

Modifications of the Digestive Tract for Holding Air in Loricariid and Scoloplacid Catfishes

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Loricariid catfishes have evolved several modifications of the digestive tract that appear to function as accessory respiratory organs or hydrostatic organs. Adaptations include an enlarged stomach in *Pterygoplichthys*, *Liposarcus*, *Glyptoperichthys*, *Hemiancistrus annectens*, *Hemiancistrus maracaiboensis*, *Hypostomus panamensis*, and *Lithoxus*; a U-shaped diverticulum in *Rhinelepis*, *Pseudorinelepis*, *Pogonopoma*, and *Pogonopomoides*; and a ringlike diverticulum in *Otocinclus*. Scoloplacids, closely related to loricariids, have enlarged, clear, air-filled stomachs similar to that of *Lithoxus*. The ability to breathe air in *Otocinclus* was confirmed; the ability of *Lithoxus* and *Scoloplax* to breathe air is inferred from morphology. The diverticula of *Pogonopomoides* and *Pogonopoma* are similar to swim bladders and may be used as hydrostatic organs. The various modifications of the stomach probably represent characters that define monophyletic clades. The ovaries of *Lithoxus* were also examined and were shown to have very few (15–17) mature eggs that were large (1.6–2.2 mm) for the small size of the fish (38.6–41.4 mm SL).

Los bagres loricariid an desarrollado varias modificaciones del canal digestivo que aparentan funcionar como órganos accesorios de respiración o órganos hidrostáticos. Las adaptaciones incluyen un estómago agrandado en *Pterygoplichthys*, *Liposarcus*, *Glyptoperichthys*, *Hemiancistrus annectens*, *Hemiancistrus maracaiboensis*, *Hypostomus panamensis*, y *Lithoxus*; un diverticulum en forma de U en *Rhinelepis*, *Pseudorinelepis*, *Pogonopoma*, y *Pogonopomoides*; y un diverticulum en forma de círculo en *Otocinclus*. Scoloplacids, de relación cercana a los loricariids, tienen estómagos claros, agrandados, llenos de aire similares a los de *Lithoxus*. La habilidad de respirar aire en *Otocinclus* fue confirmada; la habilidad de *Lithoxus* y *Scoloplax* de respirar aire es deducida por la morfología. La diverticula de *Pogonopomoides* y *Pogonopoma* es similar a las vejigas de natación y pueden ser usados como órganos hidrostáticos. Las varias modificaciones del estómago probablemente representan características que definan grupos monofiléticos. Los ovarios de *Lithoxus* tambien fueron examinados y fueron mostrados a tener muy pocos (15–17) huevos maduros que eran grandes (1.6–2.2 mm) por el tamaño pequeño del pescado (38.6–41.4 mm SL).

THE seasonal fluctuations of tropical South American rivers have profound effects upon the fish fauna (Goulding, 1980; Val and Almeida-Val, 1995). In particular, those species that occupy flooded habitats risk being subjected to hypoxic conditions in floodplain pools and swamps as the rains cease and rivers dry (Carter and Beadle, 1931). Fishes are able to survive in poorly oxygenated water using one of two methods to obtain oxygen. The first is to utilize aquatic surface respiration. Fishes such as cyprinodontiforms and some characiforms (*Copeia*, *Pyrrhulina*, and ctenoluciids) spend most of their lives at the surface; but in times of severe hypoxia, even cichlids, some catfishes, and probably most other fishes will rise to the surface to breathe in the surface layer (Carter and Beadle, 1931; Kramer and McClure, 1982).

The second method for fishes to obtain oxygen in hypoxic conditions is to utilize the air

above the water. To breathe air, a fish must possess a highly vascularized surface that can be kept moist. Examples include the lung of lungfishes, the buccal cavity of electric eels, the skin of anguillid eels, and the intestine of callichthyid catfishes (Carter and Beadle, 1931; Carter, 1957; Johansen, 1970). Most fishes that breathe air are not obligate air breathers and switch to air breathing only during times of severe hypoxia. There are few obligate air breathers because there is usually an energetic cost in rising to the surface to gulp air and a fitness cost in that rising to the surface makes the fish more exposed and susceptible to predation (Kramer, 1983; Kramer et al., 1983; Power, 1984).

Loricariidae (suckermouthed, armored catfishes) is one of the largest fish families in the world, with approximately 600 species distributed from southern Costa Rica to northern Ar-

gentina (Isbrücker, 1980; Nelson, 1994). Throughout this range, loricariids are common in all habitats from high gradient mountain streams to floodplain lakes (Burgess, 1989). Occupying such a wide range of habitats requires that loricariids have an array of adaptations for coping with varied life-history characteristics. Of particular interest are the adaptations loricariids possess for life in stagnant waters of floodplain lakes and swamps where they must breathe air to survive.

Air breathing in some loricariids is well known. Species of *Ancistrus*, *Chaetostoma*, *Dekeyseria*, *Hypoptopoma*, *Hypostomus*, *Liposarcus*, *Rhinolepis*, *Rineloricaria*, and *Sturisoma* have all been confirmed as being capable of breathing air (Kramer et al., 1983; Santos et al., 1994; Val and Almeida-Val, 1995). Gradwell (1971) discussed the behavior of air-breathing *Hypostomus* and illustrated that, to get its mouth above the water's surface to breathe air, a *Hypostomus* must orient vertically. Gee (1976) determined that the ability to breathe air was dependent upon the risk of hypoxia faced by a species. Of the species Gee examined, the torrent-dwelling astroblepids (the sister family to Loricariidae; Baskin, 1973; Schaefer, 1987; de Pinna, 1993) and *Lep-toancistrus* had no ability to breathe air; the rifle-dwelling *Chaetostoma* had only a slight ability to breathe air; and the lowland, pool-dwelling *Hypostomus* had the best ability to breathe air. However, of all loricariids for which information is available, *Liposarcus* is probably the best adapted to breathing air. Species of *Liposarcus* are commonly kept out of water and sold alive in fish markets and have been known to survive up to 30 h out of water (Val and Almeida-Val, 1995).

Few studies have been published on the morphological adaptations loricariids possess to breathe air. Only *Liposarcus* and *Hypostomus* have been examined, and both have been found to utilize the stomach to extract oxygen (Carter and Beadle, 1931; Carter, 1935; Burgess, 1989). In *Hypostomus*, the stomach was found to be only slightly modified in that it was larger and thinner than in nonair breathers (Carter, 1935). However, the stomach of *Liposarcus* was found to be greatly expanded with the posterior portion forming a long, thin sac that was much more highly vascularized than in air-breathing *Hypostomus* (Carter and Beadle, 1931).

