

Tube-snouted gymnotiform and mormyriiform fishes: convergence of a specialized foraging mode in teleosts*

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Synopsis

African mormyriiform and South American gymnotiform fishes are unique among freshwater fishes in their abilities to generate and perceive an electrical field that aids in orientation, prey detection, and communication. Here we present evidence from comparative ecology and morphology that tube-snouted electric fishes of the genera *Sternarchorhynchus* (Apterontidae) and *Campylomormyrus* (Mormyridae) may be unique among fishes in their mode of foraging by grasp-suction. The grasp-suction mode of feeding is a specialization for extracting immature stages of aquatic insects that burrow into, or hide within, interstitial spaces and holes in matrices of compacted clay particles that form the channel bottom of many tropical lowland rivers. Ecomorphological implications of the remarkable evolutionary convergence for this specialized mode of foraging by tube-snouted electric fishes provide a challenge to Liem's (1984, 1990) theory of separate aquatic and terrestrial vertebrate feeding modes.

Introduction

Biomechanical studies of the buccal apparatus of vertebrates have led to discussions of two fundamentally different biomechanical models of feeding, the terrestrial and the aquatic (Liem 1984, 1990). Because the functional morphology of suction feeding in fishes depends, in part, upon drag forces and the high density and viscosity of water, these alternative models are considered medium-dependent. According to Liem, the functional morphology of teleost fishes stresses versatility in feed-

ing performance which often gives rise to generalized diets in the field setting. In contrast, the terrestrial feeding modes are less constrained by a less-dense and less-variable physical medium and are associated with less behavioral plasticity. As a consequence, terrestrial vertebrates tend to exhibit more specialized designs for feeding (Liem 1984).

The feeding apparatus of most teleosts approximates a closed tube or cone, and feeding is accomplished by sucking prey into the mouth (Alexander 1970, Barel 1983, Motta 1984). Even though suction of whole prey appears to be the predominant feed-

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ing mode among bony fishes, teleost orobranchial morphology does not prohibit other behavioral patterns: biting and engulfing, or ram feeding (Nyberg 1971, Barel 1983, Winemiller & Taylor 1987). In contrast, the predominant mode of feeding in terrestrial vertebrates involves biting and mastication. Liem (1990) believed that these differences between terrestrial and aquatic feeding modes have not been sufficiently appreciated, and as a consequence, aquatic vertebrate ecologists have erroneously constructed their ecological paradigm based on the terrestrial vertebrate model of feeding specializations and resource partitioning. Assuming a fundamental divergence between aquatic and terrestrial feeding modes, Liem (1990) proposed four hypotheses that explain the feeding structures of teleost fishes, their implications for trophic ecology, and their evolutionary transitions. Briefly, these hypotheses are: (1) opportunism in feeding and diet shifts are prevalent among fishes, (2) evolutionary convergences among fishes are rare, (3) interspecific competition is relaxed among fishes and evidence for character displacement is lacking, and (4) the factors driving diversification in aquatic vertebrates are different than those influencing terrestrial vertebrates. Believing that little evidence had been offered to contradict these hypotheses, Liem proposed that the feeding ecology of fishes is inconsistent with the terrestrial ecological paradigm of competition, specialization, and niche partitioning (but see also, Werner & Hall 1976, 1977, Lauder 1983, Winemiller 1989, 1991a, 1991b, Winemiller et al. 1994, Yamaoka 1991).

In terms of their mode of locomotion, electrogeneration, electroreception, and functional morphology of feeding, fishes of the neotropical order Gymnotiformes and the African order Mormyriiformes represent a special case of convergent evolution among aquatic vertebrates (Roberts 1972, Lowe-McConnell 1975). In this paper, we present a brief overview of the trophic structures and ecologies of these fishes and present evidence that refutes at least two of Liem's hypotheses concerning the distinctive features of feeding ecology in fishes relative to terrestrial vertebrates. Species within the genera of tube-snouted gymnotiform and mormyriiform fishes (e.g., *Sternarchorhynchus*, Apterodontidae;

Campylomormyrus (= *Gnathonemus*), Mormyriidae) exhibit an adaptive convergence in the general form and function of the trophic apparatus. These evolutionary convergences seem to have been driven by selection for specialized trophic niches associated with electroreception and burrowing aquatic invertebrate prey in clay sediments of river channels. Moreover, the trophic apparatuses of *Sternarchorhynchus* and *Campylomormyrus* share a peculiar configuration that is a departure from the traditional suction model of the biomechanics of prey capture and ingestion. We briefly reexamine Liem's (1990) hypotheses for the relationship between feeding mode and ecological performance in teleosts. Contrary to Liem's contention, the tubular snouts and feeding modes of *Sternarchorhynchus* and *Campylomormyrus* illustrate a highly specialized mechanism for prey capture within a distinctive microhabitat.

