



South American electric knifefishes of the genus *Archolaemus* (Ostariophysi, Gymnotiformes): undetected diversity in a clade of rheophiles

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Neotropical electric knifefishes of the family Sternopygidae previously considered to represent a single relatively geographically widespread and morphologically variable species, *Archolaemus blax*, were analysed and found to represent a complex of five species, four of which are new to science. A fifth undescribed species from the Rio São Francisco basin outside the previous known range of the genus was identified. Recognized species of *Archolaemus* are: *A. blax*, previously thought to occur in the Rio Araguari, Rio Branco, Rio Tapajós, Rio Tocantins, and Rio Xingu, but which instead proved to be endemic to the Rio Tocantins; *Archolaemus ferreirai* sp. nov. from the Rio Mucajaí and Rio Uraricoera in the north-eastern portions of the Amazon basin; *Archolaemus janeae* sp. nov. of the Rio Xingu and the upper Rio Tapajós, both southern tributaries of the mainstream Amazon; *Archolaemus luciae* sp. nov. of the Rio Trombetas, Rio Jari, and Rio Tapajós basins of the eastern Amazon, and the independent Rio Araguari draining into the Atlantic Ocean north of the mouth of the Amazon; *Archolaemus orientalis* sp. nov. of the São Francisco basin in eastern Brazil; and *Archolaemus santosi* sp. nov. of the Rio Jamari in the south-western portion of the Amazon basin. The phylogenetic placements of *Archolaemus* and the recently described genus *Japigny* relative to the other members of the Eigenmanninae are discussed. A series of synapomorphies for *Archolaemus* are proposed and a hypothesis of the relationships within that genus is advanced. Rheophily of all members of *Archolaemus* is discussed, with the genus found to be the most speciose clade within the Gymnotiformes living primarily in high-energy settings. The reported anterior projection of the dentary teeth in *A. blax* was found to be a consequence of postmortem displacement.

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INTRODUCTION

Archolaemus was proposed by Korrington (1970) as a new genus of the Sternopygidae diagnosed from other members of that family, with the exception of *Sternopygus*, by the possession of a free orbital rim. In his analysis, Korrington cited various differences between

Archolaemus and *Sternopygus*, with the externally most obvious being the larger eye of *Archolaemus* relative to that in any of the species of *Sternopygus* recognized at that time. Subsequently, Meunier, Jégu & Keith (2011) described an additional new genus in the Sternopygidae, *Japigny*, which also differed from *Archolaemus* in lacking a free orbit rim.

In the original description of *Archolaemus*, Korrington (1970) assigned a single species to the genus, *Archolaemus blax*, which was based on three specimens from a

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location in the Rio Tocantins. Schwassmann & Carvalho (1985) subsequently redescribed *A. blax* from multiple population samples they equated with that species. These series of specimens significantly expanded the range of *A. blax*, both within the Rio Tocantins and beyond that drainage to four additional river systems. Two of these, the Rio Xingu and Rio Tapajós, arise from the Brazilian Shield, as does the Rio Tocantins. More notably, Schwassmann & Carvalho documented the presence of *Archolaemus* north of the mainstream Amazon in two rivers draining from the Guyana Shield: the west-flowing Rio Branco in the north-eastern portion of the Amazon basin and the east-flowing Rio Araguari that drains directly into the Atlantic Ocean. In their study, they documented that the electrogenic *A. blax* only generates monophasic wave types, a condition subsequently found to be general across the Sternopygidae, and that it produces electric organ discharges at 390–523 Hz (Kirschbaum, 1995: 175; Crampton & Albert, 2006: 673, fig. 23.9). Bichuette & Trajano (2003, 2006) more recently documented the occurrence of *A. blax* within limestone caverns of the karstic São Domingos region of the Rio Tocantins basin.

Following Schwassmann & Carvalho (1985), a monotypic *Archolaemus* was recognized in the summary treatment of the Gymnotiformes (Mago-Leccia, 1994: 18), in species compendia (Albert, 2003; Campos-da-Paz, 2007), in phylogenetic reconstructions (Albert, 2001; Albert & Crampton, 2005), and in historical biogeographical analyses (Lima & Ribeiro, 2011; Winemiller & Willis, 2011). These actions notwithstanding, it is noteworthy that Schwassmann & Carvalho (1985: fig. 2) reported that *A. blax* demonstrates pronounced intraspecific variation in the shape of the snout and overall profile of the head, and that observations at locations in the Rio Tocantins and Rio Xingu basins revealed that it is rheophilic – an inhabitant of rapid waters. In and of itself the pronounced intraspecific morphological variation is striking. Moreover, such a geographic range across major portions of the Brazilian and Guyana shields is unexpected in light of the reported rheophily of the genus. Rapids in fast-flowing rivers are patchily distributed on both shields, and many species of fishes associated with these widely spaced, high-energy locations demonstrate notable degrees of apparently small-scale endemism. This general pattern of endemicity among rheophilic fishes and the reported range in head morphology in *A. blax* raises questions about the reported broad geographic range of the species: specifically, is it actually a single morphologically variable species with a disjunct distribution across multiple separated drainages, or does the assumed monotypic *Archolaemus* instead subsume multiple species?

In this study we re-examined the samples reported on by Schwassmann & Carvalho (1985) along with a large percentage of the other known material of *Archolaemus* deposited in research collections. The aims of the analysis are:

1. to evaluate whether the standing hypothesis of the monotypy of the genus is correct;
2. if it is not, to delimit the recognizable species in the genus and provide descriptions of all of them and redefine the genus accordingly;
3. to identify characters pertinent to the hypotheses of the phylogenetic placement and monophyly of *Archolaemus* and relationships within the genus;
4. to determine whether the phylogeny and distribution of the species within the genus correlated with proposed potential vicariant events in the region of occurrence; and
5. to investigate rheophily across the genus.

MATERIAL AND METHODS

MEASUREMENTS

Gymnotiforms often suffer damage to their caudal elements, most likely as a result of predation (Lundberg *et al.*, 1996: 666), followed by partial regeneration with clearly ‘truncated, or abruptly narrowed and/or abruptly depigmented tails’ (Mago-Leccia, Lundberg & Baskin, 1985: 1). These damaged individuals are typically readily recognizable externally, and were excluded from morphometrics involving total length and caudal length, and from counts of anal-fin rays when the damage impinged on the fin. Morphological measurements were point-to-point linear distances, taken using a digital caliper accurate to 0.1 mm. The measurements and abbreviations cited in the text are: anal-fin length, from the origin of the anal fin to the posterior end of the anal-fin base; branchial opening, from the dorsal to the ventral limits of the aperture; caudal filament length (CL), from the posterior margin of the last anal-fin ray to the tip of the caudal filament; depth of caudal filament, between the dorsal and ventral margins of the caudal filament immediately posterior to the base of the last anal-fin ray; greatest body depth, the vertical distance from the origin of the anal fin to the dorsal margin of the body; head length (HL), from the tip of the snout to the posterior margin of the branchial opening; head length at opercle, from the tip of the snout to the posterior margin of the bony opercle; head depth at eye, between the dorsal and ventral margins of the head at the vertical through the eye; head depth at nape, between the dorsal and ventral margins of the head at the vertical through the nape; head width, at the middle of the opercle; internarial

distance, from the posterior margin of the anterior naris to the anterior margin of the posterior naris; internarial width, between the inner margins of the contralateral anterior nares; interorbital distance, the linear distance between the medial margins of the orbits; posterior naris to eye, from the posterior margin of the posterior naris to the anterior margin of the eye; length of mouth, from the tip of the snout to the rictus; snout to origin of anal fin, the distance from the tip of the snout to the base of first anal-fin ray; snout to anus, the distance from the tip of the snout to the anterior margin of the anus; snout to posterior naris, the distance from the anterior margin of the eye to the posterior margin of the posterior naris; length to the end of the anal fin (LEA), the distance from the tip of the snout to the end of the base of the anal fin; orbital diameter, between the anterior and posterior margins of the orbit; pectoral-fin length, the distance from the dorsal border of the fin base to the tip of the longest ray; postorbital length, the distance from the posterior margin of the eye to the posterior margin of the opercle; preanal-fin length, the distance from the tip of the snout to the origin of the anal fin; snout length, the distance from the tip of the snout to the anterior margin of the eye; total length (TL), the distance from the tip of the snout to the posterior tip of the caudal filament; and width of mouth, taken across the posterior limit of the mouth.

MERISTICS

The counts of anal- and pectoral-fin rays were primarily obtained under a microscope using transmitted light, with these data supplemented by counts taken from radiographs. In the pectoral-fin ray counts, the unbranched anterior rays are represented by lower case Roman numerals and the branched rays are represented by Arabic numerals. The branched-ray count includes all rays posterior to the anterior unbranched rays, including the posteriormost ray in the series, which is sometimes unbranched. Anal-fin ray counts are presented in terms of anterior unbranched and total rays. Values in square brackets are those of the holotype. Osteological observations were made from cleared and stained specimens prepared following Taylor & Van Dyke (1985), with these cited as CS in the lists of material examined.

The authorship of four of the new species (*Archolaemus ferreirai* sp. nov., *Archolaemus janeae* sp. nov., *Archolaemus luciae* sp. nov., and *Archolaemus santosi* sp. nov.) is the same as the authorship of this paper. The fifth new species, *Archolaemus orientalis* sp. nov., was initially recognized as possibly undescribed by Donald J. Stewart (State University of New York,

College of Environmental Science and Forestry), who is the first author for that species.

INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations are: CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MNRJ, Museu Nacional, Rio de Janeiro; MPEG, Museu Paraense Emílio Goeldi, Belém; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; and USNM, National Museum of Natural History, Smithsonian Institution, Washington.

PHYLOGENETIC POSITION AND MONOPHYLY OF *JAPIGNY*

The recent description of *Japigny* by Meunier *et al.* (2011) did not delve into the question of the phylogenetic position of the genus within the Sternopygidae, a factor that complicates the evaluation of the monophyly and intrageneric relationships within *Archolaemus*. *Japigny* can be unambiguously diagnosed by the presence of a series of conditions, including: the pattern of alternating dark bands (versus the absence of such pigmentation in other members of the Sternopygidae, with the exception of *Sternopygus astrabes*); the possession of a distinct single row of teeth at the base of the upper oral valve (versus the absence of such dentition); the ventral curvature of the lateral process of the parapophysis of the second vertebrae (versus a horizontal lateral process of the parapophysis); the distinct separation of the lateral process of the second vertebrae from the parapophysis of the fourth vertebrae (versus the parapophyses of the second and fourth vertebrae in contact); the ventrally curved parapophysis of the fourth vertebrae (versus the horizontal lateral process of parapophysis of the fourth vertebrae); and the angulo-articular not included in the socket of the lower jaw articulating with the quadrate (versus the angulo-articular being included in the socket). A comprehensive analysis of phylogenetic relationships within the Sternopygidae lies outside this study, but the osteological observations associated with the question of the relationships within *Archolaemus* indicate that *Japigny* is a component of the Eigenmanninae in the Sternopygidae. Evidence supporting this hypothesis is the possession in *Japigny* of a scapula with an included scapular foramen, a fusion of the post-temporal and the supracleithrum into a single ossification, with a profile comparable with that of the two elements when separate (e.g. *Eigenmannia virescens*; Mago-Leccia, 1978: fig. 14), and a relatively low number of precaudal vertebrae (12–16).

Alternative hypotheses have been advanced as to the relationships among *Archolaemus*, *Distocyclus*, *Eigenmannia*, and *Rhabdolichops* (the Eigenmanninae prior to the description of *Japigny*). Under the hypotheses of Mago-Leccia (1978) and Alves-Gomes (1998), *Rhabdolichops* is the basalmost genus of the Eigenmanninae. Lundberg & Mago-Leccia (1986), Albert & Fink (1996), Albert & Campos-da-Paz (1998), Albert (2001), and Correia, Crampton & Albert (2006) conversely proposed that *Archolaemus* is the basalmost taxon in that subfamily. None of the previous phylogenetic analysis included the recently described *Japigny*. Three of the examined characters variable within the Sternopygidae were informative for this question, and indicate that *Japigny* is the sister group to a clade composed of *Archolaemus*, *Distocyclus*, *Eigenmannia*, and *Rhabdolichops*. These are: (1) the angulo-articular lacking a distinct socket to receive the condyle of the quadrate (versus with a distinct socket); (2) the parapophysis of the second vertebra straight and contacting the parapophysis of the fourth vertebra (versus the parapophysis curved ventrally and clearly separated from the parapophysis of the fourth vertebra); and (3) the parapophysis of the fourth vertebra straight (versus curved ventrally). Thus, *Japigny* may resolve as the basalmost member of Eigenmanninae, with this resolution providing a foundation for the evaluation of the monophyly of *Archolaemus* and for character coding within the genus.

MONOPHYLY AND INTRARELATIONSHIPS OF *ARCHOLAEMUS*

Archolaemus shares the following unique combination of characters that define the Sternopygidae: the presence of multiple rows of small needle-like teeth in the form of a villiform band on the dentary; the relatively large eyes; the enlargement of the antorbital and infraorbitals, with expanded bony arches over the laterosensory canal segments; the anterior naris located within the vertical limits of the gape; an anal-fin origin located along the isthmus; and the lack of a caudal fin and dorsal electroreceptive organ (Hulen, Crampton & Albert, 2005).

Four proposed synapomorphies that delimit *Archolaemus* as monophyletic were identified in our analysis.

1. *A free orbital rim*. As reported by several authors (e.g. Nijssen & Isbrücker, 1972: 174; Mago-Leccia, 1994: 18; Meunier *et al.*, 2011: 48), all species of the Gymnotiformes, except for *Archolaemus* and *Sternopygus*, have the orbit covered by skin, with this surface layer attached to tissues bordering the eye. Juveniles of *Archolaemus* share this apparently primitive condition of an orbit covered

by skin and attached to the surrounding tissues, in some species up to approximately 135 mm TL; however, larger individuals of the genus all have the orbital rim free of the surrounding orbital margin. In the context of present concepts of relationships within the Gymnotiformes, the free orbital rim of *Archolaemus* and *Sternopygus* is considered a homoplastic derived character in these two genera.

