

Phylogenetic Relationships of the Suckermouth Armored Catfishes of the *Rhinelepis* Group (Loricariidae: Hypostominae)

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The loricariid catfish genera *Pogonopoma*, *Pogonopomoides*, *Pseudorinelepis*, and *Rhinelepis* form a monophyletic clade within the subfamily Hypostominae. Phylogenetic analysis of morphological characters reveals the following relationships: (*Pseudorinelepis* + (*Rhinelepis* + (*Pogonopoma* + *Pogonopomoides*))). These nodes are strongly supported with several synapomorphies, and each genus is redescribed and diagnosed. Phylogenetic analysis revealed a split between the Amazonian genus (*Pseudorinelepis*) and the remainder of the genera which occur in southeastern Brazil.

Los géneros de bagres loricariid *Pogonopoma*, *Pogonopomoides*, *Pseudorinelepis*, y *Rhinelepis* constituyen un grupo monofilético dentro de la subfamilia Hypostominae. Un análisis filogenético de características morfológicas reveló las siguientes relaciones: (*Pseudorinelepis* + (*Rhinelepis* + (*Pogonopoma* + *Pogonopomoides*))). Estos nodos son apoyados por varias sinapomorfias y cada género es redescrito y diagnosticado. Una división entre el género de Amazonia (*Pseudorinelepis*) y el resto de los géneros que ocurren en el sudeste de Brasil fue revelada por un análisis filogenético.

LORICARIIDS, the suckermouth armored catfishes, range from southern Costa Rica to northern Argentina and are traditionally placed in six subfamilies (Isbrücker, 1980). Of the subfamilies, Hypostominae is one of the largest with 18 valid genera (Isbrücker, 1980; Burgess and Finley, 1996; Armbruster and Page, 1997). Very little information is available on the relationships of the hypostomine genera to one another, and Schaefer (1986, 1987) could not find any characteristics to diagnose the subfamily. Within Hypostominae, *Pogonopoma* Regan 1904, *Pogonopomoides* Gosline 1947, *Pseudorinelepis* Bleeker 1862, and *Rhinelepis* Spix 1829 were described as the *Rhinelepis* group by Armbruster (1998) based on a large U-shaped diverticulum of the stomach.

The *Rhinelepis* group has a total of only nine species distributed in the Amazon, Paraná, and São Francisco basins and some smaller, coastal streams in southeastern Brazil (Fig. 1). *Pseudorinelepis* is the largest genus with four described species, all from the Rio Amazonas and its major tributaries in western Brazil and Peru (Armbruster and Page, 1997). *Rhinelepis* has three described species from the rios São Francisco, Paraíba, and Paraná. *Pogonopoma* and *Pogonopomoides* are both monotypic and occur in the rios Mucuri and Paraíba, respectfully (Isbrücker, 1980; Burgess, 1989).

Members of the *Rhinelepis* group are rare in collections, and few were available for examination. The number of collections is small for a variety of reasons, including their large size (*Rhinelepis* can reach at least 60 cm), their pref-

erence for large rivers, and lack of collections from the rivers in which they occur. Little is known about the ecological requirements of the group, but Armbruster (1998) suggests that *Pseudorinelepis* and *Rhinelepis* use their gut diverticula as accessory respiratory organs. In *Pogonopoma* and *Pogonopomoides*, the diverticula appear almost identical to swim bladders, and the fishes may use them as hydrostatic organs and may be more pelagic than typical loricariids.

Armbruster (1998) suggests the following as possible relationships among the *Rhinelepis* group based on characteristics associated with the gut diverticula: (*Pseudorinelepis* + (*Rhinelepis* + (*Pogonopoma* + *Pogonopomoides*))). In this paper, these findings are reviewed, a phylogeny is produced with the addition of osteological characteristics, and the genera of the *Rhinelepis* group are diagnosed and redescribed.

MATERIALS AND METHODS

Specimens were cleared and double-stained for cartilage and bone using procedures modified from Taylor and Van Dyke (1984). Drawings were prepared using a camera lucida attached to a Wild M-5 stereomicroscope. Institutional abbreviations are as in Leviton et al. (1985) with the addition of IAP for Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru and MUSM for Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos Lima, Peru.

Given that the relationships of the *Rhinelepis* group to the remainder of Loricariidae are un-

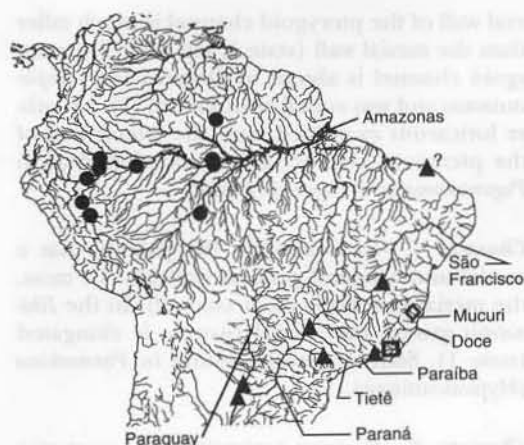


Fig. 1. Distribution of the *Rhinelepis* group. Question mark refers to a potentially introduced population of *Rhinelepis*. Diamond = *Pogonopoma*, square = *Pogonopomoides*, circles = *Pseudorinelepis*, and triangles = *Rhinelepis*.

clear, most of the genera of Hypostominae, Ancistrinae, Neoplecostominae, and several genera of Loricariinae and Hypoptopomatinae were examined. In addition, specimens of the sister family to Loricariidae, Astroblepidae (Schaefer, 1986, 1987; de Pinna 1993), were also examined. To simplify the data presentation, the outgroups used directly for this study included representatives of a variety of hypostomine genera [*Delturus*, *Hemipsilichthys*, *Hypostomus* (represented by *H. plecostomus*), and *Isbrueckerichthys* (formerly referred to as *Pareiorhaphis*; for discussion, see Derjst, 1994)] and *Neoplecostomus* the sole genus of Neoplecostominae. The outgroup taxa were chosen based on their current or former inclusion in the same subfamily as the *Rhinelepis* group and to include much of the diversity of Hypostominae. It is important to note that the relationships of the genera of the *Rhinelepis*

group were consistent when the outgroup described above was used, when all of the loricariid genera available were included as the outgroup, or when all loricariid genera available were included in the ingroup and *Astroblepus* was the sole outgroup. Polarity decisions were made based mainly on comparison to the outgroup and secondarily on how the characters plotted in preliminary analyses (Schaefer 1986; Armbruster, 1997). Note: the position of the *Rhinelepis* group in Schaefer (1986) is based on Schaefer's *Pseudorinelepis* and not on his *Pogonopomoides* because examination of the specimens of *Pogonopomoides* used by Schaefer revealed them to be *Schizolepis*. Diagnostic characters given herein are consistent with the diagnostic characters in Armbruster (1997). The character descriptions provide a general trend for the distribution of the character states in loricariids and astroblepids. A phylogeny for the majority of the genera of Hypostominae and Ancistrinae is in preparation, and the distribution of characteristics will be discussed in detail there. *Hypostomus plecostomus* in this study includes all of the species that grouped in a clade with *H. plecostomus* (including *Hypostomus micromaculatus*) in Armbruster (1997).

Characters were coded numerically (Table 1) and were unordered unless indicated otherwise. Phylogenetic analysis was accomplished using the exhaustive search algorithm of PAUP (vers. 3.1.1; D. L. Swofford, Illinois Nat. Hist. Surv. Champaign, 1993, unpubl.), and all trees were saved to the point where the *Rhinelepis* group was no longer monophyletic. A bootstrap analysis was completed using the branch-and-bound algorithm of PAUP and 1000 replicates. Trees were rooted by using the "root with a basal polytomy" option in PAUP 3.1.1. Characters considered autapomorphic for a particular genus for this analysis are indicated in the character ac-

TABLE 1. DATA MATRIX FOR PHYLOGENETIC AND DIAGNOSTIC CHARACTERS. Characters autapomorphic for a genus were excluded from the phylogenetic analysis.

Genus	Character States			
<i>Neoplecostomus</i>	00000?0000	0000011010	0000000000	1000000000
<i>Delturus</i>	00000?0000	0000011000	0010010000	0001000000
<i>Hemipsilichthys</i>	0000100000	0011000010	0000000000	1001000000
<i>Isbrueckerichthys</i>	0000000000	0011020010	0000000000	0101000100
<i>Kronichthys</i>	0000000000	0011001000	0000000000	0100000000
<i>Hypostomus</i>	0100000000	1010011000	0010000000	0000000000
<i>Pogonopoma</i>	0111111111	0100000010	0001000010	1111011113
<i>Pogonopomoides</i>	0101111111	0000011000	0001100111	1120010114
<i>Pseudorinelepis</i>	1001001001	1011011001	1011100121	1001010011
<i>Rhinelepis</i>	0111001111	0011121100	0111111010	1000110112

count and were excluded from the phylogenetic analysis. See Schaefer (1987) for a detailed description of loricariid osteology.

Meristics and morphometrics follow Armbruster and Page (1996) with the addition of dorsal-caudal length which is the length from the posterior end of the dorsal fin to penultimate dorsal procurent caudal-fin spine. Morphometric characters were restricted to those given in Table 2.

CHARACTERS

Character 1.—In most loricariids, the posterior shelf of the fourth epibranchial is present and short or else is absent (state 0, Fig. 2A). The shelf is expanded in *Pseudorinelepis* (state 1, Fig. 2B). Autapomorphy for *Pseudorinelepis*. State 1 is also found in *Scobinancistrus* (Ancistrinae).

Character 2.—In most loricariids, the second infrapharyngobranchial is a circular-shaped bone that is oriented dorsoventrally (state 0). In *Hypostomus plecostomus*, *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis*, the second infrapharyngobranchial has a lateral process located approximately in the center of the bone (state 1). This character appears to have evolved several times in loricariids (Armbruster, 1997).

Character 3.—In most loricariids, the anteromesial edge of the hypohyal is slightly concave to convex and not expanded (state 0, Fig. 2C). In *Pogonopoma* and *Rhinelepis*, the hypohyal has an extended anteromesial projection that makes the anteromesial edge of the hypohyal very concave (state 1, Fig. 2D).