Relationships of the Mormyriiformes and Gymnotiformes

The order Mormyriiformes contains two families and some 200 species and is most closely allied to the primitive bony tongues, Osteoglossiformes (Nelson 1984). The clade formed by the Mormyriiformes/Osteoglossiformes (infraclass Osteoglossomorpha) is characterized by the presence of primitive characters (plesiomorphies) and the absence of many uniquely derived traits (synapomorphies) that characterize more derived teleosts like the Percopomorpha. For example, the Osteoglossomorpha lack epipleural muscles and have an intestine that curls around the left side of the esophagus rather than the right side. Mormyriiform fishes are entirely restricted to freshwaters of the African continent (Roberts 1975). The teleost order Gymnotiformes comprises a phylogenetic clade with the Cypriniformes, Characiformes, and Siluriformes (superorder Ostariophysii; Fink & Fink 1981). The order Gymnotiformes contains 6 families and at least 100 species nearly all of which are restricted to freshwaters of South America (Mago-Leccia 1976). Five gymnotiform species occur in Panama (*Gymnotus carapo*, *Sternopygus dariensis*, *Hypopomus*

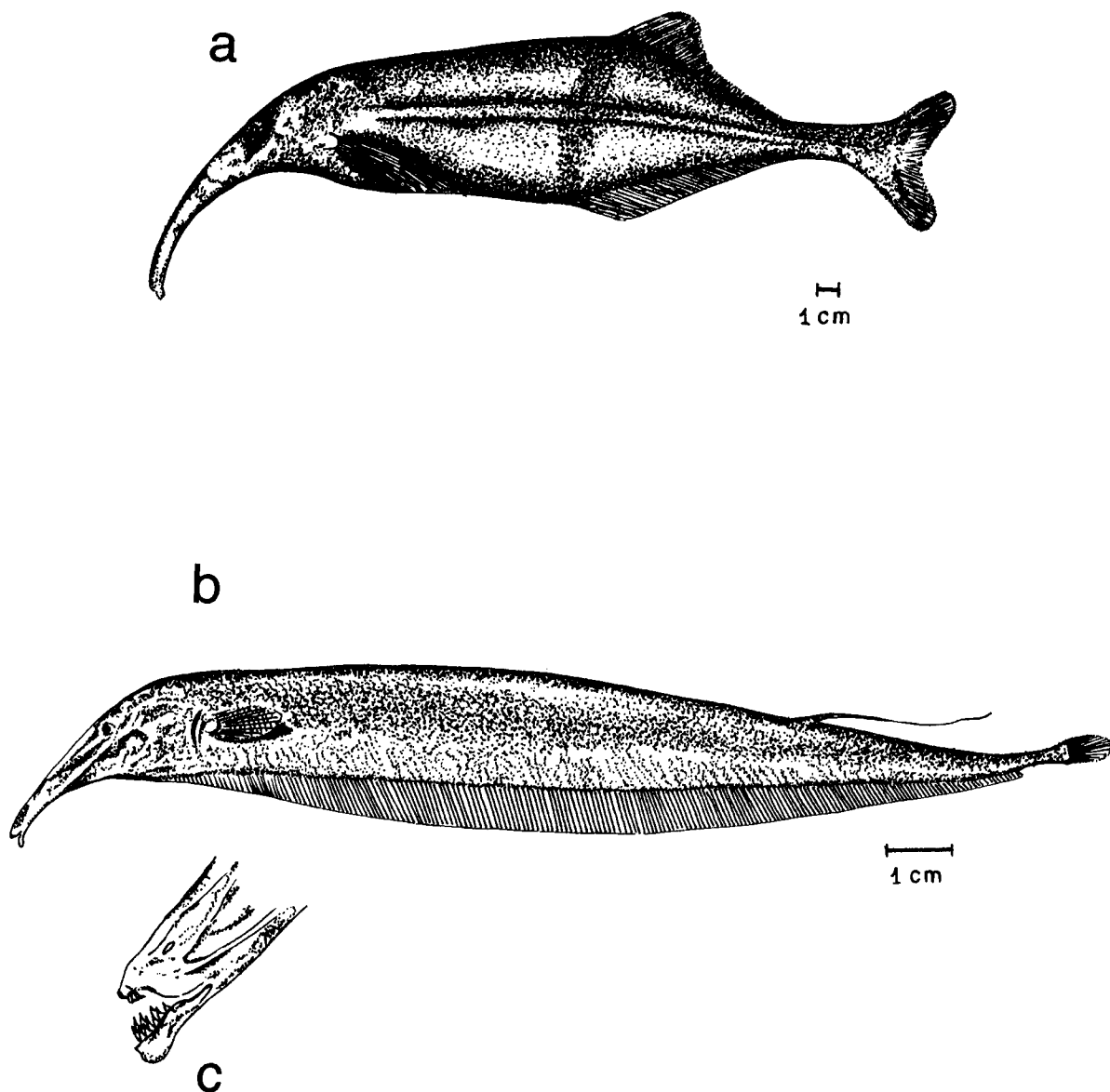


Fig. 1. Tube-snouted electric fishes: a – the African mormyrid *Campylomormyrus rhynchophorus* (drawing based on photograph in Roberts & Stewart 1976); b – South American gymnotiform *Sternarchorhynchus curvirostris*; c – detailed illustration of the anterior snout and teeth of *S. curvirostris* (b and c based on illustrations in Mago-Leccia 1976).

occidentalis, *Eigenmannia* cf. *virescens*, *Apteronotus rostratus*) and two species, *Gymnotus cylindricus* and *Gymnotus* sp., are encountered as far north as Guatemala (Miller 1976).

Based on fossil evidence and the distribution of character states among contemporary fishes, divergence between two evolutionary lineages, the present day Osteoglossomorpha and Ostariophysi,

must have occurred as far back as the middle Cretaceous (Fink & Fink 1981). Even if no date is assigned to this evolutionary divergence of lineages, we can be reasonably confident that mormyrid and gymnotiform fishes evolved electrogeneration independently (Roberts 1972, Kirschbaum 1984). Minimally, we can assume that mormyrids have enjoyed nearly exclusive occupation of a nocturnal