2. *Form of attachment of the teeth to the premaxilla*. As in all other sternopygids, the species of *Archolaemus* bear teeth on the premaxilla (approximately 22–35 teeth, depending on the species). The villiform teeth in sternopygids are typically immobile and attached to the ventral surface of the premaxilla. Conversely, in *Archolaemus* only the anterobasal margins of the teeth of the first tooth row are attached to the dentigerous surface of the premaxilla. As a consequence, these teeth are variably mobile relative to the premaxilla with the range of movement ranging between a few and 90 degrees: an apparent apomorphy for the members of the genus.
3. *Association of the posterior margin of the upper lip and the anterior margin of the premaxilla*. The anterior margin of the premaxilla lies close to and contacts, or almost contacts, the posterior margin of the upper lip from a ventral view in all species of the Sternopygidae other than for *Archolaemus*. In contrast, all species of *Archolaemus* have a pronounced gap equal to approximately one-half the width of the eye between the anterior margin of the premaxilla and the posterior margin of the upper lip (*A. blax* in Korrington, 1970: fig. 2A).
4. *Morphology of the upper lip*. The ventral surface of the upper lip is relatively flat and unelaborated from a ventral view in most members of the Sternopygidae, as well as across the Gymnotiformes. Conversely, the ventral surface of the upper lip is porous and sponge-like with raised papillae and fleshy anteroposteriorly elongate ridges of various extents in all of the species of *Archolaemus*. Elsewhere within the Sternopygidae this condition was encountered only in some populations of what is now considered to be *Eigenmannia trilineata*. Within the context of present hypotheses of relationships within the Sternopygidae (see the discussion under character 1), the occurrence of this form of upper lip in some specimens of *E. trilineata* and the species of *Archolaemus* would be homoplastic, but with the attribute a synapomorphy for the members of *Archolaemus*.

Two characters previously advanced as autapomorphies for what was then thought to be a monotypic

Archolaemus proved not to apply across the expanse of the more species-rich genus in this study. Albert (2001: 71) proposed that a lateral ethmoid contacting four bones was an autapomorphy for *A. blax*. As such it potentially served as a synapomorphy for the six species of the genus we recognize herein. Our survey shows that the complex lateral ethmoid does not universally contact four bones across the genus. A posterior naris positioned closer to the tip of the snout than to the eye was hypothesized by Albert (2001: 71) to be an autapomorphy for *A. blax*. Comparisons reveal, however, that the posterior naris is sometimes located approximately in the middle of the snout among several of the previously undescribed species of *Archolaemus* recognized herein.

Relationships within Archolaemus. The data indicate that *A. orientalis* is the sister group of a clade composed by *A. blax*, *A. ferreirai*, *A. janeae*, *A. luciae*, and *A. santosi*. The hypothesis of the monophyly of a clade formed by these five species is supported by three synapomorphies.

1. *Presence of a narrow stripe of dark pigmentation along the lateral line.* The presence of a narrow stripe of dark pigmentation extending along the lateral line is absent in *A. orientalis*, and is unique to these five species (see species accounts) among the examined members of the Sternopygidae, other than for also occurring in some species of *Eigenmannia* such as *E. trilineata*. What appears as a dark line of pigmentation proximate to the lateral line in *A. orientalis* is in fact the line of contact between the epaxial and hypaxial musculature.
2. *Presence of a band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin.* The presence of a broad band of dusky to distinctly dark pigmentation formed of individual vertical bars paralleling the pterygiophores, with the bars sometimes conjoining in darker specimens to form a variably continuous broad stripe, is limited to the members of this clade (see species accounts).
3. *Form of posterodorsal portion of the dentary.* Whereas the posterodorsal portion of the dentary is ossified in other sternopygids, this region is occupied by cartilage in these five species. Arratia (1992) made the case that given that the dentary is a dermal bone, the cartilage in the area typically occupied by the posterodorsal portion of the dentary, the 'cartilaginous coronoid process' in her terminology, is at least in some catfishes more likely to be a dorsal extension of Meckel's cartilage.

Within the clade of five species supported by characters 1–3, the evidence supports a hypothesis of two clades, each including two species (*A. blax*

plus *A. janeae* and *A. ferreirai* plus *A. luciae*). Those two clades along with *A. santosi* form an unresolved trichotomy.

Archolaemus blax and *A. janeae* are hypothesized to be sister species based on their common possession of two derived characters.

4. *Relative size of the posterior ceratohyal versus ventral hypohyal.* In these species, the posterior ceratohyal is approximately 1.5 times the length of the ventral hypohyal versus the two bones being approximately the same size in their congeners and other sternopygids.
5. *Number of tooth rows on the posterior portion of dentary.* A single tooth row on the posterior portion of the dentary occurs in both of these species, whereas other congeners have two rows of teeth in this area. The remaining sternopygids with teeth present on the posterior portion of the dentary have two or more rows of teeth in that region.

The remaining pair of sister species, *A. ferreirai* and *A. luciae*, share one hypothesized derived character.

6. *Relative size of the coronomeckelian bone versus Meckel's cartilage.* In these two species the elongate coronomeckelian bone extends along a considerable portion of the inner surface of the lower jaw, and corresponds to 50% or more of the length of Meckel's cartilage. In other congeners and outgroups the more compact coronomeckelian bone is approximately 20% or less of the length of Meckel's cartilage.

HISTORICAL BIOGEOGRAPHY

The relatively restricted geographic expanse occupied by the species of *Archolaemus* on the scale of South America, in conjunction with the long-term stability of both the Guyana and Brazilian shields that underlie most of the areas of occurrence of the members of the genus, result in relatively few major geological events being potentially informative as to the possible minimum ages of the genus and its included clades. One aspect of the phylogeny that is informative as to a minimal age of the genus as a whole is the basal dichotomy between *A. orientalis*, an endemic of the Rio São Francisco basin of eastern Brazil, versus the clade formed by its five congeners. All congeners of *A. orientalis* either inhabit rivers within the Amazon basin (Rio Branco, Rio Jari, Rio Tapajós, and Rio Xingu) or occur in drainage systems that empty in areas near the lower portions of that basin (Rio Araguari and Rio Tocantins).

Various sister-group relationships between fish taxa living in the São Francisco basin versus Rio Tocantins

and river systems further to the west have been documented in other groups of fishes (see Costa, 2003, 2010). It has been proposed that disruption of the connection between these drainages is a consequence of uplift events that date back approximately 60–40 Myr (Campos & Dardenne, 1997). Presuming that the basal division between *A. orientalis* versus the clade formed by *A. blax*, *A. ferreirai*, *A. janeae*, *A. luciae*, and *A. santosi* is a result of that geological event, then *Archolaemus* extends back at least 40 Myr. This estimated age is admittedly distinctly older than the oldest known fossil gymnotiform from the Yecua Formation in Bolivia, which dates back about 10 Myr (Gayet & Meunier, 1991), but in so far as the specimen in question represents the only identified fossil of the order, fossil information is at best minimally informative as to the age of the order and the included subunits. Evidence from molecular studies (Alves-Gomes, 1999; Lovejoy *et al.*, 2010) indicates that the order and included major taxa date to periods prior to the 40-Myr minimum possible date for *Archolaemus*. Thus, the uplift sequence that led to a separation of the São Francisco systems from drainages to the west temporally falls within the realm of possibility as a basal vicariance event within that genus.

Biogeographical analyses within the clade sister to *A. orientalis* are limited by the incomplete resolution of the scheme of relationships of the five species that resolve as a trichotomy. The units within the trichotomy at this level are *A. santosi* and two sister-species pairs: *A. blax* plus *A. janeae* on the one hand and *A. ferreirai* plus *A. luciae* on the other. These species pairs have largely disjunct distributions on either side of the mainstream Amazon. *Archolaemus blax* is limited to the Rio Tocantins and *A. janeae* is an inhabitant of the Rio Xingu and Rio Tapajós basins: all river systems to the south of the mainstream Amazon. Within the second species pair, *A. ferreirai* is limited to the upper Rio Branco and *A. luciae* is found primarily in the Rio Trombetas and Rio Araguari, all of which lie north of the Amazon, but with some populations of *A. luciae* in the Rio Tapajós south of the Amazon. This general pattern is congruent with the hypothesis of a division of *Archolaemus* populations at the level of the ancestor of *A. blax*, *A. ferreirai*, *A. janeae*, *A. luciae*, and *A. santosi*, by either marine transgressions into what is now the lower Amazon (Bloom & Lovejoy, 2011) or by the development of the present lower Amazon system following the breaching of the Purus Arch in the late Miocene (approximately 8 Mya; Lundberg *et al.*, 1998). Either of these events could have separated the ancestors of these two species pairs, with subsequent speciation events in each unit followed by a dispersal of *A. luciae* into the Rio Tapajós to the south of the main channel.

RHEOPHILY OF *ARCHOLAEMUS*

In their multifaceted ecological and taxonomic analysis of what they considered to be populations of *A. blax*, Schwassmann & Carvalho (1985: 236) reported that individuals of the species took refuge during the day 'inside crevices and between rocks at places of high current velocities' at localities in the Rio Xingu (Altamira and Belo Monte) and the Rio Tocantins (Rio Itacaiunas) basins. Our results demonstrate that Schwassmann & Carvalho's life-history observations were actually of two species, *A. janeae* (Rio Xingu localities) and *A. blax* (Rio Tocantins), both of which are clearly rheophiles (those authors did not make life observation in the Rio Araguari system, the home of the third species included in their concept of *A. blax*). *Archolaemus blax* also inhabits high water flow subterranean settings within karstic formations in the São Domingos region of the upper Rio Tocantins system (Bichuette & Trajano, 2003). Ferreira, dos Santos & Jégu (1988: 345) reported swift water habitat preferences for *A. ferreirai* (identified as *A. blax* in that study) in the rapids of the Rio Mucajá of the Rio Branco system. Ferreira (1995: 51), in turn, indicated that *A. luciae* (identified as *A. blax* in that study) is resident in swiftly moving waters within the Rio Trombetas. Observations of *A. luciae* in the Rio Tapajós system, *A. orientalis* at its type locality in the Rio São Francisco, and information on the type locality of *A. santosi* in the Rio Madeira basin (see Habitat in the accounts for these species) indicate that these three species similarly dwell in high-energy settings. Habitat preference information is unavailable for many of the lots examined of *Archolaemus* in this study, but it is noteworthy that many of these samples originated at, or proximate to, localities identified as falls (cachoeiras), attesting to the rapid water conditions in those localities. A preference for swiftly flowing waters is clearly an attribute that is general across the species of *Archolaemus*.

Recent advances in the knowledge on the alpha-taxonomy, habitat preferences, and phylogenetic relationships among Neotropical electric fishes demonstrate that life in shallow waters, including swift water conditions, evolved several times independently across the Gymnotiformes (de Santana & Vari, 2009, 2010a, b). Crampton (2011) noted that there have been multiple transitions within the Gymnotiformes from deep river habitats to life in high-energy systems, such as rapids, with no apparent reversals in habitat preferences. It is interesting that only two genera in the Gymnotiformes, *Archolaemus* and *Megadontognathus*, are composed entirely of rheophiles: species specializing in life in a high-energy aquatic environment. *Megadontognathus* includes only two species (Campos-da-Paz, 1999), which makes *Archolaemus*, with six

species, by far the most species-rich clade of exclusively rheophilic species in the Gymnotiformes.

Rheophily, the behaviour of inhabiting high-energy aquatic environments, such as occurs in all species of *Archolaemus*, is a phenomenon that is widespread among freshwater fishes, albeit limited to a small subset of the total number of species in the geographically extensive ichthyofaunas encompassing such swift water specialist species (Kullander, 1988; Lima & Zuanon, 2004; de Santana & Vari, 2010a). Adaptations for rheophily are myriad, but in some instances are apparently limited to behavioural strategies, or at least would seem to be so restricted based on externally obvious morphological adaptations. The observations by Schwassmann & Carvalho (1985: 237) document that behaviour undoubtedly contributes to the utilization of rapid flowing waters by *A. blax* in the Rio Itacaiunas and *A. janeae* in the Rio Xingu. Behavioural adaptations are supplemented in many rheophilic species by, sometimes manifold, morphological specializations for life in rapids and proximate to waterfalls. One of these specializations, the possession of a subconical downwardly oriented snout (Kullander, 1988), characterizes the species of *Archolaemus*, but many of the other specializations common in other rheophiles (e.g. dorsoventrally flattened head and body) are not feasible within the body plan of the Sternopygidae.

TAXONOMIC ACCOUNTS

ARCHOLAEMUS KORRINGA, 1970

Archolaemus Korrington, 1970: 267 (Type species *Archolaemus blax* Korrington, 1970; by original designation).

Diagnosis: *Archolaemus* is diagnosed by the synapomorphies described and discussed above, and distinguished from all remaining genera of the Sternopygidae by a pronounced gap between the anterior margin of the premaxilla and the posterior margin of the upper lip, with this separation equal to approximately one-half the width of the eye. It is further separated from *Distocyclus*, *Eigenmannia*, *Japigny*, and *Rhabdolichops* by the possession of a free orbital rim in adults (a feature uniquely shared with *Sternopygus* within the Gymnotiformes). *Archolaemus* is distinguished from *Sternopygus* by various features, with those of particular note being the possession of a postcleithrum (versus the absence of that ossification), the presence of a foramen in the scapula (versus the absence of that aperture), and the presence of some branched anal-fin rays (versus all anal-fin rays unbranched). One of the attributes that Korrington (1970) used to delimit *Archolaemus* from *Sternopygus* was the relative orbital diameter. The subsequent

description of *S. astrabes* by Mago-Leccia (1994), with a relatively large eye (13.8–19.5% HL; Hulén *et al.*, 2005), resulted in an overlap of the range of orbital diameters in the species of *Sternopygus*, with values for this feature sitting among the range of values found in species of *Archolaemus* (Tables 1 and 2).

Dentition: Jaw dentition of all species of *Archolaemus* consists of small, needle-like teeth embedded in the fleshy jaws. Consequently, details of the number of teeth and their exact distribution in each jaw are difficult to ascertain other than in cleared and counterstained specimens. Korrington (1970: fig. 2) provides a good illustration of the general dentition pattern (see, however, our comment concerning the dentary dentition in the next paragraph), with the dentary dentition consisting of bands of small teeth extending for varying distances posteriorly along the dorsal margin of the bone. Premaxillary dentition consists of two rounded to anteroposteriorly elongate patches that correspond to the form of the overlying premaxillae, and are separated from each other medially.

Korrington (1970: 267) reported that larger specimens of *A. blax* have ‘a number of dentary teeth outside the mouth and project forward in larger specimens.’ Schwassmann & Carvalho (1985: 232) were unable to confirm this condition: an observation that is in line with our results. Some larger specimens of *Archolaemus* can have the dentary dentition somewhat more prominent anteriorly, but not projecting forwards.

Distribution: Species of *Archolaemus* are known from the Rio Branco, Rio Madeira, Rio Tapajós, and Rio Xingu catchments within the Amazon basin, and outside that system in the Rio Tocantins, the easterly flowing Rio Araguari in the state of Amapá, Brazil, and the Rio São Francisco system of eastern Brazil (see species accounts).

Secondary sexual dimorphism: Secondary sexual dimorphism is manifest in several features among the species of *Archolaemus*. These include the distinctly darker overall pigmentation of the head and body in mature males, relative to the condition in females and juveniles, in *A. ferreirai*, the pronounced elongation of the snout in mature males of *A. luciae*, versus the condition in females and immatures, and the presence of teeth on the upper lip of large males of *A. ferreirai*, compared with the absence of such dentition in mature females. Limited samples of many species and the absence of mature males for others make it impossible to determine the generality of these features across the genus. This limitation notwithstanding, these modifications represent the first reported instances of secondary sexual dimorphism in the Sternopygidae.

