PHYLOGENETIC RELATIONSHIPS OF FOSSIL NEOTROPICAL ELECTRIC FISHES (OSTEICHTHYES: GYMNOTIFORMES) FROM THE UPPER MIOCENE OF BOLIVIA

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ABSTRACT— Fossil specimens of Neotropical gymnotiform electric fishes from the Yecua Formation (Upper Miocene, Parana basin, Bolivia) are analyzed in the context of a comprehensive study of gymnotiform relationships. Each fossil is analyzed individually and placed in the phylogeny according to characters it actually possesses. Some of the fossils previously referred to *Humboldtichthys kirschbaumi* can be identified only as Gymnotiformes *incertae sedis*, others as *incertae sedis* within recognized suprageneric gymnotiform taxa. The holotype of *H. kirschbaumi* shares the presence of a striated opercle with some extant species of *Sternopygus* and *Distocyclus* and can be placed in the Recent gymnotiform family Sternopygidae; *H. kirschbaumi* is diagnosed by the presence of a deeply striated opercle in which the striations extend between the dorsal and ventral opercular ridge fields. The analysis indicates the presence of several taxa among the fossil material. The presence of a multispecies assemblage is not uncommon among Recent gymnotiforms inhabiting non-floodplain forest streams, the inferred preservational environment.

INTRODUCTION

The first known fossilized remains of gymnotiform electric fishes were collected by petroleum geologists from alluvial deposits of the Río Alto Moile basin, Parana drainage, in a forest locality about 95 km west-northwest of Santa Cruz, Bolivia (López-Murillo, 1975). These specimens were taken from the Yecua Formation (Upper Miocene, c. 10 Ma, Marshall and Sempere, 1991), a proto-Parana drainage (Lundberg, 1998), and described as gymnotiform electric fish based on a number of easily recognizable features shared with extant gymnotiform species (Gayet and Meunier, 1991). Notably, the fossils exhibit an elongate anal fin with numerous fin rays and numerous proximal anal-fin pterygiophores, three rows of heavily ossified intermuscular bones, and, in one specimen, the impression of a regenerated caudal appendage. A new taxon was named, *Ellisella kirschbaumi* (Gayet and Meunier, 1991), to honor Max Ellis and Frank Kirschbaum, pioneers in the study of gymnotiform growth and regeneration (Ellis, 1913; Kirschbaum, 1994). The generic name was subsequently replaced by *Humboldtichthys* (for reasons detailed subsequently).

Based largely on the inferred presence of an adipose fin along the posterodorsal margin of the specimen with the regenerated posterior part of the body, it was hypothesized that these specimens represent a primitive gymnotiform, the sister taxon to all other gymnotiforms except Apteronotidae (Gayet et al., 1994). The 10 (perhaps 11) specimens presently known are all fragmentary, and none include a complete head or the posterior part of the abdominal cavity, regions which would provide important information for identifying this material with confidence. All of these fragments possess features of Gymnotiformes, although they differ in certain anatomical details. Here we review the anatomical characters of the specimens ascribed to *Hum-*

boldtichthys in the context of morphological data derived from recent phylogenetic studies of extant Gymnotiformes (Albert, 2001; Albert and Crampton, 2005) and Sternopygidae (Albert, 2003; Hulen et al., 2005; Correa et al., 2006). Our analysis indicates that there are several taxa among the fossil material, and that the holotype can be placed in the Recent gymnotiform family Sternopygidae.

MATERIALS AND METHODS

All fossil specimens were examined by JSA under a dissecting microscope at the Centre des Sciences de la Terre, Université Claude Bernarde, Lyon, France. They had been mechanically prepared by Dr. M. Gayet and were coated with phosphate ash before photographs were taken, to highlight shadows and increase contrast. The fragmentary nature of the fossil material makes it unsuitable for inclusion in the large data matrix of Albert (2001). Instead, we place each fragment into his tree according to the features it exhibits. In his study, Albert (2001) examined 900 museum lots containing over 4,200 specimens, representing more than 100 gymnotiform species, and all 29 of the then recognized genera. We present a subset of that data matrix, including only features available in the fossils, resulting in a table of 31 characters for 38 OTUs (Appendices 1 and 2). Character descriptions include plesiomorphic (0) and apomorphic (1) conditions based on outgroup taxa selected from previous studies on ostariophysan interrelationships (Fink and Fink, 1981, 1996; Grande, 1987; Fink and Fink, 1996).

Multiple members of each outgroup taxon were examined to estimate the plesiomorphic condition (Albert, 2001). Each fossil was placed on the tree in a position of maximum parsimony according to evidence available for that specimen using MacClade 4.03 (Maddison and Maddison, 1992) to visualize alternative placements.

Species composition of Sternopygidae follows Albert (2003). Nomenclature follows Patterson (1975) for bony elements of the

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skull, and Weitzman (1962) and Fink and Fink (1981) for the rest of the skeleton. Following Ellis (1913) and Kirschbaum and Meunier (1981) the term "caudal appendage" is used rather than "caudal filament." Whereas the term "filament" implies a one-dimensional homogenous line, the caudal appendage of gymnotiform fishes is a complex structure which, depending on taxon and extent of regeneration, may be composed of numerous skeletal elements (vertebrae or a cartilaginous/collaginous rod, pterygiophores, anal-fin rays, intermuscular bones), muscles (axial and pterygiophore), blood and lymphatic vessels, and spinal cord and segmented spinal nerves.

Meristic and mensural data were taken according to Mago-Leccia (1994), Albert and Campos-da-Paz (1998), and Albert (2001); body sizes and proportions used in character descriptions are defined by Albert and Fink (1996); and laterosensory terms are defined by Albert and colleagues (1998). Osteological data of extant gymnotiform species were taken from cleared and stained specimens using the techniques of Taylor and Van Dyke (1985). We used standardized micro-dissection methods for small teleosts (Weitzman 1974). Drawings of cleared and stained specimens were made with the aid of a drawing tube, and subsequently scanned and edited with computer software.