Character 4.—In most loricariids, the upper pharyngeal tooth plate consists of a raised, bulbous area with a shelf extending mesially or the shelf is absent (state 0, Fig. 2E). The *Rhinelepis* group also has a shelf formed laterally (state 1, Fig. 2F). State 1 is unique to the *Rhinelepis* group.

Character 5.—In most loricariids, the hyomandibula has a cartilaginous condyle that at least partially contacts the prootic (state 0). In *Hemipsilichthys*, *Pogonopoma*, and *Pogonopomoides*, the contact is solely on the pterotic-supracleithrum (state 1). State 1 is also present in *Corymbophanes bahianus* of Hypostominae and *Pseudancistrus* and *Lithoxancistrus* of Ancistrinae.

Character 6.—In most loricariids, the lateral wall of the pterygoid channel is of approximately the same height as the mesial wall (state 0, Fig. 3A). In *Pogonopoma* and *Pogonopomoides*, the lat-

eral wall of the pterygoid channel is much taller than the mesial wall (state 1, Fig. 3B). The pterygoid channel is absent in *Delturus* and *Neoplecostomus* and was coded as unknown (?). No other loricariids examined have the lateral wall of the pterygoid channel as well developed as in *Pogonopoma* and *Pogonopomoides*.

Character 7.—In loricariids, the palatine has a mesial and a lateral process ventrally. In most, the mesial process is short (state 0). In the *Rhinelepis* group, the mesial process is elongated (state 1). State 1 was also found in *Pareiorhina* (Hypostominae).

Character 8.—In most loricariids, the posterior section of the preopercle is long, and the preopercle appears to be oriented horizontally if the ventral edge of the quadrate is taken as the horizon (state 0, Fig. 3C). In *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis*, the posterior section of the preopercle is very short, giving the preopercle the appearance of being oriented at an angle to almost vertically (state 1, Fig. 3D). State 1 has evolved several times in loricariids, most notably in many Ancistrinae (Armbruster, 1997).

Character 9.—In most loricariids, the preopercular canal exits the preopercle posterior to the posterior edge of the quadrate (state 0, Fig. 3C). In *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis*, the canal exits ventral to the posterior edge of the quadrate (state 1, Fig. 3D). State 1 is also found in most Ancistrinae.

Character 10.—In most loricariids, the symplectic foramen of the preopercle is contained entirely within the preopercle (state 0, Fig. 3C). In the *Rhinelepis* group, the foramen has shifted dorsally so that the anterodorsal margin of the foramen is formed by the quadrate (state 1, Fig. 3D). State 1 appears to have evolved several times in loricariids (Armbruster, 1997).

Character 11.—In most loricariids, the quadrate is smooth laterally (state 0). In *Hypostomus plecostomus* and *Pseudorinelepis*, the quadrate has a tall ridge laterally on the articulating condyle for the lower jaw (state 1). State 1 is also found in *Pterygoplichthys* (Hypostominae).

Character 12.—In most loricariids, the opercle is broad (state 0, Fig. 3C), whereas in *Pogonopoma*, the opercle is thin (state 1, Fig. 3D). Autapomorphy for *Pogonopoma*. Ancistrines also have a narrow opercle, but the form of the opercle is

TABLE 2. SELECTED MORPHOMETRIC FEATURES OF THE *Rhinelepis* Group. Ratios expressed as percents of standard length (SL).

Morphometric feature	<i>Pogonopoma</i>			<i>Pogonopomoides</i>			<i>Pseudorhinelepis</i>			<i>Rhinelepis</i>		
	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range
Standard length (mm)	34	155.2 \pm 28.6	90.3–223.2	6	213.5 \pm 55.7	119.1–263.0	37	147.3 \pm 53.2	72.2–356.2	4	162.8 \pm 62.8	106.2–240.4
Predorsal length/SL	34	39.0 \pm 1.1	36.6–41.3	6	38.8 \pm 1.1	37.3–40.0	37	40.9 \pm 1.5	37.9–43.9	4	45.9 \pm 2.0	43.0–47.3
Head length/SL	34	29.3 \pm 1.1	26.5–32.6	6	31.6 \pm 1.1	30.4–32.6	37	31.2 \pm 1.8	27.8–35.1	4	38.0 \pm 2.3	34.7–39.6
Orbit diameter/SL	34	4.9 \pm 0.4	4.1–5.8	6	4.6 \pm 0.7	3.9–5.5	36	5.1 \pm 0.5	4.1–6.1	4	4.3 \pm 0.5	3.9–5.0
Snout length/SL	34	17.0 \pm 0.5	15.5–17.9	6	18.4 \pm 0.6	17.6–19.3	37	15.8 \pm 1.0	13.8–17.6	4	23.2 \pm 1.5	21.0–24.3
Interorbital width/SL	34	12.5 \pm 0.5	11.2–13.6	6	12.5 \pm 0.6	12.0–13.7	37		12.4–16.6	4	19.0 \pm 0.5	18.2–19.4
Thorax length/SL	34	24.5 \pm 1.7	17.3–27.2	6	21.6 \pm 1.5	18.9–23.3	37	28.7 \pm 1.6	25.8–31.7	4	18.4 \pm 2.5	15.1–20.7
Pectoral-spine length/SL	34	27.8 \pm 1.1	25.8–29.4	6	24.9 \pm 2.0	22.6–27.5	37	27.9 \pm 1.7	24.2–31.5	4	24.0 \pm 1.5	22.5–26.0
Abdomen length/SL	34	24.2 \pm 1.0	22.5–26.3	6	25.7 \pm 1.1	24.6–27.6	37	22.4 \pm 1.0	20.4–25.1	4	25.4 \pm 0.6	24.5–25.9
Pelvic-spine length/SL	34	25.1 \pm 1.4	21.8–27.8	6	24.7 \pm 2.6	21.6–28.1	35	23.0 \pm 1.4	20.6–26.9	4	23.8 \pm 1.0	23.0–24.8
Postanal length/SL	34	27.9 \pm 1.2	25.6–29.8	6	27.5 \pm 1.0	26.0–28.9	37	25.2 \pm 1.9	20.6–31.0	4	21.8 \pm 1.7	20.3–24.1
Anal-fin length/SL	34	19.0 \pm 1.1	16.4–21.0	6	18.7 \pm 1.2	16.8–20.1	34	19.5 \pm 1.6	16.3–23.0	3	18.7 \pm 2.1	16.8–21.0
Caudal depth/SL	34	9.7 \pm 0.5	8.2–10.6	6	9.4 \pm 0.8	8.6–10.5	37	10.0 \pm 0.6	8.1–10.9	4	11.7 \pm 1.1	10.2–12.6
Dorsal-caudal length/SL	29	37.3 \pm 1.4	34.2–39.6	6	33.6 \pm 0.9	32.7–35.0	36	34.1 \pm 2.5	27.3–38.0	4	31.3 \pm 1.8	29.8–33.8
Dorsal-fin length/SL	34	23.5 \pm 1.0	20.3–25.2	6	24.5 \pm 0.9	23.5–25.6	37	25.0 \pm 1.5	21.6–28.8	4	20.4 \pm 0.7	19.5–21.2
Dorsal-spine length/SL	29	27.8 \pm 2.4	17.6–31.6	4	24.9 \pm 2.5	22.4–27.5	28	26.8 \pm 2.4	23.6–34.2	4	21.3 \pm 2.0	18.5–22.9
Head depth/SL	34	18.4 \pm 0.9	16.1–19.8	6	17.5 \pm 1.4	15.5–19.0	37	22.6 \pm 1.3	20.0–26.0	4	22.6 \pm 1.2	21.4–24.3
Width at anal fin/SL	34	16.4 \pm 1.2	13.9–18.1	6	16.0 \pm 1.5	13.9–18.2	37	16.7 \pm 1.8	12.0–20.9	4	17.6 \pm 0.3	17.3–17.9
Cleithral width/SL	34	26.2 \pm 1.3	23.5–30.8	6	25.3 \pm 1.6	23.3–27.5	37	29.3 \pm 1.1	27.5–31.1	4	31.7 \pm 2.1	28.6–33.3

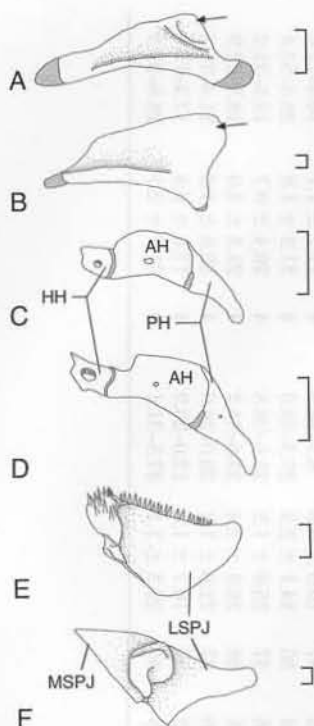


Fig. 2. Branchial elements. (A, B) Fourth epibranchial, right side, dorsal view (arrows indicate posterior shelf), scale = 0.5 mm. (A) *Baryancistrus niveatus*, INHS 40912; (B) *Pseudorinelepis genibarbis*, FMNH 95570. (C, D) Hyoid, right side, ventral view (urohyal excluded), scale = 5 mm. (C) *Pseudorinelepis genibarbis*, INHS 36938; (D) *Rhinelepis* sp., MZUSP 23067. (E, F) Upper pharyngeal jaw, right side, ventral view, scale = 0.5 mm. (E) *Hypostomus emarginatus*, FMNH 96957; (F) *Pseudorinelepis genibarbis*, FMNH 95570. AH = anterohyal, HH = hypohyal, LSPJ = lateral shelf of upper pharyngeal jaw, MSPJ = mesial shelf of upper pharyngeal jaw, PH = posterohyal.

much different. A similar opercle to *Pogonopoma* is found in *Hypostomus albopunctatus*.