Scoloplacidae, closely related to Loricariidae, consists of one genus (*Scoloplax*) and four diminutive species with a maximum reported size of about 2 cm (Bailey and Baskin, 1976; Schaefer et al. 1989; Schaefer, 1990). Scoloplacids are fairly common among leaf litter in oxbow lakes,

backwater pools, and well-vegetated streams (Bailey and Baskin, 1976; L. Page and M. Sabaj, pers. comm.). Such habitats subject the fishes to hypoxia; however, the air breathing ability of scoloplacids has never been demonstrated. Here I describe the modified stomach of *Scoloplax* and suggest it is an adaptation for air breathing.

An alternative hypothesis for the development of air sacs in loricariids is that they provide hydrostatic control or a resonating chamber for sound production. Schaefer (1997) suggested that the diverticulum in *Otocinchus* provides hydrostatic control allowing *Otocinchus* to live among plants in the upper water column. However, Gee (1976) found there was no buoyancy advantage to the air-breathing loricariids he examined (which did not include *Otocinchus*). The potential of the air sacs to act as resonating chambers must be kept in mind because loricariids do make sound, but it is unknown how important sound production is or whether the fish are using the air chambers for sound. Given the recurrent theme of air breathing in loricariids, it is likely that the initial adaptation of structures was for air breathing and that alternative uses represent exaptations.

During an ongoing study on the phylogeny of the loricariid subfamily Hypostominae, the viscera of species in 42 loricariid genera from five of the six subfamilies of Loricariidae (only the monotypic Lithogeneinae was not examined) and in Scoloplacidae were examined. Examination of the viscera of loricariids and scoloplacids has revealed several modifications of the digestive system. The modifications of the digestive system that hold air, the presumed evolution of the structures, and the phylogenetic implications of the structures are discussed.

MATERIALS AND METHODS

The viscera removed from specimens that were subsequently cleared and stained were examined for structures that could be utilized for aerial respiration. The digestive tracts were scored as either having no obvious modification, a slightly enlarged stomach, or one of seven extremely well-developed, air-filled pouches (character states are defined in the Results and summarized in Table 1 for loricariids). For some of the species with a well-developed respiratory organ, additional specimens were dissected, and the intestines were removed to determine the size of the respiratory organ relative to the abdominal cavity and circulatory patterns. Drawings were prepared using a camera lucida attached to a Wild M5 stereoscope. Insti-

TABLE 1. DISTRIBUTION OF DIGESTIVE TRACT MODIFICATION CHARACTER STATES IN LORICARIIDS^a

Species	State
Neoplecostominae	
<i>Neoplecotomus microps</i>	1
Hypoptopomatinae	
<i>Hypoptopoma</i> sp.	1
<i>Microlepidogaster</i> sp.	1
<i>Nannoptopoma spectabilis</i>	1
<i>Otocinclus</i> (all)	7
<i>Parotocinclus britskii</i>	1
Loricariinae	
<i>Crossoloricaria venezuelae</i>	1
<i>Cteniloricaria platystoma</i>	1
<i>Farlowella</i> (all)	1
<i>Lamontichthys llanero</i>	1
<i>Loricaria</i> (all)	1
<i>Loricariichthys platymetopon</i>	1
<i>Rineloricaria caracasensis</i>	1
<i>Rineloricaria rupestris</i>	1
<i>Rineloricaria uracantha</i>	2
<i>Sturisoma festivum</i>	1
Hypostominae	
<i>Aphanotorulus</i> (all)	1
<i>Cochliodon cochliodon</i>	1
<i>Cochliodon hondae</i>	1
<i>Cochliodon</i> sp.	2
<i>Cochliodon taphorni</i>	2
<i>Corymbophanes bahianus</i>	1
<i>Delturus anguillicauda</i>	1
<i>Glyptoperichthys</i> (all)	3
<i>Hemipsilichthys</i> sp. 1	1
<i>Hemipsilichthys</i> sp. 2	1
<i>Hypostomus albopunctatus</i>	1
<i>Hypostomus asperatus</i>	2
<i>Hypostomus bolivianus</i>	2
<i>Hypostomus emarginatus</i>	1
<i>Hypostomus francisci</i>	2
<i>Hypostomus panamensis</i>	3
<i>Hypostomus plecostomus</i>	2
<i>Hypostomus squalinus</i>	2
<i>Hypostomus</i> type 1 ^b	1
<i>Hypostomus</i> type 2 ^b	2
<i>Isbrueckerichthys duseni</i>	1
<i>Kronichthys</i> sp.	1
<i>Liposarcus</i> (all)	3
<i>Pogonopoma wertheimeri</i>	6
<i>Pogonopomoides parahybae</i>	6
<i>Pseudorinelepis genibarbis</i>	4
<i>Pterygoplichthys</i> (all)	3
<i>Rhinelepis aspera</i>	5
Ancistrinae	
<i>Ancistrus pireata</i>	1
<i>Ancistrus</i> sp. 1	1
<i>Ancistrus</i> sp. 2	2
<i>Chaetostoma anomalum</i>	1

TABLE 1. CONTINUED

Species	State
<i>Cordylancistrus torbesensis</i>	1
<i>Dekeyseria scaphirhynchus</i>	1
<i>Dolichancistrus cobrensis</i>	1
<i>Exastilithoxus</i> sp.	1
<i>Hemiancistrus annectens</i>	3
<i>Hemiancistrus maracaiboensis</i>	3
<i>Hemiancistrus</i> sp.	1
<i>Lasiancistrus</i> sp.	1
<i>Lithoxancistrus orinoco</i>	1
<i>Lithoxus bovallii</i>	8
<i>Lithoxus lithoides</i>	8
<i>Megalancistrus aculeatus</i>	1
<i>Oligancistrus punctatissimus</i>	1
<i>Panaque maccus</i>	1
<i>Peckoltia</i> (all)	1
<i>Pseudancistrus coquenani</i>	1
<i>Spectracanthicus murinus</i>	1

^a States are defined in the results. Polytypic species are placed in the more advanced category.

^b "Type" refers to groups of unidentified *Hypostomus* species that share a stomach modification character state.

tutional abbreviations are as in Leviton et al. (1985).