Abbreviations—**MCP**, Museu de Ciências e Tecnologia de PUCRS; **UF**, University of Florida, Florida Museum of Natural History; **RL**, collection of Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, Bolivia.

<div align="center">SYSTEMATIC PALEONTOLOGY</div>

<div align="center">Class OSTEICHTHYES Huxley, 1880
Order GYMNOTIFORMES Regan, 1911
Family STERNOPYGIDAE Cope, 1871
HUMBOLDTICHTHYS Gayet and Meunier, 2000</div>

Diagnosis—A gymnotiform fish (recognized by an elongate anal-fin with its origin anterior to the pectoral girdle) with deep radial striations extending over the majority of the lateral surface of the opercle, with the striations also extending between the dorsal and ventral opercular ridge fields. Based on the holotype of *H. kirschbaumi*, RL 1596-4.

Nomenclature—*Humboldtichthys* Gayet and Meunier (2000) is a replacement name for *Ellisella* Gayet and Meunier (1991), which is preoccupied by *Ellisella* Gray (1858), a coelenterate, and by *Ellisella* Rohr (1980), a gastropod (Bayer and Grasshoff, 1994; Rohr and Huddleston, 1982). Based on the analysis below, we restrict the name *H. kirschbaumi* to the holotype (RL 1596-4: Gayet and Meunier, 1991:fig. 1).

<div align="center">HUMBOLDTICHTHYS KIRSHBAUMI
(Gayet and Meunier, 1991)
(Fig. 1A)</div>

Diagnosis—As for genus, monotypic.

Holotype—Incompletely preserved fragment of the anterior portion of the body and the posterior portion of head, including the opercle and preopercle, oriented with anterior to the right. RL 1596-4 (Gayet and Meunier, 1991:fig. 1).

Horizon and Type Locality—Upper Yecua Formation (possibly Chasiquien or Lower Huaquérien), Lower Tortonian, Upper Miocene, from the Río Alto Moile basin, about 95 km west-northwest of Santa Cruz, Bolivia (López-Murillo, 1975; Marshall et al., 1993). The enclosing matrix is pale yellowish brown, fine mudstone.

Description—The holotype is a fragment of the right size of the body with a long axis about 5.5 cm, bearing impressions of an opercle and preopercle, and parts of the anterior portion of the body. The surface of the opercle and preopercle is lamellar with
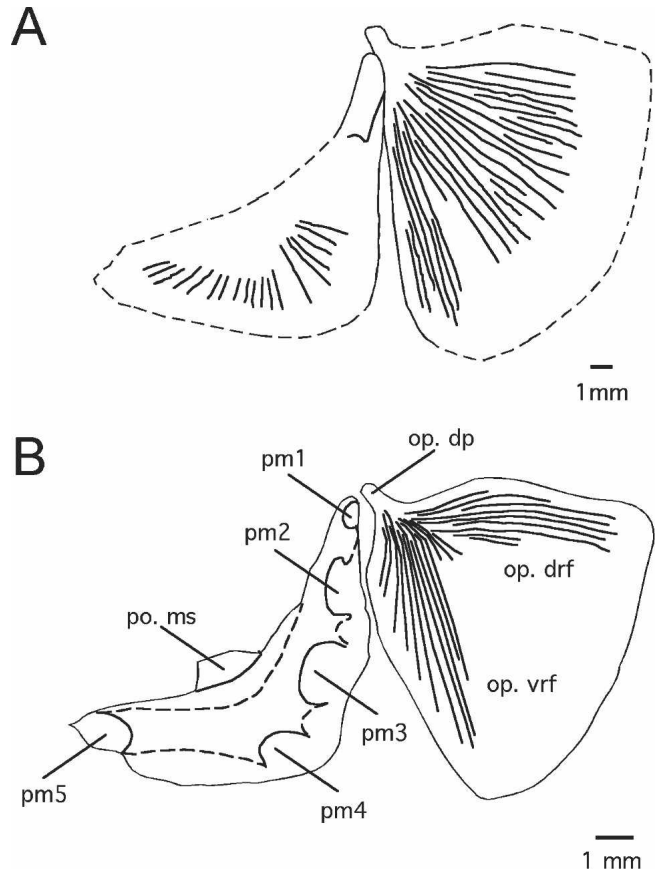

FIGURE 1. Comparisons of the preopercle and opercle in two sternopygid fishes. **A**, *Humboldtichthys kirschbaumi* RL 1596-4. **B**, *Sternopygus macrurus* UF 80862 (185 mm TL). Anterior to left; in **A** the image was flipped horizontally for purposes of comparison. Dashed lines in **A** indicate approximate bony margins. Note the thin parallel ridges on the opercle, and radiating ridges of the collapsed laterosensory canal on preopercle. **Abbreviations**: **op. dp**; dorsal process of opercle; **op. drf**, opercular dorsal ridge field; **op. vrf**, opercular ventral ridge field; **pm**, preopercular-mandibular laterosensory line pore (numbered 1-5 from medial to distal); **po. ms**, preopercular median shelf.

numerous radial striations. The preopercle is oriented oblique to the main axis of the head, and its anterior limb is broad and crescent-shaped. The dorsal limb of the preopercle has a portion of a relatively broad preopercular-mandibular laterosensory canal. The opercle is approximately triangular with slightly convex dorsal, posterior, and ventral margins. The precise shape of these bones is not known as their margins are incompletely preserved or incompletely exposed by preparation. Impressions of proximal anal-fin pterygiophores and rays indicate the origin of the anal fin is immediately posteroventral to the posterior margin of the operculum. The pectoral fin has at least 10 rays, and apparently is displaced approximately 1 to 2 cm posteriorly. The pectoral-fin insertion is not preserved. There are impressions of several thin broken ribs, eight precaudal vertebrae, and portions of six neural spines. The ribs are relatively short, compared with the body depth. The anal fin is present as parts of 28 proximal pterygiophores and proximal parts of about 15 fin rays, all of which are unbranched. Intermuscular bones are multiply branched, with three to five rami on the distal tips of most elements.