foraging/electrogeneration-reception niche in Africa for at least several million years (electrogeneration occurs in the monotypic malapterurid catfish, *Malapterurus electricus*), as have the gymnotiform fishes in South America.

External bucco-cephalic morphology of gymnotiforms and mormyriiforms in relation to foraging microhabitat

In addition to the capabilities for electrogenesis and electroreception, the external bucco-cephalic morphology of gymnotiforms and mormyriiforms reveals remarkable similarities that indicate a high degree of convergent evolution between taxa of the two orders. Among fish orders entirely restricted to freshwaters, the Mormyriiformes and Gymnoti-

formes appear to be the only ones that contain species with tube-like snouts (e.g., *Sternarchorhynchus*, *Campylomormyrus*, Fig. 1).

Several authors have speculated on the functional morphology of prey capture by tubular-snouted electric fishes. Roberts (1972) made the following remarks: 'highly peculiar and remarkably similar trophic structures [in both orders], for example diverse types of elongate tubular mouths with beak jaws and feeble dentition, are structures that permit efficient exploitation of a rich bottom fauna of small worms and worm-like insect larvae (e.g., enchytraids and chironomid larvae) which other fishes can only use marginally or not at all'. Tables 1 and 2 summarize our compilation of information on habitats and diets for genera within the orders Mormyriiformes and Gymnotiformes. The two groups of fishes clearly consume very similar prey spectra,

Table 1. A comparison of the principal mesohabitats utilized by adult size classes of several South American gymnotiform and African mormyriiform genera. Table is based on information presented in Corbet (1961), Matthes (1964), Petr (1968), Bell-Cross & Minshall (1988), and Winemiller (unpublished data for Zambezi River populations) for mormyrids; and in Marrero (1987, 1990), Marrero et al. (1987), and Winemiller (1989 unpublished data for Apure River drainage populations) for gymnotiforms. Channel bottom = the bottom substrate of larger flowing rivers; Edge/structure = undercut banks and woody debris along river and stream margins; Backwater-open = open water areas of small creeks, lagoons, and marshes; Vegetation = densely vegetated habitats of river margins, small creeks, lagoons, and marshes.

