphenoid and orbitosphenoid (CI = 1.000; RI = 1.000).

This character is associated with character 70. Outgroups to *Sternarchorhynchus* and all examined species of this genus other than *S. axelrodi* and *S. mormyrus* have a straight, vertical anterior margin of the orbitosphenoid (state 0; Fig. 20A). The cleared and stained specimens of *S. mormyrus* in contrast have a distinctly posteriorly concave anterior margin of the pterosphenoid. That concavity in conjunction with the adjoining concavity along the posterior margin of the orbitosphenoid results in a large foramen within the lateral region of the braincase. Contact of the pterosphenoid with the orbitosphenoid along the primitively continuous joint is as a consequence reduced to two separate areas of articulation; one situated dorsal to and the second ventral of the foramen (state 1; Fig. 20B). An identical posterior concavity of the anterior margin of the pterosphenoid (state 1) is obvious in radiographs of large individuals of *A. axelrodi*.

Apteronotus albifrons, *A. cuchillo*, and *'Apteronotus' apurensis* in the outgroups have a posteroventral extension of the pterosphenoid that contacts the posterior portion of the orbitosphenoid slightly above the point where that bone articulates with the parasphenoid. This process and a small anterior concavity on the orbitosphenoid jointly delimit a small transverse foramen that at first consideration might be considered homologous with the foramen discussed in the previous paragraph and under character 70 (see Hilton & Cox-Fernandes, 2006: fig. 4, for a comparable condition in *A. bonapartii*). The aperture in *A. albifrons*, *A. cuchillo*, and *'A.' apurensis* is positioned distinctly ventral of the opening in *S. axelrodi* and *S. mormyrus* and is formed by ventral extensions of the orbitosphenoid and pterosphenoid rather than by the main body of these bones such as is the case in *S. axelrodi* and *S. mormyrus*. These apertures are clearly nonhomologous with the foramen in the two species of *Sternarchorhynchus*.

72. *Anterior limit of anterior fontanel*: (0) extending anterior of anterior limit of orbitosphenoid; (1) falling short of anterior limit of orbitosphenoid (CI = 0.500; RI = 0.875).

Many ostariophysans including gymnotiforms have a median frontoparietal fontanel that is typically separated into anterior and posterior components by the transversely aligned epiphyseal bar. Variation in the extent of the anterior component of the fontanel delimited by the frontals is pertinent to the groups of interest. In both *Platyurosternarchus* and *Sternarchorhamphus* the frontal component of the fontanel system is proportionally elongate with the anterior limit of the aperture being situated anterior of the orbitosphenoid. This condition (state 0) is also present in the outgroups *Apteronotus* and *'Apteronotus'* along with *Sternarchella orthos* and *Sternarchogiton labiatus*. *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 10a) and *Sternarchorhynchus* species have less extensive frontal fontanels that fall distinctly short of the anterior limit of the orbitosphenoid (state 1).

PECTORAL GIRDLE

73. *Presence or absence of mesocoracoid*: (0) present; (1) absent (CI = 1.000; RI = 1.000).

The mesocoracoid is a relatively small, vertically elongate ossification running between the cleithrum dorsally and the region of the joint between the coracoid and scapula ventrally. The possession of a mesocoracoid is typical for gymnotiforms [e.g. species of *Gymnotus* (Albert & Miller, 1995: fig. 5; Albert *et al.*, 2005: fig. 16)] and this ossification is present in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 18b) and *Sternarchorhamphus muelleri*. A mesocoracoid is absent in *Platyurosternarchus* and *Sternarchorhynchus* and amongst the outgroups of immediate interest also in the species of *Apteronotus* and *'Apteronotus'* along with *Sternarchella orthos* and *Sternarchogiton labiatus* (state 1).

74. *Anterior extent of slender anteroventral process of coracoid*: (0) reaching to medial surface of cleithrum and terminating in small cartilage; (1) terminating anteriorly distinctly short of medial surface of cleithrum and with resultant gap filled by distinct cartilage mass (CI = 0.500; RI = 0.000).

The coracoid extends anteriorly as an elongate, typically anteriorly attenuating splint of bone amongst gymnotiforms. This condition similarly occurs in outgroups to *Sternarchorhynchus* examined in this study (Hilton *et al.*, 2007: fig. 18 for condition in *Orthosternarchus tamandua*). Anteriorly, this portion of the bone lies proximate to the medial surface of the cleithrum and is capped by at most a small cartilage body. This morphology of the coracoid process (state 0) also characterizes all *Sternarchorhynchus* species other than *S. britskii* and *S. caboclo*. In these two species there is a distinct gap between the anterior terminus of the anteroventral process and the proximate portion of the cleithrum (state 1). Filling that gap is an anteroposteriorly elongate cartilage much larger than the cartilage mass in that position in congeners. This character could not be coded for *S. axelrodi* based on radiographs of the available specimens.

POSTCLEITHRA AND PROXIMATE INDEPENDENT OSSIFICATIONS

Postcleithra are variably shaped, often flattened ossifications embedded in the superficial tissues of the body and positioned in part medial and more so posterior to the pectoral girdle, in particular the cleithrum. These elements occur broadly across within the Characiformes, albeit with zero to three postcleithra present in different families (comments by Vari, 1995: 26). Postcleithra are typically reduced to one element in the Cypriniformes and lost in the Siluriformes (Fink & Fink, 1981). Species of *Sternarchorhynchus* along with some other gymnotiforms have been reported to possess one or more postcleithra, but with these elements absent in some taxa within the order [e.g. *Sternopygus macrurus* (Lundberg & Mago-Leccia, 1986: fig. 8); *Electrophorus electricus* (Brousseau, 1976: 100)]. Nonetheless, positioning of ossifications termed postcleithra by diverse authors differs considerably across the Gymnotiformes; variation that raises questions as to the homology of some of those bones.

Amongst immediate outgroups to *Sternarchorhynchus*, we find that *Orthosternarchus tamandua* has a single large, plate-like postcleithrum partially overlapped by the pectoral girdle (Hilton *et al.*, 2007: fig. 18). This element and the ossifications in the species of *Platyurosternarchus* along with *Sternarchorhamphus muelleri* are positionally equivalent to the first postcleithrum in the Characiformes [e.g. *Brycon meeki* (Weitzman, 1962: fig. 18)] including the basal families Distichodontidae and Citharinidae (Vari, 1979: fig. 35). Ossifications located in this position in *Orthosternarchus* and *Sternarchorhamphus* are homologous with the first postcleithrum of other orders of the Ostariophysi. A comparable first postcleithrum is also present in *Sternarchorhynchus*, with the bone followed by one or more additional postcleithra in some species.

Diverse gymnotiforms have additional ossifications of uncertain homology located in the region anterodorsal to the first postcleithrum. The apteronotid genus *Adontosternarchus* bears three smaller, overlapping, longitudinally elongate ossifications in that area (Mago-Leccia *et al.*, 1985: fig. 6). A positionally homologous anteroposteriorly elongate ossification occurs in the basal gymnotiform genus *Gymnotus*. More pertinently, a subset of the species of *Sternarchorhynchus* have an anteroposteriorly elongate bone

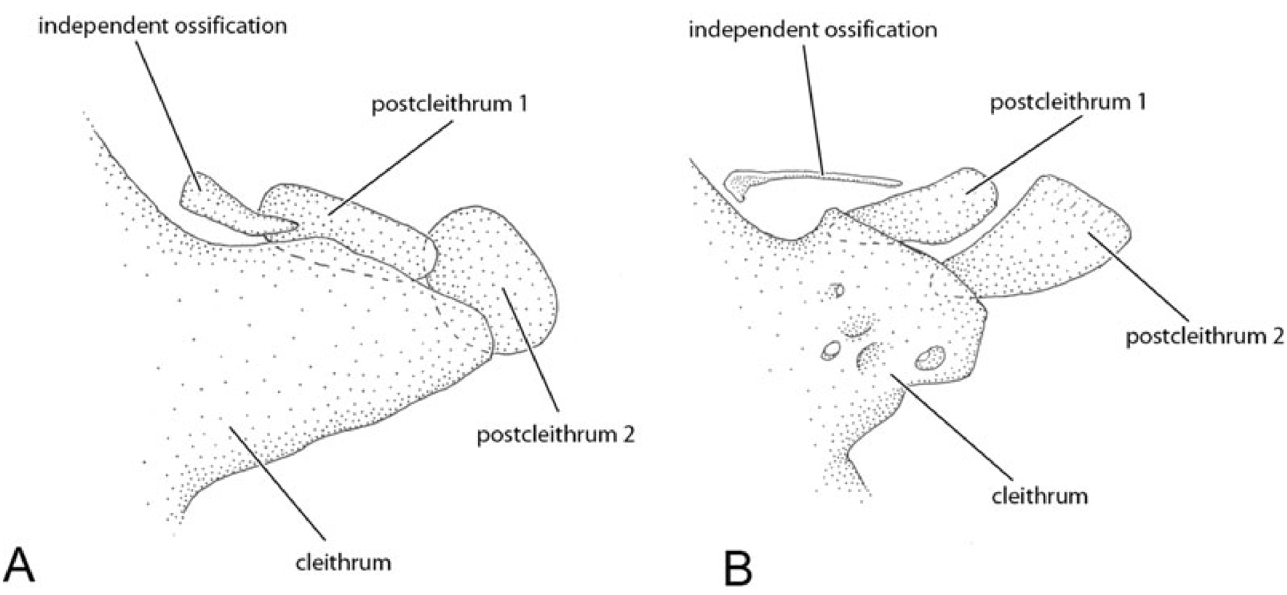

Figure 21. Posterior portion of cleithrum, postcleithra, and independent ossification in A, *Sternarchorhynchus hagedornae*, USNM 391574; and B, *Sternarchorhynchus mormyrus*, USNM 306843; left side, lateral view, anterior to left.

situated distinctly anterodorsal to the element that is positionally homologous with the first postcleithrum or the series of postcleithra in most groups in the Characiformes. The simultaneous presence in many gymnotiforms of one to three first postcleithra positionally homologous to those in many other ostariophysans plus these additional ossifications makes it clear that the more dorsally positioned bones in various species of *Sternarchorhynchus* are not postcleithra in terms of homology, notwithstanding their locations posterior to the cleithrum. This is likely to be the case with the bone or series of dorsally positioned bones present in some outgroup gymnotiforms.

For the purposes of the following discussion, we utilize a positional concept for postcleithra. The element partially overlapped by the posterior portion of the cleithrum is herein coded as the first postcleithrum in keeping with its positional equivalence to the ossification of that name in other ostariophysans [e.g. *Brycon meeki* (Weitzman, 1962: fig. 18)]. Sequentially posterior elements in that series are termed the second and third postcleithra. In light of this convention, the ossification(s) situated anterodorsal to the first postcleithrum in *Adontosternarchus*, *Gymnotus*, and some species of *Sternarchorhynchus* coded under character 75 are elements of uncertain homology.

75. *Presence or absence of ossification located in superficial tissues of body anterodorsal to first postcleithrum:* (0) absent; (1) present (CI = 0.167; RI = 0.615).

An independent ossification situated posterior of the cleithrum and anterodorsal to the first postcleithrum occurs in *S. axelrodi*, *S. britskii*, *S. chaoi*, *S. curvirostris*, *S. gnomus*, *S. goeldii*, *S. hagedornae*, *S. inpai*, *S. montanus*, *S. mormyrus*, *S. oxyrhynchus*, *S. severii*, and *S. starksi* (state 1; Fig. 21). Amongst the outgroup apteronotids examined in this study, this ossification is present in *'A.' apurensis*. No ossification occurs in this region (state 0) in the remaining *Sternarchorhynchus* species or in *A. albifrons*, *A. rostratus*, *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* in the outgroups.

Three ossifications identified as postcleithra were illustrated in the same general region by Mago-Leccia *et al.* (1985: fig. 8) in the apteronotid *Adontosternarchus devenanzii*. These bones differ in orientation and form from the ossification present in that area in some *Sternarchorhynchus* species. This makes it difficult to evaluate the possible homology between the elements in *Adontosternarchus* and the single bone present in some species of *Sternarchorhynchus.* As discussed above, in light of positional differences, we do not equate these ossifications with the postcleithra found in various gymnotiforms and characiforms. Furthermore, *Adontosternarchus* and *Sternarchorhynchus* are not close relatives (Albert, 2001) and the ossifications situated in the superficial tissues anterodorsal to the first postcleithrum even if homologous in those genera, nonetheless, demonstrate a homoplastic distribution.

76. *Form of ossification located anterodorsal to first postcleithrum*: (0) rounded or ovoid; (1) elongate (CI = 0.250; RI = 0.400).

When present, the independent ossification reported under character 75 has either of two forms in *Sternarchorhynchus* and other examined apteronotids. A rounded, ovoid, or slightly irregularly rectangular form of the bone (state 0; Fig. 21A) occurs in *S. chaoi*, *S. gnomus*, *S. hagedornae*, *S. inpai*, *S. montanus*, *S. severii*, and *S. starksi* and in the outgroup in *'A.' apurensis*. In contrast, an anterodorsally distinctly elongate form of the ossification (state 1; Fig. 21B) is present in *S. axelrodi*, *S. britskii*, *S. curvirostris*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus*. This ossification is absent and could not be coded in the remaining *Sternarchorhynchus* species examined osteologically along with *A. albifrons*, *A. rostratus*, *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* in the outgroups.

77. *Number of postcleithra*: (0) one postcleithrum; (1) two postcleithra; (2) three postcleithra (CI = 0.400; RI = 0.400).

A single postcleithrum (state 0), the first postcleithrum under the numbering system discussed above, is the only element of that series present in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 18) and *Sternarchorhamphus muelleri*. A second postcleithrum located posterior to the first postcleithrum is present in *Platyurosternarchus* and *Sternarchorhynchus* for a total of at least two postcleithra in these genera [states 1 (Fig. 20A, B) and 2]. Outgroups with a second postcleithra are *A. cuchillo*, *'A.' apurensis*, and *Sternarchogiton orthos*. *Sternarchorhynchus curvirostris*, *S. inpai*, *S. mendesi*, *S. mesensis*, and *S. roseni* have a third postcleithrum (state 2).

78. *Form of second postcleithrum*: (0) rounded or slightly longitudinally ovoid; (1) horizontally elongate (CI = 0.250; RI = 0.500).

The second postcleithrum is located immediately posterior of the first element in that series that is overlapped, in turn, by the posterior margin of the cleithrum. Two morphologies of the second postcleithrum occur within *Platyurosternarchus*, *Sternarchorhynchus*, and the other examined apteronotids bearing that ossification. In *P. crypticus*, *P. macrostoma*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus* the bone is horizontally elongate (state 1; Fig. 21B), whereas in all other species of *Sternarchorhynchus* the ossification is either round or only slightly longitudinally ovoid (state 0; Fig. 21A). An elongate morphology of the second postcleithrum (state 1) also occurs in *A. cuchillo* and *'A.' apurensis*. This character could not be coded for outgroups that lack a second postcleithrum or for *S. axelrodi* based on radiographs of the types.

WEBERIAN COMPLEX

79. *Form of intercalarium*: (0) transversely elongate; (1) rhomboidal or rectangular; (2) medially tapering and triangular overall (CI = 0.667; RI = 0.500).

The intercalarium is one of the set of ossicles within the pars auditum of the Weberian apparatus. These ossicles, along with associated soft tissues, the swimbladder, and components of the neurocranium are directly involved in the detection of sound in the water column. The intercalarium in gymnotiforms is a relatively small ossification located within the interosseus ligament that extends anterodorsally from the anterior tip of the tripus and then continues anteriorly to the scaphium (De La Hoz & Chardon, 1984: fig. 24, for illustration of arrangement in *Sternopygus macrurus*). Three morphologies of this ossification occur in *Platyurosternarchus*, *Sternarchorhynchus*, and the examined outgroup apteronotids. State 0, a transversely elongate form of the intercalarium, is limited to *P. crypticus* and *P. macrostoma* amongst examined taxa. In *Sternarchorhynchus* species with the exception of *S. mesensis* and *S. starksi* the intercalarium is overall rectangular or posteriorly narrower medially, but, nonetheless, extends a distinct distance medially along the axis of the interosseus ligament (state 1; Fig. 22A). A rhomboidal form of the ossification occurs in *A. cuchillo*, *'A.' apurensis*, *Orthosternarchus tamandua*, and *Sternarchorhamphus muelleri*. A rectangular morphology of the intercalarium is present in *A. albifrons*, *A. rostratus*, *Sternarchella orthos*, and *Sternarchogiton labiatus* (state 1). In *S. mesensis* and *S. starksi* the bone distinctly tapers medially to a point and has an overall triangular form when examined from a dorsal view (state 2; Fig. 22B). It was impossible to code this character for *S. axelrodi* from radiographs of the types.

80. *Form of tripus*: (0) progressively narrowing away from area of attachment to the centrum of the third vertebra and with relatively narrow distal tip; (1) not distinctly narrowing distally and relatively wide for distal half of bone (CI = 1.000; RI = 0.000).

The tripus, another of the set of ossicles within the pars auditum of the Weberian apparatus, progressively attenuates as it extends distally from its area of attachment on the centrum of the third vertebra both in outgroups to *Sternarchorhynchus* and most members of that genus (De La Hoz & Chardon, 1984: fig. 24, for illustration of comparable arrangement in *Sternopygus macrurus*). The distal portion of the tripus has an abrupt change in angle towards the midline in *Platyurosternarchus* and is more gradually angled in that direction in most species of *Sternarchorhynchus* (state 0; Fig. 22A). Regardless of the details of the morphology of that region of the tripus, the distal half of the ossification becomes progressively narrower and is quite narrow distally relative to the more anterior portions of the bone. This condition is also the case in the examined outgroups to the genus. In *S. mesensis* the distal half of the tripus is of approximately constant width and forms a wide overall process with a more obtuse distal tip. The width of the posterior portion of the tripus is approximately one-half that of the anterior region of the bone (state 1; Fig. 22B). Although the character is autapomorphic for *S. mesensis* amongst the species of *Sternarchorhynchus* included in this study, it may serve as a synapomorphy for a small subunit of the genus once additional species of the genus are included in the analysis. It was impossible to code this character for *S. axelrodi* based on radiographs of the types.

CAUDAL FIN

81. *Ossification of hypural plate*: (0) plate ossified; (1) plate cartilaginous (CI = 1.000; RI = 1.000).

An ossified hypural plate is common to both *Sternarchorhynchus* and *Platyurosternarchus*, whereas the plate is cartilaginous in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 17a) and *Sternarchorhamphus muelleri* [state 1; note: the specimen illustrated by Fink & Fink (1981) as *Sternarchorhamphus* with an ossified hypural plate is rather *P. crypticus*]. The plate is also ossified in other examined outgroup apteronotids, although with some specimens of *A. rostratus* having only a slightly developed ossification node in the central portion of what appears to be an otherwise cartilaginous plate. Other specimens of this species, in contrast, have a well-ossified hypural plate, with *A. rostratus* coded as having that condition (state 0).

SCALATION

82. *Scales along mid-dorsal region of body anterior to origin of electroreceptive filament*: (0) present; (1) reduced to some extent and sometimes largely absent (CI = 0.250; RI = 0.750).

The mid-dorsal region of the body in most gymnotiforms is scaled, albeit with scales sometimes sparse and hidden to varying degrees by the overlying skin (state 0). This condition is present amongst the outgroups in *A. albifrons*, *A. cuchillo*, and *A. rostratus.* Most examined species of *Sternarchorhynchus* similarly have the mid-dorsal region of the body anterior

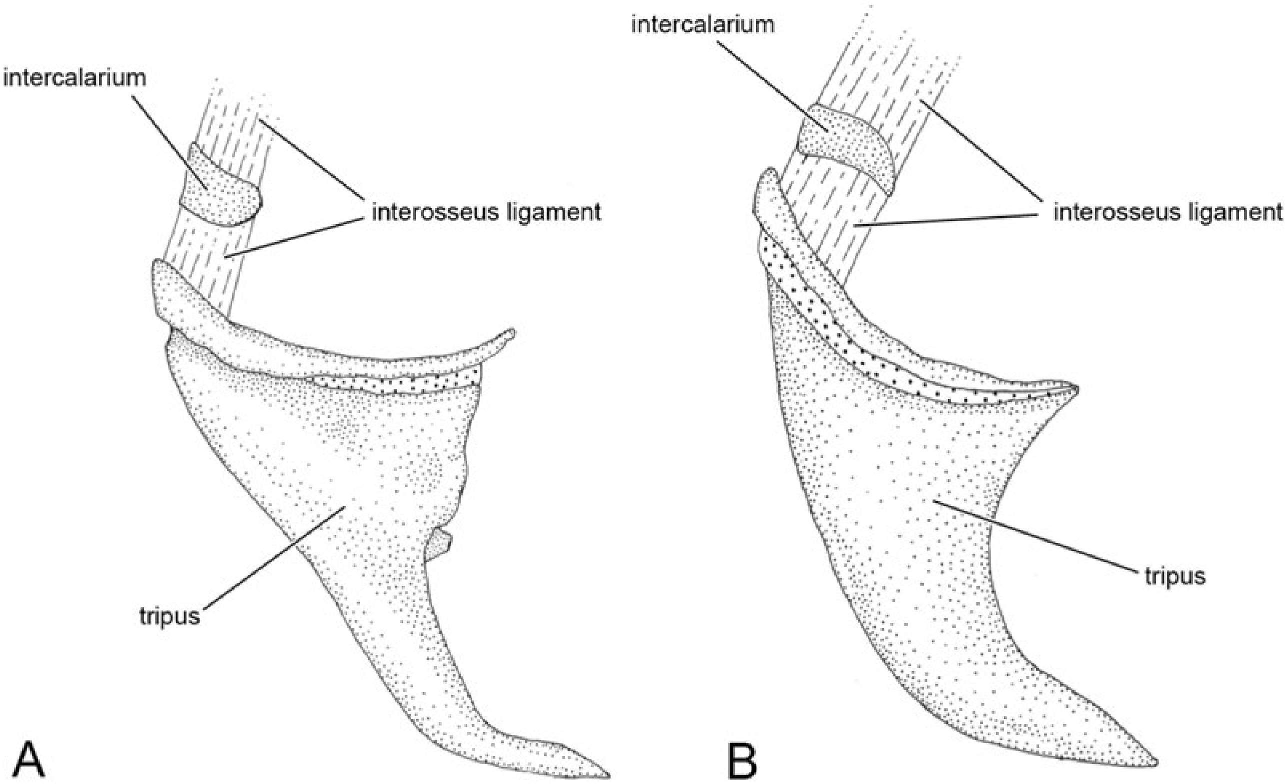

Figure 22. Tripus, intercalarium, and associated portions of interosseus ligament of A, *Sternarchorhynchus oxyrhynchus*, USNM 228787; and B, *Sternarchorhynchus mesensis*, MNRJ 13216; left side, dorsal view, anterior at top; dashed bands indicate ligament.

of the origin of the electroreceptive organ scaled (state 0). Scales are lacking in variably extensive portions of the mid-dorsal areas anterior to the origin of the electroreceptive that region of the body in *'A.' apurensis*, *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchella orthos*, *Sternarchogiton labiatus*, *Sternarchorhamphus muelleri*, *S. axelrodi*, *S. chaoi*, *S. goeldii*, *S. jaimei*, *S. mormyrus*, and *S. oxyrhynchus* (state 1).

83. *Degree of reduction of scaling along mid-dorsal portion of body anterior to origin of electroreceptive filament*: (0) scales absent along entire mid-dorsal region to origin of electroreceptive filament; (1) scales absent along mid-dorsal region only to region approximately at vertical through posterior margin of pectoral fin (CI = 1.000; RI = 1.000).

Sternarchorhynchus species and members of the outgroup with reductions in the scales along the mid-dorsal region of the body demonstrate two different degrees of that reduction. In *S. axelrodi*, *S. goeldii*, *S. mormyrus*, and *S. oxyrhynchus* along with the outgroups *'A.' apurensis*, *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, *Sternarchella orthos*, *Sternarchogiton labiatus*, and *Sternarchorhamphus muelleri* the scales are absent along the entire mid-dorsal region to the origin of the electroreceptive filament (state 0). *Sternarchorhynchus chaoi* and *S. jaimei* have less extensive reduction of the scale covering in the mid-dorsal region of the body, with the scales missing from the rear of the head approximately to the vertical through the posterior margin of the pectoral fin (state 1). This character was not coded for species that retain scales anterior by some degree to the electroreceptive filament origin, whether in the form of complete or sparse scaling.

84. *Degree of development of mid-dorsal scales when present along mid-dorsal portion of body anterior to origin of electroreceptive filament:* (0) scales well developed and obvious; (1) scales sparse and covered to different degrees by skin (CI = 0.500; RI = 0.667).

Species of *Sternarchorhynchus* that retain scales along the mid-dorsal region anterior of the origin of the electroreceptive filament vary in the degree to which the scales are present and readily obvious externally. Most species of the genus with a scaled mid-dorsal region (all species other than *S. hagedornae*, *S. higuchii*, *S. mendesi*, and *S. roseni*) have very obvious scales in that region (state 0). State 0 is also present in the outgroups in *A. albifrons*, *A. cuchillo*, and *A. rostratus*. In *S. hagedornae*, *S. higuchii*, *S. mendesi*, and *S. roseni* the mid-dorsal scales in the region anterior to the electroreceptive region, although present, are somewhat sparse and covered to varying degrees by skin (state 1). Given the presence of scales along at least part of the mid-dorsal area, this condition differs from the lack of scales in that region in characters 82 and 83. This character could not be coded for species lacking scales along the mid-dorsal region anterior to the electroreceptive filament (characters 82, 83).

COLORATION

85. *Presence or absence of narrow, mid-dorsal, lightly coloured stripe on head*: (0) mid-dorsal portion of head with pigmentation comparable to that of laterally adjoining regions or with pigmentation darker; (1) mid-dorsal region of head with narrow, mid-dorsal, lightly coloured stripe (CI = 0.333; RI = 0.833).

Immediate outgroups to *Sternarchorhynchus* (*Orthosternarchus*, *Platyurosternarchus*, *Sternarchorhamphus*) along with *Sternarchella orthos* and *Sternarchogiton labiatus* amongst more distant outgroups all have the coloration of the mid-dorsal portions of the head comparable to, or darker than, that of the laterally adjoining regions of the head (state 0). The majority of species of *Sternarchorhynchus* (state 1; Appendix 1), in contrast, have a narrow to very narrow, mid-dorsal, distinctly more lightly coloured stripe extending from, or proximate to, the tip of the snout posteriorly to at least the interorbital region and sometimes further posteriorly on the head (state 1). Some species with such a stripe have that pigmentation pattern continuous with a comparable mid-dorsal stripe along the body that extends to varying degrees posteriorly towards, or sometimes beyond, the origin of the electroreceptive filament. Amongst the outgroups, such a mid-dorsal lightly coloured stripe (state 1) is also present in *A. albifrons*, *A. cuchillo*, and *A. rostratus.* Two species of *Sternarchorhynchus*, *S. britskii* and *S. mesensis*, were reported to have only an indistinct mid-dorsal stripe on the snout in certain individuals (Campos-da-Paz, 2000), but these species are coded as state 1 in light of the presence of the stripe to some degree in the material of these species examined in this study.

86. *Presence or absence of narrow, lightly coloured stripe on lateral surface of snout*: (0) lateral surface of snout with pigmentation comparable to that of adjoining regions or with irregular marbling; (1) lateral surface of snout with distinct, more lightly coloured band (CI = 0.333; RI = 0.857).

All examined apteronotid outgroups to *Sternarchorhynchus* have uniform coloration of the lateral surface of the snout or when the pigmentation in this region is non-uniform it is marbled or otherwise irregular (state 0). Such uniform pigmentation along the snout is common to *S. curvirostris*, *S. goeldii*, *S. oxyrhynchus*, *S. roseni*, and *S. starksi*. In contrast, *S. axelrodi*, *S. britskii*, *S. caboclo*, *S. chaoi*, *S. cramptoni*, *S. curumim*, *S. gnomus*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. mareikeae*, S. *mormyrus*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. retzeri*, *S. severii*, and *S. stewarti* have a distinct, more lightly coloured band extending along the lateral surface of the snout in the region anterior to the eye and sometimes continuing nearly to the tip of the snout (state 1).

87. *Presence or absence of dark coloration along basal portion of anal fin*: (0) fin hyaline to slightly dusky overall, but lacking distinct band of dark pigmentation basally; (1) fin hyaline to slightly dusky overall, with distinct band of dark pigmentation basally (CI = 1.000; RI = 0.000).

Anal fin coloration in *Sternarchorhynchus* ranges from hyaline to somewhat dusky overall, but most species of the genus along with all outgroups in this analysis lack a band of distinctly darker pigmentation extending along the basal portion of the fin (state 0). Such a band of dark, basal pigmentation on the anal fin is limited to *S. curvirostris* amongst species of the genus (state 1). Although autapomorphic for this species in this analysis, we included this feature because future analyses may find it to be more broadly distributed with the inclusion of additional species.

Triques (2005) proposed that dark coloration of the caudal peduncle and adjoining regions was synapomorphic for a clade formed by *Platyurosternarchus*, *Sternarchorhynchus*, and *Ubidia*. This pigmentation is rare amongst the species of *Sternarchorhynchus*. As discussed under the framework for outgroup comparisons, the caudal pigmentation of *Platyurosternarchus* and *Ubidia* differs in various details with the coloration of the latter genus more similar to that of a subunit of *Apteronotus*.

88. *Presence or absence of dark coloration along distal portions of anal fin*: (0) fin hyaline to slightly dusky overall, but lacking distinct band of dark pigmentation along distal portion of fin; (1) fin hyaline to slightly dusky overall, and with distinct band of dark pigmentation distally (CI = 0.167; RI = 0.375).

Anal fin coloration in preservative in *Sternarchorhynchus* ranges from hyaline to somewhat dusky overall, but most species in the genus along with *A. albifrons*, *A. cuchillo*, *A. rostratus*, *Orthosternarchus tamandua*, *P. crypticus*, and *P. macrostoma* lack a band of distinctly darker pigmentation along the distal margin of the anal fin (state 0). *'Apteronotus' apurensis* and *Sternarchorhamphus muelleri* in the outgroups together with *S. axelrodi*, *S. camptoni*, *S. goeldii*, *S. montanus*, *S. mormyrus*, *S. oxyrhynchus*, and *S. retzeri* have instead a distinct band of dark pigmentation along the distal portions of the anal fin (state 1). This darkly pigmented band covers one-fifth to one-half of the distal portions of much of the anterior and middle anal-fin rays and in some instances all, or nearly all, of the posterior rays of the fin. The dark coloration on the anal fin in the species of *Platyurosternarchus* is limited to the posteriormost portion of the fin and extends to the base of the involved fin rays (de Santana & Vari, 2009); a very different and thus nonhomologous pattern.

Sternarchorhynchus roseni demonstrates variation in the presence or absence of dark pigmentation on the anal fin, with the presence of such coloration correlated with the possession in mature males of an anteriorly expanded dentary with enlarged dentition. This correlation raises the possibility that the presence of dark pigmentation is a seasonal, sexually dimorphic feature for males and we consequently code *S. roseni* as unknown for this character.

DISCUSSION

PHYLOGENETIC RECONSTRUCTION AND KEY INNOVATIONS

Twenty-four nodes were resolved in the phylogenetic analysis for, and within, the clade formed by *Platyurosternarchus* plus *Sternarchorhynchus* (clade numbering in Fig. 23). Reconstructed relationships amongst the outgroup taxa in this study beyond the hypothesis of a sister-group relationship between *Platyurosternarchus* and *Sternarchorhynchus* should not be viewed as well-supported phylogenetic hypotheses and support for those portions of the phylogeny is not detailed on the cladogram. The potential uncertainty in outgroup relationships is derivative of several limitations with the underlying data. Taxon sampling amongst apteronotids outside of *Platyurosternarchus* and *Sternarchorhynchus* was of necessity sparser than within those genera that were the subject of in-depth analyses by, respectively, de Santana & Vari (2009) and herein. Notwithstanding the fact that some characters were incorporated into the analysis in order to provide structure to the outgroup phylogeny, we did not search for new characters informative about relationships amongst and within the outgroup taxa incorporated into this study. Characters previously reported in the literature as informative about relationships within the Apteronotidae were typically excluded from this analysis unless germane to the core questions phylogenetic addressed in the study. The evidence for the sister-group relationship between *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri* arrived at herein does, however, conform with the hypotheses advanced by Campos-da-Paz (1995) and various subsequent authors.

The results strongly support the hypothesis of a sister-group relationship between *Platyurosternarchus* and *Sternarchorhynchus* advanced by authors starting with Albert & Campos-da-Paz (1998), albeit

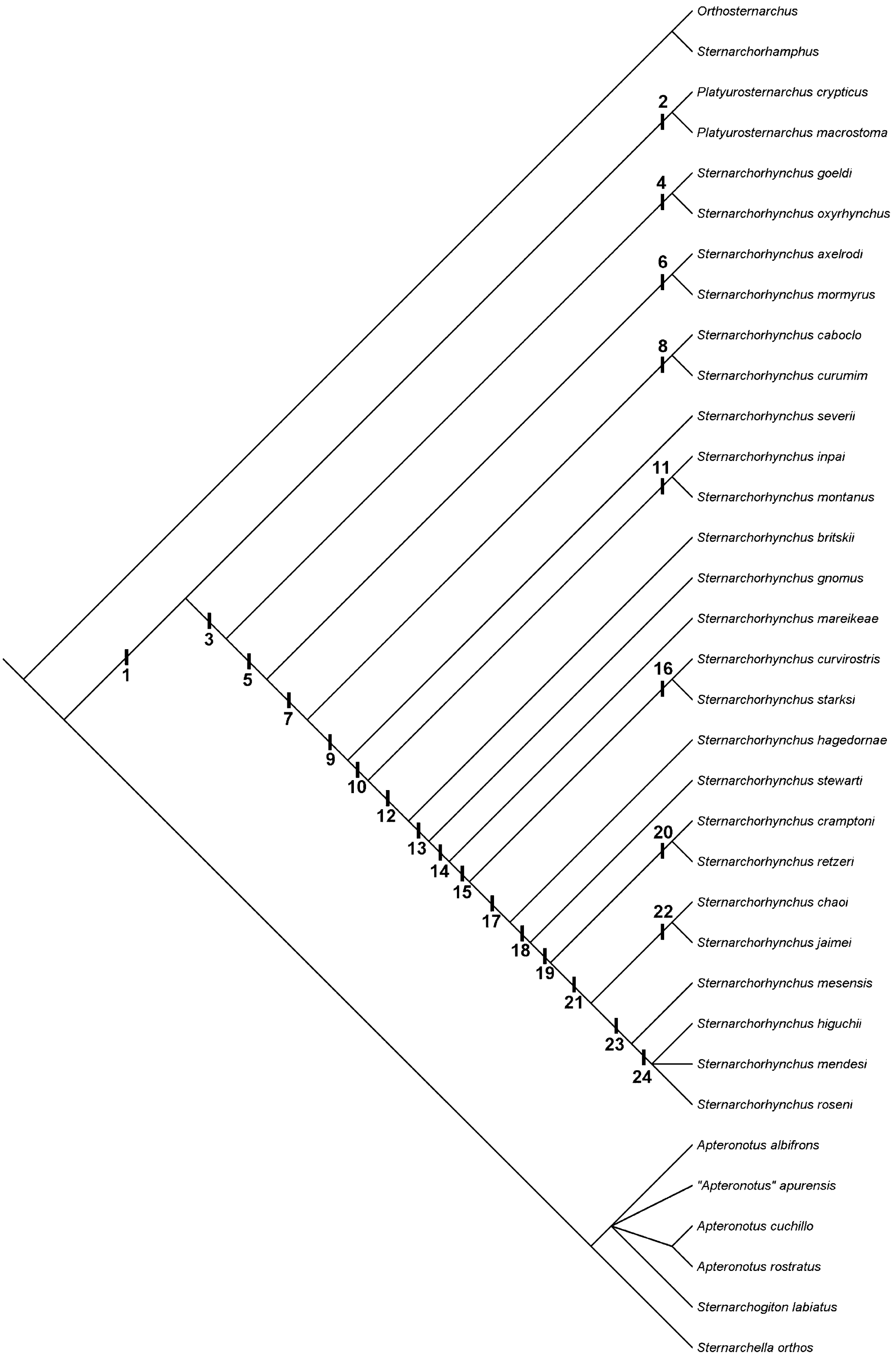

Figure 23. Strict consensus of eight most parsimonious trees generated in PAUP*, length = 193, consistency index (CI) = 0.477, and retention index (RI) = 0.814, with all branches of zero maximum length collapsed and all characters unordered. Each of the most parsimonious trees has length = 190, CI = 0.484, and RI = 0.820. Synapomorphies only mapped for and within clade consisting of *Platyurosternarchus* and *Sternarchorhynchus*.

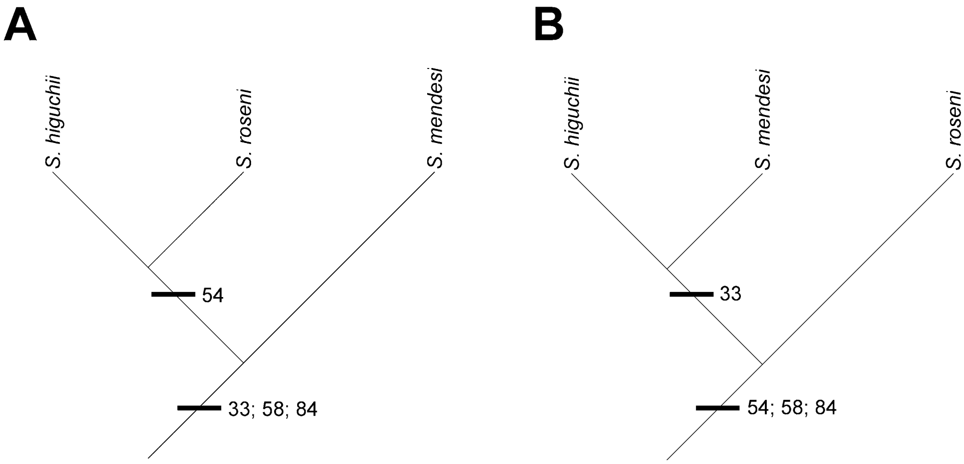

Figure 24. Two alternative topologies of species within clade 24 with characters mapped under ACCTRAN optimization.

with some differences in the underlying evidence (see Synapomorphy list in Appendix 2 for details). Several of the synapomorphies common to those two genera are of particular note in being unambiguous modifications unusual not only within the Apteronotidae but in some instances across the Gymnotiformes. Striking from that perspective are the restructuring of the posterior portion of the anguloarticular (character 17), the very distinct constriction of the medial portion of the fourth ceratobranchial (character 61), the well-ossified fourth infrapharyngobranchial (character 62), and the absence of the lateral ethmoid (character 68). The results of this study and those of de Santana & Vari (2009) also support the hypothesis of the monophyly of *Platyurosternarchus*. A number of the derived modifications at the level of *Platyurosternarchus* similarly involve the jaws and dentition. These include the absence of teeth on premaxilla (character 4), and the attachment of teeth to the exterior surface of the dentary (character 20).

Of particular note within the clade formed by *Platyurosternarchus* plus *Sternarchorhynchus* are the extensive series of synapomorphies for *Sternarchorhynchus* (Synapomorphy list in Appendix 2 for details), with a high percentage (77%) of the 27 characters informative as to the monophyly of *Sternarchorhynchus* being unambiguous characters uniquely derived at the level of the genus. These numerous synapomorphies are by far the greatest number of such features defining any genus within the Gymnotiformes (Albert, 2001, for other genera). Seven of the 27 synapomorphies for *Sternarchorhynchus* involve restructurings of components of the jaws (character 5, the form of the maxilla; character 9, the reduction of the coronomeckelian bone; character 10, the reduction of Meckel's cartilage; character 11, the relative development of the posterodorsal and posteroventral processes of the dentary; character 12, the form of the posteroventral process of the dentary; character 15, the position on the lower jaw of the articular facet contacting the quadrate; and character 16, the form of the anterior portion of the anguloarticular). Seven additional synapomorphies for *Sternarchorhynchus* involve alterations of the suspensorium so that it can be accommodated in the vertically constricted tubular snout or are correlated with the remodelling of components of the jaws (character 21, the reduction of the anterior portion of the palatoquadrate cartilage; character 22, the shift ventrally in the relative position of the endopterygoid; character 23, the reduction of the anterior portion of the endopterygoid; character 24, the reduction of the posterior portion of the endopterygoid and the closer association or fusion of that ossification with the quadrate; character 28, the loss of the dorsal portion of the quadrate; character 35, the shift of the posterior limit of the posteroventral portion of the quadrate; and character 38, the horizontal elongation of the metapterygoid). Except for character 11, none of these modifications was manifested within the examined outgroups. Of the restructurings of the neurocranium at this level of the phylogeny, one synapomorphy (character 67, the increase in the proportional distance from the tip of the mesethmoid to the vertical through the posteriormost limit of that bone) is clearly correlated with the dramatic proportional elongation of the snout characteristic of *Sternarchorhynchus*. These 15 modifications of the jaws, suspensorium, and anterior portion of the neurocranium all correlate with the distinctive form of the jaws, snout, and associated soft tissue systems that permit grasp-suction or suction assisted by mechanical grasping in the species of *Sternarchorhynchus* (comments under Adaptive radiation in the next section).

The synapomorphies for *Sternarchorhynchus* that are heavily weighed towards modifications of the jaws, suspensorium, anterior portion of the neurocranium, and associated systems are recognized herein as key innovations [i.e. special set of characteristics – *sensu* Liem (1973), Lauder (1981)] within a comparative phylogenetic framework as proposed by Stiassny & Jensen (1987). The concept of key innovation has been used in diverse fashions, usually focusing on attributes purported to account for the success for a lineage in any of several ways, including species richness and morphological diversity. Herein we focus on species richness resultant from morphological modifications, specifically asymmetrical divergence in species numbers between *Platyurosternarchus* and *Sternarchorhynchus* following the criterion of Guyer & Slowinski (1993).

That being said, there remains controversy on the issue of whether key innovations serve as triggers of diversification (e.g. Cracraft, 1990) and it is difficult to test for such features (Hodges, 1997). One difficulty with the discussion of key innovations is the lack of a standard to assess diversity and species richness (Jensen, 1990). Jensen (1990) reviewed the process for historical testing for key innovations. Historical testing uses convergence to search for independent corroboration of hypotheses relating evolutionary novelties with phylogenetic patterns (Jensen, 1990). That author proposed that historical testing must be a two-step process. The first step involves a comparison of the species diversity of a taxon exhibiting a proposed key innovation or innovations with that of its sister group. Following that is the comparison of sister groups in independent lineages in which an identical novelty has evolved. This ascertains whether comparable disparate patterns of species richness occur in each of the independent lineages.

In the present study, the first step involves a comparison of species diversity of *Sternarchorhynchus* versus *Platyurosternarchus.* The second step is a comparison of the species richness in the two genera of freshwater fishes in which grasp-suction feeding has been reported (*Sternarchorhynchus* and the African electric fish genus *Campylomormyrus*), versus their sister taxa (*Platyurosternarchus* and *Gnathonemus*, respectively) neither of which demonstrates that feeding system (for further information on the species diversity and relationships amongst Mormyriformes genera see Moller, 1995; Sullivan, Lavoué & Hopkins, 2000; Feulner *et al.*, 2007).

In both the South American and African lineages, the groups in which grasp-suction feed mode has evolved (*Sternarchorhynchus* with 32 species and *Campylomormyrus* with 14-plus species) are more diverse than are sister taxa that do not demonstrate that mode of feeding (*Platyurosternarchus* with two species and *Gnathonemus* with five species, respectively; for further details see Adaptive radiation and Convergence in elongation of snout sections). *Campylomormyrus* is forecast to be even more diverse than presently recognized (Feulner *et al.*, 2007). This consistent pattern of relative species richness between *Sternarchorhynchus* and *Campylomormyrus* versus their sister groups satisfies the second criterion advanced by Jensen (1990). We thus propose that the various synapomorphies for *Sternarchorhynchus* noted above, in particular the restructuring of components of the jaws, suspensorium, and anterior portion of the neurocranium that permit the grasp-suction feeding as likely key innovations linked to the adaptive radiation within that genus.

Looking at the distribution of synapomorphies of and within *Sternarchorhynchus*, particularly of uniquely derived features, we find a remarkable asymmetry in the occurrence of these attributes across the phylogeny of the genus (Fig. 23). Clades 1 to 7 in *Sternarchorhynchus* involve 39 such synapomorphies contrary to the presence of only one uniquely derived synapomorphy across clades 8 to 24. The pronounced loading of these characters at the basal levels within the clade formed by *Platyurosternarchus* and *Sternarchorhynchus* correlates with a number of novel modifications of various body systems at these levels. These potential key innovations particularly load at the level of clade 3 where they involve the synapomorphies for the species of *Sternarchorhynchus* associated with capture and initial processing of prey items. Such loading of major modifications applies, albeit to a lesser extent, at the level of other basal clades within that genus (clades 4 to 7), all of which are defined by multiple synapomorphies. With few exceptions, clades 8 to 24 are instead defined by single homoplastically distributed synapomorphies that involve aspects of the feeding system. The underlying cause of this pattern of synapomorphy distribution is impossible to discern from the morphological data, nor is relative timing of cladogenesis determinable in the absence of any benchmark vicariance events that provide a temporal context to the phylogeny. One explanation involves rapid speciation at less inclusive levels within the phylogeny of the genus. Such a clustering of modifications at the basal clades is congruent with expectations under the hypothesis of adaptive radiation (Foote, 1997; Schluter *et al.*, 1997; Schluter, 2000; also comments under Adaptive radiation below).

Having arrived at a series of innovations that permit the very unusual, albeit clearly highly functional, grasp-suction feeding mode at the level of *Sternarchorhynchus* (clade 3), there followed less dramatic modifications of the jaws, suspensorium, and gill arches at basal levels within the genus. Clade 4, consisting of *S. goeldii* and *S. oxyrhynchus*, is characterized by several unique distinctive modifications of these body systems (character 1, the mouth length; character 6, the reduction of the anterior portion of the maxilla; character 8, the presence of a fleshy, dorsally directed pad at the anterior margin of the dentary; character 25, the fusion of the quadrate and endopterygoid; character 30, the lateral expansion of the posterolateral portion of the quadrate; and character 39, the lateral expansion of the anterolateral portion of the metapterygoid). In sum, these result in a mouth form unique to *S. goeldii* and *S. oxyrhynchus* within *Sternarchorhynchus*. Presumably, these modifications correlate with different diets or modes of prey capture in these species versus their congeners. Unfortunately, the limited detailed available information on feeding habits in, and prey items of, the species of *Sternarchorhynchus* precludes a test of this hypothesis at this time.

Clade 5, the sister lineage to clade 4, includes all species of *Sternarchorhynchus* with the exception of *S. goeldii* and *S. oxyrhynchus.* Clade 5 is characterized by fewer unique features that clearly involve the feeding system and the elongate snout than is clade 4 (character 7, the position of the posterior limit of the dentary; character 59, the anterior extension from the main body of the second hypobranchial; character 66, the presence of a scythe-shaped process on the lateral margin of the ventral ethmoid). Clade 7, in turn, has two unique synapomorphies associated with the jaws and suspensorium (character 3, the compact form of the premaxilla; character 29, the concave dorsal margin of the quadrate). The remaining clades (8–24) either lack or have only homoplastically distributed synapomorphies associated with the food acquisition and initial processing systems and the associated elongate preorbit. The lack of further substantive modifications of the jaws, suspensorium, and anterior portion of the neurocranium at, or within, clade 8 is likely to reflect functional constraints of those portions of the head by the key innovations present at the levels of the more inclusive clades (3, 5, 7).

As would be expected, the Bremer support values [Treerot V.2C (Sorenson, 1999); 20 replicates and 10 000 trees] parallel the same pattern of asymmetry in the distribution of nonhomoplastic synapomorphies discussed above. Clade 1 (*Platyurosternarchus* plus *Sternarchorhynchus*) has a Bremer value of 4. Within that clade, *Platyurosternarchus* (clade 2) has a value of 2, whereas *Sternarchorhynchus* (clade 3) with many more synapomorphies has a value of 20. Less inclusive basal clades and their values are: clade 4, Bremer support 8; clade 5, Bremer support 4; clade 6, Bremer support 5; and clade 7, Bremer support 5. The remaining clades in the phylogeny (8–24) all have low support values of 1 other than for clade 20, which has a value of 2.

The overall pinnate form of the phylogeny at the level of *Platyurosternarchus* and *Sternarchorhynchus* and the asymmetrical distribution of the number of species across the phylogeny (Fig. 23) evokes the phenomenon discussed by Stiassny & de Pinna (1994), who documented instances in which basal taxa within lineages are proportionally depauperate in numbers of species relative to their sister groups. As discussed previously, key innovations are a potential basis for the species richness within *Sternarchorhynchus*. The underlying cause for the relatively depauperate situation in *Platyurosternarchus* is unknown, but some authors (Brooks and McLennan, 1991; Hodges, 1997) have proposed that such clades may possess attributes that constrain diversification. Stiassny & de Pinna (1994) also commented that basal taxa in pinnate phylogenetic schemes often have geographically extremely constricted distributions. The broad distribution of *P. macrostoma* in the immediate outgroup along with the extensive ranges of *S. goeldii* in the Amazon basin and of *S. oxyrhynchus* of the Río Orinoco system of the basal clade within *Sternarchorhynchus* run counter to the pattern highlighted by those authors. Although the distribution of *S. goeldii* and *S. oxyrhynchus* (Figs 42, 63) is more restrictive than the broader Amazon basin, the river systems of the Guyanas, and the upper Rio Paraná inhabited by their congeners, the distributional ranges of these two species that constitute the sister clade to all other species of *Sternarchorhynchus*, nonetheless, cover significant portions of the overall distribution of the genus.

ADAPTIVE RADIATION

The various forms of the snout and jaws in diverse groups of gymnotiforms are associated with differences in the diet and accessibility of certain food items. Restructurings of the bones, musculature, and other soft tissues of the anterior portions of the neurocranium and jaws (Aguilera, 1986) in *Sternarchorhynchus* permit the extraction of prey items from constricted refuges in compacted clay masses, decaying wood, debris, and mud on river bottoms. These dramatic restructurings are proposed above as potential key innovations that facilitate 'grasp-suction' or 'suction assisted by mechanical grasping' in the members of the genus. In that system, food items are first mechanically removed from the constricted refuges favoured by potential prey by pincer-like manipulations of the small toothed jaws and then drawn into the oral cavity via suction. Marrero & Winemiller (1993) and Winemiller & Adite (1997) pointed out that this very unusual, highly specialized feeding mode is unique to *Sternarchorhynchus* and the African mormyriform genus *Campylomormyrus* amongst those orders of fishes entirely restricted to freshwaters. Paralleling this functional similarly is the fact that *Campylomormyrus* is a strikingly speciose member of the Mormyridae (Feulner *et al.*, 2007); a situation comparable to that of *Sternarchorhynchus* within the Apteronotidae. Feulner *et al.* (2007) proposed that the phenomenon of high numbers of species represents an adaptive radiation within *Campylomormyrus*. Does that phenomenon also apply to *Sternarchorhynchus*?

In his discussion on key innovations in cichlids, Liem (1973) noted that Mayr (1960) and Bock (1965) suggested that adaptive radiations of organisms would not occur until the evolutionary novelty reached a certain degree of stability or development. The features recognized as key innovations of *Sternarchorhynchus* were primarily acquired at the level of clade 3 and achieved a degree of stability at clade 8. More recently, Schluter (2000) defined adaptive radiation as the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. Schluter proposed four criteria that characterized that phenomenon: origin from a common ancestor, rapid speciation, a correlation between environment and phenotype, and trait utility.

Common ancestry

The hypothesis of the monophyly of *Sternarchorhynchus* is supported by a series of synapomorphies thereby filling the first of the criteria proposed by Schluter (2000).

Rapid speciation

Rates of speciation are difficult to determine in the absence of any evidence (i.e. detailed fossil record or appropriate molecular data) that permits calibration of the age of the different lineages; however, the pronounced disparity between the two species within *Platyurosternarchus* (de Santana & Vari, 2009) and the minimum of 32 species within *Sternarchorhynchus* (see also comments under Possible additional undescribed species) confirm significantly different rates of speciation and/or extinction between these genera. No evidence of extinction exists for *Platyurosternarchus*, the two members of which are morphologically quite similar. That fact plus the broad range of *P. macrostoma* across the Amazon, Orinoco, and Essequibo river basins is congruent with the hypothesis of a minimal degree of speciation within *Platyurosternarchus*. Regardless of this issue, *Sternarchorhynchus* demonstrates a significantly accelerated rate of speciation over its sister clade as evidenced by the disparity in the number of species in each genus [two species of *Platyurosternarchus* (de Santana & Vari, 2009) versus 32-plus species of *Sternarchorhynchus* (results herein); also comments in Stiassny & Jensen (1987) concerning the need to evaluate concepts such as species richness in a phylogenetic context]. At least some of the studies focused on patterns of morphological divergence within clades in the fossil record have demonstrated that morphological disparity typically is maximized towards the base of the clade with that phenomenon followed by an increase in the diversity of species (Foote, 1997). The pattern highlighted by Foote (1997) is well manifested in the *Platyurosternarchus–Sternarchorhynchus* lineage, wherein the basal lineages are characterized by the possession of a disproportionate percentage of the derived morphological modifications known across that lineage. Within *Sternarchorhynchus* this is followed by a dramatic increase in species richness in clades that demonstrate relatively little pronounced morphological restructurings in the examined body systems.

Phenotype–environment correlation and trait utility

A correlation between environment and phenotype as typified by phylogeny is clear in some of the basal clades within the genus (comments at beginning of Discussion above). Different forms of the mouth in *Platyurosternarchus* versus *Sternarchorhynchus* and within basal lineages of the latter genus can be assumed to reflect different feeding regimes permitting exploitation of specific food resources; a difference fitting the criterion of trait utility. The most conspicuous phenotypic differences amongst species of *Sternarchorhynchus* involve snout size and shape; more specifically differences in the proportional length, vertical height, transverse width and degree of central curvature of the snout. To date we lack the necessary information on feeding behaviours and dietary preferences to engage in a rigorous test of the hypothesis of phenotype–environment correlation and trait utility. Nonetheless, the overall evidence indicates that adaptive radiation is a driving mechanism that accounts to some unspecified degree for the speciose nature of *Sternarchorhynchus* relative to other genera of the Apteronotidae. Further analysis incorporating data from life history studies of all species in *Sternarchorhynchus* evaluated within a phylogenetic analysis is necessary to test this hypothesis.

CONVERGENCE IN ELONGATION OF SNOUT

Elongate preorbital regions of the head (= snout) are manifested in two units of the Gymnotiformes; the Apteronotidae (*Compsaraia*, *Orthosternarchus*, *Platyurosternarchus*, *Sternarchorhamphus*, *Sternarchorhynchus*, and some species of *Apteronotus*) and the Rhamphichthyidae (*Gymnorhamphichthys* and *Rhamphichthys*). In addition, both the Apteronotidae and Rhamphichthyidae include numerous species lacking comparable elongations of the preorbital portion of the head. The extension of the snout in subunits of the two families is clearly convergent under present concepts of phylogenetic relationships within the Gymnotiformes (Albert & Campos-da-Paz, 1998; Albert, 2001).

Focusing on the Apteronotidae, the very different forms of the elongation of the anterior region of the head in *Compsaraia* and *Apteronotus* relative to the snout morphology in *Sternarchorhynchus* brings to the fore questions as to the equivalence of the preorbital expansion in these taxa (Cox-Fernandes *et al.*, 2002: fig. 1; and Hilton & Cox Fernandes, 2006: fig. 1, relative to the species of *Apteronotus*; and Mago-Leccia, 1994: fig. 90, for *Compsaraia compsus* identified as *Porotergus compsus* therein). More significantly, neither *Compsaraia* nor the species of *Apteronotus* with elongate preorbital regions are closely related to *Sternarchorhynchus* (Albert, 2001; Crampton & Albert, 2006; results of this study). Thus, the elongate snouts in these other apteronotid taxa are convergent with the lengthened preorbital portion of the head characteristic of *Sternarchorhynchus*.

Elongation of the preorbital region was proposed by Albert & Campos-da-Paz (1998) and Albert (2001) as a feature supporting a clade within the Apteronotidae consisting of *Orthosternarchus*, *Platyurosternarchus*, *Sternarchorhamphus*, and *Sternarchorhynchus*. More recently, Hilton *et al.* (2007) revisited this issue and highlighted the fact that although these four genera share an elongate preorbital region, the mode of lengthening derives from different underlying morphological modifications in *Orthosternarchus* and *Sternarchorhamphus* on the one hand versus *Platyurosternarchus* and *Sternarchorhynchus* on the other. These differences manifest themselves most clearly in the degree of proportional development of the jaws that is best reflected in the relative position of the articulation of the lower jaw with the suspensorium.

Hilton *et al.* (2007) noted that the joint of the lower jaw with the articular condyle of the quadrate is positioned distinctly further posteriorly in both *Platyurosternarchus* and *Sternarchorhynchus* (Fig. 25B for position of joint in latter genus) than is the case in *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri*. The combination of a posterior position of the joint and an elongate snout is achieved by pronounced proportional longitudinal elongation of various elements of the lower jaw (dentary, anguloarticular, Meckel's cartilage at least in juveniles) in *Platyurosternarchus* (Fig. 5) and *Sternarchorhynchus* (Figs 6, 7) relative to corresponding elements in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 12) and *Sternarchorhamphus muelleri* (Campos-da-Paz, 1995: fig. 5). Snout elongation in *Orthosternarchus tamandua* (Hilton *et al.*, 2007: fig. 11) and *Sternarchorhamphus muelleri* in which the lower jaw–quadrate joint is anteriorly positioned is in large part a function of anteroposterior elongation of elements posterior of the lower jaw–quadrate joint; most notably the preopercle, interopercle, and subopercle. Expansions of these ossifications in *Orthosternarchus* and *Sternarchorhamphus* contrasts with the more typical apteronotid morphology of these bones in *Platyurosternarchus* and *Sternarchorhynchus*.

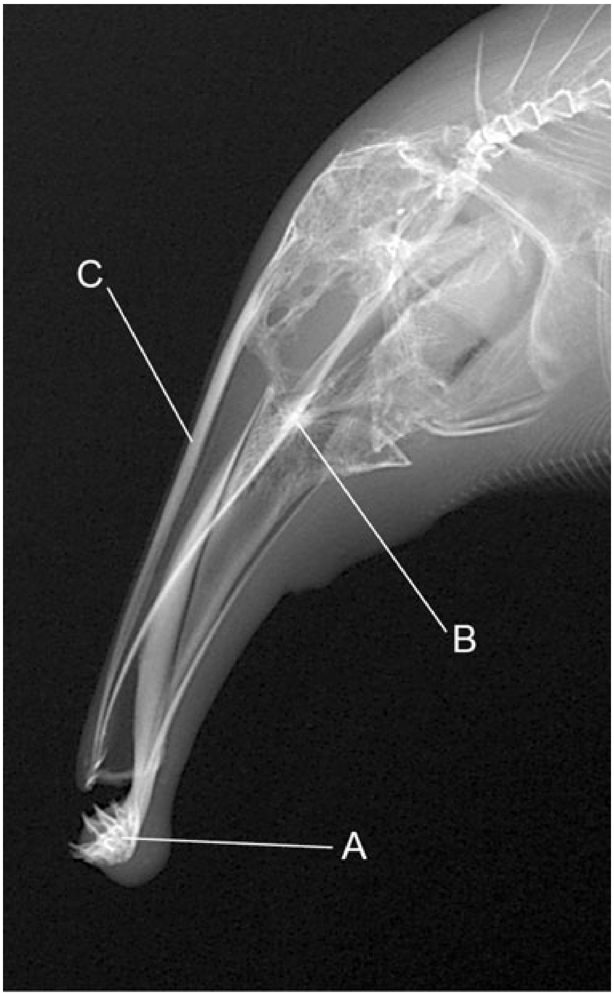

Figure 25. Radiograph of head and snout of *Sternarchorhynchus yepezi*, holotype, MCNG 44286; showing A, expanded portion of dentary and elaboration of associated dentition in sexually dimorphic males; B, point of articulation between quadrate and lower jaw; and C, elongate mesethmoid.

Preorbital elongation results from restructuring of two different systems in the species of *Platyurosternarchus* and *Sternarchorhynchus* (the anteroposterior elongation of the components of the lower jaw and anterior portions of the suspensorium) versus *Orthosternarchus tamandua* and *Sternarchorhamphus muelleri* (the anteroposterior elongation of the posterior portion of the suspensorium and some elements of the opercular series). The lengthening of the snout in these two lineages is thus patently nonhomologous, notwithstanding the external similarities in that region in the head.

Differences also occur in the mode of preorbital elongation and in particular in the morphology of the jaws in *Sternarchorhynchus* versus its sister group, *Platyurosternarchus*. Although members of each genus have what could be considered to be elongate preorbital regions, the mouth in *Platyurosternarchus* is relatively elongate, forming 30.0–37.9% of the HL (de Santana & Vari, 2009), whereas it is reduced in the species of *Sternarchorhynchus* to a small opening achieving a maximum of 12.4% of the HL in those species with longer mouths.

Looking at the underlying bones, we find that the modifications associated with the elongation of the snout in *Sternarchorhynchus* are unique to that genus, not being approximated in *Platyurosternarchus* let alone other examined apteronotids. Of particular note is the pronounced elongation of the mesethmoid in *Sternarchorhynchus* (Fig. 25C), which is a major factor in the lengthened preorbit, whereas the frontal is only moderately extended in this genus. In contrast, the mesethmoids in *Orthosternarchus tamandua*, *P. crypticus*, *P. macrostoma*, and *Sternarchorhamphus muelleri* are of proportional lengths comparable to those in outgroup apteronotids, whereas these species demonstrate a pronounced elongation of the frontals. *Orthosternarchus*, *Platyurosternarchus*, and *Sternarchorhamphus* have anteroposteriorly lengthened orbitosphenoids, whereas *Sternarchorhynchus* has a form of this bone proportionally comparable to the smaller ossification present in apteronotid taxa with shorter snouts.

A ventral curvature of the snout that terminates below the horizontal to opercular region was proposed as a synapomorphy for a clade formed by *Platyurosternarchus*, *Sternarchorhynchus*, and *Ubidia* in an analysis by Triques (2005). Elongation of the snout that is prerequisite for the extension of the snout to ventral of the horizontal to opercular region was achieved via different modifications in these genera and as such the curvature is not homologous across these genera.

As discussed above, grasp-suction or suction assisted by mechanical grasping is unique to two genera amongst freshwater fishes; *Sternarchorhynchus* in the Neotropics and *Campylomormyrus*, a member of the order Mormyriformes that inhabits rivers in the western and central portions of sub-Saharan Africa (Feulner *et al.*, 2007: fig. 1). Notwithstanding the striking convergence between these two genera in their feeding systems, numerous differences occur in the underlying osteological systems in *Sternarchorhynchus* versus *Campylomormyrus*. Given the pronounced phylogenetic distance between these genera, this result is expected and in the interests of efficiency, we discuss only a few of the larger scale differences.

The mesethmoid of *Sternarchorhynchus* is distinctly elongate anteroposteriorly (character 67), and the primary contributor amongst the bones of the dorsal portion of the neurocranium to the elongation of the snout. In *Campylomormyrus* the elongation of the preorbital region of the head is, in contrast, largely a function of the proportional lengthening of the frontal, with the mesethmoid being relatively short along its anteroposterior axis (Taverne, 1968: figs 2, 3, 6). *Campylomormyrus* has a distinctly anteroposteriorly lengthened orbitosphenoid with that elongation being one of the distinguishing characteristics of the genus (Taverne, 1968: fig. 9). *Sternarchorhynchus*, by contrast, has a relatively anteroposteriorly compact orbitosphenoid. Finally, the coronomeckelian ossification is lost ontogenetically in *Sternarchorhynchus* (character 9), but this bone is distinctly lengthened along the anteroposterior axis in *Campylomormyrus*.

These and correlated differences in other elements of the preorbital region in *Sternarchorhynchus* versus *Campylomormyrus* amply demonstrate that the two genera arrived at functionally convergent forms of jaws and associated systems for prey capture and ingestion via different evolutionary paths in South America versus sub-Saharan Africa. Interesting, the convergences in the overall external form of the preorbital region of the head in *Campylomormyrus* and *Sternarchorhynchus* correlate with the independent acquisition in these two genera of two other features; body elongation of varying degrees and electrogenic abilities. A correlation between body elongation and grasp-suction feeding may not derive directly from this feeding mode, but rather may be functionally associated with the requirements of the generative and receptive systems associated with electrolocation and electrocommunication. Both electrolocation and electrocommunication, however, provide distinct advantages in the habitats occupied by *Campylomormyrus* and *Sternarchorhynchus*. Electrolocation facilitates the targeting of potential prey items in the mud, leaf litter, and interstices of clay nodules under the limited light conditions characteristic of most tropical rivers inhabited by *Campylomormyrus* and

Sternarchorhynchus. Detection and fine-scale location of prey is a prerequisite so that the species of these genera can then bring into action their unique 'grasp-suction' feeding system. Electrocommunication is also undoubtedly critical in such habitats 'for signaling of identity or behavior states and intentions' (Crampton & Albert, 2006: 649) to at least congeners. As is the case with electrolocation, this ability provides a major advantage in the dark waters inhabited by *Campylomormyrus* and *Sternarchorhynchus* on the two continents.