Table 1. Morphometrics for examined specimens of *Archolaemus blas*, *Archolaemus ferreirai* sp. nov., and *Archolaemus janeae* sp. nov.

	<i>Archolaemus blas</i>			<i>Archolaemus ferreirai</i> sp. nov.			<i>Archolaemus janeae</i> sp. nov.				
	Range	N	Mean	H	Range	N	Mean	H	Range	N	Mean
Total length (mm)	176–382	17	–	183	68.8–342	50	–	160	110–224	13	–
Length to end of anal fin (mm)	140–300	17	–	142	67.4–286	40	–	127	118–171	8	–
Caudal filament length (mm)	36.8–77.5	12	–	34.3	16.8–67.3	32	–	32.6	21.3–42.5	6	–
Head length (mm)	20.1–45.3	16	–	23.2	12.0–40.2	50	–	19.8	16.9–26.6	12	–
Percentage of length to end of anal fin											
Anal-fin length	63.1–94.1	17	82.4	82.3	78.3–86.8	39	83.0	82.6	82.6–87.4	9	84.7
Snout to anus	6.4–10.7	17	8.6	9.0	7.4–13.3	40	9.5	13.1	8.7–13.1	9	10.7
Greatest body depth	10.6–15.9	17	13.3	13.2	10.7–16.0	39	13.4	12.3	11.4–13.7	9	12.5
Prenal-fin distance	13.1–18.6	17	16.8	17.7	14.8–26.3	39	18.1	17.8	15.2–17.8	9	16.3
Pectoral-fin length	9.0–14.2	16	11.3	11.2	8.0–15.3	40	10.6	10.7	8.2–11.8	9	10.0
Caudal filament length	22.9–38.1	12	30.4	24.2	18.1–36.6	31	26.6	25.7	16.0–25.7	7	20.5
Head length	13.5–17.0	15	14.8	16.3	14.0–18.6	39	16.1	15.6	13.8–15.8	9	14.8
Head length at opercle	13.2–16.3	16	14.2	15.8	13.9–20.9	39	15.9	14.3	13.5–14.7	9	14.1
Percentage of head length											
Head depth at eye	39.6–48.0	17	44.2	46.9	38.2–58.0	50	48.2	49.4	39.9–53.5	15	46.2
Head depth at nape	59.3–72.1	16	65.2	61.8	57.9–75.8	50	66.8	62.5	57.2–72.8	15	65.3
Head width	39.6–59.6	17	46.0	43.5	37.7–54.4	50	46.7	43.9	39.8–55.6	15	44.8
Orbital diameter	12.1–18.5	16	15.0	15.8	9.2–18.9	50	14.2	18.2	14.0–22.0	15	16.7
Interorbital distance	17.6–25.2	17	21.7	21.8	16.4–29.0	50	22.2	22.2	19.2–23.9	15	21.9
Internarial distance	7.2–9.6	17	8.4	8.4	6.0–9.4	50	7.9	8.3	7.1–9.7	15	8.2
Internarial width	9.2–11.5	17	10.2	9.4	6.5–13.5	50	9.8	14.3	8.5–14.3	15	10.5
Snout length	39.8–47.4	16	43.2	44.6	34.9–47.6	50	42.2	39.0	35.8–43.0	15	39.3
Snout to posterior naris	17.1–22.1	17	20.0	23.7	17.5–23.7	50	20.6	20.7	18.8–23.6	15	21.1
Posterior naris to eye	15.7–24.1	17	20.1	18.7	12.9–24.5	50	19.1	13.6	12.5–18.1	15	14.7
Mouth length	18.5–29.6	17	23.8	25.2	19.3–30.0	50	22.8	24.4	19.5–30.5	15	23.7
Mouth width	12.5–10.7	17	15.9	16.6	11.1–19.9	50	15.9	16.1	11.0–19.1	15	15.7
Branchial opening	26.6–31.0	17	28.5	26.4	23.2–31.1	50	27.3	28.0	22.8–31.1	15	26.2
Postorbital length	41.0–44.5	14	43.1	39.8	39.8–51.6	50	44.6	45.8	38.6–48.2	15	44.2
Percentage of caudal filament											
Caudal filament depth	5.0–6.5	12	5.7	6.1	3.6–9.2	32	6.2	5.9	5.6–11.2	7	7.3

N, number of specimens; *H*, holotype; range includes holotype of species.

Table 2. Morphometrics for examined specimens of *Archolaemus luciae* sp. nov., *Archolaemus orientalis* sp. nov., and *Archolaemus santosi* sp. nov.

	<i>Archolaemus luciae</i> sp. nov.				<i>Archolaemus orientalis</i> sp. nov.				<i>Archolaemus santosi</i> sp. nov.			
	H	Range	N	Mean	H	Range	N	Mean	H	Range	N	Mean
Total length (mm)	267	96–284	29	–	156	150.8–181	3	–	197	73–212	12	–
Length to end of anal fin (mm)	192	76–207	25	–	110.7	110.7–155	3	–	159	62–198	11	–
Caudal filament length (mm)	73.3	23.7–89.9	8	–	44.4	36.7–44.4	2	–	38.1	11.1–38.1	8	–
Head length (mm)	32.8	10.7–42.1	29	–	15.8	15.3–19.9	3	–	27.0	10.6–32.1	12	–
Percentage of length to end of anal fin												
Anal-fin length	89.9	79.8–88.9	25	82.7	83.0	70.3–83.0	3	78.5	80.5	79.7–85.3	11	82.2
Snout to anus	7.1	7.1–12.8	25	9.5	7.0	6.5–7.0	3	6.8	9.0	7.9–14.0	11	10.7
Greatest body depth	13.5	11.5–14.3	25	12.9	15.3	13.0–15.3	3	14.5	14.6	12.7–14.7	11	13.8
Preal-fin distance	17.5	15.0–20.7	25	17.7	17.0	15.0–17.6	3	16.3	17.4	16.6–19.6	11	17.9
Pectoral-fin length	12.7	8.5–17.8	25	10.9	10.0	9.4–10.0	3	9.6	10.0	9.2–11.9	11	10.4
Caudal filament length	46.1	28.6–46.1	7	35.4	40.1	32.1–40.1	2	36.1	19.3	14.4–27.0	7	20.6
Head length	16.8	13.8–20.4	25	16.0	14.3	12.8–14.3	3	13.5	17.0	15.5–17.1	11	16.4
Head length at opercle	16.4	13.2–19.4	25	15.0	13.2	11.7–13.2	3	12.5	16.0	15.0–16.3	11	15.6
Percentage of head length												
Head depth at eye	43.3	37.6–57.9	28	43.7	48.7	47.9–49.0	3	48.5	43.6	41.4–48.4	12	45.2
Head depth at nape	60.6	53.1–70.0	29	62.8	77.6	73.3–79.8	3	76.9	65.5	63.9–70.9	12	65.5
Head width	41.5	38.1–61.7	29	43.7	50.7	50.7–53.3	2	52.0	43.5	42.6–48.2	12	44.8
Orbital diameter	12.2	10.5–17.8	29	14.1	15.8	15.8–17.2	3	16.4	11.7	8.9–16.6	12	14.1
Interorbital distance	16.1	14.1–27.5	29	20.7	27.3	20.8–27.3	3	24.9	19.7	19.7–30.7	12	24.1
Internarial distance	8.6	5.4–10.5	28	7.8	9.0	8.2–9.0	2	8.6	8.3	7.0–10.3	12	8.4
Internarial width	9.7	6.6–12.4	29	8.8	13.3	13.3–15.3	2	13.3	14.3	7.6–14.3	12	10.7
Snout length	48.4	38.4–50.2	29	44.4	34.9	34.6–38.4	3	36.0	38.6	35.3–46.5	12	39.1
Snout to posterior naris	20.9	16.7–25.6	29	20.4	21.0	21.0–21.2	3	21.1	20.7	11.7–24.7	12	21.4
Posterior naris to eye	26.3	10.2–26.3	29	19.5	11.5	11.5–12.8	2	12.1	16.7	6.4–18.9	12	13.7
Mouth length	26.3	15.1–32.6	29	20.3	25.2	22.4–25.2	2	23.8	19.3	14.3–26.6	12	21.8
Mouth width	15.2	9.3–20.9	29	13.3	19.0	19.0–20.6	2	19.8	15.0	7.0–15.0	12	8.4
Branchial opening	29.6	19.0–31.6	29	24.9	28.4	27.6–28.4	3	28.0	24.5	23.1–29.2	12	26.7
Postorbital length	43.6	41.3–59.1	29	45.4	54.0	49.7–54.0	3	51.8	43.4	42.1–49.8	12	45.6
Percentage of caudal filament												
Caudal filament depth	3.3	3.3–4.8	8	3.9	3.3	3.3–4.4	2	3.9	7.6	6.7–9.1	7	8.2

N, number of specimens; H, holotype; range includes holotype of species.

Remarks: In their description of *Japigny*, Meunier *et al.* (2011) differentiated that genus from *Archolaemus* on the basis of pigmentation patterns and the total number of anal-fin rays. Their concept of *Archolaemus* was based on samples from the Rio Xingu, which presumably represent what we consider to be *A. janeae*, the only member of the genus known from that river system. *Archolaemus orientalis* described in this paper, however, has a range of total anal-fin rays (164–186) overlapping, albeit barely, with the values in *Japigny* (132–164), and lacks the pattern of longitudinal dark and light pigmentation common to the other species of *Archolaemus*. As such, the characters originally proposed to distinguish the two genera are no longer applicable. *Archolaemus* and *Japigny* differ in the association of the eye with the surrounding regions (free versus attached) and pigmentation pattern (dark pigmentation either absent or, when present, in the form of a dark stripe along the lateral line and a broad dusky to dark band over the basal pterygiophores of the anal fin versus wide alternatively dark and light vertical bars along the body).

In their analysis of *Archolaemus blax*, Schwassmann & Carvalho (1985) detailed the apparent pronounced variation in head form between populations within what they considered to be that species. In part, this variation was a consequence of ontogenetic modifications in snout and overall head morphology, as reflected in differences in the head profile from a lateral view. Supplementing these intraspecific ontogenetic alterations are alternative degrees of snout development across the species in *Archolaemus*, four of which (*A. blax*, *A. ferreirai*, *A. janeae*, and *A. luciae*) were encompassed within *A. blax* as delimited by Schwassmann & Carvalho (1985). Of note is the par-

ticularly elongate and broader snout of *A. luciae*, more so in mature males (Fig. 7). This factor contributes significantly to the range of snout profiles within what those authors considered to be *A. blax*.

Conservation status: The rapids and waterfalls patchily distributed across the gradients of the Brazilian and Guiana shields (Lima & Ribeiro, 2011; Lujan & Armbruster, 2011) are home to a number of specialized communities of plants and animals, including rheophilic fishes. Such high-energy settings significantly hinder the sampling of these communities, and as such our knowledge of the ichthyofaunas in these settings is often deficient, even within the context of the still inadequate overall understanding of the Neotropical freshwater fish fauna (Vari & Malabarba, 1998). At the same time the high-energy conditions that complicate the thorough sampling of these habitats provide the attributes that are ideal for hydroelectric facilities. The development of hydroelectric generating capacity is accelerating across the Neotropics, with the consequent submergence under reservoirs of multiple habits preferentially occupied by rheophiles. Moreover, proposed impoundments (i.e. the Belo Monte project on the lower Rio Xingu; Fearnside, 2006) threaten many as yet undeveloped high-energy settings. It is likely that various rheophilic species have been extirpated from their type localities by hydroelectric developments. Within the Gymnotiformes, this eventuality probably applies both in *Archolaemus* (e.g. *A. santosi* from the Rio Jamari at Usina Hidroelétrica Samuel in Rondônia) and *Sternarchorhynchus* (e.g. *Sternarchorhynchus britskii* in the upper Rio Paraná; Campos-da-Paz, 2005: 399). The same is likely to befall many of the locations inhabited by the species of *Archolaemus* and other rheophiles.

KEY TO THE SPECIES OF *ARCHOLAEMUS*

- 1a. 18–22 total pectoral-fin rays; 190 to 228 total anal-fin rays; dark narrow stripe running along lateral line.....2
 1b. 16 total pectoral-fin rays; 164–186 total anal-fin rays; no dark narrow stripe running along lateral line
***Archolaemus orientalis* sp. nov.** (upper Rio São Francisco basin, Brazil)
 2a. Mouth with posterior limit of opening extending posteriorly beyond vertical through posterior naris..... 3
 2b. Mouth with posterior limit of opening falling short of vertical through posterior naris.....4
 3a. Caudal-filament depth 3.3–4.8% of caudal filament length.....
***Archolaemus luciae* sp. nov.** (Rio Jari, Rio Trombetas and Rio Tapajós basins in eastern Amazon; independent Rio Araguari, Brazil)
 3b. Caudal-filament depth 5.0–6.5% of caudal filament length.....***Archolaemus blax*** (Rio Tocantins basin, Brazil)
 4a. 10–14 scales above lateral line at midbody (14 scales present only in three of 50 examined specimens.....
***Archolaemus ferreirai* sp. nov.** (Rio Mucajaí and Rio Uraricoera, Amazon basin, Brazil)
 4b. 14–17 scales above lateral line at midbody (14 scales present in none of the examined specimens of *A. janeae* sp. nov. and in only one of 12 examined specimens of *A. santosi* sp. nov.).....5
 5a. Head length to rear of opercle 13.5–14.7% of length to the end of the anal fin; mouth width 11.0–19.1% of head length.....***Archolaemus janeae* sp. nov.** (Rio Xingu and upper Rio Tapajós, Amazon basin, Brazil)
 5b. Head length to rear of opercle 15.0–16.3% of length to the end of the anal fin; mouth width 7.0–10.3% of head length.....***Archolaemus santosi* sp. nov.** (Rio Jamari, Amazon basin, Brazil)

ARCHOLAEMUS BLAX KORRINGA, 1970
(FIGS 1, 2; TABLE 1)

Archolaemus blax Korringa, 1970: 267, fig. 1 (type locality: Brazil, Goiás, Porto Nacional, Rio Tocantins, 10°40'S, 048°30'W; type species of *Archolaemus* by original designation). Mago-Leccia, 1994: 115, fig. 1A and B (Brazil, Rio Tocantins, Jatobal; drawing of head of holotype; based on information in Korringa, 1970; assignment to Eigenmanninae). Schwassmann & Carvalho, 1985: 231 (only cited specimens from the Rio Tocantins system; no samples from Rio Branco, Rio Cupixi, Rio Tapajós, or Rio Xingu; not fig. 1; reports of rheophily, behaviour, and diet of populations in the Rio Itacaiunas and Rio Tocantins basins). Albert & Fink, 1996: 87 (phylogenetic relationships). Albert & Campos-da-Paz, 1998: 423 (phylogenetic relationships). Alves-Gomes, 1998: 447 (phylogenetic relationships). Albert, 2003: 487 (in listing of members

of Sternopygidae). Bichuette & Trajano, 2003: 1109 (subterranean habits, São Domingos karst, upper Rio Tocantins basin). Bichuette & Trajano, 2006: 100 (occurrence in caves, São Domingos karst, upper Rio Tocantins basin). Campos-da-Paz, 2007: 121 (Brazil, Amazon basin). Lima & Caires, 2011: 10 (Brazil, upper Rio Tocantins basin, Rio Novo/Rio do Sono basin). Lucinda *et al.*, 2007: 82 (Brazil, Rio Tocantins basin, Lajeado Reservoir region).