genera	Habitat			
	Channel Bottom	Edge/Structure	Backwater-Open	Vegetation
Gymnotiformes:				
<i>Adontosternarchus</i>	+			+
<i>Apteronotus</i>	+	+		+
<i>Eigenmannia</i>	+	+	+	+
<i>Electrophorus</i>			+	+
<i>Gymnorhamphichthys</i>	+	+		
<i>Gymnotus</i>			+	+
<i>Hypopomus</i>				+
<i>Rhabdolichops</i>	+	+	+	
<i>Rhamphichthys</i>		+		+
<i>Sternarchorhamphus</i>	+	+		
<i>Sternarchorhynchus</i>	+			
<i>Sternopygus</i>		+		+
Mormyriiformes:				
<i>Campylomormyrus</i>	+	+		
<i>Hippopotamyrus</i>	+	+	+	
<i>Marcusenius</i>		+		+
<i>Mormyrops</i>		+	+	
<i>Mormyrus</i>		+		+
<i>Petrocephalus</i>			+	
<i>Pollimyrus</i>		+		+

and following Roberts' (1972) suggestion, genera and species with convergent diets often capture prey from similar microhabitats.

A detailed study of the microhabitat of immature stages of aquatic insects in the channel of the Río Apure in Venezuela revealed that Ephemeroptera of the family Polymitaecidae (*Campsurus* spp.), Trichoptera of the family Hidropsichidae (*Smicridea* sp., *Leptonema columbianum*), and Diptera of the family Chironomidae either inhabit narrow tunnels of their own construction, or they occupy tiny spaces already formed on the river bottom (Marrero 1990). Within the main river channel, the most abundant and conspicuous of the natural refugia for aquatic insects is bottom substrate of shifting layers of compacted clay nodules (Fig. 2). In addition to the interstitial spaces located between individual nodules, each compacted nodule generally contains numerous tiny holes and spaces that serve as refugia for numerous aquatic insects, especially burrowing

Ephemeroptera and Chironomidae (Marrero 1987, 1990, Marrero et al. 1987). The long tubular snout of species belonging to the gymnotiform genus *Sternarchorhynchus* (Apterontidae) is a specialized adaptation for probing and removing aquatic insects from small holes and tunnels in these clay substrates (Marrero 1987, Marrero et al. 1987).

Information from foraging studies of African mormyriiforms (Corbet 1961, Matthes 1964, Petr 1968, Roberts & Stewart 1976, Blake 1977) indicates that Ephemeroptera (e.g., *Povilla* sp.), Trichoptera, and Chironomidae are their principal prey (Table 1). Although the authors of these studies did not make specific mention of the phenomenon, it is almost certain that a large number of African aquatic insects construct the same type of habitations as their neotropical homologues. In all likelihood, mormyriiform fishes with long tubular snouts and small jaws armed with feeble dentition (e.g., *Campylomormyrus tamandua*) are extracting prey from

Table 2. A comparison of the principal food categories utilized by adult size classes of several South American gymnotiform and African mormyriiform genera. Table is based on information sources listed in Table 1. Chiron. = chironomid larvae; Ephem. = Ephemeroptera nymphs; Trichop. = Trichoptera larvae; Zoopla. = microcrustacea (Cladocera, Copepoda, Ostracoda); Prawns = prawns (Decapoda); Fishes = fishes.

genera	Food category					
	Chiron.	Ephem.	Trichop.	Zoopla.	Prawns	Fishes
Gymnotiformes:						
<i>Adontosternarchus</i>	+			+		
<i>Apteronotus</i>	+	+	+			
<i>Eigenmannia</i>	+			+		
<i>Electrophorus</i>						+
<i>Gymnorhamphichthys</i>	+					
<i>Gymnotus</i>					+	+
<i>Hypopomus</i>	+			+		
<i>Rhabdolichops</i>				+		
<i>Rhamphichthys</i>	+	+				
<i>Sternarchorhamphus</i>	+					
<i>Sternarchorhynchus</i>		+				
<i>Sternopygus</i>		+	+		+	
Mormyriiformes:						
<i>Campylomormyrus</i>	+	+	+			
<i>Hippopotamyrus</i>	+	+	+		+	
<i>Marcusenius</i>	+	+	+			
<i>Mormyrops</i>					+	+
<i>Mormyrus</i>	+	+	+			
<i>Petrocephalus</i>				+		
<i>Pollimyrus</i>	+			+		