RESULTS

Nine stomach modification character states were identified among the fishes examined. Primitively, in loricariids, the esophagus bends to the right upon entering the visceral cavity and then expands slightly to form the stomach after it bends to the left (Fig. 1A). Upon reaching the midline, the stomach bends to the right and travels anteriorly for a short distance before the pylorus. After the pylorus, the intestine proceeds anteriorly, bends to the left dorsal to the esophagus, turns posteroventrally, and then begins to form a tightly coiled mass that occupies most of the visceral cavity ventral to the stomach (not shown in Figs. 1–5). The stomach is a highly vascularized structure with afferent flow from a large branch of the coeliac artery and efferent flow by a branch of the hepatic portal vein. The maximum posterior extent of the stomach is about one-third of the visceral cavity (state 1). State 1 was found in nearly all Loricariinae, Neoplecostominae, most Hypoptopomatinae, most Ancistrinae, and, among the Hypostominae, in *Aphanotorulus*, *Corymbophanes*, *Delturus*, *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Parieiorhina*, and some *Hypostomus* (Table 1).

In state 2, found in some species of *Hypostomus*, *Cochliodon*, and *Ancistrus*, and in *Rineloricaria uracantha*, the stomach is expanded such

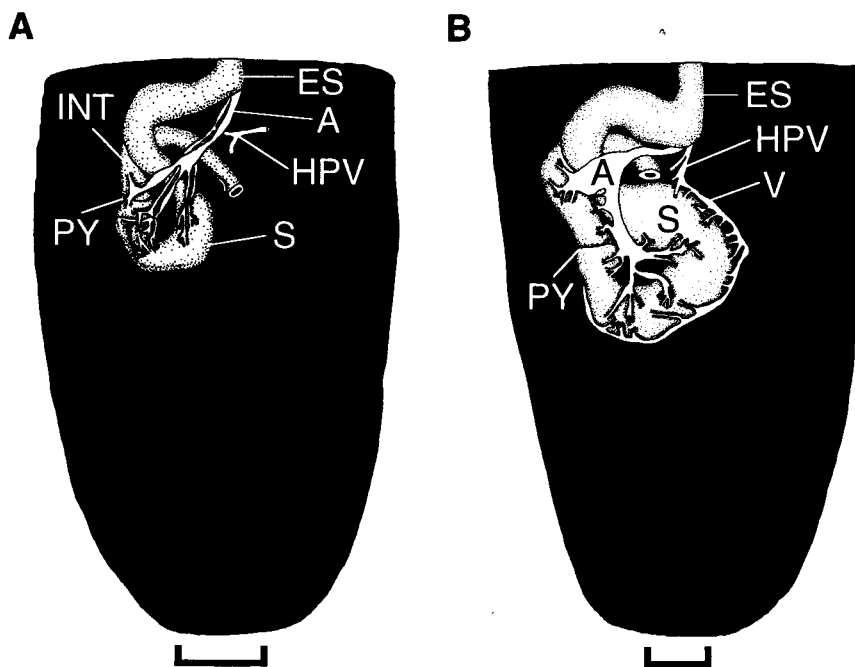


Fig. 1. States 1 (A) and 2 (B) show the visceral cavity, ventral views, of *Aphanotorulus ammophilus*, MCNG 13504, 102.0 mm SL; and *Hypostomus* sp., INHS 35660, 122.1 mm SL, respectively. Black indicates the extent of the peritoneum. Liver, gonads, and most of the intestine are not shown. Abbreviations for this figure and/or Figures 2–7 are as follows: A = branch of the coeliac artery; D = diverticulum; D1 = muscular section of diverticulum; D2 = air-filled section of diverticulum; ES = esophagus; HPV = hepatic portal vein; INT = intestine; 0 = ovary; PY = pylorus; S = stomach; TS = connective tissue sheet; V = vein to stomach. Scale = 5 mm.

that its maximum posterior extent is approximately half to three-quarters through the visceral cavity, approaching the size of the stomach in Figure 2 (Fig. 1B; Carter, 1935). Blood flow for state 2 is as in state 1. State 2 represents an ontogenetic stage described by Carter and Beadle (1931) for *Liposarcus*. A large degree of ambiguity exists between states 1 and 2, and species are often polymorphic.

Carter and Beadle (1931) were the first to describe state 3 in *Ancistrus anisitsi* (now *Liposarcus anisitsi*). In state 3, the stomach is greatly expanded and runs from three-fourths to completely through the visceral cavity (Fig. 2). The stomach is much more highly vascularized than in any of the previous states, and venous flow is by the interrenal vein instead of the hepatic portal vein. A white net consisting of connective tissue surrounds the stomach ventrolaterally and across the proximal and distal ends, leaving a circular area in the middle of the stomach free. The connective tissue sheet consists of numerous multidirectional bands that overlap one another and pass in every direction and connects to the body wall along the entire length

of the stomach, firmly holding the stomach against the body wall. The connective tissue sheet is better developed (containing more and thicker bands) in adults and is best viewed in specimens in which the stomach has been well preserved because in poorly preserved specimens it appears partially transparent. State 3 is found in *Hypostomus panamensis*, *Glyptoperichthys*, *Liposarcus*, and *Pterygoplichthys* of Hypostominae and *Hemiancistrus annectens* and *Hemiancistrus maracaiboensis* of Ancistrinae. Although the stomach in state 2 is often nearly the same size as in state 3, there is no connective tissue sheet in state 2, and the stomach is not firmly attached to the body wall.

State 4 (Fig. 3) was found only in the hypostomine *Pseudorinelepis*. In *Pseudorinelepis*, the esophagus does not bend to the right side of the body but passes straight, and the stomach branches off the right side. The stomach is short, and the opening is narrow. The intestine is slightly wider than the stomach, and it does not pass dorsally to the esophagus as it does in states 1–3. At the border between the esophagus and the stomach, there is a two-part diverticu-

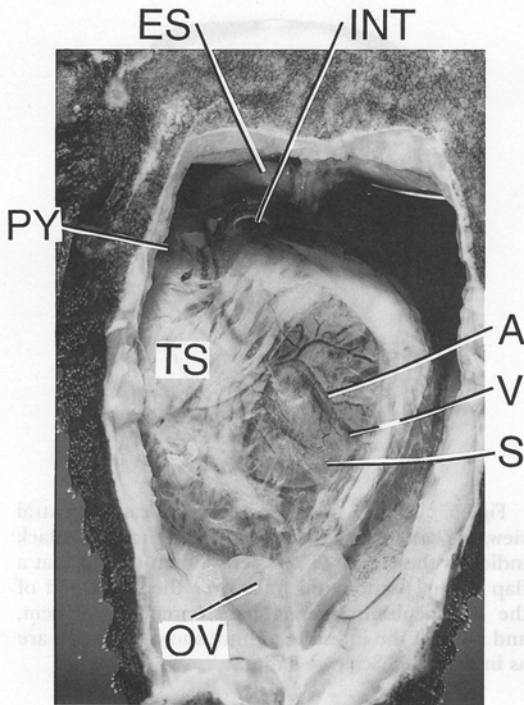


Fig. 2. State 3 shows the visceral cavity, ventral view, of *Glyptoperichthys scrophi*, INHS 38845, 178.3 mm SL. Liver and intestines have been removed. Symbols are as in Figure 1. Photo by K. S. Cummings.