Additional Materials—An additional six specimens were referred to *H. kirschbaumi* by Gayet and Meunier (1991), all presumed to be from the same locality and approximately the same

horizon. 1. RL 1596-1, caudal body with a regenerated caudal appendage, anterior to left (Fig. 2A; Gayet et al., 1994, figs. 2A, 3). 2. RL 1596-3, elongate mid-body fragment, anterior to right (photograph in Gayet et al., 1994:fig. 2B). 3. RL 1596-5, isolated opercle, lateral exposure, anterior to right. 4. RL 1596-7, long mid-body fragment, anterior to left. 5. RL 1596-13, short mid-body fragment, anterior to left. 6. RL 1596-15, long mid-body fragment, anterior to the left. In JSA's examination of these materials, he found a mid-body fragment, anterior to the left with RL 1596-5 inscribed on it; he was unable to locate the isolated opercle published with that number. Below we refer to this mid-body fragment as RL 1596-5. In addition, three unnumbered fossil gymnotiform specimens were examined: specimen RL uncat. A, long mid-body fragment, anterior to right; specimen RL uncat. B, long posterior-body fragment, anterior to right; and specimen RL uncat. C, short mid-body fragment, anterior to right.

All six of the catalogued specimens possess numerous caudal vertebrae with hemal spines, anal-fin pterygiophores, and anal-fin rays, arranged in series indicating a highly elongate body. These specimens also possess neural spines that contact the neural arches at the posterior portion of the vertebral segment, and neural arches with one to several small fenestrae. No dorsal or pelvic fins were observed in any specimens. There are numerous unbranched anal-fin rays in most specimens, although the posterior unregenerated anal-fin rays of specimen RL 1596-1 are deeply branched (Fig. 2A). The anal-fin pterygiophore blades are slender, with their tips tapering to a point, and no distal anal-fin pterygiophores are preserved.

1. Specimen RL 1596-1 possesses part of a regenerated caudal appendage (Fig. 2A; Gayet et al., 1994, figs. 2A, 3). There are 13 vertebrae (including vertebral impressions), not 12 as figured in Gayet et al. (1994), 13 complete hemal spines, and the ventral half of one hemal spine at the anterior of the specimen. There are 20 anal-fin rays in the non-regenerated portion, 10 of them are unbroken, long and deeply branched, and there are more than 50 unbranched anal-fin rays in the regenerated portion, which do not extend to the caudal margin of the fossil. The unregenerated anal-fin rays are longer than the proximal anal-fin pterygiophores and the length of these pterygiophores is greater than the length of the hemal spines at mid-body. There are three rows of intermuscular bones (sensu Patterson and Johnson, 1995), and the dorsal margin of the body outline is lacking intermuscular bones. There are impressions of numerous ridged cycloid scales above the hemal spines near their margin with the pterygiophores at the posterior of the unregenerated body portion (Gayet et al., 1994:fig. 2D, figure inverted with respect to 2A, as dorsal is to bottom and anterior to right). There is no regeneration of neural or hemal spines. An elongate relatively thick caudal rod is present, with no associated neural or hemal spines (the caudal rod of extant Gymnotiformes is a cartilaginous or collaginous bar generated to replace vertebral centra in some extant gymnotiforms). There are no clear impressions of regenerated caudal intermuscular bones. The bony elements are dark brown and flaky.

2. Specimen RL 1596-3 is part of the ventral portion of the body, with impressions of 16 vertebrae and hemal spines on the dorsal margin of the fragment, 58 pterygiophores, and the proximal parts of a similar number of anal-fin rays (Gayet et al., 1994:fig. 2B).

3. Specimen RL 1596-5 has 11 vertebrae and vertebral impressions, each with a long, curved hemal spine inserting deeply between proximal tips of the proximal anal-fin pterygiophores. The distal flexion of these hemal spines is different from the straight or curved hemal spines of the other fossil specimens and all extant gymnotiforms, and may be a preser-
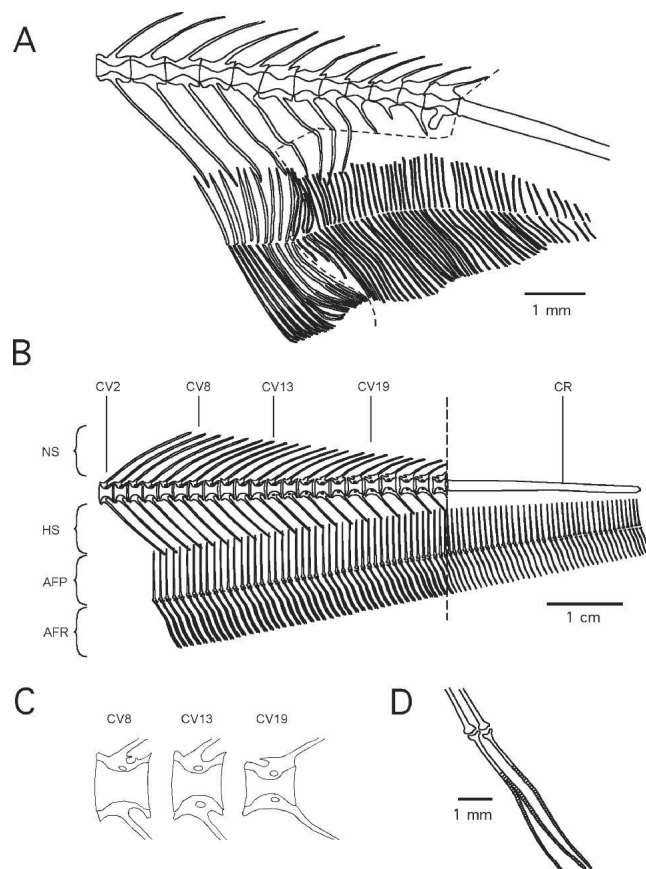

FIGURE 2. Comparisons of portions of the postcoelomic axial skeleton in two sternopygid fishes. **A**, *Humboldtichthys kirschbaumi* (RL 1596-1). **B**, *Distocyclus conirostris* (MCP uncat. WGRC 21.020999; 180 mm TL). Anterior to left; regions posterior to dashed lines in **A** are inferred to be regenerated. Intermuscular bones omitted for clarity. **C**, enlarged views of three caudal vertebrae of *D. conirostris*: CV8 with neural and hemal spines attached to arches at middle of centrum; CV13, fenestrae on neural and hemal arches. CV19, neural and hemal spines attached to arches at posterior margin of centrum. **D**, anal-fin rays of *D. conirostris*: branched (unregenerated) and unbranched (regenerated). **Abbreviations**: **AFP**, anal-fin pterygiophores; **AFR**, anal-fin rays; **CV**, caudal vertebra; **CR**, caudal rod; **HS**, hemal spines; **NS**, neural spines.

vational artifact. The distal tips of pterygiophores clearly form ball-and-socket joints with the proximal ends of the anal-fin rays. Despite this fine level of preservation and the numerous impressions of fine intermuscular bones, there are no impressions of distal anal-fin pterygiophores.