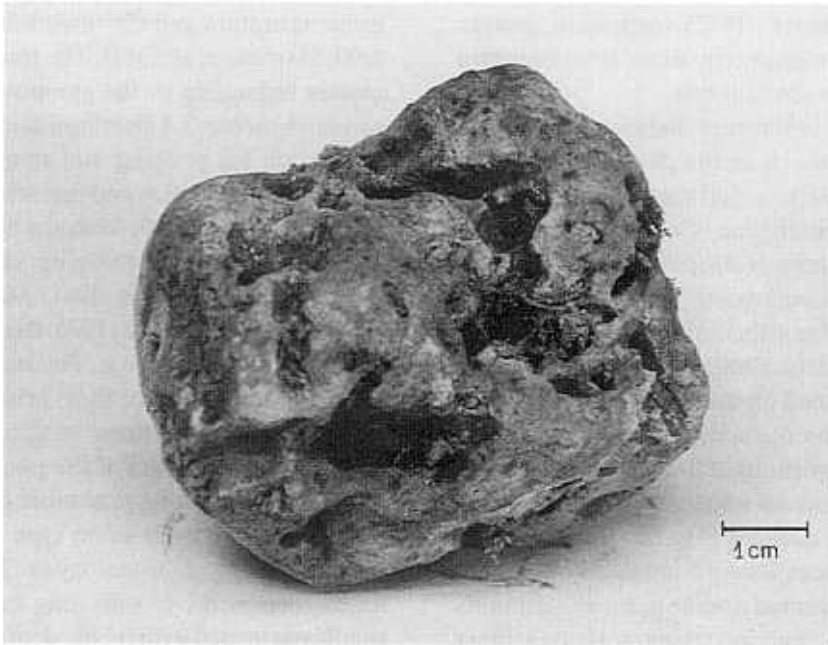


Fig. 2. Clay nodule from the bottom of the main channel of the Río Apure near Arichuna, Apure, Venezuela on 20 February 1983. Water depth was approximately 4 m. The numerous holes and spaces in the clay particle harbor immature stages of aquatic insects.

small holes and burrows in the same way as *Sternarchorhynchus*. Petr (1968) believed that *C. tamandua* were able to suck burrowing aquatic insects from crevices through its long narrow snout (and see additional discussion of Petr's findings below).

Habitat selection by mormyriforms and gymnotiforms

In the Orinoco River drainage, some gymnotiform fishes (e.g., *Sternopygus macrurus*) utilize a broad range of aquatic habitats, ranging from river channels to small creeks and swamps. Other Orinoco gymnotiforms exhibit relatively specialized habitat affinities. For example, *Sternarchorhynchus* spp. normally are found only in the main channel of rivers (Marrero & Taphorn 1991) where water currents continually reform the loose matrix of clay nodules that harbors their aquatic insect prey. In contrast, *Hypopomus* spp. inhabit densely vegetated swamps, ponds, and creeks, but are never encountered in large rivers with strong currents or in open water areas of smaller slow-flowing rivers.

Blake (1977) reported habitat affinities among mormyriform fishes in Lake Kainji, a reservoir constructed on the Niger River in Nigeria. Like *Sternarchorhynchus*, *Campylomormyrus tamandua* appears to be strongly associated with the main channel of flowing rivers. Blake (1977) reported that *C. tamandua* was abundant in the Niger River prior to impoundment, and that it was rare in the reservoir due to an apparent failure to cope with lacustrine conditions. Petr (1968) reported a virtual absence of *C. tamandua* in a reservoir on the Black Volta River in Ghana after the first year of its formation. He reported that *C. tamandua* from the river fed on a mixture of rheophilic insect larvae (e.g., ephemeropterans Leptophlebiidae, Heptageniidae, *Caenis* spp.) and wood burrowing Ephemeroptera and Coleoptera (*Potamodytes*, *Potamocares*) from slower regions of the river. Petr (1968) assumed that '*C. tamandua* can suck these (insects) out from crevices using its long downward-curved snout'.