SEXUAL DIMORPHISM

The comments in the introduction summarized the several types of sexual dimorphism that occur in the Apteronotidae. Sexual dimorphism of diverse forms, including snout form and modifications of the lower jaw and dentary teeth, arose several times in the family under present hypotheses of relationships (Rapp Py-Daniel & Cox-Fernandes, 2005). Rapp Py-Daniel & Cox-Fernandes (2005) proposed that the sexual dimorphism in some *Sternarchorhynchus* species is most parsimoniously interpreted as having arisen independently relative to other instances of that phenomenon in the Apteronotidae. Our conclusions, in particular the evidence supporting the hypothesis of a sister-group relationship of *Sternarchorhynchus* with *Platyurosternarchus*, a genus in which sexual dimorphism is unknown (de Santana & Vari, 2009), are consistent with this hypothesis. The distribution of sexual dimorphism within *Sternarchorhynchus* reveals interesting intrageneric patterns. The following comments should be considered with the caveat that various species of *Sternarchorhynchus* are known from limited samples, in some instances consisting solely of probable juveniles. It is probable that the totality of sexual dimorphism across the genus is more extensive than presently documented.

Survey of extensive samples of *Platyurosternarchus*, the sister group to *Sternarchorhynchus*, failed to reveal sexually dimorphic features in that genus (de Santana & Vari, 2009). A lack of such modifications similarly characterized the species of the basal clade 4 (*S. goeldii* and *S. oxyrhynchus*) within *Sternarchorhynchus.* Lack of sexual dimorphism in the species of clade 4 is noteworthy in that we examined large series of specimens of all sizes of those two species and the absence of the trait is unlikely to be an artefact of limited samples. Evidence as to the presence versus absence of sexual dimorphism is unavailable for some species in clade 5 (all species of *Sternarchorhynchus* with the exception of *S. goeldii* and *S. oxyrhynchus*), but notwithstanding that limitation, the phenomena manifests itself in 12 of the 22 species in clade 5 (*S. axelrodi*, *S. caboclo*, *S. camptoni*, *S. curumim*, *S. gnomus*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. mareikeae*, *S. mormyris*, *S. retzeri*, *S. roseni*) with those species distributed across the clade. Sexual dimorphism within this lineage typically involves the positions of the anus and urogenital papillae, with the variation in these features sometimes correlated with sexually dimorphic coloration differences.

One particularly striking form of sexual dimorphism is unique amongst gymnotiforms to some members of clade 17. Some mature males in five of the ten species in clade 17 (*S. cramptoni*, *S. hagedornae*, *S. higuchii*, *S. retzeri*, *S. roseni)* have the anterior portion of the dentary expanded both laterally and dorsally. The resultant dorsally bulbous structure is transversely rounded along the longitudinal axis of the snout and surmounted by a series of enlarged dentary teeth (Fig. 25A; also Rapp Py-Daniel & Cox-Fernandes, 2005: fig. 5b). Males of these species possibly use this modified lower jaw during antagonistic encounters (Marrero & Taphorn, 1991; Kirschbaum, 1995; Cox-Fernandes *et al.*, 2002). Several of the species within clade 17 not known to demonstrate sexual dimorphism in the form of the lower jaw and dentary dentition are represented by limited samples in this study. An examination of larger samples of those forms would be likely to reveal the presence of these derived modifications in other species in this lineage. These elaborations of the dentary and dentary dentition potentially represent a complex of synapomorphies for the species of clade 17. In the absence of definitive information on the presence or absence of these sexually dimorphic elaborations in all species of clade 17, we deferred from incorporating those features into the phylogenetic analysis. Two other species of *Sternarchorhynchus* not incorporated into the phylogenetic analysis because of limited samples (*S. taphorni*, *S. yepezi*) also demonstrate these pronounced elaborations of the lower jaw and associated dentition in some mature males. Thus, they are likely to be components of clade 17 or a slightly more inclusive lineage.

BODY SIZE AND HABITAT

The innovations described previously potentially provided a competitive advantage to *Sternarchorhynchus* relative to other clades of Apteronotidae during the colonization of Neotropical rivers and may account for the speciose nature of this genus within the context of the Apteronotidae. Two other aspects of morphology and behaviour may have contributed to the success of the genus. Examination of body size within the context of the arrived-at phylogeny reveals repetitive shifts in maximum body sizes within *Sternarchorhyn-*

chus that probably permit the exploitation of a more diverse suite of resources. Similarly, preferred habitats for the species of the genus demonstrate definite patterns when evaluated within the context of phylogeny, with such shifts further expanding the habitats available to members of *Sternarchorhynchus*.

Platyurosternarchus, the sister group to *Sternarchorhynchus*, grows to a relatively large body size (415 mm TL; de Santana & Vari, 2009). Basal clades within *Sternarchorhynchus* (clades 4, 6) include the largest species in the family, with examined specimens of clade 4 exceeding 460 mm TL and those of clade 6 reaching approximately 550 mm TL. Species of clade 7 are with few exceptions of shorter to distinctly shorter maximum known body sizes, with 16 of the 20 species in that clade (*S. britskii*, *S. caboclo*, *S. chaoi*, *S. curumim*, *S. curvirostris*, *S. gnomus*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. severii*, *S. stewarti*) not known to achieve TLs greater than 275 mm with some of these species sexually mature by 150 mm TL. Body sizes of those standard lengths apparently represent the primitive condition for the species of clade 7. Reversals to distinctly larger body sizes occur three times within the clade, with all of the involved species achieving TLs of at least 375 mm. These are *S. starksi* (clade 16), *S. cramptoni* and *S. retzeri* that jointly form clade 30, and *S. roseni* (clade 24).

The second transition of note within the phylogenetic scheme for *Sternarchorhynchus* involves habitat preferences. In the discussion, we follow the definitions used by Crampton & Albert (2006: 659) for streams (terra firme streams and small rivers not exposed to seasonal floodplain flooding) and rivers (deep, swiftly flowing channels). *Platyurosternarchus* species are somewhat generalists in terms of habitat, being collected both in streams and along the margins of larger rivers (de Santana & Vari, 2009). The large body size *Sternarchorhynchus* species of basal clades 4 and 6 (*S. axelrodi*, *S. goeldii*, *S. mormyrus*, *S. oxyrhynchus*) are inhabitants of large rivers. This is also the case for the large body-sized *S. roseni* of clade 24. Such a correlation between large body sizes and larger water bodies would seem logical given the reported dietary preferences for deep-water invertebrates that characterize these species. Alternative preferences for rapid water conditions were documented for an unidentified *Sternarchorhynchus* species by Schwassmann & Carvalho (1985: 237) and this attribute has been found to be broadly distributed across the genus. Twelve of the 19 intermediate-sized species of clade 7 have an overall preference for fluviatile habitats, with the other seven species in that lineage showing repeated independent transitions to life in rapids. Rheophilic habits characterize *S. caboclo* (clade 8), *S. severii* (clade 9), *S. inpai* (clade 11), *S. mareikeae* (clade 13), *S. jaimei* (clade 22), and *S. higuchii* (clade 24). *Sternarchorhynchus hagedornae* (clade 17) also lives in high-energy stream settings albeit without evidence that it occurs in rapids. Transitions from the ancestral riverine habitat preferences thus appear to have occurred multiple times independently within *Sternarchorhynchus*. Furthermore, *S. jaimei* and *S. kokraimoro*, species not included in the phylogeny because of limited samples, also were captured in the high energy habitat of the rapids of the lower Rio Xingu. An absence of information as to the phylogenetic position of these two species renders it impossible to determine whether these represent one or more additional independent transitions to rheophilic conditions. Nonetheless, the evidence indicates that rheophilic stenotopy with rapids and other high-energy situations were acquired independently on multiple occasions within *Sternarchorhynchus* as was the case with at least some groups of Neotropical cichlids (comments in Kullander & Ferreira, 2005). More extensive collecting efforts in diverse habitats throughout the river systems inhabited by the apparently rheophilic species of *Sternarchorhynchus* are prerequisite for an evaluation of the degree to which these species are actually exclusively stenotopic for rapids and other areas of very rapid water flow.

Rheophily, the tendency to thrive in or have a preference for running water, occurs in numerous groups of South American fishes [summary in Lima & Zuanon (2004: 120)] including other apteronotids [e.g. *Megadontognathus* (Campos-da-Paz, 1999); some species of *Sternarchogiton*]. Preference for rapidly flowing water and rapids is correlated with diverse morphological modifications in some groups of fish, whereas in other taxa the adaptations to high energy habitats are behavioural. We were unable to identify morphological modifications unique to all of the rheophilic species of *Sternarchorhynchus* to the exclusion of their congeners. Although a long tail such as is present in some species of the genus living in rapidly flowing waters might on first consideration be thought to correlate with rheophily, comparable elongations of the tail occur amongst congeners inhabiting lentic water bodies and slower flowing streams and rivers. Behavioural observations of the rheophilic species of *Sternarchorhynchus* in nature are lacking to date. Nonetheless, in the absence of any manifest external morphological shifts, it appears that the rheophily typical of some species of *Sternarchorhynchus* is likely to be a consequence of as-of-yet undetermined behavioural adaptations.

TAXONOMIC ACCOUNTS

The dramatic increase in the number of species of *Sternarchorhynchus* makes it impossible to associate confidently many of the literature records for the long-described species *S. curvirostris*, *S. mormyrus*, and *S. oxyrhynchus* with one of the species recognized in this revision. Particularly problematic in this respect are citations of one or more of these species of *Sternarchorhynchus* within compendia of species purportedly inhabiting various rivers, regions, or countries. Myriad drainage basins and regions originally cited as inhabited by a single species of *Sternarchorhynchus* rather include two or more often more members of the genus in their ichthyofaunas. We thus restrict the synonymies for *S. curvirostris*, *S. oxyrhynchus*, and *S. mormyrus* to the original descriptions of the species and major subsequent publications (e.g. Ellis, 1913; Mago-Leccia, 1994). Exceptions involve instances where evidence in a publication or the examination of samples that served as the basis for the record in question allowed us to associate unequivocally a published citation with a particular species.

STERNARCHORHYNCHUS CASTELNAU, 1855

Sternarchorhynchus Castelnau, 1855: 91 [Campos-da-Paz, 2000: 525, concerning page numbering; type species: *Sternarchorhynchus mulleri*, Castelnau, 1855 (= *Sternarchus oxyrhynchus*, Müller & Troschel, 1848); type by monotypy; masculine].

Rhamphosternarchus Günther, 1870: 4 (type species *Sternarchus oxyrhynchus*, Müller & Troschel, 1848; type by subsequent designation of Jordan, 1919; proposed as subgenus of *Sternarchus*, Bloch & Schneider, 1801; masculine).

Sternarchorchynchus Mago-Leccia, 1978: 14 (misspelling).

Diagnosis: Synapomorphies for *Sternarchorhynchus* were discussed under the preceding phylogenetic reconstruction and are summarized in the synapomorphy list for the genus in Appendix 2 (clade 3). Although these characters delimit the genus as monophyletic, they overwhelmingly involve internal characters and are therefore inappropriate to determine whether whole specimens at hand are members of *Sternarchorhynchus*. The following combination of derived and plesiomorphic characters serve to delimit members of the genus.

Sternarchorhynchus shares with other species of the Apteronotidae the presence of a caudal fin and a fleshy dorsal electroreceptive filament, features that readily distinguish the family from other groups in the Gymnotiformes. Species of *Sternarchorhynchus* differ from other genera in the Apteronotidae by the combination of the possession of an elongate, tubular snout that is compressed laterally and slightly to strongly curved ventrally anteriorly; the length of the snout (usually more than 50% of HL), the small mouth (usually less than 12% of HL), the pronounced distance from the posterior naris to the eye (usually more than 37% of HL), and the posterior position of the origin of the midsaggital electroreceptive filament (approximately at, or posterior to, the middle of TL and situated approximately at 55 to 70% of TL).

Remarks: Campos-da-Paz (2000: 527) detailed the history of the recognition, or lack thereof, of *Sternarchorhynchus* by authors following Castlenau's (1855) proposal of the genus. As discussed by Campos-da-Paz, various authors failed to recognize *Sternarchorhynchus* for nonspecified reasons, perhaps because they were not aware of Castlenau's description of the genus. Günther (1870: 4), for example, was apparently unaware of *Sternarchorhynchus* because he proposed *Rhamphosternarchus* as a subgenus of *Sternarchus*, with that genus including three species amongst which was *S. oxyrhynchus*, the type species of *Sternarchorhynchus*. The *Rhamphosternarchus* of Günther was based on the presence in member species of a 'snout produced into a long tube', one of the distinguishing attributes for *Sternarchorhynchus*. Eigenmann & Ward (1905: 166) rectified the problem by explicitly noting that *Rhamphosternarchus* was a synonym of *Sternarchorhynchus*.

Common features of species of Sternarchorhynchus: The species of *Sternarchorhynchus* share a distinctive bauplan with many of the features delimiting species involving meristics and specific morphometric features and/or coloration rather than significant changes in overall external head and/or body morphology. In the interest of space efficiency, we describe external features common to all species of *Sternarchorhynchus* in this section rather than reiterating them in each species description. Conditions of the intragenerically variable external features for each species are detailed in each species account.

Body elongate and distinctly laterally compressed (cultiform), more so in region posterior to abdominal region. Greatest body depth located in area of abdominal cavity or slightly posterior to that region. Dorsal profile of body ranges between straight to very slightly convex. Anteriormost perforated lateral line scale located along vertical through pectoral-fin origin.

Head laterally compressed, widest in opercular region and deepest at nape. Eye very small, laterally positioned on dorsal half of head, and completely covered by thin membrane. Cephalic pores small. Snout distinctly elongate, overall tubular but somewhat compressed laterally. Premaxilla of small size. Anterior naris located at end of small tube and proximate to tip of snout. Posterior naris ellipsoid, without tubular extension. Posterior naris located distinctly closer to tip of snout than to anterior margin of eye. Branchial opening constricted to short vertical aperture situated along posterior margin of opercle and slightly anterior to vertical through pectoral-fin origin. Branchial membranes joined at isthmus. Anus and urogenital papilla adjacent and ventrally positioned. Location of both structures intragenerically and ontogenetically variable in many species and sexually dimorphic in some species.

Scales cycloid, small and present over all, or nearly all, of body from rear of head to anterior portion of base of caudal fin. Scales absent or sparse in some species along mid-dorsal line of body anterior to origin of electroreceptive filament. Lateral line scales often larger than those of scale rows immediately dorsal and ventral of lateral line series.

Pectoral fin long, broad, and distally pointed. Anal fin elongate and extending from under head posteriorly for most of length of body. Dorsal electroreceptive filament arising on posterior portion of body and progressively narrowing posteriorly and inserting into and attached to narrow mid-dorsal grove. Caudal and pectoral fins present, but dorsal and pelvic fins absent as in all gymnotiforms.

Distribution: A distinct majority of the species of *Sternarchorhynchus* inhabit portions of the Amazon basin (22 of 32 species, Table 1), with the genus occurring across major portions of that drainage system. Many of the apparent major gaps in the distribution of the genus across the Amazon basin are most likely to be a function of the lack of collecting in habitats appropriate for the members of the genus. This issue is general for the Neotropical freshwater fish fauna (Vari & Malabarba, 1998). Seven species of *Sternarchorhynchus* occur in the Río Orinoco system and the independent river systems of north-eastern Venezuela that drain into the Golfo de Paria (Table 1). One of these species, *S. mormyrus*, is the only member of the genus shared with the Amazon basin (comments under that species description).

The sparse records of *Sternarchorhynchus* in the rivers of the Guianas (two species) may be in part a function of the limited collecting efforts in appropriate habitats, but the genus is unknown even in some relatively well sampled basins in this region (Mol *et al.*, 2007). Similar gaps in distributions at the generic level occur in other components of the ichthyofauana in the Guianas. A single species of *Sternarchorhynchus* occurs in the Essequibo River system of Guyana, one species in the Lawa River of the Marowijne River (= Fleuve Maroni) system along the border between Suriname and French Guiana. *Sternarchorhynchus* has also been reported from the Fleuve Oyapock (= Rio Oiapoque) along the boundary between French Guiana and Brazil (Planquette, Keith & Le Bail, 1996: 406). We were unable to examine the specimens that served as the basis for that report. A single species of *Sternarchorhynchus*, *S. britskii*, is known from the upper portions of the Rio Paraná basin in Brazil; that being the only member of the genus occurring in a drainage system south of the Amazon basin.

Diversity: The 32 recognized species of *Sternarchorhynchus* represent approximately 40% of the present known diversity at the species level within the Apteronotidae, making it by far the most speciose genus in the family, with the approximately 15 recognized species of *Apteronotus* (*sensu stricto*; Albert & Crampton, 2005: 363) making it the next most diverse genus in the family. As we note under the Possible additional undescribed species section, the 32 recognized species of *Sternarchorhynchus* undoubtedly represent an underestimate of the actual diversity in the genus. Under present concepts of generic limits and species richness, *Sternarchorhynchus* is one of the most speciose genera within the Gymnotiformes. Only *Gymnotus* in the Gymnotidae, that is estimated to include at least 35 species (Albert & Crampton, 2005; Albert *et al.*, 2005) is as speciose as *Sternarchorhynchus*.

An evaluation of the diversity of *Sternarchorhynchus* relative to that of *Gymnotus* shows some notable differences in the proportional density of species in the two genera across their range. Most obviously, *Sternarchorhynchus* is restricted to the cis-Andean portions of South America with only one species, *S. britskii*, known from a river basin south of the Amazon, whereas *Gymnotus* has a massive distribution from Mexico to Argentina to both sides of the Andean Cordilleras. *Gymnotus* is, furthermore, able to tolerate a much broader range of habitats, being able to absorb atmospheric oxygen via a portion of the gas-bladder (Campos-da-Paz, 2003: 483); an adaptation that opens up low oxygen-level backwaters and swamps as potential habitats. *Sternarchorhynchus* lacks such modifications and is apparently limited to well-oxygenated habitats. The more restricted geographical range and habitat tolerances of the species of *Sternarchorhynchus* render its speciose nature all the more impressive in terms of proportional density of species. In part this density is made possible by the ability by many species of *Sternarchorhynchus* to exploit deep river habitats, which contrasts with the

Table 1. Occurrence of the species of *Sternarchorhynchus* in river systems and regions of cis-Andean South America

Species	River basins and regions											
	A	B	C	D	E	F	G	H	I	J	K	L
S. axelrodi				*x*		*x*						
S. britskii										*x*		
S. caboclo												*x*
S. chaoi							*x*					
S. cramptoni			*x*			*x*	*x*					
S. curumim							*x*					
S. curvirostris									*x*			
S. freemani		*x*										
S. galibi		*x*										
S. gnomus	*x*											
S. goeldii			*x*			*x*	*x*	*x*				
S. hagedornae									*x*			
S. higuchii			*x*									
S. inpai					*x*							
S. jaimei			*x*									
S. kokraimoro											*x*	
S. mareikeae					*x*							
S. marreroi	*x*											
S. mendesi	*x*											
S. mesensis				*x*								
S. montanus									*x*			
S. mormyrus	*x*		*x*				*x*		*x*			
S. oxyrhynchus	*x*											
S. retzeri			*x*			*x*	*x*					
S. roseni	*x*											
S. schwassmanni				*x*								
S. severii												*x*
S. starksi						*x*						
S. stewarti									*x*			
S. taphorni									*x*			
S. yepezi	*x*											
S. villasboasi											*x*	

River systems and regions are as follows: A, Rio Orinoco basin; B, Guianas; C, Rio Negro; D, Rio Tocantins/Araguaia; E, Rio Trombetas; F, mainstream Amazon below Manaus; G, mainstream Amazon above Manaus; H, Rio Madeira; I, western Amazonian tributaries; J, upper Rio Paraná; K, Rio Xingu; L, Rio Branco.

absence of all genera of the Gymnotidae from such habitats (Crampton, 2007: 302).

Remarks on secondary sexual dimorphism: Various species within one clade within *Sternarchorhynchus* together with various other Gymnotiformes (e.g. *Sternarchogiton*; de Santana & Crampton, 2007: 390: fig. 1a; *Compsaraia*, Albert & Crampton, 2009: fig. 1) demonstrate particularly striking sexual dimorphic remodelling of the lower jaw of various forms. Some males with well-developed testes amongst the *Sternarchorhynchus* species in clade 17 have the dentary anteriorly lengthened and transversely expanded into a dorsally bulbous structure that is rounded from a dorsal view (Fig. 25A; comments on Sexual dimorphism under Discussion above). This enlarged portion of the dentary bears a patch of distinctly enlarged, typically slightly posteriorly recurved dentition. This patch of enlarged teeth in males of this clade may be utilized in confrontations during breeding contests (Marrero & Taphorn, 1991: 129).

Such dramatic elaborations of the lower jaw and dentary dentition are unknown in some species of the clade represented by limited numbers of specimens and larger samples are necessary to determine whether the condition is indeed absent in these species. We have examined conspecific males of the species characterized by such dentary modifications with well-developed testes that nonetheless lack elaborations of the lower jaw and associated dentition. This is despite those individuals being of body sizes comparable to conspecific males with those attributes. Thus, one cannot assume that large specimens of a species within clade 17 that lack an expansion of the dentary and elaborations of the dentary dentition are females. The significance of these differences amongst conspecific males of comparable sizes cannot be elucidated from museum specimens, but potentially reflects social structure amongst groups of males. Alternatively, it may be a function of seasonality in the manifestation of this secondary sexually dimorphic feature.

***STERNARCHORHYNCHUS AXELRODI* SP. NOV.**

(FIGS 26–28; TABLE 4)

Sternarchorhynchus cf. *mormyrus*, Campos-da-Paz, 2000: 533 [Brazil, Rio Tocantins; as probable undescribed species].

Sternarchorhynchus mormyrus, not of Steindachner, dos Santos *et al.*, 2004: 103, unnumbered figure [Brazil, lower Rio Tocantins; food habits].

Diagnosis: Sternarchorhynchus axelrodi is distinguished from all congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the origin of the electroreceptive filament, and the possession of 200–217 anal-fin rays.

Description: Morphometric data for examined specimens in Table 4.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally, and with sexual dimorphism in overall form across examined specimens of large body sizes. Snout more anteroventrally aligned in mature females than in mature males of comparable sizes as evidenced by specimens of each sex with mature gonads. Sexual dimorphism in form of lower jaw and associated dentition found in many congeners not apparent in examined samples. Mouth terminal, rictus situated anterior of vertical through anterior naris. Anus and urogenital papilla located ventral to head, with openings situated anterior to vertical through anterior margin of eye (in specimens of 433–510 mm SL). Combined opening for anus and urogenital papilla distinctly elongate longitudinally and bordered laterally by raised fleshy ridges.

Premaxilla with six to ten teeth apparent in whole specimens ($N = 4$). Dentary with one tooth row consisting of nine to 15 curved conical teeth in whole specimens ($N = 4$), with second row of apparent replacement teeth located internal to functional row.

Branchiostegal rays five; with first to third rays apparently narrow and elongate in radiographs, and with fourth and fifth rays clearly very large and broad. Precaudal vertebrae 18–19 (15 anterior; three to four transitional; $N = 10$).

Pectoral-fin rays ii + 13–17 [ii + 16] ($N = 10$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 22–34 [33] ($N = 5$). Total anal-fin rays 200–217 [205] ($N = 10$). Scales above lateral line at midbody nine to 11 [11] ($N = 10$). Scales absent along much of mid-dorsal line in region anterior to origin of midsaggital electroreceptive filament. Areas lacking scales sometimes separated by regions covered by mid-dorsal scales, but with position and extent of regions lacking scales variable across examined specimens. Origin of midsaggital electroreceptive filament located approximately at 65% of TL.

KEYS TO THE SPECIES OF *STERNARCHORHYNCHUS*

Keys are presented for the species of *Sternarchorhynchus* by major drainage basins (Amazon, Orinoco, Paraná) or region (Guianas) because each of those units have largely endemic faunas of *Sternarchorhynchus* species. As an aid to the identification of species, their distributions are detailed in Table 1. The alternative of a single, all-inclusive key for all members of the genus would be quite complex and involve working through multiple couplets in order to identify materials of many species only one of which (*S. mormyrus*) occurs in more than one river basin (Amazon plus Orinoco). *Sternarchorhynchus mormyrus* is included in the keys for the species in both of those basins. The diagnoses under each species account serve to separate differentially each species from all congeners. *Sternarchorhynchus mesensis* demonstrates variation in the degree to which the narrow, lightly coloured stripe on the head and body is obvious. Some specimens of the species in isolation might be considered to lack the stripe and the species consequently appears in two places in the key for the members of the genus in the Amazon basin.

Differences in anal-fin ray numbers, both anterior unbranched and total rays, proved to be the most informative meristic features for distinguishing *Sternarchorhynchus* species. Frequency distributions of these values for the species are provided in Tables 2 and 3 to assist readers with the identification of specimens at hand. Supplementing the information in the keys, diagnoses, and tables are the phylogenetically informative characters discussed under Character description and analysis. That evidence underpins our recognition of multiple species within a well-resolved hypothesis of relationships. Autapomorphies characterizing a number of species are listed in Appendix 2.

Key to the species of *Sternarchorhynchus* occurring in the Amazon basin

1\. Gape of mouth aligned with main axis of snout, with gape elongate and extending posteriorly distinctly beyond vertical through posterior naris …… ***S. goeldii* sp. nov.**
Gape short, terminates posteriorly at, or slightly anterior of, vertical through anterior naris …… 2

2\. Scales either lacking or sparse and covered by skin middorsally at least in part of region from rear of head to insertion of electroreceptive filament …… 3
Scales present and obvious along mid-dorsal region of body from rear of head to insertion of electroreceptive filament …… 9

3\. Mid-dorsal scales missing along entire mid-dorsal region to insertion of electroreceptive filament …… 4
Mid-dorsal scales either sparse and covered by skin, or missing along mid-dorsal region solely from rear of head to point approximately along vertical through rear of pectoral fin …… 5

4\. Total anal-fin rays 200–217 …… ***S. axelrodi* sp. nov.**
Total anal-fin rays 222–245 …… *S. mormyrus*

5\. Dorsal portion of head and body with at most obscure mid-dorsal, lightly coloured stripe on head …… ***S. higuchii* sp. nov.**
Dorsal portion of head and body with distinct narrow mid-dorsal, lightly coloured stripe on head and often on body …… 6

6\. Mid-dorsal scales completely absent along body approximately to vertical through rear of pectoral fin …… 7
Mid-dorsal region of body with scales present, but sparse and covered by skin …… 8

7\. Lateral line extending posteriorly to point three scales short of base of caudal fin; total anal-fin rays 165–178, premaxilla with eight to 13 teeth, postocular distance 39.4–41.3% of HL …… ***S. chaoi* sp. nov.**
Lateral line extending posteriorly to base of caudal fin; total anal-fin rays 180–195, premaxilla with four to seven teeth, postocular distance 41.5–49.1% of HL …… ***S. jaimei* sp. nov.**

8\. Anterior unbranched anal-fin rays 32–35, total anal-fin rays 173–193, length of anal-fin base 86.6–89.6% of LEA, head depth at nape 53.1–59.2% of HL …… ***S. hagedornae* sp. nov.**
Anterior unbranched anal-fin rays 25–26, total anal-fin rays 164–166, length of anal-fin base 80.2–83.9% of LEA, head depth at nape 49.5–49.6% of HL …… ***S. schwassmanni* sp. nov.**

9\. Mid-dorsal region of head and body without narrow, lightly coloured stripe …… 10
Mid-dorsal region of head and body with distinct, narrow, lightly coloured stripe …… 13

10\. Lateral line extending posteriorly to point three to five scales short of base of caudal fin, eight to nine series of scales present above lateral line in mid-dorsal region of body …… ***S. kokraimoro* sp. nov.**
Lateral line extending posteriorly to base of caudal fin, ten to 13 series of scales present above lateral line in mid-dorsal region of body …… 11

11\. Total anal-fin rays 153–174, branchiostegal rays four …… *S. caboclo*
Total anal-fin rays 171–189, branchiostegal rays five …… 12

12\. Premaxillary teeth seven to ten, teeth in outer tooth row of dentary seven to eight, prepectoral-fin distance 18.3–20.6% of LEA, internarial distance 2.4–2.8% of HL …… *S. curumim*
Premaxillary teeth 11–14, teeth in outer row of dentary ten to 11, prepectoral-fin distance 21.4–23.8% of LEA, internarial distance 3.2–4.7% of HL …… *S. mesensis*

13\. Mid-dorsal lightly coloured stripe limited to head …… 14
Mid-dorsal lightly coloured stripe commencing on snout and extending posteriorly to insertion of electroreceptive filament …… 17

14\. Lateral line extending posteriorly to point four to eight scales anterior of base of caudal fin …… 15
Lateral line extending posteriorly to base of caudal fin …… 16

15\. Total anal-fin rays 156–167, caudal length 12.6–15.6% of LEA, postocular distance 33.1–41.1% of HL, anal fin somewhat dusky, but not dark …… ***S. inpai* sp. nov.**
Total anal-fin rays 186, caudal length 6.8% of LEA, postocular distance 43.5–46.4% of HL, anal fin dark …… ***S. taphorni* sp. nov.**

16\. Premaxillary teeth 12–13, teeth in outer row of dentary 12–13, tip of electroreceptive filament located four to seven scales posterior of vertical through termination of base of anal fin, pectoral-fin length 35.0–40.9% of HL, postocular distance 36.0–41.3% of HL …… ***S. mareikeae* sp. nov.**
Premaxillary teeth eight to nine, teeth in outer row of dentary eight to nine, tip of electroreceptive filament located two scales posterior of vertical through termination of base of anal fin, pectoral-fin length 43.6–47.1% of HL, postocular distance 44.4–46.0% of HL …… ***S. villasboasi* sp. nov.**

17\. Distal portions of anal fin with dark band covering one-third to one-half of most of fin rays and sometimes all of posterior rays …… 18
Distal potions of anal fin without distinct dark band …… 20

18. Postocular distance 31.6–34.9% of HL, caudal length 7.1–10.3% of LEA………………………***S. retzeri* sp. nov.**
    Postocular distance 37.4–43.7% of HL, caudal length 5.3–8.4% of LEA………………………………………………19
19. Premaxillary teeth eight to 12, distance from anus to snout 8.9–12.0% of LEA, pectoral-fin length 38.0–46.5% of HL, tail depth 23.6–29.6% of caudal length……………………………………………………***S. cramptoni* sp. nov.**
    Premaxillary teeth six to seven, distance from anus to snout 6.9–7.3% of LEA, pectoral-fin length 47.8–49.1% of HL, tail depth 21.2–21.7% of caudal length……………………………………………………***S. montanus* sp. nov.**
20. Anal fin distinctly dark basally………………………………………………………………………***S. curvirostris* sp. nov.**
    Anal fin hyaline or slightly dusky, but not distinctly dark basally…………………………………………………21
21. Caudal length 6.1–7.1% of LEA……………………………………………………………………………***S. stewarti* sp. nov.**
    Caudal length 9.0–16.5% of LEA………………………………………………………………………………………………22
22. Preanal distance 14.2–17.0% of LEA, head length 20.5–23.6% of LEA, pectoral-fin length 27.0–35.3% of HL……*S. mesensis*
    Preanal distance 9.4–12.7% of LEA, head length 14.8–18.1% of LEA, pectoral-fin length 40.6–53.2% of HL……***S. starksi* sp. nov.**

KEY TO THE SPECIES OF *STERNARCHORHYNCHUS* OCCURRING IN THE RÍO ORINOCO BASIN

1. Gape of mouth aligned with main axis of snout, with gape elongate and extending posteriorly distinctly beyond vertical to posterior naris……………………………………………………………………………*S. oxyrhynchus*
   Gape short, terminates posteriorly at, or slightly anterior of, vertical through anterior naris……………………2
2. Mid-dorsal region of head and body without narrow, lightly coloured stripe or stripe obscure…………*S. gnomus*
   Mid-dorsal region of head and body with distinct, narrow, lightly coloured stripe……………………………………3
3. Scales along mid-dorsal region of body either lacking along at least part of region or scales sparse and covered by scales……4
   Scales present and obvious along mid-dorsal region of body from rear of head to insertion of electroreceptive organ……………………………………………………………………………………………………***S. marreroi* sp. nov.**
4. Total anal-fin rays 174–188…………………………………………………………………………………………………5
   Total anal-fin rays 193–245…………………………………………………………………………………………………6
5. Total anal-fin rays 174–182; anterior unbranched anal-fin rays 29–46; postocular distance 38.8–40.8% of LEA; caudal-fin length 18.1–33.0% of caudal length; scales above lateral line at midbody six to nine……***S. mendesi* sp. nov.**
   Total anal-fin rays 182–188; anterior unbranched anal-fin rays 23–29; postocular distance 43.8–46.2% of LEA; caudal-fin length 38.8% of caudal length; scales above lateral line at midbody nine to 12…….***S. yepezi* sp. nov.**
6. Total anal-fin rays 193–210; lightly coloured mid-dorsal stripe present from tip of snout to origin of electroreceptive organ; mid-dorsal region of body scaled……………………………………………………………………*S. roseni*
   Total anal-fin rays 222–245; mid-dorsal region of head and body uniformly coloured; mid-dorsal region of body lacking scales……………………………………………………………………………………………………*S. mormyrus*

KEY TO THE SPECIES OF *STERNARCHORHYNCHUS* OCCURRING IN THE COASTAL BASINS OF GUYANA AND SURINAME

1. Caudal length 8.7–10.8% of LEA; distance from anus to anal-fin insertion 6.8–12.8% of LEA; tail depth 13.8–19.2% of caudal length; premaxilla with six to ten teeth……………………………………………………***S. galibi* sp. nov.**
   Caudal length 15.1–16.9% of LEA; distance from anus to anal-fin insertion 13.0–17.4% of LEA; tail depth 8.0–8.9% of caudal length; premaxilla with four to five teeth………………………………………………***S. freemani* sp. nov.**

SPECIES OF *STERNARCHORHYNCHUS* OCCURRING IN THE UPPER RIO PARANÁ BASIN

Only a single *Sternarchorhynchus* species, *S. britskii*, is known from the upper Rio Paraná basin or indeed across the Río de La Plata system. *Sternarchorhynchus britskii* can be distinguished by all congeners by the features listed in the Diagnosis for that species.

SPECIES ACCOUNTS

In order to facilitate the location of individual species accounts and cross references between them, the species descriptions are arranged alphabetically within *Sternarchorhynchus* rather than by region of occurrence or phylogenetic affinity. Species accounts are followed by a discussion (Possible Additional Undescribed Species) of population samples that represent likely undescribed species of *Sternarchorhynchus* that are not formally described at this time.

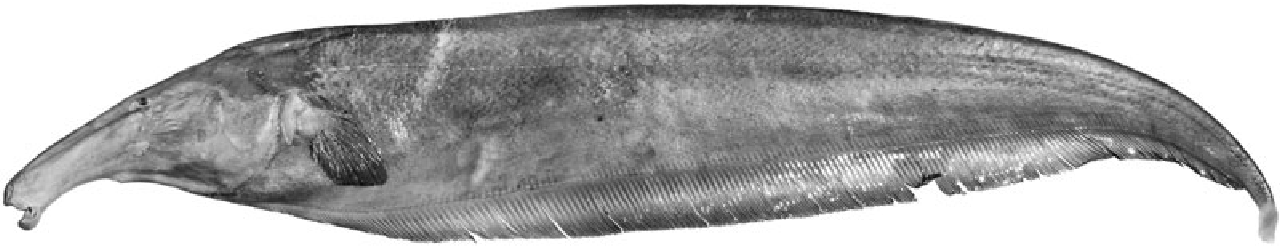

Figure 26. ***Sternarchorhynchus axelrodi* sp. nov.,** holotype, male, 444 mm total length, MNRJ 31279; Brazil, Goiás, Rio Tocantins.

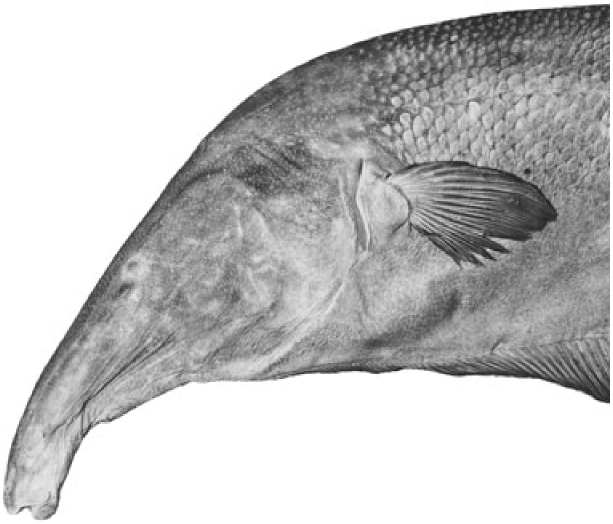

Figure 27. ***Sternarchorhynchus axelrodi* sp. nov.,** paratype, female, 493 mm total length, MNRJ 12168; Brazil, Goiás, Rio Tocantins; showing more pronounced ventral curvature of snout in mature females of species.

Filament extending posteriorly to point four scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, elongate, pointed caudal fin. Caudal-fin rays 16–20 [19] ($N = 10$).

Coloration in alcohol: Overall ground coloration brown. Head dark overall with more concentrated band of dark chromatophores present along dorsal portion of snout in region from vertical through posterior naris to slightly posterior of eye; dark pigmentation in some individuals extending anteriorly nearly to tip of snout. Body brown overall, with pigmentation darker dorsally, but without any distinct pigmentation pattern other than for dark mid-dorsal coloration in those regions that lack scales.

Pectoral fin dark, more so distally and sometimes nearly completely very darkly pigmented. Anal fin dark overall with distal pigmentation distinctly darker and forming irregular band. Caudal fin largely unpigmented, but with some individuals having variable dark pigmentation approximately midway along its length.

Distribution: Most examined specimens of *S. axelrodi* originated at one location in the upper portions of the Rio Tocantins basin; however, a single lot of the species collected in the lower portions of that river system at Tucuruí demonstrates that the species is broadly distributed along the Rio Tocantins (Fig. 28).

Ecology: The type locality of *S. axelrodi* was reported as a clear water system with the bottom formed by small stones and rocks (Vari & Harold, 2001: 164). dos Santos *et al.* (2004: 103; species cited therein as *S. mormyrus*) report that the species grows to 600 mm TL and feeds on insects and other aquatic invertebrates.

Secondary sexual dimorphism: Sternarchorhynchus axelrodi demonstrates pronounced secondary sexual dimorphism in the overall form of the snout. Large males with mature testes have the snout slightly curved ventrally, whereas mature females with well-developed ovaries have a more pronounced ventral curvature of the snout (compare Figs 26, 27). No secondary sexual dimorphism of the dentary and lower jaw dentition comparable to that present in some congeners was apparent in the available samples of the species.

Table 2. Frequency of distribution of anterior anal-fin rays in species of *Sternarchorhynchus*

	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
S. axelrodi								1									1	1	1	1						
S. britskii		1		1	1	2		3																		
S. caboclo						1		1	1			1			1											1
S. chaoi	1		1	1	1	1	1	1	1																	
S. cramptoni			1				3	3	2	1	1	1	2		1											
S. curumim									1	1																
S. curvirostris											1															
S. freemani								1				2		1												
S. galibi												2		2	1	2	1									
S. gnomus							2	1			1															
S. goeldii							1				1	3	2			3	1	1	1		1			1		1
S. hagedornae													1			1	1	1	1		1					
S. higuchii									1			2	4	3	2	1	1									
S. inpai			1			1				1																
S. jaimei									1	1	1											1				
S. kokraimoro								1	1																	
S. mareikeae	1						2		2	2		1														
S. marreroi							1									1	1									
S. mendesi															1	1			1	2	1		1			
S. mesensis									1			2	1	1												
S. montanus									1								1									
S. mormyrus												2			4	3			3	1				1		
S. oxyrhynchus									1	1	3	2														
S. retzeri			1					2	2	3	1	1	2													
S. roseni					1	1		3	1	3	3	4	2													
S. schwassmanni											1	1														
S. severii										1		1						1								
S. starksi				1			2	2	1			3														
S. stewarti													6		4	4	3		1	2						
S. taphorni																1										
S. yepezi									1						2											
S. villasboasi						1	1	1																		

Table 3. Frequency of distribution of total anal-fin rays in species of *Sternarchorhynchus*

	153	157	161	165	169	173	177	181	185	189	193	197	201	205	209	213	217	221	225	229	233	237	241	245
S. axelrodi													1	4	2		3							
S. britskii				1	3	1	2																	
S. caboclo	1	1	3	2	3	1																		
S. chaoi				3	3	3	1																	
S. cramptoni							1				2			1	3	8	4	4						
S. curumim							1	1																
S. curvirostris						2	2		1	1														
S. freemani					2	1	1																	
S. galibi					4	3	3																	
S. gnomus		1		3	2	1	2																	
S. goeldii														2		5	7	7	1	3	1	1		
S. hagedornae						2	1	1	1	1	1													
S. higuchii			2	2	7	3	1																	
S. inpai		1	2	3																				
S. jaimei				1	1		1	3	1		1	1												
S. kokraimoro						1	1																	
S. mareikeae		1	5	2	1			1																
S. marreroi			1					1																
S. mendesi						2	2	3																
S. mesensis					1	3		1		1														
S. montanus										1	1													
S. mormyrus																			2		3	2	3	5
S. oxyrhynchus																3	2		6					1
S. retzeri													2		2	4	2	4	1					
S. roseni												3	4	7	5	2								
S. schwassmanni			1	1																				
S. severii			2			1	4																	
S. starksi									2	1	3	1	3	1										
S. stewarti								6	7	3	1													
S. taphorni																								
S. yepezi									1	2														
S. villasboasi		1	1	1				1																

Anal-fin ray counts arranged in groups of four starting with listed number.

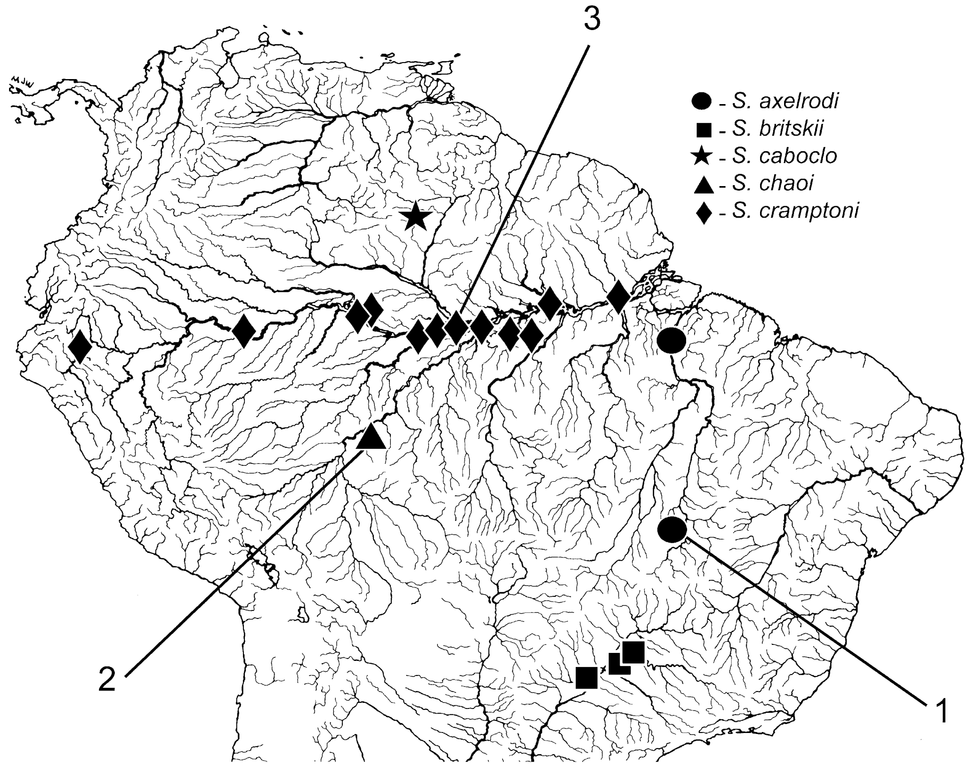

Figure 28. Map of central and northern South America showing geographical distribution of ***Sternarchorhynchus axelrodi* sp. nov.** (1 = holotype locality), *Sternarchorhynchus britskii*, *Sternarchorhynchus caboclo*, ***Sternarchorhynchus chaoi* sp. nov.** (2 = holotype locality), and ***Sternarchorhynchus cramptoni* sp. nov.** (3 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

Etymology: The species name, *axelrodi*, is in honour of Dr Herbert Axelrod, whose generous support of ichthyological research assisted with the completion of this project.

Remarks: Sternarchorhynchus axelrodi was collected at the same locality as the type series of *S. mesensis*. The two species differ in various features including the total number of anal-fin rays (200–217 versus 171–189, respectively), caudal-fin rays (16–20 versus 13–15, respectively), coloration of the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament (with distinct, narrow, lightly coloured stripe versus dark or sometimes with indistinct lightly coloured region, respectively), the greatest body depth (13.5–17.6 versus 10.0–12.3% of LEA, respectively), the caudal length (4.9–6.7 versus 9.0–14.3% of LEA, respectively), and other features.

Material examined

Holotype: – BRAZIL. *Goiás:* Município de Minaçu/Cavalcante, Rio Tocantins, at future site of Usina Hidroeléctrica Serra da Mesa (approximately 13°44′S, 48°08′W), collected by D. F. Moraes, C. N. Ricci, O. Roppa, vii.1988; MNRJ 31279 (444).

Paratypes: – BRAZIL. *Goiás:* Município de Minaçu/Cavalcante, Rio Tocantins, at future site of Usina Hidroelétrica Serra da Mesa (approximately 13°44′S, 48°08′W), collected with holotype by D. F. Moraes, C. N. Ricci, O. Roppa, vii.1988; MNRJ 12168, 8 (433–530), USNM 391570, 1 (475).

Nontype specimens: – BRAZIL. *Goiás*: Município de Minaçu/Cavalcante, Rio Tocantins, at future site of Usina Hidroeléctrica Serra da Mesa (approximately 13°44′S, 48°08′W), collected with holotype; MNRJ 31244,1 (not measured); MNRJ 31245, 1 (not measured); MNRJ 31246, 1 (not measured). *Pará*: INPA 27484, 2 (300–360); Rio Tocantins, Tucuruí, Mercado de Cametá.

STERNARCHORHYNCHUS BRITSKII CAMPOS-DA-PAZ

(FIGS 28, 29; TABLE 4)

Sternarchorhynchus sp. Britski, 1972: 91 [first citation of *Sternarchorhynchus* from Rio Paraná basin, Brazil].

Sternarchorhynchus curvirostris, not of Boulenger, Triques, 1993: 91 [details of osteology].

Table 4. Morphometrics for examined specimens of *Sternarchorhynchus axelrodi*, *Sternarchorhynchus britskii*, and *Sternarchorhynchus caboclo* (paratypes, INPA 10594)

	S. axelrodi			*S. britskii*			*S. caboclo*		
	H	Paratypes	Mean	H	Range	Mean	H	Paratypes	Mean
Total length (mm)	444	433–530 ($N = 9$)	–	261	209–250 ($N = 14$)	–	225	46.3–226 ($N = 57$)	–
Length to end of anal fin (mm)	420	410–510 ($N = 9$)	–	242	179–232 ($N = 11$)	–	206	41.1–206 ($N = 57$)	–
Head length (mm)	99.9	93.7–115.9 ($N = 9$)	–	47.5	33.1–46.9 ($N = 14$)	–	39.2	8.7–39.2 ($N = 57$)	–
Caudal length (mm)	23.3	24.9–30.5 ($N = 9$)	–	19.2	12.0–192 ($N = 10$)	–	16.8	8.7–21.6 ($N = 57$)	–
Per cent of length to end of anal fin									
Anal-fin base	83.3	76.9–97.1 ($N = 9$)	85.1	87.6	86.4–93.0 ($N = 11$)	88.3	84.0	79.3–86.4 ($N = 57$)	83.1
Distance snout to anus	8.5	4.6–8.1 ($N = 9$)	6.9	–	–	–	11.2	11.2–14.9 ($N = 10$)	12.9
Preanal-fin distance	16.5	14.1–18.5 ($N = 9$)	15.9	13.3	12.5–15.8 ($N = 11$)	13.5	16.4	12.1–20.0 ($N = 57$)	16.6
Prepectoral-fin distance	24.3	22.1–25.7 ($N = 9$)	24.0	20.1	19.4–23.6 ($N = 11$)	21.1	21.1	17.4–25.1 ($N = 57$)	21.5
Greatest body depth	14.4	13.5–17.6 ($N = 9$)	15.1	14.1	12.1–15.7 ($N = 13$)	14.3	11.0	11.3–14.7 ($N = 57$)	12.7
Head length	23.7	21.8–25.1 ($N = 9$)	23.4	19.6	18.9–23.1 ($N = 14$)	20.1	19.0	15.6–24.5 ($N = 57$)	20.9
Caudal length	5.5	4.9–6.7 ($N = 9$)	6.1	7.9	5.4–8.5 ($N = 14$)	7.8	8.2	8.8–23.9 ($N = 57$)	12.8
Per cent of head length									
Anus to anal-fin insertion	27.6	29.5–48.2 ($N = 9$)	37.1	24.8	14.4–23.9 ($N = 14$)	18.7	25.1	2.9–19.3 ($N = 57$)	11.2
Pectoral-fin length	35.7	35.3–38.7 ($N = 9$)	37.5	39.3	35.5–41.3 ($N = 14$)	38.6	39.5	31.3–46.9 ($N = 57$)	39.0
Head depth at eye	31.0	27.9–33.2 ($N = 9$)	30.1	33.3	18.2–36.5 ($N = 14$)	29.1	24.4	23.3–31.1 ($N = 10$)	26.5
Head depth at nape	50.5	46.4–60.7 ($N = 9$)	53.5	53.9	44.9–57.7 ($N = 14$)	49.2	46.6	45.4–60.3 ($N = 57$)	50.9
Head width	24.8	22.9–27.6 ($N = 9$)	25.1	28.4	15.6–28.4 ($N = 14$)	22.7	19.1	18.1–23.5 ($N = 10$)	20.7
Snout length	54.7	51.8–55.6 ($N = 9$)	54.0	63.8	59.8–65.7 ($N = 14$)	62.4	58.3	44.3–61.3 ($N = 57$)	54.6
Posterior naris to snout	10.0	8.7–10.5 ($N = 9$)	9.6	53.4	41.1–58.4 ($N = 14$)	50.9	8.1	6.4–9.1 ($N = 10$)	8.0
Posterior naris to eye	44.6	42.6–45.5 ($N = 9$)	44.4	55.8	53.9–57.9 ($N = 14$)	56.1	61.8	29.2–77.2 ($N = 57$)	56.4
Mouth length	9.1	8.0–9.7 ($N = 9$)	8.9	7.3	5.7–7.8 ($N = 14$)	6.7	7.1	5.6–12.4 ($N = 57$)	8.0
Internarial distance	3.9	2.5–4.2 ($N = 9$)	3.7	2.7	2.5–3.6 ($N = 14$)	3.1	3.7	3.0–6.4 ($N = 57$)	4.3
Eye diameter	2.9	2.6–3.5 ($N = 9$)	3.0	3.6	2.9–4.6 ($N = 14$)	3.9	6.3	4.1–10.5 ($N = 57$)	6.7
Interocular width	5.4	5.0–6.6 ($N = 9$)	5.90	6.2	4.1–7.9 ($N = 14$)	6.3	6.1	7.0–19.7 ($N = 57$)	10.0
Postocular distance	47.3	46.1–49.3 ($N = 9$)	47.8	42.7	40.0–45.9 ($N = 14$)	43.7	42.2	37.1–53.9 ($N = 57$)	45.4
Branchial opening	15.8	11.2–16.9 ($N = 9$)	15.2	15.5	12.1–17.9 ($N = 14$)	16.3	13.1	11.8–25.2 ($N = 57$)	15.6
Per cent of caudal length									
Tail depth	33.0	25.9–35.7 ($N = 9$)	30.7	22.3	18.9–25.9 ($N = 10$)	22.2	17.6	8.7–21.3 ($N = 57$)	15.3
Caudal-fin length	58.7	49.7–62.5 ($N = 9$)	54.1	37.1	33.3–46.4 ($N = 10$)	39.4	38.2	17.2–38.9 ($N = 57$)	28.6

H, holotype; range includes nontype specimens. Number of specimens indicated in parentheses.

Sternarchorhynchus britskii Campos-da-Paz, 2000: 529, fig. 9 [type locality: Brazil, Mato Grosso do Sul, Rio Paraná at Ilha Solteira dam (right margin), approximately 20°30′S 51°00′W]. – Albert, 2003: 500 [in listing of members of genus]. – Campos-da-Paz, 2005: 399 [additional locality information; threatened status]. – Triques, 2007: 125 [threatened status]. – da Graça & Pavanelli, 2007: 193, unnumbered fig. [Brazil, upper Rio Paraná; threatened status]. – Crampton, 2007: 289 [Brazil, Rio Paraná].

Diagnosis: Sternarchorhynchus britskii is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the hyaline anal fin, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends to the base of the caudal fin, the possession of five branchiostegal rays, seven teeth on the premaxilla, eight teeth in the outer row of the dentary, two teeth in the inner row of dentary, 15 precaudal vertebrae, 16–22 anterior unbranched anal-fin rays, 166–178 total anal-fin rays, 11–15 branched pectoral-fin rays, 13–15 caudal-fin rays, 16–17 precaudal vertebrae, 11–13 scales above the lateral line at the midbody, the greatest body depth (12.1–15.7% of LEA), the length of the base of the anal fin (86.4–93.0% of LEA), the prepectoral-fin distance (19.4–23.6% of LEA), the preanal distance (12.2–15.8% of LEA), the distance from the anus to the anal-fin insertion (14.4–24.8% of HL), the head length (18.9–23.9% of LEA), the snout length (59.8–65.7% of HL), the eye diameter (2.9–4.6% of HL), the distance from the posterior naris to the eye (53.9–57.9% of HL), the head depth at the nape (44.9–57.7% of HL), the caudal length (5.4–8.5% of HL), the mouth length (5.7–7.8% of HL), the postocular distance (40.0–45.9% of HL), the pectoral-fin length (35.5–46.4% of HL), the caudal-fin length (33.3–45.8% of caudal length), and the tail depth (18.9–25.9% of caudal length).

Diagnosis: Morphometric data for examined specimens in Table 4.

Lateral line extending posteriorly to point between two scales short of base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally anteriorly. Sexual dimorphism in form of lower jaw and associated dentition found in many congeners not apparent in examined samples. Anus and urogenital papilla located ventral to head. Openings shift anteriorly ontogenetically, with larger specimens having those structures situated along vertical three orbital diameters anterior of vertical through anterior margin of eye. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with seven teeth apparent in whole specimens (*N* = 1). Dentary with two tooth rows posteriorly and one sometimes somewhat irregular row anteriorly in whole specimens. Teeth in outer row eight and in inner row two (*N* = 1). Mouth small and terminal, rictus situated anterior of vertical through anterior naris.

Branchiostegal rays five; with first and second rays narrow and third to fifth rays large and broad. Precaudal vertebrae 16–17 (13–14 anterior; three transitional; *N* = 5).

Pectoral-fin rays ii + 11–13 [ii + 13] (*N* = 13). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 16–22 [19] (*N* = 13). Total anal-fin rays 166–178 [173] (*N* = 13). Scales above lateral line at midbody 11–13 [13] (*N* = 13). Scales present along mid-dorsal line in region anterior to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately at 70% of TL. Filament extending to within region delimited by verticals through point one scale short of vertical through posterior terminus of base of anal fin or point slightly beyond terminus of the base of that fin. Tail compressed and short, ending in small, elongate, slightly pointed caudal fin. Caudal-fin rays 13–15 [14] (*N* = 13).

Coloration in alcohol: Overall ground coloration ranging from light brown up to grey to brown. Head with anteriorly attenuating band of more concentrated dark chromatophores along dorsolateral region of snout in region from eye to vertical through posterior naris. Dark pigmentation on snout forms lateral border of narrow, lightly coloured, mid-dorsal stripe extending from snout to rear of head and widening

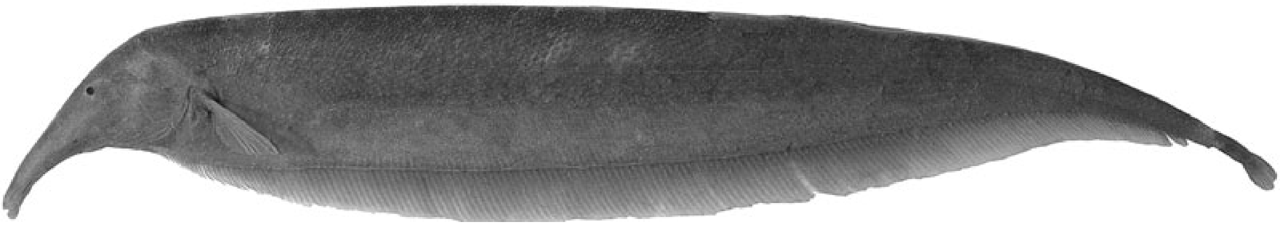

Figure 29. *Sternarchorhynchus britskii*, holotype, 272 mm total length, MZUSP 52923; Brazil, Mato Grosso do Sul, Rio Paraná.

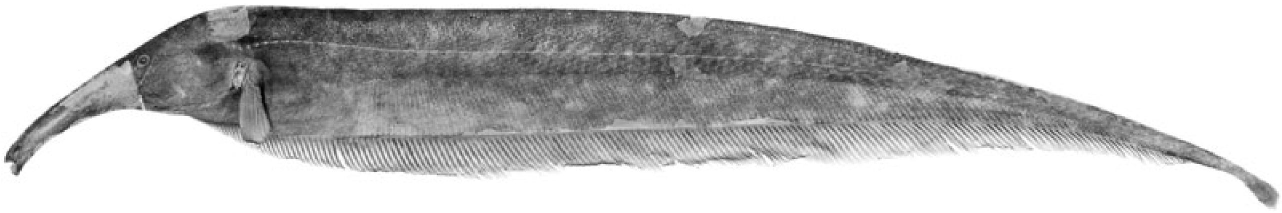

Figure 30. *Sternarchorhynchus caboclo*, holotype, male, 225 mm total length, INPA 22894; Brazil, Roraima, Rio Mucajaí.

slightly laterally along postocular portion of head (stripe indistinct, particularly in postocular region in some specimens). Remainder of head light brown other than for lightly coloured region forming anteriorly convex arch overlying preopercle in some individuals. Body pigmentation darker dorsally, but with irregular and to varying degrees obscure, narrow, more lightly coloured mid-dorsal region. Stripe sometimes continuous anteriorly with mid-dorsal stripe on head and extending posteriorly in some specimens to origin of electroreceptive filament. Pectoral fin with dark chromatophores distributed over rays and otherwise hyaline. Anal fin lightly coloured overall, with small dark chromatophores overlying rays. Caudal fin with dusky central basal spot in some individuals but otherwise hyaline over rays.

Distribution: Sternarchorhynchus britskii is only known from the upper Río Paraná basin in the states of Mato Grosso do Sul, Minas Gerais, and São Paulo, Brazil (Fig. 28).

Secondary sexual dimorphism: Sternarchorhynchus britskii is not known to demonstrate sexual dimorphism.

Remarks: Britski (1972: 91) reported that *S. britskii* (identified therein as *Sternarchorhynchus* sp.) was rare in sampled habitats with the type series having been collected in a cofferdam during the building of the Ilha da Solteira hydroelectric dam across the upper Rio Paraná. More recently, Campos-da-Paz (2005: 399) proposed that the insect larvae utilized by *S. britskii* may be associated with a specific habitat in flowing deep river channels. The extensive modifications of the upper Rio Paraná associated with the construction of major impoundments along the length of the main river channels throughout the basin and the resultant destruction of flowing deep river habitats favoured by *S. britskii* has undoubtedly adversely affected many populations of the species. As a consequence, *S. britskii* is now listed as threatened (Campos-da-Paz, 2005; Triques, 2007).

Material examined

BRAZIL. *Mato Grosso do Sul:* Rio Paraná, at Ilha Solteira dam, cofferdam at right margin of river (approximately 20°30′S, 51°00′W), MZUSP 24468 52923, 1 (262; holotype); MZUSP 24464, 8 [163–254; six specimens from this lot designated as paratypes by Campos-da-Paz (2000), but not possible to now determine which specimens were so designated]; MBUCV 13398, 1 (244; formerly MZUSP 24464, in part; nontype specimen collected with holotype). Rio Paraná, Ilha Solteira (approximately 20°30′S, 51°00′W), MZUSP 23097, 3 (125–240). Rio Paraná, ROM 37960, 1 (210). *São Paulo:* Rio Grande, Represa de Água Vermelha along boundary between state of São Paulo and Minas Gerais, MZUSP 39956, 7 (128–232). Fernandópolis (approximately 20°15′36″S, 50°13′59″W), MZUSP 50188, 1 (265).

STERNARCHORHYNCHUS CABOCLO DE SANTANA & NOGUEIRA (FIGS 28, 30; TABLE 4)

Sternarchorhynchus oxyrhynchus, not of Müller & Troschel, Ferreira, dos Santos & Jégu, 1988: 344 [in listing of species from Rio Mucajaí in vicinity of Ilha Paredão, Roraima, Brazil].

Sternarchorhynchus caboclo de Santana & Nogueira, 2006: 89: figs 1b, 2b, c [type locality: Brazil, Roraima, Rio Mucajaí, below Cachoeira Paredão].

Diagnosis: Sternarchorhynchus caboclo is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the absence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament, the lateral line that extends posteriorly to the base of the caudal fin, the dusky anal fin, the possession of four branchiostegal rays, six premaxillary teeth, 13–15 branched pectoral-fin rays, 153–174 total anal-fin rays, ten to 12 scales above the lateral line at the midbody, the greatest body depth (11.0–14.7% of LEA), the length of the base of the anal fin (79.3–86.4% of LEA), the mouth length (5.6–12.4% of HL), the snout length (44.3–61.3% of HL), the head depth at the nape

(45.4–60.3% of HL), the internarial distance (3.0–6.4% of HL), the eye diameter (4.1–10.5% of HL), the pectoral-fin length (31.3–46.9% of HL), the interocular distance (6.1–19.7% of HL), and the caudal-fin length (17.2–38.9% of caudal length).

Description: Morphometric data for examined specimens in Table 4.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and ranging from nearly straight to slightly curved ventrally. Mouth terminal and relatively small, with rictus located slightly anterior to, or along, vertical through anterior naris. Anus and urogenital papilla located ventral to head, with their position apparently somewhat ontogenetically variable in available sample. Anus and urogenital papilla in smaller individuals located along vertical slightly less than one orbital diameter posterior of rear margin of eye and very slightly anterior of vertical through anterior margin of eye in larger individuals. Combined opening for anus and urogenital papilla longitudinally ovoid in all specimens.

Premaxilla with eight to ten teeth (*N* = 8) apparent in whole specimens. Dentary with two tooth rows; outer row with seven to eight teeth and inner row with three to four teeth (*N* = 7).

Branchiostegal rays four; with first two rays narrow and elongate and fourth and fifth rays large and broad and posteriorly forked (de Santana & Nogueira, 2006: fig. 3). Precaudal vertebrae 16 (13–14 anterior; two to three transitional; *N* = 18).

Pectoral-fin rays ii + 13–15 [ii + 13] (*N* = 58). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 20–40 [23] (*N* = 58). Total anal-fin rays 153–174 [168] (*N* = 58). Scales above lateral line at midbody 10–12 [10] (*N* = 58). Scales present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located relatively far posteriorly, approximately at 67% of TL. Filament extending posteriorly to point two to four scales beyond vertical through posterior terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate caudal fin. Caudal-fin rays 12–15 [12] (*N* = 33).

Coloration in alcohol: Overall coloration dark brown. Head dark overall with stripe of slightly darker pigmentation extending anteriorly from orbit to, or nearly to, tip of snout. Slightly more lightly coloured region present on lateral surface of anterior one-third to one-half of snout. Ventral margin of snout dark. Mid-dorsal region of head dark. Body dark brown overall with mid-dorsal region uniformly dark. Pectoral fin dusky with rays covered with small dark chromatophores. Anal fin dusky with rays overlain by small, dark chromatophores. Basal portions of caudal fin dusky, but with distal portions of fin hyaline.

Distribution: Sternarchorhynchus caboclo is only known from the Rio Mucajaí basin of Roraima, Brazil (Fig. 28).