Diagnosis: *Archolaemus blax* is diagnosed from *A. ferreirai* by the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris, versus falling short of that line), the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more of the length of Meckel's cartilage), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal



Figure 1. *Archolaemus blax*, 288 mm total length; MNRJ 12158, female, Brazil, Goiás, Município de Minaçu/Cavalcante, Rio Tocantins, at site of Usina Hidroelétrica Serra da Mesa (approximately 13°44'S, 048°08'W).

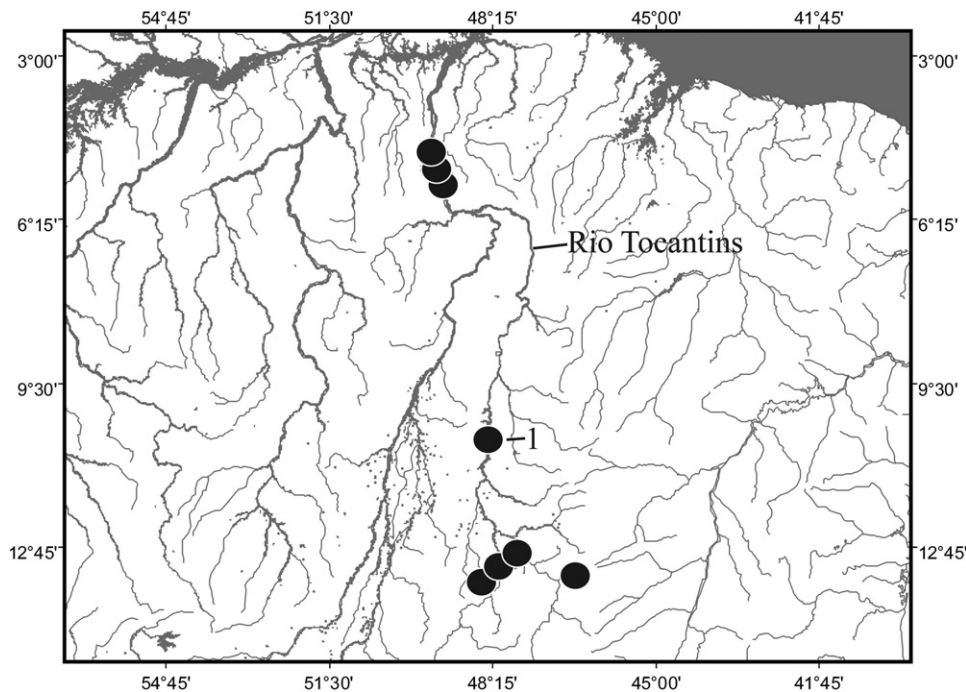


Figure 2. Map of Rio Tocantins and adjoining areas, showing geographical distribution of *Archolaemus blax* (1 = type locality; some symbols represent more than one locality and/or lot of specimens).

versus approximately the same size as the ventral hypohyal). *Archolaemus blax* is diagnosed from *A. janeae* by the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line), the number and arrangement of teeth on the internal surface of the endopterygoid (approximately six irregularly distributed teeth versus two or three teeth arranged in a single row), the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width), and the distribution of teeth on the dentary (dentition restricted to the anterior half or slightly more of the dorsal margin versus occupying most of the dorsal region). *Archolaemus blax* is diagnosed from *A. luciae* by the depth of the caudal filament (5.0–6.5% CL versus 3.3–4.8% CL), the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more of the length of Meckel's cartilage), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same length as the ventral hypohyal). *Archolaemus blax* is diagnosed from *A. orientalis* by the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad dusky to dark band of pigmentation overlying the basal pterygiophores of the anal fin, versus the lack of such dark pigmentation), the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris, versus falling short of the vertical through the posterior margin of the posterior naris), the total number of pectoral-fin rays (19–22 versus 16), the total number of anal-fin rays (193–222 versus 164–186), the form of the premaxilla (the anteroposterior length greater than the transverse width, versus the anteroposterior length equal to the transverse width), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same length as the ventral hypohyal). *Archolaemus blax* is diagnosed from *A. santosi* by the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line), the depth of the caudal filament (5.0–6.5% CL versus 6.7–9.1% CL), the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width) and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same length as of the ventral hypohyal).

Description: Morphometric data for the examined specimens of *A. blax* are presented in Table 1.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity or slightly posterior to that region. Body profile gently convex from rear of head for approximately anterior one-

third of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body distinctly convex anteriorly along anterior half of abdominal cavity, and then gradually angled posterodorsally along base of anal fin and caudal filament. Antermost perforated lateral line scale located at vertical approximately at origin of pectoral fin. Lateral line continuous, extending from immediately after vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Head profile varying from nearly straight to slightly concave along antorbital region, and then straight to slightly convex from that point to rear of head. Ventral profile of head straight and posteroventrally aligned. Snout subconical and anteroventrally directed. Eye small and located laterally on dorsal half of head. Orbital rim partially attached to surface tissues of adjoining region of head in specimen of approximately 105 mm TL, but rim totally free and without membranous attachment in larger examined individuals. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube, and located nearer to tip of snout than to anterior margin of eye in adults. Mouth distinctly inferior, with upper jaw clearly longer than and overlapping lower jaw. Gape relatively long and rictus in adults positioned posterior of vertical through posterior margin of posterior naris. Branchial opening moderately elongate, located along posterior margin of opercle and immediately anterior to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus and extending posteriorly to under pectoral-fin base. Anus proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting ontogenetically from posterior of vertical through posterior margin of orbit to more anterior position.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Scales along lateral line 131 to 152 (137 reported for the holotype by Korrington, 1970: 268) ($N = 20$). Scales above lateral line at midbody 12 to 14 ($N = 30$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad, and distally pointed with lateral rays longer. Pectoral-fin rays ii, 19 to ii, 22 (19 reported for the holotype by Korrington, 1970: 268) ($N = 30$). Anal fin elongate, extending from vertical through base of pectoral-fin base along most of length of body. Fin margin gently convex anteriorly and then straight for much of length of fin, but with rays becoming progressively shorter posteriorly. Anal fin with 23–27 unbranched rays ($N = 25$) and 193–222 total fin rays

(218 reported for the holotype by Korringa, 1970: 268) ($N = 20$). Caudal filament of moderate length.

Coloration in alcohol: Overall body coloration ranging from tan to brown. Lightly coloured specimens lacking, or with faint indications of, pigmentation pattern characteristic of darker individuals. More intensely pigmented individuals with overall brown pigmentation further developed dorsally, and with narrow band of dark pigmentation extending along lateral line; band extending from vertical through tip of pectoral fin or slightly posterior of that line to end of caudal filament. Basal pterygiophores of anal fin outlined by very narrow dark bars situated on body surface. Bars cumulatively form dark, broad, band running along ventral portion of body, with height of band gradually decreasing posteriorly. Dark pigmentation along centre of band irregularly less intense in many individuals, resulting in darker dorsal and ventral components in band. Dark stripe along lateral line distinctly separated in most specimens from dark band overlying anal-fin basal pterygiophores by more lightly pigmented, broad, midlateral stripe. Lighter midlateral stripe less obvious in some overall more darkly pigmented individuals. Head ranging from tan to dark brown. Tan specimens with upper two-thirds of head slightly dusky, but otherwise without distinct pigmentation pattern. Darkly pigmented specimens sometimes with ventral surface of head tan, but most often with head dark over nearly all surfaces. Dark pigmentation often particularly intense on opercle and around mouth, but with lips lightly coloured. Pigmentation of pectoral and anal fins variable, ranging from tan in lightly coloured specimens to quite dusky with dark pigmentation overlying fin rays in more intensely pigmented individuals.

Distribution: *Archolaemus blax* is known from multiple locations within the Rio Tocantins basin (Fig. 2).

Ecology: The concept of *A. blax* described by Schwassmann & Carvalho (1985) encompassed what has now proven to be a species complex. Analysis of a sample from the Rio Itacaiunas, in the Rio Tocantins basin, reported on by those authors (MZUSP 24158) confirmed that this population is *A. blax*. At that locality the species preferred fast-flowing waters, with individuals sheltering during the day between rocks and within crevices in locations with high-velocity currents (Schwassmann & Carvalho, 1985: 237). They observed individuals emerge from sheltered locations in the evening, but their nocturnal activities could not be tracked. Stomach content analysis showed that at that location, *A. blax* feeds most often on insect larvae, primarily of the Chironomidae, with the stomachs also containing some sand and filamentous

algae, presumably ingested incidentally with the capture of the target prey. Individuals of both sexes had mature or maturing gonads and well-developed genital papillae during the period (October) of Schwassmann & Carvalho's study, with mature males and females being of approximately the same size. The species has also been reported from subterranean habitats in the São Domingos karst formation in the upper Rio Tocantins basin, with these settings characterized by moderate to very strong water currents, particularly during the rainy season (Bichuette & Trajano, 2003: 1111).

Remarks: Multiple researchers after Schwassmann & Carvalho (1985) followed those authors in treating all samples of *Archolaemus* from a series of major river systems in the Amazon and adjoining catchments as *A. blax*. Results herein demonstrate that Schwassmann & Carvalho's concept of *A. blax* encompassed a species complex. Based on the analysis of the bulk of the specimens reported on by those authors, supplemented on the examination of numerous other samples from across the range of the genus, we consider citations of *A. blax* from the Rio Xingu to be based on *A. janeae*, those from the Rio Cupixi to be *A. luciae*, and that from the Rio Branco to be *A. ferreirai*.

Material examined

BRAZIL. Goiás: Porto Nacional, Rio Tocantins (approximately 10°40'S, 048°30'W); CAS 24743 (435; holotype). Município de Minaçu/Cavalcante, Rio Tocantins, at site of Usina Hidroelétrica Serra da Mesa (approximately 13°44'S, 048°08'W); MNRJ 12158, 22 (90–382; 4 CS). Rio Bezerra, right-bank tributary of Rio Paranã, 2 km above Fazenda Monte Alegre de Goiás (approximately 13°16'S, 047°30'10'W); MZUSP 40686, 4 (65–193). Rio Tocantinzinho and tributary, Serra da Mesa, Minaçu (approximately 13°48'S, 048°18'10'W); MZUSP 54080, 3 (215–285). Rio São Vicente, São Domingos in Lapa São Vicente II (approximately 13°30'S, 046°18'W); MZUSP 55987, 1 (139). Rio Angélica, Lapa do Angélica, São Domingos (approximately 13°31'S, 046°23'W); MZUSP 86112, 1 (not measured). Maranhão: Rio Tocantins, estreito do Tocantins (approximately 06°08'58'S, 047°29'15'W); MZUSP 4991, 1 (212). Pará: Rio Tocantins, Capuerana, upriver from Tucuruí dam (approximately 03°51'S, 049°41'W); INPA 6421, 1 (313). Rio Tocantins, above Tucuruí dam (03°45'58"S, 049°40'21"W); INPA 4828, 11 (45–340); INPA 6424, 23 (87–292; 4 CS; one *Sternopygus* intermingled with material); INPA 9071, 1 (280). Breu Branco (approximately 04°04'S, 049°38'W); INPA 20963, 1 (325). Rio Tocantins, Jatobal, sandy lagoon in front of Jatobal (04°32'S, 049°32'W); MZUSP 24158, 2 (92–133); MZUSP 24129, 24 (37–390). Rio Anapu, Estuário (01°48'25'S,

051°21'19"W); MPEG 8596, 1 (195). *Tocantins*: Rio do Sono, Cachoeira da Velha, Rio Novo basin (09°20'S, 047°44'W); MZUSP 97943, 1 (286).

***ARCHOLAEMUS FERREIRAI* SP. NOV.**

(FIGS 3, 4; TABLE 1)

Archolaemus blax, Schwassmann & Carvalho, 1985: 233 (only specimens from Brazil, Roraima, Rio Branco, Cachoeira de Bem Querer; not details of species redescription or biological information). Ferreira *et al.*, 1988: 345 (Brazil, Roraima, Rio Mucajaí, vicinity of Ilha Paredão; carnivorous diet). Ferreira *et al.*, 2007: 184 (Brazil, Roraima, Rio Branco basin).

Diagnosis: *Archolaemus ferreirai* is diagnosed from *A. blax* by the length of the gape (the rictus falling short of the vertical through the posterior naris versus extending beyond that line), the length of the coronomeckelian bone (50% or more the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage) and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus ferreirai* is diagnosed from *A. janeae* in the number of scales above the lateral line at the midbody (10–14 versus 15–17), by the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width), the



Figure 3. A, *Archolaemus ferreirai* sp. nov., holotype, female, 183 mm total length, INPA 3757; Brazil, Roraima, Rio Mucajaí, Cachoeira Paredão 2 (approximately 02°57'N, 061°27'W); B, *Archolaemus ferreirai* sp. nov., paratype, male, 342 mm total length, INPA 36379; Brazil, Roraima, Rio Mucajaí, Cachoeira Paredão 2 (approximately 02°57'N, 061°27'W).