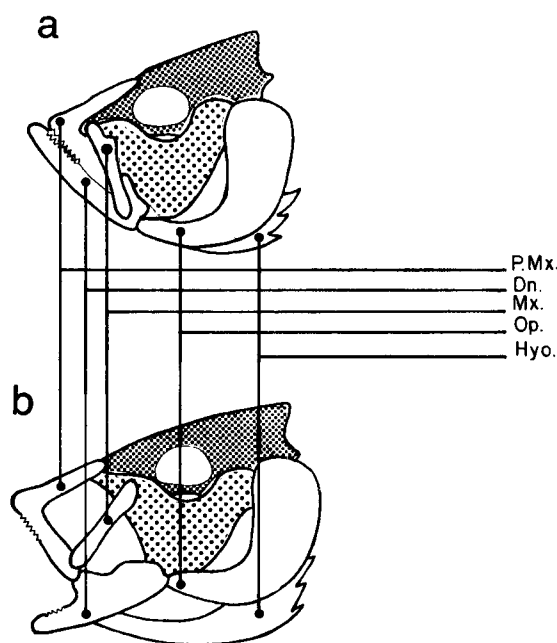


Fig. 3. Schematic diagram of a generalized teleost skull showing the bone movements associated with jaw opening and protrusion: a – positions of skeletal elements at jaw closure; b – positions of elements with jaws open and protruded (based on Hildebrand 1988). P.Mx. = premaxillary, Dn. = dentary, Mx. = maxillary, Op. = opercular, Hyo. = hyoid.

Diet variability in mormyriforms and gymnotiforms

The causes and consequences of diet variability have received much attention in studies of trophic ecology. Liem (1990) proposed that the apparent versatility in the feeding apparatus of teleosts (the expanding code model) leads to the prediction that teleosts should exhibit a high level of diet variability. Comparative estimates of diet breadth or identification of diet shifts are each dependent upon several factors, perhaps most importantly the level of prey identification. Geene & Jaksic (1983) proposed that classification of prey beyond the level of order overestimates diet variability in comparative studies involving vertebrate predators.

Marrero (1990) identified diet items from stomach contents to the highest degree of resolution that was feasible (orders and families) and observed moderate diet breadths in Río Apure apteronotid

fishes. In this case, had the diet items been classified only as 'aquatic insects', diet variability would have been nearly zero. In contrast, Liem (1990) employed a very coarse scale of classification for diet items (e.g., algae, zooplankton, insect larvae, fish) and discussed the high degree of diet variability in African haplochromine cichlids from lacustrine habitats. Based on a scale of food classification more similar to that of Marrero than Liem, Winemiller (1991b) described moderate diet breadths, yet a high degree of resource partitioning among African haplochromines (*Serranochromis* spp.) in the Zambezi River. Comparatively speaking, it appears that gymnotiform fishes may exhibit more specialized feeding habits than many of the haplochromine cichlids from either lakes or rivers.

Osteo-muscular structure of the head in mormyriform and gymnotiform fishes and the aquatic trophic model

Briefly stated, the feeding apparatus of teleosts approximates a closed cone that expands from muscular action, generating negative pressure inside of the closed jaws, followed by suction of water (with the prey item) into the buccal cavity when jaws are opened (Alexander 1967, 1970, Osse & Muller 1980, Motta 1984, Hildebrand 1988, Liem 1990). The moveable components of the euteleost skull that facilitate inertial suction following jaw opening include: the bones of the hyomandibular apparatus, maxillary, premaxillary, and dentary bones (Fig. 3). These bones are usually short with approximately rectangular shapes, and are often displaced considerably from their resting positions during the act of feeding. In terrestrial vertebrates, food is first grasped in the jaws and manipulated in the anterior part of the mouth. Food is subsequently moved posteriorly by the mechanical action of the tongue and hyoid apparatus, synchronized by successive abduction and adduction of the mandible in relation to the cranium until the item is swallowed (Liem 1990).