Ecology: The types of *S. caboclo* were collected above and below a waterfall along the Rio Mucajaí. According to Ferreira *et al.* (1988: 341) the river in that region is characterized by steep banks and with dense forest along the shore. Large amounts of aquatic plans of the family Podostemonacease were present in the area, with the water being acidic (pH 5.8) and well oxygenated (91% saturation).

Secondary sexual dimorphism: de Santana & Nogueira (2006: 90: fig. 2b, c) noted apparent differences in the angle of the snout and depth of the posterior portion of the snout in males versus females of *S. caboclo*. A definitive statement on the generality of this difference requires examination of more extensive samples of the species.

Remarks: Sternarchorhynchus caboclo and *S. severii* were collected at the type location. The two species are readily distinguishable by the number of branchiostegal rays (four versus five, respectively), pigmentation of the mid-dorsal region of the head and body (head and body dark versus with narrow, lightly coloured stripe extending posteriorly to the origin of the electroreceptive filament, respectively), the pectoral-fin length (31.3–46.9 versus 48.7–66.6% of HL, respectively), and the depth at the eye (23.3–31.1 versus 31.7–36.0% of HL, respectively).

Material examined

BRAZIL. *Roraima*: Rio Branco basin, Rio Mucajaí, below Cachoeira Paredão 2 (approximately 2°57′N, 61°27′W), INPA 22894, 1 (225.0, holotype, male); INPA 10594, 60 (46.3–226, 2 CS specimens, paratypes). Rio Branco basin, Rio Mucajaí, above Cachoeira Paredão 2 (approximately 2°57′N, 61°27′W), INPA 10578, 1 (178, paratype). Rio Branco basin, Rio Mucajaí, Estrada between Fé and Esperança, INPA 10592, 2 (156–160, paratypes). Rio Branco basin, side channel of Rio Mucajaí, INPA 10541, 1 (36). Rio Branco basin, Rio Mucajaí, approximately 2 km from Cachoeira Paredão 2, mouth of tributary igarapé (approximately 2°57′N, 61°27′W); INPA

Figure 31. ***Sternarchorhynchus chaoi*** **sp. nov.,** holotype, presumably male, 155 mm total length, INPA 28357; Brazil, Rondônia, Rio Jamari.

10580, 1 (193). Rio Branco basin, mouth of Igarapé Traíra, INPA 10590, 1 (200).

STERNARCHORHYNCHUS CHAOI SP. NOV.

(FIGS 28, 31; TABLE 5)

Diagnosis: Sternarchorhynchus chaoi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the vertical through posterior limit of the pectoral fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body that extends posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the presence of eight to 13 premaxillary teeth, 15 precaudal vertebrae, 15–23 anterior unbranched anal-fin rays, 165–178 total anal-fin rays, and ten to 13 scales above the lateral line at the midbody, the greatest body depth (10.0–11.7% of LEA), the eye diameter (3.0–4.2% of HL), the head width (19.5–23.1% of SL), the postocular distance (39.1–41.3% of HL), and the caudal length (5.7–8.9% of LEA).

Description: Morphometric data for examined specimens in Table 5.

Lateral line extending posteriorly to point approximately three scales short of base of caudal fin and absent on remainder of tail and fin. Snout elongate, compressed and nearly straight to slightly curved ventrally distally. Mouth terminal and relatively small, with rictus located within area delimited by verticals running slightly anterior to and slightly posterior of anterior naris. Anus and urogenital papilla located ventral to head, with their position somewhat ontogenetically variable in available sample. Anus and urogenital papilla located along vertical approximately three orbital diameters posterior of rear margin of eye in smaller specimens and very slightly posterior of, or along, vertical through eye in larger individuals. Combined opening for anus and urogenital papilla ovoid in one apparent female and somewhat more horizontally elongate in juveniles and apparent males.

Premaxilla with eight to 13 teeth ($N = 11$) apparent in whole specimens. Dentary with two tooth rows; outer row with seven to nine teeth and inner row with three to five teeth ($N = 11$).

Branchiostegal rays five; with first three rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (12 anterior; three transitional; $N = 11$).

Pectoral-fin rays ii + 11–13 [13] ($N = 11$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 15–23 [22] ($N = 10$). Total anal-fin rays 165–178 [176] ($N = 10$). Scales above lateral line at midbody 10–13 [12] ($N = 11$). Scales absent along mid-dorsal line for distance of one-quarter to one-third of distance between rear of head and origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 67% of TL. Filament extending posteriorly to vertical through posterior terminus of base of anal fin or one to two scales beyond that point. Tail compressed and short, ending in small, moderate, lanceolate caudal fin. Caudal-fin rays 13–16 [14] ($N = 8$).

Coloration in alcohol: Overall coloration dark brown. Snout dark overall with stripe of darker pigmentation extending anteriorly from orbit for distance one-half to two-thirds length of snout. Dorsal region of dark pigmentation on head forms lateral margin of narrow,

Table 5. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus chaoi*, *Sternarchorhynchus cramptoni*, and *Sternarchorhynchus* curumim

	S. chaoi			*S. cramptoni*			*S. curumim*		
	H	Paratypes	Mean	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	155	126–172 (N = 10)	–	290	133–315 (N = 14)	–	163	181–211 (N = 3)	–
Length to end of anal fin (mm)	148	117–163 (N = 9)	–	270	126–294 (N = 13)	–	146	168–187 (N = 3)	–
Head length (mm)	30.9	26.0–32.5 (N = 10)	–	46.4	24.1–51.3 (N = 14)	–	30.0	31.5–38.1 (N = 3)	–
Caudal length (mm)	5.5	8.4–12.1 (N = 8)	–	19.7	6.3–24.4 (N = 12)	–	16.0	20.1–22.9 (N = 2)	–
Per cent of length to end of anal fin									
Anal-fin base	83.7	80–86.5 (N = 9)	82.6	87.7	83.0–88.8 (N = 13)	86.7	85.6	83.9–94.7 (N = 3)	88.6
Distance snout to anus	12.0	11.0–14.7 (N = 9)	12.7	10.2	8.9–12.0 (N = 13)	10.5	–	–	–
Preanal-fin distance	15.6	14.2–17.6 (N = 9)	15.7	11.8	10.9–14.9 (N = 13)	12.6	13.3	12.4–14.4 (N = 3)	13.7
Prepectoral-fin distance	20.8	19.9–23.4 (N = 9)	21.2	16.8	16.5–20.3 (N = 13)	18.0	20.6	18.3–20.4 (N = 3)	19.1
Greatest body depth	11.2	10.0–11.7 (N = 9)	11.2	10.5	9.7–12.1 (N = 13)	10.8	9.9	9.0–10.0 (N = 3)	9.6
Head length	20.8	19.7–22.2 (N = 9)	20.9	17.1	16.0–19.5 (N = 13)	17.9	20.6	18.7–19.7 (N = 3)	19.0
Caudal length	3.7	5.7–8.9 (N = 8)	7.4	7.3	5.0–8.4 (N = 12)	6.8	10.9	12.0–12.2 (N = 2)	12.1
Per cent of head length									
Anus to anal-fin insertion	9.7	7.6–15.5 (N = 10)	11.0	9.7	6.7–12.3 (N = 14)	9.4	8.3	12.4–13.5 (N = 3)	12.8
Pectoral-fin length	34.5	27.5–38.3 (N = 10)	34.4	42.4	38.0–46.5 (N = 14)	42.9	34.5	36.9–37.8 (N = 3)	37.3
Head depth at eye	25.9	25.0–32.0 (N = 10)	27.8	27.9	25.6–35.4 (N = 14)	30.3	–	25.6–30.3 (N = 2)	28.0
Head depth at nape	47.7	41.4–46.6 (N = 10)	44.3	51.3	46.2–58.8 (N = 14)	51.9	41.8	42.8–48.3 (N = 3)	45.2
Head width	20.6	19.5–23.1 (N = 10)	20.9	23.6	21.3–25.9 (N = 14)	23.4	–	19.0–19.8 (N = 2)	19.5
Snout length	60.1	58.8–62.9 (N = 10)	60.9	66.3	60.6–67.0 (N = 14)	64.8	60.2	60.6–62.5 (N = 3)	61.8
Posterior naris to snout	8.1	7.2–9.1 (N = 10)	8.4	6.8	6.0–8.5 (N = 14)	7.6	–	5.9–6.2 (N = 2)	6.0
Posterior naris to eye	50.0	46.3–52.1 (N = 10)	50.1	57.6	50.9–59.3 (N = 14)	55.7	–	54.9–59.8 (N = 2)	57.4
Mouth length	5.6	5.5–6.7 (N = 10)	6.1	5.5	5.2–8.8 (N = 14)	6.5	5.3	3.5–5.6 (N = 3)	4.2
Internarial distance	3.3	2.5–3.6 (N = 10)	2.9	3.2	2.3–4.0 (N = 14)	3.2	2.8	2.4–2.6 (N = 3)	2.5
Eye diameter	3.4	3.0–4.2 (N = 10)	3.5	2.6	2.5–4.2 (N = 14)	3.1	3.9	4.1–5.0 (N = 3)	4.7
Interocular width	6.4	5.5–7.2 (N = 10)	6.5	6.1	5.2–8.5 (N = 14)	6.0	6.5	4.8–6.4 (N = 3)	5.5
Postocular distance	40.3	39.4–41.3 (N = 10)	40.5	39.3	37.4–43.7 (N = 14)	41.0	36.9	33.6–39.2 (N = 3)	37.2
Branchial opening	12.7	10.0–14.8 (N = 10)	12.2	15.4	11.7–17.7 (N = 14)	14.6	11.8	11.7–12.9 (N = 3)	12.1
Per cent of caudal length									
Tail depth	34.2	14.0–21.8 (N = 8)	16.6	25.3	23.6–29.6 (N = 12)	26.9	11.9	10.6–11.7 (N = 2)	11.1
Caudal-fin length	69.5	29.6–51.3 (N = 8)	36.4	35.5	30.9–61.4 (N = 12)	40.9	24.3	19.5–25.2 (N = 2)	22.3

Number of specimens indicated in parentheses.

somewhat obscure, lightly coloured mid-dorsal stripe. Stripe expands very slightly laterally over postocular region, but separated from lightly coloured mid-dorsal stripe on body by region of dark pigmentation. Mid-dorsal lightly coloured stripe on body commences somewhat posterior of terminus of comparable stripe on head and extends varying degrees posteriorly, reaching to origin of electroreceptive filament in some individuals. Pectoral fin distinctly dusky with rays covered with small, dark chromatophores. Anal fin dusky with rays overlain by small, dark chromatophores. Basal portions of caudal fin dusky to distinctly dark, but with distal portions of fin hyaline.

Distribution: Sternarchorhynchus chaoi is only known from one locality in the Rio Jamari basin of the state of Rondônia, Brazil (Fig. 28).

Secondary sexual dimorphism: No clear sexual dimorphism is apparent in the limited available samples of *S. chaoi.*

Etymology: The species name, *chaoi*, is in honour of Ning Labish Chao of the Universidade Federal do Amazonas, who provided invaluable assistance and financial support to the first author during his studies of gymnotiforms in Manaus, Brazil.

Material examined
Holotype: – BRAZIL. *Rondônia*: Rio Jamari, Porto Velho, canal de desvio da (diversion canal of) UHE (Usina Hidroeléctica) Samuel (approximately 8°27′S, 63°30′W), collected by G. M. dos Santos, 7.vi.1998; INPA 28357 (155).

Paratypes: – BRAZIL. *Rondônia*: Rio Jamari, Porto Velho, Canal de desvio da (diversion canal of) UHE (Usina Hidroeléctica) Samuel (approximately 8°27′S, 63°30′W), collected with holotype by G. M. dos Santos, 7.vi.1998; INPA 20851, 11 (126–174); USNM 391713, 1 (164).

Nontype specimens: – BRAZIL. *Rondônia*: amongst rocks above UHE (Usina Hidroeléctrica) Samuel (approximately 8°27′S, 63°30′W); INPA uncat., field number Polo 896, 7 (48–168).

***STERNARCHORHYNCHUS CRAMPTONI* SP. NOV.**

(FIGS 28, 32, 33; TABLE 5)

Sternarchorhynchus cf. *roseni*, Rapp Py-Daniel & Cox-Fernandes, 2005: 105, fig. 5. [Brazil, Amazon Basin; secondary sexual dimorphics in form of lower jaw].

Diagnosis: Sternarchorhynchus cramptoni is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament and sometimes beyond that point, the presence of a dark band along the distal one-fifth to one-half of much of the anal fin and over most of the posterior rays of that fin, the presence of eight to 12

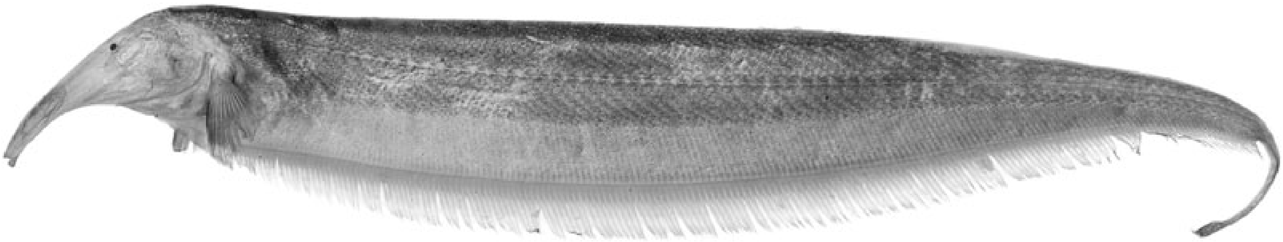

Figure 32. ***Sternarchorhynchus cramptoni* sp. nov.,** holotype, female, 290 mm total length, INPA 28376; Brazil, Amazonas, Rio Solimões, downstream from mouth of Rio Purus.

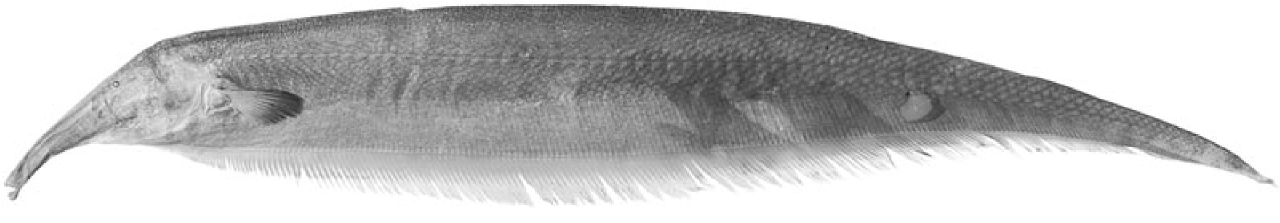

Figure 33. ***Sternarchorhynchus cramptoni* sp. nov.,** sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 331 mm total length, MCP 41638, demonstrating expanded sexually dimorphic dentary and associated dentition; Brazil, Amazonas, Rio Solimões, Ilha do Prego.

teeth on the premaxilla, six to eight teeth on the outer tooth row of the dentary, 180–221 total anal-fin-rays, 16 precaudal vertebrae, the preanal distance (10.9–14.9 of LEA), the greatest body depth (9.7–12.1% of LEA), the caudal length (5.0–8.4% of LEA), the head length (16.0–19.5% of LEA), the distance from the anus to the anal-fin insertion (6.7–12.3% of HL), the snout length (60.6–67.0% of HL), the head depth at the nape (46.2–58.8% of HL), the postocular distance (37.4–43.7% of HL), the prepectoral-fin distance (16.5–20.3% of HL), the tail depth (23.6–29.6% of caudal length), and the caudal-fin length (30.9–61.4% of caudal length).

Description: Morphometric data for holotype and paratypes in Table 5.

Lateral line extending to base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally distally. Posterior naris located closer to tip of snout than to anterior margin of eye. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla ontogenetically variable and apparently sexually dimorphic. Anus and urogenital opening in smaller individuals positioned along vertical located slight distance posterior of vertical through rear margin of eye. Larger specimens lacking secondary male characters with two openings located at vertical running slightly anterior of anterior margin of eye. Males with patch of large teeth at anterior of expanded dentary with anus and urogenital papilla positioned more anteriorly at vertical about one-third of distance between anterior margin of eye and tip of snout. Aperture for anus and urogenital opening rounded in juveniles and apparent females; longitudinally elongate in males demonstrating sexually dimorphic modifications of dentary and associated dentition.

Premaxilla of small size, somewhat rounded, with eight to 12 teeth ($N = 6$). Dentary elongate with fleshy pad on anteroventral surface in larger specimens. Dentaries approximately of same length in males and females, but with form sexually dimorphic. Anterior portion of dentary of males somewhat widened laterally into moderately dorsally bulbous structure bearing enlarged teeth (degree of expansion of dentary and of enlargement of teeth less pronounced than that present in some congeners). Dentary with two rows of curved conical teeth. Outer row with six to eight teeth ($N = 10$) and inner row with three to four teeth ($N = 8$). Mouth terminal with rictus located anterior to vertical through posterior naris in juveniles. Rictus slightly more posteriorly positioned in larger individuals.

Branchiostegal rays five; with first to third rays relatively narrow and elongate and remaining rays large and broad. Precaudal vertebrae 16 (12–13 anterior; three to four transitional, $N = 11$).

Pectoral-fin rays ii + 11–14 [ii + 14] ($N = 30$). Anal-fin origin located slightly posterior of vertical through anterior margin of opercle. Anterior unbranched anal-fin rays 17–29 [24] ($N = 15$). Total anal-fin rays 180–221 [221] ($N = 24$); number of rays apparently increases ontogenetically given evident correlation between greater body size and increased numbers of anal-fin rays amongst examined specimens. Scales above lateral line at midbody 9–12 [9] ($N = 33$). Scales along mid-dorsal region of body readily apparent. Origin of midsaggital electroreceptive filament located approximately at 62% of TL. Filament extending posteriorly to vertical running through to posterior terminus of base of anal fin. Tail compressed and short, ending in small, caudal fin with rounded distal margin. Caudal-fin rays 13–16 [15] ($N = 21$).

Coloration in life: A photo of a recently collected specimen of *S. cramptoni* from the Rio Negro, Brazil, shows a whitish-pink fish with the dark chromatophores on the head appearing as very small dots.

Coloration in alcohol: Overall ground coloration ranging from brown to dark brown. Head and body with dark chromatophores relatively densely scattered over surfaces. Size of chromatophores and intensity of their pigmentation greater in overall darker specimens. Snout with variably distinct, narrow band of darker pigmentation extending anteriorly from region somewhat anterior of eye and reaching anterior portion of snout in many specimens. Band of dark pigmentation forms lateral border of narrow, lightly coloured mid-dorsal band on head. Ventral margin of snout somewhat darker than lateral surface of that region in some specimens, more so in individuals with overall dark coloration of head and body. Mid-dorsal region of head with narrow, lightly coloured stripe apparent even in overall darkly pigmented individuals. Head stripe continuous posteriorly with narrow, lightly coloured mid-dorsal stripe on body. Body pigmentation slightly darker dorsally, but with lightly pigmented mid-dorsal stripe extending posteriorly onto basal portions of electroreceptive filament and to varying degrees posteriorly from that point in different individuals.

Pectoral-fin coloration ranging from dusky to distinctly dark, with dark pigmentation overlying pectoral-fin rays and more developed distally. Anal fin with distinct band of dark pigmentation. Dark band covering approximately distal one-fifth to one-half of fin in most examined specimens, but with dark coloration extending over all, or nearly all, of lateral surface of fin in some darkly coloured individuals. Caudal-fin rays ranging from slightly dusky to distinctly dark with extent and intensity of pigmentation greater in overall more darkly pigmented individuals.

Distribution: Sternarchorhynchus cramptoni is widely distributed along the mainstream of the Amazon River from the region of Iquitos in north-eastern Peru downstream to the Rio Trombetas, a left bank tributary of the Amazon in the state of Pará, Brazil (Fig. 28).

Ecology: Juveniles of *S. cramptoni* have been captured along the margins of main river channels in várzea, whereas adults were captured in the main channels of the sampled rivers (C. D. de Santana, pers. observ.).

Electrical organ discharge: Crampton & Albert (2006: 689) reported that *S. cramptoni* (the *Sternarchorhynchus* n. sp. C of those authors and Crampton, 2007) has a complex EOD pattern comprising four phases of alternating polarities with the weak negative phase apparently flat, but on closer examination exhibiting a gentle curve around a single peak (the type F EOD of those authors). They also noted that the multiphasic nature of this EOD form diverts the energy of the signal away from the fundamental, with the first harmonic representing the peak power frequency.

Secondary sexual dimorphism: Examined samples of *S. cramptoni* demonstrated sexual dimorphism in the form of the lower jaw and associated dentition. Although males of the species have a somewhat enlarged anterior portion of the dentary, that region is not as relatively elongate or bulbous as in males of some congeners. Dentary dentition in that region is also proportionally less developed than are the teeth in mature males of many species of *Sternarchorhynchus*.

Etymology: The species name, *cramptoni*, is in recognition of the many contributions of William Crampton, University of Central Florida, to our knowledge of the biology and systematics of gymnotiforms.

Material examined

Holotype: – BRAZIL. *Amazonas*: Rio Solimões, downstream from mouth of Río Purus (3°27′27″S, 60°45′26″W); collected by Angela Zanata *et al.*, 1.viii.1996; INPA 28376 (290, female; formerly FMNH 115489).

Paratypes: – BRAZIL. *Amazonas*: Rio Solimões, south bank of Ilha do Jaraqui, Alvarães (3°09.51'S, 64°48.76′W), collected by W. G. R. Crampton, 9.xii.1999; MCP 41637, 1 (236). Río Solimões, Ilha do Prego, opposite town of Alvarães (3°12.63'S 64°47.38′W); collected by W. G. R. Crampton, 19.ii.2001; MCP 41638, 1 (331). Rio Solimões, downstream from mouth of Rio Purus (3°27′27″S, 60°45′26″W); collected by Angela Zanata *et al.*, 1.viii.1996, collected with holotype, FMNH 115489, 3 (155–273). Rio Solimões, downstream from mouth of Río Purus (3°26′46″S, 60°45′00″W); collected by Angela Zanata *et al.*, 31.vii.1996; FMNH 115488, 4 (231–275). Rio Solimões, downstream from mouth of Rio Purus (3°27′22″S, 60°45′21″W); collected by Angela Zanata *et al.*, 1.viii.1996; FMNH 115490, 7 (133–315).

Nontype specimens: – BRAZIL. *Amazonas*: Rio Solimões, between mouths of Rio Içа and Río Tonantins, between towns of São Antônio do Iça and Nova Tonantins (2°55′00″S, 67°50′48″W); FMNH 115483, 1 (222). Rio Solimões, between mouth of Rio Iça and Río Tonantins, between towns of São Antônio do Iça and Nova Tonantins (2°55′24″S, 67°51′23″W); FMNH 115482, 1 (280). Rio Amazonas, between mouth of Rio Madeira and Paraná do Serpa, between Manaus and Itacoatiara (3°19′44″S, 58°35′28″W); FMNH 115494, 1 (128). Rio Amazonas, downstream from mouth of Rio Madeira, upstream from Itacoatiara (3°20′22″S, 58°36′31″W); FMNH 115496, 1 (267). Rio Amazonas, upstream from mouth of Rio Madeira and upstream from Itacoatiara (3°15′42″S, 58°58′24″W); FMNH 115491, 2 (154–293). Río Amazonas, downstream from mouth of Río Madeira and upstream from Itacoatiara (3°20′09″S, 58°36′11″W); FMNH 115492, 1 (240). Rio Amazonas, downstream from mouth of Rio Madeira, upstream from Itacoatiara (3°20′59″S, 58°39′32″W); FMNH 115495, 1 (307). Rio Amazonas, between mouths of Rio Negro and Rio Madeira, between towns of Nova Oriente and Itacoatiara (3°16′40″S, 58°56′56″W); FMNH 115493, 1 (215). Rio Purus, Itapuru (4°17′S, 61°54′10″W); INPA 17098, 1 (180). Rio Solimões, Ilha da Marchantaria; INPA 27491 (255); INPA 27114, 1 (245). Rio Purus, marginal lago on shore opposite Lago Surara (4°07′47S, 61°34′50″W); INPA 17099, 1 (265). Rio Purus at Beruri; INPA 17602, 1 (380). Rio Purus, Baia da Resaca, at Beruri; INPA 17603, 2 (328–358). Rio Solimões, Ilha do Careiro; INPA 17601, 3 (327–334). Rio Solimões; INPA uncat. 1 (166). Rio Solimões (3°36′19″S, 61°18′39″W); USNM 373328, 1 (163). Rio Solimões, below Purus (3°36′25″S 61°19′40″W); MZUSP 56882, 2 (150–164). *Pará*: Río Trombetas, between tributaries Lago Iripixi and Cachoeiri, between towns Oriximiná and Fazenda Paraíso; FMNH 115487, 1 (170).

PERU. *Loreto*: Iquitos, Río Amazonas, obtained from aquarium trade; UF 116761, 4 (99–121), UF 123454, 2 (167–310). Iquitos, Río Amazonas; UF 116760, 1 (241).

STERNARCHORHYNCHUS CURUMIM DE SANTANA & CRAMPTON (FIGS 34, 35; TABLE 5)

Sternarchorhynchus curumim de Santana & Crampton, 2006: 59, fig. 1 [type locality: Brazil, Amazonas, Rio Tefé, Toco Preto, Municipality of Tefé, 3°47.31′S, 64°59.91′W]. – Crampton, 2007: 289, 297 [western Amazon; occurrence in blackwater but not whitewater habitats].

Diagnosis: Sternarchorhynchus curumim is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical

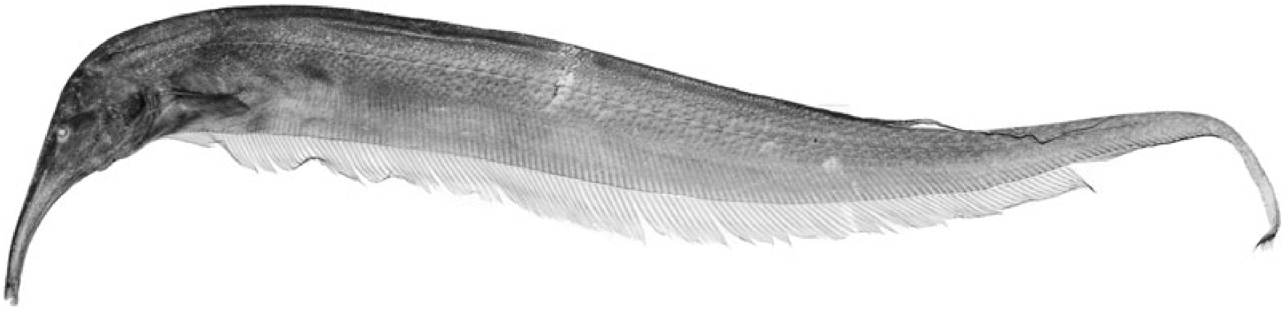

Figure 34. *Sternarchorhynchus curumim*, paratype, female, 211 mm total length, MCP 38305; Brazil, Amazonas, Río Tefé.

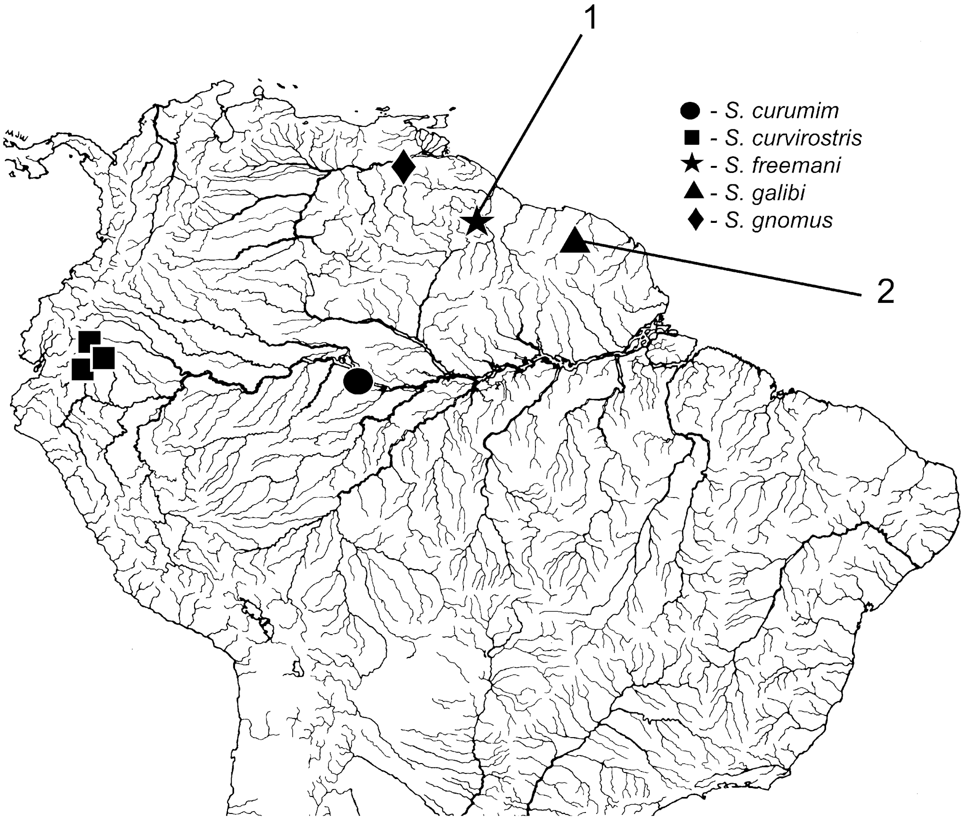

Figure 35. Map of central and northern South America showing geographical distribution of *Sternarchorhynchus curumim*, *Sternarchorhynchus curvirostris*, ***Sternarchorhynchus freemani*** **sp. nov.** (1 = holotype locality), ***Sternarchorhynchus galibi*** **sp. nov.** (2 = holotype locality), and *Sternarchorhynchus gnomus* (some symbols represent more than one locality and/or lot of specimens).

through anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the absence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament, the lateral line that extends to the base of the caudal fin, the dusky anal fin without a distinct dark band along its distal margin, the possession of seven to ten teeth on the premaxillary, seven to eight teeth in the outer row of the dentary, 15 precaudal vertebrae, 23–24 anterior unbranched anal-fin rays, 179–189 total anal-fin rays, ten to 11 scales above the lateral line at the midbody, 13–15 caudal-fin rays, the greatest body depth (9.0–10.0% of LEA), the distance from the anus to the anal-fin insertion (8.3–13.5% of HL), the preanal distance (12.4–14.4% of LEA), the caudal length (10.9–12.2% of LEA), the head length (18.7–20.6% of LEA), the snout length (60.2–62.5% of HL), the mouth length (3.5–5.6% of HL), the eye diameter (4.1–5.0% of HL), the internarial distance (2.4–2.8% of HL), the postocular distance (33.6–39.2% of HL), the pectoral-fin length (34.5–37.8% of HL), the tail depth (10.6–11.9% of caudal length), and the caudal length (10.9–12.2% of LEA).

Description: Morphometric data for examined specimens in Table 5.

Lateral line extending posteriorly to point approximately at base of caudal fin but absent on fin. Snout elongate, compressed and slightly curved ventrally distally. Mouth terminal and relatively small, with rictus located slightly posterior of vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently sexually dimorphic in limited available sample of species. Anus and urogenital papilla positioned along vertical situated approximately one orbital diameter posterior of rear margin of eye in single examined mature female and positioned at vertical one orbital diameter anterior of eye in single mature male. Combined opening for anus and urogenital papilla ovoid in one examined mature male and somewhat more horizontally elongate in mature female.

Premaxilla with seven to ten teeth ($N = 3$) apparent in whole specimens. Dentary with two rows of conical teeth; outer row with seven to eight teeth and inner row with three to four teeth ($N = 2$).

Branchiostegal rays five; with first three rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (12 anterior; three transitional; $N = 4$).

Pectoral-fin rays ii + 11–12 [ii + 12] ($N = 4$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 23–24 ($N = 2$). Total anal-fin rays 179–189 [189] ($N = 3$). Scales above lateral line at midbody ten to 11 [10] ($N = 4$). Scales clearly present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located relatively far posteriorly, approximately at 60% of TL. Filament extending posteriorly to vertical located approximately three scales posterior of vertical through terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate caudal fin. Caudal-fin rays 13–15 [15] ($N = 3$).

Coloration in alcohol: Overall coloration of head and body dark brown. Snout dark overall with stripe of slightly darker pigmentation extending anteriorly from orbit to, or nearly to, tip of snout. Pectoral fin distinctly dusky with rays covered with small dark chromatophores. Anal fin dusky with rays overlain by dark chromatophores. Basal portions of caudal fin distinctly dark, but with distal portions of fin hyaline.

Distribution: Sternarchorhynchus curumim is only known from one locality in the Rio Tefé in the state of Amazonas, Brazil (Fig. 35).

Secondary sexual dimorphism: As documented by de Santana & Crampton (2006: 1166), the single mature male of *S. curumim* has the posterior region of the snout distinctly more developed vertically than do the three known females. No other sexually dimorphic features are present other than for the relatively minor difference in the positions of the anus and urogenital papilla described above.

Material examined

BRAZIL. *Amazonas*: Rio Tefé, Toco Preto, Município de Tefé (3°47.31′S, 64°59.91′W); MCP 38304, 1 (holotype; female, 163 mm); MCP 38305, 2 (paratypes: female 211 mm, male 183 mm); INPA 25256, 1 (cleared and stained paratype; female, 181 mm).

STERNARCHORHYNCHUS CURVIROSTRIS (BOULENGER) (FIGS 35, 36, 37; TABLE 6)

Sternarchus (*Rhamphosternarchus*) *curvirostris* Boulenger, 1887: 282, pl. 24 [type locality; Ecuador, Canelos]. – Eigenmann & Eigenmann, 1891: 62 [assignment to *Sternarchorhynchus*]. – Ellis, 1913: 141 [*Sternarchorhynchus curvirostris* placed in synonymy of *S. oxyrhynchus*]. – Fernández-Yépez, 1967: 18 [*Sternarchorhynchus curvirostris* resurrected from synonymy of *S. oxyrhynchus*]

Sternarchorhynchus curvirostris, Eigenmann & Bean, 1907: 666 [*S. curvirostris* as possible synonym of *S. mormyrus*]. – Fernández-Yépez, 1967: 18 [*S. curvirostris* resurrected from synonymy of *S. oxyrhynchus*]. – Mago-Leccia, 1994: 37, fig. 55 [as valid

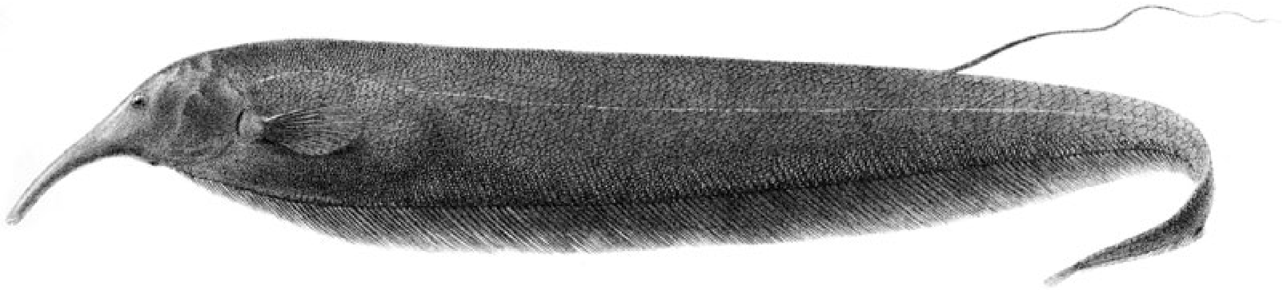

Figure 36. *Sternarchorhynchus curvirostris*, illustration of syntype from Boulenger (1887).

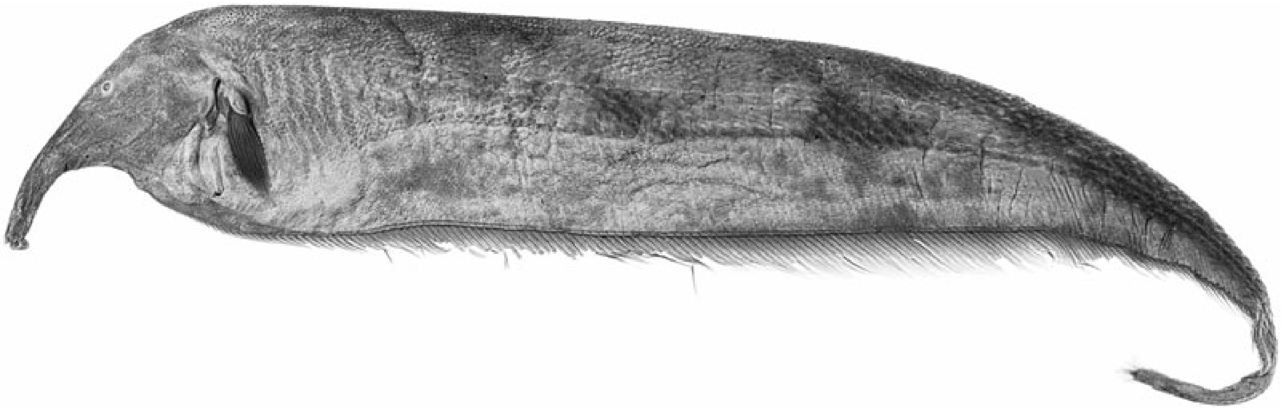

Figure 37. *Sternarchorhynchus curvirostris*, female, 235 mm total length, MCZ 46676; Ecuador, Pastaza, Río Putuno.

species in listing of members of genus]. – Campos-da-Paz, 2000: 528, fig. 3 [in key to species of *Sternarchorhynchus*; syntype illustrated]. – Albert, 2003: 500 [in listing of members of genus].

Diagnosis: Sternarchorhynchus curvirostris is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends posteriorly to the base of the caudal fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and sometimes the mid-dorsal region of the body anterior of the origin of the electroreceptive filament, the darkly coloured anal fin with darker basal coloration but without a distinct, dark, distal band, the presence of eight to 11 teeth on the premaxilla, six teeth in the outer row of the premaxilla, four teeth on the inner row of the premaxilla, 25 unbranched anal-fin rays, 173–180 total anal-fin rays, 16 precaudal vertebrae, 15–16 caudal-fin rays, the preanal distance (11.3–13.4% of LEA), the greatest body depth (12.5–15.0% of LEA), the caudal length (7.9–10.4% of LEA), the distance from the anus to the anal-fin insertion (6.0–6.8% of HL), the head depth at the eye (27.2–35.4% of HL), the head depth at the nape (50.9–67.3% of HL), the snout length (64.5–66.1% of HL), the distance from the posterior naris to the snout (6.9–7.4% of HL), the internarial distance (3.0–4.5% of HL), the eye diameter (3.6–5.8% of HL), the interocular distance (5.6–6.8% of HL), the postocular length (36.7–40.3% of HL), the height of the branchial opening (13.8–16.6% of HL), the pectoral-fin length (38.5–45.7% of HL), and the tail depth (12.7–17.5% of caudal length).

Description: Morphometric data for examined specimens in Table 6.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and distinctly curved ventrally. Mouth terminal and relatively small, with rictus located anterior to vertical through posterior naris. Anus and urogenital papilla located ventral to head, situated along vertical through eye. Combined opening for anus and urogenital papilla ovoid, with intraspecific proportional variation in width of opening.

Premaxilla with eight to 11 teeth ($N = 2$) apparent in whole specimen. Dentary with two tooth rows; outer row with six teeth and inner row with four teeth ($N = 2$).

Table 6. Morphometrics for examined specimens of *Sternarchorhynchus curvirostris*, *Sternarchorhynchus freemani*, and *Sternarchorhynchus* galibi

	S. curvirostris		*S. freemani*			*S. galibi*		
	Range	Mean	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	203–237 ($N = 4$)	–	201	163–172 ($N = 2$)	–	168	80–202 ($N = 9$)	–
Length to end of anal fin (mm)	188–220 ($N = 4$)	–	171	142–146 ($N = 2$)	–	153	75–183 ($N = 9$)	–
Head length (mm)	38.5–41.0 ($N = 5$)	–	37.9	31.3–32.7 ($N = 2$)	–	32.3	16.3–38.9 ($N = 9$)	–
Caudal length (mm)	17.0–20.3 ($N = 3$)	–	28.9	21.5–24.2 ($N = 2$)	–	14.7	8.7–18.4 ($N = 8$)	–
Per cent of length to end of anal fin								
Anal-fin base	83.1–90.2 ($N = 4$)	85.7	88.8	84.5–86.9 ($N = 2$)	85.7	86.2	79.5–86.2 ($N = 9$)	82.4
Distance snout to anus	9.5–12.0 ($N = 4$)	10.7	11.9	12.2–12.7 ($N = 2$)	12.4	11.4	11.3–15.4 ($N = 9$)	13.7
Preanal-fin distance	11.3–13.4 ($N = 3$)	12.6	15.0	16.0–16.7 ($N = 2$)	16.2	14.3	14.2–18.3 ($N = 9$)	16.3
Prepectoral-fin distance	18.7–22.5 ($N = 4$)	20.3	21.6	22.6–23.2 ($N = 2$)	22.9	21.8	19.9–24.6 ($N = 9$)	22.7
Greatest body depth	12.5–15.0 ($N = 4$)	13.4	11.9	11.0–11.2 ($N = 2$)	11.1	12.6	11.1–12.7 ($N = 9$)	11.8
Head length	18.5–21.8 ($N = 4$)	20.0	22.1	21.4–23.0 ($N = 2$)	22.2	21.1	20.2–23.7 ($N = 9$)	22.1
Caudal length	7.9–10.4 ($N = 6$)	9.0	16.9	15.1–16.6 ($N = 2$)	15.8	9.6	8.7–10.8 ($N = 8$)	9.9
Per cent of head length								
Anus to anal-fin insertion	1.6–6.8 ($N = 4$)	3.2	15.0	13.0–17.4 ($N = 2$)	15.2	11.1	6.8–12.8 ($N = 9$)	9.5
Pectoral-fin length	38.5–45.7 ($N = 4$)	42.4	34.8	35.6–37.0 ($N = 2$)	36.3	31.5	31.5–40.7 ($N = 9$)	34.6
Head depth at eye	27.2–35.4 ($N = 5$)	30.2	27.7	25.6–27.0 ($N = 2$)	26.3	30.4	26.2–30.8 ($N = 9$)	28.6
Head depth at nape	50.9–67.3 ($N = 3$)	57.4	41.4	39.5–42.2 ($N = 2$)	40.9	43.2	39.5–47.6 ($N = 9$)	43.0
Head width	18.7–30.3 ($N = 5$)	23.1	20.4	18.8–19.9 ($N = 2$)	19.4	20.9	17.9–23.3 ($N = 9$)	21.1
Snout length	64.5–66.1 ($N = 5$)	65.5	66.0	63.8–64.6 ($N = 2$)	64.2	63.4	57.2–66.0 ($N = 9$)	61.8
Posterior naris to snout	6.9–7.4 ($N = 2$)	7.2	6.5	7.2–7.5 ($N = 2$)	7.4	9.6	7.9–10.7 ($N = 9$)	9.4
Posterior naris to eye	54.5–57.1 ($N = 2$)	55.8	58.0	53.0–54.6 ($N = 2$)	53.8	52.5	42.5–55.5 ($N = 9$)	50.0
Mouth length	5.1–5.7 ($N = 2$)	5.4	5.0	4.8–5.3 ($N = 2$)	5.0	6.6	5.8–7.6 ($N = 9$)	6.5
Internarial distance	3.0–4.5 ($N = 2$)	3.8	2.0	2.3–3.1 ($N = 2$)	2.7	2.9	2.2–3.5 ($N = 9$)	2.7
Eye diameter	3.6–5.8 ($N = 5$)	4.6	4.0	3.8–4.3 ($N = 2$)	4.1	4.6	3.9–6.7 ($N = 9$)	5.0
Interocular width	5.6–6.8 ($N = 5$)	6.2	5.2	5.4–6.2 ($N = 2$)	5.8	6.3	5.6–13.5 ($N = 9$)	8.3
Postocular distance	36.7–40.3 ($N = 5$)	38.2	38.7	36.1–38.6 ($N = 2$)	37.3	39.8	35.6–39.8 ($N = 9$)	37.9
Branchial opening	13.8–16.6 ($N = 4$)	15.5	9.5	10.2–10.8 ($N = 2$)	10.5	11.5	9.8–14.0 ($N = 9$)	11.8
Per cent of caudal length								
Tail depth	12.7–17.5 ($N = 4$)	14.7	8.9	8.0–8.6 ($N = 2$)	8.3	17.1	13.8–19.2 ($N = 8$)	15.8
Caudal-fin length	30.3–56.9 ($N = 2$)	43.6	19.7	17.2–21.7 ($N = 2$)	19.1	29.4	26.6–45.0 ($N = 8$)	34.3

Number of specimens indicated in parentheses. H, holotype; range includes nontype specimens.

Branchiostegal rays five; with first three rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (13 anterior; three transitional; $N = 1$).

Pectoral-fin rays ii + 11–14 [ii + 11] ($N = 5$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 25 ($N = 1$). Total anal-fin rays 173–180 [180] ($N = 4$). Scales above lateral line at midbody nine to 11 [10] ($N = 5$). Scales present along mid-dorsal line to origin of electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 59% of TL. Filament extending posteriorly to vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, elongate, pointed caudal fin. Caudal-fin rays 15–16 ($N = 3$).

Coloration in alcohol: Available specimens including syntypes variably depigmented. Overall coloration tan to brown, but missing on some regions in some nontype specimens as consequence of apparent postmortem damage. Head slightly lighter midventrally and with narrow, lightly coloured mid-dorsal stripe that commences midway along length of snout and expands laterally in region above orbit into longitudinally ovoid, more lightly pigmented area on dorsal surface of postocular portion of head. Lightly coloured region terminates posteriorly approximately at vertical through anterior margin of opercle. Stripe obscure in some individuals. Body tan to dark overall and lacking distinct, narrow, lightly coloured mid-dorsal stripe present in some congeners. Pectoral fin dusky to dark. Anal fin nearly hyaline to dark, more so basally. Caudal fin dusky to dark.

Distribution: Sternarchorhynchus curvirostris is known from the Río Bobanaza, eastern Ecuador and perhaps from north-eastern Peru (Fig. 35; under Remarks below).

Remarks: The original description of *Sternarchus* (*Rhamphosternarchus*) *curvirostris* by Boulenger (1887: 282) reported the length as 125 mm TL. The two specimens now identified as the syntype series (BMNH 1880.12.890-891) are, however, distinctly longer than that length [note: Mago-Leccia (1994: fig. 55) and Campos-da-Paz (2000: fig. 3) both labelled a specimen as the 'type', whereas there are two syntypes]. Searches through the collections of the BMNH failed to yield any other specimens of *S. curvirostris* that correspond to the length reported in the species description. It is impossible to determine whether the reported original length was a lapsus or the purported types are not the material on which the species was based. This question notwithstanding, the specimens identified as the syntypes of *Sternarchus curvirostris* (= *Sternarchorhynchus curvirostris*) otherwise conform to the details in the original description of that species.

Eigenmann & Bean (1907: 666) proposed that *S. curvirostris* might be a synonym of *S. mormyrus* on the basis of specimens that originated in the lower Amazon River between Manaus and Pará (= Belém). They believed that those eastern Amazonian specimens bridged the differences in morphometrics and meristics purported to differentiate *S. curvirostris* from *S. mormyrus*. *Sternarchorhynchus curvirostris* along with *S. mormyrus* were, in turn, considered to be junior synonyms of *S. oxyrhynchus* by Ellis (1913: 141), who recognized the latter species as a monotypic, morphologically highly variable form.

Fernández-Yépez (1967: 18) resurrected *S. curvirostris* (and *S. mormyrus*) from the synonymy of *S. oxyrhynchus* on the basis of external features of the head. The recognition of *S. curvirostris* as a distinct species continued with Mago-Leccia (1994: 37), Campos-da-Paz (2000: 528), and other authors. Based on the information provided by Fernández-Yépez (1967), the specimens that he considered to be *S. mormyrus* were misidentified and it is highly questionable whether the specimen he identified as *S. curvirostris* was that species. Notwithstanding the fact that Fernández-Yépez based his conclusions on erroneous information, our results confirm that *S. curvirostris* is a distinct species. Various authors followed Fernández-Yépez (1967) in considering *S. curvirostris* a component of the Venezuelan ichthyofauna, but we have not examined any specimens of the species that originated in that country or regions proximate to it. It is likely that the original citation represents a misidentification.

We located only five specimens of *S. curvirostris* in museum collections, the two apparent syntypes (BMNH 1880.12.8.90-91) and three other specimens (MCZ 48676; USNM 163887) that were also collected in the Río Bobonaza, Ecuador, the river system from which the type series originated. Three other specimens from portions of north-eastern Peru proximate to the type region (LACM 36324-2, LACM 36327-3) would be considered conspecific with *S. curvirostris* based on counts and overall form of the head and body, but differ from Ecuadorian samples in the degree of pigmentation on the snout. Although this difference may be a consequence of differential preservation or geographical variation, we defer from formally equating these specimens with *S. curvirostris* at this time.

Secondary sexual dimorphism: Sternarchorhynchus curvirostris is not known to demonstrate sexual dimorphism.

Material examined

ECUADOR. *Pastaza*: Canelos (1°35′S, 77°45′W); BMNH 1880.12.8.90-91, 2 (length undetermined because of missing tail-203.2; syntypes of *Sternarchorhynchus* (*Rhamphosternarchus*) *curvirostris*; See remarks concerning the reported type status of these specimens). Río Putuno, tributary of Río Bobonaza; MCZ 48676, 1 (235). Upper Río Pastaza basin, Río Bobonaza, Chicirota (2°22′S, 76°38′W), USNM 163887, 2 (217–240).

The following specimens may be *S. curvirostris* (see Remarks above).

PERU. *Amazonas*: Río Santiago at La Poza (4°01′S, 75°18W); LACM 36324-2, 1 (189), LACM 36327-3, 2 (150–238).

STERNARCHORHYNCHUS FREEMANI SP. NOV.

(FIGS 35, 38; TABLE 6)

Sternarchorhynchus oxyrhynchus, not of Müller & Troschel, Eigenmann, 1912: 438 [in part, specimens from Guyana, Warraputa, and Amatuk]. – Ellis, 1913: 141, 174 [in part, specimens from Guyana, Warraputa, and Amatuk; diet].

Diagnosis: Sternarchorhynchus freemani is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the vertical through posterior limit of the pectoral fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending as far posteriorly as the origin of the electroreceptive filament and sometimes beyond that point, the presence of four to five premaxillary teeth, 16–17 precaudal vertebrae, 26–28 anterior unbranched anal-fin rays, 170–177 total anal-fin rays, eight to nine scales above the lateral line at the midbody, the termination of the electroreceptive filament at the vertical running through a point four scales posterior of the posterior limit of the base of the anal fin, the termination of the lateral line at a point four scales anterior of the base of the caudal fin, the greatest body depth (11.0–11.9% of LEA), the distance from the anus to the anal-fin insertion (13.0–17.4% of HL), the caudal length (15.1–16.9% of LEA), the head width (18.8–20.4% of HL), the distance from the posterior naris to the snout (6.5–7.5% of HL), the interocular width (5.2–6.2% of HL), the postocular distance (36.1–38.7% of HL), the height of the branchial opening (9.5–10.8% of HL), the head depth at the eye (25.6–27.7% of HL), and the tail depth (8.0–8.9% of caudal length).

Description: Morphometric data for examined specimens in Table 6.

Lateral line extending posteriorly to point four scales from base of caudal fin and absent on remainder of tail and on caudal fin. Snout elongate, compressed and slightly curved ventrally along its anterior portion. Mouth terminal. Rictus located slightly anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head, either situated approximately at vertical through eye or along vertical one eye diameter anterior to margin of eye. Combined opening for anus and urogenital papilla longitudinally ovoid in all specimens.

Figure 38. *Sternarchorhynchus freemani* sp. nov., holotype, male, 201 mm total length, CAS 72246; Guyana, Amatuk, Lower Potaro River.

Premaxilla with four to five teeth (*N* = 2) apparent in whole specimens. Dentary with two tooth rows; outer row with eight teeth and inner row with one to two teeth (*N* = 2).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16–17 (12–14 anterior; two to four transitional; *N* = 4).

Pectoral-fin rays ii + 11–12 [ii + 11] (*N* = 4). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 22–28 [22] (*N* = 4). Total anal-fin rays 170–177 [176] (*N* = 4). Scales above lateral line at midbody eight to nine [8] (*N* = 4). Scales absent along mid-dorsal region of body from rear of head posteriorly to point approximately along vertical through posterior limit of pectoral fin. Scaleless region followed by area with sparse mid-dorsal scales and then fully scaled region extending to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately 60% of TL. Filament extending posteriorly four scales beyond vertical through posterior terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate, pointed caudal fin. Caudal-fin rays 13–16 [13] (*N* = 4).

Coloration in alcohol: Overall coloration of head and body ranging from tan to brown. More lightly pigmented specimen with narrow band of darker pigmentation extending anteriorly from eye nearly to tip of snout and with second darker band extending along ventral portions of snout. Two bands of darker pigmentation border more lightly pigmented region extending along lateral surface of snout. Dark bands and intervening more lightly coloured area on snout less apparent in overall darkly pigmented individuals. Dorsal dark band forms lateral margin of narrow, lightly coloured stripe running along mid-dorsal region of snout; mid-dorsal stripe terminates above eye, or slightly posterior of that point. Mid-dorsal stripe on anterior portion of head separated from mid-dorsal stripe on body by dark pigmentation on dorsal surface of head in postocular region. Body with mid-dorsal more lightly pigmented stripe extending from rear of head to origin of electroreceptive filament or to varying degrees posterior of that point. Pectoral fin in overall more lightly coloured specimens hyaline but somewhat dusky with small dark chromatophores overlying fin rays in darker individuals. Anal fin ranging from hyaline to dusky, with darker individuals having small, dark chromatophores overlying fin rays. Caudal fin dark, more so in overall darker individuals, with distal regions somewhat more lightly coloured.

Distribution: Sternarchorhynchus freemani is only known from locations in the lower portions of the Essequibo River basin in Guyana (Fig. 35).

Ecology: Ellis (1913: 174) reported that *S. freemani* (specimens identified as *S. oxyrhynchus* by that author) feeds on various types of aquatic larvae and annelids.

Secondary sexual dimorphism: No sexual dimorphism was apparent in the limited available sample of *S. freemani.*

Etymology: The species name, *freemani*, is in honour of Bryon J. Freeman of the University of Georgia who provided the senior author with invaluable assistance at the Georgia Museum of Natural History.

Remarks: Eigenmann (1912: 438) and Ellis, 1913: 141) reported *S. oxyrhynchus* from Amatuk and Warraputa in the Essequibo River system of Guyana. More recently Watkins *et al.* (2004) cited that species from streams of the Iwokrama forest along the left bank of the Essequibo. As discussed under Remarks for *S. oxyrhynchus*, none of the examined samples of *Sternarchorhynchus* from Guyana proved to be *S. oxyrhynchus*. Examination of the material that served at least in part as the basis of the Eigenmann and Ellis citations of S. *oxyrhynchus* (CAS 72248 formerly CM 1807; CAS 72246, formerly IU 12590) have shown that they are *S. freemani*, a new species described in this study.

Müller & Troschel (1848) reported that the material on which they based their description of *S. oxyrhynchus* originated in the Essequibo River, Guyana. As mentioned within the Remarks section under *S. oxyrhynchus*, none of the samples of that species we examined originated in the Essequibo River or any other river in the Guianas. Rather, all examined specimens of *S. oxyrhynchus* were captured in the Río Orinoco basin. Samples of *Sternarchorhynchus* that originated in the Essequibo River are all *S. freemani*, a species distinguished from *S. oxyrhynchus* by numerous features. One other species of *Sternarchorhynchus* was discovered in samples from the easterly flowing rivers of the Guianas; that being *S. galibi*, a species apparently endemic to the Marowijne River (= Fleuve Maroni) system along the border between Suriname and French Guiana. *Sternarchorhynchus galibi* and *S. oxyrhynchus* differ in diverse features, most notably in mouth form.

Material examined
Holotype: – GUYANA. Essequibo River basin, Lower Potaro River at Amatuk (approximately 5°18′N, 59°18W), collected by C. H. Eigenmann, 10.x.1908; CAS 72246, (201, male).

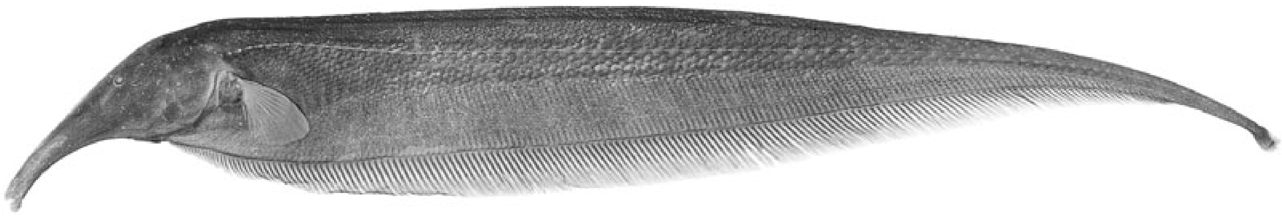

Figure 39. ***Sternarchorhynchus galibi*** **sp. nov.,** holotype, female, 168 mm total length, ZMA 109.366; Suriname, Marowijne District, Lawa River at Stroomafwaarts Rapids near Anapaikekondre.

Paratypes: – GUYANA. Essequibo River basin, Lower Potaro River at Amatuk (approximately 5°18′N, 59°18W), collected by C. H. Eigenmann with the holotype, CAS 227622 ex CAS 72246, 1 (163, female; originally two specimens, but one female was lost during the clearing and staining process but photographed and radiographed), Essequibo River basin, lower Potaro River at Warraputa cataract; CAS 72248, 1 (185).

STERNARCHORHYNCHUS GALIBI SP. NOV.

(FIGS 35, 39; TABLE 6)

Diagnosis: Sternarchorhynchus galibi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the vertical through the posterior limit of the pectoral fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending as far posteriorly as the origin of the electroreceptive filament and sometimes beyond that point, the presence of six to ten premaxillary teeth, 26–31 anterior unbranched anal-fin rays, 169–179 total anal-fin rays, and seven to ten scales above the lateral line at the midbody, the termination of the electroreceptive filament at the vertical running through a point one or two scales anterior of the posterior limit of the base of the anal fin, the termination of the lateral line at a point three or four scales anterior of the base of the caudal fin, the greatest body depth (11.1–12.7% of LEA), the caudal length (8.7–10.8% of LEA), the distance from the anus to the anal-fin insertion (6.8–12.8% of HL), the head width (17.9–23.3% of HL), eye diameter (3.9–6.7 of HL), the head depth at the eye (26.2–30.8% of HL), the head depth at the nape (39.5–47.6% of HL), the postocular distance (35.6–39.8% of HL), the pectoral-fin length (31.5–40.7% of HL), and the tail depth (13.8–19.2% of caudal length).

Description: Morphometric data for examined specimens in Table 6.

Lateral line extending posteriorly to point three or four scales anterior of base of caudal fin but absent on remainder of tail and on caudal fin. Snout elongate, compressed and slightly curved ventrally along anterior portion. Mouth terminal. Rictus located along vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position in smaller specimens located within area delimited anteriorly by vertical running approximately to eye and posteriorly one orbital diameter posterior of eye. Openings positioned one eye diameter anterior to vertical through eye in larger individuals. Combined opening for anus and urogenital papilla circular in smaller individuals and longitudinally ovoid in larger specimens.

Premaxilla with six to ten teeth ($N = 4$) apparent in whole specimens. Dentary with two tooth rows; outer row with six to nine teeth and inner row with one to three teeth ($N = 4$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15–16 (11–12 anterior; four transitional; $N = 2$).

Pectoral-fin rays ii + 12–13 [ii + 12] ($N = 10$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 26–31 [26] ($N = 8$). Total anal-fin rays 169–179 [175] ($N = 10$). Scales above lateral line at midbody seven to ten [10] ($N = 10$). Scales absent along mid-dorsal region of body from rear of head posteriorly to point approximately one-third of distance along length of body and three times length of pectoral fin from rear of head. Scaleless region followed by fully scaled mid-dorsal area to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately 70% of TL. Filament extending to point one or two scales short of vertical through posterior terminus of base of anal fin to vertical through latter landmark. Tail compressed and short, ending in small, elongate, pointed caudal fin. Caudal-fin rays 15–17 [15] ($N = 9$).

Coloration in alcohol: Overall coloration of head and body dark brown. Slightly darker bands of pigmentation extending anteriorly from eye along dorsolateral portion of snout and along ventral portions of snout. Dark bands border more lightly pigmented region on midlateral surface of anterior half of snout. Dorsal dark band forms lateral margin of narrow, lightly coloured stripe running along mid-dorsal region of snout; stripe terminates above eye, or slightly posterior of that point. Mid-dorsal stripe on snout separated from mid-dorsal stripe on body by dark pigmentation on dorsal surface of head in postocular region. Body with more lightly pigmented, mid-dorsal stripe extending from rear of head to origin of electroreceptive filament or to varying degrees posterior of that point. Pectoral fin dusky with small, dark chromatophores overlying fin rays. Anal fin dusky with small, dark chromatophores overlying fin rays. Caudal fin dark with distal regions hyaline.

Distribution: Sternarchorhynchus galibi is known from the Lawa River, Marowijne River (= Fleuve Maroni) basin along the border between Suriname and French Guiana (Fig. 35).

Secondary sexual dimorphism: No sexual dimorphism was apparent in the limited available sample of *S. galibi.*

Etymology: The species name, *galibi*, is in reference to the town of that name begun as a major settlement of the indigenous Caribs. The town is at the mouth of the Marowijne, the drainage system that includes the type locality of *S. galibi.*

Remarks: Sternarchorhynchus oxyrhynchus was cited by Meunier (2004: 89) as occurring in the upper portions of the Fleuve Maroni (= Marowijne River in French Guiana); however, it is likely that this citation was based on *S. galibi.*

Material examined
Holotype: – SURINAME. *Marowijne District*: Lawa River at Stroomafwaarts Rapids near Anapaikekondre (= Anapaike country; Anapaike at 3°34′N, 54°39′W), collected by J. P. Gosse, 18.xi.1966, ZMA 109.366 (168, originally part of IRSCNB 16793, apparently female).

Paratypes: – SURINAME. *Marowijne District*: Lawa River at Stroomafwaarts Rapids near Anapaikekondre (= Anapaike country; Anapaike at 3°34′N, 54°39′W), ZMA 124.524, 1 (121), IRSCNB 16793, 7 (80–202); collected with the holotype by J. P. Gosse, 18.xi.1966. Lawa River base camp, approximately 8 km south-south-west of Anapaike/Kawahaken (airstrip) (3°19′31″N, 54°03′48″W), collected by J. Lundberg, M. Sabaj, P. Willink, and J. Mol, 18.iv.2007, ANSP 187155, 1 (200).

Nontype specimen: – FRENCH GUIANA. Upper Maroni River (no specific locality), MHNG 2167.45, 1 (143).

STERNARCHORHYNCHUS GNOMUS DE SANTANA & TAPHORN (FIGS 35, 40; TABLE 7)

Sternarchorhynchus gnomus de Santana & Taphorn, 2006: 2, figs 1, 2 [type locality: Venezuela, Bolivar, Río Caroni, at confluence with Río Claro, 7°54′30″N, 63°02′50″W].

Diagnosis: Sternarchorhynchus gnomus is distinguished from congeners by the following combination

Figure 40. *Sternarchorhynchus gnomus*, holotype, female, 133.5 mm total length, MCNG 53963; Venezuela, Bolivar, Río Caroní.