4. Specimen RL 1596-7 is the largest of the fossil gymnotiform fragments ascribed to *H. kirschbaumi* by Gayet and colleagues (1994). Its long axis is 11.3 cm. There are 20 vertebrae and 7 additional vertebral impressions, 34 complete hemal spines or impressions, with the anterior hemal spines more curved than the posterior. There are about 137 short unbranched anal-fin rays, no distal anal-fin pterygiophores, and numerous intermuscular bones arranged into three rows. The anal-fin pterygiophores are longer than the hemal spines at the mid-body.

5. Specimen RL 1596-13 has 60 unbranched anal-fin rays, but the tips are not preserved. There are three rows of intermuscular bones, three intact vertebrae, and the impressions of six more vertebrae.

6. Specimen RL 1596-15 has 84 deeply branched anal-fin rays, and the distal tips of 5 hemal spines.

7. Specimen RL uncat. A has 98 deeply branched anal-fin rays, and an approximately equal number of pterygiophores of about equal length to the fin rays.

8. Specimen RL uncat. B has anal-fin pterygiophores longer than the hemal spines at the mid-body, resembling RL 1596-7. There are about 30 neural spines, vertebrae and vertebral impressions, and anal-fin pterygiophores, and about 60 unbranched anal-fin rays.

9. Specimen RL uncat. C has 20 anal-fin rays and 4 vertebrae.

Paleoenvironment—The Yecua Formation in the northern Río Alto Moile basin is mainly composed of continental alluvial facies (Marshall and Sempere, 1991). There are no volcanic basalts or tuffs in the Yecua Formation so radioisotope dating is not possible, and paleomagnetic and stratigraphic studies have not yet been performed. Specimen RL 1596-14 contains the caudal portion of the body of a catfish, specimen RL 1596-9 contains pieces of the caudal fin of an unidentified small-bodied characin, and specimen RL 1596-6 contains pieces of the blades of an aquatic macrophyte resembling grass. Other organisms described in this formation by Marshall and Sempere (1991) include an unidentified distal limb bone of a litoptern mammal (cf. *Thesodon* sp.), an indeterminate rodent tooth, and characin and catfish remains. Marshall and colleagues (1993) report the presence of teleost vertebrae, several pelycopods, wood fragments, and leaf impressions from a nearby locality (base of Tariquía Formation). The presence of *Thesodon* sp. implies the locality is Chasicoan in age (i.e., 11 to 9 Ma.; Marshall and Sempere, 1991). These data indicate the environment of preservation was a small, terra firme (non floodplain) stream with slowly moving water (Marshall et al., 1993), a common habitat for multispecies assemblages among Recent gymnotiforms (Crampton, 1998; Albert, 2001).

PHYLOGENETIC POSITIONS OF
FOSSIL GYMNOTIFORMES

Gayet and colleagues (1994:fig. 11) proposed that *H. kirschbaumi* (then called *Ellisella kirschbaumi*) is the sister group to a clade consisting of all extant gymnotiforms except Apteronotidae. This position was based primarily on the presence of a regenerated caudal appendage and the inferred presence of an adipose fin in specimen RL 1596-1, as well as a large proximal articulation of the hyomandibula in specimen RL 1596-4. The caudal appendage of gymnotiforms is the portion of the body posterior to the last anal-fin ray (Kirschbaum and Meunier, 1981). The significance of the hyomandibula articulation is unclear; outgroup comparison shows the "large" articulation to be a primitive feature at this level. Additional characters posited as evidence for this placement by Gayet and colleagues in support of their hypothesis include the position and shape of the anguloarticular, the number of post-cleithra, and a lack of regenerated intermuscular bones; none of these features is discernable on the fossil specimens.

In this study, we individually analyzed the fossil fragments ascribed to *H. kirschbaumi,* placing them in our phylogenetic hypothesis according to their particular traits. We do this for two reasons. First, the fragments preserve different amounts of morphological data, ranging from impressions of the anal fin to segments of the middle and posterior portions of the body. Also, it is common for extant gymnotiforms to occur in multi-species assemblages (Crampton, 1998; Albert and Crampton, 2001; Albert and Crampton, 2005), so there is reason to doubt that the fragments necessarily represent a single species. Figure 3 summarizes their placement on a reduced taxon cladogram from Albert (2001). The main phylogenetic results of this analysis are presented below, in which we describe the particular features that allow most precise placement of each fossil specimen. We
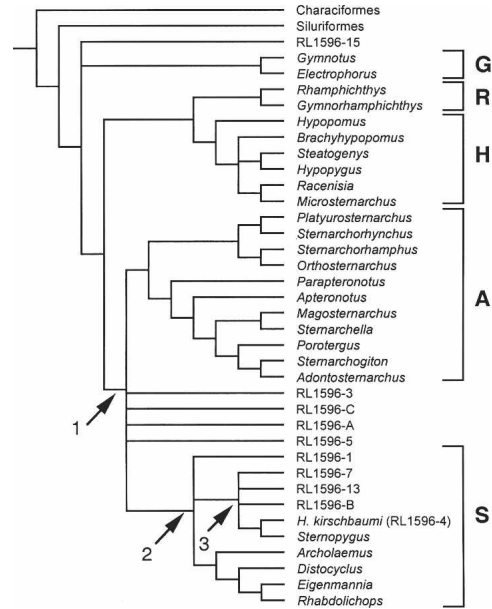