Character 13.—Schaefer (1986, 1987, 1988) and Schaefer and Lauder (1986, 1996) state that loricariids have lost both the interopercle and the interoperculo-mandibular ligament. *Delturus*, *Neoplecostomus*, *Pogonopoma*, and *Pogonopomoides* have a small ossification mesial to the preopercle and connected by a ligament to the opercle and the angulo-articular (state 0, Fig. 3D). Although this bone is similar in position to the interopercle, its structure suggests that it is a sesamoid ossification and is not likely to be homologous to the interopercle of other catfishes. The ligament has a wide connection to the opercle and then narrows such that it is a band where it connects with the angulo-articular. The

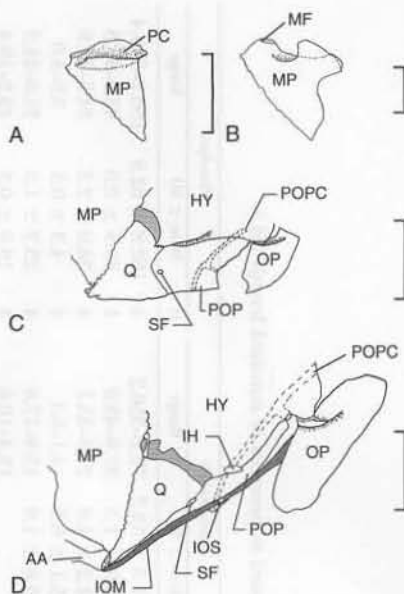


Fig. 3. Suspensorium elements. (A, B) Metapterygoid, right side, lateral view, scale = 5 mm. (A) *Hemipsilichthys cameroni*, USNM 279585; (B) *Pogonopoma wertheimeri*, USNM 301001. (C, D) Suspensorium, right side, mesial view, scale = 5 mm. (C) *Hypostomus* sp., CAS 59487; (D) *Pogonopoma wertheimeri*, USNM 301001. AA = angulo-articular, HY = hyomandibula, IH = interhyal, IOS = interopercular sesamoid, IOM = interoperculo-mandibular ligament, MF = facet for articulation of the metapterygoid to the lateral ethmoid, OP = opercle, PC = pterygoid channel, POP = preopercle, POPC = preopercular canal, SF = symplectic foramen, and Q = quadrate.

sesamoid always forms at the point where the fibers of the ligament first narrow to form a band. The sesamoid is also found in some Loricariinae. Most loricariids lack the sesamoid (state 1, Fig. 3C).

Character 14.—In *Delturus*, *Hypostomus plecostomus*, *Neoplecostomus*, *Pogonopoma*, and *Pogonopomoides*, the interoperculo-mandibular ligament is present (state 0, Fig. 3D). In most loricariids, the interoperculo-mandibular ligament is absent (state 1, Fig. 3C). Although it is unknown whether the interoperculo-mandibular ligament in loricariids is homologous to the same ligament in other catfishes, it is analogous. Loricariids with the ligament do not have a loss of, and probably have reevolved, one of the mechanical couples whose loss Schaefer and Lauder (1986, 1996) suggest may have allowed for the increased variability in the shape of the jaw mechanism of loricariids. See character 13 for more information. Characters 13 and 14 were coded separately because the presence of the

ligament is not always concomitant with the presence of the sesamoid. The ligament appears to have evolved several times in loricariids and is also present in some loricariines and some ancistrines (Armbruster, 1997).

Character 15.—Most loricariids lack plates or have small plates between the opercle and the ventral margin of the pterotic-supracleithrum (state 0). *Rhinelepis* has a unique, large ossification, which probably represents a dermal plate, between the opercle and pterotic-supracleithrum (state 1). Autapomorphy for *Rhinelepis*.

Character 16.—In loricariids, the preopercular canal has an anterior extension into a plate termed the canal plate (Schaefer, 1986, 1987). In *Pogonopoma*, *Hemipsilichthys*, and *Kronichthys*, the canal plate is large and deflected ventrally (state 0), whereas it is much smaller in most Hypostominae and *Neoplecostomus* (state 1). *Rhinelepis* and *Isbrueckerichthys* have two canal plates (state 2). State 0 is also found in Hypoptopomatinae.

Character 17.—*Hemipsilichthys*, *Kronichthys*, and *Pogonopoma* lack plates between the opercle and the canal plate (state 0). Most loricariids have at least one plate between the canal plate and the exposed portion of the opercle (state 1).

Character 18.—In most loricariids, the most posterior infraorbital forms the posteroventral margin of the orbit (state 0). In *Rhinelepis*, the posterior infraorbital forms the entire posterior border of the orbit (state 1). Autapomorphy for *Rhinelepis*. State 1 was also found in *Hypoptopoma* (Hypoptopomatinae).

Character 19.—In most loricariids, the lateral ethmoid is flat posteriorly or else just slightly concave (state 0). In *Hemipsilichthys*, *Isbrueckerichthys*, *Neoplecostomus*, and *Pogonopoma*, the posterolateral corner of the lateral ethmoid is deeply concave such that the posterolateral edge of the lateral ethmoid appears as a ridge (state 1). State 1 is found in several loricariids, particularly in Ancistrinae.

Character 20.—In most loricariids, the parasphenoid is narrow and forms a ridge (state 0). In *Pseudorhinelepis*, the parasphenoid is very wide and forms only a slight ridge (state 1). Other members of the *Rhinelepis* group also have low, wide parasphenoids, but they are not as modified as *Pseudorhinelepis*. Autapomorphy for *Pseudorhinelepis*.

Character 21.—In most loricariids, the pterotic-supracleithrum is fairly smooth laterally or else has only slight ridges formed by bone and odontodes (state 0). In *Pseudorhinelepis*, the ridges are very tall (state 1). Autapomorphy for *Pseudorhinelepis*. *Acanthicus*, *Megalancistrus*, *Pseudacanthicus*, and some *Panaque* (Ancistrinae) have a similar development of the ridges on the pterotic-supracleithrum but not to the extent of *Pseudorhinelepis*.

Character 22.—In most loricariids, the sphenotic at least forms the posterodorsal corner of the orbit (state 0). In *Rhinelepis*, the sphenotic does not contact the orbit exteriorly (state 1). Autapomorphy for *Rhinelepis*. State 1 is also found in *Hypoptopoma* (Hypoptopomatinae).

Character 23.—*Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Neoplecostomus*, *Pogonopoma*, and *Pogonopomoides* have one to several centra above (and sometimes behind) the anal fin with bifid hemal spines (state 0). Most loricariids have no bifid hemal spines (state 1). Bifid hemal spines are found in most hypoptopomatines, most loricariines, *Lithoxus*, and astroblepids but appear to have been separately evolved in *Pogonopoma* and *Pogonopomoides*.

Character 24.—Most loricariids have ribs behind the expanded rib of the sixth vertebral centrum (state 0). In the *Rhinelepis* group, the ribs are absent behind the expanded rib of the sixth vertebral centrum (state 1). Of the loricariids examined, only *Hypoptopoma* (Hypoptopomatinae) lacks ribs.

Character 25.—In astroblepids and most loricariids, the adipose fin is present (state 0). The adipose fin has been lost in several loricariids including *Pogonopomoides*, *Pseudorhinelepis*, and *Rhinelepis* (state 1). An adipose fin is also absent in *Acanthicus*, some *Chaetostoma*, *Leptoancistrus*, and *Lipopterygichthys* of Ancistrinae; *Cochliodon levis*, *Corymbophanes andersoni*, and *Pareiorhina* of Hypostominae; all loricariines; and many hypoptopomatines.

Character 26.—In most loricariids, the abductor fossa of the pectoral girdle is deep to the midline (state 0, Fig. 4A). In *Delturus* and *Rhinelepis*, the fossa is nearly flat anteromesially (state 1, Fig. 4B). State 1 is also found in some loricariines and in *Dekeyseria* (Ancistrinae).

Character 27.—In most loricariids, the anterior margin of the cleithrum is straight (state 0, Fig. 4A). In *Rhinelepis*, the anterior margin is shaped

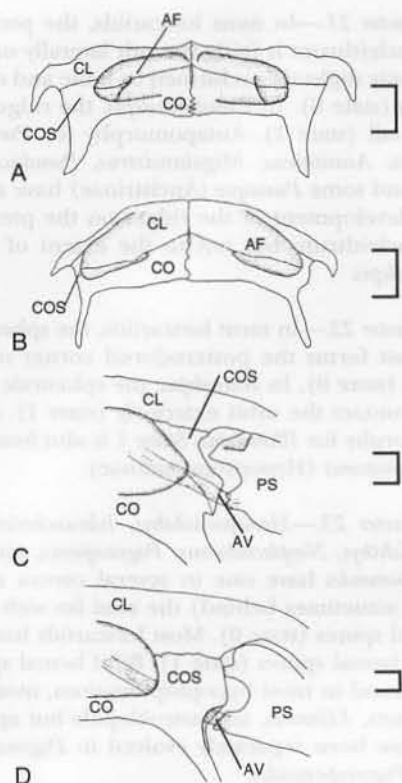


Fig. 4. Pectoral girdle, ventral view. (A, B) Scale = 5 mm. (A) *Pseudorinelepis genibarbis*, INHS 36938; (B) *Rhinelepis* sp., MZUSP 23067. (C, D) Coracoid strut, left side, scale = 1 mm. (C) *Aphanotorulus unicolor*, USNM 319355; (D) *Pseudorinelepis genibarbis*, FMNH 95570. AF = abductor fossa, AV = arrector ventralis, CL = cleithrum, CO = coracoid, COS = coracoid strut, and PS = pectoral spine.

such that the cleithrum forms a trapezoid (state 1, Fig. 4B). Autapomorphy for *Rhinelepis*. State 1 is also found in some loricariines and in *Dekeyseria* (Ancistrinae).

Character 28.—Most loricariids have a thin, lateral strut on the ventral surface of the coracoid, ventral to which the arrector ventralis runs (Schaefer 1986, 1987; state 0, Fig. 4B). In *Pogonopomoides* and *Pseudorinelepis*, the coracoid strut is wide (state 1, Fig. 4A). State 1 is also found in hypoptopomatines, *Corymbophanes bahianus*, and some loricariines.