Table 7. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus gnomus*, *Sternarchorhynchus goeldii*, and *Sternarchorhynchus* hagedornae

	S. gnomus			*S. goeldii*			*S. hagedornae*		
	H	Paratypes	Mean	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	133.5	76.5–152 (*N* = 9)	–	306.6	193–333.4 (*N* = 9)	–	249	162–206 (*N* = 5)	–
Length to end of anal fin (mm)	116.5	69.1–137 (*N* = 8)	–	280	165–293 (*N* = 7)	–	233	150–193 (*N* = 5)	–
Head length (mm)	23.7	15.6–30.7 (*N* = 9)	–	48.8	34.9–50.0 (*N* = 5)	–	40.9	28.7–35.0 (*N* = 5)	–
Caudal length (mm)	17.3	9.9–14.9 (*N* = 5)	–	27.4	26.7–41.9 (*N* = 3)	–	17.1	10.0–14.4 (*N* = 5)	–
Per cent of length to end of anal fin									
Anal-fin base	81.8	82.4–86.9 (*N* = 7)	84.5	87.1	80.4–87.3 (*N* = 7)	85.3	87.5	86.6–89.6 (*N* = 5)	88.2
Distance snout to anus	13.4	11.8–17.4 (*N* = 8)	15.0	15.6	9.5–15.4 (*N* = 5)	12.9	6.4	8.4–12.0 (*N* = 5)	10.0
Preanal-fin distance	14.7	14.1–17.7 (*N* = 7)	16.6	14.2	12.8–18.9 (*N* = 5)	16.0	11.6	10.4–13.9 (*N* = 5)	11.9
Prepectoral-fin distance	20.0	20.0–23.2 (*N* = 7)	22.3	17.3	17.1–20.9 (*N* = 5)	19.0	17.6	17.9–20.8 (*N* = 5)	19.1
Greatest body depth	9.6	9.3–11.4 (*N* = 7)	10.4	7.5	8.2–10.8 (*N* = 7)	9.3	11.4	12.9–13.3 (*N* = 5)	13.1
Head length	20.3	20.1–24.3 (*N* = 9)	22.2	17.4	17.0–21.1 (*N* = 4)	19.2	17.5	17.7–20.0 (*N* = 5)	18.8
Caudal length	14.8	10.1–17.4 (*N* = 5)	14.6	9.8	14.3–16.2 (*N* = 3)	14.9	7.3	5.5–8.3 (*N* = 5)	7.1
Per cent of head length									
Anus to anal-fin insertion	15.0	7.8–19.9 (*N* = 8)	12.3	23.1	10.1–20.1 (*N* = 5)	14.5	23.3	8.0–10.1 (*N* = 5)	8.9
Pectoral-fin length	38.8	34.8–41.0 (*N* = 9)	36.9	42.7	33.7–37.8 (*N* = 5)	36.4	43.8	39.1–46.9 (*N* = 5)	42.9
Head depth at eye	–	37.4–39.0 (*N* = 3)	38.3	26.5	20.2–25.3 (*N* = 5)	23.7	39.8	29.6–37.2 (*N* = 5)	34.0
Head depth at nape	41.7	39.7–44.9 (*N* = 9)	41.8	45.4	35.0–44.8 (*N* = 5)	39.4	55.4	53.1–59.2 (*N* = 5)	55.8
Head width	20.3	20.0–21.5 (*N* = 5)	20.6	21.0	17.5–20.7 (*N* = 5)	19.0	26.8	24.1–28.3 (*N* = 5)	25.8
Snout length	62.8	57.6–65.4 (*N* = 9)	61.1	61.3	61.6–64.7 (*N* = 5)	62.7	59.6	57.4–58.9 (*N* = 5)	58.1
Posterior naris to snout	11.4	10.9–11.5 (*N* = 5)	11.3	4.9	5.6–6.8 (*N* = 5)	6.2	9.0	8.7–9.8 (*N* = 5)	9.0
Posterior naris to eye	52.7	47.6–55.7 (*N* = 9)	50.3	54.2	53.3–57.5 (*N* = 5)	55.3	48.9	44.6–47.9 (*N* = 5)	46.5
Mouth length	6.3	5.5–9.2 (*N* = 9)	7.3	9.2	6.5–7.9 (*N* = 5)	7.2	8.6	6.4–7.9 (*N* = 5)	7.0
Internarial distance	5.9	2.7–7.0 (*N* = 9)	4.4	3.3	1.8–3.6 (*N* = 5)	2.6	2.7	2.3–3.5 (*N* = 5)	3.1
Eye diameter	5.4	4.1–7.6 (*N* = 9)	5.4	4.5	3.8–5.1 (*N* = 5)	4.2	4.3	4.1–5.9 (*N* = 5)	4.8
Interocular width	8.8	4.2–9.6 (*N* = 9)	6.9	5.6	6.1–7.3 (*N* = 5)	5.0	7.5	6.0–8.5 (*N* = 5)	7.7
Postocular distance	39.2	36.9–41.6 (*N* = 9)	38.7	39.5	34.3–37.1 (*N* = 5)	35.7	44.1	43.6–46.2 (*N* = 5)	45.3
Branchial opening	11.8	9.5–12.3 (*N* = 9)	10.9	16.4	11.0–13.8 (*N* = 5)	12.6	14.8	11.9–14.9 (*N* = 5)	13.6
Per cent of caudal length									
Tail depth	10.9	8.3–13.8 (*N* = 5)	9.9	22.6	13.2–16.3 (*N* = 3)	14.8	22.0	21.3–30.4 (*N* = 5)	25.0
Caudal-fin length	25.4	19.6–31.8 (*N* = 5)	24.9	46.3	22.3 (*N* = 1)	–	40.3	25.8–54.3 (*N* = 5)	38.3

Number of specimens indicated in parentheses.

of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends to the base of the caudal fin, the absence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament or with the stripe very obscure, the hyaline anal fin lacking a dark band along its distal margin, the possession of six to eight premaxillary teeth, one row of dentary dentition with seven to eight teeth, 12 branched pectoral-fin rays, 15 precaudal vertebrae, 21–25 anterior unbranched anal-fin rays, 156–177 total anal-fin rays, six to seven scales above the lateral line at the midbody, ten to 12 caudal fin-rays, the greatest body depth (9.3–11.4% of LEA), the distance from the snout to the anus (11.8–17.4% of LEA), the preanal distance (14.1–17.7% of LEA), the prepectoral-fin distance (20.0–23.2% of LEA), the caudal length (10.1–17.4% of LEA), the head length (20.1–24.3% of LEA), the snout length (57.6–65.4% of HL), the head depth at the nape (39.7–44.9% of HL), the postocular distance (36.9–41.6% of HL), the pectoral-fin length (34.8–41.0% of HL), and the tail depth (8.3–13.8% of caudal length).

Description: Morphometric data for examined specimens in Table 7.

Lateral line extending posteriorly to approximately three to four scales anterior of base of caudal fin, but absent fin. Snout elongate, compressed and slightly curved ventrally along anterior portion. Mouth terminal. Rictus located distinctly anterior of vertical through anterior naris. Anus and urogenital papilla located ventral to head. Openings located at vertical approximately two eyes diameter posterior of margin of orbit in largest specimens. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with six teeth (*N* = 1) in cleared and stained specimen, seven to eight apparent in whole specimens (*N* = 4). Dentary with one tooth row with seven functional and five replacement teeth in cleared and stained specimen (*N* = 1), six to eight functional plus three replacement teeth apparent in whole specimens (*N* = 4).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (13 anterior; two transitional; *N* = 4).

Pectoral-fin rays ii + 12 [ii + 12] (*N* = 10). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 21–25 (*N* = 5). Total anal-fin rays 159–177 [175] (*N* = 9). Scales above lateral line at midbody six to seven [7] (*N* = 10). Scales present along mid-dorsal region of body to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately 60% of TL. Filament extending posteriorly to vertical through posterior terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate, pointed caudal fin. Caudal-fin rays ten to 12 (*N* = 4).

Coloration in alcohol: Overall coloration of head and body dark brown. Slightly darker bands of pigmentation extending from anterior of orbit anteriorly along dorsolateral portion of snout and along ventral portions of snout. Two dark bands border more lightly pigmented region on midlateral surface of anterior half of snout. Mid-dorsal region of head and body with narrow, more lightly coloured, irregularly interrupted stripe extending to origin of midsaggital electroreceptive filament. Pectoral and anal fins hyaline. Caudal fin dark with distal regions hyaline.

Distribution: Sternarchorhynchus gnomus is known from the lower portions of the Río Caroni basin, Venezuela (Fig. 35). The type locality is now submerged by the waters of the Caruachi Reservoir (de Santana & Taphorn, 2006: 1).

Ecology: The type locality of *S. gnomus* was a side channel of the Río Caroni near its confluence with the Río Claro. At that site, the water was clear with a visibility of approximately 2 m and the pH ranging from 6.6–7.6. Stomach contents of the species included chironomids, ephemeropterans, and trichopterans.

*Secondary sexual dimorphism: S*exually mature males of *S. gnomus* appear to have the ventral curvature of the snout more pronounced than do females of comparable sizes (de Santana & Taphorn, 2006: fig. 2).

Material examined
VENEZUELA. *Bolivar*: Río Caroní, at its confluence with Río Claro (7°54′30″N 63°02′50″W); ANSP 182798, 1 (108.8; paratype); INPA 182798, 3 (one cleared and stained, 145.0–152.0; paratypes); MCNG 53963, 1 (133.5; holotype, female); MCNG 18435, 5 (76.5–152.0; paratypes).

STERNARCHORHYNCHUS GOELDII SP. NOV.

(FIGS 41, 42; TABLE 7)

Diagnosis: Sternarchorhynchus goeldii is distinguished from all congeners with the exception of *S. oxyrhynchus* by having the gape of the mouth aligned with main axis of snout, with the gape elongate and extending posteriorly distinctly beyond the vertical

Figure 41. ***Sternarchorhynchus goeldii* sp. nov.,** holotype, female, 306 mm total length, INPA 28378; Brazil, Amazonas, Rio Purus.

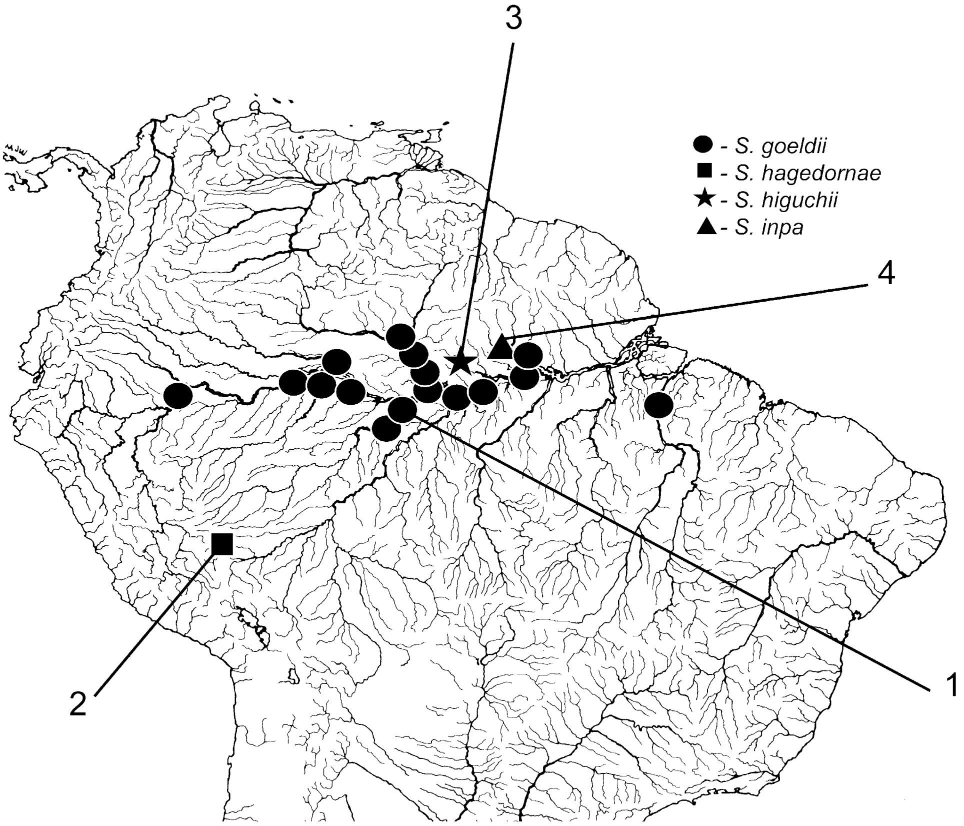

Figure 42. Map of central and northern South America showing geographical distribution of ***Sternarchorhynchus goeldii* sp. nov.** (1 = holotype locality; species also collected in region of type locality of ***Sternarchorhynchus higuchii* sp. nov.**, star), ***Sternarchorhynchus hagedornae* sp. nov.** (2 = holotype locality), ***S. higuchii* sp. nov.** (3 = holotype locality), and ***Sternarchorhynchus inpai* sp. nov.** (4 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

through posterior naris contrary to a shorter gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares. *Sternarchorhynchus goeldii* differs from *S. oxyrhynchus* in the number of total vertebrae (92–94 versus 97–108, respectively), the greatest body depth (8.2–10.8 versus 6.3–8.2% of TL, respectively), and to a large degree in the head depth at the nape (35.0–44.8 versus 26.8–37.7% of SL, respectively).

Description: Morphometric data for holotype and paratypes specimens in Table 7.

Lateral line extending posteriorly to base of caudal fin, but not extending onto fin. Snout elongate, compressed and very slightly curved ventrally along its distal portion, but having overall anteroventral orientation. Anus and urogenital papilla located ventral to head, with position ranging from slightly anterior of vertical through anterior margin of orbit to vertical located two orbital diameters posterior of vertical through rear of orbit. Anus and urogenital papilla generally more anteriorly positioned in larger specimens. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with ten to 11 teeth with six replacement teeth in cleared and stained specimen ($N = 6$). No sexual dimorphism in form of dentary or dentary dentition apparent in examined samples. Dentary with two rows of teeth. Outer row consisting of 13–20 curved conical teeth and inner row with three to five teeth ($N = 7$). Mouth terminal. Gape of mouth aligned with main axis of snout, elongate and extending posteriorly distinctly beyond vertical through posterior naris (Fig. 1A). Lower jaw with terminal fleshy pad that extends anteriorly beyond vertical through anterior limit of snout. Fleshy pad directed dorsally and overlaps tip of snout when mouth closed.

Branchiostegal rays five; with first and second ray narrow and elongate, third to fifth rays becoming progressively wider. Precaudal vertebrae 16–17 (three anterior; three to four transitional; $N = 15$). Total vertebrae 92–94 ($N = 10$).

Pectoral-fin rays ii + 12–14 [ii + 13] ($N = 29$). Anal-fin origin located anterior to vertical through opercle. Anterior unbranched anal-fin rays 21–40 [26] ($N = 17$). Total anal-fin rays 204–237 [215] ($N = 29$). Scales above lateral line at midbody three to six [5] ($N = 21$). Scales absent along mid-dorsal line from rear of head to origin of electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 62% of TL. Filament extending posteriorly beyond vertical through posterior terminus of base of anal fin for distance of approximately five scales. Tail compressed and short, ending in small, elongate caudal fin with rounded posterior margin. Caudal-fin rays 16–22 [20] ($N = 13$).

Coloration in alcohol: Overall ground coloration tan to dark brown. Head and body with small dark chromatophores relatively densely scattered over surfaces. Chromatophores more densely packed and more intensely pigmented in darker specimens. Portion of head anterior of orbit somewhat darker than remaining region of head in some specimens. Some specimens with posteriormost portion of body and all of tail distinctly darker than remainder of body.

Pectoral fin ranging from nearly completely hyaline to overall darkly pigmented, but with dark pigmentation most developed on distal portions and along dorsal margin of fin. Very lightly pigmented specimens with dark pigmentation limited to distalmost portions and dorsal margin of fin. Overall darkly pigmented specimens with dark pigmentation covering distal half to two-thirds of pectoral fin. Distal portions of anal fin variably dark. Overall more lightly pigmented specimens often with distal dark pigmentation barely apparent on anteriormost portion of anal fin and with obvious dark coloration present only as narrow band along distal portion of fin. Some other individuals with distal dark pigmentation extending forward to anterior limit of fin and with broad irregular band of dark pigmentation extending along most of distal portion of fin. Caudal fin dark even in overall lightly pigmented individuals and very dark in most specimens.

Distribution: Sternarchorhynchus goeldii is distributed along the main stream of the Amazon from the region of Óbidos, Brazil, in the eastern portions of the Amazon basin westwards to north-eastern Peru. The species also occurs to varying degrees in the lower courses of tributary rivers of the main Amazon (Fig. 42).

Electrical organ discharge: Crampton (1998) and Crampton & Albert (2006) reported that individuals of *S. goeldii* (identified therein as *Sternarchorhynchus oxyrhynchus*) have a type D EOD pattern with a fundamental frequency of 1321–1390 Hz.

Habits: Crampton (2007: 330) reported on the activity pattern of *S. goeldii* (identified by that author as *S. oxyrhynchus*) in an aquarium setting under subdued natural light. In that setting the species demonstrated increased activity levels at night, but only sporadic foraging activities in the course of the day.

Secondary sexual dimorphism: No secondary sexual dimorphism comparable to that found in many congeners was apparent in exampled samples of *S. goeldii.*

Etymology: The species name, *goeldii*, is in honour of Emilio Goeldi, who made many contributions to our knowledge of many groups of Amazonian animals including fishes.

Material examined

Holotype: – BRAZIL. *Amazonas*: Rio Purus (3°50′06″S, 61°23′59″W); collected by M. Toledo-Piza *et al.*, 26.vii.1996; INPA 28378 (306, formerly USNM 375467).

Paratypes: – BRAZIL. *Amazonas*: Rio Solimões, downstream from mouth of Río Purus, upstream from town of Manacapuru (3°27′22″S, 60°45′21″W) FMNH 115520, 1 (193). Rio Purus (4°53′47″S, 62°54′53″W); INPA 17104, 2 (175–202). Rio Amazonas, 20.6 km above Itacoatiara, 35.5 km below Santa Antonia (3°15′46″S, 58°36′02″W), collected by F. Langeani *et al.*, 20.x.1994; USNM 373081, 1 (212). Rio Solimões, Costa do Marimba, Ilha do Careiro, collected by C. Cox-Fernandes *et al.*; INPA 17633, 4 (285–336). Rio Solimões, near 'encontro das águas' (area of mixing of waters of Rio Negro and Rio Amazonas, collected by C. Cox-Fernandes *et al.*; INPA 24109, 5 (335–367).

Nontype specimens: – BRAZIL. *Amazonas*: Rio Negro, between tributary Rios Cuieras and Taruma-Açu, between towns of Santa Maria and Leprosário (3°01′45″S, 60°24′7″W); FMNH 115505, 4 (213–263), FMNH 115506, 4 (162–244). Rio Jaú, curve of Jaú, Novo Airão; INPA 11355, 1 (184). Rio Jaú, mouth of Río Preto, Novo Airão; INPA 12548, 1 (133), INPA 12551, 2 (176–217), INPA 12656, 1 (194). Rio Negro, 12 km above Leprosário, 16.3 km below Santa Maria (3°02′58″S, 60°22′10″W); USNM 373069, 3 (221–257). Rio Negro 4 km above Manaus (3°08′S, 60°03′W); USNM 373044, 2 (231–251). Rio Negro, between Paraná da Floresta and Paraná da Cotia, between towns of Moura and São Francisco (1°33′48″S, 61°33′3″W); FMNH 115507, 1 (231). Rio Negro, 18.5 km above São Francisco (1°33′45″S, 61°33′01″W); USNM 373075, 1 (221). Rio Negro, USNM 373046, 2 (225–243). Rio Negro, above Manaus; MCZ 98360, 1 (210). Rio Negro, between tributary drainages Curidique and Paraná Jacaré, between towns of Novo Caioe and São Francisco de Assis (1°58′30″S, 61°14′20″W); FMNH 115508, 4 (180–256). Rio Negro, upstream from tributary drainage Tarumã-Mirim and upstream from city of Manaus (3°04′11″S, 60°11′03″W); FMNH 115517, 1 (272). Rio Negro, upstream from Manaus (3°1′18″S, 60°23′29″W); FMNH 115516, 1 (326). Rio Negro, Praia Grande, Manaus; INPA 27495 1 (235). Rio Solimões, Manaus; INPA 24111, 2 (335–339). Rio Negro, near Manaus; INPA 4435, 3 (180–303). Rio Negro, 5.6 km below São Francisco de Assis (1°42′42″S 61°24′27″W); USNM 373106, 3 (173–207). Rio Negro, 33 km below Novo Caioe, 7 km above São Francisco de Assis (1°58′24″S, 61°14′30″W); USNM 373886, 1 (214). Rio Jaú, mouth of Jaú; INPA 12551, 2 (176–217). Rio Jaú, mouth of Rio Preto; INPA 11355, 1 (184), INPA 12656, 1 (191). Rio Amazonas, Paraná do Tapará; INPA 19991, 1 (203). Rio Solimões, Paraná do Xiborena, INPA 17636, 1 (354). Rio Solimões, Paraná do Xiborena; INPA 24110 1 (285). Rio Solimões, Ilha do Careiro, Paraná do Rei; INPA 27497, 1 (353). Rio Solimoes, Lago Januacá, Manaquiri, INPA 27499, 5 (345–360). Rio Solimões, Paraná do Tapará, Autazes; INPA 19991, 1 (200). Rio Purus, Beabá (4°53′47″S, 62°54′51″W); INPA 17104, 2 (173–211). Rio Solimões, Ilha do Careiro, Paraná do Rei; INPA 17634 1 (288), INPA 17637, 1 (347), INPA uncat., 1 (353), INPA uncat., 1 (370). Rio Japurá between mouth of Lagos Mamirauá and Joaquim; INPA 18274, 1 (334). Rio Japurá, at mouth of Lago Mamirauá; INPA uncat., 1 (214). Rio Tefé at Tefé; INPA 15821, 6 (315–370). Rio Tefé, Toco Preto; INPA 15821, 6 (311–369). Rio Amazonas, upstream from mouth of Rio Madeira/Paraná da Eva, upstream from town of Novo Oriente (3°13′37″S, 59°3′32″W); FMNH 115519, 7 (193–295). Rio Solimões, below mouth of Rio Madeira; INPA 20221, 28 (230–313). Rio Solimões, Paraná Xiborena; INPA 16636, 1 (357). Rio Amazonas downstream from Rio Madeira, upstream from town of Itacoatiara (3°20′9″S, 58°36′11″W); FMNH 115518, 1 (289). Rio Uatumã, Presidente Figueiredo at Balbina Dam; INPA 4833, 1 (341). Rio Juruá, tributaries Lago Pauapixuna and Rio Solimões, between towns of Pauapixuna and Vitória (2°41′11″S, 65°48′30″W); FMNH 115503, 2 (257–282). Rio Juruá between Lago Pauapixuna and Rio Solimões, between towns of Pauapixuna and Vitória (2°41′11″S, 65°48′30″W); FMNH 115503, 2 (257–282). Rio Juruá, Lago Pauapixuna and Lago Meneroa, between towns of Pauapixuna and Tamanicoa (2°46′31″S, 65°50′00″W); FMNH 115509, 1 (283). Rio Juruá, between Lago Pauapixuna and Rio Solimões, between towns of Pauapixuna and Vitória (2°41′08″S, 65°48′29″W); FMNH 115502, 1 (289). Rio Jutaí, between mouths of Rio Zinho and Rio Solimões, between towns of Porto Antunes and Copatana (2°51′16″S, 66°57′23″W); FMNH 115510, 1 (257). Rio Juruá tributaries Lago Pauapixuna and Meneroa, between towns of Pauapixuna and Tamanicoa (2°46′31″S, 65°50′00″W); FMNH 115509, 1 (283). Rio Juruá, between Lago Pauapixuna and Rio Solimões, between towns of Pauapixuna and Vitória (2°41′08″S, 65°48′29″W); FMNH 115502, 1 (289). Rio Solimões, downstream from mouth of Rio Purus, upstream from Manacapuru (3°27′22″S, 60°45′21″W); FMNH 115520, 1 (193). Rio Solimões, Lago Manacapuru; MCZ 9340, 2 (200–355), MCZ 24934, 1 (350). Rio Jutaí, between Rio Zinho and Rio Solimões, between towns of Porto Antunes and Copatana (2°51′16″S, 66°57′23″W); FMNH 115510, 1 (257). Rio Jutaí, between Porto Antunes and Foz do Jutaí (2°53′00″S, 66°58′22″W); USNM 375482, 2 (351–353). Rio Solimões (3°36′19″S, 61°18′39″W); USNM 375398, 2 (210–216). Rio Solimões (3°35′43″S, 61°07′16″W); USNM 375399, 1 (261). *Pará*: Rio Tocantins, Tucuruí; INPA 1501, 1 (220). Rio Amazonas between tributaries Paraná de Jurutí and Trombetas, between towns of Jurutí and Óbidos (2°00′39″S, 55°55′17″W); FMNH 115511, 1 (259). Rio Trombetas between tributaries Furo Maria Tereza and Amazonas, between towns of Fazenda Santana and Óbidos (1°52′53″S, 55°38′13″W); FMNH 115512, 1 (183). Rio Trombetas, between tributaries Lago Bacabal and Lago Samauma (1°31′3″S, 56°9′57″W); FMNH 115513, 2 (not measured). Rio Trombetas, between Rio Cumina and Lago Axipica, between towns of Bom Jesus and Santa Cecilia (1°32′40″S; 56°01′07″W); FMNH 115514, 1 (245). Rio Amazonas, 58.5 km below Jurutí, 21.1 km above Óbidos (1°55′48″S, 55°40′41″W); USNM 373040, 4 (329–368). *Roraima*: Rio Negro, at confluence with Rio Branco or along lower 30 mi (48 km) below Rio Branco (approximately 1°24′S, 61°27′W); MCZ 46887, 3 (1 CS, 190–215).

PERU. *Loreto*: Rio Amazonas, beach along east bank of east channel of river, opposite Iquitos; INHS 55418, 3 (224–283).

STERNARCHORHYNCHUS HAGEDORNAE SP. NOV.

(FIGS 42–44; TABLE 7)

Sternarchorhynchus sp., Ortega, 1996: 469 [Peru, Manu Biosphere Reserve, Rio Manu and Quebrada de Pachija, tributary to Rio Manu]. – Hagedorn & Keller, 1996: 493, fig. 2f [Peru, Manu Biosphere Reserve, Quebrada de Pachija, tributary to Rio Manu; habitat, EOD, secondary sexual dimorphism].

Diagnosis: Sternarchorhynchus hagedornae is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the distinctly longitudinally elongate combined opening for the anus and the urogenital opening, the sparse scales covered by skin along the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament, the consistently dark overall coloration of the head and body, the presence of a more lightly coloured, narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament and sometimes posterior of that point, the absence of a very dark band of pigmentation at the base of the enlarged patch of dentition on the dentary in mature males, the possession of five to six teeth in the outer tooth row of the dentary, 27–35 anterior unbranched anal-fin rays, 173–193 total anal-fin rays, nine to 13 scales above the lateral line at the midbody, the greatest body depth (11.4–13.3% of LEA), the length of the anal-fin base (86.6–89.6% of LEA), the prepectoral-fin distance (17.6–20.8% of LEA), the caudal length (5.5–8.3% of LEA), the head depth at the nape (53.1–59.2% of HL), the head width (24.1–28.3% of HL), the distance from the posterior naris to the snout (8.7–9.8% of HL), the mouth length (6.4–8.6% of HL), the interocular width (6.0–8.5% of HL), the distance from the posterior naris to the eye (44.6–48.9% of HL), the postocular distance (43.6–46.2% of HL), the pectoral-fin length (39.1–46.9% of HL), and the tail depth (21.3–30.4% of caudal length).

Description: Morphometric data for holotype and paratypes in Table 7.

Lateral line extending to base of caudal fin, but absent on fin. Snout elongate, compressed and straight. Posterior naris closer to tip of snout than to anterior margin of orbit. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla apparently ontogenetically and perhaps sexu-

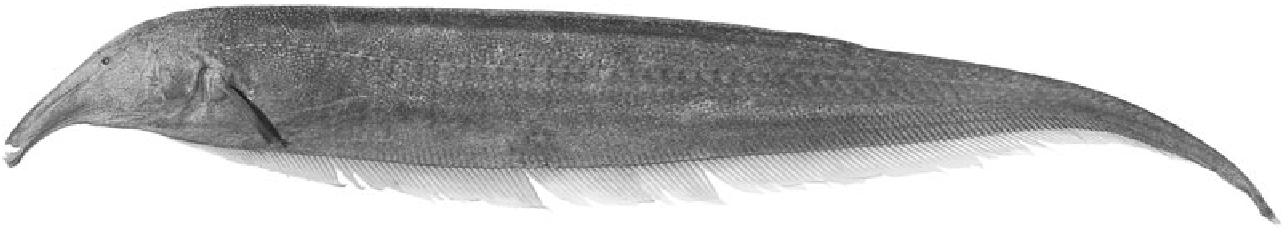

Figure 43. *Sternarchorhynchus hagedornae* sp. nov., holotype, sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 249 mm total length, MUSM 30534; Peru, Madre de Dios, Río Manu.

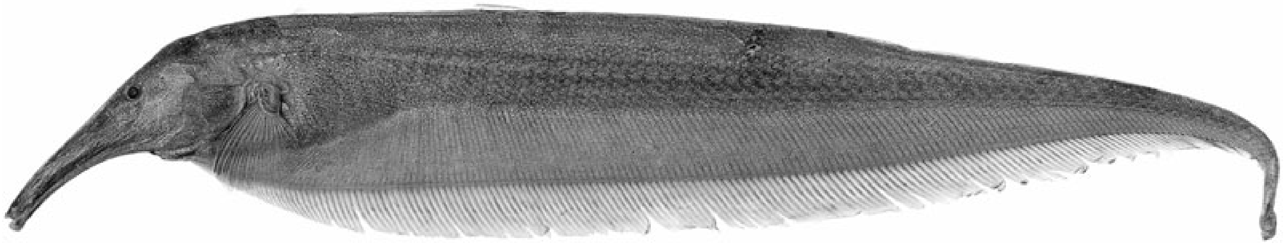

Figure 44. *Sternarchorhynchus hagedornae* sp. nov., female, approximately 192 mm total length, ANSP 180637; Peru, Madre de Dios, Quebrada Pachija, Río Manu.

ally variable, but definite pattern uncertain because of limited sample size. Anus and urogenital papilla in smaller individual (162 mm TL) located at vertical running two orbital diameters posterior of eye. Mid-sized specimen (206 mm SL) with structures positioned slightly anterior of vertical through eye. Male with definite patch of enlarged dentition on expanded anterior portion of dentary (249 mm TL) with anus and urogenital papilla more anteriorly positioned, and located along vertical approximately one-quarter of distance between anterior limit of orbit and tip of snout. Combined opening for anus and urogenital papilla longitudinally elongate.

Premaxilla of small size, somewhat rounded, with five to eight teeth (*N* = 4). Dentary with two tooth rows. Outer tooth row with five to six curved conical teeth and inner tooth row with three to four teeth (*N* = 3). Mature males with dentary expanded anteriorly and widened laterally into dorsally bulbous region rounded from dorsal view, with expansion bearing patch of enlarged dentition. Mouth terminal with rictus in juveniles located slightly posterior to vertical through anterior naris. Rictus in adults shifted somewhat anteriorly and located anterior to vertical through anterior naris.

Branchiostegal rays five; with first to third rays relatively narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16–17 (13 anterior; three to four transitional; *N* = 4).

Pectoral-fin rays ii + 12–14 [ii + 14] (*N* = 6). Anal-fin origin located slightly posterior of vertical through anterior margin of opercle. Anterior unbranched anal-fin rays 27–35 [27] (*N* = 6). Total anal-fin rays 173–193 [173] (*N* = 6). Scales above lateral line at midbody nine to 13 [13] (*N* = 6). Scales along mid-dorsal region of body somewhat sparse and not readily apparent on body surface. Origin of midsaggital electroreceptive filament located approximately at 70% of TL. Filament in juveniles extending posteriorly to vertical one scale posterior of vertical through posterior terminus of base of anal fin; filament in adults reaching to vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small and moderate caudal fin. Caudal-fin rays 12–16 [18] (*N* = 6).

Coloration in alcohol: Overall ground coloration dark brown. Series of whitish, papillae-like structures broadly distributed over lateral and dorsal portions of posterior two-thirds of snout, lateral surface of head, and dorsalmost portion of body. Lightly coloured spots limited to irregular single series to each side of electroreceptive filament on posterior portion of body. Snout with variably distinct, narrow band of darker pigmentation extending anteriorly from region somewhat anterior of orbit; and reaching anterior portion of snout in some individuals and apparent even in overall darkly pigmented specimens. Band of dark pigmentation forms lateral border of narrow, more lightly coloured mid-dorsal band present on head. Anterior portion of lightly coloured mid-dorsal stripe on head less apparent in male with well-developed patches of enlarged dentition on lower jaw. Body pigmentation very slightly darker dorsally, but with mid-dorsal more lightly coloured stripe continuous with corresponding stripe on head and extending posteriorly onto basal portions of electroreceptive filament.

Pectoral fin dark in all specimens, with dark chromatophores overlying fin rays. All examined specimens with anal fin dusky and posterior margin of fin outlined by series of dark chromatophores. Caudal fin dark overall, but with distal margin hyaline.

Distribution: All examined specimens of *S. hagedornae* originated in the Manu Biosphere Reserve, in the upper Río Madeira basin in south-eastern Peru (Fig. 42).

Ecology: Hagedorn & Keller (1996: 488, 490 493) remarked that the type locality for *S. hagedornae*, Quebrada Pachija, is an open-gallery, high flow stream with a flow of 0.748 m/s, a mean stream depth of 0.397 ± 0.059 m, and a mean stream width of 19.1 ± 1.0 m. According to these authors this species, (their *Sternarchorhynchus* sp.) 'lived in the fastest flowing water sampled; most adult specimens were captured from a single rocky rapids'. Their collecting efforts also yielded numerous fry and small juveniles from within floating debris along the fast-flowing edges of the Río Manu that they considered to be the same species. We have not examined these samples.

Electrical organ discharge: Sternarchorhynchus hagedornae was studied in the field by Hagedorn & Keller (1996: 493, figs 2f, 4) who reported that it is a high frequency, wave-type fish with peak-power EOD frequencies ranging from 977–2832 Hz and a mean of 1608.5 ± 160.6 Hz SE in the 14 specimens examined. They remarked on the variety of EOD types observed in the species (Hagedorn & Keller, 1996: fig. 4), but pointed out that they lacked sufficient specimens to determine whether this variation reflected sexual dimorphism in this feature; however, they did comment that the heterogeneity might reflect changes with 'age, sex and/or activity pattern'.

Secondary sexual dimorphism: The obvious sexually dimorphic feature in *S. hagedornae* is the anteriorly lengthened and transversely widened anterior portion of the dentary in males and the associated patch of enlarged, posteriorly recurved teeth on this region.

Figure 45. ***Sternarchorhynchus higuchii* sp. nov.,** holotype, sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 246 mm total length, INPA 28358; Brazil, Amazonas, Cachoeira do Miriti, Rio Uatumã.

The male (249 mm TL) had the anus and urogenital papilla more anteriorly positioned than did the slightly shorter, possibly female, specimen (206 mm TL) and the juveniles. In the male, the anus and the urogenital papilla are located along the vertical running approximately one-quarter of the distance between the anterior limit of the orbit and the tip of the snout. This position is distinctly anterior of the location of the anus and urogenital papilla in smaller specimens, in which these structures are positioned from slightly anterior to variably posterior of the vertical through the eye.

Etymology: The species name, *hagedornae*, is in honour of Mary Hagedorn of the Smithsonian Institution who collected the type series and has made many contributions to our understanding of the diversity of gymnotiforms.

Material examined

Holotype: – PERU. *Madre de Dios*: Manu Biosphere Reserve, Quebrada Pachija, tributary emptying into Río Manu 3 km upstream of Pakitza (Pakitza at 11°55′48″S, 71°15′18″W), MUSM 30534, 1 (249, male); collected by M. Hagedorn *et al.*

Paratypes: – PERU. *Madre de Dios*: Manu Biosphere Reserve, Quebrada Pachija, tributary emptying into Río Manu 3 km upstream of Pakitza (Pakitza at 11°55′48″S, 71°15′18″W), collected by M. Hagedorn *et al.*, with holotype, USNM 391574, 2 (169–206); MUSM 30535, 1 (202); MBUCV 33742, 2 (162–194). MUSM 23755, (174); Manu Biosphere Reserve, Río Los Amigos.

Nontype specimens: – PERU. *Cuzco*: Río Inambari and mouth of Quebrada Hondonado, Madre de Dios drainage, upstream of Puerto Mazuko (13°06′23″S, 70°24′44″W), ANSP 180637, 2 (200–208).

STERNARCHORHYNCHUS HIGUCHII SP. NOV.

(FIGS 42, 45, 46; TABLE 8)

Diagnosis: Sternarchorhynchus higuchii is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through anterior nares, the presence of scales although sometimes sparse and covered by skin along the mid-dorsal region of the body to the origin of the electroreceptive filament, the presence of an obscure, more lightly coloured, narrow band of mid-dorsal pigmentation on the head and anterior mid-dorsal region of the body, the slightly dusky anal fin without a distinct dark band along its distal margin, the lateral line extending posteriorly to a point approximately four to seven scales short of the base of the anal fin, the possession of two rows of dentary teeth with the outer row having nine to ten teeth, 23–31 anterior unbranched anal-fin rays, 162–178 total anal-fin rays, eight to 12 scales above the lateral line at the midbody, ten to 12 caudal-fin rays, the caudal length (14.7–18.9% of LEA), and the tail depth (5.9–7.5% of caudal length).

Description: Morphometric data for holotype and paratypes in Table 8.

Lateral line falling short of base of caudal fin by distance equal to four to seven scales and absent on remainder of tail and on caudal fin. Snout elongate,

Figure 46. ***Sternarchorhynchus higuchii* sp. nov.,** female, 180 mm total length, INPA 20855; Brazil, Amazonas, Cachoeira do Miriti, Rio Uatumã.

compressed and slightly curved ventrally distally. Posterior naris closer to tip of snout than to anterior margin of orbit. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla apparently sexually dimorphic. Anus and urogenital papilla in smaller individuals and apparently mature females located within area between vertical located two orbital diameters posterior of orbit and vertical running through eye. Males with definite patch of enlarged dentition on dentary with anus and urogenital papilla more anteriorly positioned, located along verticals two to four orbital diameters anterior of anterior margin of eye (most anterior position approximately one-quarter of distance between anterior margin of orbit and tip of snout). Combined opening for anus and urogenital papilla distinctly elongate longitudinally.

Premaxilla of small size, somewhat rounded, with seven to eight teeth ($N = 5$). Dentary with two tooth rows with six curved conical teeth in outer row and three to four teeth on inner row ($N = 5$) in juveniles and females. Mature males demonstrating sexual dimorphism in lower jaw with anterior portion of dentary extending further anteriorly than in females and juveniles and with dentary distinctly expanded laterally into dorsally bulbous structure rounded from dorsal view. Expanded portion of dentary bearing series of enlarged, slightly posteriorly recurved teeth. Mouth terminal in juveniles and females and somewhat dorsally directed in males with anteriorly and transversely expanded dentaries. Rictus located slightly anterior to vertical through anterior naris in all specimens.

Branchiostegal rays five; with first to third rays relatively narrow and elongate and remaining rays large and broad. Precaudal vertebrae 15–16 (12–13 anterior; two to four transitional; $N = 16$).

Pectoral-fin rays ii + 11–13 [ii + 13] ($N = 14$). Anal-fin origin located slightly posterior of vertical through anterior margin of opercle. Anterior unbranched anal-fin rays 23–31 [28] ($N = 14$). Total anal-fin rays 162–178 [171] ($N = 15$). Scales above lateral line at midbody eight to 12 [10] ($N = 16$). Scales along mid-dorsal region of body present, but somewhat sparse and not readily apparent on body surface. Origin of midsaggital electroreceptive filament located approximately at 59% of TL. Filament in specimens of all sizes extending six to eight scales posterior of vertical through posterior terminus of base of anal fin. Tail compressed and long, ending in very small, somewhat elongate caudal fin. Caudal-fin rays ten to 12 [11] ($N = 11$).

Coloration in alcohol: Overall ground coloration dark brown. Snout with variably distinct, narrow band of slightly darker pigmentation extending from region somewhat in advance of eye to anterior portion of snout. Second stripe of dark pigmentation running ventrally on snout to lower jaw. Two dark stripes delimit intermediate, more lightly pigmented region running along lateral surface of snout. Dorsal band of dark pigmentation forms lateral border of narrow, lightly coloured, mid-dorsal band on head that terminates posteriorly in region dorsal to eye. Body pigmentation very slightly darker dorsally and without distinct mid-dorsal lightly coloured stripe present in that region in many congeners. Mid-dorsal region of body irregularly less intensely pigmented in some individuals, but with these lighter areas not confluent and not forming distinct, narrow stripe.

Pectoral fin coloration dark in all specimens, with dark chromatophores overlying fin rays. All examined specimens with anal fin dusky and posterior margin of fin-rays outlined by series of dark chromatophores. Caudal fin dark overall, but with distal margin hyaline.

Table 8. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus higuchii*, *Sternarchorhynchus inpai*, and *Sternarchorhynchus jaimei*

	S. higuchii			*S. inpai*			*S. jaimei*		
	H	Paratypes	Mean	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	246	88.0–243 (*N* = 15)	–	191	54.0–222 (*N* = 11)	–	200	72.2–123 (*N* = 11)	–
Length to end of anal fin (mm)	208	76–205 (*N* = 15)	–	165	47.0–192.4 (*N* = 11)	–	182	64.4–115 (*N* = 8)	–
Head length (mm)	40.9	18.8–39.0 (*N* = 15)	–	34.6	10.8–39.4 (*N* = 11)	–	34.9	14.0–23.4 (*N* = 11)	–
Caudal length (mm)	38.6	12.1–37.7 (*N* = 11)	–	23.3	9.7–27.4 (*N* = 5)	–	18.1	8.3–10.6 (*N* = 7)	–
Per cent of length to end of anal fin									
Anal-fin base	84.6	81.1–86.8 (*N* = 15)	84.2	81.8	79.7–97.7 (*N* = 7)	84.7	86.8	79.9–89.4 (*N* = 8)	83.9
Distance snout to anus	10.0	9.0–15.0 (*N* = 15)	12.4	8.1	6.7–12.2 (*N* = 6)	9.2	11.1	11.1–15.3 (*N* = 8)	13.1
					13.4				
Preanal-fin distance	13.9	14.5–17.5 (*N* = 15)	15.9	16.3	15.2–16.3 (*N* = 6)	15.7	13.9	13.9–17.1 (*N* = 8)	15.6
					18.9				
Prepectoral-fin distance	19.2	19.2–40.7 (*N* = 15)	22.3	20.8	20.0–22.9 (*N* = 6)	21.5	19.8	19.5–23.7 (*N* = 8)	21.2
Greatest body depth	9.2	8.7–11.0 (*N* = 15)	10.0	12.2	9.6–13.2 (*N* = 6)	11.5	10.8	10.8–12.6 (*N* = 8)	11.7
					10.3				
Head length	19.6	18.6–22.6 (*N* = 15)	21.0	20.9	19.8–23.1 (*N* = 11)	21.5	19.2	18.7–23.9 (*N* = 11)	20.7
					20.4				
Caudal length	18.5	14.7–18.9 (*N* = 11)	17.1	14.1	12.6–15.6 (*N* = 4)	14.3	9.9	8.0–15.1 (*N* = 7)	10.6
Per cent of head length									
Anus to anal-fin insertion	16.5	6.9–14.7 (*N* = 14)	10.5	13.6	12.0–20.0 (*N* = 2)	15.2	12.3	4.8–12.3 (*N* = 8)	8.3
Pectoral-fin length	36.7	31.0–41.2 (*N* = 15)	35.1	39.3	27.9–42.3 (*N* = 6)	37.4	47.9	35.7–58.4 (*N* = 8)	45.8
					27.9				
Head depth at eye	27.5	22.8–31.1 (*N* = 15)	26.1	26.8	26.8–34.1 (*N* = 2)	29.1	30.3	26.1–35.7 (*N* = 11)	31.8
					26.3				
Head depth at nape	41.9	36.6–47.2 (*N* = 15)	41.2	40.5	40.7–48.6 (*N* = 6)	45.5	49.5	43.9–58.7 (*N* = 11)	50.3
					44.9				
Head width	21.0	18.5–24.4 (*N* = 15)	20.1	20.8	20.2–21.4 (*N* = 2)	20.8	23.9	22.7–28.9 (*N* = 11)	24.9
Snout length	64.7	54.6–63.8 (*N* = 15)	61.7	65.8	57.3–64.7 (*N* = 6)	60.9	58.7	52.7–67.2 (*N* = 11)	57.7
Posterior naris to snout	7.8	6.6–9.6 (*N* = 15)	7.5	8.1	6.7–9.0 (*N* = 2)	7.9	8.3	8.1–12.9 (*N* = 11)	10.0
Posterior naris to eye	55.2	39.4–55.1 (*N* = 15)	52.0	57.4	43.7–59.7 (*N* = 6)	51.2	49.5	37.0–55.1 (*N* = 11)	45.0
					59.7				
Mouth length	5.5	4.9–7.3 (*N* = 15)	5.8	6.7	4.7–8.7 (*N* = 6)	6.9	6.5	4.3–8.4 (*N* = 11)	6.5
Internarial distance	2.8	2.0–4.3 (*N* = 15)	2.7	3.3	2.3–4.1 (*N* = 6)	3.1	2.9	1.9–4.2 (*N* = 11)	3.1
					2.6				
Eye diameter	3.6	3.1–5.2 (*N* = 15)	4.1	4.1	3.6–5.6 (*N* = 6)	4.7	4.0	4.0–6.3 (*N* = 11)	5.1
Interocular width	4.7	3.3–12.3 (*N* = 11)	7.0	6.9	5.9–8.7 (*N* = 6)	7.0	6.6	6.6–10.7 (*N* = 11)	8.7
					5.9				
Postocular distance	37.0	35.5–42.5 (*N* = 15)	38.8	33.1	38.0–41.1 (*N* = 6)	39.0	44.7	41.5–49.1 (*N* = 11)	44.1
Branchial opening	10.5	9.6–12.3 (*N* = 15)	10.9	12.3	9.4–13.4 (*N* = 6)	11.7	12.9	11.4–17.9 (*N* = 11)	14.1
					10.9				
Per cent of caudal length									
Tail depth	6.1	5.9–7.5 (*N* = 11)	6.4	9.1	8.0–11.1 (*N* = 4)	9.6	16.5	10.1–19.2 (*N* = 7)	15.5
Caudal-fin length	10.3	12.5–20.6 (*N* = 10)	15.2	23.9	20.1–23.6 (*N* = 4)	22.1	34.1	17.3–46.0 (*N* = 7)	33.9

Sexually dimorphic features for *S. inpai* are presented as two entries. First entry is data for all specimens other than sexually dimorphic mature males with information for sexually dimorphic male in second entry based on one specimen of 222 mm total length. Number of specimens indicated in parentheses.

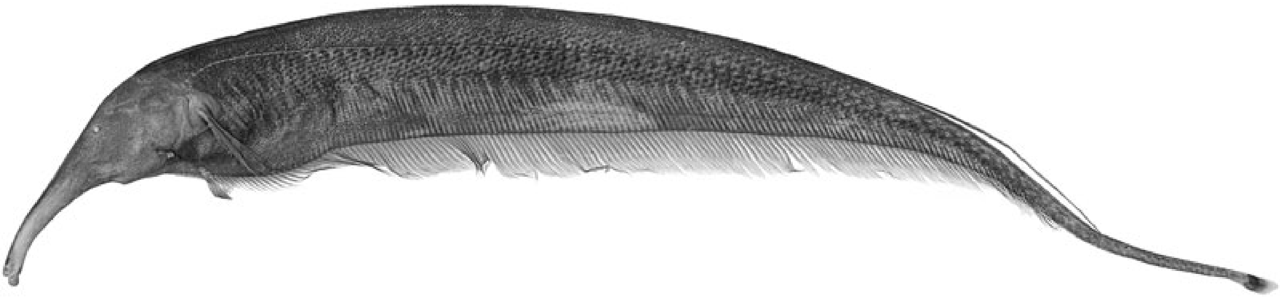

Figure 47. *Sternarchorhynchus inpai* sp. nov., holotype, female, 191 mm total length, INPA 22895; Brazil, Pará, Cachoeira Porteira, Rio Mapuera.

Distribution: All examined specimens of *S. higuchii* were collected at the Cachoeira do Miriti and Cachoeira do Morena in the Rio Uatumã in the eastern portions of Amazonas, Brazil (Fig. 42).

Secondary sexual dimorphism: Mature males of *S. higuchii* have an anteriorly extended and laterally enlarged anterior portion of the dentary with the associated patch of enlarged teeth. Males bearing such elaborations of the lower jaw and dentary teeth have the anus and urogenital papilla more anteriorly positioned than in examined conspecifics of comparable body sizes. Both the anus and urogenital papillae in these males are located distinctly anterior of the vertical through the eye, rather than at, or posterior of, that position as in males lacking modified dentaries and associated dentition. Females and juveniles similarly have these structures in a posterior position. Examined females of *S. higuchii* with mature ovaries are smaller than available males demonstrating sexual dimorphism in the lower jaw and dentary dentition.

Etymology: The species name, *higuchii*, is in honour of Horácio Higuchi of the Museu Paraense Emilio Goeldi, who provided invaluable assistance to the first author during his early studies of gymnotiforms.

Remarks: Sternarchorhynchus higuchii was collected at the same type locality as *S. jaimei*. The two species differ in the posterior extent of the lateral line (falling short of base of caudal fin by four to seven scales versus reaching the base of the caudal fin, respectively), total anal-fin rays (162–178 versus 180–195, respectively), the pigmentation of the mid-dorsal region of the body anterior to the origin of the electroreceptive filament (dark versus with narrow, lightly coloured stripe, respectively), and caudal depth (5.9–7.5 versus 10.1–19.2% of caudal length, respectively), and nearly completely in body depth (8.7–11.0 versus 10.8–12.6 of LEA, respectively).

Material examined
Holotype: – BRAZIL. *Amazonas*: Rio Uatumã, Cachoeira do Miriti, Presidente Figueredo (approximately 2°01′S, 59°28′W), INPA 28358 (246), collected by E. Ferreira, R. Leite, and S. Kullander, 4.x.1987.

Paratypes: – BRAZIL. *Amazonas*: Rio Uatumã, Cachoeira do Miriti, Presidente Figueredo (approximately 2°01′S, 59°28′W), collected by E. Ferreira, R. Leite, and S. Kullander, with holotype, INPA 20855, 15 (88–243); USNM 391714, 1 (189).

Nontype specimens: – BRAZIL. *Amazonas*: Rio Uatumã, Cachoeira do Miriti (approximately 2°01′S, 59°28′W), INPA uncat., 2 (158–181). Rio Uatumã, Cachoeira do Morena, INPA 20854, 25 (125–233).

STERNARCHORHYNCHUS INPAI SP. NOV.

(FIGS 42, 47, 48; TABLE 8)

Sternarchorhynchus oxyrhynchus Ferreira, 1995: 51 [Brazil, Pará, Rio Trombetas, Cachoeira Porteira].

Diagnosis: Sternarchorhynchus inpai is distinguished from all congeners by having a very short first branchiostegal ray that is distinctly shorter than the second ray rather than being approximately subequal in length to that ossification. It is furthermore differentiated from all other species of *Sternarchorhynchus* by possessing the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the more lightly coloured mid-dorsal stripe on the head sometimes extending posteriorly to the vertical through the insertion of the pectoral fin, the dusky anal fin, the very short first branchiostegal ray, the possession of four to seven

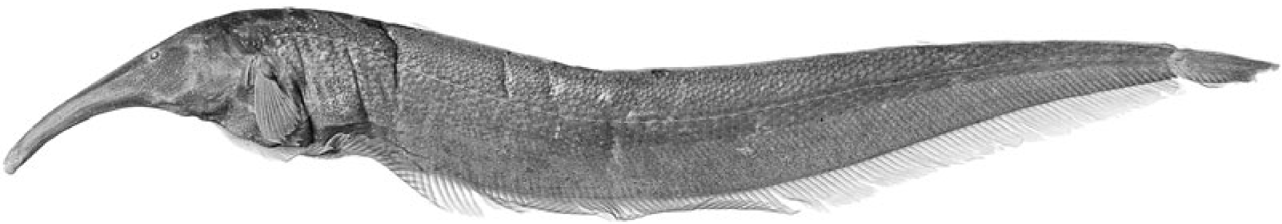

Figure 48. ***Sternarchorhynchus inpai* sp. nov.,** paratype, male (tail broken), 222 mm total length, INPA 22899; Brazil, Pará, Cachoeira Porteira, Rio Mapuera.

premaxillary teeth, five to six teeth in the outer row of the dentary, 15 precaudal vertebrae, the distance from the snout to the anus in mature males (13.4% of LEA), the preanal distance (15.2–16.3% of LEA; 18.9 in mature male), the caudal length (12.6–15.6% of LEA), the pectoral-fin length (27.9–42.3% of HL; 27.9 in mature male), the head depth at the eye in mature males (26.3 of HL), the head depth at the nape (40.5–48.6% of HL), the distance from the posterior naris to the eye in mature males (59.7 of HL), the postocular distance (33.1–41.1% of HL), the height of the branchial opening (9.4–13.4% of SL; 10.9% in mature males), the tail depth (8.0–11.1% of caudal length), and the caudal-fin length (20.1–23.9% of caudal length).

Description: Morphometric data for examined specimens in Table 8.

Lateral line extending posteriorly to point four scales anterior of base of caudal fin but absent on fin. Snout elongate, compressed and slightly curved ventrally along anterior portion. Mouth terminal to very slightly anterodorsally orientated and relatively small with distinct fleshy pad at anterior of lower jaw. Rictus located anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically variable. Anus and urogenital papilla located along vertical about one orbital diameter posterior of eye in juveniles and along verticals through to one orbital diameter anterior of eye in mature males and females. Combined opening for anus and urogenital papilla longitudinally ovoid in all specimens.

Premaxilla with four to seven teeth ($N = 6$) apparent in whole specimens. Dentary with two tooth rows; outer row with five to six teeth and inner row with three teeth ($N = 4$).

Branchiostegal rays five; with first ray distinctly shorter than second and first three rays narrow. Fourth and fifth rays large and broad with fifth ray branched distally on both sides in cleared and stained specimen. Precaudal vertebrae 15 (13 anterior; two transitional; $N = 6$).

Pectoral-fin rays ii + 12–13 ($N = 7$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 17–24 [17] ($N = 3$). Total anal-fin rays 156–167 [161] ($N = 7$). Scales above lateral line at midbody eight to 11 ($N = 9$). Scales present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately at 60% of TL. Filament extending posteriorly three to seven scales beyond vertical through posterior terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate, pointed caudal fin. Caudal-fin rays 13–16 [14] ($N = 6$).

Coloration in alcohol: Overall coloration brown. Head dark brown overall other than for more lightly coloured stripe along lateral surface of snout and very narrow, lightly coloured mid-dorsal stripe on snout that terminates posteriorly approximately at vertical through eye. Body dark overall, somewhat more so dorsally. Pectoral fin dusky with rays somewhat darker than membranes. Anal fin dusky with rays darker than membranes. Caudal fin dark with distal regions somewhat lighter.

Distribution: Sternarchorhynchus inpai is only known from the type locality at Cachoeira Porteira on the Rio Mapuera, Pará, Brazil (Fig. 42).

Secondary sexual dimorphism: The single mature examined male of *S. inpai* as evidenced by the well-developed testes has a slightly longer snout than do females of comparable sizes. This species matures at relatively small body sizes with a 154 mm TL female bearing well-developed eggs and the single mature male being at least 222 mm (a portion of the caudal is lacking in this specimen).

Etymology: The species name, *inpai*, is in reference to the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Brazil, that has been the centre for the study of the biodiversity of the Brazilian Amazon for over five decades.

Remarks: Specimens reported as *S. oxyrhynchus* by Ferreira (1995: 51) from Cachoeira Porteira have proved to be *S. inpai. Sternarchorhynchus inpai* occurs in the same river basin as *S. mareikeae* and the two species have similar coloration patterns. They differ in the numbers of teeth on the premaxilla (four to seven versus 12–13, respectively), and in the outer row of the dentary (five to six versus 12–13, respectively), and the number of precaudal vertebrae (15 versus 16, respectively). Mature males of the two species can be furthermore distinguished on various sexually dimorphic morphometric features detailed in tables 15 and 18 of Ferreira (1995), most notably the distance from the snout to the anus (13.4% in *S. inpai* versus 8.8–10.8% in *S. mareikeae*), the preanal distance (18.9 versus 12.7–15.2%, respectively), and the height of the branchial opening (10.9 versus 12.3–15.4%, respectively).

Material examined

Holotype: – BRAZIL. *Pará*: Rio Mapuera, Cachoeira Porteira, last fall before Rio Trombetas (approximately 1°05′S 57°02′W); collected by E. Ferreira and M. Jégu, 19.iv.1985; INPA 22895, 191.0 mm TL, female.

Paratypes: – BRAZIL. *Pará*: Rio Mapuera, Cachoeira Porteira, last fall before Rio Trombetas (approximately 1°05′S 57°02′W); collected with holotype by E. Ferreira and M. Jégu, 19.iv.1985; INPA 22899, 10 (1 CS; 54–222); USNM 391715, 1 (195).

STERNARCHORHYNCHUS JAIMEI SP. NOV.

(FIGS 49, 50; TABLE 8)

Diagnosis: Sternarchorhynchus jaimei is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the vertical through the posterior limit of the pectoral fin, the presence of a narrow, more lightly coloured band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the lateral line that extends to the base of the caudal fin, the presence of four to seven premaxillary teeth, 23–26 anterior unbranched anal-fin rays, and 180–195 total anal-fin rays, the distance from the anus to the anal-fin insertion (4.8–12.3% of HL), the distance from the posterior naris to the snout (8.1–12.9% of HL), the head width (22.7–28.9% of HL), the head depth at the nape (41.8–43.2% of HL), the interocular distance (6.6–10.7% of HL), the postocular distance (41.5–49.1% of HL), the height of the branchial opening (11.4–17.9% of HL), the postocular distance (41.5–58.7% of HL), the pectoral-fin length (35.7–58.4% of HL), the caudal depth (10.1–19.2% of caudal length), and the caudal-fin length (17.3–46.0% of caudal length).

Description: Morphometric data for examined specimens in Table 8.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly curved ventrally along anterior portion; curvature more pronounced in larger individuals. Mouth terminal. Dentary with distinct fleshy pad anteriorly. Rictus located anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically variable. Anus and urogenital papilla located along vertical about two orbital diameters posterior of eye in juveniles and along vertical through eye in larger specimens. Combined opening for anus and urogenital papilla ranging from circular to longitudinally ovoid.

Premaxilla with four to seven teeth ($N = 5$) apparent in whole specimens. Dentary with two tooth rows; outer row with eight to nine teeth and inner row with two to three teeth ($N = 5$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (12–13 anterior; three to four transitional; $N = 12$).

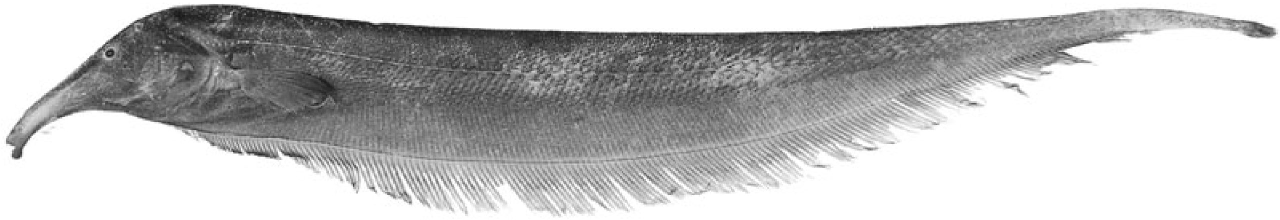

Figure 49. ***Sternarchorhynchus jaimei* sp. nov.,** holotype, female, 200 mm total length, INPA 28359; Brazil, Amazonas, Cachoeira do Miriti, Rio Uatumã.

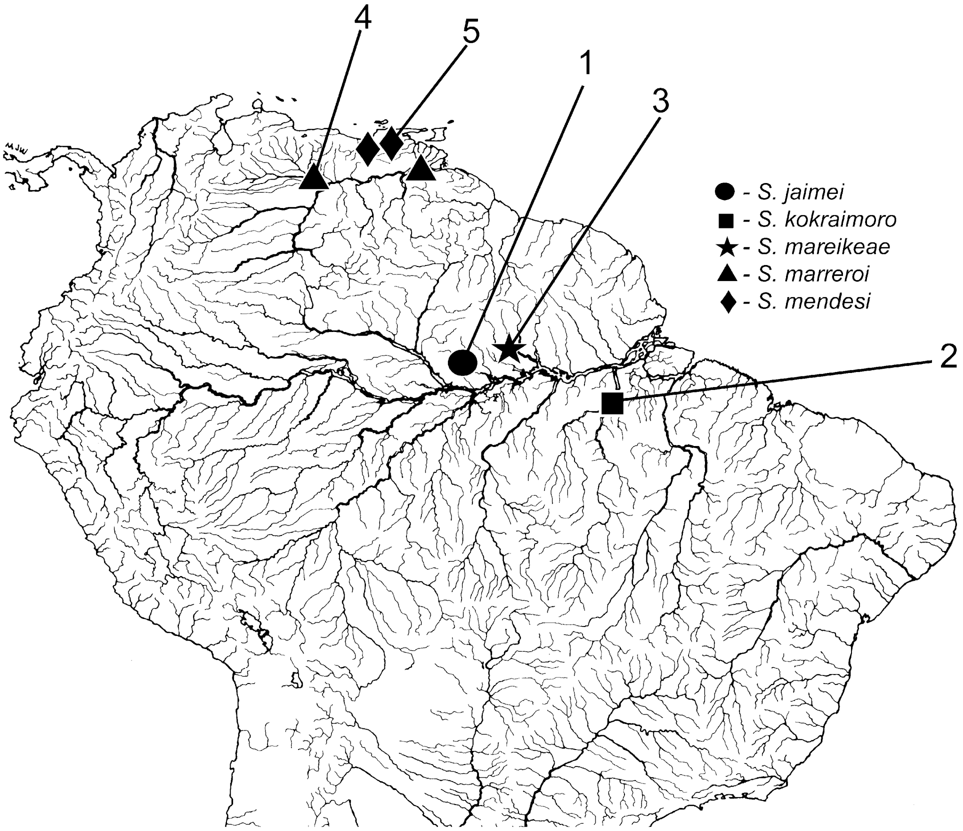

Figure 50. Map of central and northern South America showing geographical distribution of *Sternarchorhynchus jaimei* (1 = holotype locality), ***Sternarchorhynchus kokraimoro* sp. nov.** (2 = holotype locality), ***Sternarchorhynchus mareikeae* sp. nov.** (3 = holotype locality), ***Sternarchorhynchus marreroi* sp. nov.** (4 = holotype locality), and ***Sternarchorhynchus mendesi* sp. nov.** (5 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

Pectoral-fin rays ii + 11–14 [ii + 11] ($N = 12$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 23–36 [25] ($N = 12$). Total anal-fin rays 180–195 [184] ($N = 7$). Scales above lateral line at midbody nine to 12 [12] ($N = 12$). Scales along mid-dorsal midline of body absent or sparse to midlength of body in smaller specimens, and absent in larger specimen as far posteriorly as vertical through posterior limit of pectoral fin, then sparse to midlength of body and followed by regular series of scales as far posteriorly as origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, at point approximately 65% of TL. Filament extending posteriorly four to six scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, somewhat rounded caudal fin in juveniles and in small, somewhat lanceolate fin in large individuals. Caudal-fin rays 11–18 [14] ($N = 7$).

Coloration in alcohol: Overall coloration of head and body brown. Head with variably intense band of dark pigmentation extending along dorsolateral surface of snout nearly to tip of snout. Ventrolateral portion of snout dark. Two dark bands on snout border intermediate more lightly coloured region on anterior half of snout. Dorsal band of dark coloration forms lateral margin of narrow, lightly coloured stripe extending from tip to snout to varying degrees beyond vertical through eye and onto mid-dorsal postocular portion of head. Stripe on head variably obscurely continuous with narrow, lightly coloured mid-dorsal stripe on body. Mid-dorsal stripe on body extending posteriorly to origin of electroreceptive filament. Pectoral fin dusky with rays somewhat darker than membranes. Anal fin dusky with rays darker than membranes. Caudal fin dark with distal regions somewhat lighter.

Distribution: Sternarchorhynchus jaimei is only known from the Rio Uatumã, Amazonas, Brazil (Fig. 50).

Secondary sexual dimorphism: No sexual dimorphism was apparent in the examined samples of *S. jaimei.*

Etymology: The species name, *jaimei*, is in honour of Jaime Ribeiro Carvalho Júnior, of the Centro do Jovem Aquarista, in recognition of his invaluable assistance to the first author during the early phases of his studies of gymnotiforms.

Remarks: One of the examined specimens, a female of 115 mm TL, had clearly developing eggs and it seems likely that the species matures at relatively small body sizes. *Sternarchorhynchus jaimei* was collected at the same type locality as *S. higuchii.* The species differ in various details of pigmentation, meristics, and morphometrics detailed in Remarks under *S. higuchii*.

Material examined

Holotype: – BRAZIL. *Amazonas*: Rio Uatumã, Cachoeira do Miriti, Presidente Figueredo (approximately 2°01′S, 59°28′W), collected by E. Ferreira, R. Leite, and S. Kullander, 4.x.1987; INPA 28359 (200, maturing female).

Paratypes: – BRAZIL. *Amazonas*: Rio Uatumã, Cachoeira do Miriti, Presidente Figueredo (approximately 2°01′S, 59°28′W), collected with holotype by E. Ferreira, R. Leite, and S. Kullander, 4.x.1987; INPA 22902, 2 (72.2–75.6). Rio Uatumã, Cachoeira Morena, Presidente Figueredo, collected by E. Ferreira, R. Leite, and S. Kullander, 7.x.1987; INPA 26122, 10 (one cleared and stained, 88–123); USNM 391716, 1 (127).