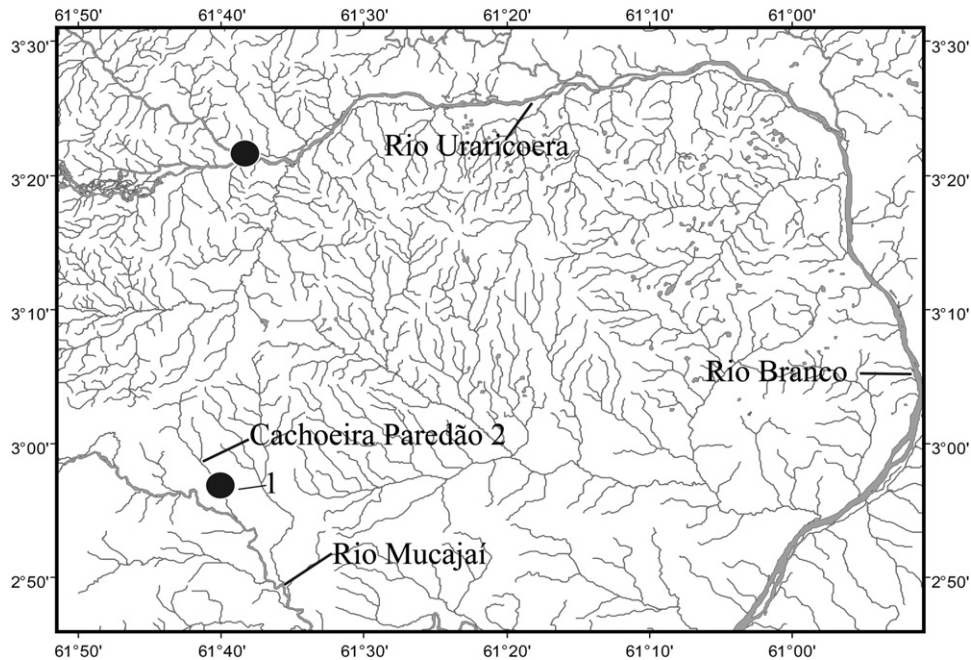


Figure 4. Map of upper Rio Branco and adjoining areas showing geographical distribution of *Archolaemus ferreirai* sp. nov. (1, holotype locality; some symbols represent more than one locality and/or lot of specimens).

distribution of the teeth on the dentary (dentition restricted to anterior one-half or slightly more of the dorsal margin versus occupying most of the dorsal margin), the length of the coronomeckelian bone (50% or more the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus ferreirai* is diagnosed from *A. luciae* by the length of the gape (the rictus not extending posteriorly beyond the vertical through the posterior naris versus extending beyond that line) and the distribution of the teeth on the internal surface of the endopterygoid (five or six teeth arranged in single row versus between seven and ten irregularly distributed teeth). *Archolaemus ferreirai* is diagnosed from *A. orientalis* in the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin, versus the lack of such dark pigmentation), the total number of pectoral-fin rays (18–21 versus 16), the total number of anal-fin rays (190–222 versus 164–186), the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width), and the length of the coronomeckelian bone (50% or more of the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage). *Archolaemus ferreirai* is diag-

nosed from *A. santosi* in the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width) and the length of the coronomeckelian bone (50% or more the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage).

Description: Morphometric data for the examined specimens of *A. ferreirai* are presented in Table 1.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity. Body profile gently convex from rear of head for approximately anterior one-third of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body slightly convex anteriorly along anterior half of abdominal cavity, and then gradually angled postero-dorsally along base of anal fin and caudal filament. Anterior most perforated lateral line scale located at vertical approximately at origin of pectoral fin. Lateral line continuous, extending from immediately after vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Head profile nearly straight dorsally. Ventral profile of head straight and posteroventrally aligned. Snout subconical and anteroventrally directed. Eye small and located laterally on dorsal half of head. Orbital rim covered by

membrane and partially free of surface tissues of adjoining region of head in specimens of up to approximately 119 mm TL, but rim totally free and without membranous attachment in larger examined individuals. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube and located nearer tip of snout than to anterior margin of eye. Mouth distinctly inferior, with upper jaw clearly longer than, and overlapping, lower jaw. Gape relatively short and in adults falling short posteriorly of vertical through posterior margin of posterior naris. Branchial opening moderately elongate; located along posterior margin of opercle and immediately anterior to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus and extending posteriorly to under pectoral-fin base. Anus proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting anteriorly ontogenetically from posterior of vertical through posterior margin of orbit to position along, or anterior of, vertical through anterior margin of orbit in larger specimens.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Scales along lateral line 136 to 150 (145) ($N = 25$). Scales above lateral line at midbody 10 to 14 (12) ($N = 50$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad, and distally pointed with lateral rays longer. Pectoral-fin rays between ii, 16 and ii, 19 (18) ($N = 50$). Anal-fin elongate, extending from vertical through base of pectoral-fin base along most of length of body. Fin margin gently convex anteriorly and then straight, but with rays becoming progressively shorter posteriorly. Anal fin with 24–33 (28) unbranched rays ($N = 30$) and 190–222 (197) total fin rays ($N = 30$). Caudal filament of moderate length.

Coloration in alcohol: Overall body coloration ranging from tan to light brown, with lightly coloured specimens demonstrating a less intense version of pigmentation pattern characteristic of darker individuals. Overall brown pigmentation more developed dorsally, with narrow dark stripe extending along lateral line from vertical through tip of pectoral fin, or slightly posterior of that line to end of caudal filament. Band less apparent, but still obvious in very darkly pigmented adult male specimens. Skin overlying basal pterygiophores of anal fin with pterygiophores outlined by very narrow dark bars on body surface. Bars cumulatively form dusky to dark, broad, band running along ventral portion of body, with height of band gradually decreasing posteriorly. Dark pigmentation along centre of band often less intense, with

resultant darker dorsal and ventral components to band. Dark stripe along lateral line and ventral band above anal fin separated by more lightly pigmented, broad, midlateral stripe. Lighter midlateral stripe less obvious in some overall more darkly pigmented individuals, and obscured to significant degree by overall dark pigmentation in the single examined large male specimen. Head ranging from tan ventrally and dark dorsally to dark brown over all surfaces, other than for narrow lightly coloured mid-ventral stripe. Lips of darkly pigmented specimens distinctly lighter than proximate areas. Region anteroventral and posteroventral of pectoral-fin base more darkly pigmented than adjoining regions. Pigmentation of pectoral and anal fins ranging from tan in more lightly coloured specimens to quite dusky with dark pigmentation overlying fin rays in more intensely pigmented individuals.

Distribution: *Archolaemus ferreirai* is known from north-eastern portions of the Amazon basin in the Rio Mucajaí at Cachoeira Paredão 2 and the Rio Uraricera at Ilha de Maracá, both in Roraima, Brazil (Fig. 4).

Secondary sexual dimorphism: The only examined mature male of *Archolaemus ferreirai* (INPA 3757) has an overall body coloration (Fig. 3B) much darker than in the juveniles and females (Fig. 3A) captured at the same time. This darker pigmentation largely obscures the lighter longitudinal band present in mature females and juveniles between the dark stripe along the lateral line and the dark band overlying the basal pterygiophores of the anal fin. The upper lip of this large male is also notable in bearing some teeth, contrary to the absence of such dentition in mature females and juveniles.

Habitat: Ferreira *et al.* (1988: 342) reported the type region of *Archolaemus ferreirai*, the Rio Mucajaí at Cachoeira Paredão 2, as characterized by rapidly flowing waters and a 20 m high waterfall. The sample of *A. ferreirai* (reported as *A. blax* in that paper) was captured above these falls, in an area with many rapids and no still backwaters.

Etymology: The species name, *Archolaemus ferreirai* sp. nov., is in honor of Efreim Ferreira of the Instituto Nacional de Pesquisas da Amazônia, one of the collectors of the type series, in recognition of his many contributions to our understanding of the Amazonian fish fauna.

Material examined

Holotype: BRAZIL. Roraima: Rio Mucajaí, Cachoeira Paredão 2 (approximately 02°57'N, 061°27'W), collected by E. G. Ferreira & M. Jégu, 19 February 1987; INPA 3757 (183).

Paratypes: BRAZIL. *Roraima:* collected with holotype; INPA 36379, 21 (119–342; 1 CS); MPEG 21683, 1 (286); MZUSP 110183, 1 (150); USNM 404354, 1 (172). Rio Mucajaí, mouth of Igarapé Traira (approximately 02°57'N, 061°27'W), collected by E. G. Ferreira & M. Jégu, 21 February 1987; INPA 6422, 12 (131–269; 4 CS).

Non-type specimens: BRAZIL. *Roraima:* Rio Uraricoera, Ilha Maracá, Furo Santa Rosa (approximately 03°22'N, 061°22'W); INPA 2038, 6 (122–176). Rio Uraricoera, Ilha Maracá, below Furo Santa Rosa (approximately 03°22'N, 061°22'W); INPA 2054, 4 (135–184). Rio Uraricoera, Ilha Maracá (approximately 03°22'N, 061°22'W); INPA 2675, 1 (54). Rio Uraricoera, Ilha Maracá, below Furo Santa Rosa (approximately 03°22'N, 061°22'W); INPA 3747, 1 (60). Rio Mucajaí, station Fé-Esperança; INPA 3758, 3 (83–145). Rio Mucajaí, 2 km above Cachoeira Paredão (approximately 02°57'N, 061°27'W); INPA 6423, 1 (338). Rio Mucajaí, 2 km above Cachoeira Paredão, mouth of Igarapé (approximately 02°57'N, 061°27'W); INPA 6495, 1 (136); INPA 6500, 7 (115–223). Rio Mucajaí, near Cachoeira Paredão (approximately 02°57'N, 061°27'W); INPA 6496, 11 (69–196). Rio Mucajaí, above Cachoeira Paredão (approximately 02°57'N, 061°27'W); INPA 6499, 1 (192).

ARCHOLAEMUS JANEAE SP. NOV.

(FIGS 5, 6; TABLE 1)

Archolaemus blax, Schwassmann & Carvalho, 1985: 233, fig. 1 (in part, specimens from Rio Xingu, Belo Monte, Pará, Brazil; not details in species redescription or biological information). Moller, 1995: 451, 455, 453 (illustration, feeding habits). Camargo, Giarrizzo & Isaac, 2004: 139 (Brazil, lower and middle Rio Xingu). Montag, Freitas, Wosiacki, & Barthem, 2008: 20 (Brazil, Para, Rio Xingu basin, Floresta Nacional de Caxiuanã).

Diagnosis: *Archolaemus janeae* is diagnosed from *A. blax* in the length of the gape (the rictus falling short posteriorly of the vertical through the posterior naris versus extending beyond that line), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), the distribution of the teeth on the dentary (dentition occupying most of the dorsal margin versus restricted to the anterior one-half or slightly more of the margin), and the number and arrangement of teeth on the internal surface of the endopterygoid (two or three teeth arranged in a single row versus six irregularly distributed teeth). *Archolaemus janeae* is diagnosed from *A. ferreirai* by the number of scales above the lateral line at the midbody (15–17 versus 10–14), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), the distribution of the teeth on the dentary (dentition occupying most of the dorsal margin versus restricted to the anterior one-half or slightly more of the margin), the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more of length of Meckel's cartilage), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same size as the ventral hypohyal). *Archolaemus janeae* is diagnosed from *A. luciae* in the length of the gape (the rictus falling short posteriorly of the vertical through the posterior naris versus extending beyond that line), the length of the caudal filament (16.0–25.7% LEA versus 28.6–46.1% LEA), the depth of the caudal filament (5.6–11.2% CL versus 3.3–4.8% CL), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), the distribution of the teeth on the dentary (dentition occupying most of the dorsal margin versus restricted

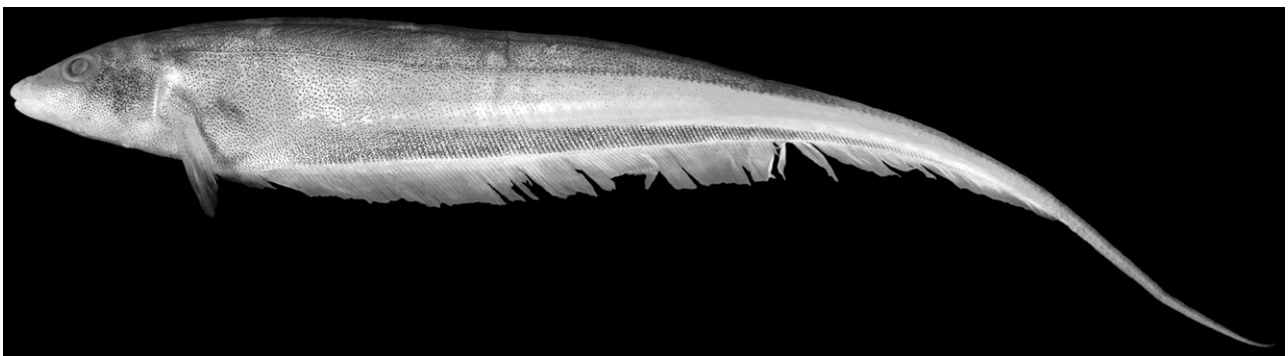


Figure 5. *Archolaemus janeae* sp. nov., holotype, 160 mm total length, INPA 30832; Brazil, Pará, Rio Iriri, just upriver of its mouth into Rio Xingu, Município de Altamira (03°48'54"S, 052°37'09"W).

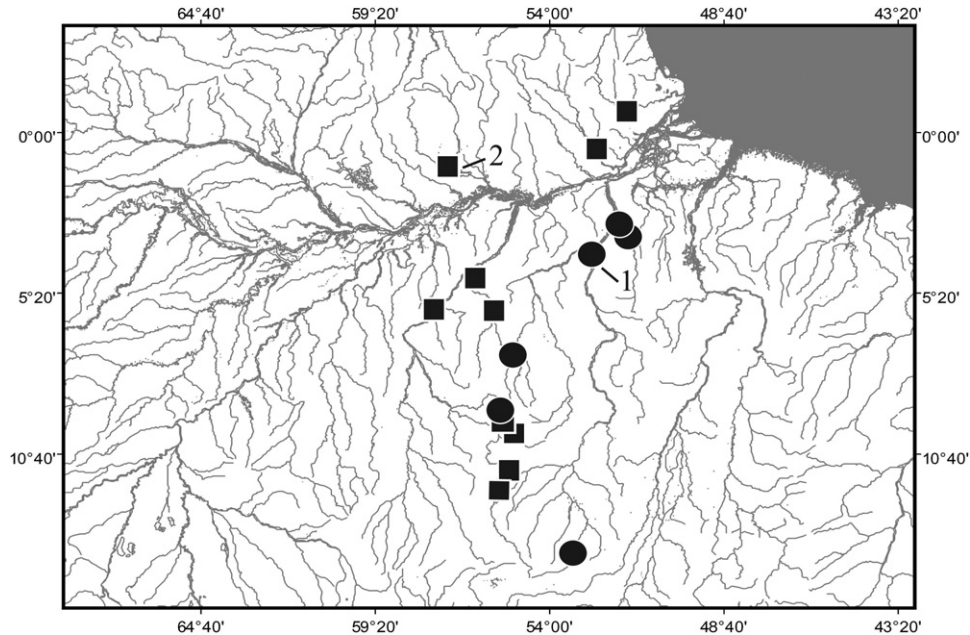


Figure 6. Map of lower portion of Amazon basin and adjoining areas, showing geographical distribution of *Archolaemus janeae* sp. nov. (dots; 1, holotype locality) and *Archolaemus luciae* sp. nov. (squares; 2, holotype locality) (some symbols represent more than one locality and/or lot of specimens).

to the anterior one-half or slightly more of the margin), the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more of the length of Meckel's cartilage), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same size as the ventral hypohyal). *Archolaemus janeae* is diagnosed from *A. orientalis* by the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin, versus the lack of such dark pigmentation), the total number of pectoral-fin rays (19–21 versus 16), the total number of anal-fin rays (205–228 versus 164–186), the distribution of the teeth on the dentary (dentition occupying most of the dorsal margin versus restricted to the anterior one-half or slightly more of the margin), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same size as the ventral hypohyal). *Archolaemus janeae* is diagnosed from *A. santosi* by the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin, versus the lack of such dark pigmentation), the head length at the opercle (13.5–14.7% LEA versus 15.0–16.3% LEA), the distribution of the teeth on the dentary (dentition occupying most of the dorsal margin versus restricted to the anterior one-half or

slightly more of the margin), and the length of the posterior ceratohyal (1.5 times the length of the ventral hypohyal versus approximately the same size as the ventral hypohyal).