Character 29.—In most loricariids, the coracoid strut is covered in skin or plates (state 0). In *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis*, the coracoid strut supports at least a few odontodes (state 1). In *Pseudorinelepis*, the lateral strut of the coracoid is almost completely exposed and

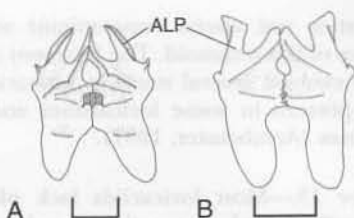


Fig. 5. Pelvic basiptyerygium, dorsal view. (A) *Hypostomus squalinus*, MCNG 18340; (B) *Rhinelepis* sp., MZUSP 23067.

covered in odontodes (state 2). Because most loricariids lack exposure of the coracoid strut, it is most parsimonious to assume that exposure of the coracoid strut was at first slight and that the exposure of the strut increased through evolution; hence, this character was ordered. Schaefer (1991) uses characteristics associated with the exposure of the pectoral girdle to diagnose Hypoptopomatinae. Although exposure of the coracoid appears to have occurred several times (Armbruster, 1997), the condition in Hypoptopomatinae where the abductor fossa becomes covered by bone and the cleithrum is also exposed appears to be unique (Armbruster, 1997).

Character 30.—In astroblepids and most loricariids, the arrector ventralis passes ventral to the coracoid strut and attaches onto the posterior condyle of the pectoral fin spine (state 0, Fig. 4C). In *Pogonopomoides* and *Pseudorinelepis*, the arrector ventralis passes through a channel in the coracoid strut (state 1, Fig. 4D). Passage of the arrector ventralis through a channel is also found in hypoptopomatines, loricariines, and *Corymbophanes bahianus*.

Character 31.—In astroblepids and most loricariids, the anterolateral process of the pelvic basiptyerygium is thin (state 0, Fig. 5A). In several *Hemipsilichthys*, *Neoplecostomus*, and the *Rhinelepis* group, the anterolateral process is widened along its entire length (state 1, Fig. 5B). Wide anterolateral processes of the pelvic basiptyerygium have evolved several times (Armbruster, 1997).

Character 32.—Most loricariids have a ridge anteroventrally on the pelvic basiptyerygium (state 0). In *Isbrueckerichthys*, *Pogonopoma*, and *Pogonopomoides*, the ridge is represented by only a small, short section laterally or is absent (state 1).

Character 33.—In most loricariids, the posterior processes of the pelvic basiptyerygium are round-

ed and broad (state 0), whereas in *Pogonopoma*, they are pointed and thin (state 1), and in *Pogonopomoides*, they are very elongate and pointed (state 2). The reason for the elongation of the posterior processes of the pelvic basipterygium is unknown; however, the extreme elongation of the posterior processes in *Pogonopomoides* is further derived from what is seen in the outgroup than the moderate elongation seen in *Pogonopoma*, and it was hypothesized that the posterior processes evolved by a successive lengthening and thinning. Hence, this character was ordered. No other loricariids have long, pointed posterior processes of the pelvic basipterygium; however, astroblepids have a similar state to that of *Pogonopomoides*.

Character 34.—Most loricariids in the analysis lack elongate odontodes on the cheek (state 0). *Delturus*, *Hemipislichthys*, *Isbrueckerichthys*, *Pogonopoma*, and *Pseudorinelepis* have elongated odontodes on the cheek (state 1). Elongated odontodes are also found on the cheeks of some breeding males of Loricariinae and *Isorineloricaria*. Elongated cheek odontodes are found in both males and females of many *Pterygoplichthys* and most Ancistrinae; however, the odontodes are located on an evertible patch of plates, whereas the cheek odontodes of the other loricariids are not evertible.

Character 35.—In most loricariids, the gill openings are restricted (state 0), whereas in *Rhinelepis*, the gill openings are large (state 1). Autapomorphy for *Rhinelepis*. Expanded gill openings are also found in *Parancistrus* (Ancistrinae).

Character 36.—In most catfishes and in the *Rhinelepis* group, the iris is circular (state 0). In other loricariids, the iris has a dorsal flap of skin causing the eye to appear bilobed (state 1).

Character 37.—In most loricariids, the odontodes of the lateral plates are either generally distributed or located on the top of short, bony ridges (state 0). In *Pogonopoma*, the ridges of the lateral plates are well developed but lack odontodes. The odontodes in *Pogonopoma* are located only in the spaces between the ridges (state 1). Autapomorphy for *Pogonopoma*.

Character 38.—Most loricariids have either just a few small plates (one to three), a naked area, or a medium-sized plate posterior to the pterotic-supracleithrum at the level of the lateral line (state 0). *Isbrueckerichthys*, *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis* have a patch of numerous small plates (five or more) just posterior to

the pterotic-supracleithrum (state 1). *Paraorhina* (Hypostominae) also has state 1.

Character 39.—In most loricariids, the esophagus normally bends to the right upon entering the visceral cavity and the proximal part of the intestine passes dorsal to the esophagus before turning ventrally to form a large coil (state 0). In the *Rhinelepis* group, the esophagus passes straight to the stomach and the anterior intestine does not pass dorsal to the esophagus (state 1; see Armbruster, 1998). State 1 is also found in *Lithoxus* (Ancistrinae) and *Otocinclus* (Hypopommatinae).

Character 40.—The *Rhinelepis* group has several unique modifications of the digestive tract. In most loricariids, the digestive tract is little modified and lacks a diverticulum at the distal end of the esophagus (state 0). In *Pseudorinelepis*, a large, expandable, two-part diverticulum exits at the distal margin of the esophagus and is loosely held to the abdominal wall (state 1). In *Rhinelepis*, the diverticulum is similar to that of *Pseudorinelepis* but is tightly attached to the abdominal wall (state 2). In *Pogonopoma*, the diverticulum is retroperitoneal (lying outside of the peritoneum), much wider, not expandable, and the initial, muscular section of the diverticulum is reduced (state 3). In *Pogonopomoides*, the diverticulum is similar to that of *Pogonopoma* except that it lacks the initial anterior extension of the second part of the diverticulum seen in all other members of the *Rhinelepis* group and forms a perfect U-shape rather than a U-shape with an inside curve on the right side (state 4). This character was coded as ordered as was suggested by Armbruster (1998). *Otocinclus* has a similar diverticulum; but the distal tip of the diverticulum passes through the peritoneum, the muscular bulb is lacking, and the diverticulum begins on the right, not the left, side of the body. The diverticulum of *Otocinclus* is not considered to be homologous to that of the *Rhinelepis* group (Armbruster, 1998). The posterior section of the diverticulum can be viewed without dissection in small- to medium-sized *Pogonopoma* and *Pogonopomoides* by shining a bright light just dorsal to the pelvic girdle. Because the intestines do not cover the diverticulum below the pelvic fins, the body glows red.

RESULTS

The rarity of species of the *Rhinelepis* group in collections has precluded the examination of large series of specimens. Despite an extensive search of museum collections for lots with large

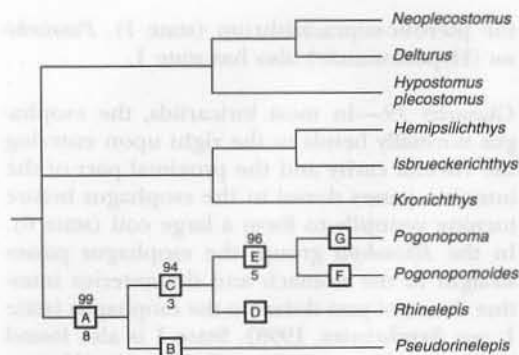


Fig. 6. Single most-parsimonious phylogenetic tree of 61 steps. Upper numbers are bootstrap values based on 1000 replicates. Lower numbers are decay values and indicate the number of steps above the most-parsimonious tree in which the node appears. The relationships of the outgroup taxa to one another and the position of the *Rhinelepis* group within Loricariidae were not explored in this analysis. Letters refer to the following character state changes: (A) 4-1, 7-1, 10-1, 24-1, 25-1, 31-1, 36-0, 39-1, 40-1; (B) 1-1, 11-1, 20-1, 21-1, 28-1, 29-2, 30-1, 34-1; (C) 2-1, 8-1, 9-1, 38-1, 40-2; (D) 15-1, 16-2, 18-1, 22-1, 26-1, 27-1, 35-1; (E) 5-1, 6-1, 13-0, 14-0, 23-0, 32-1, 33-1, 40-3; (F) 28-1, 30-1, 33-2, 40-4; (G) 12-1, 16-0, 17-0, 19-1, 25-0, 34-1, 37-1.

enough numbers of individuals, only one cleared-and-stained specimen of *Pogonopomoides*, two each of *Pogonopoma* and *Rhinelepis*, and three *Pseudorinelepis* were prepared. Given the small sample size, it is possible that characteristics found to be apomorphic for genera could be anomalous in the specimens available. However, many of the apomorphic characteristics for the genera were external and were able to be examined on a greater number of individuals. The material presented herein represents the best possible examination of the data given the few specimens that are now available, but it should be noted that diagnostic characters should be examined in greater detail before they become widely accepted.

Phylogenetic analysis resulted in a single most-parsimonious tree of 61 steps and a consistency index of 0.59 which supported Armbruster's (1998) hypothesis (Fig. 6). Note: characters were not examined to resolve the relationships of the genera of the outgroup or the relationships of the outgroup with the ingroup; thus, no hypothesis of relationships of any taxa other than within the *Rhinelepis* group can be made. Removal of the diverticulum (character 40) upon which the previous hypothesis (Armbruster, 1998) was based resulted in the same tree. Bootstrap values and decay indices (Fig. 6)

were high, indicating strong support for the relationships. Number of trees saved for steps between the most-parsimonious tree (61 steps) and the point where the *Rhinelepis* group was no longer monophyletic (70 steps) are as follows: 61-1, 62-13, 63-33, 64-97, 65-196, 66-265, 67-308, 68-279, 69-405, 70-687 for a total of 2279 trees.

DESCRIPTIONS

Diagnosis.—The *Rhinelepis* group is diagnosed by several synapomorphies: a lateral shelf of the upper pharyngeal tooth plate (4-1); an elongated mesial process of the palatine (7-1); a symplectic foramen that has shifted dorsally such that the anterodorsal margin is formed by the quadrate (10-1); lack of ribs beyond the enlarged rib of the sixth vertebral centrum (24-1); loss of the adipose fin (25-1); an exposed portion of the coracoid strut (29-1); widened lateral processes of the pelvic basipterygium (31-1); circular (vs bilobed) iris (36-0); a straight esophagus to which the intestine does not pass dorsally (39-1); and a large, U-shaped, two-part diverticulum of the digestive tract (40-1). Within the *Rhinelepis* group, the clade of *Pogonopoma*, *Pogonopomoides*, and *Rhinelepis* is diagnosed by a lateral process on the second infrapharyngobranchial (2-1); an angled preopercle (8-1); an anterior exit of the preopercular canal (9-1); a patch of small plates posterior to the pterotic-supracleithrum (38-1); and a diverticulum that has become firmly attached to the abdominal wall (40-2). *Pogonopoma* + *Pogonopomoides* is diagnosed by contact of the hyomandibular condyle solely to the pterotic-supracleithrum (5-1); a taller lateral than mesial wall of the pterygoid channel (6-1); a sesamoid ossification located in the interoperculo-mandibular ligament (13-0 and 14-0); bifid hemal spines (23-0); reduction of the anteroventral ridge of the pelvic basipterygium (32-1); pointed posterior processes of the pelvic basipterygium (33-1); and a diverticulum that has become retroperitoneal, nonexpandable, and has a reduced first section (40-3).