STERNARCHORHYNCHUS KOKRAIMORO SP. NOV.

(FIGS 50–52; TABLE 9)

Diagnosis: Sternarchorhynchus kokraimoro is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the absence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament, the dusky anal fin, the termination of the lateral line three to five scales anterior of the base of the caudal fin, the possession of seven to ten premaxillary teeth, two tooth rows on the dentary with eight to ten teeth in the outer row, 175–177 total anal-fin rays, eight to nine scales above the lateral line at the midbody, 16–17 precaudal vertebrae, 15 caudal-fin rays, the distance from the snout to the anus (13.6–15.0% of LEA), the preanal distance (16.9–17.1% of LEA), the prepectoral-fin distance (23.1–24.0% of LEA), the head length (22.9–23.1% of LEA), the caudal length (14.3–15.5% of LEA), the distance from the anus to the anal-fin insertion (8.2–12.5% of HL), the head width (18.6–20.2% of HL), the snout length (63.7–66.2% of HL), and the interocular distance (4.6–5.1% of HL).

Figure 51. *Sternarchorhynchus kokraimoro* sp. nov., holotype, male, showing deeper snout of males, 197 mm total length, INPA 28360; Brazil, Pará, Cachoeira de Kaituká, Rio Xingu.

Figure 52. ***Sternarchorhynchus kokraimoro* sp. nov.,** paratype, female, 171 mm total length, INPA 3932; Brazil, Pará, Cachoeira de Kaituká, Rio Xingu.

Description: Morphometric data for examined specimens in Table 9.

Lateral line extending posteriorly to point approximately three to five scales anterior of base of caudal fin but absent on remainder of tail and on fin. Snout elongate, compressed and curved ventrally distally. Male with dorsomedial fleshy ridge on anterior half of snout; ridge absent in female. Ridge makes that portion of snout of male overall distinctly deeper than in female (compare Figs 51, 52). Mouth moderate, with opening anterodorsally orientated, and rictus located at, or slightly posterior of, vertical through anterior naris. Dentary in mature male lengthened anteriorly, slightly expanded transversely and bearing patch of somewhat enlarged teeth. Anus and urogenital papilla located ventral to head, with position apparently sexually dimorphic in limited available sample. Anus and urogenital papilla positioned along vertical through eye in mature female and slightly more anteriorly in single mature male. Combined opening for anus and urogenital papilla ovoid in both sexes.

Premaxilla with seven to ten teeth ($N = 2$) apparent in whole specimens. Dentary with two tooth rows; outer row with eight to ten teeth and inner row with two to three teeth ($N = 2$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16–17 (14 anterior; two to three transitional; $N = 2$).

Pectoral-fin rays ii + 12–13 [ii + 13] ($N = 2$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 22–23 [23] ($N = 2$). Total anal-fin rays 175–177 [175] ($N = 2$). Scales above lateral line at midbody eight to nine [9] ($N = 2$). Scales clearly present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 64% of TL. Filament extending posteriorly to vertical located two scales posterior of vertical through terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate caudal fin. Caudal-fin rays 15 [15] ($N = 2$).

Coloration in alcohol: Overall coloration of head and body dark brown. Snout dark overall with stripe of distinctly darker pigmentation extending from orbit anteriorly to, or nearly to, tip of snout. Ventral portion of snout darkly pigmented; that pigmentation along with dark pigmentation on dorsolateral portion of snout delimits intermediate, more lightly coloured band running along lateral surface of snout. Head and body uniformly dark along mid-dorsal region contrary to condition present in many congeners. Pectoral fin distinctly dusky with rays covered with small, dark chromatophores. Anal fin slightly dusky, with rays overlain by spots of dark pigmentation. Caudal fin dark overall, but with distal most margin hyaline.

Distribution: Sternarchorhynchus kokraimoro is only known from the Cachoeira de Kaituká in the Rio Xingu (Fig. 50).

Ecology: Little information is available about the type locality of *S. kokraimoro* other than that it was a rapids area in the northern portions of the Rio Xingu (also Campos-da-Paz, 1999).

Table 9. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus kokraimoro*, *Sternarchorhynchus mareikeae*, and *Sternarchorhynchus marreroi*

	S. kokraimoro		*S. mareikeae*			*S. marreroi*		
	H	Paratype	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	197	171	192	131–221 (*N* = 9)	–	182	231–278 (*N* = 2)	–
Length to end of anal fin (mm)	172	148	165	120–192 (*N* = 9)	–	166	209–252 (*N* = 2)	–
Head length (mm)	39.4	34.2	31.2	25.8–35.1 (*N* = 9)	–	27.1	34.3–41.3 (*N* = 2)	–
Caudal length (mm)	26.7	21.2	22.1	19.8–27.8 (*N* = 8)	–	14.6	22.8–26.4 (*N* = 2)	–
Per cent of length to end of anal fin								
Anal-fin base	86.0	85.1	85.4	82.0–86.9 (*N* = 9)	85.1	85.5	88.4–92.3 (*N* = 2)	90.4
Distance snout to anus	13.6	15.0	9.6	8.8–13.5 (*N* = 9)	11.4	9.0	5.8–7.7 (*N* = 2)	6.7
				8.8–10.8	9.7			
Preanal-fin distance	16.9	17.1	13.9	12.2–17.8 (*N* = 9)	15.2	10.8	9.2–10.1 (*N* = 2)	9.7
				12.7–15.2	13.7			
Prepectoral-fin distance	24.0	23.1	19.0	17.9–23.1 (*N* = 9)	20.6	17.6	17.0–17.0 (*N* = 2)	17.0
				37.5–40.9	39.1			
Greatest body depth	10.1	12.3	10.0	10.9–13.6 (*N* = 9)	11.9	13.4	11.2–14.1 (*N* = 2)	12.6
				10.9–11.8	11.2			
Head length	22.9	23.1	18.9	18.3–23.2 (*N* = 9)	20.6	16.6	16.4–16.4 (*N* = 2)	16.4
				18.3–20.2	19.11			
Caudal length	15.5	14.3	13.4	13.4–17.4 (*N* = 8)	15.6	8.8	10.4–10.9 (*N* = 2)	10.6
Per cent of head length								
Anus to anal-fin insertion	12.5	8.2	73.7	66.9–78.3 (*N* = 9)	73.5	10.1	16.2–17.6 (*N* = 2)	16.9
Pectoral-fin length	31.0	31.1	38.5	35.0–40.9 (*N* = 9)	38.6	47.5	52.0–75.8 (*N* = 2)	63.9
				37.5–40.9				
Head depth at eye	26.3	26.7	30.0	28.7–38.4 (*N* = 9)	32.5	32.9	34.1–35.4 (*N* = 2)	34.8
				29.9–38.4	33.5			
Head depth at nape	43.6	46.3	49.5	45.1–53.4 (*N* = 9)	49.5	62.6	55.1–65.5 (*N* = 2)	60.3
Head width	20.2	18.6	24.4	19.7–25.4 (*N* = 9)	22.5	29.9	25.9–28.7 (*N* = 2)	27.3
Snout length	66.2	63.7	61.0	51.2–65.4 (*N* = 9)	60.9	62.4	62.3–63.6 (*N* = 2)	62.9
Posterior naris to snout	8.3	7.4	–	–	–	7.8	6.4–7.9 (*N* = 2)	7.2
Posterior naris to eye	55.0	55.0	50.5	48.2–53.7 (*N* = 9)	51.8	48.8	50.7–53.4 (*N* = 2)	52.1
				52.3–53.7	52.9			
Mouth length	6.5	5.9	6.8	4.3–9.4 (*N* = 9)	5.7	7.0	5.3–6.4 (*N* = 2)	5.8
Internarial distance	1.8	2.0	3.1	2.9–4.6 (*N* = 9)	3.5	4.3	3.0–3.5 (*N* = 2)	3.3
				3.2–3.5	3.4			
Eye diameter	3.9	3.8	4.8	3.5–5.3 (*N* = 9)	4.5	4.5	3.3–4.4 (*N* = 2)	3.9
Interocular width	5.1	4.6	9.0	6.6–8.1 (*N* = 9)	7.3	8.1	6.8–8.1 (*N* = 2)	7.4
				6.6–7.4	7.0			
Postocular distance	38.8	37.6	37.7	36.0–41.3 (*N* = 9)	38.6	49.0	45.3–45.4 (*N* = 2)	45.4
Branchial opening	12.0	12.1	10.9	11.9–15.4 (*N* = 9)	12.9	15.3	15.6–19.6 (*N* = 2)	17.6
				12.3–15.4	13.2			
Per cent of caudal length								
Tail depth	10.1	12.3	9.7	7.1–10.2 (*N* = 9)	8.8	20.2	15.7–19.2 (*N* = 2)	17.5
Caudal-fin length	19.8	22.5	–	18.5–24.7 (*N* = 7)	20.8	39.0	32.4 (*N* = 1)	–

Sexually dimorphic features for *Sternarchorhynchus mareikeae* are presented as two entries. First entry is data for all specimens other than sexually dimorphic mature males with information for sexually dimorphic male in second entry based on four specimens of 176–221 mm total length. Number of specimens indicated in parentheses.

Secondary sexual dimorphism: The single examined male of *S. kokraimoro* has the lower jaw lengthened and somewhat expanded laterally, albeit to a lesser degree than that in congeners that share this sexually dimorphic feature. The available material of the species does not permit us to determine whether the lesser degree of development of this feature is characteristic of *S. kokraimoro* or alternatively may represent ontogenetic variation or seasonality in the expression of that modification. The male also has a well-developed, mid-dorsal fleshy ridge along the anterior half of the snout that is lacking in the female (compare Figs 51, 52). This feature is unique to this species within *Sternarchorhynchus*.

Etymology: The species name, *kokraimoro*, is in reference to the Kokraimoro, a group within the Kayabo tribe whose ancestral lands included the type locality of the species.

Material examined

Holotype: – BRAZIL. *Pará*: Rio Xingu, Cachoeira de Kaituká, at Altamira (3°12′S, 52°12′W), collected by L. Rapp Py-Daniel and J. A. Zuanon, 9.x.1990; INPA 28360 (197, mature male).

Paratype: – BRAZIL. *Pará*: Rio Xingu, Cachoeira de Kaituká, Altamira (3°12′S, 52°12′W), collected with holotype by L. Rapp Py-Daniel and J. A. Zuanon, 9.x.1990; INPA 3932, 1 (171, mature female).

STERNARCHORHYNCHUS MAREIKEAE SP. NOV. (FIGS 50, 53, 54; TABLE 9)

Sternarchorhynchus oxyrhynchus, Ferreira, 1995: 51 [in listing of species from Brazil, Rio Trombetas, Pará, Cachoeira Porteira].

Diagnosis: Sternarchorhynchus mareikeae is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the lateral line that extends posteriorly to the base of caudal fin, the presence of a definite series of scales along the mid-dorsal region of the body, the presence of a narrow, more lightly coloured mid-dorsal stripe on the head with the stripe sometimes extending posteriorly along the body to the vertical through the insertion of the pectoral fin, the dark anal fin, the possession of 12–13 teeth in the outer row of the dentary, 12–13 teeth in the outer row of the dentary with a total of 16–17 teeth on that jaw, 159–181 total anal-fin rays, nine to 11 scales above the lateral line at the midbody, 16 precaudal vertebrae, the distance from the snout to the anus in mature males (8.8–10.8% of LEA), the preanal distance (12.2–17.8% of LEA; 12.2–15.2% in mature

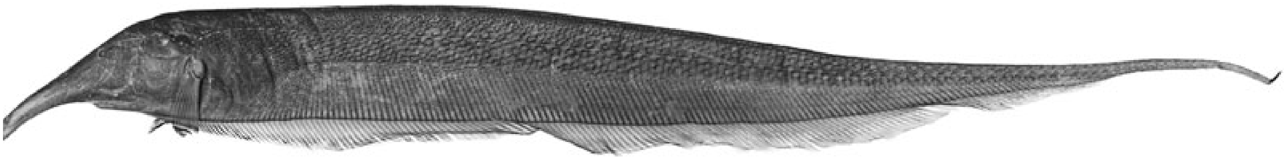

Figure 53. ***Sternarchorhynchus mareikeae*** **sp. nov.,** holotype, male, 192 mm total length, INPA 22896; Brazil, Pará, Cachoeira Porteira, Rio Mapuera.

Figure 54. ***Sternarchorhynchus mareikeae*** **sp. nov.,** paratype, female, 135 mm total length, INPA 22901; Brazil, Pará, Cachoeira Porteira, Rio Mapuera.

males), the caudal length (13.4–17.4% of LEA), the head length (18.3–23.2% of LEA), the prepectoral-fin distance (17.9–23.1% of LEA), the postocular distance (36.0–41.3% of HL), the pectoral-fin length (35.0–40.9% of HL; 37.5–40.9% in mature males), the head depth at the eye in mature males (29.9–38.4% of HL), the head depth at the nape (45.1–53.4% of HL), the distance from the posterior naris to the eye in mature males (52.3–53.7% of HL), the eye diameter (3.5–5.3% of HL), the interocular width (6.6–9.0% of HL), the postocular distance (36.0–41.3% of HL), the height of the branchial opening in mature males (12.3–15.4% of HL), the tail depth (7.1–10.2% of caudal length), and the caudal-fin length (18.5–24.7% of caudal length).

Description: Morphometric data for examined specimens in Table 9.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly curved ventrally along anterior portion. Mouth terminal to very slightly anterodorsally orientated and relatively small with distinct fleshy pad at anterior of lower jaw. Rictus located anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head and along vertical about three orbital diameters anterior of eye in both mature males and females. Combined opening for anus and urogenital papilla longitudinally ovoid in all specimens.

Premaxilla with 12–13 teeth ($N = 7$) apparent in whole specimens. Dentary with two tooth rows; outer row with 12–13 teeth and inner row with three to four teeth ($N = 5$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (12 anterior; four transitional; $N = 9$).

Pectoral-fin rays ii + 10–12 [ii + 12] ($N = 10$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 15–26 [23] ($N = 8$). Total anal-fin rays 159–181 [170] ($N = 10$). Scales above lateral line at midbody nine to 11 [9] ($N = 10$). Scales present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately at 60% of TL. Filament extending posteriorly four to seven scales beyond vertical through posterior terminus of base of anal fin. Tail compressed and moderate, ending in small, elongate, pointed caudal fin. Caudal-fin rays 12–14 ($N = 6$).

Coloration in alcohol: Overall coloration brown. Head dark brown overall laterally other than for more lightly coloured stripe extending along lateral surface of snout. Darker coloration anterior of eye along dorsal surface of snout forms lateral margin of very narrow, lightly coloured mid-dorsal stripe along snout that terminates in rear portion of head. Body dark overall, somewhat more so dorsally. Pectoral fin dusky with rays somewhat darker than membranes. Anal fin dusky with rays darker than membranes. Caudal fin dark.

Distribution: Sternarchorhynchus mareikeae is only known from the type locality at Cachoeira Porteira along the Rio Mapuera, Pará, Brazil (Fig. 50).

Secondary sexual dimorphism: Sternarchorhynchus mareikeae is possibly sexually dimorphic in terms of body size. Mature females($N = 5$) reach a maximum of 160 mm TL, whereas mature males collected with those specimens attain a maximum of 221 mm TL. This species matures at relatively small body sizes as indicated by a 131 mm TL female filled with well-developed eggs and a 176 mm TL male with mature testes.

Etymology: The species name, *mareikeae*, is in honour of the German biologist Mareike Roeder who has greatly added to the senior author's life.

Remarks: Examination of the specimens cited from Cachoeira Porteira as *S. oxyrhynchus* by Ferreira (1995: 51) has shown that some are rather *S. mareikeae. Sternarchorhynchus mareikeae* occurs in the same river basin as *S. inpai* and the two species have similar coloration patterns. They differ both in the numbers of teeth in the upper and lower jaws and also in the various features involving mature males that were cited in the Diagnosis and summarized under Remarks for *S. inpai*.

Material examined

Holotype: – BRAZIL. *Pará*: Rio Trombetas, Cachoeira Porteira, last fall before Rio Trombetas (approximately 1°05′S 57°02′W), collected by E. Ferreira and M. Jégu, 19.iv.1985; INPA 22896, 192.0 mm TL, male.

Paratypes: – BRAZIL. *Pará*: Rio Trombetas, Cachoeira Porteira, last fall before Rio Trombetas (approximately 1°05′S 57°02′W), collected by E. Ferreira and M. Jégu, 19.iv.1985, INPA 22901, 9 (60–120, one specimen cleared and stained); INPA 22900, 3 (125–148); USNM 391717, 1 (177).

STERNARCHORHYNCHUS MARREROI SP. NOV.

(FIGS 50, 55; TABLE 9)

Diagnosis: Sternarchorhynchus marreroi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the hyaline anal fin with slight dusky pigmentation distally in some specimens, the extension of the lateral line posteriorly to a point four to five scales anterior of the base of the caudal fin, the possession of eight premaxillary teeth, two rows of teeth on the dentary with eight teeth in the outer row, 14 caudal-fin rays, 15 precaudal vertebrae, 21–31 anterior unbranched anal-fin rays, 162–181 total anal-fin rays, ten to 11 scales above the lateral line at the midbody, 14 caudal-fin rays, the greatest body depth (11.2–14.1% of LEA), the distance from the snout to the anus (5.8–9.0% of LEA), the distance from the anus to the anal-fin insertion (10.1–17.6% of HL), the preanal distance (9.2–10.8% of LEA), the prepectoral-fin distance (17.0–17.6% of LEA), the head length (16.4–16.6% of LEA), the caudal length (8.8–10.9% of LEA), the distance from the posterior naris to the snout (6.4–7.9% of HL), the head width (25.9–29.9% of HL), the pectoral-fin length (45.7–75.8% of HL), the head depth at the eye (32.9–35.4% of HL), the head depth at the nape (55.1–65.5% of HL), the snout length (62.3–63.6% of HL), the distance from the posterior naris to the eye (48.8–53.4% of HL), the internarial distance (3.0–4.3% of HL), the interocular width (6.8–8.1% of HL), the height of the branchial opening (15.3–19.6% of HL), the postocular distance (45.3–49.0% of HL), and the tail depth (15.7–20.2% of caudal length).

Description: Morphometric data for examined specimens in Table 9.

Lateral line extending posteriorly to point approximately four or five scales short of base of caudal fin, but absent on remainder of tail and fin. Snout elongate, compressed and distinctly curved ventrally. Mouth terminal and relatively small, with rictus located slightly posterior to vertical through posterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically somewhat variable. Openings positioned along vertical slightly posterior of rear margin of eye in smaller specimens and along vertical two orbital diameters anterior of anterior margin of orbit in larger individuals. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with eight teeth ($N = 2$) apparent in whole specimens. Dentary with two tooth rows; outer row with eight teeth and inner row with three teeth ($N = 2$).

Branchiostegal rays five; with first three rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (12–13 anterior; two to three transitional; $N = 3$).

Pectoral-fin rays ii + 12–13 [ii + 12] ($N = 3$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 21–31 [30] ($N = 3$). Total anal-fin rays 162–181 [162] ($N = 3$). Scales above lateral line at midbody ten to 11 [10] ($N = 3$). Scales present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 60% of TL. Filament extending posteriorly to point two to five scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, moderate, pointed caudal fin. Caudal-fin rays 14 [14] ($N = 2$).

Coloration in alcohol: Overall coloration ranging from light to medium brown, but missing on some regions because of apparent postmortem damage. Head with narrow stripe of slightly darker pigmentation extending anteriorly from orbit for distance a half to two-thirds length of snout. Darker pigmentation forms lateral margin of lightly coloured mid-dorsal stripe on

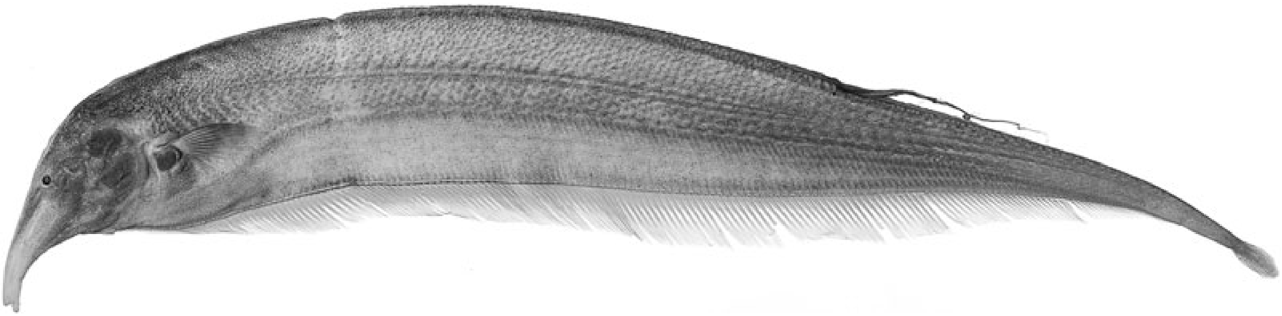

Figure 55. ***Sternarchorhynchus marreroi* sp. nov.,** holotype, presumably female, 182 mm total length, MBUCV 15806; Venezuela, Apure, Río Apure.

snout. Lightly coloured stripe expands posteriorly into longitudinally elongate ovoid, lightly coloured area located above postocular portion of head. Ovoid region continuous posteriorly with mid-dorsal, lightly coloured stripe on body that extends posteriorly for varying degrees towards origin of electroreceptive filament. Pectoral fin dark distally and dorsally. Anal fin hyaline overall, but with distal portions slightly dusky in largest examined specimen. Caudal fin dusky to dark.

Distribution: Sternarchorhynchus marreroi is known from the central and delta regions of the Río Orinoco (Fig. 50).

Secondary sexual dimorphism: No sexual dimorphism is apparent in the limited available samples of *S. marreroi*.

Etymology: The name, *marreroi*, is in honour of Críspulo Marrero of the Universidad Nacional Experimental de los Llanos Occidentales, who has greatly contributed to our knowledge of the biology of gymnotiforms in Venezuela.

Material examined

Holotype: – VENEZUELA. *Apure*: Río Apure, in front of Isla Apurito, left bank (8°00′N, 67°31′W), collected by O. Castillo and F. Provenzano, 25.i.1984; MBUCV 15806 (182).

Paratypes: – VENEZUELA. *Apure*: Río Apure, in front of Isla Apurito, left bank (8°00′N, 67°31′W), collected with holotype by O. Castillo and F. Provenzano, 25.i.1984; MBUCV 33750, 1 (278; formerly MBUCV V-15806, in part). *Delta Amacuro*: Río Orinoco, south of Isla Portuguesa (approximately 8°37′N, 61°49′W), collected by J. G. Lundberg *et al.*, 20.ii.1978; MBUCV 10637, 1 (231).

STERNARCHORHYNCHUS MENDESI SP. NOV.

(FIGS 50, 56; TABLE 10)

Diagnosis: Sternarchorhynchus mendesi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, having the scales along the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament sparse and covered by skin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament and sometimes posterior of that point, the extension of the mid-dorsal filament to a point approximately two to three scales beyond the vertical through the posterior terminus of the anal fin, the lateral line that extends to the base of the caudal fin, the possession of ten to 11 teeth in the outer row of the dentary, 29–37 anterior unbranched anal-fin rays, 174–182 total anal-fin rays, six to seven scales above the lateral line at the midbody, 12–17 caudal-fin rays, the length of the base of the anal fin (80.8–85.9% of LEA), the caudal length (8.8–11.1% of LEA), the length of the pectoral fin (33.9–44.2% of HL), the postocular distance (38.8–40.8% of HL), the distance from the posterior naris to the eye (46.6–55.3% of HL), the height of the branchial opening (10.2–14.1% of HL), and the tail depth (15.1–20.7% of caudal length).

Description: Morphometric data for examined specimens in Table 10.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and straight overall, but slightly curved ventrally along anterior portion. Mouth slightly anterodorsally directed, with fleshy process at anterior limit of dentary. Rictus located along vertical ranging from slightly anterior of, to slightly posterior of, anterior naris. Anus and urogenital papilla located ventral to head, with position ontogenetically variable. Openings located along vertical approximately three orbital diameters posterior of eye in smaller specimens and maximum of one eye diameter anterior of orbit in largest specimens. Combined opening for anus and urogenital papilla ranging from circular to longitudinally ovoid.

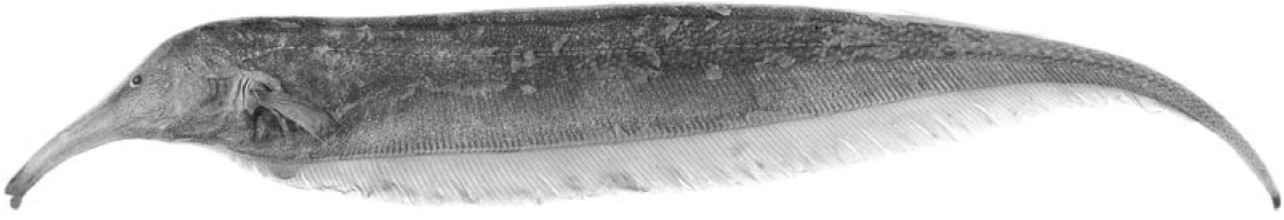

Figure 56. ***Sternarchorhynchus mendesi* sp. nov.,** holotype, presumably female, 155 mm total length, MCNG 29129; Venezuela, Monagas, Río Guanipa.

Premaxilla with six to nine teeth ($N = 4$) apparent in whole specimens. Dentary with two tooth rows; outer row with ten to 11 teeth and inner row with three teeth ($N = 4$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15–16 (12 anterior; three to four transitional; $N = 8$).

Pectoral-fin rays ii + 10–14 [ii + 14] ($N = 8$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 29–37 [33] ($N = 8$). Total anal-fin rays 174–182 [176] ($N = 8$). Scales above lateral line at midbody six to nine [9] ($N = 8$). Scales along mid-dorsal region of body sparse and covered by thick skin. Origin of midsaggital electroreceptive filament located on posterior half of body situated approximately at 55% of TL. Filament extending posteriorly to within area delimited anterior by vertical through posterior terminus of base of anal fin and posteriorly by vertical two to three scales beyond that landmark. Tail compressed and short, ending in small, caudal fin with posteroventrally angled oblique margin. Caudal-fin rays 12–17 [12] ($N = 5$).

Coloration in alcohol: Overall coloration of head and body of specimens brown to dark brown. Snout dark overall on lateral surface with little or no indication of somewhat lighter central band present along at least anterior one-third of snout in some congeners. Dark pigmentation on lateral surface of snout forms lateral margin of narrow, lightly coloured stripe running along mid-dorsal region of snout. Lightly coloured mid-dorsal stripe continues onto, and expands laterally on, postocular portion of head. Expanded lightly coloured mid-dorsal region on rear of head continuous posteriorly with narrow, lightly coloured mid-dorsal

Table 10. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus mendesi*, *Sternarchorhynchus mesensis*, and *Sternarchorhynchus montanus*

	S. mendesi			*S. mesensis*		*S. montanus*		
	H	Paratypes	Mean	H	Range	Mean	H	Paratype
Total length (mm)	155	77.7–192	–	249	116–228 ($N = 8$)	–	226	258
Length to end of anal fin (mm)	142	70.4–146	–	226	106–209 ($N = 8$)	–	221	233
Head length (mm)	29.9	16.9–35.5	–	46.5	23.2–38.8 ($N = 10$)	–	37.7	38.0
Caudal length (mm)	13.8	6.2–15.3	–	23.0	10.0–27.0 ($N = 8$)	–	5.25	7.23
Per cent of length to end of anal fin								
Anal-fin base	82.4	80.8–85.9 ($N = 5$)	84.2	88.0	83.0–88.0 ($N = 8$)	85.2	85.0	90.9
Distance snout to anus	12.5	11.3–16.2 ($N = 6$)	13.3	–	13.5–15.2 ($N = 3$)	14.4	7.3	6.9
Preanal-fin distance	15.2	13.2–18.2 ($N = 5$)	15.1	14.4	14.2–17.0 ($N = 8$)	15.6	10.2	9.5
Prepectoral-fin distance	21.3	20.0–23.8 ($N = 5$)	21.3	21.4	21.5–23.8 ($N = 8$)	22.4	16.6	10.9
Greatest body depth	11.5	7.4–12.9 ($N = 5$)	10.6	10.4	10.0–12.3 ($N = 8$)	10.9	7.5	13.0
Head length	21.4	19.5–24.0 ($N = 5$)	21.0	20.5	20.5–23.6 ($N = 8$)	21.8	17.0	16.3
Caudal length	9.4	8.8–11.1 ($N = 4$)	10.1	10.1	9.0–14.3 ($N = 8$)	10.5	6.5	5.3
Per cent of head length								
Anus to anal-fin insertion	8.7	6.8–15.0 ($N = 6$)	9.6	14.8	7.5–15.4 ($N = 10$)	11.2	12.3	9.8
Pectoral-fin length	37.0	33.9–42.2 ($N = 7$)	38.3	30.1	27.0–35.3 ($N = 10$)	31.3	47.8	49.1
Head depth at eye	24.6	28.1–33.3 ($N = 6$)	30.3	–	24.3–26.4 ($N = 3$)	25.4	34.5	34.0
Head depth at nape	48.3	44.5–60.3 ($N = 6$)	49.7	42.3	39.1–45.2 ($N = 10$)	41.9	53.5	55.7
Head width	21.2	21.5–26.4 ($N = 6$)	23.3	–	17.3–22.1 ($N = 3$)	19.4	24.0	24.0
Snout length	61.3	58.7–63.9 ($N = 6$)	62.2	65.8	60.1–65.1 ($N = 10$)	63.4	63.7	65.3
Posterior naris to snout	8.8	7.0–10.0 ($N = 6$)	8.6	4.3	4.6–5.6 ($N = 10$)	4.9	7.3	7.0
Posterior naris to eye	50.3	46.6–55.3 ($N = 6$)	52.7	56.5	49.0–55.9 ($N = 10$)	53.5	54.4	54.6
Mouth length	6.6	5.2–6.8 ($N = 6$)	6.1	5.8	5.4–6.4 ($N = 10$)	6.0	5.2	4.3
Internarial distance	3.5	2.5–3.5 ($N = 6$)	3.1	3.8	3.2–4.7 ($N = 10$)	4.0	2.1	2.2
Eye diameter	4.5	3.8–5.6 ($N = 6$)	4.6	3.6	3.8–4.7 ($N = 10$)	4.1	4.3	4.0
Interocular width	7.9	7.2–11.6 ($N = 6$)	9.1	4.7	4.8–6.0 ($N = 10$)	5.2	5.4	5.3
Postocular distance	40.2	38.8–40.8 ($N = 6$)	40.1	37.2	36.4–41.0 ($N = 10$)	38.8	42.3	43.2
Branchial opening	11.6	10.2–14.1 ($N = 6$)	11.8	9.6	8.6–13.1 ($N = 10$)	10.6	15.5	18.1
Per cent of caudal length								
Tail depth	17.5	15.1–20.7 ($N = 4$)	18.2	8.7	5.5–11.4 ($N = 8$)	9.0	21.2	21.7
Caudal-fin length	13.4	18.1–33.0 ($N = 4$)	24.7	23.9	21.5–33.5 ($N = 8$)	27.3	36.5	58.2

Number of specimens indicated in parentheses.

stripe on body. Mid-dorsal stripe on body very obvious and extending from rear of head posteriorly to beyond origin of electroreceptive filament to varying degrees. Pectoral fin dusky with small, dark chromatophores overlying fin rays. Anal fin dusky with small, dark chromatophores overlying fin rays. Caudal fin dark overall with distal regions hyaline. One small examined specimen apparently albino.

Distribution: Sternarchorhynchus mendesi is only known from the Río San Juan and Río Guanipa basins of north-eastern Venezuela, both of which drain into the Golfo de Paria (Fig. 50).

Secondary sexual dimorphism: No sexual dimorphism was apparent in the limited sample of *S. mendesi.*

Etymology: The species name, *mendesi*, is in honour of George Nilson Mendes of the Universidade Federal de Pernambuco, in recognition of his assistance to the first author during the early phases of his studies of gymnotiforms.

Material examined
Holotype: – VENEZUELA. *Monagas*: Department of Maturín, Morichal Largo, Río Guanipa, 5 km south of Aguasay (Aguasay at 9°25′N, 63°44′W), Golfo de Paria drainage, collected by D. C. Taphorn, L. Page *et al.*, 2.vii.1998; MCNG 29129, (155).

Paratypes: – VENEZUELA. *Monagas*: Department of Maturín, Morichal Largo, Río Guanipa, 5 km south of Aguasay (Aguasay at 9°25′N, 63°44′W), Golfo de Paria drainage, collected by D. C. Taphorn, L. Page *et al.*, with holotype, 2.vii.1998; MCNG 55850, 1 (118 CS; formerly MCNG 29129, in part). Río Guanipa, bridge on Highway 5, Golfo de Paria drainage (9°22′06″N 63°46′47″W), collected by L. Page *et al.*, 7.i.1994; INHS 31374, 3 (77.7–157). Río de Oro, Ríos Guarapiche–San Juan basins, Golfo de Paria drainage, L. Page *et al.*, 7.i.1994, INHS 31453, 1 (192). Department of Maturín, Río de Oro, south-west of Jusepín (Jusepín at 9°45′N, 63°31′W), Golfo de Paria drainage, collected by D. C. Taphorn, L. Page *et al.*, 2.vii.1998; MCNG 29194, 1 (157). Department of Maturín, Río Amaná, north-west of Santa Bárbara (Santa Bárbara at 9°37′N, 63°37′W), Golfo de Paria drainage, collected by D. C. Taphorn, L. Page *et al.*, 2.vii.1998; MCNG 29166, 1 (104).

STERNARCHORHYNCHUS MESENSIS CAMPOS-DA-PAZ
(FIGS 57, 58; TABLE 10)

Sternarchorhynchus mesensis Campos-da-Paz, 2000: 531, figs 5, 6 [type locality: Brazil, Goiás, Río Tocantins (upper Río Tocantins region), at Serra de Mesa dam, municípios Minaçu/Uruaçu ('Minaçu/Cavalcante'), approximately 13°50′S, 18°19′W]. – Albert, 2003: 501 [in listing of members of genus]. – Triques, 2007: 125 [Brazil, Rio Tocantins basin].

Diagnosis: Sternarchorhynchus mesensis is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the first and second branchiostegal rays of approximately the same size, the presence of a definite series of scales along the mid-dorsal region of the body, the hyaline anal fin, the lateral line extending posteriorly to the base of the caudal fin, the possession of five branchiostegal rays, 11–14 premaxillary teeth, two rows of teeth on the dentary with ten to 11 teeth in the outer row, 171–189 total anal-fin rays, 13–18 anterior unbranched anal-fin rays, 16–17 precaudal vertebrae, 11–13 scales above the lateral line at the midbody, the greatest body depth (10.0–12.3% of LEA), the preanal distance (14.2–17.0% of LEA), the prepectoral-fin distance (21.4–23.8% of LEA), the caudal length (9.0–14.3% of LEA), the distance from the anus to the insertion of the anal fin (7.5–15.4% of HL), the caudal length (9.0–14.3% of LEA), the head length (20.5–23.6% of LEA), the distance from the posterior nares to the eye (49.0–56.5% of HL), the eye diameter (3.6–4.7% of HL), the height of the branchial opening (8.6–13.1% of LEA), the head depth at the nape (39.1–45.2% of HL), the interocular distance (4.7–6.0% of HL), the distance from the posterior naris to the snout (4.3–5.6% of HL), the postocular length (36.4–41.0% of HL), the length of the pectoral fin (27.0–35.3% of HL), and the tail depth (5.5–11.4% of caudal length).

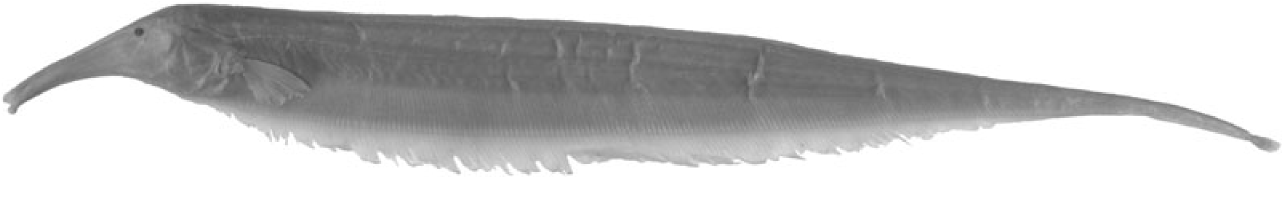

Figure 57. *Sternarchorhynchus mesensis*, paratype, 127 mm total length, MNRJ 11613; Brazil, upper Rio Tocantins, municípios de Minaçu and Uruaçu, at Serra de Mesa dam.

Description: Morphometric data for examined specimens in Table 10.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally. Mouth terminal with fleshy process at anterior limit of dentary. Rictus located along vertical slightly anterior of anterior naris. Anus and urogenital papilla located ventral to head, with position ontogenetically variable. Structures located approximately at vertical one orbital diameter posterior of eye in small specimens, and within area delimited posteriorly by vertical running through eye and anteriorly by vertical approximately one orbital diameter anterior of eye in larger specimens. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with 11–14 teeth ($N = 5$) apparent in whole specimens and nine to ten teeth ($N = 3$) in cleared and stained material. Dentary with two tooth rows; outer row with eight teeth and inner row with three teeth ($N = 5$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16–17 (13–14 anterior; three transitional; $N = 5$).

Pectoral-fin rays ii + 12–13 [ii + 13] ($N = 9$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 23–28 ($N = 10$). Total anal-fin rays 171–189 [181] ($N = 8$). Scales above lateral line at midbody 11–13 [13] ($N = 10$). Scales present along mid-dorsal region to origin of electroreceptive filament. Origin of midsaggital electroreceptive filament located on posterior half of body, approximately at 60% of TL. Filament extending posteriorly to vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, caudal fin. Caudal-fin rays 13–15 [14] ($N = 8$).

Coloration in alcohol: Overall ground coloration ranging from light tan to brown with pigmentation darker on dorsal portions of head and body. Snout and remainder of head with narrow, lightly coloured stripe extending to rear of head. Stripe extending in some individuals onto mid-dorsal region. Stripe on head and anterior portion of body indistinct in some specimens. Anal, caudal, and pectoral fins hyaline overall, but with some dark chromatophores along margins of rays, but lacking distinct bands of dark pigmentation along distal margins of fins.

Distribution: Sternarchorhynchus mesensis is known from sites in the upper Rio Tocantins system (Fig. 58) and has been collected in caves of the São Domingos karst region (see Ecology below).

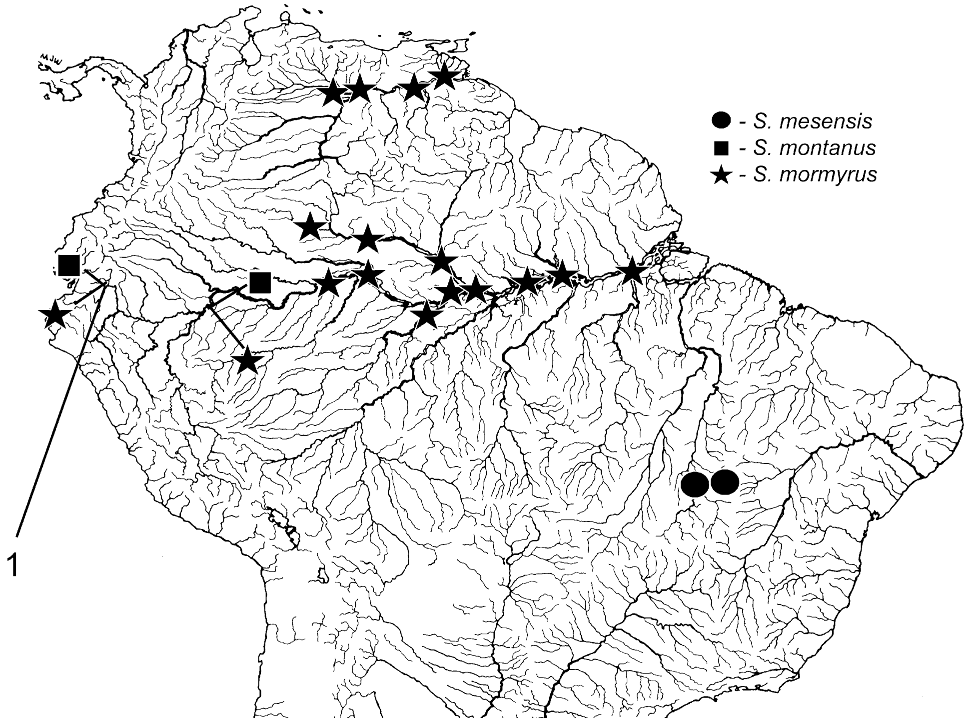

Figure 58. Map of central and northern South America showing geographical distribution of *Sternarchorhynchus mesensis*, ***Sternarchorhynchus montanus* sp. nov.** (1 = holotype locality), and *Sternarchorhynchus mormyrus* (some symbols represent more than one locality and/or lot of specimens).

Ecology: Several examined lots of *S. mesensis* originated in caves within the São Domingos karst region in the upper portions of the Rio Tocantins basin. The region is home to numerous epigean fishes (Bichuette & Trajano, 2003, 2004), some of which are limited to the cave systems whereas some others occur in both subterranean and surface drainages. *Sternarchorhynchus mesensis* demonstrates the latter pattern, occurring in both settings, with several population samples originating in caves (MZUSP 88577, MZUSP 24993, MZUSP 62652, MZUSP 44116) and others (MZUSP 58623, MZUSP 24497) from surface waters in the vicinity of those caves. *Sternarchorhynchus mesensis* appears to be well adapted to epigean habitats as indicated by the overall condition and sexual maturity of the individuals from cave habitats. Given the continuity between surface and epigean waters in the São Domingos region (Bichuette & Trajano, 2004), it is impossible to determine whether the cave populations live their entire life cycles and reproduce in that epigean settings.

Secondary sexual dimorphism: No sexual dimorphism was reported for the species by Campos-da-Paz (2000) or is apparent in examined specimens.

Remarks: The samples of *S. mesensis* from epigean and surface locations around São Domingos differ somewhat from those from the main river channels of the Rio Tocantins. Variation in the available samples does not unequivocally separate the São Domingos samples from individuals of *S. mesensis* from the type region. Samples from intervening regions are necessary to resolve the question of whether these differences represent geographical variation or a possible second form.

Sternarchorhynchus mesensis was collected at the same locality as the type series of *S. axelrodi*. The two species differ in various details of pigmentation along with the meristic and morphometric features detailed under Remarks for *S. axelrodi*.

Material examined

BRAZIL. *Goiás*: Rio Tocantins, upper Rio Tocantins region, municípios Minaçu and Uruaçu, at Serra da Mesa dam (approximately 13°50′S, 48°19′W); MNRJ 11611, 2 of 4 (cleared and stained paratypes), MNRJ 11613, 4 of 7 (115–127, paratypes); MZUSP 57497, 1 (170). Serra da Mesa, Município de Minaçu. MZUSP 58623, 1 (220), re-emergence of Rio Angélica/Bezerra, Parque Estadual da Terra Ronca, São Domingos; MZUSP 54100, 1 (180). Lagos of Ribeirão do Bezerra, São Domingos; MZUSP 24497, 2 (145–212). Rio Angélica, Caverna Angélica, near its point of re-emergence, below cachoeira; MZUSP 88577, 1 (81). Rio São Mateus, Gruta Matilde, Município de São Domingos; MZUSP 24993, 1 (170). Caverna São Mateus, Imbira, Matilde II; MZUSP 62652, 1 (143). Rio São Mateus, Gruta São Mateus, Imbira, São Domingos; MZUSP 44116, 1 (188).

STERNARCHORHYNCHUS MONTANUS SP. NOV.

(FIGS 58, 59; TABLE 10)

Diagnosis: Sternarchorhynchus montanus is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends to a point one scale anterior of the base of the caudal fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the distinctly dusky anal fin without a dark basal band, the possession of six to seven teeth on the premaxilla, six to seven teeth in the outer row of the dentary, 23–31 anterior unbranched anal-fin rays, 187–191 total anal-fin rays, 12–13 pectoral-fin rays, 16 precaudal vertebrae, the greatest body depth (7.5–13.0% of LEA), the preanal distance (9.5–10.2% of LEA), the prepectoral-fin distance (10.9–16.6% of LEA), the head length (16.3–17.0% of LEA), the distance from the anus to the anal-fin insertion (9.8–12.3% of HL), the caudal length (5.3–6.5% of LEA), the head depth at the eye (34.0–34.5% of HL), the head depth at the nape (53.5–55.7% of HL), the mouth length (4.3–5.2%

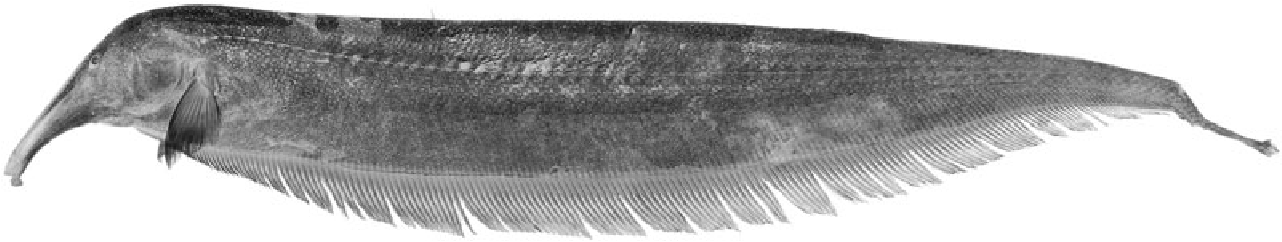

Figure 59. *Sternarchorhynchus montanus* sp. nov., holotype, male, 226 mm total length, MUSM 31312; Peru, Amazonas, Río Marañon.

of HL), the snout length (63.7–65.3% of HL), the distance from the posterior naris to the eye (54.4–54.6% of HL), the eye diameter (4.0–4.3% of HL), the internarial distance (2.1–2.2% of HL), the interocular distance (5.3–5.4% of HL), the postocular distance (42.3–43.2% of HL), the height of the branchial opening (15.5–18.1% of HL), the pectoral-fin length (47.8–49.1% of HL), and the tail depth (21.1–21.7% of caudal length).

Description: Morphometric data for examined specimens in Table 10.

Lateral line extending posteriorly to point one scale anterior of base of caudal fin and absent on remainder of tail and on caudal fin. Snout elongate, compressed and curved ventrally. Mouth terminal with fleshy process arising from anterior limit of dentary. Rictus located along vertical slightly anterior of anterior naris. Anus and urogenital papilla located ventral to head, with position of openings variable; located within area delimited posteriorly by vertical through eye and anteriorly by vertical approximately four orbital diameters anterior of eye (secondary sexual dimorphism). Combined opening for anus and urogenital papilla ranging from circular to longitudinally ovoid.

Premaxilla with six to seven teeth ($N = 2$) apparent in whole specimens. Dentary with two tooth rows; outer row with six to seven teeth and inner row with two teeth ($N = 2$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (13 anterior; three transitional; $N = 2$).

Pectoral-fin rays ii + 12–13 [12] ($N = 2$). Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 23–31 [23] ($N = 2$). Total anal-fin rays 187–191 [187] ($N = 2$). Scales above lateral line at midbody nine to 12 [9] ($N = 2$). Scales present along mid-dorsal region to origin of electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 65% of TL. Filament extending to point one to two scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, elongate caudal fin. Caudal-fin rays 12–16 ($N = 2$).

Coloration in alcohol: Overall coloration of head and body ranging from tan to dark brown. Snout with distinct dark band extending from slightly anterior of eye nearly to tip of snout. Ventrolateral surface of snout somewhat darker than ground coloration. Two dark regions on snout together delimit somewhat lighter intermediate band along lateral surface of anterior two-thirds of snout. Dorsal margin of dark pigmentation on snout forms lateral margin of narrow, lightly coloured stripe running along mid-dorsal region of snout. More lightly coloured mid-dorsal stripe continues onto and expands somewhat laterally on postocular portion of head. Expanded lightly coloured region slightly less apparent over posteriormost portion of head, but nonetheless continuous posteriorly with narrow, mid-dorsal stripe on body. Mid-dorsal stripe on body obvious, more so in darker holotype and extending from rear of head posteriorly to origin of electroreceptive filament or slightly beyond that point. Pectoral fin dusky, more so distally; very dark in overall more intensely pigmented holotype. Anal fin dusky with small, dark chromatophores overlying fin rays and inter-radial filaments. Intensity of pigmentation more pronounced along distal third to half of fin and forming obvious distal dark band. Caudal fin dark overall.

Distribution: Sternarchorhynchus montanus is known from two locations in the Río Marañon of Peru (Fig. 58). It is uncertain where the two nontype specimens originated because they were secured from a dealer in the aquarium trade based in Iquitos, northeastern Peru. If the locality information associated with the nontypes is correct, it would extend the distribution of *S. montanus* to the Iquitos region. The two nontypes agree with the type series in all features that can be unequivocally determined, but both have regenerated tails, which makes it impossible to count the total number of anal-fin rays or determine morphometric values dependent on measurements taken to the end of the anal fin.

Secondary sexual dimorphism: Sternarchorhynchus montanus does not demonstrate the sexual dimorphism of the dentary and associated dentition present in some congeners. The male holotype is distinctly darker overall than the female paratype. A similar difference in coloration occurs between the nontype male and female. The female nontype, which is larger than the paratypic female, also has the posterior portion of the snout deeper than in the males. This specimen has the combined opening for the anus and urogenital papilla positioned approximately four orbital diameters anterior of the vertical through the eye contrary to the location of those combined openings approximately at the vertical through the eye in the nontype male of similar size and the male holotype and female paratype, both of which are of smaller sizes. This may indicate both ontogenetic and sexual dimorphism in the location of that opening comparable to that in congeners.

Etymology: The species name, *montanus*, from the Latin for mountains, refers to the type location of the type series in the foothills of the Andean Cordilleras.

Material examined

Holotype: – PERU. *Amazonas*: Río Marañon, pongo above Borja, 35.5 km north-east Juan Velasco, Santa Maria de Nieva (4°27′36″S, 77°34″53′W), collected by N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, K. A. Capps, D. P. German, D. Osorio, 6.viii.2006; MUSM 31312 (226; formerly AUM 46270, in part).

Paratype: – PERU. *Amazonas*: Río Marañon, vicinity of Santa Maria de Nieva (Santa Maria de Nieva at 4°27′36″S, 77°34′53′W), collected by D. J. Stewart, 16.iv.1980; LACM 41741–44, 1 (258, female).

Nontype specimens: **–** PERU. *Amazonas*: Río Amazonas, near Iquitos, 1 h above or below, purchased from aquarium fish dealer at Belen, 20.i.2004; UF uncatalogued, 2 (276–277, male and female).

*S*TERNARCHORHYNCHUS MORMYRUS (STEINDACHNER) (FIGS 58, 60, 61; TABLE 11)

Sternarchus mormyrus Steindachner, 1868a: 176 [description of species in abstract of primary description that appeared in Steindachner, 1868b]. Steindachner, 1868b: 253, pl. 1, fig. 3 [more detailed description following from Steindachner, 1868a; type locality reported as Brazil, Marabitanos (= Río Negro, north of Marabitanas at foot of Cocui mountains; Remarks); head and anterior portion of body of type illustrated]. – Eigenmann & Eigenmann, 1891: 62 [assignment to *Sternarchorhynchus*]. – Ellis, 1913: 141 [placed as junior synonym of *S. oxyrhynchus*]. – Fernández-Yépez, 1967: 18 [species resurrected from synonymy of *S. oxyrhynchus*]. – Eschmeyer, 1998: 1122 [discussion as to which publication constitutes original description of species]. *Sternarchorhynchus oxyrhynchus*, Fowler, 1951: 431 [in part; citations of *Sternarchus mormyrus* and *S. mormyrus*, not other references].

Sternarchorhynchus mormyrus, Mago-Leccia, 1970: 76 [Venezuela]. – Machado-Allison, 1987: 132 [llanos of Venezuela]. – Mago-Leccia, 1994: 37, fig. 54 [as valid species in listing of members of genus]. – Taphorn *et al.*, 1997: 80 [Venezuela]. – Campos-da-Paz, 2000: 528, fig. 2 [as valid species of *Sternarchorhynchus* in key to species of genus; syntype illustrated]. – Albert, 2003: 501 [in listing of members of genus]. – Lasso *et al.*, 2004b: 142 [Río Orinoco basin in Colombia and Venezuela]. – Lasso *et al.*, 2004a: 181 [Venezuela; Río Orinoco basin]. – Crampton, 2007: 289 [widespread in Amazon and Orinoco basins]. – Triques, 2007: 125 [Amazon basin].

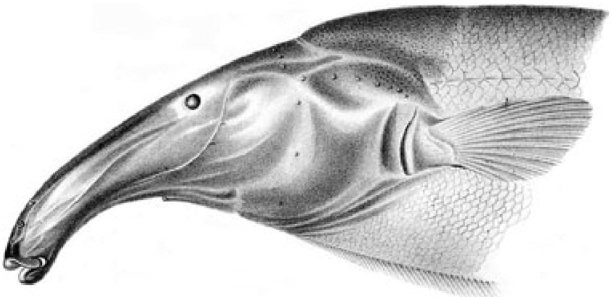

Figure 60. *Sternarchorhynchus mormyrus*, illustration of head of one of the syntypes (from Steindachner, 1868b: table 1, fig. 3). Figure reversed from original orientation.

Diagnosis: Sternarchorhynchus mormyrus is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the absence of scales along the mid-dorsal region of the body as far posteriorly as the origin of the electroreceptive filament, and the possession of 222–245 anal-fin rays.

Description: Morphometric data for examined specimens in Table 11.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally. Mature males with wider snout than females (de Santana & Crampton, 2006: 58). Mouth terminal and relatively small, with rictus located anterior to vertical through posterior naris. Anus and urogenital papilla located ventral to head, with position ontogenetically variable. Smaller examined specimens (*c.* 190 mm TL) with both structures positioned along vertical midway between rear of eye and

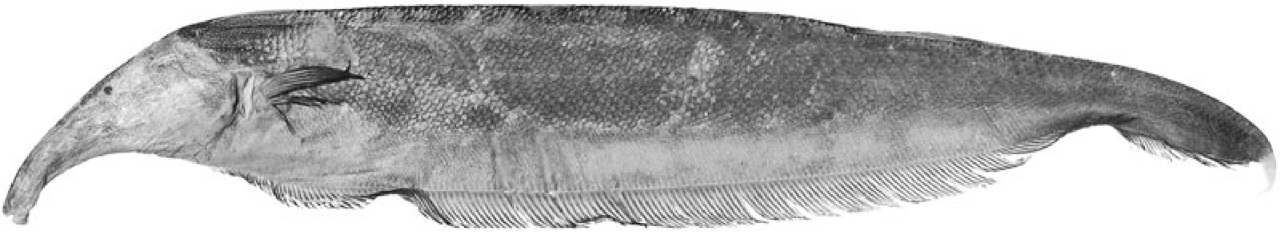

Figure 61. *Sternarchorhynchus mormyrus*, male, 315 mm total length, USNM 375479; Brazil, Amazonas, Rio Amazonas.

Table 11. Morphometrics for examined specimens of *Sternarchorhynchus mormyrus*, *Sternarchorhynchus oxyrhynchus*, and *Sternarchorhynchus retzeri*

	S. mormyrus		*S. oxyrhynchus*		*S. retzeri*			
	Range	Mean	H	Range	Mean	H	Paratypes	Mean
Total length (mm)	119–315 ($N = 15$)	–	469	207–348.3 ($N = 22$)	–	372	281–264 ($N = 5$)	–
Length to end of anal fin (mm)	236–255 ($N = 2$)	–	388	279–193 ($N = 22$)	–	342	226–269 ($N = 4$)	–
Head length (mm)	27.0–67.6 ($N = 15$)	–	57.0	35.8–47.8 ($N = 21$)	–	67.8	52.3–68.0 ($N = 6$)	–
Caudal length (mm)	14.1–15.3 ($N = 2$)	–	81.0	25.4–69.3 ($N = 18$)	–	24.6	25.2–30.1 ($N = 2$)	–
Per cent of length to end of anal fin								
Anal-fin base	81.7–84.3 ($N = 2$)	83.0	87.8	82.2–93.3 ($N = 22$)	86.0	85.6	84.2–86.9 ($N = 5$)	85.4
Distance snout to anus	14.1–14.2 ($N = 2$)	14.1	–	10.1–15.2 ($N = 21$)	13.8	3.7	9.8–12.8 ($N = 8$)	11.6
Preanal-fin distance	15.5–16.2 ($N = 2$)	15.9	12.5	13.7–19.3 ($N = 21$)	16.1	13.5	13.0–15.2 ($N = 6$)	13.8
Prepectoral-fin distance	21.0–21.4 ($N = 2$)	21.2	15.3	16.7–20.4 ($N = 22$)	18.6	19.8	18.5–21.3 ($N = 5$)	19.6
Greatest body depth	11.7–12.1 ($N = 2$)	11.9	9.4	6.3–8.2 ($N = 22$)	7.4	8.3	8.7–10.1 ($N = 5$)	9.2
Head length	21.3–21.8 ($N = 2$)	21.5	14.6	17.0–23.2 ($N = 21$)	19.0	19.8	18.5–20.2 ($N = 5$)	19.4
Caudal length	6.0 ($N = 2$)	6.0	20.8	14.4–31.2 ($N = 20$)	23.9	7.1	9.2–10.3 ($N = 2$)	9.7
Per cent of head length								
Anus to anal-fin insertion	5.2–16.1 ($N = 15$)	10.3	–	6.1–19.9 ($N = 21$)	10.8	25.8	5.7–14.8 ($N = 6$)	11.1
							17.7–25.6 ($N = 3$)	22.0
Pectoral-fin length	37.5–47.4 ($N = 15$)	41.7	38.0	27.0–37.7 ($N = 21$)	34.7	35.4	34.4–39.1 ($N = 9$)	36.5
Head depth at eye	24.9–30.8 ($N = 15$)	27.7	24.9	18.3–23.1 ($N = 21$)	21.5	25.0	21.4–27.7 ($N = 9$)	24.7
Head depth at nape	43.6–54.3 ($N = 15$)	48.0	–	26.8–37.7 ($N = 21$)	34.2	34.7	34.1–41.8 ($N = 9$)	37.2
Head width	21.0–29.4 ($N = 15$)	24.8	16.6	13.7–21.5 ($N = 21$)	18.0	15.9	16.4–18.7 ($N = 9$)	17.6
Snout length	52.9–63.3 ($N = 15$)	55.6	65.7	49.5–65.7 ($N = 21$)	62.7	68.4	65.4–71.2 ($N = 9$)	68.0
Posterior naris to snout	8.0–10.6 ($N = 15$)	9.3	7.0	4.8–6.8 ($N = 21$)	5.8	6.9	5.7–7.0 ($N = 9$)	6.3
Posterior naris to eye	39.7–47.4 ($N = 15$)	44.9	58.7	45.4–58.4 ($N = 21$)	55.1	61.7	57.3–74.0 ($N = 9$)	61.9
Mouth length	6.1–9.8 ($N = 15$)	8.1	8.5	6.0–11.0 ($N = 20$)	7.9	6.0	4.2–6.6 ($N = 9$)	5.1
Internarial distance	3.4–4.8 ($N = 15$)	4.1	3.5	0.9–4.1 ($N = 20$)	2.8	3.3	2.2–3.4 ($N = 9$)	2.9
Eye diameter	3.2–6.3 ($N = 15$)	4.1	4.0	3.2–5.7 ($N = 21$)	4.3	2.8	2.5–3.4 ($N = 9$)	2.8
Interocular width	4.2–9.9 ($N = 15$)	6.0	5.6	4.6–7.6 ($N = 21$)	6.1	4.6	3.9–6.4 ($N = 9$)	4.8
Postocular distance	27.7–48.5 ($N = 15$)	45.9	20.1	26.0–36.8 ($N = 21$)	34.3	31.9	31.6–34.9 ($N = 9$)	33.5
Branchial opening	10.7–16.2 ($N = 12$)	13.6	6.2	8.3–14.5 ($N = 21$)	11.3	11.3	10.0–12.5 ($N = 9$)	11.4
Per cent of caudal length								
Tail depth	29.7–31.8 ($N = 2$)	30.7	4.9	3.7–14.2 ($N = 20$)	7.3	21.4	15.3–21.4 ($N = 2$)	17.5
Caudal-fin length	42.4–64.9 ($N = 2$)	53.6	–	6.15–34.9 ($N = 18$)	14.7	27.7	21.8–27.7 ($N = 2$)	24.1

Number of specimens indicated in parentheses. H, holotype; range includes nontype specimens.

Many specimens of *S. mormyrus* that served as basis for measurements had tails damaged as a consequence of apparent predation and various proportions could not be determined for these individuals. Sexually dimorphic features for *S. retzeri* are presented as two entries. First entry is data for all specimens other than sexually dimorphic mature males with information for sexually dimorphic male in second entry based on three specimens of 371–390 mm total length.

posterior border of opercle. Midsized specimens (*c*. 315 mm TL) with anus and urogenital papilla located along vertical one-third of distance between posterior margin of eye and posterior border of opercle. Largest examined specimens (*c*. 450–470 mm SL) with openings shifted distinctly anteriorly and positioned along verticals falling within region delimited posteriorly by vertical located slightly anterior to eye and anteriorly by vertical approximately one-third of distance between anterior margin of eye and tip of snout. Combined opening for anus and urogenital papillae circular to longitudinally ovoid in females, longitudinally ovoid in males.

Premaxilla with ten to 11 [ten in both syntypes] teeth and ten replacement teeth in cleared and stained specimen (122 TL) and with ten to 14 functional teeth apparent in whole specimens ($N = 5$). Sexual dimorphism in form of dentary and associated dentition present in some congeners not apparent in examined specimens. Dentary in cleared and stained specimen (122 TL) with one functional tooth row of nine curved conical teeth bordered medially by eight replacement teeth. Whole specimens with two tooth rows with 11–16 [13 in both syntypes] teeth in outer row and three to four [four in one syntype] teeth apparent in inner row ($N = 4$).

Branchiostegal rays five; with first ray narrow and elongate, second and third rays somewhat wider, and fourth and fifth rays very large and broad with triangular ventral margins. Precaudal vertebrae 17–18 (four anterior; three to four transitional; $N = 23$).

Pectoral-fin rays ii + 13–15 ($N = 23$) [13 and 14 branched rays in syntypes]. Anal-fin origin located anterior to opercle. Anterior unbranched anal-fin rays 22–38 ($N = 14$). Total anal-fin rays 222–245 ($N = 15$) [226 in syntypes according to Steindachner (1868b: 254) but with 228 rays in smaller and 225 in larger syntypes; both specimens with regenerated tails]. Scales above lateral line at midbody nine to 12 [11 scales in syntypes] ($N = 20$). Scales along mid-dorsal line absent in many specimens along most of body anterior to origin of midsaggital electroreceptive filament. Larger specimens with areas lacking scales sometimes separated by scaled mid-dorsal patches, and with position and extent of unscaled regions variable both ontogenetically and within some population samples. Origin of midsaggital electroreceptive filament located approximately at 60% of TL. Filament extending posteriorly beyond vertical through posterior terminus of base of anal fin for distance of approximately four scales. Tail compressed and short, ending in small, elongate, pointed caudal fin. Caudal-fin rays 16–19 ($N = 6$) [16–17 in syntypes according to Steindachner (1868b: 254) but fins regenerated in both specimens].

Coloration in alcohol: Overall ground coloration light brown. Head in smaller specimens with scattered, small, dark chromatophores dorsally and on lateral surface of postocular region. More concentrated band of dark chromatophores located along dorsal region of snout in region from vertical through posterior naris to slightly posterior of eye. Dark pigmentation on head more obvious in larger individuals, with dark dorsal preorbital region often more obvious and sometimes extending anteriorly nearly to snout tip. Body in small specimens with light brown pigmentation overlain by relatively dense pattern of irregularly positioned, small, dark chromatophores. Larger individuals with overall coloration distinctly darker, but without any distinct pigmentation pattern.

Pectoral fin in smaller specimens hyaline to very slightly dusky distally. Distal pigmentation on fin increasingly pronounced in both extent and intensity ontogenetically. Largest individuals with pectoral fin sometimes nearly completely very darkly pigmented and with overall pigmentation distinctly darker than that present in juveniles. Anal fin in smallest examined individuals hyaline to very slightly pigmented distally, with distal pigmentation distinctly darker in largest specimens and sometimes covering distal two-thirds of fin and forming irregular band. Caudal fin unpigmented.