lum (Fig. 3). The first part of the diverticulum is a tube consisting of thick musculature and appears as if it is an extension of the esophagus. The muscular tube passes a short distance before the second or main section of the diverticulum, which is a long, U-shaped sac. The second part of the diverticulum passes anteriorly for a short distance and then bends 360° to the left so that it runs posteriorly along the left side of the body. The diverticulum reaches a maximum extent about three-quarters to entirely through the visceral cavity, bends anteriorly so that it runs up the right side of the body, and then terminates at about the maximum anterior extent of the diverticulum on the left side of the body. The muscular section of the diverticulum is generally dark yellow to red-orange in preserved specimens and is lined with numerous large folds. In contrast, the remainder of the diverticulum is lighter in color and lacks folds. The outside of the second part of the diverticulum consists of numerous longitudinal folds that allow the diverticulum to expand, whereas the internal lining of the diverticulum is textured to increase the surface area for respiration. The diverticulum is loosely attached to the abdominal wall.

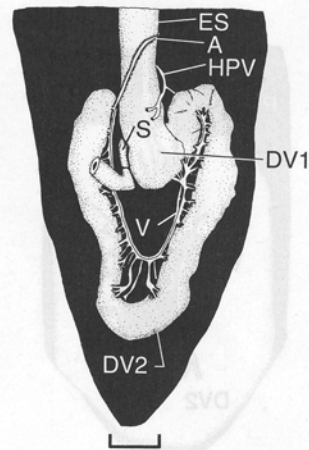


Fig. 3. State 4 (state 5 has same shape, but is firmly, not loosely, attached to the abdominal wall) shows the visceral cavity, ventral view, of *Pseudorinelepis genibarbis*, INHS 36938, 100.4 mm SL. Black indicates the extent of the peritoneum. Liver, gonads, and most of the intestine are not shown. Symbols are as in Figure 1. Scale = 5 mm.

A branch of the coeliac artery feeds the diverticulum and is located ventrally on the structure, whereas a branch of the hepatic portal vein that drains the diverticulum is located dorsally. Both blood vessels are located mesially to the diverticulum with the vein running parallel to the diverticulum and the artery running antiparallel. The blood vessels give off numerous branches, which break into capillaries upon contact with the diverticulum.

State 5 is found in *Rhinelepis* (Hypostominae). The state is nearly identical to state 4 except that the diverticulum has become firmly attached to the abdominal wall, and the interior of the diverticulum is more textured.

State 6 (Fig. 4) is found in the hypostomines *Pogonopoma* and *Pogonopomoides* and is similar to that of states 4 and 5, except that the first part of the diverticulum is greatly reduced, whereas the second part of the diverticulum is much larger than in states 4 and 5 and has a smooth interior surface. The diverticulum is not as well vascularized as in states 4 and 5, and it passes through the peritoneum so that it lies entirely outside the visceral cavity (retroperitoneal). Unlike in states 4 and 5, the walls of the diverticulum are inflexible, and it appears that the diverticulum is always inflated. The diverticulum of state 6 is similar to a swim bladder but is not contiguous with the swim bladder. The shape of the diverticulum in *Pogonopoma* is as in state 4 but differs slightly in *Pogonopomoides*, in which the diverticulum does not first pass anteriorly.

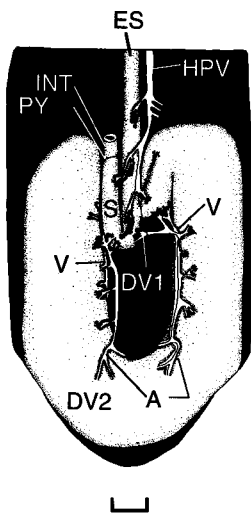


Fig. 4. State 6 shows the visceral cavity, ventral view, of *Pogonopoma wertheimeri*, USNM 318202, 152.6 mm SL. Black indicates the extent of the peritoneum except that the peritoneum also covers the diverticulum. Liver, gonads, and most of the intestine are not shown. Symbols are as in Figure 1. Scale = 5 mm.

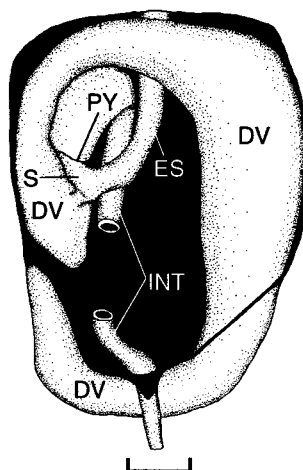


Fig. 5. State 7 shows the visceral cavity, ventral view, of *Otocinclus* sp., INHS 28083, 24.8 mm SL. Black indicates the extent of the peritoneum except that a flap of the peritoneum folds over the distal end of the diverticulum. Liver, gonads, circulatory system, and most of the intestine are not shown. Symbols are as in Figure 1. Scale = 1 mm.

The diverticulum of *Pogonopomoides* is also shorter and wider than in *Pogonopoma*, *Pseudorinelepis*, or *Rhinelepis*.

State 7 (Fig. 5) is found in *Otocinclus* (Hypopomatinae). In *Otocinclus*, a small duct forms on the right side of the digestive tract at the junction of the stomach and esophagus and then expands into an enlarged diverticulum (Schaefer, 1997). The diverticulum has a small section posterior to the duct and then passes anteriorly along the right side of the body to the anterior margin of the abdominal cavity. There, the diverticulum turns mesially and passes ventrally to the esophagus and parallel to the anterior wall of the abdominal cavity. The diverticulum then widens and passes posteriorly along the left side of the body. At the end of the abdominal cavity, the diverticulum passes through the peritoneum and turns to the right. The diverticulum passes dorsally to the rectum and urogenital canal and then proceeds anteriorly along the right side of the body between the peritoneum and the lateral musculature. The diverticulum ends approximately at the level of the most posterior expansion of the proximal end of the diverticulum. It appears as though the diverticulum may have blood flow similar to that of states 4–6; however, because of the small size of the *Otocinclus*, it was difficult to examine the blood vessels without accidentally deflating the diverticulum. When the diverticulum is deflated, it is impossible to see the blood

vessels. I have witnessed *Otocinclus* in apparently hypoxic water gulping air. Prior to surfacing, the fish released air through their mouth and gill openings. Upon returning to the bottom, the fish either infrequently or never engaged in buccal pumping. Because they were not pumping water over the gills, it can be assumed that they were obtaining oxygen from the swallowed air.

