

Redescription of *Pseudorinelepis genibarbis* (Loricariidae: Hypostominae) with comments on behavior as it relates to air-holding

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The loricariid catfish genus *Pseudorinelepis* is revised. Analysis revealed no difference between the nominal species of *Pseudorinelepis* and only *P. genibarbis* is recognized as valid. The *Pseudorinelepis* from the Rio Branco of Brazil may represent an undescribed species. *Pseudorinelepis* was examined for its behavior as it relates to the ability of a large esophageal diverticulum to hold air. *Pseudorinelepis* was shown to breathe air, and, when disturbed, would swim through the water column remaining neutrally buoyant.

Introduction

Pseudorinelepis Bleeker is a small genus (4 nominal species) of suckermouth armored catfish from the Amazon basin characterized by a peculiar modification of the digestive tract. At the distal end of the esophagus is a large, U-shaped diverticulum that was hypothesized by Armbruster (1998b) to be an accessory respiratory organ. This diverticulum is also found in *Pogonopoma* Regan, *Pogonopomoides* Gosline, and *Rhinelepis* Spix which, together with *Pseudorinelepis*, represent the *Rhinelepis* group of Loricariidae (Armbruster, 1998a-b). The evolution of the diverticulum appears to mirror the evolution of the lung/swim bladder in other fishes, and may represent a useful model for studying the behavioral, morpho-

logical, and physiological evolution of the lung/swim bladder in sarcopterygians and basal actinopterygians. Unfortunately, very little information is available on the life history characteristics of members of the *Rhinelepis* group, and only *Rhinelepis* is known to breathe air (Santos et al., 1994). It has been suggested that *Pseudorinelepis* and *Rhinelepis* use their diverticula mainly for respiration, but may also use it for hydrostatic control. The diverticulum in *Pogonopoma* and *Pogonopomoides* is similar to a swim bladder and is suggested to function only as a hydrostatic organ (Armbruster, 1998a-b).

The four species currently recognized in *Pseudorinelepis* are: *P. genibarbis* (Valenciennes, 1840), *P. agassizii* (Steindachner, 1877), *P. pellegrini* (Regan, 1904), and *P. carachama* (Fowler, 1940) (Arm-

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bruster & Page, 1997). Despite this small number of species, the taxonomic history of *Pseudorinelepis* is complex. *Pseudorinelepis genibarbis* was originally described by Valenciennes (in Cuvier & Valenciennes, 1840) in *Rhinelepis*. Bleeker (1862) described *Pseudorinelepis* to include *P. genibarbis* which is the type species by monotypy; however, *Pseudorinelepis* was not recognized by subsequent authors until Isbrücker (1980). Steindachner (1877) described *P. agassizii* in *Rhinelepis*. Regan (1904) placed *P. agassizii* into the synonymy of *P. genibarbis* and described *P. pellegrini* based on minor differences with the types of *P. agassizii* and *P. genibarbis*. Regan (1904) placed *P. genibarbis* and *P. pellegrini* in the subgenus *Pogonopoma* of *Plecostomus* Gronovius (= *Hypostomus* Lacepède). Eigenmann (1910) described *Canthopomus* to include *P. genibarbis* as the type species, *P. agassizii* as a synonym of *P. genibarbis*, and *P. pellegrini* as valid. Fowler (1940) described *Monistiancistrus carachama* and suggested that it was closely related to *Ancistrus*. Eigenmann & Allen (1942) recognized all four species currently in *Pseudorinelepis*; however, they placed *P. agassizii* in *Canthopomus* with it now erroneously cited as the type species, returned *P. genibarbis* to *Rhinelepis* and retained *P. pellegrini* in the subgenus *Plecostomus* (*Pogonopoma*) and *P. carachama* in *Monistiancistrus*. Eigenmann & Allen (1942) incorrectly suggested that *Canthopomus* Eigenmann (1910) was a nomen nudum. In Eigenmann (1910), the genus name *Canthopomus* is clearly stated as a new genus and described species are indicated as belonging to *Canthopomus*, thereby satisfying Article 12 of the International Code of Zoological Nomenclature for genus-group names described prior to 1931 (ICZN, 1985). Gosline (1947) returned *P. genibarbis*, and *P. pellegrini* to *Canthopomus* in which he also recognized *P. agassizii* as valid. Isbrücker (1980) recognized *Canthopomus* as a synonym of *Pseudorinelepis*, retained *P. carachama* in *Monistiancistrus*, and concluded that *Monistiancistrus* belonged in the Ancistrinae. Isbrücker & Nijssen (1982) moved *Monistiancistrus* to the Hypostominae and later placed *Monistiancistrus* into the synonymy of *Pseudorinelepis* (Nijssen & Isbrücker, 1986). Isbrücker (1992) removed *Monistiancistrus* from the synonymy of *Pseudorinelepis* and placed it in the synonymy of *Hypostomus*, and, finally, Armbruster & Page (1997) returned *Monistiancistrus* to the synonymy of *Pseudorinelepis*.

Recent collecting efforts in the Iquitos region of Peru has resulted in the collection of several

Pseudorinelepis specimens and provided the impetus to examine the species of *Pseudorinelepis*, examine behavior in aquaria, and to examine the ability to breathe air. In this study, 41 specimens of *Pseudorinelepis*, including all types except that of *P. genibarbis* (which is lost) were examined to determine if *P. agassizii*, *P. carachama*, and *P. pellegrini* are valid. A neotype is designated for *Rhinelepis genibarbis*. The behavior of *Pseudorinelepis* as it relates to buoyancy and air-breathing is also described.