Distribution: Sternarchorhynchus mormyrus is known from the mainstream of the Amazon River from Manaus in the central portions of the basin to the vicinity of Iquitos in north-eastern Peru, the Río Negro, and from the Río Orinoco basin in both Venezuela and south-eastern Colombia (Fig. 58). A photograph that we examined shows a specimen that either *S. mormyrus* or a very similar undescribed species captured in the central portions of the Rio Madeira in the vicinity of Porto Velho. This location lies a considerable distance from the mainstream Amazon. Two questionable records of the species (see comments under Remarks below) would extend its distribution to the lower portions of the Amazon River basin.

The distribution of this species is the greatest in *Sternarchorhynchus*, but we did not identify any differences across that range (e.g. Orinoco versus Amazon basins) that justified the recognition of more than one species. Comparable broad ranges occur in some fish species that have been critically analysed across those basins within the Apteronotidae (e.g. *Sternarchorhamphus muelleri*, Campos-da-Paz, 1995: fig. 2) and other major groups in those ichthyofaunas (e.g. Siluriformes: *Hoplosternum littorale*, Reis, 1997: fig. 4; *Cetopsis coecutiens*, Vari, Ferraris & de Pinna, 2005: fig. 19. Cichlidae: *Cichla ocellaris*, *Cichla* *temensis*, Kullander & Ferreira, 2007: figs 9, 75. Characidae: *Roeboides affinis*, de Lucena, 2007: fig. 3).

Ecology: Juveniles of *S. mormyrus* live within várzea along the shores of the main river (C. D. de Santana, pers. observ.) whereas adults are inhabitants of main river channels (Cox-Fernandes, Podos & Lundberg, 2004: supplemental information).

Electrical organ discharge: Crampton & Albert (2006: 688) briefly described the EOD in *S. mormyrus* as resembling the IR Type B pattern, but 'in which the descending voltage curve has no, or only a very slight, outward inflection giving the waveform an asymmetrical aspect in the horizontal plane'. These authors consequently termed this EOD pattern as type C.

Secondary sexual dimorphism: de Santana & Crampton (2006: 58) remarked that *S. mormyrus* demonstrates sexual dimorphism in the form of the anterior portion of the neurocranium, with mature males having a wider snout than do conspecific females. Hilton & Cox-Fernandes (2006: 836) reported that *S. mormyrus* demonstrates sexual dimorphism of the lower jaw, with males having distended jaws relative to females. These authors also reported that males have many more teeth on that jaw than do females. We have not found such differences in the form of the lower jaw and dentary dentition in the material of *S. mormyrus* examined in this study.

Remarks: The two extant known syntypes of *Sternarchus mormyrus* (NMW 65336, 65345; Eschmeyer, 1998: 1122), both have regenerated tails makes it impossible to determine the total length and other distances and proportions that are a function of that measurement. The count of the anal-fin rays is also likely to be reduced as a consequence of that damage.

Steindachner (1868b: 253) reported the type locality of *Sternarchus mormyrus* as 'Maribitanos' without elaboration as to the river basin and country within which the collecting site was located. That site is undoubtedly Marabitanas, the type locality for various other lots of fishes deposited at NMW (e.g. *Heros psittacus* Heckel) collected at 'Rio-negro, nordlich von Marabitanas am Fusse des Berges Cocui' (= Río Negro, north of Marabitanas at foot of Cocui mountains; Kullander, 2003: 637). Marabitanas is at approximately 00°58′N, 66°51′W in the region where Colombia, Brazil, and Venezuela border each other along the upper Río Negro.

Steindachner often published two accounts of species that he described as new. One paper was typically a brief abstract in the *Anzeiger de Akademie der Wissenschaften*, *Wien* with the name of the species and a brief listing of certain diagnostic characters. He complimented these brief initial accounts with a second more detailed account that was often accompanied by detailed illustrations. These accounts were typically published in the *Sitzungsberichte der Akademie der Wissenschaften*, *Matematicsh-Naturwissenschafrliche Classe*, *Wien*, although on occasion in other outlets. In the case of *Sternarchus mormyrus*, the *Sternarchorhynchus mormyrus* of this study, previous authors (e.g. Mago-Leccia, 1994; Campos-da-Paz, 2000) understandably assumed that the detailed description with an associated illustration of the head and anterior portion of the body of a syntype (Steindachner, 1868b) constituted the formal description. In this instance the abstract (Steindachner, 1868a) was published first (Eschmeyer, 1998: 1122) and, thus, constitutes the formal original description of *Sternarchus mormyrus*.

Eigenmann & Bean (1907) proposed that *S. curvirostris* was a likely senior synonym of *S. mormyrus*. *Sternarchorhynchus mormyrus* and *S. curvirostris* were, in turn, placed as junior synonyms of *S. oxyrhynchus* by Ellis (1913: 141), who considered the latter species to be a monotypic, morphologically highly variable form. Fernández-Yépez (1967: 18) resurrected *S. mormyrus* and *S. curvirostris* from synonymy on the basis of various external features of the head. Based on the illustration provided by Fernández-Yépez (1967: 19), the material that he reported as *S. curvirostris* differed from that species in various details and is likely to be another species. It is also questionable whether Fernández-Yépez had material of *S. mormyrus* at hand given the differences between the illustrated specimen and *S. mormyrus*, most notably in the form of the snout and position of the anus and urogenital papilla. That question notwithstanding, the practice of recognizing *S. mormyrus* as a distinct species was continued by Mago-Leccia (1994: 37) and Campos-da-Paz (2000: 528). Our results confirm the distinctiveness of *S. mormyrus*. Indeed it is one of the more easily recognized species within *Sternarchorhynchus*.

Eigenmann & Bean (1907: 666) reported on specimens of what they identified as *S. mormyrus* from along the Amazon River in the region between Manaus and Pará (= Belém). Although *S. mormyrus* does occur in that region, those specimens had 191 to 194 anal-fin rays, a range distinctly lower than the 222 to 245 rays present in *S. mormyrus*. Examination of the specimens (USNM 52542) that served as the basis for that record has shown them to be *S. starksi*.

The easternmost records for *S. mormyrus* within the Amazon basin in this study (Fig. 58) are based on two specimens (USNM 373026, USNM 373050) lacking portions of their tails. This damage renders a definitive identification problematic, but these specimens are assigned to *S. mormyrus* based on their correspondence to that species in other features including morphometrics of the head, overall head and body form, and coloration.

Material examined

BRAZIL. *Amazonas*: Marabitanas (approximately 00°58′N, 66°51′W), NMW 65345, approximately 315 [syntype of *Sternarchus mormyrus*, tail regenerated]; NMW 65336, 384 [syntype of *Sternarchus mormyrus*, tail regenerated]. Rio Solimões, Ilha do Careiro, Lago Juanico; INPA 4899, 2 (378–413), INPA 27473, 3 (243–251), INPA 27474, 1 (214); INPA 4900, 1 (505). Rio Solimões, Ilha da Machantaria, INPA 17608, 1 (342), INPA 17609, 3 (310–350), INPA 27470, 1 (300). Rio Solimões, Paraná do Xiborena; INPA 17610, 1 (240), INPA 27475, 1 (270), INPA 27746, 1 (382). Rio Solimões, Paraná do Cuarí; INPA 17611, 1 (180). Rio Japurá, mouth of Lago Caxinguba; INPA 18295, 1 (243). Rio Purus, Beruri; INPA 27477, 1 (365). Lago Manacapuru (3°06′S, 61°30′W); MCZ 34338, 1 (250). Rio Amazonas, 28.5 km below Manaus (3°05′33″S, 59°46′27″W); USNM 306843, 2 (1CS, 119–122); USNM 229916, 1 (133); USNM 375479, 1 (315). Rio Jutaí, near Zinho (2°57′40″S 67°00′48″W); MZUSP 55855, 1 (257). Rio Amazonas, Parintins (2°38′S, 56°46′W); MZUSP 79856, 1 (105). Rio Uaupés (2°55′S 69°38′W); MZUSP 91647, 1 (410). Rio Negro, 5.4 km below Unini (1°41′41″S 61°29′19″W); MZUSP 55852, 1 (279). Rio Negro, below Daraá (approximately 0°30′S, 64°40′W); MZUSP 32202, 2, 335–379. Rio Negro, at Manaus (3°06′S, 60°00′W); MCZ 9347, 1 (258).

COLOMBIA. Río Orinoco basin, Río Meta, no specified locality; IAVHP 2674; 1 (520).

PERU. *Amazonas*: Río Marañon, pongo above Borja, 35.5 km north-east of Juan Velasco at Santa Maria de Neiva (approximately 4°50′S, 77°51′W); AUM 47285, 1 (305; formerly AUM 46270, in part). *Loreto*: Río Amazonas, vicinity of Iquitos, upstream and downstream of mouth Río Itaya (3°40′36″S, 73°14′37″W); ANSP 182583, 1 (190).

VENEZUELA. *Apure*: Río Guariquito at confluence with Río Orinoco; MBUCV 15711, 1 (300). Río Apure, in front of mouth of Caño Manglar (approximately 7°52′N, 67°36′W); MBUCV 20670, 1 (522). Río Matyure, just south of village of Achaguas (7°45′N, 68°15′W); CU 72165, 1 (148). *Delta Amacuro*: Caño at mouth of Anabata into Río Orinoco, north of Isla Portuguesa (approximately 8°37′12″N, 61°47′33″W); CU 80960, 2 (252–275). Río Orinoco, south of Isla Portuguesa, 116 nautical miles (= 214.6 km) upstream from sea buoy (approximately 8°37′N, 61°49′W); LACM 43044–5, 1 (420). Río Orinoco, on north shore at Isla Portuguesa (approximately 8°37′N, 61°49′W); LACM 43295–84, 2 (261–273). Río Orinoco, in front of Isla Iguana; MBUCV 10512, 1 (200). Río Orinoco, in front of Isla Tres Caños (8°40′N, 62°00″W; MBUCV 10885, 1 (239), MBUCV 12081, 1 (229). Río Orinoco, shallow river downstream from buoy 82, near mouth of small caño (8°28′24″N, 61°17′12″W); USNM 228646, 1 (264). Río Orinoco (8°40′12″N, 62°00′00″W); USNM 228875, 1 (495). *Guárico*: Caño Casi Seco, 42 km east of Guayabal (8°01′67″N, 67°07′50″W); MCNG 14427, 1 (110).

The following material is tentatively identified as *S. mormyrus* (comments under Remarks above):

BRAZIL. *Pará*: Rio Amazonas, between Almerim and Gurupá (01°28′38″S, 52°04′00″W); USNM 373026, 1 (261). Rio Amazonas, 58.5 km below Jurutí, 21.1 km above Óbidos (1°55′56″S, 55°40′58″W); USNM 373050, 1 (235).

STERNARCHORHYNCHUS OXYRHYNCHUS (MÜLLER & TROSCHEL) (FIGS 62, 63; TABLE 11)

Sternarchus oxyrhynchus Müller & Troschel, 1848: 640 [type locality: Guyana, Essequibo River; locality information problematic, Remarks]. – Müller &

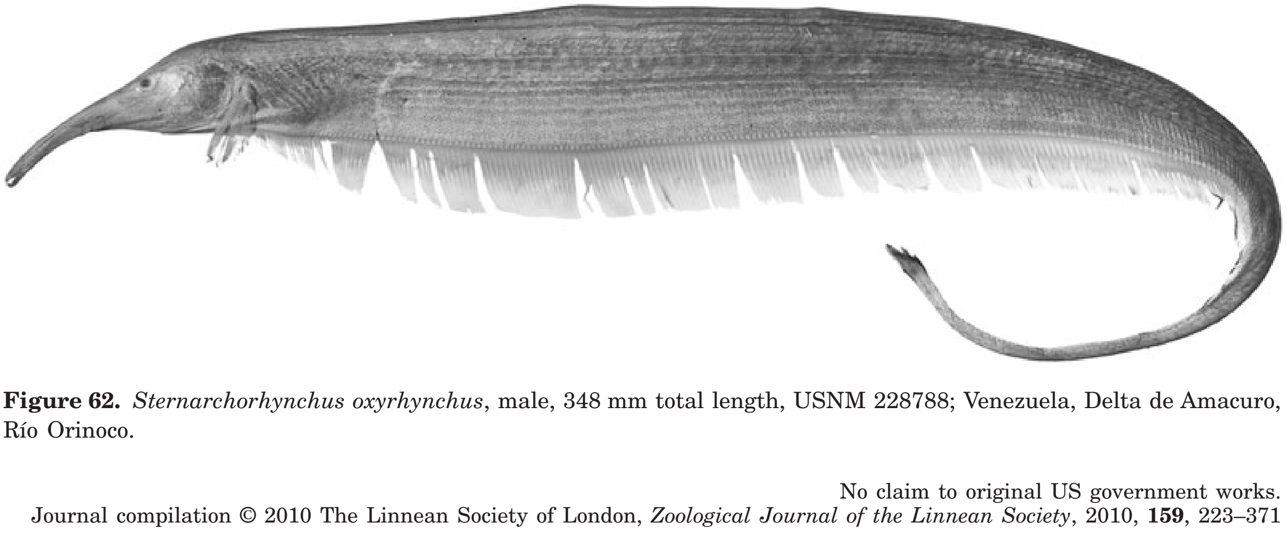

Figure 62. *Sternarchorhynchus oxyrhynchus*, male, 348 mm total length, USNM 228788; Venezuela, Delta de Amacuro, Río Orinoco.

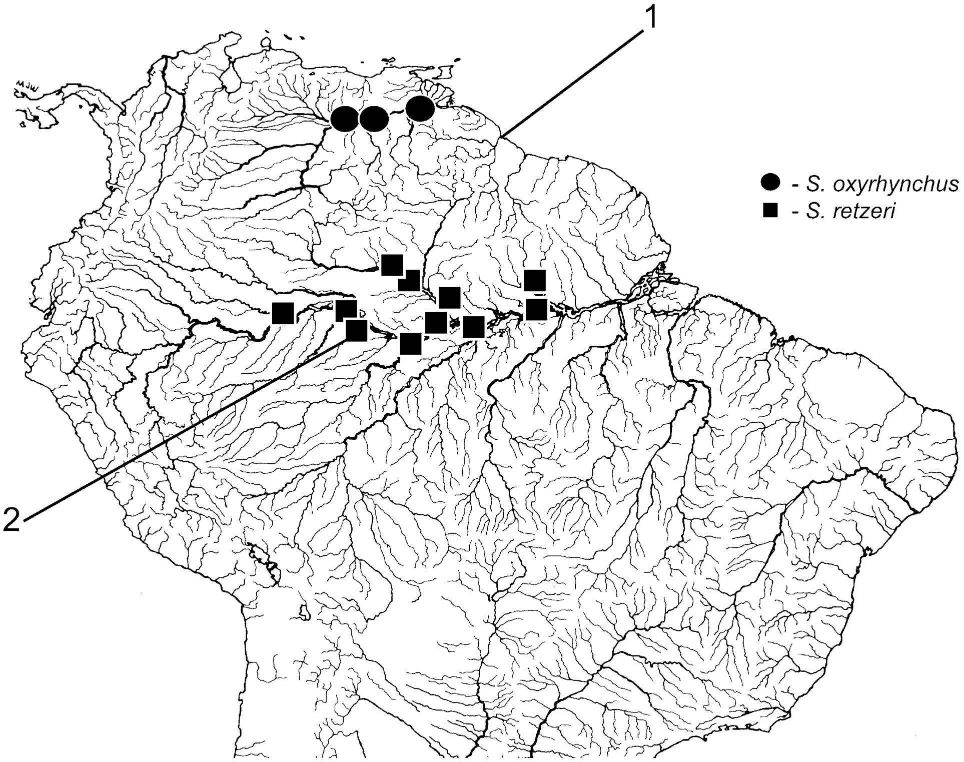

Figure 63. Map of central and northern South America showing geographical distribution of *Sternarchorhynchus oxyrhynchus* (1 – Essequibo River, reported type locality of species, but see Remarks in species account concerning possible erroneous locality information), and ***Sternarchorhynchus retzeri* sp. nov.** (2 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

Troschel, 1849: 16, pl. 2, figs 1, 2 [expanded description of species with accompanying illustration]. – Günther, 1870: 4 [British Guiana; based on original description]. – Eigenmann & Eigenmann, 1891: 62 [assignment to *Sternarchorhynchus*].

Sternarchorhynchus mulleri Castelnau, 1855: 95 [type locality: Guyana, Essequibo River; based on *Sternarchus oxyrhynchus* Müller & Troschel, 1848]. – Mago-Leccia, 1994: 36 [as junior synonym of *S. oxyrhynchus*]. – Campos-da-Paz, 2000: 521 [as junior objective synonym of *S. oxyrhynchus*].

Sternarchorhynchus oxyrhynchus, Ellis, 1913: 140, 174 [meristic and morphometric data for holotype reported; diet; *Sternarchus mormyrus* and *S. curvirostris* placed into synonymy of *S. oxyrhynchus*; not cited records of species from localities in Guyana]. – Fowler, 1951: 431 [in part; not records based on synonymy of *S. mormyrus* and *S. curvirostris* into *S. oxyrhynchus*; not cited occurrence in the Amazon basin and Guianas]. – Fernández-Yépez, 1967: 18 [*Sternarchus mormyrus* and *S. curvirostris* resurrected from synonymy of *S. oxyrhynchus*]. – Mago-Leccia, 1994: 36, fig. 53 [as valid species in listing of members of genus]. – Taphorn *et al.*, 1997: 80 [Venezuela]. – Albert & Campos-da-Paz, 1998: 423 [phylogenetic relationships]. – Campos-da-Paz, 2000: 528, fig. 1 [recognized as valid species in key to species of *Sternarchorhynchus*; head and anterior portion of body of holotype illustrated]. – Albert, 2001: 13 [in study of phylogenetic relationships]. – Albert, 2003: 501 [in listing of members of *Sternarchorhynchus*]. – Lasso *et al.*, 2004b: 142 [Río Orinoco basin in Colombia and Venezuela]. – Lasso *et al.*, 2004b: 181 [Venezuela; Río Orinoco basin]. – Crampton, 2007: 289 [widespread in Orinoco basin; not cited occurrence in river systems outside that basin].

Diagnosis: Sternarchorhynchus oxyrhynchus is distinguished from all congeners other than *S. goeldii* by possessing the following combination of characters: the gape of the mouth is aligned with main axis of snout, with the gape elongate and extending posteriorly distinctly beyond the vertical through the posterior naris. *Sternarchorhynchus oxyrhynchus* differs from *S. goeldii* in the number of total vertebrae (97–108 versus 92–94, respectively), the greatest body depth (6.3–9.2 versus 8.2–10.8 of TL, respectively), and to a notable degree in head depth at the nape (26.8–37.7 versus 35.0–44.8 of HL).

Description: Morphometric data for examined specimens in Table 11.

Lateral line extending posteriorly at least to base of caudal fin and continuing for short distance onto basal portions of fin in some specimens. Snout elongate, compressed and very slightly curved ventrally distally, but with snout having overall anteroventral orientation. Anus and urogenital papilla located ventral to head, with position demonstrating little intraspecific variation and located about two to four orbital diameters posterior of vertical through posterior margin of eye.

Premaxilla with ten functional teeth and six replacement teeth in cleared and stained specimen (*N* = 1; 280 mm TL). Whole specimens with ten to 13 functional teeth on premaxilla. No obvious sexual dimorphism present in form of dentary and associated dentition in examined samples. Dentary with two rows of teeth along at least anterior portion of bone. Outer row more elongate, with ten to 12 teeth in cleared and stained specimens (*N* = 2; 210–240 mm TL) and with teeth in region situated short distance posterior of symphysis shifted somewhat laterally and pointed slightly dorsolaterally. Outer tooth row with six associated replacement teeth in that specimen. Mouth terminal. Gape of mouth aligned with main axis of snout, elongate and extending posteriorly distinctly beyond vertical through posterior naris (Fig. 1A). Lower jaw with terminal fleshy pad that extends beyond vertical through anterior limit of snout. Pad orientated dorsally and overlaps tip of snout in closed mouth.

Branchiostegal rays five; with first and second ray narrow and elongate, third to fifth rays becoming increasingly wider and with fourth and fifth rays with triangular ventral margins. Precaudal vertebrae 16–17 (13 anterior; three to four transitional; *N* = 12). Total vertebrae 97–108 [108].

Pectoral-fin rays ii + 12–15 [ii + 12] (*N* = 16). Anal-fin origin located anterior to vertical through opercle. Anterior unbranched anal-fin rays 24–26 [23] (*N* = 7). Total anal-fin rays 212–242 [215] (*N* = 12) [215 anal-fin rays reported by Müller & Troschel (1848: 640) in original description]. Scales above lateral line at midbody three to eight [3] (*N* = 12). Scales absent along mid-dorsal line from rear of head to electroreceptive filament origin. Origin of midsaggital electroreceptive filament located approximately at 54% of TL. Filament extending posteriorly beyond vertical through posterior terminus of base of anal fin for distance of approximately seven scales. Tail compressed and long, ending in small, elongate, pointed caudal fin. Caudal-fin rays 15–18 (*N* = 14).

Coloration in alcohol: Overall ground coloration tan to light brown. Head and body with small dark chromatophores relatively densely scattered over surfaces. Dark pigmentation somewhat more developed dorsally. Some specimens with posteriormost portion of body and all of tail distinctly darker than remainder of body.

Pectoral fin coloration ranging from nearly completely hyaline to overall darkly pigmented, but with dark pigmentation most developed distally. Very lightly pigmented specimens with dark pigmentation limited to distal most portions of fin. Distal pigmentation on fin increasingly pronounced ontogenetically in both extent and intensity. Anal fin with variably developed dark pigmentation distally. Overall more lightly pigmented specimens often with dark pigmentation limited to posterior half of anal fin and/or forming narrow band along distal fin margin. Specimens with dark overall coloration with extent of dark pigmentation increasing both in terms of extension anteriorly and also in degree to which pigmentation extends basally from margin of fin. Distal pigmentation in some darker individuals extending forward nearly to anteriormost rays of fin and forming irregular dark band along entire fin margin. Caudal fin dark even in overall lightly pigmented individuals.

Distribution: Sternarchorhynchus oxyrhynchus is only known from the Río Orinoco basin (Fig. 63; see under Remarks concerning purported occurrence of species in the Essequibo River, Guyana).

Remarks: Sternarchorhynchus was proposed by Castelnau (1855) on the basis of a species, *S. mulleri*, described in the same publication (this species erroneously cited by some authors as *S. muelleri* or *S. mulleri*; Campos-da-Paz, 2000: 521). Mago-Leccia (1994: 36) noted that *S. mulleri* was based on *S. oxyrhynchus* and as such was a junior synonym of the latter species. That conclusion was reiterated by Campos-da-Paz (2000: 521), who specifically pointed out that *S. mulleri* was a junior objective synonym of *S. oxyrhynchus* under the rules of the International Code of Zoological Nomenclature.

Sternarchorhynchus oxyrhynchus and *S. goeldii* have a distinctive mouth form with the extent of the gape extending further posteriorly than in all other congeners and terminating distinctly posterior of the vertical through the posterior naris. The remaining species of *Sternarchorhynchus* have a shorter gape that fails to extend nearly as far posteriorly. The mouth form of *S. oxyrhynchus* was clearly illustrated by Müller & Troschel (1849: 16, pl. 2, fig. 2), albeit without the posterior naris indicated. The 108 total vertebrae in the type specimen of *Sternarchus oxyrhynchus* (the *Sternarchorhynchus oxyrhynchus* of this study; ZMB 4086) fall at the upper end of the range for that feature (97–108 vertebrae) amongst the radiographed specimens of *S. oxyrhynchus*, but that count lies distant from the 98–99 vertebrae present in *S. goeldii*, the only other species within *Sternarchorhynchus* characterized by this distinctive elongate gape.

All specimens examined in the course of this study that agree with the original description of *S. oxyrhynchus* and the type specimen of the species in terms of overall appearance, mouth form, and meristics originated within the Río Orinoco basin. In their original description of *Sternarchus oxyrhynchus* (the *Sternarchorhynchus oxyrhynchus* of this study), Müller & Troschel (1848: 640) reported that the type locality was the Essequibo River of British Guiana (= Guyana) with the collector being 'Schomb.' (= Schomburgk). Müller & Troschel reiterated that locality in their more encompassing description of the species that was accompanied by illustrations (Müller & Troschel, 1849: 16, pl. 2, figs 1, 2). None of the specimens of *Sternarchorhynchus* that originated in the Essequibo River basin examined during this study agree with the original description of *S. oxyrhynchus.* The only species of *Sternarchorhynchus* we examined that originated in the Essequibo River system is *S. freemani*, a species distinguished from *S. oxyrhynchus* in numerous features including the presence of an unpigmented stripe along the dorsal midline from the snout to at least the origin of the electroreceptive filament (versus the lack of such a stripe in *S. oxyrhynchus*), the presence of scales along the mid-dorsal portion of the body to the origin of the electroreceptive filament (versus the absence of scales along at least part of that region in *S. oxyrhynchus*), and the number of anal-fin rays [170–177 in *S. freemani* versus 212–242 in *S. oxyrhynchus*, with 215 reported by Müller & Troschel (1848: 640) in the original description].

Schomburgk collected in the Río Orinoco basin in 1838–1839 in association with some of his collecting efforts in British Guiana (Kullander & Stawikowski, 1997: 113; Riviere, 1998: 2). Given that all examined samples of *S. oxyrhynchus* were collected in the eastern portions of the Río Orinoco basin, this raises the possibility that some of the material reported by Müller & Troschel (1848: 1849) as having originated in the Essequibo River might represent specimens collected in the Río Orinoco basin with incorrect associated locality information.

The original description of *Sternarchus oxyrhynchus* (Müller & Troschel, 1848: 640) cited a range of size of examined specimens (16–18 Zoll) presumably indicative of least two specimens at hand. The subsequent Müller & Troschel paper that discussed the species in greater detail (Müller & Troschel, 1849: 16) lists, however, only a single length (18 Zoll), which was indicative of a unique specimen. Eigenmann (in Ellis, 1913: 142) similarly reported a unique 'type' as No. 4086 in the 'Berlin Mus.' (= ZMB) and only that specimen is now present in the ZMB holdings (Eschmeyer, 1998; P. Bartsch, ZMB, pers. comm.). The original description possibly incorrectly listed a range of sizes despite a unique type specimen or alternatively a second syntype was lost subsequent to the original description. Given the brief timeframe between the two Müller & Troschel publications (1848, 1849), the option of an lapsus in the original description seems the more likely possibility.

In his study of the Gymnotidae (the Gymnotiformes of this study), Ellis (1913: 142) considered *S. curvirostris* and *S. mormyrus* to be junior synonyms of *S. oxyrhynchus* and ascribed the apparent differences between the nominal species as 'being in part due to the size of the fish'. The concept of a monotypic *Sternarchorhynchus* was followed by subsequent authors (e.g., Eigenmann & Allen, 1942; Fowler, 1951) until Fernández-Yépez (1967: 18) resurrected *S. mormyrus* and *S. curvirostris* from the synonymy of *S. oxyrhynchus* based on differences in external features, albeit on the basis of misidentified specimens in the case of the purported *S. curvirostris* and probably also for *S. mormyrus* (see Remarks under that species). The results of our study, nonetheless, confirm the distinctiveness of those two nominal species with respect to *S. oxyrhynchus*.

Eigenmann (1912: 438) and Ellis (1913: 141) reported *S. oxyrhynchus* from Amatuk and Warraputa in the Essequibo River system of Guyana. As detailed above, none of the samples of *Sternarchorhynchus* that we examined from the river systems of the Guianas proved to be *S. oxyrhynchus*. Examination of the material that served, at least in part, as the basis of the Eigenmann and Ellis records (CAS 72248 formerly CM 1807; CAS 72246, formerly IU 12590) have shown that they are *S. freemani*, a species described as new in this study.

Material examined

GUYANA. Essequibo River, no specified locality (both locality information and possible number of specimens in original description problematic; see under Remarks; photograph and radiograph of type examined, with meristic and morphometric data provided by P. Bartsch, ZMB); ZMB 4086, 1 (469; type of *Sternarchus oxyrhynchus* Müller & Troschel).

VENEZUELA. *Bolivar*: Río Orinoco, approximately 50 km above mouth of Río Cuchivero (7°40′N, 65°57′W); ANSP 162670, 4 (268–290). Río Orinoco, near mouth of Río Caura (7°38′N, 64°52′W); ANSP

163044, 1 (283). *Delta Amacuro*: Río Orinoco, shallow river, north side of river across from Isla Tres Caños, 131.8 nautical miles (= 243.8 km) from sea buoy (8°39′48″N, 62°01′W); USNM 228787, 8 (1 CS, 207–314). Río Orinoco, deep river channel, at Isla Tres Caño, 130 nautical miles (= 240.5 km) upstream from sea buoy (8°40′N, 61°59′W); USNM 228788, 1 (348); MBUCV 10886, 2 (227–297). Río Orinoco, north shore, in front of Isla Tres Caños (approximately 8°39′48″N, 62°01′W); MBUCV 11853, 1 (305); MBUCV 10691, 1 (250). MBUCV 12079, 4 (235–275).

STERNARCHORHYNCHUS RETZERI SP. NOV.

(FIGS 63–65; TABLE 11)

Sternarchorhynchus cf. *roseni* – Crampton, 2007: 320, fig. 11.13c [sexual dimorphism in form of anterior portion of dentary].

Diagnosis: Sternarchorhynchus retzeri is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales

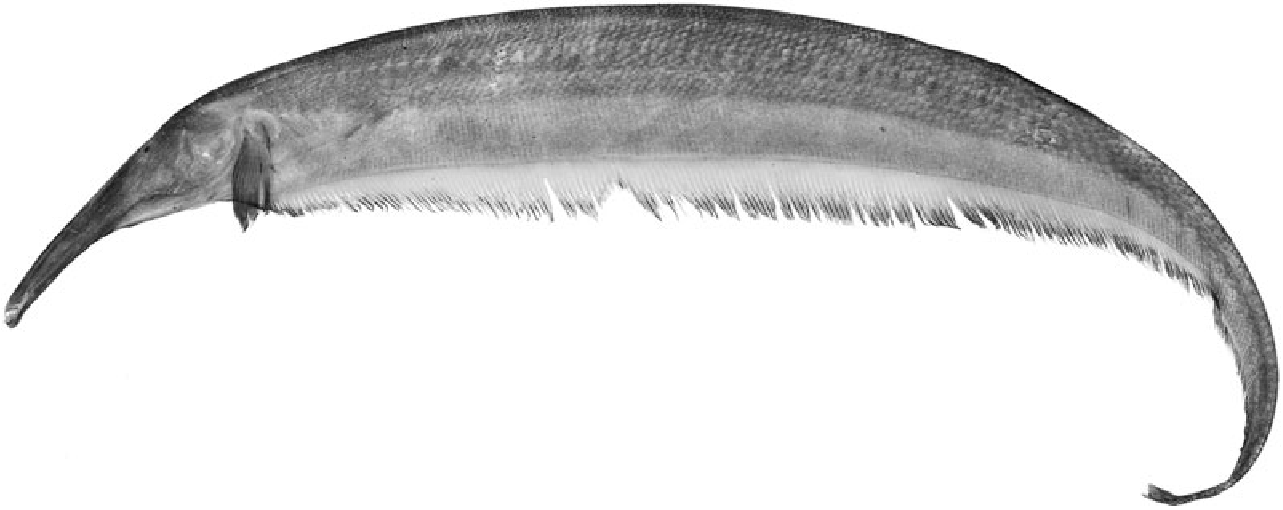

Figure 64. ***Sternarchorhynchus retzeri* sp. nov.,** holotype, sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 297 mm total length, MCP 41636; Brazil, Amazonas, Rio Solimões, Rio Tefé, Tefé.

Figure 65. ***Sternarchorhynchus retzeri* sp. nov.**, female, 382 mm total length, MCP 41635; Brazil, Amazonas, Rio Solimões.

along the mid-dorsal region of the body, the lateral line that extends posteriorly to the base of the caudal fin, the presence of a narrow, more lightly coloured band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the distinct band of dark pigmentation along the distal third to half of most of the anal fin and covering most of the posterior rays on that fin, the possession of eight to 11 teeth on the premaxilla, five to nine teeth in the outer tooth row of the dentary, one to two teeth in the inner tooth row of the dentary, 17–25 anterior unbranched anal-fin rays, 198–225 total anal-fin rays, 14–18 caudal-fin rays, 15 precaudal vertebrae, the greatest body depth (8.3–10.1% of LEA), the preanal distance (13.0–15.2% of LEA), the caudal length (7.1–10.3% of LEA), the head width (15.9–18.7% of HL), the head depth at the eye (21.4–27.7% of HL), the head depth at the nape (34.1–41.8% of HL), the snout length (65.4–71.2% of HL), the distance from the posterior naris to the eye (57.3–74.0% of HL), the distance from the posterior naris to the snout (5.7–7.0% of HL), the eye diameter (2.5–3.4% of HL), the postocular distance (31.6–34.9% of HL), the height of the branchial opening (10.0–12.5% of HL), the pectoral-fin length (34.4–39.1% of HL), and the tail depth (15.3–15.8% of caudal length).

Description: Morphometric data for holotype and paratypes in Table 11.

Lateral line extending to base of caudal fin, but absent on fin. Snout elongate, compressed and straight to very slightly curved ventrally distally. Posterior naris closer to tip of snout than to anterior margin of eye. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla ontogenetically variable and apparently sexually dimorphic. Openings in smaller individuals positioned along vertical located slight distance posterior of vertical through rear margin of orbit. Anus and urogenital papilla located at vertical slightly anterior of anterior margin of orbit in mature females and also in mature males lacking patch of large teeth at anterior of dentary. Males with patch of large teeth at anterior of dentary with anus and urogenital papilla positioned further anteriorly approximately at vertical one-third of distance between anterior margin of eye and tip of snout. Combined opening relatively rounded in juveniles and somewhat to distinctly horizontally elongate in larger specimens.

Premaxilla of small size, somewhat rounded, with eight to 11 teeth ($N = 3$). Dentary sexually dimorphic. Dentary in mature males extended further anteriorly than in females and juveniles and with anterior portion widened transversely into bulbous structure rounded from dorsal view and bearing series of enlarged, posteriorly recurved teeth on dorsal surface. Dentary bearing two irregular tooth rows with approximately five to nine teeth present in outer row and one to two in inner row ($N = 3$). Mouth terminal with rictus located anterior to vertical through posterior naris.

Branchiostegal rays five; with first to third rays relatively narrow and elongate and fourth and fifth branchiostegals large and broad. Precaudal vertebrae 16 (12–13 anterior; three to four transitional, $N = 10$).

Pectoral-fin rays ii + 12–15 [ii + 14] ($N = 20$). Anal-fin origin located slightly posterior of vertical through anterior margin of opercle. Anterior unbranched anal-fin rays 17–27 [27] ($N = 12$). Total anal-fin rays 198–225 [225] ($N = 14$); number of rays apparently increases ontogenetically based on correlation between increased body length and greater numbers of rays in examined samples. Scales above lateral line at midbody ten to 11 [10] ($N = 20$). Scales along mid-dorsal region of body readily apparent. Origin of midsaggital electroreceptive filament located approximately at 67% of TL. Filament typically extending posteriorly to vertical through posterior terminus of base of anal fin. Tail compressed and of moderate length, ending in small and elongate caudal fin. Caudal-fin rays 14–18 ($N = 13$).

Coloration in alcohol: Overall ground coloration ranging from light to dark brown. Head and body with dark chromatophores relatively densely scattered over surfaces. Relative size of chromatophores and intensity of pigmentation greater in overall darker specimens. Snout with variably distinct, narrow band of pigmentation somewhat darker than ground coloration extending anteriorly from region slightly forward of orbit to, or slightly short of, anterior portion of snout. Band of dark pigmentation on snout borders narrow, lightly coloured, mid-dorsal band on head; lightly pigmented band apparent even in overall darkly pigmented specimens. Ventral margin of snout somewhat darker than lateral surface of snout in some specimens. Body pigmentation slightly darker dorsally, but with mid-dorsal, more lightly coloured stripe extending from stripe on head posteriorly onto basal portions of electroreceptive filament and then to varying degrees further posteriorly.

Pectoral fin coloration ranging from dusky to distinctly dark, with pigmentation more pronounced over fin rays and distally. Anal fin with distinct band of dark pigmentation along distal third to half of fin along most of its length, but with dark pigmentation covering nearly all of shorter fin rays posteriorly. Caudal-fin rays dark.

Distribution: Sternarchorhynchus retzeri is broadly distributed across the Amazon basin from the Rio Iça basin in the western portions of Amazonas, Brazil, to the Rio Trombetas in Pará, Brazil (Fig. 63).

Electrical organ discharge: Crampton & Albert (2006: 688) reported that *S. retzeri* (identified by those authors as *S.* cf. *roseni*) had an EOD resembling their type B, but 'in which the descending voltage curve has no, or only a very slight, outward inflection giving the waveform an asymmetrical aspect in the horizontal plane'. In light of this difference they proposed that it be separated as a type C EOD pattern.

Secondary sexual dimorphism: Specimens of *S. retzeri* examined in this study demonstrate a striking sexual dimorphism in the form of the dentary and in the position of the anus and urogenital opening. At least some males have the dentary extended further anteriorly and widened transversely into a dorsally bulbous structure that is distinctly rounded from dorsal view and bears a series of enlarged, posteriorly recurved teeth (Crampton, 2007: fig. 11.13c; species identified therein as *S.* cf. *roseni*). Juveniles and adults without these elaborations instead have the anus and urogenital opening positioned approximately along the vertical through the eye. Males as evidenced by the presence of a well-developed patch of teeth on the anterior portion of the dentary have these structures instead significantly shifted anteriorly and positioned within the region delimited by the verticals falling one-quarter to one-third of the distance from the anterior margin of the orbit to the tip of the snout.

Geographical variation: Nearly all specimens of *S. retzeri* examined in this study have the termination of the electroreceptive filament located at the vertical through the posterior terminus of the base of the anal fin. One possible specimen of the species captured in the Rio Negro (FMNH 115484), has the filament extending somewhat more posteriorly for a distance of about four scales beyond the vertical through the posterior termination of the base of the anal fin. This specimen is a mature male as evidenced by the gonads, but has the anus and urogenital papilla anteriorly positioned along a vertical approximately one-third of the distance between the anterior margin of the orbit and the tip of the snout. This anterior position of the anus and urogenital papilla occurs elsewhere in *S. retzeri* only in mature males with a distinct batch of enlarged dentition on the anterior portion of the dentary. The specimen from the Rio Negro may represent a male of this species without such modifications of the anterior portions of the dentary and associated dentition, a situation that occurs in males of some congeners. Additional samples are necessary to determine whether it represents a geographical variant, possible differential expression of secondary sexual characters in males because of seasonality in the presence of such dentary modifications, or an undescribed species.

Etymology: The specific name, *retzeri*, is in honour of Michael Retzer of the Illinois Natural History Survey who provided invaluable assistance through the years to both authors in the course of this and other research projects.

Material examined

Holotype: – BRAZIL. *Amazonas*: Rio Tefé, Toco Preto, Tefé (3°47′19″S, 64°59′54″W), collected by W. G. R. Crampton, 25.x.1999; MCP 41636, 1 (372).

Paratypes: – BRAZIL. *Amazonas*: Rio Tefé, Toco Preto, Tefé (3°47′19″S, 64°59′54″W), collected by W. G. R. Crampton, 22–25.x.1999; MCP 41635, 10 (281–390).

Nontype specimens: – BRAZIL. *Amazonas*: FMNH 115481, 1 (279), FMNH 115504, 1 (222); Río Iça, between Paraná do Curumim and Rio Solimões, between towns of Betânia and São Antônio do Iça (3°8′48″S, 68°02′07″W). FMNH 115484, 1 (327); Rio Negro between Paraná Cantagalo and Paraná Onças, between São Francisco and São Francisco de Assis (1°44′22″S, 61°24′56″W). MZUSP 55847, 1 (200), Río Negro, 24.4 km below Paraná Aliaque (1°13′32″S 62°13′49″W). INPA 27493 1 (374); Rio Negro, Lago do Prato, Anavilhanas. USNM 375475, 1 (270); Rio Solimões (3°35′43″S, 61°07′16″W). MZUSP uncat.; 1 (197), Rio Solimões, below Purus (3°36′25″S, 61°19′40″W). MZUSP 56161, 2 (240–290), Rio Solimões, 15.4 km below Paraná do Taiacutuba (2°36′24′S 65°44′23″W). INPA 27490, 1 (362); INPA 17607, 1 (237); Rio Solimões, Ilha da Machantaria. INPA 17606, 1 (242); Rio Solimões. INPA 17604, 1 (308); Rio Purus, at Beruri. INPA 17605 2 (190–279); Rio Solimões, Costa do Marimba, Ilha do Careiro. *Pará*: FMNH 115515, 3 (188–236); Rio Amazonas between Paraná de Santa Rita and Rio Trombetas, between towns of Jurutí and Óbidos (1°56′7″S, 55°41′19″W). USNM 373027, 3 (186–286); Rio Trombetas, 9.9 km above Vila Aracuá (1°30′48″S, 56°10′19″W).

*S*TERNARCHORHYNCHUS ROSENI MAGO-LECCIA

(FIGS 66–68; TABLE 12)

Sternarchorhynchus roseni (nomen nudum), Marrero & Taphorn, 1991: 129 [use of manuscript name; secondary sexual dimorphism in species discussed]. –

Figure 66. *Sternarchorhynchus roseni*, sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 383 mm total length, MBUCV 19844; Venezuela, Apure, Río Apure.

Figure 67. *Sternarchorhynchus roseni*, female, 377 mm total length, LACM 43252-3; Venezuela, Delta de Amacuro, Río Orinoco.

Machado-Allison & Moreno, 1993: 88 [use of manuscript name; Venezuela, Guarico, Río Orituco].

Sternarchorhynchus roseni Mago-Leccia, 1994: 99, fig. 92 [type locality: Venezuela, Río Orinoco basin, Estado Apure, Río Apure in front of Jarina, near San Fernando de Apure]. – Taphorn *et al.*, 1997: 80 [Venezuela]. – Campos-da-Paz, 2000: 528 [recognized as valid species in key to species of *Sternarchorhynchus*]. – Albert, 2003: 501 [in listing of members of *Sternarchorhynchus*]. – Lasso *et al.*, 2004b: 142 [Río Orinoco basin in Colombia and Venezuela]. – Lasso *et al.*, 2004a: 181 [Venezuela; Río Orinoco basin]. – Machado-Allison, 2006: 26 [Venezuela]. – Crampton, 2007: 289 [widespread in Orinoco basin; not cited occurrence in Amazon].

Diagnosis: Sternarchorhynchus roseni is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, having the scales along the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament sparse and covered by skin, the presence of a more lightly coloured, narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the possession of a total of eight to 11 teeth on the dentary, 16 precaudal vertebrae, 19–27 anterior unbranched anal-fin rays, 193–210 total anal-fin rays, the greatest body depth (8.6–10.9 of LEA), the caudal length (10.7–12.8 of LEA), the head depth at the nape (40.1–46.3 of HL), the head depth at the eye (23.0–29.9 of HL), the head width (19.7–23.0 of HL), the distance from the posterior naris to the snout (6.0–8.4 of HL), the distance from the posterior naris to the eye (49.8–63.4 of HL), the postocular distance (34.0–40.7 of HL), the pectoral-fin length (34.4–41.0 of HL), and the tail depth (11.0–16.1 of caudal length).

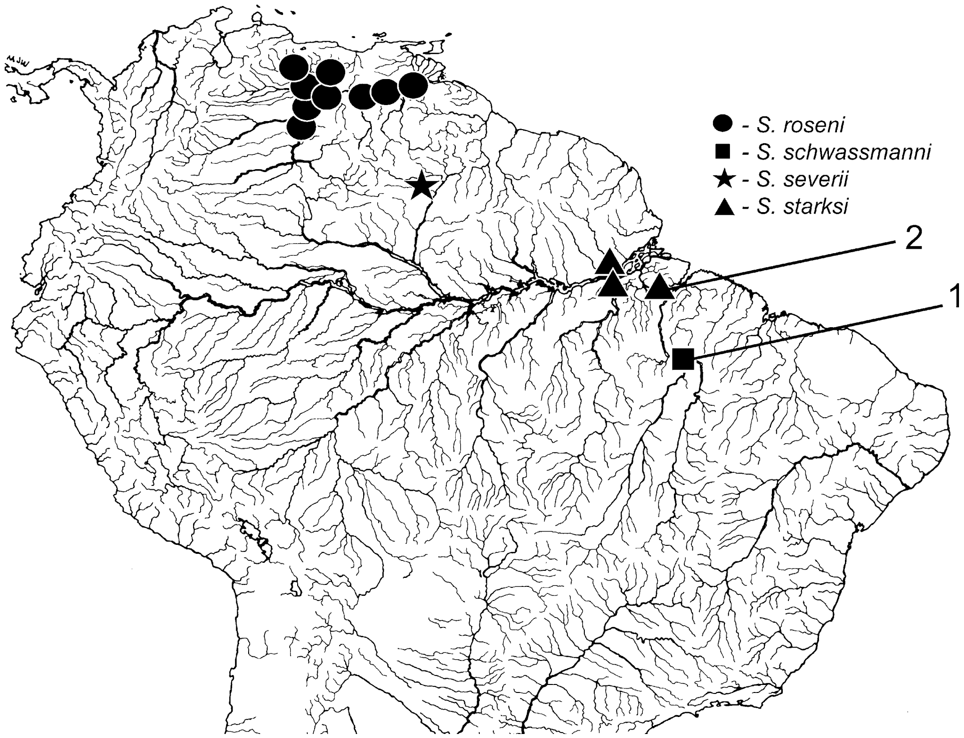

Figure 68. Map of central and northern South America showing geographical distribution of *Sternarchorhynchus roseni*, ***Sternarchorhynchus schwassmanni* sp. nov.** (1 = holotype locality), *Sternarchorhynchus severii*, and ***Sternarchorhynchus starksi* sp. nov.** (2 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

Description: Morphometric data for holotype and paratypes in Table 12.

Lateral line extending to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly curved ventrally, more so distally. Posterior naris located closer to tip of snout than to anterior margin of eye. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla apparently sexually dimorphic. Openings positioned within range between verticals running slightly anterior to slightly posterior to eye in smaller individuals, females, and mature males lacking expanded dentary and patch of enlarged dentition on dentary. Anus and urogenital aperture much more anteriorly positioned in males with definite patch of enlarged dentition on dentary and located between verticals approximately one-quarter to one-third distance between anterior limit of eye and tip of snout. Combined opening for anus and urogenital papilla slightly horizontally elongate in males with well-developed patch of teeth on dentary; opening more rounded in other examined specimens.

Premaxilla of small size, somewhat rounded, with seven to eight teeth ($N = 2$). Dentary with two rows of teeth with total of eight to 11 teeth ($N = 2$). Dentary form sexually dimorphic. Dentary in some males extending further anteriorly than in females and widened transversely into dorsally bulbous structure, rounded from dorsal view and bearing series of enlarged, slightly posteriorly recurved teeth. Mouth terminal with rictus located anterior to vertical through anterior naris in juveniles, posterior of that vertical in males with enlarged dentary with patch of teeth, but still located distinctly anterior of vertical through posterior naris.

Branchiostegal rays five; with first to third rays relatively narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (12–13 anterior, three to four transitional; $N = 10$).

Pectoral-fin rays ii + 11–14 [ii + 12] ($N = 25$). Anal-fin origin located slightly posterior of vertical through anterior margin of opercle. Anterior unbranched anal-fin rays 19–27 ($N = 18$). Total anal-fin rays 193–210 [208] ($N = 21$); number of fin rays apparently increases ontogenetically based on correlation between greater body size and increased numbers of fin rays within examined samples. Scales above lateral line at midbody seven to 12 [12] ($N = 25$). Scales along mid-dorsal region of body somewhat sparse and not readily apparent on body surface. Origin of midsaggital electroreceptive filament located approximately at 62% of TL. Filament extending one to two scales posterior of vertical through

Table 12. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus roseni*, *Sternarchorhynchus schwassmanni*, and *Sternarchorhynchus severii*

	S. roseni		*S. schwassmanni*			*S. severii*	
	Range	Mean	H	Paratype	H	Paratypes	Mean
Total length (mm)	154–417 (*N* = 17)	–	98.5	115.8	161	67.0–169 (*N* = 12)	–
Length to end of anal fin (mm)	138–375 (*N* = 17)	–	87.4	111.7	145	61.7–149 (*N* = 12)	–
Head length (mm)	27.7–53.9 (*N* = 17)	–	19.7	23.0	23.7	9.0–28.6 (*N* = 12)	–
Caudal length (mm)	14.9–46.8 (*N* = 15)	–	7.0	–	14.6	5.7–14.6 (*N* = 12)	–
Per cent of length to end of anal fin							
Anal-fin base	82.6–97.7 (*N* = 17)	87.0	83.9	80.2	85.5	78.9–89.5 (*N* = 12)	85.0
Distance snout to anus	8.0–13.2 (*N* = 17)	11.1	11.8	10.6	19.6	10.0–13.5 (*N* = 12)	11.6
Preanal-fin distance	11.4–15.0 (*N* = 17)	13.7	15.2	13.6	12.0	12.9–16.7 (*N* = 12)	14.4
Prepectoral-fin distance	16.2–20.7 (*N* = 17)	19.1	22.2	21.8	17.0	16.4–21.2 (*N* = 12)	19.1
Greatest body depth	8.6–10.9 (*N* = 17)	9.8	12.7	12.4	13.5	12.7–14.0 (*N* = 12)	13.4
Head length	16.0–20.9 (*N* = 17)	19.0	22.5	20.6	16.4	16.4–20.7 (*N* = 12)	18.5
Caudal length	10.7–12.8 (*N* = 15)	11.6	8.0	–	10.1	7.7–11.3 (*N* = 12)	9.7
Per cent of head length							
Anus to anal-fin insertion	7.0–20.0 (*N* = 17) 27.5–32.5 (*N* = 2)	12.230.0	10.5	14.4	15.0	7.8–19.9 (*N* = 12)	12.3
Pectoral-fin length	34.4–41.0 (*N* = 19)	37.5	35.5	38.3	66.6	48.7–59.8 (*N* = 12)	52.2
Head depth at eye	23.0–29.9 (*N* = 19)	26.9	31.6	30.4	35.4	31.7–36.0 (*N* = 5)	34.4
Head depth at nape	40.1–46.3 (*N* = 19)	43.3	49.6	49.5	63.2	53.8–72.0 (*N* = 12)	61.2
Head width	19.7–23.0 (*N* = 19)	21.0	25.6	22.6	23.7	23.6–26.0 (*N* = 5)	24.5
Snout length	56.7–70.6 (*N* = 19)	65.8	56.8	57.3	50.2	44.7–53.2 (*N* = 12)	49.4
Posterior naris to snout	6.0–8.4 (*N* = 19)	7.5	9.6	10.2	8.0	7.4–10.0 (*N* = 5)	8.3
Posterior naris to eye	49.8–63.4 (*N* = 19)	57.5	44.2	45.4	65.5	48.8–67.2 (*N* = 12)	58.8
Mouth length	4.1–6.4 (*N* = 19)	5.1	6.3	5.7	9.7	7.8–9.8 (*N* = 12)	8.9
Internarial distance	2.5–3.5 (*N* = 18)	3.0	3.6	3.0	5.0	4.0–6.0 (*N* = 12)	5.1
Eye diameter	2.3–4.2 (*N* = 19)	3.1	6.4	5.3	8.0	6.2–9.2 (*N* = 12)	7.9
Interocular width	4.8–7.8 (*N* = 19)	6.0	9.1	9.7	8.6	6.0–15.3 (*N* = 12)	10.2
Postocular distance	34.0–40.7 (*N* = 19)	37.1	42.4	43.3	56.8	45.2–54.2 (*N* = 12)	49.6
Branchial opening	9.4–14.3 (*N* = 19)	12.1	14.8	15.2	21.3	15.4–21.7 (*N* = 12)	19.2
Per cent of caudal length							
Tail depth	11.0–16.1 (*N* = 15)	13.6	22.3	–	17.3	14.5–24.1 (*N* = 12)	18.8
Caudal-fin length	16.8–29.5 (*N* = 15)	21.9	41.7	–	37.2	28.6–49.3 (*N* = 12)	39.8

Sexually dimorphic features for *S. roseni* are presented as two entries. First entry is data for all specimens other than sexually dimorphic mature males. Information for sexually dimorphic male in second entry based on two specimens of 385–405 mm total length. Number of specimens indicated in parentheses.

posterior terminus of base of anal fin. Tail compressed and of moderate length, ending in small and elongate caudal fin. Caudal-fin rays 12–16 [16] (*N* = 14).

Coloration in life: In his original description of *S. roseni*, Mago-Leccia (1994: 102) reported that recently collected males from the Río Apure, had a 'dark, almost black' life coloration with a dark snout and hyaline midsaggital electroreceptive filament (the thong of that author). Females collected together with the males were 'gray with a snout clear which had a dark line contacting the midline pale stripe' and the filament was reported as 'grayish' and the anal fin was reported to have a 'dark border'.

Coloration in alcohol: Overall ground coloration light to dark brown. Head and body covered with relatively densely packed dark chromatophores. Size of individual chromatophores and intensity of pigmentation greater in overall darker specimens. Snout with variably distinct, narrow band of somewhat darker pigmentation extending forward from region anterior of orbit and reaching to anterior portion of snout in many specimens. Anterior portion of snout darker than adjoining areas in some males with well-developed patches of enlarged dentition on lower jaw. Dark band on lateral surface of snout apparent even in overall darkly pigmented specimens and forms lateral margin of narrow, lightly coloured, mid-dorsal band on snout. Lightly coloured mid-dorsal band on head expands laterally along dorsal portion of postocular region of head and continuous posteriorly with narrow, mid-dorsal lightly coloured stripe on body. Body pigmentation overall slightly darker dorsally, but with narrow, lightly coloured mid-dorsal stripe extending from rear of head posteriorly onto basal portions of electroreceptive filament and then to varying degrees further posteriorly in various specimens.

Pectoral-fin coloration ranging from nearly hyaline in many specimens to dusky in darker individuals, with dark chromatophores overlying pectoral-fin rays. Anal-fin pigmentation apparently sexually dimorphic. Anal fin completely hyaline in most examined specimens, including apparently mature females. Some of darker individuals with overall hyaline anal fins having basal portions of rays outlined by series of dark chromatophores and forming very faint band. Males with anteriorly and laterally expanded dentary with patch of enlarged dentary teeth have distal half of most of anal fin darker and forming distinct band; band extends across all rays in narrower posterior portion of fin. Caudal-fin pigmentation variable, with coloration of rays ranging from somewhat to distinctly dark and with pigmentation always more developed on basal portions of rays. Some males with expanded dentaries have additional distal dark pigmentation on caudal fin.

Distribution: Examined specimens of *S. roseni* all originated in the central portions of the Río Orinoco system in Colombia and Venezuela (Fig. 68). Lasso *et al.* (2004b: 142) reported the species as inhabiting other portions of the basin ranging from the state of Delta Amacuro in eastern Venezuela to the Río Meta system in the western portions of the Río Orinoco system.

Ecology: Specimens of *S. roseni* collected at Caño Bravo in the Río Apure drainage of Venezuela came, in part, from a white water habitat over a substrate of sand and clay covered with leaf litter and at water depths of up to 1.5 m (de Santana *et al.*, 2006: 279).

Secondary sexual dimorphism: Sternarchorhynchus roseni demonstrates sexual dimorphism of the anterior portion of the dentary and associated dentition comparable to that present in some congeners. The species also demonstrates a striking sexual dimorphism in the position of the anus and urogenital papilla. Females along with juveniles have the anus and urogenital papilla positioned approximately at the vertical through the eye. Mature males, as evidenced by the presence of a well-developed patch of enlarged teeth on the expanded anterior portion of the dentary, have the anus and urogenital papilla instead significantly shifted anteriorly and positioned in the region delimited by verticals running one-quarter to one-third of distance from the anterior margin of the orbit to the tip of the snout.

Remarks: As aforementioned under Coloration in life, Mago-Leccia (1994) reported a distinct sexual dimorphism in the coloration in *S. roseni*, with males being much darker than females. Our samples demonstrate a significant degree of variation in overall coloration with the species. We found, however, that in preserved samples the mature males with well-developed patches of enlarged teeth on the expanded dentary had only a slightly darker coloration than did females collected at the same time. It is possible that the distinct sexual dimorphism in pigmentation reported by Mago-Leccia (1994) for *S. roseni* is apparent only in life or is limited to the breeding season.

Material examined

COLOMBIA. Río Meta, unspecified localities; IAVHP 2981, 1 (221), IAVHP 6278, 1 (129).

VENEZUELA. *Apure*: Río Apure, near of mouth of Río Manglar (approximately 7°52′N, 67°36′W); MCNG 50521, 1 (192). Río Apure, near San Fernando de Apure; INHS 28403, 1 (240); Río Apure (7°16.26′N, 71°5.20′W). AMNH 58665, 2 (233–253; paratypes), MBUCV 15809, 6 (212–273; paratypes), MBUCV 19839, 8 (144–256; paratypes). Río Apure, 1 km upstream from San Fernando de Apure; MBUCV 19843, 1 (400). Río Apure, 3 to 5 km downstream from bridge of San Fernando de Apure; MBUCV 19844, 1 (383). Río Apure, near Isla del Medio; MBUCV 20025, 2 (208–289; paratypes). Río Apure, between mouth of Río Portuguesa and San Fernando de Apure airport (7°54′00″N, 67°32′00″W); ANSP 165215, 2 (202–330). Río Apure, near San Fernando de Apure; MCNG 24068, 1 (216). Río Apure at confluence with Río Portuguesa; MBUCV 7562, 1 (143; paratype). Río Meta, upstream from confluence with Río Orinoco; MBUCV 15722, 1 (171; paratype). MBUCV 15807, 5 (170–245; paratypes), MBUCV 15811, 1 (117; paratype); Río Apure, in front of Isla Apurito (8°00′N, 67°31′W). Río Apure, at Jarina (7°56′N, 67°30′W). MCNG 52591, 18 (115–172), Río Aruaca, Caño Bucaral; MBUCV 20037, holotype (267), MBUCV 20066, 1 (166; paratype); MBUCV 15808, 2 (154–247; paratypes). Río Arauca, mouth of Caño Bucaral; MBUCV 15810, 1 (108; paratype). Río Apure, at La Rompia; MBUCV 15813, 1 (180; paratype). Río Apure, 10 km downstream of San Fernando de Apure (7°86′39″N, 67°39′17″W); MCNG 13875, 5 (161–285). Río Apure, mouth of Río Portuguesa near San Fernando de Apure (7°95′00″N, 67°52′78″W); MCNG 14040, 1 (206), MCNG 14041, 1 (145). Río Portuguesa, between Estudos Barinas and Guarico; MCNG 51457, 2 (175–323), MCNG 51458, 5 (172–240), MCNG 51459, 3 (166–222). Río Apure, Caño Caujarito; MCNG 45131, 2 (152–221). Río Apure, Caño Caicara, where crossed by bridge on road from Mantecal (7°22′N, 69°21′W); USNM 260248, 4 (164–222). *Barinas*: Río Apure, mouth of Río Portuguesa; MCNG 52552, 3 (185–335), MCNG 52546, 1 (326). Río Masparro, 5 km north-west from Libertad to Barinas; INHS 29916, 1 (255). Río Apure, Caño Bravo (8°00′00″N, 67°98′33″E); MCNG 49176, 1 (196), MCNG 49284, 1 (171), MCNG 49314, 3 (131–180), MCNG 49341, 1 (168), MCNG 49462, 1 (78), MCNG 49614, 1, (184), MCNG 51727, 1 (96), MCNG 51747, 4 (105–170), MCNG 51770, 1 (228), MCNG 51790, 2 (137–170), MCNG 52106, 1 (310), MCNG 52233, 8 (123–222), MCNG 52264, 1 (52). *Bolivar*: Río Orinoco, near Puerto Las Majadas, at confluence with Río Caura; MBUCV 15697, 1 (217). Río Portuguesa (9°06′67″N, 69°50′00″W); MCNG 15827, 3 (91–120). Río Orinoco, near Isla de Farjado (8°22′N, 62°42W); USNM 228879, 1 (410). *Delta de Amacuro*: Río Orinoco, LACM 43252–3, 4 (186–377). Río Orinoco, old shipping channel south of Isla Portuguesa; MBUCV 10411, 1 (235; paratype). Río Orinoco, downstream from El Concejo; MBUCV 12201, 3 (228–260). Río Orinoco, at Isla Tres Caños (8°39′48″N, 61°58′40″W); USNM 228786, 1 (226). *Guarico*: Río Orituco; MBUCV 5491, 1 (93; paratype). Río Orinoco, mouth of Caño Guine (8°39′54″N, 62°02′06″W); USNM 228880, 2 (333–413). Río Orituco (8°52′N, 67°18′W); USNM 260246, 1 (123). Río Guarico, at Flores Moradas ranch approximately 3–4 km east of road from Calabozo to San Fernando de Apure (8°27″N, 67°25″W); USNM 260249, 1 (242).

STERNARCHORHYNCHUS SCHWASSMANNI SP. NOV.

(FIGS 68, 69; TABLE 12)

Diagnosis: Sternarchorhynchus schwassmanni is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, in having the scales along the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament sparse and covered by skin to varying degrees, the presence of a more lightly coloured, narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the extension of the dorsal filament to a point one or two scales posterior of the vertical through the posterior terminus of the base of the anal fin, the possession of ten teeth in the outer tooth row on the dentary, 15 precaudal vertebrae, 25–26 anterior unbranched anal-fin rays, nine to ten scales above the lateral line at the midbody, 164–166 total anal-fin rays, the greatest body depth (12.4–12.7% of LEA), the length of the base of the anal fin (80.2–83.9% of LEA), the prepectoral-fin distance (21.8–22.2% of LEA), the head depth at the nape (49.5–49.6% of HL), the snout length (56.8–57.3% of SL), the mouth length (5.7–6.3% of HL), the interocular width (9.1–9.7% of HL), the eye diameter (5.3–6.4% of HL), the distance from the posterior naris to the eye (44.2–45.4% of HL), the postocular distance (42.4–43.3% of HL), the height of the branchial opening (14.8–15.2% of HL), and the pectoral-fin length (35.5–38.2% of HL).

Description: Morphometric data for examined specimens in Table 12.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and curved ventrally distally. Mouth terminal and relatively small, with rictus located slightly anterior to

Figure 69. ***Sternarchorhynchus schwassmanni* sp. nov.,** holotype, female, 98.5 mm total length, MZUSP 95633, Brazil, Pará, Rio Araguaia.

vertical through anterior naris. Anus and urogenital papilla located ventral to head. Those structures situated along, or slightly anterior of, vertical through eye. Combined opening for anus and urogenital papilla ovoid.

Premaxilla with six to eight teeth ($N = 2$) apparent in whole specimens. Dentary with two tooth rows; outer row with ten teeth and inner row with two to three teeth ($N = 2$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (12 anterior; three transitional; $N = 2$).

Pectoral-fin rays ii + 12–13 [ii + 13] ($N = 2$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 25–26 [25] ($N = 2$). Total anal-fin rays 164–166 [166] ($N = 2$). Scales above lateral line at midbody nine to ten [9] ($N = 2$). Scales present but sparse and covered to varying degrees by skin along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of electroreceptive filament located approximately at 65% of TL. Filament extending posteriorly to point one to two scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, moderate, posteriorly rounded caudal fin. Caudal-fin rays 16 ($N = 1$).

Coloration in alcohol: Overall coloration brown. Head brown overall other than for slightly lighter region on midlateral surface of snout. Fleshy pad on anterior of dentary largely unpigmented. Darker pigmentation on snout forms lateral margin of lightly coloured, mid-dorsal stripe on snout. Mid-dorsal stripe continues posteriorly and expands very slightly laterally above postocular portion of head. Mid-dorsal stripe on head continuous posteriorly with narrow, lightly coloured, mid-dorsal stripe that extends posteriorly from rear of head to, or beyond, origin of electroreceptive filament. Posterior portion of tail darker than remainder of body. Pectoral fin dusky with rays overlain by dark chromatophores. Anal fin dusky with rays overlain by dark chromatophores. Caudal fin dark basally, but with hyaline posterior margin.

Distribution: Sternarchorhynchus schwassmanni is only known from the type locality in the Rio Araguaia of eastern Brazil (Fig. 68).

Etymology: The species name, *schwassmanni*, is in honour of Horst O. Schwassmann, University of Florida, for his contributions to the knowledge of Neotropical electric knifefishes.

Secondary sexual dimorphism: No sexual dimorphism was apparent in the limited examined sample of *S. schwassmanni.*

Remarks: One of the striking attributes of *S. schwassmanni* is its relatively small size at maturity. The 98.5 mm TL holotype is a female with developed white eggs and the 115.8 mm TL paratype is a male with developed testes.

Material examined

Holotype: – BRAZIL. *Pará*: Rio Araguaia, small stream between São João do Araguaia (5°23′S, 48°46′W) and São Bento (5°28′S, 48°20′W), collected by R. Stawikowski, 12.xi.1990; MZUSP 95633 (98.5, female, formerly MHNG 2566.093, in part).