State 8 is found in *Lithoxus*, an extremely dorsoventrally flattened fish with a very limited visceral cavity. In *Lithoxus*, the stomach is expanded, thin-walled, and clear (Fig. 6). A thin, clear tube exits the main body of the stomach anterodorsally, terminating at the pylorus just anterior to the posterior extent of the stomach. The intestine has fewer coils than in most other Ancistrinae and is displaced to the left of the stomach. *Lithoxus* are sexually dimorphic in the size of the stomach. In mature females, the stomach ends anterior to the pelvic girdle, whereas it continues through much of the visceral cavity in males. This difference appears to be related to the size of the gonads. Males have larger stomachs than females because there is more space available in the male visceral cavity. Blood vessels could not be examined effectively on the specimens of *Lithoxus*. The ovaries of two adult female *Lithoxus* (38.6 and 41.4 mm SL) were also examined, and there appeared to be three size classes of ova with mature ova arranged in a single layer. Few mature eggs, averaging 1.85

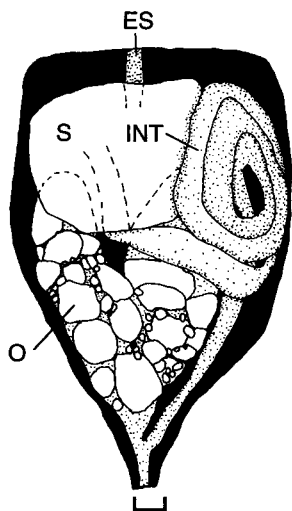


Fig. 6. State 8 shows the visceral cavity, ventral view, of *Lithoxus lithoides*, BMNH 1972.7.17:66-115, 38.6 mm SL. Black indicates the extent of the peritoneum. Liver and circulatory system are not shown. Symbols are as in Figure 1. Scale = 5 mm.

mm in maximum diameter ($n = 20$), were found in the ovaries (15 and 17, respectfully).

State 9 is found in *Scoloplax* and is similar to the stomach of *Lithoxus* except that the intestine exits ventrally on the stomach. Only two specimens of *Scoloplax dicra* were examined, and one had a stomach that was extremely expanded and was initially air filled (Fig. 7). In this specimen (INHS 37242), the esophagus entered the stomach along the dorsal side just posterior to the anterior margin of the stomach. A small patch of muscular tissue, which presumably represents the extent of the digestive portion of the stomach, was located from the entrance of the esophagus to where the intestine exits. The remainder of the stomach was a clear, air-filled sac that filled the majority of the abdominal cavity. In the second specimen examined (INHS 37195), the stomach was not as enlarged as in the first specimen but still had a clear, air-filled portion. Because of the small size of the specimens, blood vessels were extremely difficult to see and are not shown in Figure 7.

DISCUSSION

Functional aspects of air-holding structures.—The evolution of air sacs in loricariids and scoloplacids is difficult to explain. Given the requirements of a working stomach, it is interesting to note that at least five times (based on plotting the characters on the phylogenies of Schaefer, 1986; de Pinna, 1993) these fishes have evolved

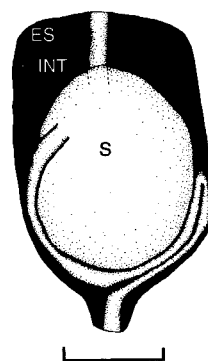


Fig. 7. State 9 shows the visceral cavity, ventral view, of *Scoloplax dicra*, INHS 37242, 12.5 mm SL. Black indicates the extent of the peritoneum. Liver, gonads, and circulatory system are not shown. Symbols are as in Figure 1. Scale = 5 mm.

complex structures that could severely hamper their prospects at obtaining and digesting food. However, based on aquarium observations, loricariids will only use their respiratory stomachs in times of duress; and when oxygen levels are high, they will rely on their gills alone (Gee, 1976; Kramer, 1983). The dry season, when the fishes would need to rely on their respiratory stomachs, is likely a time of severe competition for limited food resources, and it is possible that loricariids and scoloplacids eat sparingly or not at all. Lack of feeding would allow the fishes to use their stomachs almost exclusively for air breathing. Formation of diverticula with narrow openings in the *Rhinelepis* group (*Pogonopoma*, *Pogonopomoides*, *Pseudorhinelepis*, and *Rhinelepis*) and *Otoclinchus* serve to better separate the air-holding and digestive attributes of the digestive tract and may have led to the possible secondary use of the diverticula as hydrostatic organs.

Voiding of gas through the mouth and gill openings in fishes has been suggested by Gradwell (1971), Liem (1988), and Brainerd (1994) to be a result of several possible actions: hydrostatic pressure could compress the air sac; the buccal cavity expands and draws air out of the stomach; the muscles of the stomach could compress to force the air out of the stomach; the rectus abdominis could contract to press the viscera against the stomach to squeeze the air out of the stomach; or contraction of the epaxial musculature could compress the stomach. It is unknown how these actions interplay or upon which loricariids and scoloplacids rely. Val and Almeida-Val (1995) suggested that air may be released through the anus, but Gradwell (1971) suggested that *Hypostomus* released all gas through the gill openings. Because both *Hypos-*

tomus and *Otocinclus* release air through the gill openings and mouth prior to taking a breath of air, it is likely that any air released through the anus is inconsequential and may be only the result of the poor separation of the respiratory and digestive aspects of the stomach.

In *Scoloplax*, the rectus abdominis muscles are larger than those of loricariids, and it is possible that they do use these muscles to compress the stomach; however, no fish have been shown to use the rectus abdominis to void the stomach. In the *Pterygoplichthys* group, the connective tissue sheet may compress the stomach against the dorsal body wall upon springing back to shape after air is released (elastic recoil). The tight net of tissue may be oriented so that the maximum amount of air is voided, and expiration may be faster than in those species without a connective tissue sheet. In *Pseudorinelepis* and *Rhinelepis*, the first part of the diverticulum is muscular and may function in some manner to drain or fill the diverticulum or may act to seal the air chamber from the stomach. If the first section of the diverticulum does serve some purpose in draining or filling the diverticulum, its reduction in *Pogonopoma* and *Pogonopomoides* may suggest that the genera have limited ability to drain or fill the diverticulum. In *Otocinclus*, the distal end of the diverticulum is retroperitoneal, and this may be an adaptation to void the diverticulum of air. By bending the body to the right, the lateral musculature would push the distal end of the diverticulum against the viscera and push air from the diverticulum.