Description.—The *Rhinelepis* group is an assemblage of four genera, with medium- to large-sized species. The *Rhinelepis* group is unique among loricariids for possessing a round (normal) iris versus a bilobed iris (although it is often hard to see the flap in bilobed, preserved fishes). The species have thick plates. The anus is placed far posteriorly so that it is just anterior to the anal fin. The teeth are fairly unusual among loricariids in that they are usually numerous (up to 96) and have stalks that are

much longer than those seen in other loricariids. In *Pogonopoma*, *Pogonopomoides*, and *Pseudorhinelepis*, the crowns of the teeth are small but otherwise shaped like most loricariids (a large mesial and a small lateral cusp). In *Rhinelepis*, the mesial cusp is long and thin, and the lateral cusp is often absent making the teeth look peg-like.

Comparisons.—The *Rhinelepis* group can be distinguished from other Hypostominae by a combination of the following characters: six anal-fin rays; lack of postdorsal ridge formed of raised, median, unpaired plates; an exposed portion of the coracoid strut of the pectoral girdle; a circular (vs bilobed) pupil; and if elongate odontodes are present on the head, they are developed in a large, nonevertible patch.

Pogonopoma Regan, 1904

Figure 7A

Diagnosis.—*Pogonopoma* is diagnosed by a narrow opercle (12-1); a large, ventrally deflected canal plate (16-0); no plates between the opercle and the canal plate (17-0); a lateral ethmoid that is very concave ventrally and has a strong posterolateral ridge (19-1); an adipose fin (25-0); elongated odontodes on the cheek (34-1); and odontodes on the lateral plates that are not present on ridges of bone but only on the gaps between the ridges (37-1).

Description.—*Pogonopoma* is a cylindrically shaped loricariid. Ground color in alcohol preserved specimens is grayish-brown with large dark spots occasionally developed on the head, upper sides, and dorsal fin. Abdomen is gray. The abdomen is mostly unplated except for a row of large plates along the sides, a large patch of small plates between the pelvic fins, and a few scattered small plates along the pectoral girdle. An adipose fin is present although occasionally only the spine is present and is fused with the dorsal plates. The cheek is covered in long but thin odontodes that form a dense patch. Dorsal II-7, pectoral I-6, pelvic I-5, anal 6 (one unbranched and five branched), caudal I-14-I; 23-26 lateral line plates, 6-7 plates under the base of the dorsal fin, 10-12 plates in the depressed dorsal fin, 14-15 postdorsal plates, 10-12 postanal plates, and 38-89 teeth per jaw ramus. Morphometrics given in Table 2.

Distribution.—There is only one species, *Pogonopoma wertheimeri*, in the Rio Mucuri in southeast Brazil (Fig. 1).

Comparisons.—*Pogonopoma* can be distinguished from other Hypostominae by a combination of the following characteristics: a dense patch of odontodes on the cheek that are very elongate and not evertible (the odontodes in most Hypostominae with cheek odontodes, are not dense, are not as long, or are evertible), a well-developed dorsal-fin spinelet (vs a small, rectangular spinelet or no spinelet in *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Pareiorhina*, and *Corymbophanes andersoni*), six anal-fin rays, one preadipose plate (vs 3 or more in *Delturus* and *Upsilonodus*), and a coracoid that is exposed ventrally. Within the *Rhinelepis* group, *Pogonopoma* differs from all others by the presence of an adipose fin. In addition, *Pogonopoma* differs from *Pogonopomoides* by the presence of elongate cheek odontodes and large (vs small) plates along the sides of the abdomen; from *Pseudorhinelepis* by the presence of an incompletely plated abdomen, unkeeled plates, lack of tall ridges on the pterotic-supracleithrum, and a smaller head depth/SL ratio (0.161–0.198 vs 0.200–0.260; Table 2); and from *Rhinelepis* by presence of a smaller gill opening, an incompletely plated abdomen, large (vs small) plates along the sides of the abdomen, elongate cheek odontodes, lack of a large plate between the opercle and pterotic-supracleithrum, and the following morphometric features (see Table 2): a smaller predorsal length/SL ratio (0.366–0.413 vs 0.430–0.473), a smaller head length/SL ratio (0.265–0.326 vs 0.347–0.396), a smaller snout length/SL ratio (0.155–0.179 vs 0.210–0.243), a smaller interorbital width/SL ratio (0.112–0.136 vs 0.182–0.194), a larger dorsal-caudal length/SL ratio (0.342–0.396 vs 0.298–0.338), and a smaller head depth/SL ratio (0.155–0.190 vs 0.214–0.243).

Pogonopomoides Gosline, 1947

Figure 7B

Diagnosis.—*Pogonopomoides* is diagnosed by a wide ventrolateral strut of the coracoid (28-1); passage of the arrector ventralis muscle of the pectoral girdle through a channel (30-1); very elongate and pointed posterior processes of the pelvic basipterygium (33-2); and loss of the initial anterior section of the diverticulum (40-4).

Description.—*Pogonopomoides* appears intermediate in shape between *Rhinelepis* and *Pogonopoma*. *Pogonopomoides* is fairly dorsoventrally flattened with long pectoral and pelvic fins compared with others in the *Rhinelepis* group. The body is charcoal gray and without spots in alcohol preserved specimens. The abdomen is naked ex-

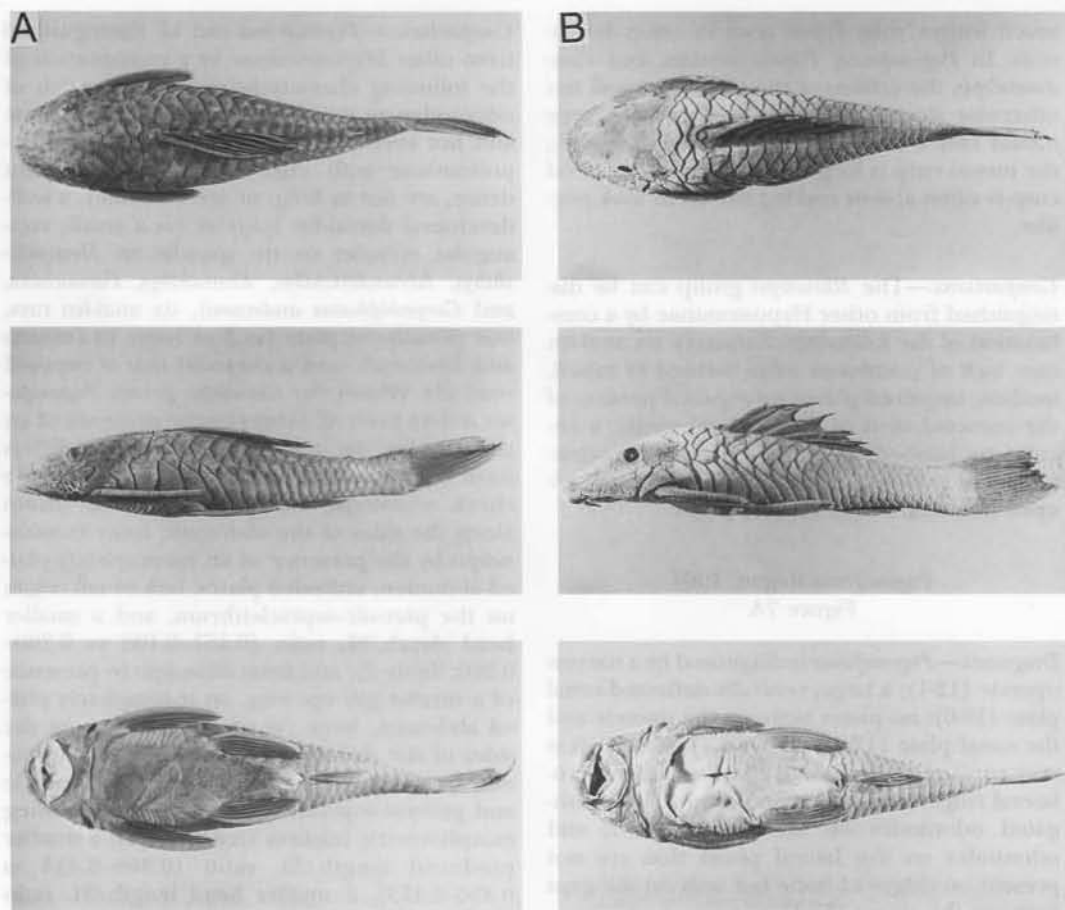


Fig. 7. (A) *Pogonopoma wertheimeri*, USNM 301001, SL = 166.0 mm. (B) *Pogonopomoides parahybae*, MNRJ 13503, SL = 239.6 mm. Dorsal, lateral, and ventral views. Photos by K. S. Cummings.

cept for a row of plates laterally (they are not as large as those in *Pogonopoma*) and a few randomly placed small plates along the pectoral girdle as well as elsewhere. Gill openings are large but not as large as in *Rhinelepis*. The cheek lacks elongate odontodes. Dorsal II-7, pectoral I-6, pelvic I-5, anal 6 (1 unbranched, 5 branched), caudal I-14-I; 24-26 lateral-line plates, seven plates under the base of the dorsal fin, 11-13 plates in the depressed dorsal fin, 12-15 postdorsal plates, 11-13 postanal plates, and 73-98 teeth per jaw ramus. Morphometrics given in Table 2.

Distribution.—There is one species, *Pogonopomoides parahybae*, in the Rio Paraíba of southeast Brazil (Fig. 1).