Description: Morphometric data for examined specimens of *A. janeae* are presented in Table 1.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity or slightly posterior to that region. Body profile very gently convex from rear of head for approximately anterior one-third of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body distinctly convex anteriorly below anterior one-half to two-thirds of abdominal cavity, more so in specimens with distended abdomens, and then gradually angled posterodorsally along base of anal fin and caudal filament. Antermost perforated lateral line scale located at vertical situated approximately at origin of pectoral fin. Lateral line continuous, extending from immediately after vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Head profile ranging from nearly straight to slightly concave from tip of snout to vertical through orbit, and then straight from that area to rear of head. Ventral profile straight and posteroventrally aligned. Snout subconical, anteroventrally directed and moderately developed.

Eye small and located laterally on dorsal one-half of head. Orbital rim partially attached to surface tissues of adjoining region of head in examined specimen of approximately 105 mm TL, but rim totally free and without membrane in larger individuals. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube and located nearer to tip of snout than to anterior margin of eye. Mouth distinctly inferior, with upper jaw clearly longer than, and overlapping, lower jaw. Gape relatively long, and extending posteriorly beyond vertical through posterior margin of posterior naris. Branchial opening moderately elongate; located along posterior margin of opercle and immediately anterior to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus and extending posteriorly to under pectoral-fin base. Anus proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting ontogenetically from posterior of vertical through posterior margin of orbit to more anterior position.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Scales along lateral line 146 to 161 (155) ($N = 15$). Scales above lateral line at midbody 15 to 17 (15) ($N = 15$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad, and distally pointed with lateral rays longer. Pectoral-fin rays ii, 19 to ii, 21 (19) rays ($N = 15$). Anal-fin elongate, extending from vertical through base of pectoral-fin base along most of length of body. Fin margin gently convex anteriorly and then straight for length of fin, but with rays becoming progressively shorter posteriorly. Anal fin with 22–33 (33) unbranched rays ($N = 15$) and 205–228 total fin rays (220) ($N = 9$). Caudal filament of moderate length.

Coloration in alcohol: Overall ground body coloration ranging from tan to dark brown. More lightly coloured specimens with pigmentation pattern characteristic of darker specimens less pronounced. More intensely pigmented individuals with overall brown pigmentation more developed dorsally, and narrow dark stripe extending over lateral line from vertical through tip of pectoral fin or slightly posterior of that line to end of caudal filament. Stripe particularly dark in intensely pigmented specimens, such that it stands out even against an overall dark anterior portion of body. Area overlying anal-fin basal pterygiophores with ossifications outlined by variably dark bars on body surface. Bars narrow, distinct, and dusky in overall more lightly coloured specimens, in which they cumula-

tively form dusky band along ventral portion of body with height of band gradually decreasing posteriorly. More darkly pigmented band in dark specimens quite intense, and individual narrow bars sometimes merge into continuous dark broad band running along ventral portion of body. Dark stripe along lateral line and ventral band overlying basal pterygiophores separated in most specimens by more lightly pigmented, broad midlateral stripe. Lighter stripe less obvious in overall very lightly coloured specimens, and obscured anteriorly in some overall more darkly pigmented individuals. Head ranging from tan ventrally and dusky dorsally in lightly coloured individuals to totally dark brown in large, dark specimens. Smaller darkly pigmented specimens sometimes with lightly coloured area on ventral surface of head. Fleishy covering of branchial opening lightly pigmented, even in dark specimens. Larger specimens in some samples with dark pigmentation patch present immediately anterior to base of pectoral fin. Pectoral and anal fins ranging from hyaline in smaller individuals to dusky in larger specimens.

Coloration in life: (Based on photograph of recently captured specimen from São Felix do Xingu along the Rio Xingu.) Dark coloration overall quite intense, with head, portion of body dorsal of lateral line, and region overlying basal pterygiophores of anal fin nearly black. Rays of anal fin overlain by black pigmentation. Pectoral fin black. Midlateral more lightly pigmented stripe present in most preserved specimens, obscured anteriorly by darker pigmentation that gradually becomes more diffuse posteriorly.

Distribution: *Archolaemus janeae* is known from the upper and lower portions of the Rio Xingu basin at the Rio Iriri, the Cachoeira de Kaituká at Município de Altamira, and localities in the Rio Culuene, as well as the upper Rio Tapajós basin, where it was collected in the Rio Jamanxim at the Município do Novo Progresso, Brazil (Fig. 6).

Remarks: Two specimens of *A. janeae* from the Rio Xingu listed by Schwassmann & Carvalho (1985: 233; cited therein as *A. blax*) as MPEG 1370 are now registered as MZUSP 31491.

Etymology: The species name, *Archolaemus janeae*, is in honor of Jane Mertens of Humboldt Universität zu Berlin for her assistance to the second author.

Habitat: The holotype and a portion of the paratype series of *A. janeae* were collected between 21:00 and 23:00 h in the Rio Iriri, just upriver of a sandbank that separated the tributary from the mainstream Rio Xingu. In this area the river had a pronounced

current that was faster towards the centre of the channel, with the substrate in the sampled areas formed by pebbly sand. The depth of the fishing effort varied between < 10 cm and about 120 cm, and water parameters at that location were: pH = 5.5; T = 31.1 °C at night and 31.9 °C during the day; dissolved oxygen (D.O.) = 5.9 mg L⁻¹; conductivity 32.9 uScm⁻¹; and Secchi depth = 187 cm (H. López-Fernández, pers. comm.). Some non-type specimens of *A. janeae* that originated in the Rio Xingu were captured in the main stream of shallow rapids and small waterfalls, always over a rocky bottom (J.L.O. Birindelli, pers. comm.).

Material examined

Holotype: BRAZIL. *Pará:* Rio Iriri, just upriver of its mouth into Rio Xingu, Município de Altamira (03°48'54"S, 052°37'09"W), collected by H. López-Fernández, G. Ortí, N. Meliciano, and C. Röepke, 15 August 2008; INPA 30832 (160).

Paratypes: BRAZIL. *Pará:* collected with holotype, INPA 36380, 16 (136–225; 2 CS); MPEG 21684, 1 (141); USNM 404355, 1 (191). Rio Xingu near cachoeira, collected by M. Goulding, 14 October 1983; MZUSP 31491, 2 (115–206).

Non-type specimens: BRAZIL. *Pará:* Rio Xingu, Cachoeira de Kaituká, Altamira (03°33'47"S, 51°51'20"W); MZUSP 3930, 13 (113–340). Rio Xingu, Furo da Mirandolina (approximately 03°12'43"S, 052°12'12"W); INPA 4131, 1 (221). Rio Jamaxim, Rio Tapajós basin, Novo Progresso near Vila Mil (07°43'51"S, 055°16'36"W); MZUSP 97383, 10 (197–402). Rio Jamaxim, Rio Tapajós basin, small beach near Novo Progresso (09°17'59"S, 054°50'00"W); MZUSP 97514, 9 (213–222). Rio Iriri (03°48'49"S, 052°38'06"W), MZUSP 105843, 1 (300). Rio Xingu, above Belo Monte (approximately 03°17'S, 052°12'W); MZUSP 106054, 1 (341). Rio Xingu at Altamira, near Kaituká (03°33'48"S, 051°51'49"W); MZUSP 106223, 1 (372). Rio Xingu, Boa Esperança (03°33'44"S, 052°20'59"W); MZUSP 106287, 1 (only anterior half of specimen). Rio Xingu, Arroz Crú, Altamira (03°22'05"S, 051°58'02"W); MZUSP 106290, 1 (209); MZUSP 106049, 1 (230). *Mato Grosso:* Rio Xingu basin, Rio Culuene, Paranatinga, cachoeira at site of Pequena Centrais Hidrelétrica Paranatinga II (13°51'08"S, 053°15'22"W); MZUSP 89741, 3 (191–232). Rio Xingu basin, Rio Culuene, Paranatinga, cofferdam of Pequena Centrais Hidrelétrica 2 (13°49'00"S, 053°15'00"W); MZUSP 94909, 6 (253–368).

***ARCHOLAEMUS LUCIAE* SP. NOV.** (FIGS 6, 7; TABLE 2)

Archolaemus blax, Schwassmann & Carvalho 1985: 233 (in part, specimens from Rio Tapajós and

Rio Cupixi; not species redescription or biological information). Ferreira, 1995: 51 (Brazil, Rio Trombetas basin, Cachoeira Porteira, Cachoeira Vira-Mundo, inhabitant of swift-flowing waters).

Diagnosis: *Archolaemus luciae* is diagnosed from *A. blax* by the depth of the caudal filament (3.3–4.8% CL versus 5.0–6.5% CL), the length of the coronomeckelian bone (50% or more the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus luciae* is diagnosed from *A. ferreirai* in the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line) and the distribution of teeth on the internal surface of the endopterygoid (between seven and ten irregularly distributed teeth versus five or six teeth arranged in a single row). *Archolaemus luciae* is diagnosed from *A. janeae* in the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line), the length of the caudal filament (28.6–46.1% LEA versus 16.0–25.7% LEA), the depth of the caudal filament (3.3–4.8% CL versus 5.6–11.2% CL), the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width), the distribution of the teeth on the dentary (dentition restricted to the anterior one-half or slightly more of the dorsal margin versus occupying most of the dorsal margin), the length of the coronomeckelian bone (50% or more of the length of Meckel's cartilage versus less than 20% of the length of Meckel's cartilage), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus luciae* is diagnosed from *A. orientalis* by the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin, versus the lack of such dark pigmentation), the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line), the total number of pectoral-fin rays (19–21 versus 16), the total number of anal-fin rays (192–213 versus 164–186), the form of the premaxilla (the anteroposterior length greater than the transverse width versus the anteroposterior length equal to the transverse width), and the length of the coronomeckelian bone (50% or more the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage). *Archolaemus luciae* is diagnosed from *A. santosi* by the pigmenta-



Figure 7. A, *Archolaemus luciae* sp. nov., holotype, female, 267 mm total length, INPA 20960; Brazil, Pará, Rio Trombetas, Cachoeira Porteira, below Furo nas Pedras (approximately 01°05'S, 057°02'W); B, *Archolaemus luciae* sp. nov., male, 497 mm total length, INPA 6767; Brazil, Pará, Rio Jamanxim, Rio Tapajós basin, Ilha Terra Preta (05°27'04"S, 055°52'40"W).

tion pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin versus the lack of such dark pigmentation), the length of the gape (the rictus extending posteriorly beyond the vertical through the posterior naris versus falling short of that line), the length of the caudal filament (28.6–46.1% of LEA versus 14.4–27.0%), the depth of the caudal filament (3.3–4.8% of CL versus 6.7–9.1%), and the length of the coro-

nomeckelian bone (50% or more of the length of Meckel's cartilage versus less than 20% the length of Meckel's cartilage).

Description: Morphometric data for the examined specimens of *A. luciae* are presented in Table 2.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity or slightly posterior to that region. Body profile gently convex from rear of head for approximately anterior one-third

of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body distinctly convex anteriorly along anterior half of abdominal cavity, and then gradually angled posterodorsally along base of anal fin and caudal filament. Anteriormost perforated lateral line scale located approximately at vertical through origin of pectoral fin. Lateral line continuous, extending from immediately posterior of vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Dorsal profile of head varying from nearly straight to slightly concave along antorbital region, and then from straight to slightly convex from that point to rear of head. Ventral profile of head straight and posteroventrally aligned. Snout subconical, anteroventrally directed, and moderately developed to elongate with elongation particularly pronounced in largest examined specimen (INPA 6767; 497 mm TL). Eye small and located laterally on dorsal half of head. Orbital rim covered by membrane and attached to surface tissues of adjoining region of head in six specimens of approximately 97–135 mm TL, partially free on one side in two specimens of approximately 96–97 mm TL, and without membrane and unattached in individuals larger than 135 mm TL. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube, and located nearer tip of snout than anterior margin of eye. Mouth distinctly inferior, with upper jaw clearly longer than, and overlapping, lower jaw. Gape relatively long and extending posteriorly beyond vertical through posterior margin of posterior nares. Branchial opening moderately elongate, located along posterior margin of opercle and immediately anterior to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus, and extending posteriorly to under pectoral-fin base. Anus situated proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting ontogenetically from posterior of vertical through posterior margin of orbit to under or slightly anterior of orbit.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Between 127 and 148 (127) scales along lateral line ($N = 15$). Between 13 and 16 scales above lateral line at midbody (14) ($N = 29$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad and distally pointed, with rounded margin, and lateral rays longer overall. Pectoral-fin rays between ii, 17 and ii, 19 ($N = 29$). Anal-fin elongate, extending from vertical through base of

pectoral-fin base along most of length of body. Fin margin gently convex anteriorly, and then straight for length of fin, but with rays becoming progressively shorter posteriorly. Anal fin with 22–32 (24) unbranched rays ($N = 29$) and 192 to 213 (192) total fin rays ($N = 29$). Caudal filament long, with elongation particularly pronounced in largest examined specimen (INPA 6767; 497 mm TL).

Coloration in alcohol: Available specimens somewhat faded compared with obvious coloration in live specimens (see Coloration in life). Overall ground head and body coloration tan. Body with obvious but not dark, narrow stripe along lateral line. Extent of stripe variable anteriorly, even in specimens of comparable size, with anterior limit ranging from above centre of pectoral fin to point slightly posterior to vertical through tip of pectoral fin. Body pigmentation darker than overall ground pigmentation along dorsal portion of body. Area overlying basal anal-fin pterygiophores with pterygiophores outlined by very narrow dark surface bars that cumulatively form dusky broad band running along ventral portion of body, with depth of band gradually decreasing posteriorly. Dusky stripe along lateral line and dark ventral band above anal fin separated by more lightly pigmented, broad midlateral stripe. Head lightly coloured ventrally, and somewhat darker on opercle and above horizontal between tip of snout and areas somewhat below orbit. Pectoral and anal fins hyaline.