Evolution of air-breathing structures.—A common theme within the loricarioids is the evolution of air breathing. Studies by Gee (1976) suggest that all except high montane species have at least some ability to extract oxygen through their alimentary tract. Elucidating the evolution of the respiratory stomachs of loricariids is likely to be important in understanding phylogenetic relationships within the family; however, it is difficult to assign polarity to character states because of the widespread ability to breathe air through various structures within the alimentary tract. It is probable that primitively, within Loricariidae, there was no modification of the stomach as is seen in *Neoplecostomus*, the presumed sister to all other loricariids excluding *Lithogenes* (Schaefer, 1987) and in Astroblepidae. Carter and Beadle (1935) also determined that the modified stomach of *Liposarcus* went through ontogenetic stages that included states 1–3.

Fishes with the primitive state of having no modification to the stomach (state 1) often have

a slight ability to breathe air. Both *Chaetostoma* and *Sturisoma* possess state 1, yet Gee (1976) found them to have a rudimentary ability to breathe air under hypoxia. The stomach is an excellent structure to evolve air breathing because it is connected to the outside of the body and is already a highly vascularized organ.

In loricariid lineages that began to rely on the stomach for extracting oxygen during times of hypoxia, the stomach probably became further modified, perhaps several times independently, by expansion and thinning of the stomach wall. By thinning the stomach wall, the stomach presumably can expand more and a greater surface area of blood vessels could come in contact with the air to increase gas exchange. Also, the thinning of an area of the stomach is associated with the loss of digestive cells (Carter and Beadle, 1931; Carter, 1935) allowing the area to specialize in extracting oxygen. Air breathing in these fishes is probably fairly good, but preference of most of the fishes with this state for muddy streams and not for swamps suggests that they cannot rely on the structure in severe cases of oxygen deprivation. State 2 is likely to have evolved several times and occurs in three subfamilies of Loricariidae: Ancistrinae, Hypostominae, and Loricariinae.

Ambiguity in states 1–2 and the indication that similarly sized individuals in the same population may possess different character states suggest that species may be able to change the condition of their stomachs based on oxygen levels. Under low oxygen conditions, gulping air would expand the stomach. The stomach may contract back to state 1 under high oxygen levels. Because of the problem in assigning character states 1–2 to species, the ability of a loricariid species possessing state 1 to breathe air can only be determined by subjecting the fish to hypoxia.

State 3 appears very similar to state 2, differing mainly in the extent of vascularization, the size of the stomach, and the connective tissue sheet that covers the stomach. Fishes that possess state 3 (e.g., *Liposarcus*) are typical members of floodplain lakes, swamps, and borrow pits, where oxygen levels are very low and the fishes must rely on air breathing for long periods of time. State 3 is almost certainly derived from states 1 or 2 because juvenile members of *Hypostomus panamensis* (a relative of *Hemiancistrus annectens* and *Hemiancistrus maracaiboensis*, see below) have only the anterior section of the connective tissue sheet developed, but adults have full development. I have witnessed adult *Glyptoperichthys gibbiceps* in large aquaria swimming through the middle of the water column

with no effort, so the stomach probably also acts as a hydrostatic organ.

Evolution of the U-shaped diverticulum probably proceeded state 4, to state 5, to state 6 (see Armbruster, 1998). In state 4, the diverticulum is attached to the abdominal wall much in the same way as the stomach of other loricariids, that is, loosely. State 5 probably evolved as the membrane that loosely held the diverticulum to the abdominal wall, in state 4 and shrunk and became stronger. *Pseudorinelepis* is an air breather whose habits are under investigation, and *Rhinelepis* has been confirmed as an air breather (Santos et al., 1994). Little is known about the ecology of either genus, but it appears that *Pseudorinelepis* lives in flooded areas and swamps of the Rio Amazonas (Burgess, 1989; Armbruster and Page, 1997). Kramer et al. (1978) suggest that *Pseudorinelepis* (which they called *Canthopomus*) might be able to cross land, based on artificial trials where fish were released on a boat deck and on mud. Of the five loricariid species tested (*Pseudorinelepis genibarbis*, *Liposarcus pardalis*, *Hypostomus* sp., *H. emarginatus*, and *Ancistrus* sp.), *P. genibarbis* was best able to locomote out of water. *Rhinelepis* is said to be found near waterfalls (Santos et al., 1994) but is also common in reservoirs (Fernandes et al., 1995).

It is probable that state 6 has evolved from state 5 rather than vice versa because the digestive tract is intraperitoneal and it seems less parsimonious for the diverticulum to have evolved retroperitoneally and then to move back inside the peritoneum. Neither *Pogonopoma* nor *Pogonopomoides* have been confirmed as air breathers, and it is possible that they are not. The air sac in these fishes is thin, not expandable, not particularly well vascularized; and the first section of the diverticulum is reduced over that seen in states 4 and 5. The diverticulum is extremely similar to a swim bladder, which this structure has been called in the past (Gosline, 1947) and to which it may be analogous. The diverticulum cannot be homologous to the swim bladder because the two structures are not contiguous, and the swim bladder in loricarioids is restricted to an encapsulated region under the pterotic-supracleithrum (Alexander, 1962; Gee, 1976). Also, unlike the swim bladders of most other fishes, it is U-shaped and not located mesially. The diverticula of *Pogonopoma* and *Pogonopomoides* are also thicker-walled than most swim bladders, perhaps to allow the diverticula to secondarily act as resonating chambers in sound production.

If the diverticulum in *Pogonopoma* and *Pogonopomoides* is not for air breathing, the other likely use is for buoyancy control, which seems odd

because loricariids are generally considered to be benthic. In other loricariids, Gee (1976) found no buoyancy effect of air stored in the stomach, but the species he examined all have much smaller reservoirs than do *Pogonopoma* and *Pogonopomoides*, and the hypothesis that state 6 is analogous to a swim bladder deserves further testing. If state 6 acts as a hydrostatic organ, it raises the possibility that the diverticulum evolved in *Pseudorinelepis* and *Rhinelepis* as a buoyancy control organ rather than for air breathing, and the fishes should be tested for their air-breathing ability as well as for buoyancy control. Because the evolution of the diverticulum in the *Rhinelepis* group parallels that of the evolution of the lung/swim bladder in the bony fishes, determining the function of the diverticulum in the members of the *Rhinelepis* group may provide insight into the function and origin of the lung in early fishes.

Because of the different shapes of the diverticula and the notion that *Otocinclus* and the *Rhinelepis* group are not considered to be closely related (Isbrücker, 1980; Schaefer, 1986, 1990), state 7 is not considered to be homologous to states 4–6. That *Otocinclus* nearly stop irrigating their gills when they commence gulping air supports the contention that they are air breathers. However, it does not prove that *Otocinclus* are using the diverticulum to extract oxygen; they may be using the diverticulum only for hydrostatic control. The diverticulum in *Otocinclus* has extremely thin walls (much thinner than air-breathing structures in all other loricariids), further suggesting the use of the diverticulum as a hydrostatic organ.