FIGURE 3. Phylogenetic positions suggested by available data of 10 fossil gymnotiform fragments on the tree topology of Albert (2001). Note four fossil fragments are placed *incertae sedis* within the Sinusoidea (1, Apteronotidae + Sternopygidae), the fossil fragment with the regenerated caudal region (RL-1596-1) is placed within the Sternopygidae (2), and four fossil fragments (including the holotype of *Humboldtichthys kirschbaumi* RL-1596-4) are placed closer to *Sternopygus* (3) than any other extant gymnotiform genus. **Abbreviations: A,** Apteronotidae; **G,** Gymnotidae; **H,** Hypopomidae; **R,** Rhamphichthyidae; **S,** Sternopygidae. Numbered nodes indicate three inclusive clades within which the fossils are placed: 1, Sinusoidea. 2, Sternopygidae. 3, *Sternopygus+ Humboldtichthys+*3 fossil specimen. Note RL 1596-15 is placed as Gymnotiformes *incertae sedis*.

also include information about data present in specimens that might exclude them from some groups (e.g., retention of primitive features that might exclude membership from a crown group [although the trait could be reversed]). Given the incompleteness of the specimens, there are alternative placements that are equally parsimonious for some specimens. The features, including those apomorphies that support more inclusive clade membership, are summarized for each taxon in Appendix 2. We emphasize that the placement of each fragment is not to be interpreted as the actual phylogenetic position of the specimen; rather, it is the placement allowed by available data. In some cases, the specimen could be moved to other places in the tree, giving the same tree length. But because of the large number of missing characters, we have hand-placed each fragment according to the most restrictive feature(s) available.

Fragment 1596-15 is identifiable only as a gymnotiform, sharing with members of that group an elongate anal fin (character 17) and the anal-fin articulation being with the proximal pterygiophores (character 18). This specimen also lacks one of the diagnostic features of S*ternopygus*, character 19 (also found in *Sternarchorhamphus* and *Orthosternarchus*).

Specimens 1596-3, 1596-5, 1596-A and 1596-C are identifiable as Sinusoidea *incertae sedis* (Albert, 2001) based on the attachment of neural spines to the posterior portions of the neural arches (character 10). Specimens 1596-3, 1596-5, 1596-A also have a sinusoid feature: presence of vertebral fenestrae (character 11). The following characters are scored as plesiomorphic for these specimens: slender descending blades of proximal anal-fin pterygiophores (character 21, present in some apteronotids); anal-fin pterygiophores tapered smoothly to tips (character 22,

present in some apteronotids); and hemal spines present (characters 25, diagnostic of *Electrophorus*). Specimens 1595-3 and 1596-5 have anal-fin pterygiophores shorter than hemal spines at midbody (the plesiomorphic condition of character 20; derived condition diagnostic of Gymnotidae, Rhamphichthyidae, some apteronotids, and a group comprised of *Distocyclus*, *Rhabdolichops*, and *Eigenmannia*). Specimen 1596-A has the plesiomorphic morphology of branched anal-fin rays (character 19; unbranched anal-fin rays present in the sternopygid *Sternopygus*, and the apteronotids *Sternarchorhamphus* and *Orthosternarchus*).

Specimen 1596-4, the holotype of *H. kirschbaumi*, is placed as sister group to extant species of *Sternopygus* by the presence of a striated opercle. The striations on the opercle of *H. kirschbaumi* are significantly more deeply etched than we have found in *Sternopygus*. Specimen 1596-4 also has an anteriorly placed anal-fin origin (character 16), which is a feature of the Sinusoidea. The anterior placement of the anal-fin origin is also present in rhamphichthyids, where it is located at the branchial isthmus. Specimen 1596-4 also retains primitive states for a large number of features, including a lamellar surface texture of the bones (character 3, vs. a highly pitted or reticulate surface in many deep river channel apteronotids and sternopyids), the orientation of the hyomandibula oblique to that of the head (character 4, vs. parallel in Rhamphichthyidae), preopercle robustly ossified and crescent-shaped (character 6, vs. approximately parallel with main axis of head poorly ossified, anterior limb narrow in Rhamphichthyoidea, *Steatogenys* and Apteronotidae), dorsal margin of opercular (character 8, vs. straight or convex in *Electrophorus* and some apteronotids), eight or more pairs of ribs (character 26, vs. five to seven pairs of ribs in *Distocyclus*, *Rhabdolichops*, and *Eigenmannia*), relatively short anterior ribs (character 27, vs. relatively long anterior ribs in *Archolaemus*, *Distocyclus*, *Rhabdolichops*, and *Eigenmannia*), and narrow anterior ribs (character 28, vs. broad anterior ribs in *Electrophorus*, some *Gymnotus,* and some apteronotids).

Specimen 1596-1 can be placed as Sternopygidae *incertae sedis*, due to its possession of a relatively thick caudal rod with neural and hemal spines (character 31, state 2). Features that exclude this specimen from other gymnotiform taxa include the presence of scales (character 2, vs. no scales in *Electrophorus*), absence of a dorsal organ (character 13, vs. present in Apteronotidae), branched anal-fin rays (character 19, vs. unbranched in *Sternopygus*, *Sternarchorhamphus*, and *Orthosternarchus*), anal-fin pterygiophores shorter than hemal spines (character 20, vs. short [character with wide homoplastic distribution, see Appendix 2]), slender descending blades of proximal anal-fin pterygiophores (character 21, vs. broad in some apteronotids), anal-fin pterygiophore tapered smoothly to tips (character 22, vs. broad and arrow-head shaped in some apteronotids), free neural and hemal spines associated with regenerated cartilaginous rod (character 24, vs. no regenerated spines in Gymnotidae), presence of hemal spines (character 25, vs. no hemal spines in *Electrophorus*), and inferred absence of a caudal fin or hypural plate (character 30, vs. presence of caudal fin and hypural plate in apteronotids). Gayet and colleagues (1994) and Meunier and Gayet (1991) claim that this specimen totally lacks regenerated intermuscular bones; if that is true then such lack would be unique within sinusoids, implying that the specimen lies outside that group. However, the fossil preservation is, as Meunier and Gayet put it, "mediocre." Lack of fine and poorly ossified regenerated intermuscular bones in the fossil is here regarded as equivocal. The specimen also has anal-fin rays that are exceptionally long in relation to body depth; this feature serves to distinguish the specimen from extant sternopygids.