Paratype: – BRAZIL. *Pará*: Rio Araguaia, small stream between São João do Araguaia (5°23′S, 48°46′W) and São Bento (5°28′S, 48°20′W), collected with holotype by R. Stawikowski, 12.xi.1990; MHNG 2566.093, 1 (115.8, male).

STERNARCHORHYNCHUS SEVERII DE SANTANA & NOGUEIRA (FIGS 68, 70; TABLE 12)

Sternarchorhynchus oxyrhynchus, not of Müller & Troschel, Ferreira *et al.*, 1988: 344 [in listing of species from Rio Mucajaí].

Sternarchorhynchus severii de Santana & Nogueira, 2006: 89, figs 1b, 2b, c [type locality: Brazil, Roraima, Rio Mucajaí, below Cachoeira Paredão].

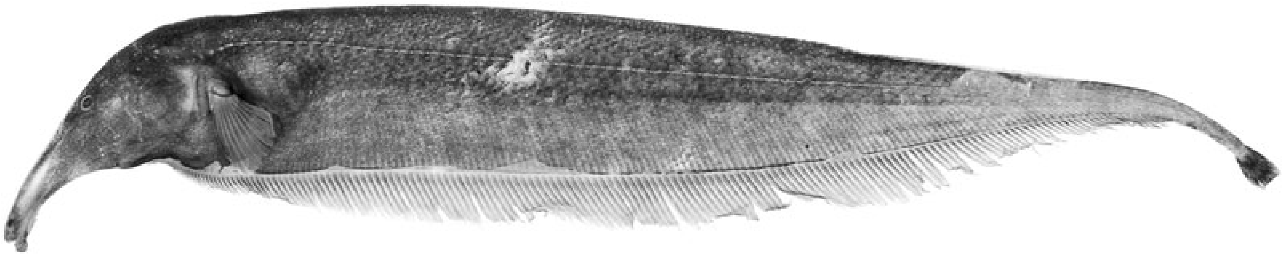

Figure 70. *Sternarchorhynchus severii*, holotype, male, 161 mm total length; Brazil, Roraima, Rio Mucajaí.

Diagnosis: Sternarchorhynchus severii is distinguished from congeners in the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends posteriorly to the base of the caudal fin, the dorsal filament that extends to a point two scales beyond the vertical through the posterior terminus of the base of the anal fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body anterior of the origin of the electroreceptive filament and sometimes extending posteriorly beyond that point, the dusky anal fin without a distinct dark band along the distal portions, the possession of nine to ten premaxillary teeth, seven to eight teeth on the outer row of the dentary, two to three teeth on the inner row of the dentary, 24–32 anterior unbranched anal-fin rays, 161–175 total anal-fin rays, 12–14 caudal-fin rays, the greatest body depth (12.7–14.0% of LEA), the caudal length (7.7–11.3% of LEA), the preanal distance (12.0–16.7% of LEA), the distance from the anus to the anal-fin insertion (7.8–19.9% of HL), the prepectoral-fin distance (16.4–21.2% of LEA), the caudal length (7.7–11.3% of LEA), the snout length (44.7–53.2% of HL), the head depth at the nape (53.8–72.0% of HL), the height of the branchial opening (15.4–21.7% of HL), the postocular length (45.2–56.8% of HL), the internarial distance (4.0–6.0% of HL), the pectoral-fin length (48.7–66.6% of HL), and the tail depth (14.5–24.1% of caudal length).

Description: Morphometric data for examined specimens in Table 12.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly curved ventrally distally. Mouth terminal and relatively small, with rictus located slightly anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head. Those structures situated within region delimited anteriorly by vertical less than one orbital diameter anterior of eye and posteriorly by vertical less than one orbital diameter posterior of eye. Combined opening for anus and urogenital papilla circular to longitudinally ovoid.

Premaxilla with nine to ten teeth (*N* = 6) apparent in whole specimens. Dentary with two tooth rows; outer row with seven to eight teeth and inner row with two to three teeth (*N* = 6).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15–16 (12–14 anterior; two to four transitional; *N* = 6).

Pectoral-fin rays ii + 12–13 [ii + 12] (*N* = 13). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 24–32 [26] (*N* = 12). Total anal-fin rays 161–175 [164] (*N* = 12). Scales above lateral line at midbody seven to 12 [9] (*N* = 13). Scales clearly present along mid-dorsal line of body to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 65% of TL. Filament extending posteriorly to point two scales anterior of vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in small, moderate, posteriorly rounded caudal fin. Caudal-fin rays 12–15 [15] (*N* = 11).

Coloration in alcohol: Overall coloration brown. Head brown overall laterally other than for slightly lighter region on midlateral surface of snout. Fleshy pad on anterior of dentary less intensely unpigmented than adjoining regions. Darker pigmentation on dorsolateral portion of snout forms lateral margin of anterior region of lightly coloured, mid-dorsal stripe on head. Lightly coloured, mid-dorsal area on head slightly laterally expanded above orbit and along anterior portion of postocular region of head and variably continuous posteriorly with narrow, mid-dorsal lightly pigmented stripe on body that extends posteriorly to, or beyond, origin of electroreceptive filament. Pectoral fin dusky with rays overlain by dark chromatophores. Anal fin dusky with rays overlain by dark chromatophores. Caudal fin very dark basally, but with hyaline region along rounded posterior margin.

Distribution: Sternarchorhynchus severii is only known from the type locality in the Rio Mucajaí, below Cachoeira Paredão (Fig. 68).

Secondary sexual dimorphism: No sexual dimorphism was observed in the limited available material of *S. severii.*

Ecology: According to Ferreira *et al.* (1988: 341), the area where the samples of *S. severii* were collected is characterized by steep banks and a shoreline bordered by dense forest. Large amounts of aquatic plans of the family Podostemonacease were present in the river, with the water being acidic (pH 5.8) and well oxygenated (91% saturation).

Remarks: The type series of *S. severii* and *S. caboclo* were collected at the same location. The two species are readily distinguishable by the number of branchiostegal rays (five versus four, respectively), pigmentation of the head and body (with narrow, lightly coloured stripe extending posteriorly to the origin of the electroreceptive filament versus mid-dorsal region of head and body dark, respectively), the pectoral-fin length (48.7–66.6 versus 31.3–46.9% of HL, respectively), and the head depth at the eye (31.7–36.0 versus 23.3–31.1% of HL, respectively).

Material examined
BRAZIL. *Roraima*: Rio Mucajaí, below falls of Cachoeira Paredão (approximately 2°57′N, 61°27′W); INPA 22893, 1 (161, male, holotype); INPA 22898, 13 (paratypes; 67–169, 2 cleared and stained).

STERNARCHORHYNCHUS STARKSI **SP. NOV.**
(FIGS 68, 71; TABLE 13)

Sternarchorhynchus mormyrus, not of Steindachner, Eigenmann & Bean, 1907: 666 [Brazil, lower Amazon between Pará (= Belém) and Manaus].

Sternarchorhynchus curvirostris, not of Boulenger, Starks, 1913: 23 [Brazil, Pará (= fish market at Belém].

Diagnosis: Sternarchorhynchus starksi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the anterior naris, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line extending posteriorly to the base of the caudal fin, the presence of a more lightly coloured, narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the hyaline anal fin without a distal dark band, the extension of the dorsal filament posteriorly to a point along the vertical approximately eight scales posterior of the terminus of the base of the anal fin, the possession of ten to 13 premaxillary teeth, eight teeth on the outer row of the dentary, four to five teeth on the inner row of the dentary, 18–26 anterior unbranched anal-fin rays, 185–202 total anal-fin rays, 11–14 scales above the lateral line at the midbody, 11–13 caudal-fin rays, the greatest body depth (9.7–12.5% of LEA), the head length (14.8–18.1% of LEA), the distance from the snout to the anus (7.0–10.8% of LEA), the distance from the anus to the anal-fin origin (8.3–18.3% of LEA), the prepelvic distance (14.4–18.3% of LEA), the caudal length (12.2–16.5% of LEA), the snout length (56.3–61.6% of HL), the distance from the posterior naris to the eye (47.8–53.7% of HL), the pectoral-fin length (40.6–53.2% of HL), the head depth at the eye (26.9–36.2% of HL), the head depth at the nape (50.5–69.3% of HL), the head width (23.1–28.4% of HL), and the tail depth (9.9–13.2% of caudal length).

Description: Morphometric data for examined specimens in Table 13.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly to distinctly curved ventrally; degree of curvature more pronounced in larger individuals. Mouth terminal and relatively small, with rictus located slightly anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically somewhat variable. Those structures situated along vertical approximately four orbital diameters posterior of rear margin of eye in smaller specimens and approaching, or along, vertical through eye in larger individuals. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla with ten to 13 teeth ($N = 9$) apparent in whole specimens. Dentary with two tooth rows; outer row with eight teeth and inner row with four to five teeth ($N = 6$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15–16 (12–13 anterior; two to three transitional; $N = 13$).

Pectoral-fin rays ii + 12–14 [ii + 13] ($N = 13$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 18–26 [22] ($N = 13$). Total anal-fin rays 185–202 [199] ($N = 11$). Scales above lateral line at midbody 11–14 [11] ($N = 13$). Scales present along mid-dorsal line to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 56% of TL. Filament extending posteriorly to point eight to ten scales posterior of vertical through posterior terminus of base of anal fin. Tail compressed and long, ending in small, moderate, pointed caudal fin. Caudal-fin rays 11–13 ($N = 7$).

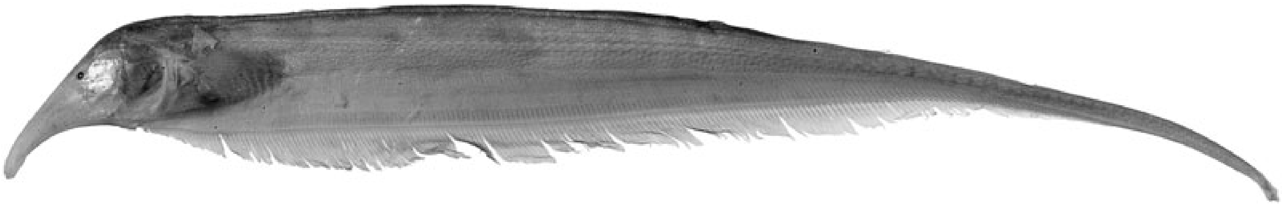

Figure 71. ***Sternarchorhynchus starksi*** **sp. nov.,** holotype, 231 mm total length, INPA 28377; Brazil, Pará, Rio Pará.

Table 13. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus starksi*, *Sternarchorhynchus stewarti*, and *Sternarchorhynchus taphorni*

	S. starksi			*S. stewarti*			*S. taphorni*		
	H	Paratypes	Mean	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	231	203–374 (*N* = 12)	–	182	195–229 (*N* = 8)	–	310	77.3–216	–
Length to end of anal fin (mm)	198	182–327 (*N* = 11)	–	168	182–217 (*N* = 8)	–	290	–	–
Head length (mm)	35.9	30.2–51.2 (*N* = 12)	–	35.6	35.7–43.3 (*N* = 8)	–	54.9	16.9–36.4	–
Caudal length (mm)	32.5	25.4–45.2 (*N* = 9)	–	10.9	11.2–15.5 (*N* = 8)	–	20.0	–	–
Per cent of length to end of anal fin									
Anal-fin base	88.3	87.0–91.7 (*N* = 11)	89.5	86.9	85.8–92.8 (*N* = 8)	88.2	84.8	–	–
Distance snout to anus	10.8	7.0–10.1 (*N* = 11)	8.2	12.6	9.3–12.0 (*N* = 8)	10.4	11.0	–	–
Preanal-fin distance	12.7	9.4–11.9 (*N* = 11)	10.6	13.9	12.0–13.6 (*N* = 8)	12.9	11.0	–	–
Prepectoral-fin distance	18.3	14.4–17.0 (*N* = 11)	15.9	21.8	18.3–21.1 (*N* = 8)	19.6	18.8	–	–
Greatest body depth	10.2	9.7–12.5 (*N* = 11)	11.4	12.6	11.4–13.7 (*N* = 8)	12.5	12.8	–	–
Head length	18.1	14.8–16.6 (*N* = 11)	15.9	21.1	18.3–19.9 (*N* = 8)	19.3	18.9	–	–
Caudal length	16.4	12.2–16.5 (*N* = 9)	14.5	6.5	6.1–7.1 (*N* = 8)	6.5	6.8	–	–
Per cent of head length									
Anus to anal-fin insertion	8.3	9.0–18.3 (*N* = 12)	13.7	8.2	7.8–13.2 (*N* = 8)	11.0	18.5	3.9–11.7	7.8
Pectoral-fin length	44.7	40.6–53.2 (*N* = 12)	48.1	42.9	35.1–58.4 (*N* = 8)	43.4	47.8	37.4–45.2	41.3
Head depth at eye	29.7	26.9–36.2 (*N* = 12)	31.0	32.8	26.2–33.9 (*N* = 8)	30.0	36.4	31.8–46.8	39.3
Head depth at nape	50.5	52.4–69.3 (*N* = 12)	60.4	50.4	52.0–59.0 (*N* = 8)	55.8	62.2	55.7–62.3	59.0
Head width	23.7	23.1–28.4 (*N* = 12)	25.2	23.7	22.5–25.5 (*N* = 8)	24.0	23.9	27.5–31.1	29.3
Snout length	58.5	56.3–61.6 (*N* = 12)	59.3	64.0	61.7–65.7 (*N* = 8)	63.2	62.2	51.1–61.0	56.1
Posterior naris to snout	7.8	6.6–9.5 (*N* = 12)	7.6	8.1	8.2–9.3 (*N* = 8)	8.6	7.7	9.2–10.1	9.6
Posterior naris to eye	49.1	47.8–53.7 (*N* = 12)	50.5	53.5	51.2–55.7 (*N* = 8)	52.8	52.4	35.9–49.4	42.6
Mouth length	4.5	4.6–6.7 (*N* = 12)	5.3	6.2	6.1–7.5 (*N* = 8)	6.8	7.7	8.0–9.0	8.5
Internarial distance	2.4	2.1–3.2 (*N* = 12)	2.7	2.3	2.5–3.3 (*N* = 8)	2.9	2.7	2.9–3.7	3.3
Eye diameter	3.6	3.1–4.1 (*N* = 12)	3.6	4.0	3.6–4.1 (*N* = 8)	3.7	3.8	5.7–6.0	5.9
Interocular width	5.3	5.1–7.4 (*N* = 12)	6.4	37.3	5.3–7.1 (*N* = 8)	6.4	8.1	7.8–11.5	9.6
Postocular distance	28.8	41.5–49.2 (*N* = 12)	45.3	38.6	38.9–42.6 (*N* = 8)	41.0	43.5	45.2–46.4	45.8
Branchial opening	9.7	10.8–16.6 (*N* = 12)	14.2	11.8	12.0–14.5 (*N* = 8)	13.3	11.6	13.4–14.8	14.1
Per cent of caudal length									
Tail depth	11.5	9.9–13.2 (*N* = 9)	12.1	23.9	19.8–25.7 (*N* = 8)	23.2	24.4	–	–
Caudal-fin length	13.5	14.4–19.6 (*N* = 7)	17.6	51.2	41.6–52.7 (*N* = 8)	47.4	50.2	–	–

Morphometric values for paratypes of *S. taphorni* that are functions of length from tip of snout to end of anal fin and caudal length not available because of damage of tails. Number of specimens indicated in parentheses.

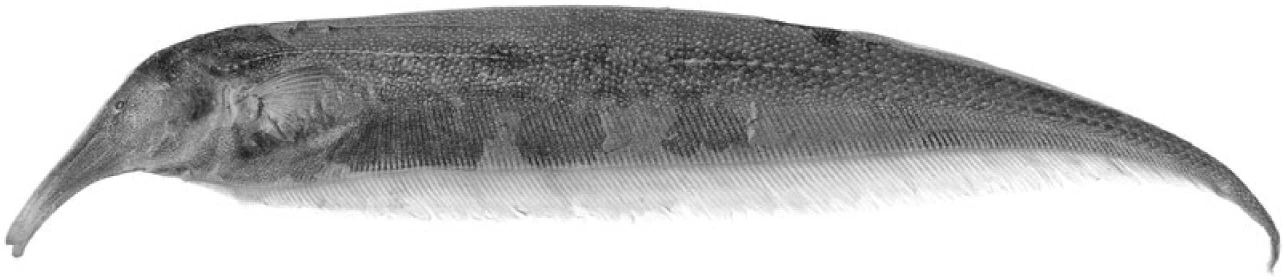

Figure 72. ***Sternarchorhynchus stewarti* sp. nov.,** holotype, 182 mm total length, MUSM 30409; Peru, Amazonas, Río Marañon.

Coloration in alcohol: Overall coloration light brown. Head with narrow, faint stripe of slightly darker pigmentation extending anteriorly from orbit for distance half to two-thirds length of snout. Darker pigmentation on snout forms lateral margin of lightly coloured, mid-dorsal stripe on snout. Lightly coloured mid-dorsal stripe on snout expands into longitudinally elongate ovoid area above postocular portion of head. Ovoid region continuous posteriorly with barely apparent mid-dorsal, lightly coloured stripe that extends posteriorly from rear of head for varying degrees, but which falls short of origin of electroreceptive filament. Pectoral fin hyaline to dusky. Anal fin hyaline. Caudal fin slightly dusky.

Distribution: Samples of *S. starksi* with definite locality information originated in the easternmost portions of the Amazon basin or were purchased in the fish market at Belém (Starks, 1913: 4, 23); cited therein as *S. curvirostris*). Given the fishing and transportation technology of that era, it is likely that those market samples were captured close to that city in the lowermost portion of the Amazon River (Fig. 68).

Secondary sexual dimorphism: No sexual dimorphism apparent in limited available samples of *S. starksi*.

Etymology: The species name, *starksi*, is in honour of Edwin Chapin Starks of Stanford University, who in the early part of the twentieth century collected a portion of the series that served as the basis for this description and who made a number of contributions to our knowledge of the anatomy of fishes.

Remarks: Examination of the specimens (CAS SU 22193; USNM 52542) that served, at least in part, as the basis for the citation of *S. mormyrus* from the lower Amazon between Pará (= Belém) and Manaus (Eigenmann & Bean, 1907: 666) and of *S. curvirostris* from the Belém region (Starks, 1913: 23) has shown them to be *S. starksi*.

Material examined

Holotype: – BRAZIL. *Pará*: Rio Pará between Rio Boa Vista and Rio Tocantins, between towns of Boa Vista and Abaetetuba (1°45′30″S, 49°29′17″W), collected by A. M. Zanata *et al.*, 18.xi.1994; INPA 28377 (231, formerly FMNH 115485).

Paratypes: – BRAZIL. *Pará*: Pará (= fish market at Belém), collected by E. C. Starks, 1911; CAS SU 22193, 10 (203–374). Rio Amazonas between Pará (= Belém) to Manaus, collected by J. B. Steere, 1901; USNM 52542, 2 [229 (tail broken)-267]. Río Jari, Monte Dourado, upstream of Rio Amazonas, L. Py-Daniel *et al.*, 13.xi.1994; MZUSP 58196, 1 (260).

Nontype specimens: – BRAZIL. *Pará*: Rio Amazonas, above Rio Xingu and town of Gurupá (1°28′38″S, 52°04′00″W), USNM 373029, 1 (278 regenerated tail). Pará (= fish market at Belém); AMNH 3776, 1 (307), AMNH 9869, 1 (259).

STERNARCHORHYNCHUS STEWARTI SP. NOV.

(FIGS 72, 73; TABLE 13)

Sternarchorhynchus curvirostris, not of Boulenger, Stewart, Barriga & Ibarra, 1987: 37 [Ecuador, Río Napo basin].

Diagnosis: Sternarchorhynchus stewarti is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line that extends posteriorly to the base of the caudal fin, the dorsal filament that extends posteriorly to a vertical approximately eight to ten scales posterior of the vertical through the posterior terminus of the

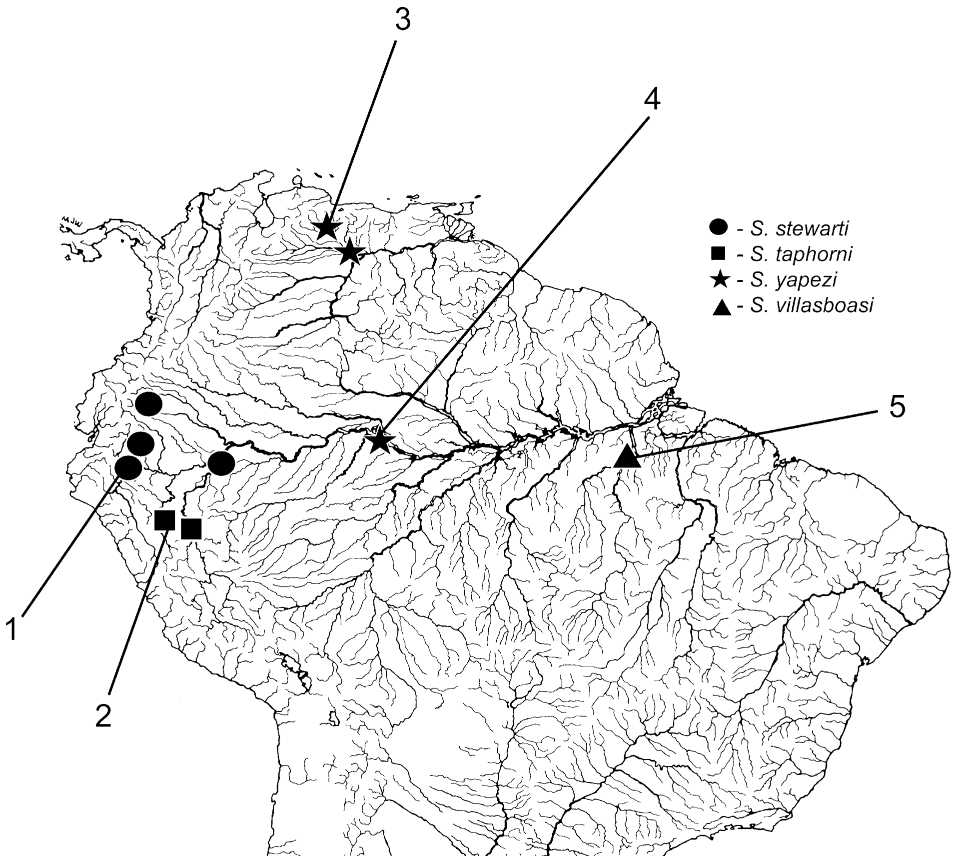

Figure 73. Map of central and northern South America showing geographical distribution of ***Sternarchorhynchus stewarti* sp. nov.** (1 = holotype locality), ***Sternarchorhynchus taphorni* sp. nov.** (2 = holotype locality), ***Sternarchorhynchus yepezi* sp. nov.** (3 = holotype locality; 4 = collecting location of possibly conspecific sample from central Amazon; under Remarks concerning that specimen and second specimen from aquarium trade possibly collected in the region of Iquitos, Peru), and ***Sternarchorhynchus villasboasi* sp. nov.** (5 = holotype locality) (some symbols represent more than one locality and/or lot of specimens).

base of the anal fin, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posterior to the origin of the electroreceptive filament and sometimes beyond that point, the hyaline to slightly dusky anal fin without a distinct band of dark pigmentation either distally or basally, the possession of seven to eight teeth on the premaxilla, six to seven teeth on the outer tooth row of the dentary, three to four teeth on the inner tooth row of the dentary, 16 precaudal vertebrae, 13–15 branched pectoral-fin rays, 26–34 anterior unbranched anal-fin rays, 180–191 total anal-fin rays, eight to nine scales above the lateral line at the midbody, 15–17 caudal-fin rays, the greatest body depth (11.4–13.7% of LEA), the distance from the anus to the anal-fin insertion (7.8–13.2% of HL), the preanal distance (12.0–13.9% of LEA), the prepectoral-fin distance (18.3–21.8% of LEA), the caudal length (6.1–7.1% of LEA), the head length (18.3–21.1% of LEA), the distance from the posterior naris to the snout (8.1–9.3% of HL), the mouth length (6.1–7.5% of HL), the snout length (61.7–65.7% of HL), the internarial distance (2.3–3.3% of HL), the head width (22.5–25.5% of HL), the head depth at the nape (50.4–59.0% of HL), the height of the branchial opening (11.8–14.5% of HL), and the tail depth (19.8–25.7% of caudal length).

Description: Morphometric data for examined specimens in Table 13.

Lateral line extending posteriorly to base of caudal fin, but absent on fin. Snout elongate, compressed and slightly to distinctly curved ventrally. Mouth terminal and relatively small, with rictus located slightly anterior to vertical through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically somewhat variable. Both structures positioned along vertical running approximately two to three orbital diameters posterior of rear margin of eye in smaller specimens and at, or up to one orbital diameter anterior of, vertical running through anterior margin of eye in larger individuals. Opening for anus and urogenital papilla ovoid, but with fleshy puckered margin.

Premaxilla with seven to eight teeth ($N = 15$) apparent in whole specimens. Dentary with two tooth rows; outer row with six to seven teeth and inner row with three to four teeth ($N = 10$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (12–13 anterior; three to four transitional; $N = 25$).

Pectoral-fin rays ii + 13–15 [ii + 14] ($N = 27$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 26–34 [27] ($N = 20$). Total anal-fin rays 179–191 [179] ($N = 20$). Scales above lateral line at midbody eight to nine [9] ($N = 25$). Scales present along mid-dorsal region of body to origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 64% of TL. Filament extending posteriorly to vertical running through posterior terminus of base of anal fin. Tail compressed and short, ending in small, moderate, fan-shaped caudal fin. Caudal-fin rays 15–17 [16] ($N = 21$).

Coloration in alcohol: Overall coloration ranging from tan to dark brown. Snout with distal portions pale even in darkly pigmented specimens. Overall lightly pigmented specimens with narrow, stripe of slightly darker pigmentation extending anteriorly from orbit for distance one-half to two-thirds length of snout. Dark pigmentation on snout masked to varying degrees in overall more darkly pigmented individuals. Darker specimens with second band of dark pigmentation running along ventral portion of snout. Two bands of dark coloration separated by very narrow, more lightly pigmented stripe along lateral surface of snout. Dorsolateral region of dark pigmentation on head forms lateral margin of narrow, somewhat obscure and more lightly coloured mid-dorsal stripe. Stripe somewhat laterally expanded over postocular region and continuous posteriorly with more lightly coloured mid-dorsal stripe on body that extends varying degrees posteriorly, sometimes to origin of electroreceptive filament. Lightly coloured stripes on head and body more obvious in darker specimens. Pectoral and anal fins in lightly pigmented specimens hyaline. Pectoral fin in darker specimens dusky with dark chromatophores concentrated over fin rays. Anal fin in dark specimens slightly dusky, with dark chromatophores overlying fin rays but without any indication of distinct dark band along the distal margin. Caudal fin with basal portions ranging from dusky to distinctly dark and with distal region hyaline.

Distribution: Sternarchorhynchus stewarti is known from the rivers of south-eastern Peru and eastern Ecuador (Fig. 73).

Secondary sexual dimorphism: No sexual dimorphism was apparent in the available samples of *S. stewarti*.

Etymology: The species name, *stewarti*, is in honour of Donald Stewart, College of Environmental Science of Forestry, State University of New York, who collected the specimens that first brought this species to our attention, and who has made many contributions to our knowledge of the fishes of the western portions of the Amazon basin.

Remarks: Examination of the specimens that served, at least in part, as the basis for the citation of *S. curvirostris* from the Río Napo basin (Stewart *et al.*, 1987: 37) have shown them to be *S. stewarti*. *Sternarchorhynchus stewarti* is very similar to *S. cramptoni*, a species distributed in the Amazon basin from Iquitos to the eastern portions of that drainage system. Although the two species demonstrate overlap in a number of meristic and morphometric features, even the overall very dark individuals of *S. stewarti* lack the distinct band of dark pigmentation along the distal portions of the anal fin that is present in all examined material of *S. cramptoni* including overall lightly coloured individuals. These species also differ to a large extent in the tail depth and distance from the posterior nares to the snout.

Material examined

Holotype: – PERU. *Amazonas*: Río Marañon, log riffle, 1.57 km east-north-east of Juan Velasco Santa Maria de Nieva (4°50′S, 77°51′W), collected by N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, K. A. Capps, D. P. German, D. Osorio, 3.viii.2006; MUSM 30409 (182).

Paratypes: – PERU. *Amazonas*: Río Marañon, log riffle, 1.57 km east-north-east of Juan Velasco Santa Maria de Nieva (4°50′S, 77°51′W), collected with holotype; MUSM 30410, 2 (105–132); AUM 46266, 2; (164–180); UF 168165, 2 (96–126); CU 93464, 1 (74); USNM 391571, 2 (155–242); ANSP 187150, 1 (170). Río Marañon, log riffle, 1.57 km east-north-east of Juan Velasco Santa Maria de Nieva (4°50′S, 77°51′W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, K. A. Capps, D. P. German, D. Osorio, 8.viii.2006; AUM 46272, 4 (186–260); UF 168166, 3 (121–164), CU 93465, 3 (136–157); USNM 391572, 4 (133–155); ANSP 187151, 3 (116–183). Río Marañon, 6.3 km north-east of Juan Velasco, Santa Maria de Nieva (4°50′S, 77°51′W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, D.

Osorio, 4.viii.2006; AUM 46267, 1 (71); UF 168167,1 (95). Río Marañon, 1.5 km east-north-east of Juan Velasco, Santa Maria de Nieva (4°50′S, 77°51′W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, D. Osorio, 4.viii.2006; AUM 46268, 1 (111); UF 168168, 1 (128); CU 93466, 1 (202). Río Nieva, 7.4 km south-south-west of Juan Velasco, Santa Maria de Nieva (4°39′36″S, 77°53′24″W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, D. Osorio, 5.viii.2006; AUM 46269, 3 (63–120); UF 168169, 2 (160–177); CU 93467, 2 (183–215); USNM 391573, 2 (189–207); ANSP 187152, 2 (124–200). Río Marañon, pongo above Borja, 35.5 km north-east of Juan Velasco, Santa Maria de Nieva (4°26′36″S, 77°34′54″W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, D. Osorio, 6.viii.2006; AUM 46270, 1 (251); UF 168170, 1 (253); CU 93468, 1 (226); AUM 46271, 1 (223). Río Marañon, 12 km north of Imacita (4°56′54″S, 78°20′24″W), N. K. Lujan, D. C. Werneke, D. C. Taphorn, A. S. Flecker, B. Rengifo, D. Osorio, 10.viii.2006; AUM 46273, 1 (110); UF 168171, 1 (154); CU 93469, 1(138).

Nontype specimens: – ECUADOR. *Napo*: Río Payamino, 23.3 km upstream from mouth in Río Napo, sandy beach on right bank (0°26′54″S, 77°06′12″W); FMNH 103364, 2 (214–222). Río Aguarico, few kilometres upstream from mouth of Río Eno (0°11′S, 76°30′W); FMNH 100616, 1 (154).

PERU. *Amazonas*: Río Marañon, vicinity of Santa Maria de Nieva (Santa Maria de Nieva at 4°27′36″S, 77°34′53′W), collected by D. J. Stewart, 16.iv.1980; LACM 41741–7, 8 (195–229). *Loreto*: Río Marañon, along south side of Río Marañon, opposite Nauta (4°30′39″S, 73°34′5′W); INHS 52735, 1 (94).

STERNARCHORHYNCHUS TAPHORNI SP. NOV.

(FIGS 73, 74; TABLE 13)

Diagnosis: Sternarchorhynchus taphorni is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the presence of a narrow, more lightly coloured mid-dorsal stripe on the head and body extending posteriorly to the vertical through the insertion of the pectoral fin at least in smaller individuals, the dark anal fin, the lateral line terminating at a point approximately eight scales anterior of the base of the caudal fin, the possession of eight premaxillary teeth, ten teeth in total on the dentary, 14 branched pectoral-fin rays, 30 anterior unbranched anal-fin rays, 186 total anal-fin rays, 12–13 premaxillary teeth, the length of the anal-fin base (84.8% of LEA), the preanal distance (11.0% of LEA), the prepectoral-fin distance (18.8% of LEA), the pectoral-fin length (37.4–47.8% of HL), the caudal length (6.8% of LEA), the head length (18.9% of LEA), the snout length (51.1–62.2% of HL), the head depth at the eye (31.8–46.8% of HL), the head depth at the nape (55.7–62.3% of HL), the eye diam-

Figure 74. ***Sternarchorhynchus taphorni* sp. nov.,** holotype, sexually dimorphic male demonstrating modifications of dentary and dentary dentition, 310 mm total length, MUSM 6635; Peru, San Martin, Río Huallaga.

eter (5.7–6.0% of HL), the distance from the posterior naris to the eye (35.9–52.4% of HL), the postocular distance (43.5–46.4% of HL), the interocular width (7.8–11.5% of HL), the length of the mouth (7.7–9.0% of HL), the height of the branchial opening (11.6–14.8% of HL), the tail depth (24.4% of caudal length), and the caudal-fin length (50.2% of caudal length).

Description: Morphometric data for holotype and nontype specimens in Table 13.

Lateral line extending to position about eight scales anterior of hypural joint and absent on remainder of tail and on caudal fin. Snout elongate, compressed and notably curved ventrally distally. Posterior naris closer to tip of snout than to anterior margin of eye. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla apparently both ontogenetically and sexually dimorphic based on limited available sample. Anus and urogenital papilla in small individual located along vertical running three orbital diameters posterior of eye. Midsized specimen with those structures located along vertical through eye. Larger male with patch of enlarged dentition on expanded dentary having anus and urogenital papilla more anteriorly positioned and located along vertical two orbital diameters anterior of anterior margin of orbit. Combined opening for anus and urogenital papilla longitudinally ovoid.

Premaxilla of small size, somewhat rounded, with eight teeth ($N = 1$). Dentary with two rows of irregularly arranged teeth with total of ten teeth. Male demonstrating sexual dimorphism in lower jaw with anterior portion of jaw extending further anteriorly than in females and juveniles and with dentary distinctly expanded laterally into dorsally bulbous structure rounded from dorsal view. Expanded portion of dentary bearing series of enlarged, slightly posteriorly recurved teeth. Mouth terminal in juveniles and females and somewhat anterodorsally directed in male with expanded dentary. Position of rictus ontogenetically slightly variable. Rictus located slightly posterior to vertical through anterior naris in smallest examined specimen (77 mm TL), approximately at, or slightly anterior of, vertical running through anterior naris in midsized specimen (216 mm TL) and in male with large patch of dentition on enlarged dentary (310 mm TL).

Branchiostegal rays five; with first to third rays somewhat narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 16 (13 anterior; three transitional; $N = 1$).

Pectoral-fin rays ii + 13–15 [ii + 15] ($N = 3$). Anal-fin origin variable, located posterior to vertical running through eye in small specimen (77 mm TL), along vertical running through eye in midsized specimen (216 mm TL), and anterior to vertical through eye in largest specimen (male with large patch of enlarged dentition on expanded dentary; 310 mm TL). Anterior unbranched anal-fin rays 30 ($N = 1$). Total anal-fin rays 186 ($N = 1$; largest specimen, only examined individual without regenerated tail and damaged posterior portion of anal fin). Scales above lateral line at midbody 11–12 [11] ($N = 3$). Scales along mid-dorsal region of body readily apparent on surface. Origin of midsaggital electroreceptive filament located distinctly posterior of midlength of body. Filament in large male (only specimen without regenerated tail and damaged posterior portion of anal fin) terminating posteriorly two scales anterior of vertical running through posterior terminus of base of anal fin. Tail compressed and short, ending in small, somewhat elongate caudal fin. Caudal-fin rays 14 ($N = 1$, largest specimen; only individual without regenerated caudal fin).

Coloration in alcohol: Overall ground coloration brown to dark brown. Snout in smallest specimen darker dorsolaterally and ventrally, with those areas separated by very narrow, distinctly more lightly coloured stripe. No such midlateral stripe on snout present in other specimens, although dorsal region of snout somewhat darker than lateral and ventral portion of that portion of head in midsized individual. Male with anteriorly expanded lower jaw bearing patch of distinct enlarged teeth having head very dark overall on lateral and ventral portions. Smallest specimen (77 mm TL) with narrow, lightly coloured, mid-dorsal stripe extending from snout along top of head and mid-dorsal portion of body as far posteriorly as vertical through posterior limit of pectoral fin. Stripe apparent but less extensive in larger specimens, reaching only to vertical about four orbital diameters posterior of rear of eye in midsized specimen (216 mm TL) and only to vertical running through anterior margin of eye in larger male (310 mm TL).

Pectoral fin variably dark in all specimens and particularly so in largest examined individual. Anal fin dark in all individuals, with chromatophores overlying fin rays. Dark pigmentation particularly intense along basal portion of fin in large male and forming posteriorly attenuating dark band. Caudal fin dark with distal portions less intensely pigmented.

Distribution: Examined specimens of *S. taphorni* originated in the upper portions of the Río Huallaga and adjoining left bank tributaries of the Río Ucayali basin of eastern Peru (Fig. 73).

Secondary sexual dimorphism: The examined male of *S. taphorni* has an anteriorly extended and laterally enlarged anterior portion of the dentary with the

Figure 75. ***Sternarchorhynchus yepezi* sp. nov.,** holotype, sexually dimorphic male, 280 mm total length, MCNG 44286; Venezuela, Portuguesa, Río Portuguesa.

associated patch of enlarged teeth comparable to the modifications of the jaw and teeth of some congeners. The male also has the anus and urogenital papilla more anteriorly positioned than in the examined female and juvenile.

Etymology: The species name, *taphorni*, is in honour of Donald Taphorn of the Universidad Nacional Experimental de los Llanos Occidentales, who generously assisted the authors with this and other publications over the years and who has made many contributions to our understanding of the South American freshwater fish fauna.

Remarks: The two paratypes of *S. taphorni* examined in this study agree with the holotype in examined details and were collected in the same general region in the Peruvian Amazon. The holotype originated, however, within the Río Huallaga system whereas the two nontypes came from tributaries of the Río Ucayali. The common presence of a species in both the Río Huallaga system and left bank tributaries of the Río Ucayali was reported by Vari & Harold (2001: 172) for the characid *Creagrutus ortegai.* Some tributaries of the Río Ucayali approach portions of the Río Huallaga system (Isbrücker & Nijssen, 1983: fig. 5) and commonality of species across those portions of the two river basins may be found to be a phenomenon of greater generality once the ichthyofauna of that region is better explored ichthyologically.

Material examined
Holotype: – PERU. *Departamento de San Martin*: Río Huallaga, Uchiza (approximately 8°29″59″S, 76°22′59″W); MUSM 6635 (310), collected by L. P. Davilla, viii.1948.

Paratypes: – PERU. *Departamento de Huánuco*: Río Llullapichis, 2 km upstream from mouth into Río Pachitea (9°37′S, 74°57′W), ROM 55531, 1 (216), collected by E. Holm, B. Alvarado, H. Sisniegas. Río Llullapichis, 1.5 km west of Panguana Station (9°37′S, 74°57′W), ROM 55530, 1 (77.3), collected by E. Holm, B. Alvarado.

STERNARCHORHYNCHUS YEPEZI SP. NOV.

(FIGS 73, 75, 76; TABLE 14)

Diagnosis: Sternarchorhynchus yepezi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, having sparse scales covered by skin along the mid-dorsal portion of the body anterior to the origin of the electroreceptive filament, the longitudinally ovoid, but not distinctly horizontally elongate combined opening for the anus and the urogenital papilla, the consistently light overall coloration of the head and body, the presence of very dark pigmentation in the region at the base of the anterior and lateral margins of the enlarged teeth on the bulbous dentary in mature males, the presence of a more lightly coloured narrow band of mid-dorsal pigmentation on the head and mid-dorsal region of the body extending posteriorly to the origin of the electroreceptive filament and sometimes beyond that point, the possession of seven teeth on the outer tooth row of the dentary, 15 precaudal vertebrae, 182–188 total anal-fin rays, the greatest body depth (11.3–13.2% of LEA), the caudal length (8.1–8.4% of LEA), the pectoral-fin length (43.1–44.2% of HL), the head depth at the eye (30.5–40.0% of HL), the head depth at the nape (48.2–

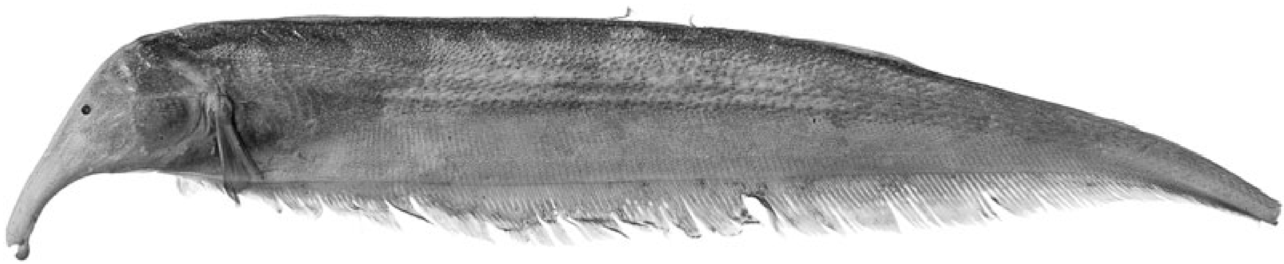

Figure 76. ***Sternarchorhynchus yepezi* sp. nov.,** immature specimen, 177 mm total length, ANSP 165222; Venezuela, Apure, Río Apure.

Table 14. Morphometric data for holotype (H), and paratypes of *Sternarchorhynchus yepezi* and Sternarchorhynchus *villasboasi*

	S. yepezi			*S. villasboasi*		
	H	Paratypes	Mean	H	Paratypes	Mean
Total length (mm)	282	108.2–177 (*N* = 2)	–	135	97.0–136 (*N* = 2)	–
Length to end of anal fin (mm)	260	98.9–173 (*N* = 2)	–	120	85.7–126 (*N* = 2)	–
Head length (mm)	46.46	22.5–34.0 (*N* = 2)	–	24.2	18.3–24.3 (*N* = 2)	–
Caudal length (mm)	21.09	8.37 (*N* = 1)	–	15.7	10.2 (*N* = 1)	–
Per cent of length to end of anal fin						
Anal-fin base	91.1	81.9–87.8 (*N* = 2)	84.9	85.8	83.6–84.8 (*N* = 2)	84.2
Distance snout to anus	6.9	13.1–13.6 (*N* = 2)	13.3	9.4	9.5–11.6 (*N* = 2)	10.6
Preanal-fin distance	10.9	13.5–16.3 (*N* = 2)	14.9	12.8	12.5–14.7 (*N* = 2)	13.6
Prepectoral-fin distance	17.9	18.9–23.7 (*N* = 2)	21.3	19.9	19.4–21.1 (*N* = 2)	20.3
Greatest body depth	11.8	11.3–13.2 (*N* = 2)	12.2	12.3	12.9–11.9 (*N* = 2)	12.4
Head length	17.8	19.6–22.7 (*N* = 2)	21.2	20.2	19.4–21.3 (*N* = 2)	20.4
Caudal length	8.1	8.4 (*N* = 1)	–	13.1	11.9 (*N* = 1)	–
Per cent of head length						
Anus to anal-fin insertion	21.8	10.4–17.8 (*N* = 2)	14.1	14.3	12.1–15.0 (*N* = 2)	13.6
Pectoral-fin length	43.1	43.2–44.2 (*N* = 2)	43.7	44.3	43.6–47.1 (*N* = 2)	45.4
Head depth at eye	40.0	30.5–33.2 (*N* = 2)	31.9	27.4	29.8–30.6 (*N* = 2)	30.2
Head depth at nape	56.0	48.2–54.0 (*N* = 2)	51.1	55.4	52.6–52.9 (*N* = 2)	50.7
Head width	26.1	22.0–26.3 (*N* = 2)	24.2	23.2	25.3–27.5 (*N* = 2)	26.4
Snout length	61.7	58.7–60.1 (*N* = 2)	59.4	53.3	53.6–56.1 (*N* = 2)	54.8
Posterior naris to snout	8.5	8.8–9.3 (*N* = 2)	9.0	9.0	8.9–9.6 (*N* = 2)	9.2
Posterior naris to eye	52.7	47.5–49.9 (*N* = 2)	48.7	41.5	39.7–45.4 (*N* = 2)	42.5
Mouth length	7.8	6.0–6.4 (*N* = 2)	6.2	7.0	5.8–7.3 (*N* = 2)	6.5
Internarial distance	3.2	2.7–3.7 (*N* = 2)	3.2	2.5	3.6–3.8 (*N* = 2)	3.7
Eye diameter	4.2	4.1–4.8 (*N* = 2)	4.4	5.7	5.0–5.9 (*N* = 2)	5.5
Interocular width	7.7	6.6–8.1 (*N* = 2)	7.4	6.9	9.4–13.1 (*N* = 2)	11.3
Postocular distance	40.5	43.8–46.2 (*N* = 2)	45.0	44.4	44.4–46.0 (*N* = 2)	45.2
Branchial opening	16.2	10.9–17.0 (*N* = 2)	13.9	13.7	15.3–15.4 (*N* = 2)	15.3
Per cent of caudal length						
Tail depth	31.0	18.6 (*N* = 1)	–	14.2	12.2 (*N* = 1)	–
Caudal-fin length	33.2	38.8 (*N* = 1)	–	25	36.6 (*N* = 1)	–

Number of specimens indicated in parentheses.

56.0% of HL), the snout length (58.7–61.7% of HL), the eye diameter (4.1–4.8% of HL), the interocular width (6.6–8.1% of HL), and the caudal-fin length (33.2–38.8% of caudal length).

Description: Morphometric data for holotype and paratypes in Table 14.

Lateral line extending to base of caudal fin but absent on fin. Snout elongate, compressed and notably curved ventrally distally. Posterior naris located closer to tip of snout than to anterior margin of eye. Branchial opening restricted and situated slightly anterior to vertical through pectoral-fin origin. Location of anus and urogenital papilla sexually dimorphic based on limited available sample. Structures in small individual (112 mm TL) and apparently mature female (177 mm TL) located along vertical running two orbital diameters posterior of eye. Males (280 mm TL) with definite patch of enlarged dentition on dentary with anus and urogenital papilla more anteriorly positioned and located along vertical running two orbital diameters anterior of anterior margin of orbit. Combined opening for anus and urogenital papillae longitudinally ovoid.

Premaxilla of small size, somewhat rounded, with five to eight teeth ($N = 3$). Dentary in males transversely expanded into dorsally bulbous structure rounded from dorsal view and bearing series of enlarged, posteriorly recurved teeth. Dentary in single examined juvenile (112 mm TL) less elongate and lacking such expansion. Form of dentary in adults without expansion of anterior portion of dentary unknown. Teeth in two rows, with total of 11 teeth, with seven teeth in outer row and four teeth on inner row ($N = 1$). Mouth terminal in juveniles and somewhat dorsally directed in males with expanded dentaries. Location of rictus ontogenetically variable. Rictus located slightly posterior to vertical through anterior naris in smallest examined specimen (112 mm TL), approximately at vertical through anterior naris in midsized specimen (177 mm TL) and clearly anterior of vertical running through that naris in largest examined individual (280 mm TL).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15 (two anterior; three transitional; $N = 3$).

Pectoral-fin rays ii + 13–14 [ii + 13] ($N = 3$). Position of anal-fin origin either ontogenetically variable or sexually dimorphic, but with underlying basis impossible to ascertain from limited available sample. Located slightly posterior of vertical through anterior margin of opercle in smallest examined specimen (112 mm TL), but positioned along vertical slightly anterior of midpoint between anterior margin of opercle and posterior margin of eye in largest examined specimen (male, 280 mm TL). Anterior unbranched anal-fin rays 23–29 [29] ($N = 3$). Total anal-fin rays 182–188 [187] ($N = 3$). Scales above lateral line at midbody nine to 12 [11] ($N = 3$). Scales along mid-dorsal region of body somewhat sparse and not readily apparent on surface. Origin of midsaggital electroreceptive filament located approximately at 65% of TL. Filament in specimens of all sizes extending to vertical through posterior terminus of base of anal fin. Tail compressed and short, ending in very small, somewhat elongate caudal fin. Caudal-fin rays 16–17 [17] ($N = 2$).

Coloration in alcohol: Overall ground coloration tan to light greyish-tan. Snout ranging from nearly hyaline in small and midsized specimens to slightly grey in larger male with anteriorly expanded lower jaw bearing patch of distinct enlarged teeth. Skin around base of outer margin of patch of enlarged teeth in that male much more darkly pigmented than adjoining areas. Lower jaw without such dark pigmentation in other examined specimens (presumably females and juveniles). Snout in all specimens with distinct, narrow, anteriorly attenuating band of somewhat darker pigmentation extending from region anterior of eye to anterior portion of snout. Dark stripe nearly completely masked by ground coloration in examined males. Dark pigmentation on snout forms lateral border of narrow, more lightly coloured mid-dorsal band on head that continues from tip of snout to posterior margin of head. More lightly pigmented mid-dorsal band on head continuous posteriorly with lightly coloured mid-dorsal stripe extending along body to origin of electroreceptive filament.

Pectoral fin hyaline in smallest examined specimen, with some scattered dark pigmentation in somewhat larger female and with fin rays overlain by series of dark chromatophores in largest examined individual. Anal fin hyaline in small specimen and female paratype, with dark chromatophores overlying fin rays in male (largest specimen examined). Caudal fin hyaline or with faint dark pigmentation.

Distribution: The limited available samples of *S. yepezi* all originated in the central portions of the Río Orinoco basin in Venezuela (Fig. 73). The range of the species possibly extends to the Peruvian Amazon (see discussion under Remarks; also under Possible additional undescribed species).

Secondary sexual dimorphism: Males of *S. yepezi* share the anteriorly extended and laterally enlarged anterior portion of the dentary and associated patch of enlarged teeth present in some congeners. These mature males also have the anus and urogenital papilla more anteriorly positioned than do females and juveniles, but with the degree of difference in the position of those structures less pronounced than that present in some congeners. The reduction is both a consequence of the relatively more anterior position of the anus and urogenital papilla in the immature specimens and in the less distinctly advanced position of those structures in the single examined male with sexually dimorphic modifications of the lower jaw. It is possible that the examination of more extensive series of specimens will demonstrate a more pronounced degree of sexual dimorphism in this feature.

Etymology: The species name, *yepezi*, is in honour of Augustin Fernández-Yépez whose research on *Sternarchorhynchus* demonstrated that the diversity within the genus was greater than then recognized.

Remarks: Two specimens from the Peruvian Amazon examined during this study are very similar in many details to *S. yepezi* or more likely represent yet another undescribed species of the genus (see Possible additional undescribed species, below).

Material examined

Holotype: – VENEZUELA. *Portuguesa*: Río Portuguesa, fort at Nueva Florida, Santa Rosalía (approximately 8°57′N, 69°01′W), MCNG 44286 (280), collected by O. Castillo and RNR students, 2001.

Paratypes: – VENEZUELA. *Apure*: Río Apure, between mouth of Río Portuguesa and San Fernando de Apure (7°54′N, 67°32′W), ANSP 165222, 2 (112–177), collected by S. A. Schaefer *et al.*, 4.xi.1989.

Nontype specimens: – VENEZUELA. *Apure*: Río Chirere, in Camachero, MBUCV-V-17394, 1 (320).

STERNARCHORHYNCHUS VILLASBOASI SP. NOV.
(FIGS 73, 77; TABLE 14)

Diagnosis: Sternarchorhynchus villasboasi is distinguished from congeners by the following combination of characters: a short gape that terminates posteriorly at, or slightly short of, the vertical through the anterior nares, the presence of a definite series of scales along the mid-dorsal region of the body, the lateral line extending posteriorly to the base of the caudal fin, the narrow, more lightly coloured mid-dorsal stripe on the head that sometimes extends posteriorly to the vertical through the insertion of the pectoral fin, the slightly dusky anal fin, the possession of eight to nine teeth on the premaxilla, eight to nine teeth in the outer row of the dentary, 20–21 anterior unbranched anal-fin rays, 160–166 total anal-fin rays, the length of the base of the anal fin (83.6–85.8% of LEA), the preanal distance (12.5–14.7% of LEA), the caudal length (11.9–13.1% of LEA), the distance from the anus to the anal-fin insertion (12.1–15.0% of HL), the pectoral-fin length (43.6–47.1% of HL), the head depth at the eye (27.4–30.6% of HL), the head depth at the nape (52.6–55.4%), the mouth length (5.8–7.3% of HL), the snout length (53.3.56.1% of HL), the distance from the posterior naris to eye (39.7–45.4% of HL), the postocular distance (44.4–46.0% of HL), the height of the branchial opening (13.7–15.4% of HL), the tail depth (12.2–14.2% of caudal length), and the caudal-fin length (25.0–36.6% of caudal length).

Description: Morphometric data for examined specimens in Table 14.

Lateral line extending posteriorly to base of caudal fin but absent on fin. Snout elongate, compressed and slightly curved ventrally distally. Mouth small and terminal, with rictus located slightly anterior of vertical running through anterior naris. Anus and urogenital papilla located ventral to head, with position apparently ontogenetically variable in limited available sample. Structures located slightly posterior of vertical running through eye in juvenile (97 mm TL) and slightly anterior of vertical through eye in single mature female (135 mm TL) and single mature male (136 mm TL). Opening for anus and urogenital papilla longitudinally ovoid both sexes.

Premaxilla with eight to nine teeth ($N = 2$) apparent in whole specimens. Dentary with two tooth rows; outer row with eight to nine teeth and inner row with three teeth ($N = 2$).

Branchiostegal rays five; with first to third rays narrow and elongate and fourth and fifth rays large and broad. Precaudal vertebrae 15–16 (12 anterior; three to four transitional; $N = 3$).

Pectoral-fin rays ii + 12–13 [ii + 12] ($N = 3$). Anal-fin origin located anterior to vertical through margin of opercle. Anterior unbranched anal-fin rays 20–22 [22] ($N = 3$). Total anal-fin rays 160–166 [164] ($N = 3$). Scales above lateral line at midbody ten to 12 [12] ($N = 3$). Scales clearly present along mid-dorsal line to

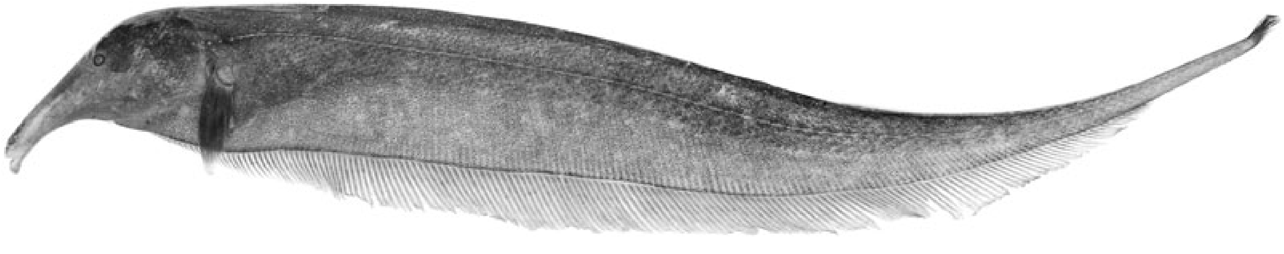

Figure 77. ***Sternarchorhynchus villasboasi* sp. nov.,** holotype, female, 135 mm total length, INPA 28361; Brazil, Pará, Cachoeira de Kaituká, Rio Xingu.

origin of midsaggital electroreceptive filament. Origin of midsaggital electroreceptive filament located approximately at 64% of TL. Filament extending posteriorly to point located approximately two scales anterior of vertical running through terminus of base of anal fin in juvenile and single mature male, but extending posteriorly one scale past terminus of base of anal fin in single examined female. Tail compressed and moderate, ending in small, elongate caudal fin. Caudal-fin rays 16–17 [17] ($N = 2$).

Coloration in alcohol: Overall coloration of head and body brown but darker dorsally. Snout dark overall with stripe of distinctly darker pigmentation extending anteriorly from orbit to, or nearly to, tip of snout. Ventral portion of snout dark. This dark coloration along with dark pigmentation on dorsolateral region of snout delimits distinctly more lightly pigmented band running along lateral surface of snout. Mid-dorsal region of head with narrow, lightly coloured band extending from tip of snout to point approximately two-thirds of distance to vertical through eye. Remainder of head and body dark along mid-dorsal region. Pectoral distinctly dusky with rays covered with small, dark chromatophores. Anal fin slightly dusky with rays overlain by dark chromatophores. Caudal fin dark with distal most margin hyaline.

Distribution: Sternarchorhynchus villasboasi is only known from the type locality in the Rio Xingu at the Cachoeira de Kaituká (Fig. 73).

Secondary sexual dimorphism: The available sample of *S. villasboasi* included a single mature male (135 mm TL) and single mature female (136 mm TL) as indicated by the examination of the gonads. No sexual dimorphism was apparent between those two individuals, but these specimens demonstrate that the species matures at relatively small body sizes.

Ecology: Little information is available about the type locality of *S. villasboasi* other than that it was a rapids area in the Rio Xingu, Brazil (see also Campos-da-Paz, 1999).

Etymology: The species name, *villasboasi*, is in honour of Orlando Villa Bôas, who was instrumental in the designation of the Xingu National Park, in recognition of his diverse endeavours to ameliorate the impact of development projects on the indigenous peoples of that region.

Material examined

Holotype: – BRAZIL. *Pará*: Rio Xingu, Cachoeira de Kaituká, at Altamira (3°12′S, 52°12′W), L. Rapp Py-Daniel and J. A. Zuanon, 9.x.1990; INPA 28361 (135, mature female).

Paratype: – BRAZIL. *Pará*: Rio Xingu, Cachoeira de Kaituká, at Altamira (3°12′S, 52°12′W) L. Rapp Py-Daniel and J. A. Zuanon, 1990; INPA 32084, 1 (136, mature male); INPA 3934, 1 (97).

POSSIBLE ADDITIONAL UNDESCRIBED SPECIES

The apparent tendency towards relatively small scale endemicity in many species of *Sternarchorhynchus* and the many regions within the known range of the genus that are yet-to-be collected using methods appropriate for securing samples of the genus make it certain that *Sternarchorhynchus* is undoubtedly more speciose, perhaps significantly more speciose, than we document in this study. The limited samples of *Sternarchorhynchus* from some locations rendered it difficult to determine the status of some specimens that we had at hand. In some instances these samples may represent additional undescribed forms. The following summary will hopefully encourage further collecting and analysis of relevant population samples from the cited areas in order to resolve the issue of the state of these problematic specimens.

1. Two samples from the Río Paragua basin (MBUCV-V 20686; AMNH 91009). These are similar to *S. gnomus* of the Río Caroní basin (which includes the Río Paragua) in overall appearance and morphometrics. The two samples differ from *S. gnomus* in details of pigmentation (primarily the presence of a narrow, lightly coloured, mid-dorsal stripe on the head versus the uniformly dark dorsal region of the head in *S. gnomus*) and possibly osteology as evidenced by differences apparent in radiographs. Additional samples of *Sternarchorhynchus* from throughout the Río Caroní drainage system are necessary to determine whether these differences are constant across samples and, thus, indicative of an additional undescribed species.
2. One specimen that originated from the Río Caura (MCNG 34618), a right bank tributary of Río Orinoco, was cited as *S. oxyrhynchus* by Rodríguez-Olarte *et al.* (2003: 198) and is probably the basis for the citation of that species for the ichthyofauna of the Río Caura basin by Lasso *et al.* (2003: 239). The specimen is distinguished from all other congeners in that basin other than *S. oxyrhynchus* by the uniformly dark mid-dorsal region of the head and body (versus the presence of a narrow, lightly coloured, mid-dorsal stripe on the head and body in all other congeners in the Río Orinoco basin). The Río Caura specimen differs, however, from *S. oxyrhynchus* in its mouth form (extends posteriorly only to a point distinctly short

of the vertical through the posterior nares versus extending posteriorly beyond the vertical through the posterior nares, respectively). Other features further separate this specimen from all other congeners. Additional material is necessary to adequately describe this probable undescribed species.

3. Two specimens from the Peruvian Amazon that were examined probably represent an undescribed species of *Sternarchorhynchus* similar to *S. yepezi* a Río Orinoco endemic. The specimens share the overall head and body form of *S. yepezi* along with the distinctive dark pigmentation of the lower lip in the area ventral to the external margin of the patch of enlarged teeth on the bulbous dentary of males. One of the individuals (UF 12354) originated from the aquarium trade at Iquitos, Peru, which draws its material from a somewhat wide area. This specimen is of relatively small body size (167 mm TL), but nonetheless has a significantly higher anal-fin ray count (197) than that in the samples of *S. yepezi* examined in this study (182–188). The second specimen (MCP 41639) is a large male (261 mm TL) that bears a well-developed patch of enlarged teeth on the expanded anterior portion of the dentary. This specimen originated in the Tefé region in the western Amazon and was reported as *Sternarchorhynchus* n. sp. B by Crampton & Albert (2006: 689) and Crampton (2007: 289) on the basis of its EOD pattern. The regenerated tail makes it impossible to secure accurate counts of critical meristics and proportional measurements, most importantly the anal-fin ray count. In light of the differences and the significant distance between the known range of *S. yepezi* in the Río Orinoco basin and sites of origin of these two specimens in the western Amazon, they probably represent an undescribed form. The limited available sample of this form, the small size of one individual, and the damage to a critical region of the body in the other specimen, led us to defer from proposing this form as a new species.

Above and beyond the three highlighted examples, photographs of specimens that originated from some of the apparent geographical gaps within the range of the genus but for which we did not have samples, revealed populations that in some instances clearly differ from the species of *Sternarchorhynchus* we recognize herein. This fact plus the large gaps in the known distribution of the genus in the Amazon basin make it likely that future studies will significantly increase the known diversity of the species of *Sternarchorhynchus* beyond the 32 species that we recognize in this revision.

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REFERENCES

Aguilera O. 1986. La musculature estriada en los peces Gymnotiformes (Teleostei-Ostariophysi): musculature facial. *Acta Biologica Venezuelica* **12:** 13–23.

Albert JS. 2001. Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). *Miscellaneous Publication, Museum of Zoology, University of Michigan* **190:** 1–127.

Albert JS. 2003. Gymnotiformes: Apteronotidae – ghost knifefishes. In: Reis RE, Kullander SO, Ferraris CJ Jr, eds.

Check list of the freshwater fishes of South and Central America. Porto Alegre, Brazil: EDIPUCRS, 497–502.

Albert JS, Campos-da-Paz R. 1998. Phylogenetic systematics of Gymnotiformes with diagnoses of 58 clades: a review of available data. In: Malabarba LR, Reis RE, Vari RP, Lucena ZM, Lucena C, eds. *Phylogeny and classification of Neotropical fishes*. Porto Alegre, Brazil: EDIPUCRS, 419–446.

Albert JS, Crampton WGR. 2005. Diversity and phylogeny of neotropical electric fishes (Gymnotiformes). In: Bullock H, Hopkins CD, Popper AN, Fay RR, eds. *Electroreception*, Vol. 21. New York: Springer Handbook of Auditory Research, 360–409.

Albert JS, Crampton WGR. 2009. A new species of electric knifefish, genus *Compsaraia* (Gymnotiformes: Apteronotidae) from the Amazon fiver, with extreme sexual dimorphism in snout and jaw length. *Systematics and Biodiversity* **7:** 81–92.

Albert JS, Crampton WGR, Thorson DH, Lovejoy NR. 2005. Phylogenetic systematics and historical biogeography of the neotropical electric fish *Gymnotus* (Teleostei: Gymnotidae). *Systematics and Biodiversity* **2:** 375–417.

Albert JS, Miller RR. 1995. *Gymnotus maculosus*, a new species of electric fish (Chordata: Teleostei: Gymnotoidei) from Middle America, with a key to the specie of *Gymnotus*. *Proceedings of the Biological Society of Washington* **108:** 662–678.

Alves-Gomes JA, Ortí G, Haywood W, Heligenberg W, Meyer A. 1995. Phylogenetic analysis of the South American electric fishes (Order Gymnotiformes) and the evolution of their electrogenic system: a synthesis based on morphology, electrophysiology, and mitochondrial sequence data. *Molecular Biology and Evolution* **12:** 298–318.

Barbarino Duque A, Winemiller KO. 2003. Dietary segregation amongst large catfishes of the Apure and Arauca Rivers, Venezuela. *Journal of Fish Biology* **63:** 410–427.

Bichuette ME, Trajano E. 2003. Epigean and subterranean ichthyofauna from the São Domingos karst area, upper Tocantins River basin, central Brazil. *Journal of Fish Biology* **63:** 1100–1121.

Bichuette ME, Trajano E. 2004. Three new subterranean species of *Ituglanis* from Central Brazil (Siluriformes: Trichomycteridae). *Ichthyological Exploration of Freshwaters* **15:** 243–256.

Bloch ME, Schneider JG. 1801. *M.E. Blochii. Systema ichthyologiae iconibus ex illustratum. Post obitum auctoris opun inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider. Saxo Berolini*. Berlin: Sumtibus Austoris Impressum et Bibliopolio Sanderiano Commissum.