The possession of an air sac in *Lithoxus* is impressive because these fish are extremely dorsoventrally flattened and the visceral cavity is very small, leaving little room for the modification of the viscera. Because of the small area for the visceral cavity and the possession of the air sac, *Lithoxus* have a much shorter intestine than most other loricariids.

Little information is available on the habitat requirements of *Lithoxus*. Boeseman (1982) suggests that *Lithoxus* is found under rocks in flowing water in rivulets, often in very shallow water; however, Eigenmann (1912) describes the habitat as fairly deep, rocky pools in larger creeks. The habitats mentioned by Eigenmann and Boeseman are both fairly well oxygenated, but rivulets tend to be intermittent, and drying of the rivulets may have led to the modification of the stomach in *Lithoxus*. Because *Lithoxus* are so flat and probably live underneath rocks, it seems unlikely that they are exploiting the water

column by using the stomach as a hydrostatic organ.

In the two female *Lithoxus* examined, the ovaries were extremely well developed with mature ova. Interestingly, these eggs were extremely large (1.6–2.2 mm) for such small fish (38.6–41.4 mm SL). Fecundity for the fish must be very low because the average number of mature eggs per fish was only 16. Low numbers of very large eggs suggests that *Lithoxus* exhibit well-developed parental care, but nothing has been reported on their breeding behavior.

The presence of an air sac in *Scoloplax* could also be for air breathing or for buoyancy control. Given the habitat preference of *Scoloplax* and that air breathers such as *Erythrinus* and *Hoplosternum* were collected along with the *Scoloplax* used in this study, it is likely that the stomach is acting as a respiratory organ. Due to lack of comparative material, it is impossible to determine how *Scoloplax* evolved an inflatable stomach, but it was likely through steps similar to those of loricariids. It is tempting to call an expanded stomach (states 2–3, 8) a primitive characteristic in Loricariidae based on the presence of an expanded stomach in *Scoloplax*. However, the different morphologies of the expanded stomach in loricariids and scoloplacids suggests that they are convergent.

Phylogenetic patterns.—Although stomachs may have been modified as air-holding organs several times within catfishes, the modifications are all fairly distinct and complex enough to be uniquely derived. Therefore, it is likely that the analysis of the complex air-breathing structures in loricariids (states 3–8) will help determine phylogenetic relationships within the family. Because of the ambiguity of states 1–2, their phylogenetic utility is more limited and will require large series of fishes to determine to which state a particular species belongs.

The presence of an extremely enlarged stomach with a connective tissue sheet (state 3) may be very important in resolving relationships within Hypostominae. State 3 was found mainly in species formerly ascribed to *Pterygoplichthys*. Weber (1991, 1992) believed that *Pterygoplichthys* was a paraphyletic genus with three distinct lineages, *Pterygoplichthys*, *Liposarcus*, and *Glyptoperichthys* (the *Pterygoplichthys* group) forming a monophyletic group with *Megalancistrus*. Schaefer (1986, 1987) also suggested a close relationship between *Pterygoplichthys* and *Megalancistrus*. Weber and Schaefer site two main characters considered synapomorphic for *Pterygoplichthys*, *Liposarcus*, *Glyptoperichthys*, and *Megalancistrus*: an increased number of dorsal-fin rays (to 10+

from 7 in most other loricariids) and an associated increased number of bifid neural spines. However, *Megalancistrus* has an opercle morphology characteristic with Ancistrinae (as described by Schaefer, 1986, 1987), is phenetically similar to the ancistrines *Pseudacanthicus* and *Acanthicus*, and lacks a modified respiratory stomach. With the presence of state 3 and the lack of an ancistrine opercle in the *Pterygoplichthys* group, it is likely that the increase in the numbers of dorsal-fin rays and bifid neural spines are correlated with one another and are convergent between the *Pterygoplichthys* group and *Megalancistrus*.

Hemiancistrus is another taxonomic problem that can be aided by examination of the respiratory stomach. It appears that *Hemiancistrus*, as currently recognized (Isbrücker, 1980), is a polyphyletic genus with the lineage that contains the type species of the genus similar to the ancistrine *Peckoltia* (Isbrücker, 1992) and another lineage consisting of *Hemiancistrus annectens*, *Hemiancistrus aspilogaster*, *Hemiancistrus holostictus*, *Hemiancistrus maracaiboensis*, and *Hemiancistrus wilsoni* as well as *Hypostomus panamensis*. True *Hemiancistrus* examined did not possess an enlarged stomach, whereas the examined members of the *H. annectens* group did. The *H. annectens* group also lacks either opercle morphology that diagnoses Ancistrinae. Presence of state 3 in the *Pterygoplichthys* group and the *H. annectens* group suggests the two may be sisters. If the *H. annectens* group is the sister to the *Pterygoplichthys* group, it would probably deserve separate generic status. Placement of the *H. annectens* group into a different genus is reserved until the phylogenetic position of the species can be assessed.

The U-shaped diverticula of *Rhinelepis*, *Pseudorhinelepis*, *Pogonopoma*, and *Pogonopomoides* (the *Rhinelepis* group) clearly diagnose a monophyletic clade. Although the genera are all fairly divergent in appearance, other characters support the group's monophyly: a lack of ribs beyond the enlarged rib of the sixth vertebral centrum, widened lateral processes of the basipterygium of the pelvic girdle, and an esophagus that does not bend to the right upon entering the visceral cavity. Based on the proposed evolutionary sequence of the diverticulum, the relationships for the genera of the *Rhinelepis* group would be: (*Pseudorhinelepis* + (*Rhinelepis* + (*Pogonopoma* + *Pogonopomoides*))). In an examination of the relationships of the *Rhinelepis* group, Armbruster (1998) suggests that this indeed is the phylogeny of the group. The same relationships were found with and without use of the diverticulum character, which suggests

that the hypothesized evolutionary sequence for the diverticulum is correct.

Expanded stomachs may be characteristics that can be used to separately diagnose *Lithoxus* and *Scoloplax*; however, more species of each genus must be examined before such a claim can be made. The sister to *Lithoxus* is believed to be *Exastilithoxus* (Schaefer, 1986; Isbrücker and Nijssen, 1985; 1990), but *Exastilithoxus* has no modification of the stomach, suggesting that the expanded stomach is a synapomorphy for *Lithoxus*. The ringlike diverticulum was found by Schaefer (1997) to diagnose *Otocinclus*.