Comparisons.—*Pogonopomoides* can be identified from most other loricariids by a combination of a loss of the adipose fin and median preadipose plate, a well-developed dorsal-fin spinelet (vs a

small, rectangular spinelet or no spinelet in *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Paraciorhina*, and *Corymbophanes andersoni*), six anal-fin rays, and a coracoid that is exposed ventrally. Within the *Rhinelepis* group, *Pogonopomoides* differs from *Pogonopoma* by the lack of elongate cheek odontodes and lack of an adipose fin; from *Pseudorhinelepis* by the lack of tall ridges on the pterotic-supracleithrum, lack of cheek spines, an incompletely plated abdomen, and the following morphometric features (Table 2): a longer snout length/SL ratio (0.176-0.193 vs 0.138-0.176), a shorter thorax length/SL ratio (0.189-0.233 vs 0.258-0.317), a smaller head depth/SL ratio (0.155-0.190 vs 0.200-0.260), and a smaller cleithral width/SL ratio (0.233-0.275 vs 0.275-0.311); and from *Rhinelepis* by having smaller gill openings, only a few plates on the abdomen (vs fully plated), an exposed posteroventral projection of the coracoid, lack of a plate between the opercle and the pterotic-supracleithrum, and the following morphomet-

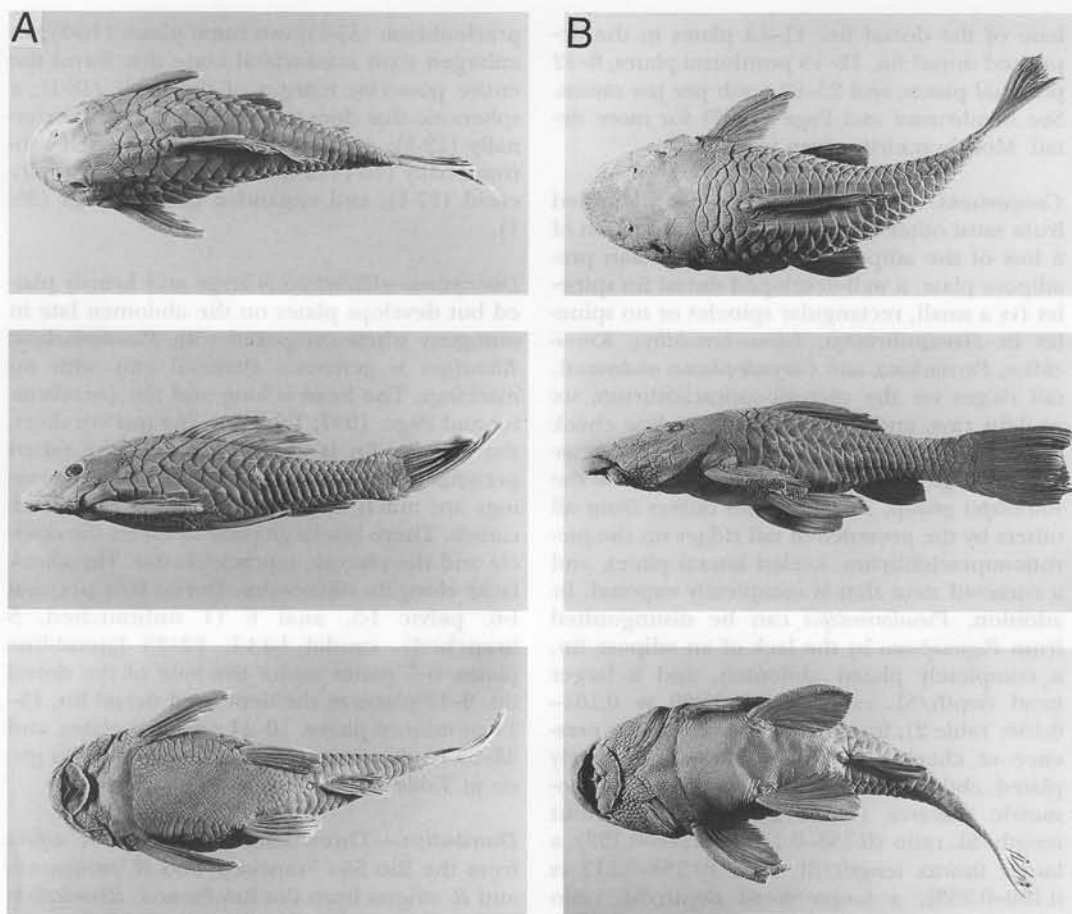


Fig. 8. (A) *Pseudorinelepis genibarbis*, FMNH 95569, SL = 171.2 mm. (B) *Rhinelepis aspera*, MNRJ 13564, SL = 237.9 mm. Dorsal, lateral, and ventral views. Photos by K. S. Cummings.

ric features (Table 2): a smaller predorsal length/SL ratio (0.373–0.400 vs 0.430–0.473), a smaller head length/SL ratio (0.304–0.326 vs 0.347–0.396), a smaller snout length/SL ratio (0.176–0.193 vs 0.210–0.243), a smaller interorbital width/SL ratio (0.120–0.137 vs 0.182–0.194), a larger postanal length/SL ratio (0.260–0.289 vs 0.203–0.241), a larger dorsal-fin length/SL ratio (0.235–0.256 vs 0.195–0.212), a smaller head depth/SL ratio (0.155–0.190 vs 0.214–0.243), and a smaller cleithral width/SL ratio (0.233–0.275 vs 0.286–0.333).

Pseudorinelepis Bleeker, 1862

Figure 8A

Diagnosis.—*Pseudorinelepis* is diagnosed by an enlarged posterior shelf of the fourth epibranchial (1-1); a tall, lateral ridge on the quadrate (11-1); a parasphenoid that is wide and flat at the anterior margin of the orbitosphenoid (20-1); tall ridges on the pterotic-supracleithrum (21-

1); a wide ventrolateral strut of the coracoid that is wholly exposed and covered in odontodes (28-1, 29-2); passage of the arrector ventralis muscle of the pectoral girdle through a channel (30-1); and elongate cheek odontodes (34-1).

Description.—*Pseudorinelepis* are medium to large fishes that are shaped much like an American football. The body is typically very deep and squat with a caudal peduncle that is almost round in cross-section. Almost the entire body is covered in plates even in juveniles. The pterotic-supracleithrum has very tall ridges formed by bone and odontodes. Color pattern is variable from mottled tan and dark brown, to tan and spotted, to completely dark brown. The leading edges of the fins, the dorsal and ventral caudal spines, and the cheek may be colored orange. Dorsal II (7–8), pectoral I-6, pelvic I-5, anal 6 (1 unbranched, 5 branched), caudal I-14 I; 23–26 lateral-line plates, 6–7 plates under the

base of the dorsal fin, 11–14 plates in the depressed dorsal fin, 12–15 postdorsal plates, 8–12 postanal plates, and 23–62 teeth per jaw ramus. See Armbruster and Page (1997) for more detail. Morphometrics given in Table 2.

Comparisons.—*Pseudorinelepis* can be identified from most other loricariids by a combination of a loss of the adipose fin and the median preadipose plate, a well-developed dorsal fin spinelet (vs a small, rectangular spinelet or no spinelet in *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Pareiorhina*, and *Corymbophanes andersoni*), tall ridges on the pterotic-supracleithrum, six anal-fin rays, and a dense patch of fine cheek odontodes that are not evertible. See Armbruster and Page (1997) for more detail. Within the *Rhinelepis* group, *Pseudorinelepis* differs from all others by the presence of tall ridges on the pterotic-supracleithrum, keeled lateral plates, and a coracoid strut that is completely exposed. In addition, *Pseudorinelepis* can be distinguished from *Pogonopoma* by the lack of an adipose fin, a completely plated abdomen, and a larger head depth/SL ratio (0.200–0.260 vs 0.161–0.198; Table 2); from *Pogonopomoides* by the presence of cheek spines in adults, a completely plated abdomen, and the following morphometric features (Table 2): a smaller snout length/SL ratio (0.138–0.176 vs 0.176–0.193), a larger thorax length/SL ratio (0.258–0.317 vs 0.189–0.233), a larger head depth/SL ratio (0.200–0.260 vs 0.155–0.190), and a larger cleithral width/SL ratio (0.275–0.311 vs 0.233–0.275); and from *Rhinelepis* by the presence of cheek spines in adults, lack of a plate between the pterotic-supracleithrum and the exposed opercle, small (vs large) gill openings, and the following morphometric features (Table 2): a smaller snout length/SL ratio (0.138–0.176 vs 0.210–0.243), a smaller interorbital width/SL ratio (0.124–0.166 vs 0.182–0.194), a larger thorax length/SL ratio (0.258–0.317 vs 0.151–0.207), a larger postanal length/SL ratio (0.260–0.289 vs 0.203–0.241), and a larger dorsal fin spine length/SL ratio (0.236–0.342 vs 0.185–0.229).

Distribution.—Four species, *P. agassizii*, *P. carachama*, *P. genibarbis*, and *P. pellegrini* all from the Rios Amazonas, Ucayali, Madeira, Napo, and Negro in Brazil and Peru (Fig. 1).

Rhinelepis von Spix, 1829

Figure 8B

Diagnosis.—*Rhinelepis* is diagnosed by a large plate between the opercle and the pterotic-su-

pracleithrum (15-1); two canal plates (16-2); an enlarged sixth infraorbital bone that forms the entire posterior margin of the orbit (18-1); a sphenotic that does not contact the orbit externally (22-1); a cleithrum that is flattened ventromesially (26-1) and that is shaped like a trapezoid (27-1); and expanded gill openings (35-1).

Description.—*Rhinelepis* is large and heavily plated but develops plates on the abdomen late in ontogeny when compared with *Pseudorinelepis*. *Rhinelepis* is generally charcoal gray with no markings. The head is long and flat (Armbruster and Page, 1997; Table 2). The fins are short; the adipose fin is absent although the raised preadipose plate is often present. The gill openings are much larger than in most other loricariids. There is a large plate between the opercle and the pterotic-supracleithrum. The cheek lacks elongate odontodes. Dorsal II-7, pectoral I-6, pelvic I-5, anal 6 (1 unbranched, 5 branched), caudal I-14-I; 22–25 lateral-line plates, 6–7 plates under the base of the dorsal fin, 9–12 plates in the depressed dorsal fin, 13–14 postdorsal plates, 10–11 postanal plates, and 43–57 teeth per jaw ramus. Morphometrics given in Table 2.