Bock WJ. 1965. The role of adaptative mechanism in the origin of higher levels of organization. *Systematic Zoology* **14:** 272–287.

Boulenger GA. 1887. An account of the fishes collected by Mr. C. Buckley in eastern Ecuador. *Proceedings of the Zoological Society, London* **2:** 274–283.

Britski HA. 1972. Peixes da água doce do Estado de São Paulo: Sistemática. In: *Poluição e piscicultura*. São Paulo: Comisão Interestadual da bacia Paraná-Paraguai, 79–108.

Britski HA, Silimon KS, Lopes B. 1999. *Peixes do Pantanal. Manual de identifição*. Corumbá, Brazil: Empresa Brasileira de Pesquisa Agropecuária.

Brooks DR, McLennan DA. 1991. *Phylogeny, ecology, and behavior: a research program in comparative biology*. Chicago: University of Chicago Press.

Brousseau RA. 1976. The pectoral anatomy of selected Ostariophysi. I. The Characiniformes. *Journal of Morphology* **148:** 89–136.

Campos-da-Paz R. 1995. Revision of the South American freshwater fish genus *Sternarchorhamphus* Eigenmann, 1905 (Ostariophysi: Gymnotiformes: Apteronotidae), with notes on its relationships. *Proceedings of the Biological Society of Washington* **108:** 29–44.

Campos-da-Paz R. 1999. New species of *Megadontognathus* from the Amazon basin, with phylogenetic and taxonomic discussions on the genus (Gymnotiformes: Apteronotidae). *Copeia* **1999:** 1041–1049.

Campos-da-Paz R. 2000. On *Sternarchorhynchus* Castelnau: a South American electric knifefish with descriptions of two new species (Ostariophysi, Gymnotoidei, Apteronotidae). *Copeia* **2000:** 521–535.

Campos-da-Paz R. 2003. Gymnotiformes: Gymnotidae – naked-back knifefishes. In: Reis RE, Kullander SO, Ferraris CJ Jr, eds. *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Brazil: EDIPUCRS, 483–486.

Campos-da-Paz R. 2005. Previously undescribed dental arrangement amongst electric knifefishes, with comments on the taxonomic and conservation status of *Tembeaussu marauna* Triques (Otophysi: Gymnotiformes: Apteronotidae). *Neotropical Ichthyology* **3:** 395–400.

Carr CE, Maler L. 1986. *Electroreception* in gymnotiform fish: central anatomy and physiology. In: Bullock TH, Heiligenberg W, eds. *Electroreception*. New York: John Wiley & Sons, 319–374.

Castelnau F. 1855. *Poissons nouveaux ou rares récuillis pendant l'expedition dans les parties centrales de Amerique du Sud, de Rio de Janeiro a lima et de lima au Pará*. Paris: Chez P. Bertrand.

Chardon M, De La Hoz E. 1974. Towards an improved classification of the gymnotid fishes by the use of splanchnocranium characters. *Ichthyologia* **6:** 15–25.

Cox-Fernandes C. 1998. Sex-related morphological variation in two species of apteronotid fishes (Gymnotiformes) from the Amazon River basin. *Copeia* **1998:** 730–735.

Cox-Fernandes C. 1999. Detrended canonical correspondence analysis (DCCA) of electric fish assemblages in the Amazon. In: Val AL, Almeida-Val VMF, eds. *Biology of tropical fishes*. Manaus: INPA, 21–39.

Cox-Fernandes C, Lundberg JG, Riginos C. 2002. Largest of all electric-fish snouts: hypermorphic facial growth in male *Apteronotus hasemani* and the identity of *Apteronotus anas* (Gymnotiformes: Apteronotidae). *Copeia* **2002:** 52–61.

Cox-Fernandes C, Podos J, Lundberg JG. 2004. Amazon Ecology. Tributaries enhance the diversity of electric fishes. *Science* **305:** 1960–1962.

Cracraft J. 1990. The origin of evolutionary novelties:

pattern and process at different hierarchical levels. In: Nitecki MH, ed. *Evolutionary innovations*. Chicago: The University of Chicago Press, 21–44.

Crampton WGR. 1998. Electric signals, design and habitat preference in a rich assemblage of gymnotiform fishes from the upper Amazon basin. *Anais da Academia Brasileira de Ciências* **70:** 805–847.

Crampton WGR. 2007. Diversity and adaptation in deep-channel neotropical electric fishes. In: Sébert P, Onyango DW, Kapoor BG, eds. *Fish life in special environments*. Enfield, NH: Science Publishers Inc., 283–339.

Crampton WGR, Albert JS. 2006. Evolution of electric signal diversity in gymnotiforms fishes. In: Ladich F, Collin SP, Moller P, Kapoor BG, eds. *Communication in fishes*. Enfield, NH: Science Publishers Inc., 647–731.

De La Hoz E, Chardon M. 1984. Skeleton, muscles, ligaments and swimbladder of a gymnotid fish, *Sternopygus macrurus* (Ostariophysi Gymnotoidei). *Bulletin de la Société Royale des Sciences de Liège* **53:** 9–53.

Eigenmann CH. 1912. The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum* **5:** 1–578.

Eigenmann CH, Allen WR. 1942. *Fishes of western South America, I: The intercordilleran and Amazonian lowlands of Peru, II: The High Pampas, Bolivia, and northern Chile, with a revision of the Peruvian Gymnotidae, and of the genus Orestias*. Lexington: University of Kentucky.

Eigenmann CH, Bean BA. 1907. An account of Amazon River fishes collected by J. B. Steere: with a note on *Pimelodus clarias*. *Proceedings of the United States National Museum* **36:** 659–668.

Eigenmann CH, Eigenmann R. 1891. A catalogue of the fresh-water fishes of South America. *Proceedings of the United States National Museum* **16:** 1–81.

Eigenmann CH, Ward DP. 1905. The Gymnotidae. *Proceedings of the Washington Academy of Sciences* **4:** 157–186.

Ellis MM. 1913. The gymnotid eels of tropical America. *Memoirs of the Carnegie Museum* **6:** 109–195.

Eschmeyer W, ed. **1998.** *Catalog of fishes*. San Francisco: California Academy of Sciences.

Fernández-Yépez A. 1967. Diferencias cefálicas em las especies del género *Sternarchorhynchus* de la familia Apteronotidae. *Natura, Fundación La Salle, Caracas* **34:** 18–19.

Ferreira E, dos Santos GM, Jégu M. 1988. Aspectos ecológicos da ictiofauna do rio Mucajaí, na ilha da Paredão, Roraima. *Amazoniana* **3:** 339–352.

Ferreira E, Zuanon J, Fosberg B, Goulding M, Briglia-Ferreira R. 2007. *Rio Branco. Peixes, Ecología e Conservação de Roraima*. Manaus, Brazil: Amazon Conservation Association, Instituto Nacional de Pesquisas da Amazônia, Sociedade Civil de Mamirauá.

Ferreira EFG. 1995 (issue for 1993). Composição, distribuição e aspectos ecológicos da ictiofauna de um trecho do rio Trombetas, na área de influência da future UHE cachoeira Porteira, Estado do Pará, Brasil. *Acta Amazonica* **23** (suplemento 1–4)**:** 1–89.

Feulner PGD, Kirshbaum F, Mamonekeve V, Ketmaier V, Tiedemann R. 2007. Adaptive radiation in African weakly electric fish (Teleostei: Mormyridae: *Campylomormyrus*): a combined molecular and morphological approach. *Journal of Evolutionary Biology* **20:** 403–414.

Fink SV, Fink WL. 1981. Interrelationships of the Ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72:** 297–353.

Fink SV, Fink WL. 1996. Interrelationships of Ostariophysan fishes (Teleostei). In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. San Diego: Academic Press, 209–249.

Foote M. 1997. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28:** 129–152.

Forey PL, Littlewood DTJ, Ritchie P, Meyer A. 1996. Interrelationships of elopomorph fishes. In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. New York: Academic Press, 175–191.

Fowler HW. 1951. Os peixes de água doce do Brasil (3.ª entrega). *Arquivos de Zoologia do Estado do São Paulo* **6:** 205–625.

Franchina CR, Hopkins CD. 1996. The dorsal filament of the weakly electric Apteronotidae (Gymnotiformes, Teleostei) is specialized for electroreception. *Brain, Behavior and Evolution* **47:** 165–178.

Goloboff P. 1999. *NONA. (NO NAME) version 2*. Published by the author, Tucumán, Argentina.

Gottschalk B, Scheich H. 1979. Phase sensitivity and phase coupling. Common mechanisms for communication behaviors in gymnotoid wave and pulse species. *Behavioral Ecology and Sociobiology* **4:** 395–408.

Goulding M, Leal Carvalho M, Ferreira E. 1988. *Rio Negro; rich life in poor water. Amazonian diversity and foodchain ecology as seen through fish communities*. The Hague: SPB Academic Publishing.

da Graça WF, Pavanelli CS. 2007. *Peixes da planície de inundação do alto rio Paraná e áreas adjacentes*. Maringa, Brazil: Editora da Universidade Estadual da Maringá.

Günther A. 1870. Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi . . . . *Leptocardii in the British Museum* **8:** 1–549.

Guyer C, Slowinski JB. 1993. Adaptive radiation of topology of large phylogenies. *Evolution* **47:** 253–263.

Hagedorn M, Keller CH. 1996. Species diversity of gymnotiform fishes in Manu Biosphere, Pakitza, Perú. In: Wilson DE, Sandoval A, eds. *Manu: the biodiversity of southeastern Peru*. Washington DC: Smithsonian Institution Press, 483–502.

Hennig W. 1966. *Phylogenetic systematics*. Urbana: University of Illinois Press.

Hilton EJ, Cox-Fernandes C. 2006. Sexual dimorphism in *Apteronotus bonapartii* (Gymnotiformes: Apteronotidae). *Copeia* **2006:** 826–833.

Hilton EJ, Cox-Fernandes C, Sullivan JP, Lundberg JG, Campos-da-Paz R. 2007. Redescription of *Orthosternarchus tamandua* (Boulenger, 1898) (Gymnotiformes, Apteronotidae), with reviews of its ecology, electric organ discharges, external morphology, osteology, and phylogenetic affinities. *Proceedings of the Academy of Natural Sciences of Philadelphia* **156:** 1–25.

Hodges SA. 1997. Rapid radiation due to a key innovation in columbines (Rananculaceae: *Aquilegia*). In: Givinish TJ, Sytsma K, eds. *Molecular evolution and adaptive radiation*. Cambridge: Cambridge University Press, 391–405.

Hopkins CD. 1991. *Hypopomus pinnicaudatus* (Hypopomidae), a new species of gymnotiform fish from French Guiana. *Copeia* **1991:** 151–161.

Isbrücker IJK, Nijssen H. 1983. *Crossoloricaria rhami* n. sp., un nouveau poisson-chat cuirassé du Río Huacamayo, Pérou (Pisces. Siluriformes. Loricariidae). *Revue Française de Aquariologie Herpétologie* **10:** 9–12.

Jensen JS. 1990. Plausibility and testability: assessing the consequences of evolutionary innovation. In: Nitecki MH, ed. *Evolutionary innovations*. Chicago: The University of Chicago Press, 171–190.

Johnson GD, Patterson C. 1996. Relationships of lower eutelostean fishes. In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. San Diego: Academic Press, 251–332.

Jordan DS. 1919. *The genera of fishes. Part III. A contribution to the stability of zoological nomenclature*. Palo Alto: Leland Stanford Junior University Publications. University Series.

Kirschbaum F. 1995. Taxonomy, zoogeography and general ecology of South American knifefishes (Gymnotiformes). In: Moller P, ed. *Electric fishes; history and behavior*. London: Chapman and Hall, 446–464.

Kullander SO. 2003. Family Cichlidae – cichlids. In: Reis RE, Kullander SO, Ferraris CJ Jr, eds. *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Brazil: EDIPUCRS, 605–654.

Kullander SO, Ferreira EFG. 2005. Two new species of *Apistogramma* Regan (Teleostei: Cichlidae) from the rio Trombetas, Pará, Brazil. *Neotropical Ichthyology* **3:** 361–371.

Kullander SO, Ferreira EFG. 2007. A review of the South American cichlid genus *Cichla*, with descriptions of nine new species (Teleostei: Cichlidae). *Ichthyological Exploration of Freshwaters* **17:** 289–398.

Kullander SO, Stawikowski R. 1997. Jardines Cichliden. *Deutsche Cichliden-Gesselscahaft* **28:** 112–119.

Langner G, Scheich H. 1978. Active phase coupling in electric fish: behavioral control with microsecond precision. *Journal of Comparative Physiology* **128:** 235–240.

Lasso CA, Machado-Allison A, Taphorn D, Rodríguez-Olarte D, Vispo CR, Chernoff B, Provenzano F, Lasso-Alcalá O, Cervó A, Nakamura K, González N, Meri J, Silvera C, Bonilla A, López-Rojas H, Machado-Aranda D. 2003. The fishes of the Caura River basin, Orinoco drainage, Venezuela. Annotated Checklist. *Scientia Guianae* **12:** 223–245.

Lasso CA, Lew D, Taphorn DC, DoNascimiento C, Lasso-Alcalá O, Provenzano F, Machado-Allison A. 2004a. Biodiversidad ictiologico continental de Venezuela. parte 1. Lista de especies y distribución por cuencas. *Memoria de la Fundación La Salle de Ciencias Naturales* **159–160 (for 2003):** 105–195.

Lasso CA, Mojica JI, Usma JS, Maldonaldo JA, DoNascimiento C, Taphorn DC, Provenzano F, Lasso-Alcalá OM, Galvis G, Vásquez L, Lugo M, Machado-Allison A, Royero R, Suárez C, Ortega-Lara A. 2004b. Peces de las cuencas del río Orinoco. Parte I: lista de especies y distribucíon por subcuencas. *Biota Colombiana* **5:** 95–158.

Lauder GV. 1981. Form and function; structural analysis in evolutionary morphology. *Paleobiology* **7:** 430–442.

Liem KF. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **4:** 425–441.

Lima FCT, Zuanon J. 2004. A new species of *Astyanax* (Characiformes: Characidae) from the rapids of the lower rio Xingu, Brazil. *Neotropical Ichthyology* **2:** 117–122.

Lopez-Rojas H, Lundberg JG, Marsh E. 1984. Design and operation of a small trawling apparatus for use with dugout canoes. *North American Journal of Fisheries Management* **4:** 331–334.

de Lucena CAS. 2007. Revisão taxonômica das espécies do gênero *Roeboides* group-*affinis* (Ostariophysi, Characiformes, Characidae). *Iheringia, series Zoologia, Porto Alegre* **97:** 117–136.

Lundberg JG, Cox-Fernandes C, Albert JS, Garcia M. 1996. *Magosternarchus*, a new genus with two new species of electric fishes (Gymnotiformes: Apteronotidae) from the Amazon River basin, South America. *Copeia* **1996:** 657–670.

Lundberg JG, Lewis WM Jr, Saunders JF III, Mago-Leccia F. 1987. A major food web component in the Orinoco River channel: evidence from planktivorous electric fishes. *Science* **237:** 81–83.

Lundberg JG, Mago-Leccia F. 1986. A review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a genus of South America freshwater fishes, with descriptions of four new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **138:** 53–85.

McAllister DE. 1968. Evolution of branchiostegals and classification of Teleostome fishes. *Bulletin, National Museum of Canada* **221:** 1–239.

Machado-Allison A. 1987. *Los peces de las llanos de Venezuela. Un esayo sobre su historia natural*. Caracas: Universidad Central de Venezuela.

Machado-Allison A. 2006. Contributions to the knowledge of freshwater ichthyology in Venezuela. *Acta Biologica Venezuelica* **26:** 13–52.

Machado-Allison A, Moreno H. 1993. Estudios sobre la comunidad de peces del Río Orituco, Estado Guarico, Venezuela. Parte 1. Inventario, abundancia relative y diversidad. *Acta Biologica Venezuelica* **14:** 77–94.

Maddison DR, Maddison WP. 2005. *MacClade, analysis of phylogeny and character evolution.* Version 4.08. Sunderland, MA: Sinauer Associates, Inc.

Mago-Leccia F. 1970. *Lista de los peces de Venezuela*. Caracas: Ministerio de Agricultura y Curia.

Mago-Leccia F. 1978. Los peces de la familia Sternopygidae de Venezuela. *Acta Scientífica Venezolana* **29** (suplemento 1**)**: 1–89.

Mago-Leccia F. 1994. *Electric fishes of the continental waters of America. Classification and catalogue of the electric fishes of the order Gymnotiformes (Teleostei: Ostariophysi) with descriptions of new genera and species*. Caracas: Biblioteca de la academia de ciencias fisicas, matematics y naturales.

Mago-Leccia F, Lundberg JG, Baskin JN. 1985. Systematics of the South American freshwater fish genus *Adontosternarchus* (Gymnotiformes, Apteronotidae). *Contributions in Sciences, Natural History Museum of Los Angeles County* **358:** 1–19.

Marrero C. 1987. Notas preliminares acerca de la historia natural de los peces del bajo llano. I. Comparación de los hábitos alimentarios de tres especies de Gymnotiformes del Río Apure (Edo. Apure) Venezuela. *Revista de Hidrobiologia Tropical* **20:** 57–63.

Marrero C, Castillo O, Machado-Allison A. 1987. Primera cita del genero *Traverella* Edmunds 1948 (Insecta, Ephemeroptera, Leptophlebidae), para Venezuela y comentarios preliminares acerca de la importancia del bentos en la dieta de los peces Gymnotiformes del Río Apure. *Biollania* **5:** 123–128.

Marrero C, Taphorn D. 1991. Notas sobre la historia natural y la distribution de los peces Gymnotiformes en la cuenca del río Apure y otros rios de la Orinoquia. *Biollania* **8:** 123–142.

Marrero C, Winemiller KO. 1993. Tube-snouted gymnotiform and mormyriform fishes: convergence of a specialized foraging mode in teleosts. *Environmental Biology of Fishes* **38:** 299–309.

Mayr E. 1960. The emergence of evolutionary novelties. In: Tax S, ed. *The evolution of life*. Chicago: University of Chicago Press, 349–380.

Meunier FJ. 2004. (Coordinator). Piranhas enivrés, des poissons et des hommes en Guyane. Paris: Societé Française d'Ichthologie – Réunion des Musées Nationaux.

Miles C. 1945. Some newly recorded fishes from the Magdalena River system. *Caldasia* **3:** 453–464.

Mojica JI. 1999. Lista preliminar de las especies duleacuícolas de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales* **23:** 547–566.

Mol JH, de Merona B, Oubeter PE, Sahdew A. 2007. The fish fauna of Brokopondo Reservoir, Suriname, during 40 years of impoundment. *Neotropical Ichthyology* **5:** 351–368.

Moller P. 1995. Taxonomy, zoogeography, general ecology. Order: Mormyriformes. In: Moller P, ed. *Electric fishes: history and behavior*. London: Chapman and Hall.

Müller J, Troschel FH. 1848. Fische. In: Schomburgk R, ed. *Reisen in British-Guiana in den Jahren 1840–1844*. Leipzig: Verlagsbuchhandlung von JJ Weber, 618–644.

Müller J, Troschel FH. 1849. *Horae Ichthyologicae. Beschreibung und Abbildung neuer Fische*. Berlin: Verlag von Veit und Comp.

Nelson G. 1969. Gill arches and the phylogeny of fishes with notes on the classification of the vertebrates. *Bulletin of the American Museum of Natural History* **141:** 475–522.

Nelson GJ, Platnick NI. 1981. *Systematics and biogeography: cladistics and vicariance*. New York: Colombia University Press.

Nixon KC. 1999–2002. *WinClada version 1.0000*. Published by the author, Ithaca, NY.

Novaceck MJ. 1992. Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals. *Systematic Biology* **41:** 58–73.

Ortega H. 1996. Ictiofauna del Parque Nacional Manu, Perú. In: Wilson DE, Sandoval A, eds. *Manu: the biodiversity of southeastern Peru*. Washington DC: Smithsonian Institution Press, 453–482.

Patterson C. 1975. The braincase of pholidophorid and leptolepid fishes with a review of the Actinopterygian braincase. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **269:** 275–579.

de Pinna MCC. 1991. Concepts and test of homology in the cladistic paradigm. *Cladistics* **7:** 367–394.

Planquette P, Keith P, Le Bail PY. 1996. *Atlas des poissons d'eau douce de Guyane (tome 1)*. Paris: IEGB – MNHN, INRA, CSP, Ministere de l'Environment.

Rapp Py-Daniel L, Cox-Fernandes C. 2005. Dimorfismo sexual em Siluriformes e Gymnotiformes (Ostariophysi) da Amazônia. *Acta Amazonica* **35:** 97–110.

Reis RE. 1997. Revision of the neotropical catfish genus Hoplosternum (Ostariophysi: Siluriformes: Callichthyidae), with the description of two new genus and three new species. *Ichthyological Exploration of Freshwaters* **7:** 299–326.

Reis RE, Kullander SO, Ferraris CJ Jr. 2003. *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Brazil: EDIPUCRS.

Riviere P. 1998. From science to imperialism: Robert Schomburgk's humanitarianism. *Archives of Natural History* **25:** 1–8.

Rodríguez-Olarte D, Taphorn DC, Lasso C, Vispo CR. 2003. Fishes of the lower Caura, Orinoco basin, Venezuela. *Scientia Guianae* **12:** 181–221.

de Santana CD, Castillo O, Taphorn D. 2006. *Apteronotus magoi*, a new species of ghost knifefish from the Río Orinoco basin, Venezuela (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **17:** 275–280.

de Santana CD, Crampton WGR. 2006. *Sternarchorhynchus curumin* (Gymnotiformes: Apteronotidae), a new species of tube-snouted ghost electric knifefish from the lowland Amazon basin, Brazil. *Zootaxa* **1166:** 57–68.

de Santana CD, Crampton WGR. 2007. Revision of the deep-channel electric fish genus *Sternarchogiton* (Gymnotiformes: Apteronotidae). *Copeia* **2007:** 387–402.

de Santana CD, Maldonado-Ocampo JA. 2005. *Apteronotus milesi*, new species of ghost knifefish (Gymnotiformes: Apteronotidae) from the Cauca river, with a key to apteronotids from the Magdalena-Cauca basin, Colombia. *Ichthyological Exploration of Freshwaters* **16:** 223–230.

de Santana CD, Maldonado-Ocampo J, Severi W, Mendes GN. 2004. *Apteronotus eschmeyeri*, a new species of ghost knifefish from Magdalena basin, Colombia (Gymnotiformes: Apteronotidae). *Zootaxa* **410:** 1–11.

de Santana CD, Nogueira A. 2006. Two new species of *Sternarchorhynchus* Castelnau from the Amazon basin, Brazil (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **17:** 85–92.

de Santana CD, Taphorn DC. 2006. *Sternarchorhynchus gnomus*, a new species of electric knifefish from the lower Rio Caroni, Venezuela (Gymnotiformes: Apteronotidae). *Ichthyological Exploration of Freshwaters* **17:** 1–8.

de Santana CD, Vari RP. 2009. The South America electric fish genus *Platyurosternarchus* (Gymnotiformes: Apteronotidae). *Copeia* **2009:** 233–244.

dos Santos GM, de Mérona B, Juras AA, Jégu M. 2004. *Peixes da baixo Rio Tocantins, 20 anos depois da Usina Hidroeléctrica Tucuruí*. Brasilia: Electronorte.

Schluter D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Schluter D, Price TD, Mooers Ø, Ludwig G. 1997. Likelihood on ancestor states in adaptive radiation. *Evolution* **51:** 1699–1711.

Schultz LP. 1949. A further contribution to the ichthyology of Venezuela. *Proceedings of the United States National Museum* **99:** 1–211.

Schwassmann HO, Carvalho ML. 1985. *Archolaemus blax* Korringa (Pisces, Gymnotiformes, Sternopygidae); a redescription with notes on ecology. *Spixiana* **8:** 231–240.

Sorenson MD. 1999. *TreeRot, version 2*. Boston, MA: Boston University.

Starks EC. 1913. *The fishes of the Stanford expedition to Brazil*. Palo Alto: Stanford Publications University Series.

Steindachner F. 1868a. Abhandlung über die Gymnotiden des Weiner Museum. *Anzeiger de Akademie der Wissenschaften, Wien* **5:** 176–177.

Steindachner F. 1868b. Die Gymnotidae des k. k. Hof-Naturaliencabinetes zu Wien. *Sitzungsberichte der Akademie der Wissenschaften, Matematicsh-Naturwissenschaftliche Classe, Wien* **58:** 249–264.

Stewart D, Barriga R, Ibarra M. 1987. Ictiofauna de la cuenca del Río Napo, Ecuador Oriental: Lista anotada de especies. *Politecnica, Revista de Información Tecnico-Cientifíca* **12:** 9–63.

Stiassny MLJ, Jensen JS. 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. *Bulletin of the Museum of Comparative Zoology* **151:** 269–319.

Stiassny MLJ, de Pinna MCC. 1994. Basal taxa and the role of cladistic patterns in the evaluation of conservation priorities: a view from freshwaters. In: Forey PL, Humphries CJ, Vane-Wright RI, eds. *Systematics and conservation evaluation*, Special Vol. 50. London: The Systematics Association, 235–249.

Sullivan JP, Lavoué S, Hopkins CD. 2000. Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *Journal of Experimental Biology* **203:** 665–683.

Swofford DL. 2003. *PAUP* version 4.0. Phylogenetic analyses using parsimony*. Washington, D.C.: Sinauer Associates, Inc.

Swofford DL, Maddison WP. 1987. Reconstructing ancestral states under wagner parsimony. *Mathematical Biosciences* **87:** 199–229.

Taphorn D, Royero R, Machado-Allison A, Mago Leccia F. 1997. Lista actualizada de los peces de aqua dulce de Venezuela. In: La Marca E, ed. *Vertebrados actuales y fósiles de Venezuela*. Merida, Venezuela: Museo de Ciencia y Tecnología de Mérida, 55–100.

Taverne L. 1968. Ostéologie du genre *Campylomormyrus* Bleeker (Pisces Mormyriformes). *Annales de la Société royale Zoologique de Belgique* **98:** 147–188.

Taylor WR, Van Dyke GC. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9:** 107–119.

Triques M. 1993. Filogenia dos gêneros de Gymnotiformes (Actinopterygii, Ostariophysi) com base em caracteres esqueléticos. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Séries Zoologia, Porto Alegre* **6:** 85–130.

Triques M. 2005. Análise cladística dos caracteres de anatomia externa e esquelética de Apteronotidae (Teleostei: Gymnotiformes). *Lundiana* **6:** 121–149.

Triques M. 2007. Família Apteronotidae. In: Buckup PA, Menezes NA, Ghazzi MS, eds. *Catálogo das espécies de peixes de água doce do Brasil*. Rio de Janeiro: Museu Nacional, Universidade Federal do Rio de Janeiro, 123–125.

Vari RP. 1979. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). *Bulletin of the British Museum (Natural History)* **36:** 261–344

Vari RP. 1995. The neotropical fish family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): supra and intrafamilial phylogenetic relationships, with a revisionary study. *Smithsonian Contributions to Zoology* **564:** 1–97.

Vari RP, Ferraris CJ Jr, de Pinna MCC. 2005. The neotropical whale catfishes (Siluriformes: Cetopsidae: Cetopsinae), a revisionary study. *Neotropical Ichthyology* **3:** 127–238.

Vari RP, Harold AS. 2001. Phylogenetic study of the neotropical fish genera *Creagrutus* Günther and *Piabina* Reinhardt (Teleostei: Ostariophysi: Characiformes), with a revision of the cis-Andean species. *Smithsonian Contributions to Zoology* **613:** 1–239.

Vari RP, Malabarba LR. 1998. Neotropical ichthyology: an overview. In: Reis RE, Kullander SO, Ferraris CJ Jr, eds. *Check list of the freshwater fishes of South and Central America*. Porto Alegre: EDIPUCRS, 1–11.

Watkins G, Saul W, Holm E, Watson C, Arjoon D, Bicknell J. 2004. The fish fauna of the Iwokrama Forest. *Proceedings of the Academy of Natural Sciences of Philadelphia* **15:** 39–53.

Weitzman SH. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* **8:** 1–77.

Weitzman SH. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. *Bulletin of the American Museum of Natural History* **153:** 327–478.

Wiens JJ. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* **52:** 528–538.

Wiens JJ. 2005. Can incomplete taxa rescue phylogenetic analyses from long-branch attraction? *Systematic Biology* **54:** 731–742.

Wiley EO. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. New York: John Wiley and Sons.

Wiley EO, Siegel-Causey D, Brooks DR, Funk VA. 1991. The compleat cladist: a primer of phylogenetic procedures. University of Kansas Museum of Natural History, Special Publication **19:** 1–158.

Winemiller KO, Adite A. 1997. Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environmental Biology of Fishes* **49:** 175–186.

Winterbottom R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceeding of the Academy of Natural Sciences of Philadelphia* **125:** 225–317.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Cleared and stained material examined.

APPENDIX 1

CHARACTER MATRIX

Phylogenetic character matrix for 88 characters for the examined species of *Sternarchorhynchus* and outgroups. Characters numbers correspond to those in the text and in Appendix 2. Characters inapplicable and missing data for particular taxa are indicated by dashes and “?” respectively.

	Character								
Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	88888888 12345678
Outgroups									
Apteronotus									
A. albifrons	-011000000	0001000111	00000100-0	1100010000	0000100-00	0-0000000	0000100000	00100-1010	00-01000
“A.” *apurensis*	-011000000	0001000111	00000100-0	1100010000	0100100-00	0-0000000	0000100000	0010101110	010-0001
“A.” *cuchillo*	-011000000	0001000111	00000100-0	0100000000	0000100-00	0-0000000	0000000000	00100-1110	00-01000
A. rostratus	-011000000	0001000111	00000000-0	0100000000	0010100-00	0-0000000	0000000000	00100-1010	00-01000
Orthosternarchus									
O. tamandua	0001001000	0000-00001	00000000-0	0100000000	0010101-01	0000001000	0000000000	01000-0-10	110-0000
Platyurosternarchus									
P. crypticus	-0000-0000	0001001010	00000100-0	0100000000	0000000-00	0100000000	1110000100	00100-1100	010-0000
P. macrostoma	-0000-0000	0001001010	00000000-0	0100010000	0100100-00	0100000000	1110000100	00100-1100	010-0000
Sternarchorhamphus									
S. muelleri	0001000000	0000-00001	00000000-0	0100000000	0000001-01	0000001000	0000000000	00000-0-10	110-0001
Sternarchella									
S. orthos	0111000000	1001000111	00000100-0	0100010000	0011000-00	0100000000	0000000000	00100-1010	010-0000
Sternarchogiton									
S. labiatus	-010000000	0001000111	00000100-0	1100010000	0000100-00	0-0000000	0000000000	00100-1010	010-0000
Sternarchorhynchus									
S. axelrodi	0101121011	1101111111	11110??100	110011010?	0111110000	0????10???	111?111111	111?111???	010-0101
S. britskii	0111101011	1111111111	1111001110	0100100101	1011010000	0100010010	1111111110	0111111010	00-01100
S. caboclo	0111101011	1111111111	1111000110	0110100101	1111000-00	1101010011	1111111110	01110-1010	00-00100
S. chaoi	0111101011	1101111111	1111000110	0110100101	0111010000	0111010110	1112011110	0110101010	01101100
S. cramptoni	0111101011	1101111111	1111001110	0110101101	0111010000	0111010110	1111111110	01100-1010	00-01101
S. curumim	0111101011	1101111111	1111000110	0100101101	1111010000	0111010010	1111011110	01100-1010	00-00100
S. curvirostris	0111101011	1101111111	1111000110	0001101101	1011010000	0101010110	1111011110	0110112010	00-01010
S. gnomus	0111101011	1111111111	1111001110	0101100101	1011010000	0101010010	1111011110	0110101010	00-01100
S. goeldii	1001110111	1101111011	1111100101	0000111110	1111010010	0000010000	1110101110	0110111110	010-0001
S. hagedornae	0111101011	1101111111	1111001110	0101101101	0011010000	0111010110	1111111110	0110101010	00-11100
S. higuchii	0111101011	1111111111	1111000110	0101100101	1011010000	0110010011	1111111110	01100-1010	00-11100
S. inpai	0111101011	1101111111	1111001110	0100100101	1011010100	0101110010	1111111110	0110102010	00-01100
S. jaimei	0111101011	1101111111	1111001110	0110100101	1011010000	0110010110	1111011110	01100-1010	01101100
S. mareikeae	0111101011	1111111111	1111001110	0101101101	1011010000	0101010010	1111111110	01100-1010	00-01100
S. mendesi	0111101011	1101111111	1111000110	0100100101	1011010000	0101010010	1111111110	01100-2010	00-11100
S. mesensis	0111101011	1101111111	1111000110	0110100101	1011010000	0111010110	1111111110	01100-2021	00-01100
S. montanus	0111101011	1101111111	1111001110	0100100101	0011010000	0111110010	1111111110	0110101010	00-01101
S. mormyrus	0101121011	1101111111	1111010100	1100110100	0111110000	0001010110	1111111111	1110111110	010-0101
S. oxyrhynchus	1001110111	1101111011	1111100101	0000111110	1111010010	0000010000	1111001110	0110111110	010-0001
S. retzeri	0111101011	1101111111	1111001110	0110101101	1111010000	0101010110	1111111110	01100-1010	00-01101
S. roseni	0111101011	1101111111	1111000110	0110100101	1011010000	0110010010	1111111110	01100-2010	00-1100?
S. severii	0111101011	1101111111	1111001110	0100100101	1111010000	0101010110	1111111110	0110101010	00-01100
S. starksi	0111101011	1101111111	1111001110	0101101101	0011010000	01?1010110	1111011110	0110101020	00-01000
S. stewarti	0111101011	1111111111	1111001110	0100101101	1011010000	0111010110	1111111110	01100-1010	00-01100

APPENDIX 2

SYNAPOMORPHY LIST

The 24 numbered clades that appear in Figure 23 and in the following list are present in all of the most parsimonious trees recovered during the phylogenetic analysis. A list of the character state transitions that optimize unambiguously at the branch encompassing each numbered clade in the strict consensus phylogeny is provided, as are transitions that optimized as autapomorphies for species. We limited the discussion to characters pertinent to the hypothesis of a sister group relationship of *Platyurosternarchus* and *Sternarchorhynchus* and subunits of those genera. The scheme of outgroup relationships shown in Figure 23 should not be considered well supported because we did not search for characters pertinent to the resolution of relationships amongst those taxa nor necessarily include published characters pertinent solely to the question of relationships amongst the outgroup taxa.

A brief description of each synapomorphy is provided with more detailed information available under the description of the character. Each synapomorphic character state transition for *Sternarchorhynchus* or a subunit of that genus is followed by information on whether that state transition is a reversal within *Sternarchorhynchus*, whether other clades within *Sternarchorhynchus* have acquired that character state independently, and whether additional character state transitions in the character under discussion occur within the clade defined by the synapomorphy.

Clade 1: *Platyurosternarchus* plus *Sternarchorhynchus* (Tribe Sternarchorhynchini)

- Character 17, state 0→1; anguloarticular terminating posteriorly at, to posteriorly distinctly posterior of, vertical through dorsal portion of joint between angulo-articular and retroarticular and with distinct, posteriorly attenuating process extending along anterior margin of retroarticular
- Character 42, state 0→1 (ACCTRAN); laterosensory canal segment in vertical arm of preopercle in form of two deeply anteriorly concave segments; reversed to state 0 in *Platyurosternarchus crypticus* and clade 10, reacquired in clade 20
- Character 61, state 0→1; very distinct constriction of medial portion of fourth ceratobranchial
- Character 62, state 0→1; well-ossified fourth infrapharyngobranchial with an overall triangular, posteriorly widening form from dorsal view
- Character 63, state 0→1; cartilage along anterior margin of first epibranchial expanded medially and extending along all, or nearly all, of anterior margin of cartilage at anterior of second infrapharyngobranchial
- Character 68, state 0→1; absence of lateral ethmoid
- Character 78, state 0→1 (DELTRAN); second postcleithrum horizontally elongate; reversed in clade 7

Clade 2: *Platyurosternarchus*

- Character 4, state 1→0; absence of teeth on premaxilla; also present in *Sternarchogiton labiatus* in outgroups
- Character 20, state 1→0; teeth attaching to exterior surface of dentary
- Character 43, state 1→0 (ACCTRAN); dorsal margin of opercle very slightly concave to distinctly convex
- Character 52, state 0→1; anterior portion of urohyal relatively wide and one-third or more of length of main body of bone; also present in clade 7
- Character 79, state 1→0; intercalarium transversely elongate

In a separate study focused on *Platyurosternarchus*, de Santana & Vari (2009) identified three additional synapomorphies for the species of the genus:

- the extension of the posterodorsal corner of the maxilla into a posteriorly attenuating process
- the reduction of the posterior fontanel to a small round opening bordered by the posteriormost portions of the contralateral parietals and median region of the anterior margin of the supraoccipital
- the distinct pigmentation pattern of dark ventrolateral and light dorsolateral pigmentation with a patch of very dark pigmentation on the posterior portion of the anal fin

Platyurosternarchus crypticus

- Character 26, state 0→1; presence of ascending process of endopterygoid; also in clade 6
- Character 36, state 1→0; overall form of symplectic bone relatively slender, with height of posteriormost portion of symplectic approximately one-fifth length of that bone; also occurs in clade 7

Character 42, state 1→0 (ACCTRAN); laterosensory canal segment in vertical arm of preopercle in form of two shallowly anteriorly concave segments; also present in clade 10

Platyurosternarchus macrostoma

- Character 42, state 0→1 (DELTRAN); laterosensory canal segment in vertical arm of preopercle in form of two deeply anteriorly concave segments; also present in clade 3, reversed in clade 10, and reacquired in clade 20 and *S. chaoi*
- Character 45, state 0→1; association of posterodorsal corner of opercle and supracleithrum rounded posterior extension of opercle extending over ventralmost portion of supracleithrum; also occurs in clade 6

- In their study of *Platyurosternarchus* de Santana & Vari (2009) identified an additional synapomorphy for *P. macrostoma*:
- The fusion of the extrascapular with the neurocranium

Clade 3: *Sternarchorhynchus*

- Character 5, state 0→1; anterior portion of maxilla with distinct anteriorly pointed process without distinct anterior process
- Character 9, state 0→1; coronomeckelian bone present as small rounded ossification in smaller specimens, but absent in adults
- Character 10, state 0→1; Meckel's cartilage well developed in smaller individuals, but reduced ontogenetically and highly reduced in adults
- Character 11, state 0→1; posterodorsal and posteroventral processes of dentary approximately of same length
- Character 12, state 0→1; posteroventral process of dentary very narrow and in form of elongate narrow strut of bone
- Character 15, state 0→1; separation along dorsal margin of anguloarticular between joint for articulation with quadrate and anguloarticular–retroarticular joint approximately about 4–4.5 times width of articular facet on anguloarticular that forms joint
- Character 16, state 0→1; anterior portion of anguloarticular distinctly pointed with medial surface of bone unelaborated
- Character 21, state 0→1; anterior portion of palatoquadrate cartilage poorly developed and reduced to narrow, somewhat thread-like process
- Character 22, state 0→1; endopterygoid positioned along medial surface of dentary and anguloarticular with dorsal margin of endopterygoid located distinctly ventral of dorsal margins of dentary and anguloarticular
- Character 23, state 0→1; anterior portion of endopterygoid very narrow and compressed transversely and distinctly higher than wide
- Character 24, state 0→1; posterior portion of endopterygoid reduced to very elongate, approximately horizontally aligned process extending along, and tightly attached to, lateral surface of quadrate and metapterygoid or fused to quadrate in some species
- Character 28, state 0→1; dorsal portion of quadrate without broad anterodorsal plate-like process
- Character 35, state 0→1; posterior limit of posteroventral portion of quadrate terminating approximately at vertical through two-thirds of length of metapterygoid or posterior of that point
- Character 38, state 0→1; metapterygoid somewhat to distinctly horizontally elongate and approximately quadrilateral
- Character 41, state 0→1 (ACCTRAN); preopercle extending anteriorly to anterior of vertical through ventral portion of joint between quadrate and metapterygoid; reversed in clade 6, *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. montanus*, and *S. starksi*
- Character 42, state 0→1 (DELTRAN); laterosensory canal segment in vertical arm of preopercle in form of two deeply anteriorly concave segments; reversed in clade 10, and reacquired in clade 20 and *S. chaoi*
- Character 43, state 0→1 (DELTRAN); dorsal margin of opercle distinctly concave
- Character 44, state 0→1; posterodorsal corner of opercle extended in form of distinct process
- Character 46, state 0→1; presence of anteriormost branchiostegal ray attaching to ventral margin of anterior ceratohyal; reversed in *S. caboclo*
- Character 56, state 0→1; basihyal distinctly separated from second basibranchial, with posterior of basihyal extending posteriorly only to or proximate to anterior region of ossified portion of first hypobranchial
- Character 64, state 0→1 (ACCTRAN); central portion of myorhadoi with ventral elaboration; transition to state 2 in *S. chaoi*
- Character 65, state 0→1 (ACCTRAN); position of anus notably ontogenetically variable and shifting anteriorly to location anterior to vertical through eye in adults; reversed in *S. curumim*, *S. gnomus*, *S. oxyrhynchus*, and clades 16, 22
- Character 67, state 0→1; distance from tip of mesethmoid to vertical through posteriormost limit of that bone equal to, or longer than, distance from anteriormost point on frontal to anterior margin of parietal distance
- Character 69, state 0→1; ventral portion of orbitosphenoid relatively narrow along anteroposterior axis and not extending anteriorly along dorsal margin of parasphenoid
- Character 72, state 0→1; anterior limit of anterior fontanel falling short of anterior limit of orbitosphenoid
- Character 75, state 0→1; presence of ossification located in superficial tissues of body anterodorsal to first postcleithrum; reversed in clades 8 with reacquisition in *S. chaoi*, clade 18, and *S. mareikeae*
- Character 88, state 0→1 (ACCTRAN); anal fin hyaline to slightly dusky overall, and with distinct band of dark pigmentation distally; reversed in clade 7 and then reacquired independently in *S. montanus* and clade 20

Clade 4: *Sternarchorhynchus goeldii* and *S. oxyrhynchus*

- Character 1, state 0→1; mouth short and posterior terminus of gape extending posteriorly to beyond vertical through posterior nares
- Character 6, state 0→1; anterior portion of maxilla reduced and only slightly wider than main portion of bone
- Character 8, state 0→1; fleshy pad at anterior of dentary well developed, dorsally directed, and overlapping tip of snout in closed mouth
- Character 25, state 0→1; quadrate and endopterygoid fused
- Character 30, state 0→1; posterolateral portion of quadrate with lateral expansion into rounded ridge terminating posteriorly in articular facet
- Character 32, state 1→0; anterior portion of symplectic fitting into notch or pocket along posteroventral margin of quadrate located distinctly posterior of ventral limit of joint between quadrate and metapterygoid; also present in *S. curvirostris*
- Character 37, state 0→1; anterodorsally directly process on dorsal margin of symplectic present; evolved independently in *S. curumim* and clade 14, reversed in clade 21
- Character 39, state 0→1; lateral surface of dorsal portion of metapterygoid with distinct rounded lateral ridge terminating anteriorly in well-developed articular surface
- Character 41, state 0→1 (DELTRAN); anterior extent of preopercle extending to location anterior of vertical through ventral portion of joint between quadrate and metapterygoid; also present in clade 7, reversed in *S. chaoi*, *S. cramptoni*, *S. hagedornae*, and *S. montanus*
- Character 49, state 0→1; anterodorsal margin of third branchiostegal ray with distinct angular process
- Character 76, state 0→1 (DELTRAN); ossification located anterodorsal to first postcleithrum elongate; also occurs in clade 6, *S. britskii*, and *S. curvirostris*
- Character 88, state 0→1 (DELTRAN); fin hyaline to slightly dusky overall, and with distinct band of dark pigmentation distally; acquired independently in clades 6, 20, and *S. montanus*

Sternarchorhynchus goeldii

- Character 64, state 1→0 (ACCTRAN); central portion of myorhadoi without ventral or dorsal elaborations; also occurs in *Platyurosternarchus*
- Character 65, state 0→1 (DELTRAN); position of anus notably ontogenetically variable and shifting anteriorly to location anterior to vertical through eye in adults; also evolved independently in clade 5 with subsequent reversals in *S. curumim*, *S. gnomus*, clade 16, and clade 22

Sternarchorhynchus oxyrhynchus

- Character 64, state 0→1 (DELTRAN); central portion of myorhadoi with ventral elaboration; also occurs in clade 5
- Character 65, state 1→0 (ACCTRAN); position of anus relatively invariant in juveniles and adults with anus situated posterior to vertical through eye in adults; also occurs independently in *S. gnomus*, clade 16, and clade 22

Clade 5: *Sternarchorhynchus axelrodi*, *S. britskii*, *S. caboclo*, *S. chaoi*, *S. cramptoni*, *S. curumim*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. gnomus*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. mormyrus*, *S. retzeri*, *S. roseni*, *S. severii*, *S. starksi*, and *S. stewarti*

- Character 2, state 0→1; skin of upper lip with distinct fold; also occurs in *Sternarchella orthos* in outgroups
- Character 7, state 0→1; ventral margin of maxilla with distinct concavity
- Character 18, state 0→1; posterior limit of dentary located along vertical through vertical component of orbitosphenoid
- Character 54, state 0→1 (ACCTRAN); basihyal with lateral processes; reversed in *S. britskii*, *S. jaimei*, and clade 24 with reacquisition in *S. mendesi*
- Character 54, state 0→1 (DELTRAN as an exclusive synapomorphy); basihyal with lateral processes; independently reversed in *S. britskii*, *S. higuchii*, *S. jaimei*, and *S. roseni*
- Character 59, state 0→1; anterior portion of second hypobranchial with distinct anterior extension from main body
- Character 64, state 0→1 (DELTRAN); central portion of myorhadoi with ventral elaboration; also present in *S. oxyrhynchus*; modified to state 2 in *S. chaoi*
- Character 65, state 0→1 (DELTRAN); position of anus notably ontogenetically variable and shifting anteriorly to location anterior to vertical through eye in adults; reversed independently in *S. curumim*, *S. gnomus*, clade 16, and clade 22
- Character 66, state 0→1; presence of scythe-shaped process along lateral margin of ventral ethmoid
- Character 86, state 0→1; presence of narrow, lightly coloured stripe on lateral surface of snout; reversed independently in clade 16 and *S. roseni*

Clade 6: *Sternarchorhynchus axelrodi* and *S. mormyrus*

- Character 6, state 0→2; anterior portion of maxilla distinctly expanded into somewhat square plate with irregular margins
- Character 26, state 0→1 (ACCTRAN); presence of ascending process of endopterygoid; also present in *P. crypticus* in outgroup
- Character 31, state 0→1; posteroventral margin of main body of quadrate that receives anterior tip of symplectic with notch very small or absent and enclosed laterally and medially by vertical sheet of bone
- Character 41, state 1→0 (ACCTRAN); preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also present independently in *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. montanus*, and *S. starksi*
- Character 45, state 0→1; rounded posterior extension of opercle extending over ventralmost portion of supracleithrum; also present in *P. macrostoma*
- Character 58, state 0→1(ACCTRAN); second basibranchial with lateral margins running approximately in parallel; occurs independently in *S. severii*
- Character 70, state 0→1; posterior margin of orbitosphenoid concave and contacting pterosphenoid only at dorsal and ventral limits of areas of contact of orbitosphenoid and pterosphenoid
- Character 71, state 0→1; anterior margin of pterosphenoid concave and contacting orbitosphenoid only at dorsal and ventral limits of areas of contact of pterosphenoid and orbitosphenoid
- Character 76, state 0→1 (DELTRAN); ossification located anterodorsal to first postcleithrum elongate; also occurs independently in clade 4, *S. britskii*, and *S. curvirostris*
- Character 88, state 0→1 (DELTRAN); anal fin hyaline to slightly dusky overall with distinct band of dark pigmentation distally; also occurs independently in clade 4, clade 22, and *S. montanus* within *Sternarchorhynchus*

Clade 7: *Sternarchorhynchus britskii*, *S. caboclo*, *S. chaoi*, *S. cramptoni*, *S. curumim*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. gnomus*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. retzeri*, *S. roseni*, *S. severii*, *S. starksi*, and *S. stewarti*

- Character 3, state 0→1; premaxilla compact with longitudinal length approximately equal to transverse width
- Character 29, state 0→1; dorsal margin of quadrate concave
- Character 36, state 1→0; Symplectic relatively slender, with height of posteriormost portion of bone approximately one-fifth length of bone.
- Character 40, state 0→1; tip of posteroventral process of quadrate fitting into variably developed notch along dorsal margin of preopercle
- Character 41, state 0→1 (DELTRAN); preopercle extending anteriorly to location anterior of vertical through ventral portion of joint between quadrate and metapterygoid; also present in clade 4; reversed to state 0 in *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. montanus*, and *S. starksi*
- Character 52, state 0→1; anterior portion of urohyal relatively wide and one-third or more of length of main body of bone; also occurs independently in clade 2, and in *Sternarchella orthos* in outgroups
- Character 76, state 1→0 (ACCTRAN); ossification located anterodorsal to first postcleithrum rhomboid or ovoid; reversed to state 1 independently in *S. britskii* and *S. curvirostris*
- Character 78, state 1→0; second postcleithrum rounded or slightly longitudinally ovoid
- Character 82, state 1→0; scales present along mid-dorsal region of body anterior to origin of electroreceptive filament; reversed in clade 22
- Character 83, state 0→1 (ACCTRAN); scales absent along mid-dorsal region only to region approximately at vertical through posterior margin of pectoral fin
- Character 88, state 1→0 (ACCTRAN); anal fin hyaline to slightly dusky overall, but lacking distinct band of dark pigmentation distally; also present in *P. crypticus* and *P. macrostoma*; reversed in clade 20

Clade 8: *Sternarchorhynchus caboclo* and *S. curumim*

- Character 75, state 1→0; absence of ossification located in superficial tissues of body anterodorsal to first postcleithrum; also occurs in clade 18, reversed to state 1 in *S. chaoi*

Sternarchorhynchus caboclo

- Character 13, state 0→1; posteroventral process of dentary not reaching margin of posteroventral process of anguloarticular; reversed in clade 15; also occurs independently in *S. britskii*, *S. gnomus*, *S. higuchii*, *S. mareikeae*, and *S. stewarti*
- Character 33, state 0→1; absence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; also present in clade 19 with reversal in clade 24 and reacquisition in *S. roseni*
- Character 46, state 1→0; absence of anteriormost branchiostegal ray attaching to ventral margin of anterior ceratohyal
- Character 51, state 0→1; dorsal margin of proximate portion of anterior branchiostegal ray attaching to lateral surface of the anterior ceratohyal concave with angled margins

- Character 60, state 0→1; medial portion of second hypobranchial in adults without distinct medial process and with contralateral second hypobranchials separated by second basibranchial; also present in *S. higuchii*
- Character 74, state 0→1; slender anteroventral process of coracoid, terminating anteriorly distinctly short of medial surface of cleithrum and with gap filled by distinct cartilage mass; also present in *S. britskii*

Clade 9: *Sternarchorhynchus britskii*, *S. chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. gnomus*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. retzeri*, *S. roseni*, *S. severii*, *S. starksi*, and *S. stewarti*

- Character 27, state 0→1 (ACCTRAN); pterygocranial ligament attaching to both endopterygoid and quadrate; reversed in *S. curvirostris* and clade 21 with reacquisition in *S. jaimei*
- Character 27, state 0→1 (DELTRAN); pterygocranial ligament attaching to both endopterygoid and quadrate; reversed in *S. curvirostris*, *S. chaoi*, and clade 23
- Character 85, state 0→1; mid-dorsal region of head with narrow, mid-dorsal, lightly coloured stripe

Sternarchorhynchus severii

- Character 58, state 0→1; second basibranchial with lateral margins running approximately in parallel; also occurs in clade 15 with reversal in clade 24

Clade 10: *Sternarchorhynchus britskii*, *S. chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. inpai*, *S. jaimei*, *S. gnomus*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. montanus*, *S. retzeri*, *S. roseni*, *S. starksi,* and *S. stewarti*

- Character 42, state 1→0; laterosensory canal segment in vertical arm of preopercle in form of two shallowly anteriorly concave segments; reversed independently in clade 20 and *S. chaoi*

Clade 11: *Sternarchorhynchus inpai* and *S. montanus*

- Character 51, state 0→1; form of dorsal margin of proximate portion of anterior branchiostegal ray attaching to lateral surface of the anterior ceratohyal dorsally pointed or rounded

Sternarchorhynchus inpai

- Character 48, state 0→1; first branchiostegal ray approximately one-third length of second branchiostegal ray
- Character 77, state 1→2; three postcleithra present; also occurs independently in *S. curvirostris* and clade 23

Sternarchorhynchus montanus

- Character 41, state 1→0; preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also occurs independently in *S. axelrodi*, *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. mormyrus*, and *S. starksi*
- Character 53, state 0→1; anterior margin of urohyal with distinct medial notch; also occurs in clade 17 with independent reversals in *S. retzeri* and *S. mendesi*
- Character 88, state 0→1; anal fin hyaline to slightly dusky overall with distinct band of dark pigmentation distally; also occurs independently in clade 20

Clade 12: *Sternarchorhynchus britskii*, *S. chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. gnomus*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, *S. starksi*, and *S. stewarti*

- Character 13, state 0→1; posteroventral process of dentary not reaching margin of posteroventral process of anguloarticular; reversed in clade 15 with state 1 reacquired independently in *S. higuchii* and *S. stewarti*

Sternarchorhynchus britskii

- Character 54, state 1→0; basihyal without lateral processes; also occurs independently in *S. jaimei* and clade 24 with reversal in *S. mendesi*
- Character 74, state 0→1; slender anteroventral process of coracoid terminating anteriorly distinctly short of medial surface of cleithrum and with gap filled by distinct cartilage mass; also occurs independently in *S. caboclo*
- Character 76, state 0→1; ossification located anterodorsal to first postcleithrum elongate; also present independently in *S. curvirostris*, and clades 3 and 5

Clade 13: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. curvirostris*, *S. gnomus*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, *S. starksi*, and *S. stewarti*

- Character 34, state 0→1; presence of overlap laterally of anteroventral corner of metapterygoid by bony process of quadrate; reversed in clade 18 with reacquisition in *S. higuchii*

Sternarchorhynchus gnomus

- Character 65, state 1→0; anus position relatively invariant in juveniles and adults with anus situated posterior to vertical through eye in adults; also occurs in clades 16 and 22

Clade 14: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. mareikeae*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, *S. starksi*, and *S. stewarti*

- Character 37, state 0→1; presence of anterodorsally directed process on dorsal margin of symplectic; reversed in clade 21

Sternarchorhynchus mareikeae

- Character 75, state 1→0; absence of ossification located in superficial tissues of body anterodorsal to first postcleithrum; also occurs independently in clade 18 with subsequent reversal in *S. chaoi*

Clade 15: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. curvirostris*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, *S. starksi*, and *S. stewarti*

- Character 13, state 1→0; posteroventral process of dentary reaching margin of posteroventral process of anguloarticular; reversed independently in *S. higuchii* and *S. stewarti*
- Character 58, state 0→1; second basibranchial with lateral margins running approximately in parallel; reversed in clade 24

Clade 16: *Sternarchorhynchus curvirostris* and *S. starksi*

- Character 65, state 1→0; position of anus relatively invariant in juveniles and adults with anus situated posterior to vertical through eye in adults; also present independently in clade 22
- Character 86, state 1→0; lateral surface of snout with pigmentation comparable to that of adjoining regions or with irregular marbling; further present in *S. roseni*

Sternarchorhynchus curvirostris

- Character 27, state 1→0; pterygocranial ligament attachment limited to dorsal surface of endopterygoid; also reversed independently in *S. jaimei*
- Character 32, state 1→0; anterior portion of symplectic fitting into notch or bony pocket along posteroventral margin of quadrate located anterior of ventral limit of joint between quadrate and metapterygoid; also present in clade 4
- Character 76, state 0→1; ossification located anterodorsal to first postcleithrum elongate; also occurs independently in *S. britskii*
- Character 77, state 1→2; three postcleithra present; also occurs independently in *S. inpai* and clade 23
- Character 87, state 0→1; anal fin hyaline to slightly dusky overall, and with distinct band of dark pigmentation basally

Sternarchorhynchus starksi

- Character 41, state 1→0; preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also occurs independently in clade 6, *S. chaoi*, *S. cramptoni*, *S. hagedornae*, and *S. montanus*
- Character 79, state 0→2; intercalarium medially tapering and triangular overall; also present in *S. mesensis*

Clade 17: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. hagedornae*, *S. higuchii*, *S. jaimei*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, and *S. stewarti*

- Character 53, state 0→1; anterior margin of urohyal, with distinct medial notch; also occurs in *S. montanus*; reversed in *S. retzeri* and further in *S. mendesi*

Sternarchorhynchus hagedornae

- Character 41, state 1→0; preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also occurs independently in *S. chaoi*, *S. cramptoni*, *S. montanus*, and *S. starksi*
- Character 84, state 0→1; scales sparse and covered to different degrees by skin; also occurs in clade 24

Clade 18: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. higuchii*, *S. jaimei*, *S. mendesi*, *S. mesensis*, *S. retzeri*, *S. roseni*, and *S. stewarti*

- Character 34, state 1→0; absence of overlap laterally of anteroventral corner of metapterygoid by bony process of quadrate
- Character 75, state 1→0; absence of ossification located in superficial tissues of body anterodorsal to first postcleithrum; character reversed in *S. chaoi*: state 0 also occurs in *S. mareikeae*

Sternarchorhynchus stewarti

- Character 13, state 0→1; posteroventral process of dentary not reaching margin of posteroventral process of anguloarticular; also occurs independently in *S. britskii*, *S. caboclo*, *S. gnomus*, *S. higuchii*, and *S. mareikeae*

Clade 19: *Sternarchorhynchus chaoi*, *S. cramptoni*, *S. higuchii*, *S. jaimei*, *S. mendesi*, *S. mesensis*, *S. roseni*, and *S. retzeri*

- Character 33, state 0→1; absence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; reversed in clade 24 and reacquired in *S. roseni*; state 1 also present independently in *S. caboclo*

Clade 20: *Sternarchorhynchus cramptoni* and *S. retzeri*

- Character 42, state 0→1; laterosensory canal segment in vertical arm of preopercle in form of two deeply anteriorly concave segments; also present independently in clades 4, 6, *S. caboclo*, *S. chaoi*, *S. curumim*, and *S. severii*
- Character 88, state 0→1; anal fin hyaline to slightly dusky overall, and with distinct band of dark pigmentation distally; also occurs in clades 4, 6, and *S. montanus*

Sternarchorhynchus cramptoni

- Character 41, state 1→0; preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also present independently in clade 6, *S. chaoi*, *S. cramptoni*, *S. hagedornae*, *S. montanus*, and *S. starksi*

Sternarchorhynchus retzeri

- Character 53, state 1→0; anterior margin of urohyal straight or slightly irregular, but without distinct medial notch; also present in *S. mendesi*

Clade 21: *Sternarchorhynchus chaoi*, *S. higuchii*, *S. jaimei*, *S. mendesi*, *S. mesensis*, and *S. roseni*

- Character 27, state 1→0 (ACCTRAN); pterygocranial ligament attachment limited to dorsal surface of endopterygoid; reversed to state 1 in *S. jaimei*; state 0 also occurs independently in clade 4, *S. caboclo*, *S. curvirostris*, and *S. mormyrus*
- Character 37, state 1→0; absence of anterodorsally directed process on dorsal margin of symplectic

Clade 22: *Sternarchorhynchus chaoi* and *S. jaimei*

- Character 65, state 1→0; position of anus relatively invariant in juveniles and adults with anus situated posterior to vertical through eye in adults; also present independently in clade 16
- Character 82, state 1→0; scales reduced to some extent and sometimes largely absent along mid-dorsal region of body anterior to origin of electroreceptive filament
- Character 83, state 0→1 (DELTRAN); scales absent along mid-dorsal region only to region approximately at vertical through posterior margin of pectoral fin

Sternarchorhynchus chaoi

- Character 27, state 1→0 (DELTRAN); pterygocranial ligament attachment limited to dorsal surface of endopterygoid; also occurs independently in clade 4, *S. caboclo*, *S. curvirostris*, and *S. mormyrus*
- Character 41, state 1→0; preopercle terminating anteriorly variably posterior of vertical through ventral portion of joint between quadrate and metapterygoid; also present independently in *S. cramptoni*, *S. hagedornae*, *S. montanus*, *S. mormyrus*, and *S. starksi*
- Character 42, state 0→1; laterosensory canal segment in vertical arm of preopercle in form of two deeply anteriorly concave segments; also present independently in clades 4, 6, and 20
- Character 64, state 1→2; central portion of myorhadoi with ventral and dorsal elaborations
- Character 75, state 0→1; presence of ossification located in superficial tissues of body anterodorsal to first postcleithrum; also occurs in clades, 4, 6, *S. britskii*, *S. curvirostris*, *S. gnomus*, *S. hagedornae*, *S. inpai*, *S. montanus*, *S. severii*, and *S. starksi*

Sternarchorhynchus jaimei

- Character 27, state 0→1 (ACCTRAN); pterygocranial ligament involving both endopterygoid and quadrate; also occurs in clade 9, with reversal in *S. curvirostris* and clade 20
- Character 54, state 1→0; basihyal without lateral processes; also present independently in *S. britskii* and clades 4 and 24 with reversal in *S. mendesi*

Clade 23: *Sternarchorhynchus higuchii*, *S. mendesi*, *S. mesensis*, and *S. roseni*

- Character 27, state 1→0 (DELTRAN); pterygocranial ligament attachment limited to dorsal surface of endopterygoid; also occurs independently in clade 4, *S. caboclo*, *S. chaoi*, *S. curvirostris*, and *S. mormyrus*
- Character 77, state 1→2; three postcleithra present; also occurs independently in *S. inpai* and *S. curvirostris*

Sternarchorhynchus mesensis

- Character 79, state 0→2; intercalarium medially tapering and triangular overall; also present in *S. starksi*
- Character 80, state 0→1; tripus not distinctly narrowing distally and relatively wide for distal half of bone

Clade 24: *Sternarchorhynchus higuchii*, *S. mendesi*, and *S. roseni*

- Character 33, state 1→0 (ACCTRAN); presence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; reversed in *S. roseni*
- Character 54, state 1→0; basihyal without lateral processes; reversed in *S. mendesi*; state 0 also present independently in *S. britskii* and *S. jaimei*

- Character 58, state 1→0; second basibranchial with midlength constriction
- Character 84, state 0→1; scales sparse and covered to different degrees by skin; also occurs in *S. hagedornae*

Two equally parsimonious trees were found in the analyses for the relationships amongst *S. higuchii*, *S. mendesi*, and *S. roseni*. These alternatives resulted in an unresolved trichotomy at this level. Details on the characters that supported each alternative are as follows:

Sternarchorhynchus roseni as sister group to clade formed by *S. higuchii* and *S. mendesi*

- Character 33, state 1→0 (ACCTRAN and DELTRAN); presence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic.

Sternarchorhynchus mendesi as sister group to clade formed by *S. higuchii* and *S. roseni*

- Character 54, state 1→0; basihyal without lateral processes; state 0 also present independently in *S. britskii* and *S. jaimei*

Autapomorphies for the three species in this unresolved tricotomy are:

Sternarchorhynchus higuchii

- Character 13, state 0→1; posteroventral process of dentary not reaching margin of posteroventral process of anguloarticular; also occurs independently in *S. caboclo* and *S. stewarti*
- Character 33, state 1→0 (DELTRAN); presence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; also present in *S. mendesi*
- Character 34, state 0→1; presence of overlap laterally of anteroventral corner of metapterygoid by bony process of quadrate; also occurs independently in *S. gnomus* and *S. higuchii*
- Character 54, state 1→0 (DELTRAN); basihyal without lateral processes; also present independently in *S. jaimei* and *S. roseni*
- Character 60, state 0→1; medial portion of second hypobranchial in adults without distinct medial process and with contralateral second hypobranchials separated by second basibranchial; also occurs in *S. caboclo*
- Character 77, state 0→1; two postcleithra present

Sternarchorhynchus mendesi

- Character 33, state 1→0 (DELTRAN); presence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; also present independently in *S. higuchii*
- Character 53, state 1→0; anterior margin of urohyal, straight or slightly irregular, but without distinct medial notch; also present independently in *S. retzeri*
- Character 54, state 0→1 (ACCTRAN); basihyal with lateral processes; also occurs in clade 5

Sternarchorhynchus roseni

- Character 33, state 0→1 (ACCTRAN); absence of lateral closure of notch along posteroventral margin of quadrate that receives symplectic; also present in *S. caboclo* and clade 19
- Character 54, state 1→0 (DELTRAN); basihyal without lateral processes; also present independently in *S. britskii*, *S. higuchii*, and *S. jaimei*
- Character 86, state 1→0; lateral surface of snout with pigmentation comparable to that of adjoining regions or with irregular marbling; also occurs in clade 16