Here I have attempted to infer ecological status for morphological structures based on gross morphology. Actual utility of the air-holding structures requires the tissues to be examined histologically and the behavior of the fishes to be elucidated. Loricariids represent an excellent group to study the evolution of air breathing; and studies of functional morphology, histology, and behavior should be performed to address the evolution of these very interesting products of evolution.

SPECIMENS EXAMINED

Scoloplacidae: *Scoloplax dicra*: INHS 37242 (1 examined), INHS 37195 (1).

Neoplecostominae: *Neoplecostomus microps*: MNRJ 12802 (1), MNRJ 13555 (1), MNRJ 13556 (2).

Hypoptopomatinae: *Hypoptopoma* sp.: INHS 28696 (2), INHS 28997 (4), INHS 29973 (2). *Microlepidogaster* sp.: INHS 37356 (2). *Nannoptopoma spectabilis*: INHS 28298 (2), INHS 61281 (1). *Otocinclus* sp. 1: INHS 28083 (2), INHS 30093 (5), and INHS 60418 (3). *Otocinclus* sp. 2: INHS 37469 (6). *Parotocinclus britskii*: INHS 31733 (2).

Loricariinae: *Crossoloricaria venezuelae*: INHS 60378 (1). *Cteniloricaria platystoma*: INHS 31687 (1). *Farlowella curtirostra*: INHS 60037 (1). *Farlowella mariaelenae*: INHS 28973 (3). *Lamontichthys llanero*: INHS 29957 (2). *Loricaria cataphracta*: INHS 31415 (1), INHS 34780 (1). *Loricaria* sp.: INHS 31689 (1). *Loricariichthys platymetopon*: INHS 29926 (1), INHS 35413 (3). *Rineloricaria caracasensis*: INHS 27632 (1). *Rineloricaria rupestris*: INHS 35602 (3), INHS 60354 (1), INHS 60381 (1). *Rineloricaria uracantha*: INHS 36105 (1), INHS 62740 (1). *Sturisoma festivum*: INHS 35575 (3), INHS 35603 (1), INHS 59948 (1).

Hypostominae: *Aphanotorulus ammophilus*: ANSP 165832 (1), MCNG 13504 (3). *Aphanotorulus franki*: LACM 41738-9 (2). *Cochliodon cochliodon*: UMMZ 206338 (3). *Cochliodon honda*: INHS 60463 (1). *Cochliodon* sp.: AMNH 97880

(1). *Cochliodon taphorni*: ANSP 168195 (2). *Corymbophanes bahianus*: USNM 318203 (3). *Delturus anguillicauda*: USNM 218209 (1), USNM 315901 (1), USNM 318180 (1). *Glyptoperichthys gibbiceps*: MZUSP 24340 (3). *Glyptoperichthys lituratus*: AMNH 39945 (1). *Glyptoperichthys scrophus*: INHS 36937 (1), INHS 41107 (1). *Hemipsilichthys* sp. 1: USNM 320377 (3). *Hemipsilichthys* sp. 2: MZUSP 42205 (3). *Hypostomus* type 1 ("type" refers to an artificial group of unidentified species with the same stomach character state): INHS 31683 (1), INHS 35660 (1), UF 82322 (2). *Hypostomus* type 2: ANSP 160774 (3), CAS 77265 (1), UF 77909 (2). *Hypostomus albopunctatus*: MZUSP 24458 (2). *Hypostomus asperatus*: SU 51772 (1). *Hypostomus bolivianus*: CAS 77246 (1). *Hypostomus emarginatus*: AMNH 12607 (1), AMNH 77378 (1), INHS 29085 (1). *Hypostomus francisci*: ANSP 172107 (2), MNRJ 13559 (2). *Hypostomus panamensis*: ANSP 126440 (3), USNM 78315 (2), USNM 7823 (1), USNM 293166 (1). *Hypostomus plecostomus*: YPM 4194 (1), ZMA 105306 (2). *Hypostomus robinii*: MCNG 8215 (2). *Hypostomus squalinus*: ANSP 134182 (2), SU 50695 (1), MCNG 18340 (1). *Isbrueckerichthys duseni*: UMMZ 215262 (2). *Kronichthys* sp.: MZUSP 27545 (2), MZUSP 35286 (1). *Liposarcus multi-radiatus*: INHS 28260 (1), INHS 29787 (1), INHS 35490 (1). *Liposarcus pardalis*: CAS 77274 (1), FMNH 101384 (1). *Pogonopoma wertheimeri*: USNM 301001 (1), USNM 301985 (2). *Pogonopomoides parahybae*: MNRJ 13562 (1). *Pseudorinelepis genibarbis*: INHS 36938 (2), INHS 39730 (1), MZUSP 6339 (1), ZMA 107867 (1). *Pterygoplichthys etentaculatus*: ANSP 172096 (2), ANSP 172097 (1). *Pterygoplichthys zuliaensis*: INHS 35384 (1). *Rhinelepis aspera*: MHNG 2475.6 (1), MHNG 2475.61 (1), MHNG 2475.68 (1), MNRJ 13561 (1).

Ancistrinae: *Ancistrus pirareta*: UMMZ 296085 (4). *Ancistrus* sp. 1: INHS 31835 (2). *Ancistrus* sp. 2: INHS 29996 (4). *Chaetostoma anomala*: INHS 69496 (4). *Cordylancistrus torbesensis*: MCNG 8066 (1). *Dolichancistrus pediculatus*: MCNG 6470 (1). *Dekeyseria scaphirhyncha*: USNM 269958 (1). *Exastilithoxus* sp.: AMNH 91400 (1). *Hemiancistrus annectens*: BMNH 1902.5.27.49 (Holotype). *Hemiancistrus maracaiboensis*: EBRG 2855 (2), INHS 35580 (1). *Hemiancistrus* sp.: MNRJ 13304 (2), UF 77850 (2). *Lasiancistrus* sp.: INHS 28283 (4). *Lithoxancistrus orinoco*: AMNH 91023 (1). *Lithoxus bovallii*: AMNH 54961 (1). *Lithoxus lithoides*: BMNH 1972.7.17:66-115 (3). *Megalancistrus aculeatus*: MZUSP 21143 (1), MZUSP 24435 (1). *Oligancistrus punctatissimus*: INHS 40913 (1cs), MZUSP 34265 (1). *Panaque maccus*: INHS 29862 (1). *Peckoltia brevis*: USNM 305824 (3), *Peckoltia ucayalensis*: INHS 40916

(1), *Peckoltia vittata*: CAS 6476 (1), *Peckoltia* sp.: FMNH 70863 (1), INHS uncataloged (1), *Spectracanthicus murinus*: MZUSP 34279 (1).

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