Species of the gymnotiform genus *Sternarchorhynchus* and the mormyriform genus *Campylomormyrus* represent a variation of the traditional tele-

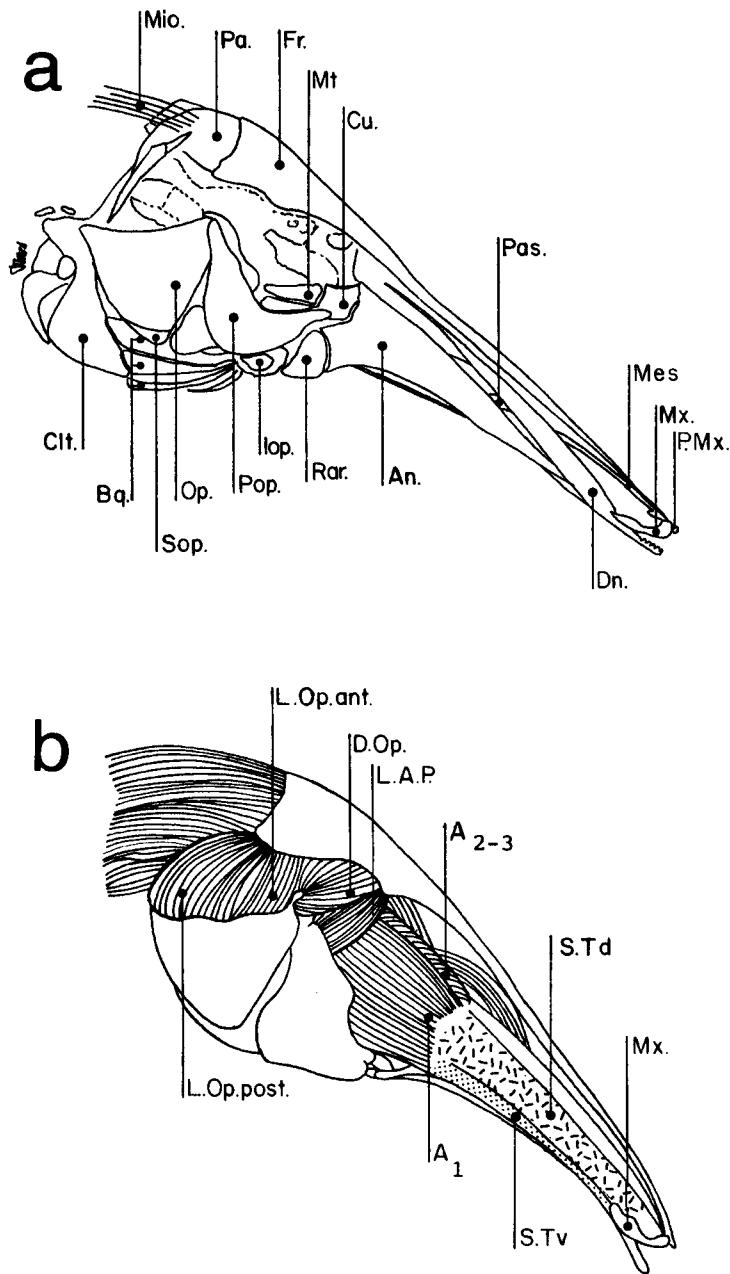


Fig. 4. Osteology (a, based on Mago-Leccia 1976) and myology (b, based on Aguilera 1986) of the head of *Sternarchorhynchus curvirostris*. Mio. = myorhabdals, Pa. = parietal, Fr. = frontal, Mt. = metapterigoid, Cu. = quadrate, Pas. = parasphenoids, Mes. = mesopterygoid, Mx. = maxillary, PMx. = premaxillary, Dn. = dentary, An. = angular, Rar. = retroarticular, Iop. = interopercular, Pop. = preopercular, Op. = opercular, Sop. = subopercular, Bq. = radial branchiostegals, Clt. = cleithrum, L.Op.ant. = levator operculi anterior, D.Op. = dilator operculi, L.A.P. = levator arcus palatini, A₁ = section 1 of abductor mandibulae, A₂₋₃ = sections 2-3 of abductor mandibulae, L.Op.post. = levator operculi posterior, S.Td. = section of dorsal tendons, S.Tv. = section of ventral tendons.