Distribution.—Three described species, *R. aspera* from the Rio São Francisco, and *R. paraguensis* and *R. strigosa* from the Rio Paraná. *Rhinelepis* is also present in the Rio Paraíba and in a reservoir near Fortaleza in Ceará (Fig. 1). The population in Ceará is likely to be an introduction because the region is very dry and the large river habitat preferred by *Rhinelepis* is not naturally present. I have also examined a specimen of *etentaculatus* from this reservoir. *Pterygoplichthys etentaculatus* is also thought to be restricted to the Rio São Francisco (Weber, 1992) where it is sympatric with *Rhinelepis*.

Comparisons.—*Rhinelepis* can be distinguished from most other loricariids by the combination of a loss of the adipose fin, a well-developed dorsal-fin spinelet (vs a small, rectangular spinelet or no spinelet in *Hemipsilichthys*, *Isbrueckerichthys*, *Kronichthys*, *Pareiorhina*, and *Corymbophanes andersoni*), a large plate between the opercle and the pterotic-supracleithrum, expanded gill openings, six anal-fin rays, and a coracoid that is exposed ventrally. Within the *Rhinelepis* group, *Rhinelepis* differs from all others by the presence of expanded gill openings and presence of a plate between the opercle and the pterotic-supracleithrum. In addition, *Rhinelepis* differs from *Pogonopoma* by the absence of an adipose

fin, a completely plated abdomen in adults, no elongate cheek odontodes, and the following morphometric features (Table 2): a larger predorsal length/SL ratio (0.430–0.473 vs 0.366–0.413), a larger head length/SL ratio (0.347–0.396 vs 0.265–0.326), a larger snout length/SL ratio (0.210–0.243 vs 0.155–0.179), a larger interorbital width/SL ratio (0.182–0.194 vs 0.112–0.136), a smaller dorsal-caudal length/SL ratio (0.298–0.338 vs 0.342–0.396), and a larger head depth/SL ratio (0.214–0.243 vs 0.155–0.190); from *Pogonopomoides* by a completely plated abdomen in adults and the following morphometric features (Table 2): a larger predorsal length/SL ratio (0.430–0.473 vs 0.373–0.400), a larger head length/SL ratio (0.347–0.396 vs 0.304–0.326), a larger snout length/SL ratio (0.210–0.243 vs 0.176–0.193), a larger interorbital width/SL ratio (0.182–0.194 and 0.120–0.137), a smaller postanal length/SL ratio (0.203–0.241 vs 0.260–0.289), a smaller dorsal-fin length/SL ratio (0.195–0.212 vs 0.235–0.256), a larger head depth/SL ratio (0.214–0.243 vs 0.155–0.190), and a larger cleithral width/SL ratio (0.286–0.333 vs 0.233–0.275); and from *Pseudorhinelepis* by the absence of tall ridges on the pterotic-supracleithrum, a lack of keels on the lateral plates, presence of a longer, lower head (Armbruster and Page, 1997), and the following morphometric features (Table 2): a larger snout length/SL ratio (0.210–0.243 vs 0.138–0.176), a larger interorbital width/SL ratio (0.182–0.194 vs 0.124–0.166), a smaller thorax length/SL ratio (0.151–0.207 vs 0.258–0.317), a smaller postanal length/SL ratio (0.203–0.241 vs 0.260–0.289), and a smaller dorsal-fin spine length/SL ratio (0.185–0.229 vs 0.236–0.342).

DISCUSSION

The *Rhinelepis* group is a well-diagnosed, monophyletic group of genera and phylogenetic analysis confirmed Armbruster's (1998) hypothesis of the relationships of the group. Analysis of the phylogeny with and without the use of the diverticulum character resulted in the same tree indicating that the hypothesis for the evolution of the diverticulum is most likely correct. The phylogenetic analysis revealed a split between the Amazon and the eastern river systems (Fig. 9). Retzer (1994) also suggested a close relationship of the Amazon with the Paraná-Paraguay based on the relationships of *Farlowella*. The presence of the *Rhinelepis* group in the São Francisco and the smaller, coastal tributaries allows a more detailed picture of the relationships of the rivers in the area.

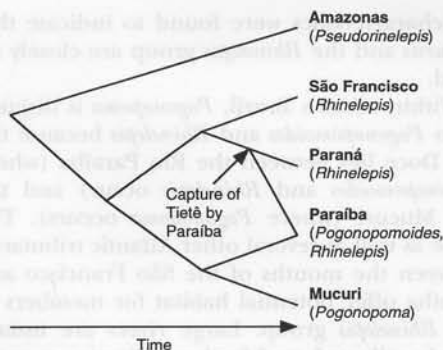


Fig. 9. Drainage relationships based on the phylogenetic analysis. Part of the Paraná was probably captured by the Paraíba after the split of the Paraná + São Francisco and the Paraíba + Mucuri, hence the complex relationships of the river systems shown.

The close relationship of *Pogonopoma* and *Pogonopomoides* suggests that the coastal streams of southeastern Brazil share a recent faunal ancestry. Also, presence of *Rhinelepis* in both the Paraná and the São Francisco suggests a close faunal relationship between the two river systems, and the phylogenetic analysis suggests that the Paraná + São Francisco has a common faunal ancestry with the Paraíba + Mucuri. The additional presence of *Rhinelepis* in the Paraíba confounds the relationships somewhat; however, capture of part of the Tietê (Paraná drainage) may have allowed *Rhinelepis* access to the Paraíba. The Paraíba flows mainly to the northeast; however, there is sharp, almost 360° bend at its extreme southwestern point, such that the river is actually flowing southwest when it originates. A tributary of the Tietê flows very close to the area where the Paraíba reverses direction, suggesting that the upper Paraíba was formed by stream capture from the Tietê (Fig. 1). Invasion of the Paraíba by *Rhinelepis* likely occurred after the split of *Rhinelepis* and the *Pogonopoma* + *Pogonopomoides* clade; hence, the relationships of the river systems shown in Figure 9 are complex.

Of the hypostomine genera, only *Corymbophanes* and *Upsilodus* have not been examined, and it is possible that they may be related to the *Rhinelepis* group. However, examination of radiographs of the type of *Corymbophanes andersoni* (FMNH 52675) revealed that it has ribs beyond the enlarged rib of the sixth vertebral centrum and no diverticulum was evident. Although *Corymbophanes* cannot be ruled out as a sister to the *Rhinelepis* group, the presence of ribs in *Corymbophanes* suggests that the *Rhinelepis* group as diagnosed is a monophyletic entity. *Upsilodus* is very similar to *Delturus* and is probably related.

No characteristics were found to indicate that *Delturus* and the *Rhinelepis* group are closely related.

Within eastern Brazil, *Pogonopoma* is disjunct from *Pogonopomoides* and *Rhinelepis* because the Rio Doce lies between the Rio Paraíba (where *Pogonopomoides* and *Rhinelepis* occur) and the Rio Mucuri (where *Pogonopoma* occurs). The Doce as well as several other Atlantic tributaries between the mouths of the São Francisco and Paraíba offer potential habitat for members of the *Rhinelepis* group. Large rivers are usually poorly collected, and further collecting may expand the range of the *Rhinelepis* group to include more of the Atlantic tributaries in southeastern Brazil.

SPECIMENS EXAMINED

Ingroup.—*Pogonopoma wertheimeri*: MCZ 7757 (5 examined, cotypes), Brazil, Santa Clara, Rio Mucuri; USNM 301001 (9, 1 cleared and stained) and USNM 318175 (4), Brazil, Minas Gerais, rio Mucuri, 9 km west of town of Presidente Pena along a dirt road on Fazenda Gaviao, 17°41'S, 40°55'W; USNM 301985 (15, 1 cleared and stained), Brazil, Minas Gerais, rio Mucuri, approximately 26 km southeast of town of Nanuque on Fazenda Santa Clara, 17°54'S, 40°13'W; USNM 318172 (1), Brazil, Minas Gerais, rio Mucuri, 22 km south and east of Nanuque at Santa Clara. *Pogonopomoides parahybæ*: FMNH 59724 (2), Brazil, Rio de Janeiro, Entre Rios; FMNH 59726 (1), Brazil, Rio de Janeiro, Barra de Pirahy; MCZ 7756 (2, cotypes), Brazil, Rio Parahyba, Rio Paraíba do Sul, between Barra do Pirai and Tres Rios (D. Pedro II Railroad), 22°16'S, 42°45'W; MNRJ 13562 (5, 1 cleared and stained) and MNRJ 13563 (5), Brazil, Rio de Janeiro, rio Paraíba do Sul, área fronteira à cidade de Itaocara, 21°41'S, 42°5'W. *Pseudorinelepis agassizii*: MCZ 8007 (1, syntype?), NMW 44559 (3, syntypes), NMW 44560 (1, syntype), and NMW 44561 (1, syntype), Brazil, Amazonas, lago Manacapuru, Manacapuru (lago Grande de Manacapuru), 3°6'S, 61°30'W. *Pseudorinelepis carachama*: ANSP 68654 (1, holotype), Peru, Loreto, Rio Ucayali Basin, at Contamana. *Pseudorinelepis genibarbis*: BMNH 18035 (1), Peru, Loreto, Cashiboya; CAS 42325 (1), Peru, Loreto, Quebrada Yaguas Yacu near Pebas; CAS 58801 (1), Peru, Loreto, Iquitos; FMNH 95569 (1), FMNH 95570 (1cs), MZUSP 6339 (17, 1 cleared and stained), and ZMA 107858 (3), Brazil, Amazonas, lago Castro do Rio Purus; IAP 114 (6), Peru, Loreto, Rio Samiria (Caño Ungurahui); INHS 36938 (5, 1 cleared and stained), Peru, Loreto, Rio Amazonas, at Pueblo Gallito; INHS