Coloration in life: (Based on recently collected specimens from Rio Teles Pires, Rio Tapajós basin.) Head dark overall, more so dorsal of horizontal between mouth and base of pectoral fin. Body dark from lateral line dorsally, with lateral line more intensely pigmented. Basal portions of anal-fin basal pterygiophores outlined by dark bars on body surface; pigmentation cumulatively forming dark band above base of fin, with height of band gradually decreasing posteriorly. Pigmentation overlying distal portions of basal pterygiophores less intense than that near base of fin, resulting in faint dusky band variably separate, other than anteriorly, from dark band along ventral margin of body. Pectoral fin dusky. Anal fin with rays outlined by dark pigmentation and dusky overall.

Distribution: *Archolaemus luciae* is known within the Amazon basin from the Rio Trombetas basin at Cachoeira Porteira, Cachoeira Vira-Mundo, and the Rio Mapuera, all in the state of Pará, as well as the Rio Tapajós basin, where it has been collected in the Rio Jamaxim and Rio Teles Pires in the state of Mato Grosso. In the state of Amapá, north of the lower Amazon, it has been collected in the Rio Jari that

empties into the Amazon and the Rio Araguari that drains independently into the Atlantic Ocean (Fig. 6).

Secondary sexual dimorphism: *Archolaemus luciae* demonstrates pronounced sexual dimorphism in the form of the snout in mature individuals (Fig. 7). Whereas the snout in mature females of the species is overall comparable with that in mature males and females of various congeners, the snout in the large male of *A. luciae* is distinctly lengthened and more massive anteriorly.

Habitat: Ferreira (1995: 51) reported *A. luciae* (as *A. blax*) from swift-flowing water habitats around Cachoeira Porteira and Cachoeira Vira-Mundo in the Rio Trombetas basin. Some of the non-type specimens of the species that originated in the Rio Tapajós were captured in the main stream of shallow rapids and small waterfalls, always over a rocky bottom (J. L. O. Birindelli, pers. comm.).

Etymology: The species name, *Archolaemus luciae*, is in honor of Lucia Py-Daniel of the Instituto Nacional de Pesquisas da Amazônia, in recognition of her many contributions to the knowledge of the fishes of the Amazon and her assistance to the authors over the years.

Material examined

Holotype: BRAZIL. *Pará:* Rio Trombetas, Cachoeira Porteira, below Furo nas Pedras (approximately 01°05'S, 057°02'W), collected by Equipe de Ictiologia do INPA, 19 April 1985; INPA 20960 (267).

Paratypes: BRAZIL. Collected with holotype: INPA 36381, 3 (137–276); Rio Trombetas, Cachoeira Porteira (approximately 01°05'S, 057°02'W), collected by Equipe de Ictiologia do INPA, 19 April 1985; INPA 20962, 23 (40–202); INPA 20964, 12 (110–210; 4 CS); MPEG 21685, 1 (138); MZUSP 110184 (135); USNM 404356 (158). Rio Mapuera, Cachoeira Porteira (approximately 01°05'S, 057°02'W); collected by E. Ferreira & M. Jegú; INPA 20961, 2 (130–180).

Non-type specimens: BRAZIL. *Amapá:* Rio Cupixi, Rio Araguari basin, bridge on road to Serra do Navio, in channel of river (approximately 00°53'45"N, 052°00'07"W); MZUSP 34920, 1 (238). Rio Iratapuru, left bank tributary of Rio Jari, Laranjal do Jari, at Cachoeira de São Raimundo, above Cachoeira de Santo Antonio (00°33'59"S, 052°34'40"W); MZUSP 103446, 1 (206). *Pará:* Rio Trombetas, Oriximiná, above Cachoeira Porteira (approximately 01°03'S, 057°01'W); INPA 3289, 1 (210). Rio Trombetas, Oriximiná, near Igarapé Caxipacoré (approximately 01°03'S, 057°01'W); INPA 3354, 1 (173); INPA 3386, 1 (160). Rio Trombetas, Oriximiná, above Cachoeira Vira-Mundo (approximately 01°03'S,

057°01'W); INPA 3356, 3 (230–269); INPA 3378, 1 (250). Rio Mapuera, Cachoeira Porteira (approximately 01°05'S, 057°02'W); INPA 4371, 10 (140–235); INPA 20957, 2 (130–141). Rio Trombetas, Cachoeira Porteira (approximately 01°05'S, 057°02'W); INPA 4372, 1 (102); INPA 19989, 1 (275); INPA 19990, 1 (181); INPA 20965, 1 (60). Trombetas, Oriximiná, Cachoeira Vira-Mundo (approximately 01°05'S, 057°02'W); INPA 5081, 1 (220); INPA 5082, 1 (180). Rio Jamaxim, Rio Tapajós basin, Ilha Terra Preta (05°27'04"S, 055°52'40"W); INPA 6767, 1 (497); INPA 6812, 6 (92–130). Rio Tapajós, São Luis do Tapajós (approximately 04°25'S, 056°13'W); MZUSP 24268, 1 (400). Rio Tapajós basin, Jacaracanga, rapids along Rio Teles Pires, below Sete Quedas (approximately 06°13'20"S, 057°45'10"W); MZUSP 96130, 1 (229). *Mato Grosso:* Rio Tapajós, Paranaíta, Rio Teles Pires, near ferry crossing of rodovia MT-416; MZUSP 95630, 4 (148–186). Rio Peixoto de Azevedo, Município do Peixoto de Azevedo, tributary of Rio Teles Pires near Peixoto de Azevedo (approximately 10°10'S, 054°50'W); MZUSP 96618, 1 (203). Rio Teles Pires, Itaúba, below mouth of Rio Renato (approximately 11°03'43"S, 055°16'33"W); MZUSP 99362, 2 (363–445). Rio Tapajós, Itaúba, Rio Teles Pires (approximately 11°39'11"S, 055°42'14"W); MZUSP 95909, 1 (409). Rio Braço Norte, Novo Mundo, above Pequena Centrais Hidrelétrica Braço Norte IV (approximately 09°47'S, 054°54'W); MZUSP 106461, 1 (292). Rio Teles Pires, Município da Paranatinga, Fazenda do Antônio Bezerra (approximately 10°20'S, 054°45'W); MZUSP 107923, 1 (447).

***ARCHOLAEMUS ORIENTALIS* SP. NOV. STEWART, VARI, DE SANTANA & WOSIACKI (FIGS 8, 9; TABLE 2)**

Diagnosis: *Archolaemus orientalis* is diagnosed from all congeners by the pigmentation pattern (the lack of a narrow dark stripe along the lateral line and absence of a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin, versus the presence of such dark pigmentation). *Archolaemus orientalis* is further distinguished from *A. blax* by the length of the gape (the rictus falling short of the vertical through the posterior border of the posterior nares versus extending beyond that line), the total number of pectoral-fin rays (16 versus 19–22), the total number of anal-fin rays (164–186 versus 193–222), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus orien-*

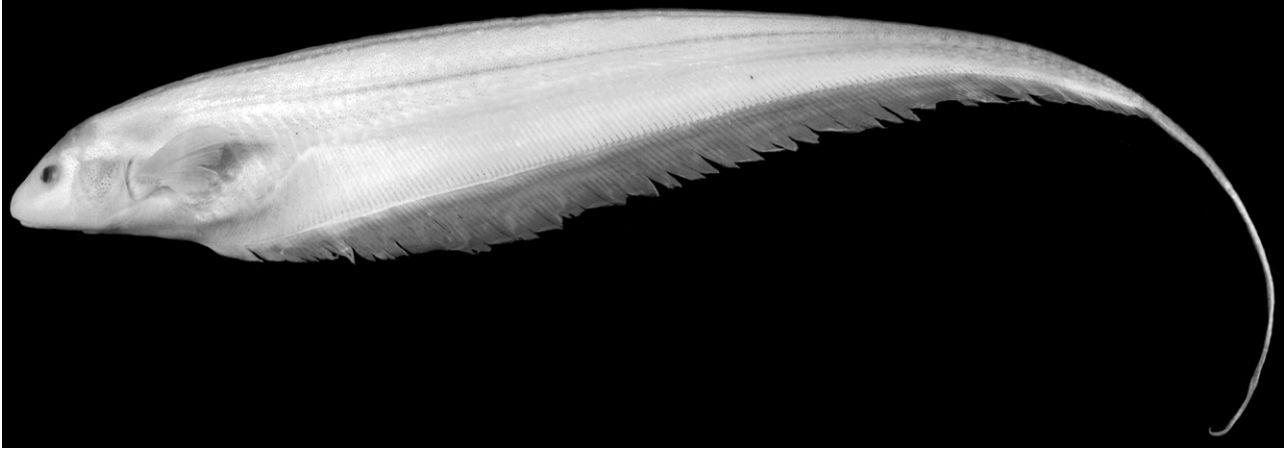


Figure 8. *Archolaemus orientalis* sp. nov., holotype, 156 mm total length, MPEG 21508; Brazil, Minas Gerais, Rio São Francisco system, Rio Piracutu basin, Município Buritizero, Rio do Sono (17°18'S, 045°20'59"W).

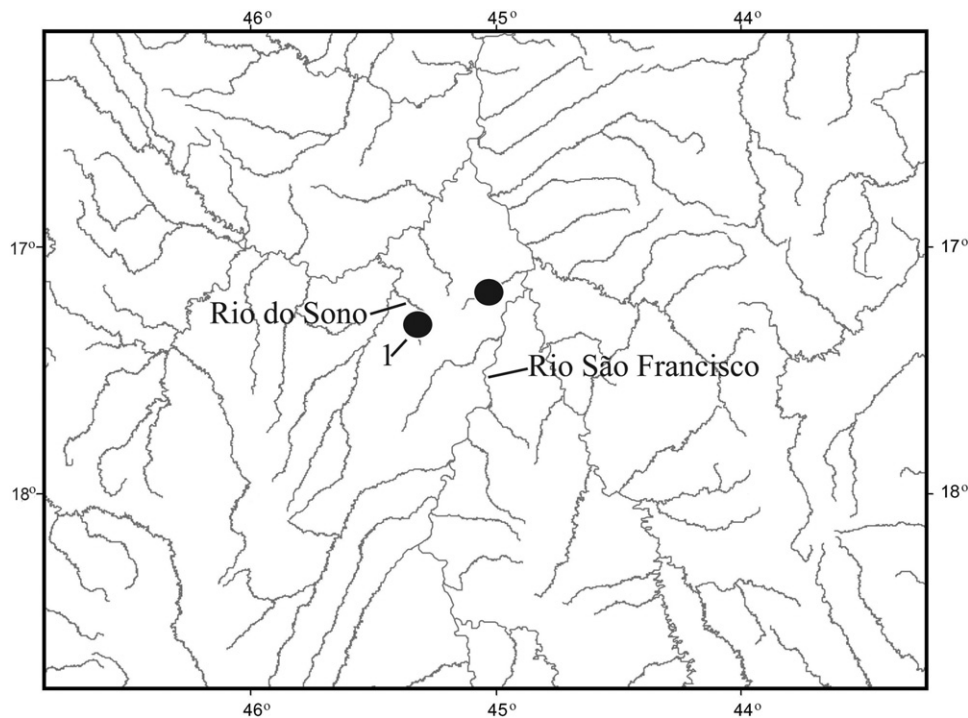


Figure 9. Map of upper portions of Rio São Francisco basin and adjoining areas showing geographical distribution of *Archolaemus orientalis* sp. nov. (1, holotype locality; some symbols represent more than one locality and/or lot of specimens).

talis is additionally diagnosed from *A. ferreirai* in the total number of pectoral-fin rays (16 versus 18–21), the total number of anal-fin rays (164–186 versus 190–222), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), and the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more the length of Meckel's cartilage).

Archolaemus orientalis is further diagnosed from *A. janeae* in the total number of pectoral-fin rays (16 versus 19–21), the total number of anal-fin rays (164–186 versus 205–228), the distribution of the teeth on the dentary (dentition restricted to the anterior one-half or slightly more of the dorsal margin of the dentary versus occupying most of the dorsal margin of the dentary), and the length of the posterior ceratohyal (approximately the same length as the ventral

hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus orientalis* is additionally diagnosed from *A. luciae* in the length of the gape (the rictus falling short of the vertical through the posterior border of the posterior nares versus extending beyond that line), the total number of pectoral-fin rays (16 versus 19–21), the total number of anal-fin rays (164–186 versus 192–213), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), and the length of the coronomeckelian bone (less than 20% of the length of Meckel's cartilage versus 50% or more of the length of Meckel's cartilage). *Archolaemus orientalis* is further diagnosed from *A. santosi* in the total number of pectoral-fin rays (16 versus 19–21) and the total number of anal-fin rays (164–186 versus 192–213).

Description: Morphometric data for the examined specimens of *A. orientalis* are presented in Table 2.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity or slightly posterior to that region. Body profile very gently convex from rear of head for approximately anterior one-third of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body straight to slightly convex along anteriormost portion of base of anal fin, and then gradually angled posterodorsally along base of anal fin and caudal filament. Anterior-most perforated lateral line scale located at vertical approximately at origin of pectoral fin. Lateral line continuous, extending from immediately posterior of vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Head profile convex anteriorly proximate to upper lip, and then straight from that point to rear of head. Ventral profile straight and posteroventrally aligned. Snout subconical and anteroventrally directed; length comparatively short. Eye small and located laterally on dorsal half of head. Orbital rim free, without membrane or attachment to surface tissues of adjoining region of head. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube, and located approximately same distance from tip of snout and anterior margin of eye in adults. Mouth distinctly inferior, with upper jaw clearly longer than, and overlapping, lower jaw. Gape short in specimens of all sizes, extending posteriorly to point short of vertical through posterior naris. Branchial opening moderately elongate, located along posterior margin of opercle and immediately anterior

to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus and extending posteriorly to under pectoral-fin base. Anus proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting ontogenetically from posterior of vertical, through posterior margin of orbit, to under orbit.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Scales along lateral line 120 to 143 (143) ($N = 2$). Fifteen scales above lateral line at midbody (15) ($N = 2$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad, and distally pointed with lateral rays longer. Pectoral-fin rays ii, 16 (16) ($N = 4$). Anal-fin elongate, extending from vertical through base of pectoral-fin base along most of length of body. Fin margin gently convex anteriorly, and then straight for much of length of fin, but with rays becoming progressively shorter posteriorly. Anal fin with 27–32 (27) unbranched rays ($N = 2$) and 164–186 (164) total fin rays ($N = 3$). Caudal filament of moderate length.

Coloration in alcohol: Overall body coloration of head and body tan, with scattered small dark spots somewhat more concentrated dorsally, but not forming any discrete pigmentation pattern. Subset of specimens with series of small dark spots aligned on body surface between basal pterygiophores of anal fin, but with that region of body otherwise hyaline. Line of contact between hypaxial and epaxial muscle sometimes gives appearance of narrow dark line in vicinity of lateral line. Pectoral and anal fins hyaline.