ost model of aquatic suction feeding. These electric fishes possess morphologies that result in a mode of suction feeding that could be termed 'grasp-suction', or 'suction assisted by mechanical grasping'. In the traditional aquatic suction model, the mouth forms the aperture at the tip of a cone, or cylinder, and regulates the passage of water and food into the mouth following expansion of the orobranchial chamber. In the tube-snouted electric fishes, the small jaws form tiny pincers used for grasping aquatic insects hidden inside of small openings. The compact grasping jaws of these fishes are formed by a bone complex consisting of the dentaries, vomer, and mesethmoids (Fig. 4a). In stark contrast to the majority of other teleosts, all bones in the anterior head region are elongate and thin, and together form a kind of narrow wedge. The jaws of these tube-snouted electric fishes exhibit none of the protrusibility that is normally encountered in suction feeding fishes. The terminal jaw bones of these tube-snouted electric fishes seem to be effectively fixed in such a manner that the jaws are only able to swing open and shut for grasping small prey items.

In *Sternarchorhynchus*, the arrangement of the muscles and tendons controlling the mobility of these bony pincers appears to be nearly unique among gymnotiforms (attachment of the A1 division of the adductor mandibulae to the maxilla is also found in some acanthomorphs and several siluriforms; J.G. Lundberg personal communication). Aguilera (1986) described the insertion of the adductor mandibulae on the internal surface of the maxillary near the tip of the snout (Fig. 4b). In addition to lengthening the snout, this manner of long-distance connection results in the delivery of strong pressure to a small area between the pincer-like jaws. Based on the morphological observations we just described, we conclude that ingestion by *Sternarchorhynchus* proceeds through the following sequence: the prey item is first grasped within the pincer-like jaws, the item is then pulled from the substrate via backward locomotion, and the item is then sucked through the tube snout into the mid-buccal chamber via the normal orobranchial expansion mechanism of suction. This specialized functional morphology of the feeding apparatus allows *Sternarchorhynchus* to extract Ephemeroptera

nymphs and chironomid larvae from constructed burrows and natural spaces within the clay matrix on the bottom of river channels. *Sternarchorhynchus* is sometimes captured near the bottom of floodplain lakes, where they probably feed on aquatic insects that are hidden in spaces among leaf litter and other forms of coarse organic detritus. The taxonomic composition of mormyriiform diets suggests that an analogous behavioral sequence occurs during feeding by African *Campylomormyrus* as well.

The grasp-suction feeding mode involves a degree of additional complexity to the basic model of suction feeding in teleosts (sensu Osse & Muller 1980), and to some extent presents a challenge for the distinction between a versatile aquatic feeding mode versus a terrestrial feeding mode that facilitates specialized feeding behavior (Liem 1984, 1990). In some respects, the grasping of prey in pincer-like jaws and extraction from substrates prior to its ingestion by tube-snouted electric fishes resembles the foraging mode exhibited by terrestrial insectivores (e.g., birds, squamate reptiles) more than the foraging mode used by most other insectivorous teleosts.

Lauder (1992) recently discussed the integration of biophysics with historical biology as a means for understanding the evolution of complex structures. One could hypothesize that electroreception in mormyriiforms and gymnotiforms first evolved as an adaptation for orienting, foraging, and communicating in the nearly constant darkness of benthic areas of large lowland rivers. Alternatively, electroreception could have evolved as an adaptation for nocturnal foraging in shallow freshwater habitats, and a subset of electric fishes subsequently colonized large river bottoms to exploit abundant invertebrate prey. Phylogenetic analyses may ultimately shed light on these alternative evolutionary scenarios. Yet clearly, the rostral morphology and grasp-suction feeding mode of the gymnotiform genus *Sternarchorhynchus* are adaptations for extracting aquatic insects from the clay matrix of river bottoms. Unlike a number of earlier discussions of neotropical fishes that have highlighted diet flexibility (e.g., Knöppel 1970, Saul 1975), we believe that rostral morphological features associated with feeding

by gymnotiform fishes limits the spectrum of exploitable prey. Potentially, the tube-snouted electric fishes could consume prey located either on top of or burrowed within porous substrates, yet they would have nearly exclusive access to those prey nested in burrows and holes. The limited published data on diets of gymnotiform and mormyrid fishes supports the idea that tube-snouted species eat mostly burrowing aquatic insects. Other ostariophysan fishes, including short-snouted electric fishes, are less capable of extracting burrowing insects, and they are presumably more efficient foragers above and on the surface of the substrate than tube-snouted species.

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