36941 (1), Peru, Loreto, Felipe Cocha (Rio Itaya), 12 km south Iquitos on road to Quistococha near the community of 29 Enero 1995; INHS 39730 (5, 1 cleared and stained), Peru, Loreto, Ushpa and Moena Caños, Rio Itaya—Rio Amazonas drainage, 1.73 miles NNE Iquitos; MUSM 1847 (1), Peru, Ucayali, Ivita, Pucallpa; MHNG 2358.87 (1), Peru, Ucayali, Pucallpa, Utuquinia; MUSM 1869 (1), Peru, Ucayali, Santa Carmela de Machangay (laguna), Pucallpa; MUSM 6064 (1), Peru, Ucayali, Yarinacocha, Coronel Portillo; ZMA 107858 (3), Brazil, Amazonas, ZMA 119401 (1), Brazil, Rondônia, small pool on Rio Jamari near confluence with Rio Madeira just below Samuel Hydroelectric; ZMA 107867 (1), Peru, Ucayali, Coronel Portillo Prov., Rio Ucayali basin, Cashiba Cocha; ZMA 120102 (1), Brazil, Roraima, Rio Branco, Marará, floodplain lake (Lago Central). *Rhinelepis aspera*: FMNH 59725 (1), Brazil, São Paulo, Piracicaba; MHNG 2475.60 (1), MHNG 2475.61 (1), and MHNG 2475.68 (1), Paraguay, Central, Villeta; MNRJ 13561 (2, 1 cleared and stained), Brazil, Rio de Janeiro, Resende represa do Funil, rio Paraíba do Sul; MNRJ 13564 (9), Brazil, Minas Gerais, rio São Francisco, em Itacarembi; MZUSP 23067 (28, 1 cleared and stained), Brazil, São Paulo, rio Paraná, Ilha Solteira, 20°30'S, 51°0'W; UMMZ 203406 (1), Brazil, Ceará, Acude al Mecejana, near Fortaleza; UMMZ 205600 (1), Paraguay, Rio Paraguay, overflowing inlet along east shore, 1 km south from Puente Remanso.

Outgroup.—Hypostominae: *Delturus anguicauda*—USNM 318209 (4, 1 cleared and stained); *Hemipsilichthys cameroni*—USNM 279585 (17, 3 cleared and stained); *Hemipsilichthys* sp.—USNM 320377 (27, 3 cleared and stained); *Hypostomus micromaculatus*—ANSP 160774 (12, 3 cleared and stained); *Hypostomus plecostomus*—YPM 4194 (3, 1 cleared and stained); ZMA 105.306 (7, 2 cleared and stained); *Hypostomus* sp. 1—INHS 33435 (1, 1 cleared and stained); INHS 30039 (1, 2 cleared and stained); UF 77909 (9, 2 cleared and stained); *Hypostomus* sp. 2—UF 91915 (9, 2 cleared and stained); *Isbrueckerichthys duseni*—UMMZ 215262 (18, 2 cleared and stained); and *Kronichthys* sp.—FMNH 71334 (1 cleared and stained); FMNH 92364 (12, 3 cleared and stained); MZUSP 27545 (20, 2 cleared and stained); MZUSP 35286 (5, 1 cleared and stained). Neoplecostominae: *Neoplecostomus microps*—MNRJ 12802 (4, 1 cleared and stained), MNRJ 13555 (6, 1 cleared and stained), MNRJ 13556 (13, 2 cleared and stained).

Additional Material.—Only cleared-and-stained material indicated. Ancistrinae: *Acanthicus hystrix*—INHS 36803 (1); INHS 39840 (1); *Ancistrus pirareta*—UMMZ 206085 (5); *Ancistrus* sp. 1—INHS 31835 (1); INHS 31858 (1); *Ancistrus* sp. 2—INHS 29996 (2); *Baryancistrus niveatus*—INHS 40912 (1); *Chaetostoma anomala*—INHS 59863 (1); *Chaetostoma pearsei*—INHS 34589 (2); *Chaetostoma sovichthyis*—INHS34957 (1); *Chaetostoma stannii*—INHS 28838 (1); INHS 60478 (1); *Chaetostoma* sp.—FMNH 96945 (2); FMNH 97569 (2); *Cordylancistrus torbesensis*—MCNG 8066 (1); *Dekeyseria pulcher*—INHS 37471 (1); *Dekeyseria scaphirhyncha*—FMNH 85832 (1); USNM 269958 (1); *Dekeyseria* sp.—FMNH 103494 (2); *Dolichancistrus cobrensis*—MCNG 6470 (1); *Dolichancistrus pediculatus*—FMNH 58566 (2); *Dolichancistrus setosus*—FMNH 76213 (1); *Exastilithoxus fimbriatus*—AMNH 91400 (1); *Hemiancistrus* sp. 1—UF 77850 (2); ANSP 162173 (2); *Hemiancistrus* sp. 2—MNRJ 13304 (2); *Hemiancistrus landoni*—FMNH 93099 (1); *Hemiancistrus maracaiboensis*—EBRG 2855 (1); *Hypancistrus zebra*—INHS 37472 (1); *Lasiancistrus maracaiboensis*—INHS 59866 (4); INHS 60465 (2); *Lasiancistrus* sp.—INHS 28263 (4); INHS 29866 (6); *Leporacanthicus galaxias*—INHS 40910 (1); *Leptoancistrus canensis*—INHS 36108 (1); *Lithoxancistrus orinoco*—AMNH 31023 (1); *Lithoxus bovalii*—AMNH 54961SW (1); *Lithoxus lithoides*—BMNH 1972.7.17:66–115 (2); *Megalancistrus aculeatus*—MZUSP 21143 (1); MZUSP 24435 (1); *Neblinichthys pilosus*—AMNH 56138SW (2, paratypes); *Oligancistrus punctatissimus*—FMNH 95556 (1); INHS 40913 (1); MZUSP 34265 (1); *Panaque albomaculatus*—FMNH 96951 (1); *Panaque maccus*—INHS 28933 (1); INHS 29862 (2); INHS 29906 (1); *Panaque nigrolineatus*—INHS 29902 (1); INHS 37470 (1); *Parancistrus aurantiacus*—INHS 40911 (1); *Peckoltia ucayalensis*—INHS 40916 (1); *Peckoltia vittata*—CAS 6476 (1); *Peckoltia* sp.—FMNH 70863 (1); *Pseudacanthicus histrix*—FMNH 95554 (1); *Pseudancistrus* sp.—USNM 226181 (1); *Scobinancistrus pariolispos*—ZMA uncataloged aquarium specimen (1); *Spectracanthicus murinus*—MZUSP 34279 (1). Hypoptopomatinae: *Hypoptopoma* sp.—INHS 28696 (2); INHS 28997 (3); INHS 29973 (2); *Microlepidogaster* sp.—INHS 37356 (3); *Otocinclus* sp.—INHS 28298 (2); INHS 30093 (3); INHS 60418 (1); *Parotocinclus eppleyi*—INHS 31733 (5); *Schizolecis guentheri*—FMNH 71338 (2); INHS 37362 (3). Hypostominae: *Aphanotorulus unicolor*—AMNH 77429 (1); AMNH 77434 (2); FMNH 84145 (6); FMNH 101120 (2); FMNH 103282 (4); UMMZ 205129 (2); USNM 301642 (3); USNM 319355 (2); USNM 319357 (2); USNM 329281 (1); *Cochliodon cochliodon*—UMMZ

206338 (3); UMMZ 207988 (2); AMNH 97880 (1); *Cochliodon taphorni*—ANSP 168195 (2); *Corymbophanes bahianus*—USNM 318203 (3); *Hypostomus albopunctatus*—MZUSP 24458 (2); *Hypostomus boulengeri*—USNM 326313 (1); *Hypostomus commersoni*—FMNH 95548 (1); *Hypostomus cordovae*—UF 82322 (2); *Hypostomus emarginatus*—AMNH 12607 (1); AMNH 77378 (1); CAS 59487 (1); CAS 150695 (1); FMNH 96957 (1); INHS 29085 (1); UMMZ 187225 (1); *Hypostomus francisci*—ANSP 172107 (2); MNRJ 13559 (2); *Hypostomus panamensis*—ANSP 126440 (2); *Hypostomus punctatus*—INHS 37350 (2); MNRJ 13557 (1); *Hypostomus robinii*—MCNG 8215 (1); *Hypostomus squalinus*—ANSP 134182 (2); MCNG 7389 (1); MCNG 18340 (1); USNM 258283 (4); *Hypostomus* sp. 3—USNM 302485 (2); *Hypostomus* sp. 4—USNM 300999 (2); USNM 300997 (2); *Hypostomus* sp. 5—INHS 31683 (1); *Hypostomus* sp. 6—USNM 300099 (1); USNM 318199 (3); *Isorineloricaria spinosissimus*—CAS 32461 (1); FMNH 58546 (1); *Pareiorhina rudolphi*—MNRJ 13560 (3); *Pterygoplichthys anisitsi*—UMMZ 205481 (1); *Pterygoplichthys disjunctivus*—AMNH 77486 (4); *Pterygoplichthys elentaculatus*—ANSP 172096 (2); ANSP 172097 (1); FMNH 59730 (1); *Pterygoplichthys gibbiceps*—FMNH 95576 (1); MZUSP 24340 (3); *Pterygoplichthys lituratus*—AMNH 39945 (1); *Pterygoplichthys multiradiatus*—INHS 28133 (2); INHS 28260 (1); INHS 29787 (1); *Pterygoplichthys pardalis*—CAS 77274 (1); FMNH 95546 (1); FMNH 101384 (1); *Pterygoplichthys punctatus*—FMNH 96959 (1); FMNH 96960 (1); *Pterygoplichthys scrophus*—INHS 41107 (1); INHS 36937 (1); *Pterygoplichthys zulianensis*—INHS 35384 (1). Loricariinae: *Farlowella mariaelena*—INHS 28973 (3); INHS 31992 (1); *Harttia platystoma*—AMNH 14408SW (1); *Lamontichthys llanero*—INHS 29957 (2); *Loricaria* sp.—INHS 31689 (1); *Loricariichthys* sp.—INHS 35413 (3); *Rineloricaria rupestris*—INHS 35602 (3); INHS 60381 (1); *Sturisoma festivum*—INHS 35575 (1); INHS 59948 (1). Astroblepidae: *Astroblepus chotae*—USNM 121129 (1); *Astroblepus longifilis*—FMNH 70017 (1); *Astroblepus whympersi*—MCZ 31512 (1); *Astroblepus* sp.—MCNG 6468 (1); MCNG 16251 (1); USNM 302674 (1).

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