Distribution: *Archolaemus orientalis* sp. nov. is only known from a relatively limited portion of the Rio São Francisco in the state of Minas Gerais, Brazil (Fig. 9).

Habitat: The holotype and paratype from the Rio do Sono in the Rio São Francisco system were collected in a portion of the river characterized by large rapids and a major waterfall, the Cachoeira das Almas, and rocky and sandy substrates. Those specimens were captured approximately 200 m downstream from the Cachoeira das Almas under a partially submerged grassy bank in swiftly flowing, approximately 1.5-m deep water over a sand substrate (T. C. Pessali, pers. comm.)

Remarks: The description of *A. orientalis* from the Rio São Francisco basin represents the first record of the genus from outside the drainages within the Amazon catchment or the Rio Tocantins and Rio Araguari, which empty into or near the lower reaches of that massive drainage system. The holotype

(MPEG 21508) and the paratypes originating with it (MPEG 21509) were collected and originally intermingled with a large series of *Eigenmannia microstoma* (MPEG 20010). The two species are similar to a pronounced degree in their overall external appearances, albeit differing in the form of the mouth and the position of the eye.

Etymology: The species name, *Archolaemus orientalis*, from the Latin for 'of the east' refers to the presence of the species in the Rio São Francisco, the easternmost known occurrence of a species of *Archolaemus*.

Material examined

Holotype: BRAZIL. *Minas Gerais*: Rio São Francisco system, Rio Piracutu basin, Município Buritizério, Rio do Sono (17°18'S, 045°20'59"W), collected by T. C. Pessali, 1 November 2010, MPEG 21508 (156).

Paratypes: BRAZIL. *Minas Gerais*: collected with holotype; MPEG 21509, 1 (150). Pirapora, Rio São Francisco (17°15'S, 045°00'W), collected by J. D. Hase-man, 15 July 1907; FMNH 94418, 3 (120–181; 1 CS).

***ARCHOLAEMUS SANTOSI* SP. NOV.**

(FIGS 10, 11; TABLE 2)

Diagnosis: *Archolaemus santosi* is diagnosed from *A. blax* in the length of the gape (the rictus falling short of the vertical through the posterior border of the posterior naris versus extending beyond that line), the depth of the caudal filament (6.7–9.1% CL versus 5.0–6.5% CL), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus santosi* is diagnosed

from *A. ferreirai* in the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width) and the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more the length of Meckel's cartilage). *Archolaemus santosi* is diagnosed from *A. janeae* by the head length to the rear of the opercle (15.0–16.3% LEA versus 13.5–14.7% LEA), the mouth width (7.0–10.3% HL versus 11.0–19.1% HL), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), the distribution of the teeth on the dentary (dentition restricted to the anterior one-half or slightly more of the dorsal margin versus occupying most of the dorsal margin), and the length of the posterior ceratohyal (approximately the same length as the ventral hypohyal versus 1.5 times the length of the ventral hypohyal). *Archolaemus santosi* is diagnosed from *A. luciae* in the length of the gape (the rictus falling short of the vertical through the posterior border of the posterior nares versus extending beyond that line), the length of the caudal filament (14.4–27.0% LEA versus 28.6–46.1% LEA), the depth of the caudal filament (6.7–9.1% CL versus 3.3–4.8% CL), the form of the premaxilla (the anteroposterior length equal to the transverse width versus the anteroposterior length greater than the transverse width), and the length of the coronomeckelian bone (less than 20% the length of Meckel's cartilage versus 50% or more of the length of Meckel's cartilage). *Archolaemus santosi* is diagnosed from *A. orientalis* by the pigmentation pattern (the presence of a narrow dark stripe along the lateral line and a broad band of dusky to dark pigmentation overlying the basal pterygiophores of the anal fin versus the lack of such dark pigmentation), the total number of pectoral-fin rays (19–21

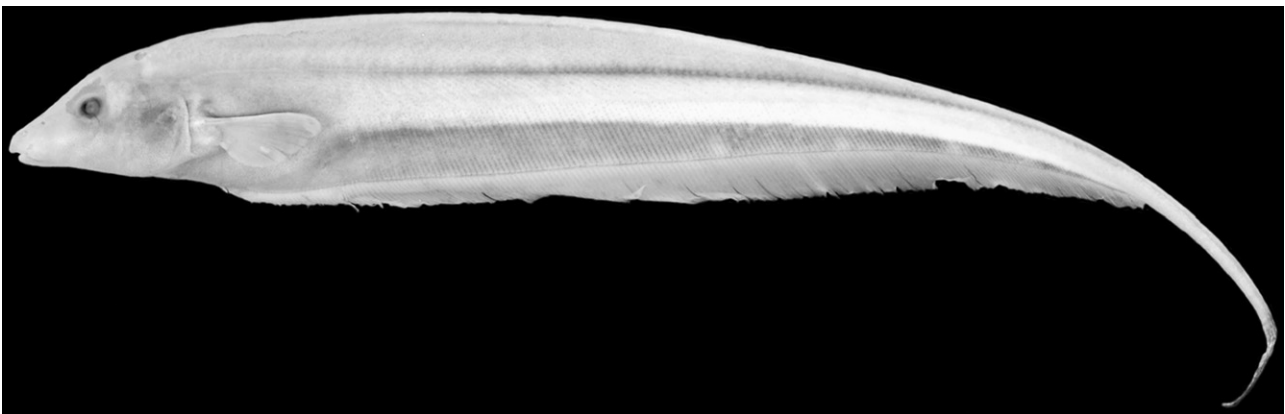


Figure 10. *Archolaemus santosi* sp. nov., holotype, female, 197 mm total length, INPA 20966; Brazil, Rondônia, Rio Jamari, above site of future Usina Hidroelétrica Samuel (approximately 08°27'S, 063°30'W).

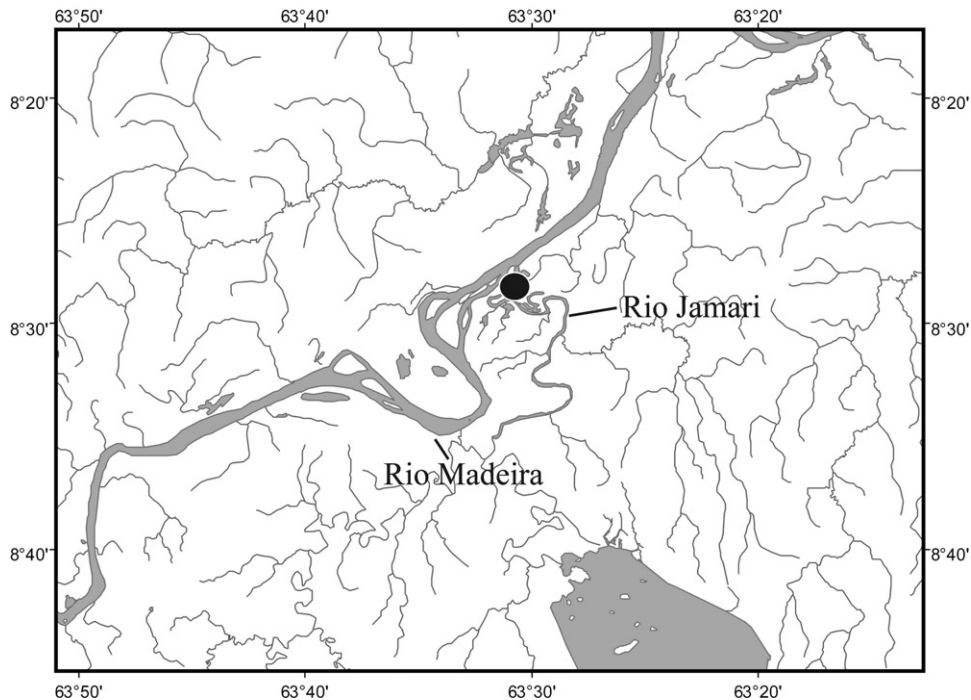


Figure 11. Map of middle portions of Rio Madeira basin and adjoining areas, showing the geographical distribution of *Archolaemus santosi* sp. nov. (the dot indicates the holotype locality and more than one lot of specimens).

versus 16), and the total number of anal-fin rays (204–221 versus 164–186).

Description: Morphometric data for the examined specimens of *A. santosi* are presented in Table 2.

Body elongate and laterally compressed. Greatest body depth located along abdominal cavity in specimens of all sizes. Body profile gently convex from rear of head for approximately anterior one-third of body, and then gradually angled posteroventrally along progressively tapering body and caudal filament. Ventral profile of body straight and posteroventrally aligned in juveniles and convex anteriorly along anterior half of abdominal cavity in larger individuals, and then gradually angled posterodorsally along base of anal fin and caudal filament. Antermost perforated lateral-line scale located at vertical situated approximately at origin of pectoral fin. Lateral line continuous, extending from immediately posterior of vertical through origin of pectoral fin to end of caudal filament.

Head laterally compressed, widest at opercular region and deepest at nape. Head profile convex anteriorly from margin of upper lip in specimens of all sizes, then convex to varying degrees along antorbital region, with concavity more pronounced in larger specimens, and then straight to slightly convex from that point to rear of head in specimens of all sizes. Ventral profile straight and posteroventrally aligned. Snout subconical and anteroventrally directed, mod-

erately elongate in smaller specimens to elongate in larger individuals. Eye small and located laterally on dorsal half of head. Orbital rim covered by membrane and attached to surface tissues of adjoining region of head in two specimens of approximately 73–104 mm TL, partially free on one side in an individual of 103 mm TL, and completely free in larger examined specimens. Anterior naris located at end of short tube and positioned short distance posterior of tip of snout, but distant from anterior margin of eye. Posterior naris elliptical, without tube, and located nearer to tip of snout than to anterior margin of eye in adults. Mouth distinctly inferior, with upper jaw clearly longer than, and overlapping, lower jaw. Gape short in adults, not extending posteriorly to vertical through anterior margin of posterior naris. Branchial opening moderately elongate, located along posterior margin of opercle and immediately anterior to anterior margin of pectoral-fin origin. Branchial membranes joined at isthmus and extending posteriorly to under pectoral-fin base. Anus situated proximate to elongate urogenital papilla, and both structures positioned approximately ventral of orbit. Position of anus and urogenital papilla shifting ontogenetically from distinctly posterior of vertical through posterior margin of orbit in juveniles, to along vertical through eye in largest specimens.

Scales small, cycloid, and present from immediately posterior of head to end of caudal filament. Scales

along lateral line 132 to 147 (147) ($N = 10$). Scales above lateral line at midbody 14 to 17 (17) ($N = 12$). Scales absent on head.

Pectoral fin long, approximately two-thirds of head length, broad, and distally pointed, with lateral rays longer. Pectoral-fin rays between ii, 19 and ii, 21 (21) ($N = 12$). Anal-fin elongate, extending from vertical through base of pectoral fin along most of length of body. Fin convex anteriorly, and then straight for length of fin, but with rays becoming progressively shorter posteriorly. Anal fin with 26–35 unbranched rays (26) ($N = 12$) and 204–221 total fin rays (208) ($N = 12$). Caudal filament of moderate length.

Coloration in alcohol: Overall ground body coloration ranging from tan to brown. Head more lightly pigmented ventrally in specimens across all intensities of dark coloration, with dorsal two-thirds of head together with most of opercle distinctly darker in largest examined specimen. Narrow, dark stripe overlying lateral line for varying distances. Dark pigmentation along lateral line starts posterior of vertical through tip of pectoral fin in very small individuals, but extends anteriorly to beginning of lateral line in larger specimens. Basal anal-fin pterygiophores outlined on body surface by very narrow dark bars that cumulatively form dusky broad band running along ventral portion of body, with height of band gradually decreasing posteriorly. Surface bars along pterygiophore margins expand ontogenetically and coalesce to varying degrees to form solid dark band in larger specimens. Dark stripe along lateral line and dark ventral band separated by more lightly pigmented, broad midlateral stripe. Some specimens with ventral surface of the head tan, but most often with head dark over all surfaces. Pectoral fin hyaline overall, with scattered dark chromatophores. Anal fin hyaline.

Distribution: *Archolaemus santosi* is only known from the type locality at the Rio Jamari in Rondônia, Brazil (Fig. 11).

Habitat: The area of the type locality of *A. santosi* was reported by Santos (1996: 249) as being rapids (= corredeira), indicative of the rapid water flow conditions at the site.

Remarks: *Archolaemus santosi* is only known from juveniles and mature females.

Etymology: The species name, *Archolaemus santosi*, is in honor of Geraldo Mendes dos Santos of the Instituto Nacional de Pesquisas da Amazônia, the collector of the type series, in recognition of his many contributions to our knowledge of the Amazonian fish fauna.

Material examined

Holotype: BRAZIL. Rondônia, Rio Jamari, above site of Usina Hidroelétrica Samuel (approximately 08°27'S, 063°30'W), station Polo 666, collected by G. M. Santos, 4 April 1985; INPA 20966 (197).

Paratypes: BRAZIL. Collected with holotype, INPA 36382, 9 (73–212; 3 CS); MPEG 21686, 1 (100); MZUSP 110185, 1 (132); USNM 404357, 1 (100).

COMPARATIVE CLEARED AND STAINED MATERIAL EXAMINED

Apteronotidae. *Apteronotus* cf. *albifrons*, MPEG 2434, 1 (114), Brazil, Rio Goiapi. *Adontosternarchus sachsi*, INPA 18277, 2 (119–1220), Brazil, Rio Japurá. *Compsaraia compsus*, INPA 28916, 2 (116–120), Brazil, Rio Negro. *Sternarchogiton preto*, INPA 28906 1 (69), Brazil, Rio Negro. *Sternarchorhynchus mesensis*, MNRJ 11611 (2), 130–140 mm, Brazil, Rio Tocantins.

Sternopygidae. *Distocyclus conirostris*, INPA 28879, 2 (142–239); INPA 28915, 2 (135–158), Brazil, Rio Negro. *Eigenmannia limbata*, INPA 18288, 2 (137–176), Brazil, Rio Japura. *Eigenmannia* cf. *macrops*, INPA 22687, 2 (65–153), Brazil, Rio Uatumã. *Eigenmannia macrops*, INPA 33259, 2 (67.7–94.1), Brazil, Rio Solimões. *Eigenmannia* gr. *trilineata*, MPEG 6887, 1 (167), Brazil, Rio Capim. *Japigny kirschbaum*, FMNH 50185, 3 (100–130), Guyana, New River. *Rhabdolichops eastwardi*, INPA 12361, 2 (60–172), Brazil, Rio Negro. *Rhabdolichops troscheli*, INPA 12363, 3 (70–174), Brazil, Rio Negro. *Sternopygus astrabes*, INPA 30502, 2 (112–156), Brazil, Rio Negro. *Sternopygus macrurus*, INPA 4869, 4 (31.9–84.1), Brazil, Rio Solimões, Lago Castanho; INPA 16001, 1 (27), Brazil, Rio Urubu.

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