Specimens 1596-7, 1596-13, and 1596-B are all placed as *Sternopygus incertae sedis* by their possession of unbranched anal-fin rays (character 19). This feature is found homoplastically in the rhamphichthyid *Gymnorhamphichthys* and the apteronotids *Sternarchorhamphus* and *Orthosternarchus*. However, these specimens lack synapomorphies that would place them with other gymnotiform taxa; for example, tapered anal fin pterygiophores (the plesiomorphic state of character 22) which diagnoses the clade composed of *Sternarchorhamphus* and *Orthosternarchus*. Specimen 1596-7 and 1596-B both have distal anal-fin pterygiophores, the primitive state of character 23, which is found in its derived state in Gymnotidae and Rhamphichthyoidea. In addition, all three specimens have slender anal-fin pterygiophores (the primitive state of character 21), which is derived in some apteronotids, and they also have hemal spines (the absence of which characterizes *Electrophorus*).

DISCUSSION

Comparisons among the Fossil Fragments

The 11 fragments of the nominal taxon *H. kirschbaumi* described here were collected from approximately the same locality and geological formation. Because the majority of the features exhibited by these specimens are similar, superficially they might be thought to represent a single taxon. This is because most of the specimens lack critical features used to identify higher gymnotiform taxa. One feature clearly shows that some of the specimens attributed to *H. kirschbaumi* represent more than one species. Specimens 1596-1, 1596-15, and 1596-A all have branched anal-fin rays (the plesiomorphic state of character 19) while 1596-7, 1596-13, and 1596-B all have unbranched rays (the derived state of character 19).

Preservational Concerns

Several of the characters originally used in the placement of these fossils may have been defined or coded incorrectly as the result of preservational artifacts. For example, our interpretation that there is no adipose fin in RL 1596-1 contradicts the interpretation of Gayet and Meunier (1994). No extant gymnotiform possess an adipose fin; based on histological and morphological criteria, the dorsal organ of apteronotids is not regarded as an adipose fin (Franchina and Hopkins, 1996; Albert, 2001). We suspect that the zone of the dorsal body outline, which is free of intermuscular bones in RL 1596-1, is a preservational artifact resulting from compression. Among extant gymnotiforms, the dorsal carinal muscles extend along the dorsal body margin, and do not contain strongly ossified intermuscular bones. The supposed absence of intermuscular bones in the regenerated caudal region was also used by Gayet and colleagues (1994) to indicate plesiomorphic affinity with apteronotids, which do not regenerate the caudal intermuscular bones. We consider the presence or absence of regenerated intermuscular bones as problematic; these bones are fewer and more lightly ossified than the original bones in the extant gymnotiforms that regenerate these bones, and unlike the original bones, are rarely observed in radiographs.

No extant *Sternopygus* or other gymnotiform species possess striations on the preopercle. We interpret the supposed preopercular striations in *H. kirschbaumi* as impressions of collapsed laterosensory canals. The portion of the laterosensory canal extending over the preopercle in sternopygid fishes is large and partially fused with the bone. The incomplete preservation of this canal on the dorsal portion of the bone is not unexpected given the relatively poor quality of preservation. The preopercle illustrated by Gayet and colleagues (1994) depicting specimen 1596-4 is interpreted by them as possessing a sensory canal adjacent to the dorsal tip of the bone. Clear preservation of only this dorsal portion of the canal would be unusual in gymnotiforms, which have similarly sized and largely closed, ossified

canals over other parts of the preopercle. This morphology could result from fossilization of a sternopygid; however, because the other portions of the preopercular canals on sternopygids are not closed over with ossification but are mostly open, with thin roofing ossification and only a few thin struts attaching the roofing ossification of the canals to the main body of the bone. Crushing of these large, open canals in the fossilization process would result in a pattern resembling striations.

The opercular striations in *H. kirschbaumi* are more extensive than, yet not qualitatively different from, those of extant *Sternopygus* species. Opercular striations in mature specimens of *Sternopygus* range from complete absence in certain specimens collected in Amazonian black waters, to the fully striated dorsal and ventral fields observed in *Sternopygus macrurus* collected from Amazonian and Orinocoan white waters (e.g., UF 80862; Fig. 1B). The margins of the opercle and preopercle of *H. kirschbaumi* are poorly preserved, which obscures interpretation of their shapes; uncertain margins of these bones are indicated by dashed lines in Figure 1A. The posterior and ventral margins of the opercle and preopercle in many extant gymnotiforms are thin and membranous, often being incompletely ossified, grading from very thin and transparent bone to an unssossified membrane. In *Sternopygus*, the extent and rugosity of these striations may be reduced or lost in individuals of larger body sizes (c. 300-600 mm TL). In some populations of *Distocyclus conirostris* and *Gymnotus carapo* striations are observed in medium to large specimens (150-400 mm TL).

Characters of Regeneration—Three of the characters used in the phylogenetic placement of the fossilized fragment RL 1596-1 involve aspects of caudal appendage morphology and regeneration. Regeneration is a natural and common aspect of the life history and ontogeny of gymnotiform fishes (Ellis, 1913) and the developmental biology of caudal appendage regeneration has been well studied in a comparative context (Kirschbaum and Meunier, 1981; Meunier and Kirschbaum, 1984; Zakon and Unguez, 1999; Albert, 2001). Two features of caudal appendage regeneration and one of unregenerated caudal vertebral morphology permit the phylogenetic position of specimen RL 1596-1 to be estimated as a member of the Sternopygidae: the presence of a regenerated caudal rod, the absence of regenerated (free) hemal spines, and the posterior position at which the neural spines contact the neural arches. A survey of radiographs and cleared-and-stained specimens representing all extant gymnotiform genera showed that all species of *Gymnotus*, Hypopomidae, Rhamphicthyidae, and Sternopygidae replace caudal vertebral centra during regeneration with a cartilaginous or collaginous rod (Albert, 2001). The presence of a caudal rod in specimen RL 1596-1 therefore excludes it from *Electrophorus* or Apteronotidae. The absence of free hemal spines in specimen RL 1596-1 further excludes it from *Gymnotus*, which is the only gymnotiform genus that exhibits free hemal spines (Albert, 2001; Albert et al., 2004). Free hemal spines are regenerated bones similar in size, shape, and position to unregenerated hemal spines, but not associated with individual vertebral centra (Meunier and Gayet, 1991). Rhamphichthyids and hypopomids with regenerated caudal regions were not observed with regenerated hemal spines (contra Gayet et al., 1994, character 43). The posterior position at which the neural spines contact the neural arches in specimen RL 1596-1 indicate this specimen is a member of either the Sternopygidae or Apteronotidae. In combination, the regenerated caudal rod, the absence of regenerated hemal spines, and the posterior position of the neural spines contact uniquely diagnose specimen RL 1596-1 as a member of the Sternopygidae among extant Gymnotiformes.

The survey of radiographs and cleared-and-stained specimens referred to previously (Albert, 2001) recovered several discrepancies with character states previously reported in the literature. The capacity to regenerate damaged portions of hemal spines was reported for specimen RL 1596-1 (Meunier and Gayet 1991, fig. 1.2), who also report regenerated portions of damaged hemal spines in *Eigenmannia virescens* (their fig. 3), *Gymnotus carapo* (their fig. 4), and *Apteronotus leptorhynchus* (their fig. 5). Regenerated portions of existing hemal spines were confirmed in material available for the present study in species of *Sternopygus* and *Apteronotus*. However, the inferred capacity of specimen RL 1596-1 to regenerate the damaged posterior vertebral centrum (Gayet et al., 1994: fig. 3) is enigmatic. If this were to be confirmed such a capacity would be unique among gymnotiforms. Specimens from field collections have not been observed with regenerated portions of damaged posterior vertebrae, and the regeneration experiments of Meunier and Gayet (1991) did not involve severed vertebral centra.

CONCLUSION

The available evidence indicates that most of these gymnotiform fossil fragments are members of extant gymnotiform generic-level taxa. We come to this conclusion after considering the data present on each fossil fragment, rather than assuming that all features from all specimens can be combined into a single taxonomic entity. The only diagnostic feature of *H. kirschbaumi* not called into question because of poor preservation and resulting interpretation is the deeply striated opercle, a feature shared with some extant *Sternopygus*, although no examined *Sternopygus* has the striations as pronounced as that of the fossil. Ambiguities of interpretation and analysis will remain until more specimens can be collected, and we look forward to that information.

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APPENDIX 1. Descriptions of 31 phylogenetically informative characters used to place 11 fossil specimens from the Río Alto Moile in relation to extant gymnotiform taxa.

1. Body shape: body deep, depth at mid-body (excluding anal fin) 11% to 14% total length (0); body slender, depth at midbody less than 9% to 11% total length (1).
2. Body squamation: scales present on entire body surface (0); body surface entirely without scales (Fink and Fink, 1981, character 124) (1).
3. Cranial skeleton texture: surface of endochondral and dermal ossifications of cranial skeleton composed of lamellar or cancellous bone (0); surface of many cranial bones pitted and/or reticular in appearance (Albert, 2001, fig. 18; Triques, 1993, fig. 3) (1).
4. Orientation of the hyomandibula: oblique to head (0); parallel to head (1).
5. Preopercle orientation: long axis of preopercle oriented at an oblique angle to main axis of neurocranium (0); long axis roughly parallel

with main axis of neurocranium (Chardon and de la Hoz, 1974, figs. 2-6; Triques, 1993, figs. 5 and 6) (1).

6. Preopercle ossification: preopercle robustly ossified, crescent-shaped; anterior limb broad (0); preopercle poorly ossified along its posteroventral margin; anterior limb narrow (Albert, 2001, figs. 3, 30A; Chardon and de la Hoz, 1974, figs. 2-6; Fink and Fink, 1981, figs. 8-12) (1).

7. Opercle shape: outline of opercle approximately rectangular; dorsal margin shorter than posterior margin, and interrupted by a pronounced angle (0); opercle approximately triangular; dorsal margin about as long as posterior margin, and either slightly curved or straight (Fink and Fink, 1981, character 36, figs. 8-12) (1).

8. Opercular dorsal margin: convex (0); straight or concave (Fink and Fink, 1981, figs. 8-12; Albert, 2001) (1).

9. Lateral surface of opercle: smooth or reticulate (0); rugose or striated (Fig. 1A; Gayet and Meunier, 1991, fig. 1) (1).

10. Articulation of neural spines and arches in posterior body regions: neural spines contact middle of neural arches (0); neural spines contact neural arches at their posterior margin (Fig. 2C) (Albert, 2001, fig. 35) (1).

11. Vertebral fenestrae: neural arches completely ossified, their lateral walls complete (0); lateral walls with 1 - 3 small fenestrae (Albert, 2001, figs. 36 and 37; Meunier and Gayet, 1991, figs. 3-5; Gayet et al., 1994, fig. 6) (1).

12. Epineural and epipleural intermuscular bones: simple or with one branch on the proximal tip (0); multiply branched, three to five rami on proximal and distal tips of most elements (1).

13. Dorsal organ: posterodorsal margin of body without a fleshy strap of ectodermal tissue (0); posterodorsal margin of body with a fleshy midsaggital flattened strap of ectodermal tissue, extending parallel with dorsal margin of the dorsal carinalis musculature (Franchina and Hopkins, 1996; Albert, 2001, figs. 37 and 38) (1).

14. Dorsal and pelvic fins and bony supports (pterygiophores, girdles): present (0); absent (1).

15. Pectoral fin: longer than operculum (0); about as long as or shorter than operculum (1).

16. Anal fin origin: anal-fin origin posterior to posterior margin of cleithrum (0); anal-fin origin ventral to posterior margin of cleithrum (1); anal-fin origin near branchial isthmus (2).

17. Anal-fin base length. Anal fin short, extending less than 0.2 times total length of body, with less than 50 rays (0); anal fin long, extending along majority of ventral body margin, with 50 – 350 fin rays (Albert, 2001; figs. 39 - 42) (1). A long anal-fin base in RL1596-4 is inferred from the anterior location of the fin rays.

18. Anal-fin ray articulation: anal-fin rays articulate with distal anal-fin pterygiophores (0); anal-fin rays articulate with proximal anal-fin pterygiophores (Fink and Fink, 1981, character 107; fig. 22) (1).

19. Anal-fin ray branching: all but anterior-most 1-10 rays branched (0); most or all anal-fin rays unbranched (1).

20. Anal-fin ray and pterygiophore lengths: anal-fin pterygiophores shorter than hemal spines at midbody, less than one-third total body depth (0); anal-fin pterygiophores longer than hemal spines at midbody, more than one-third total body depth (1).

21. Shape of anal-fin pterygiophore blades: descending blades of proximal anal-fin pterygiophores slender, approximately cylindrical in cross section (0); descending blades of anal-fin pterygiophores broad, anterior and posterior margins extending into ventral median septum in cross section (1).

22. Shape of (proximal) anal-fin pterygiophore tips: tapered smoothly to tips (0); arrow-head shaped (1).

23. Distal anal-fin pterygiophores: distal anal-fin pterygiophores present (0); no distal anal-fin pterygiophores (1).

24. Regeneration of hemal spines: no regenerated hemal spines (0); free hemal spines associated with regenerated cartilaginous rod (Gayet et al., 1994, character 2.2; Gayet et al., 1994, characters 43 and 56) (1).

25. Hemal spines: present in tail (post-thoracic) region (0); absent from tail region (1).

26. Number of ribs: eight to ten pairs of ribs (0); five to seven pairs of ribs (1).

27. Length of anterior ribs: anterior two or three ribs relatively short, less than 80% body depth at pectoral girdle (0); length of anterior two ribs long, greater than 80% body depth at pectoral girdle (1).

28. Shape of anterior ribs: anterior pair of ribs (associated with 5th vertebrae) narrow, less than twice width of ribs associated with 6th vertebrae (0); anterior ribs broad; more than twice width of ribs associated with 6th vertebrae (1).

29. Caudal appendage regeneration: no regeneration of caudal appendage (rod or fin) after damage or removal (0); capacity to fully regenerate entire caudal appendage, including muscle, electric organ, bone, spinal cord, integument, and supportive tissues (blood vessel and nervous innervation) (1).

30. Caudal fin with hypural plate and segmented rays: present (0); absent (1).

31. Caudal rod regeneration: regeneration of caudal appendage without replacement of axial support structure(s) (0); regeneration of caudal appendage with a single elongate cartilaginous or collagenous rod or bar in place of vertebral centra (1).

APPENDIX 2.   Summary of 31 character-states used to place the fossil gymnotiform specimens (listed as RL).

Taxon	1–10	11–20	21–30	31
Characiformes	0000000000	0000000000	0000000000	0
Siluriformes	0100001000	0000000000	0000000000	0
Gymnotus carapo	10000010P0	0101101101	0011000011	1
Electrophorus electricus	1100001100	0101101101	001?100111	0
Rhamphichthys rostratus	1001101000	0101121101	0010000011	1
Gymnorhamphichthys hypostomus	1001101000	0101121111	0010000011	1
Steatogenys elegans	1000110000	0101101100	0010000011	1
Hypopygus lepturus	1000100000	0101101100	0010000011	1
Hypopomus artedi	1000100000	0101101100	0010000011	1
Brachyhypopomus brevirostris	1000100000	0101101100	0010000011	1
Microsternarchus bilineatus	1000100000	0101101100	0010000011	1
Racenisia fimbriipinna	1000100000	0101101100	0010000011	1
RL 1596-1	?0??????1	1?0???1100	00000???11	1
RL 1596-3	?????????1	1??????11?0	00??0?????	?
RL 1596-4 (*H. kirschbaumi,* type)	??000?101?	?1??111???	?????000??	?
RL 1596-5	?????????1	1??????11?0	000?0?????	?
RL 1596-7	1????????1	11?1??1110	000?0?????	?
RL 1596-13	?????????1	1?????111?	00??0?????	?
RL 1596-15	??????????	??????110?	00??0?????	?
RL 1596-A	?????????1	??????110?	00??0?????	?
RL 1596-B	1????????1	1?????1111	000?0?????	?
RL 1596-C	?????????1	1???????1??	00??0?????	?
Sternopygus macrurus	1000001011	1101111110	0000000011	1
Archolaemus blax	10000?100?	1101111100	000?001011	1
Distocyclus conirostris	10100010P1	1101111101	0000011011	1
Rhabdolichops eastwardi	1000001001	1101111101	0000011011	1
Eigenmannia virescens	1000001001	1101111101	0000011011	1
Platyurosternarchus macrostomus	1010011100	1111121101	1000000110	0
Sternarchorhynchus oxyrhynchus	1010011101	1111121101	1000000110	0
Sternarchorhamphus muelleri	1010011101	1111121111	1100000010	0
Orthosternarchus tamandua	1010011101	1111121111	1100000010	0
Magosternarchus raptor	1010011101	1111111101	0000000110	0
Sternarchella sima	1010011101	1111111101	0000000110	0
Parapteronotus hasemani	1010011101	1111111100	0000000110	0
Apteronotus albifrons	1000011101	1111111100	0000000110	0
Porotergus gymnotus	1010011101	1111111101	0000000110	0
Adontosternarchus sachsi	1010011001	1111111101	0010000110	0
Sternarchogiton nattereri	1010011101	1111111101	1000000110	0

A "?" indicates missing data or character state not pertinent; a "P" indicates polymorphic characters. Character descriptions are in Appendix 1. Phylogenetically informative character-states mostly adapted from Albert (2001).