Methods

Morphometric features were measured with digital calipers to the nearest 0.1 mm. Measurements are as defined below or as defined in Boeseman (1968) or Armbruster & Page (1996) and include: standard length, head length (from the snout tip to the posterior tip of the supraoccipital), cleithral width (width of the body just posterior to the posterior margin of the cleithral process that is just dorsal to the pectoral fin), snout length, orbit diameter, interorbital width, dorsal spine length, folded dorsal fin length, dorsal base length (from the point between the dorsal-fin spinelet and spine to the posterior end of the membrane connecting the last dorsal-fin ray to the body), dorsal-caudal length (from the posterior end of the membrane that connects the last dorsal-fin ray to the body to the posterior edge of the penultimate dorsal procurrent caudal-fin spine), thorax length (from the insertion of the pectoral-fin spine to the insertion of the pelvic-fin spine [pelvic insertion defined as a bony, subcutaneous process just anterior to the point where the pelvic-fin spine passes through the skin]), pectoral spine length, abdominal length (from the insertion of the pelvic-fin spine to the insertion of the anal-fin spine), pelvic spine length (from the insertion of the pelvic-fin spine to the tip of the spine), postanal length (from the posterior insertion of the anal fin to the posterior margin of the penultimate ventral procurrent caudal-fin spine), caudal peduncle depth (measured vertically from the posterior margin of the adipose fin membrane), anal width (body width at the anal-fin spine), snout-opercle length, and head width.

Counts are as in Armbruster & Page (1996) except that the unbranched ray of the anal fin was counted as a spine and dorsal-caudal plates are the number of plates in a dorsal series start-

ing from the plate just posterior to the last plate contacted by the dorsal-fin membrane up to and including the elongate plate covering the base of the dorsal-most caudal-fin ray. Values for the neotype are given in parentheses when different. Maximum number of teeth is the number of teeth in the jaw ramus with the most teeth. Institution abbreviations are as in Leviton et al. (1985) with the addition of ILAP, Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru. Numbers following catalog numbers are the number of specimens examined. Specimens were grouped into five populations: the Rio Branco (upper Rio Negro drainage), the Brazilian Amazon (in and near the mainstem Amazon), the Rio Madeira, the Peruvian Amazon (in and near the mainstem Amazon from the Brazilian border to the confluence of the Rios Marañon and Ucayali), and the Ucayali/Marañon (all collections examined were from the Rio Ucayali proper or the swampy area between the two rivers near their confluence). The locality of the type of *P. pellegrini* is given only as Upper Amazon (Regan, 1904); *P. pellegrini* was coded as an unknown population.

All measurements were natural log-transformed and a principal components analysis was performed using a covariance matrix in Systat (ver. 5.0, Systat Inc., 1992). Measurements were also compared univariately through the use of notched-box plots to determine the extent of overlap between the populations.

Nine live specimens were captured from Ushpa Caño, Río Itaya – Río Amazonas drainage, 1.73 miles NNE Iquitos, 3°46'20"S, 73°14'17"W, Loreto, Peru and observed in aquaria (specimens preserved at the site cataloged as INHS 39730). Habitat measurements, including water temperature, conductivity, total dissolved solids (TDS), pH and dissolved oxygen, were made at the site during collection. Water temperature was sampled with a standard laboratory mercury thermometer; conductivity was sampled with the Jenway Electronic Conductivity Meter #4071; total dissolved solids were sampled with the Jenway Electronic TDS Meter #4076; and pH and dissolved oxygen were sampled with TetraTest reagent test kits designed for aquarium use.

Results and discussion

No gross morphological differences could be found between the various population of *Pseu-*

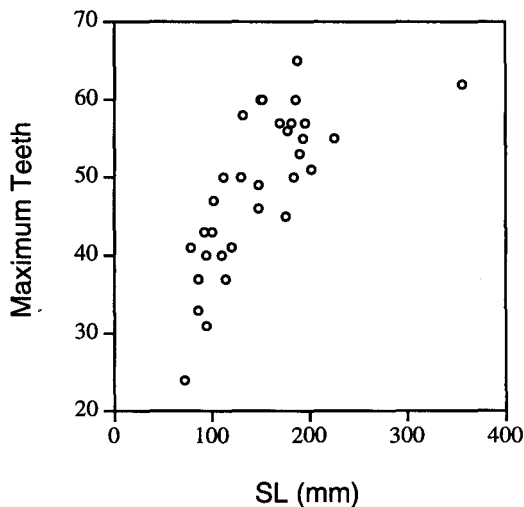


Fig. 1. Maximum number of teeth vs. standard length in *Pseudorinelepis genibarbis*.

dorinelepis. Color is variable, but observations on the live specimens suggests that they may change their color to match the substrate. Color patterns in live specimens range from tan to almost black, and specimens may have spots or mottling variously placed on the body (specimens generally become almost black upon preservation). Only the one specimen examined from the Rio Branco (Rio Negro drainage; ZMA 120.102; 356.2 mm SL) deviates significantly in color. The Rio Branco specimen is a male with long, numerous cheek odontodes, orange on the edges of its cheeks and dorsal- and caudal-fin spines, and very intense spots located on the sides and abdomen (see photo of a similar individual in Burgess, 1989: 748). No other specimens examined have the color pattern of the Rio Branco specimen, but it is possible that the color is a breeding male characteristic and that other breeding males examined lost the color as an artifact of preservation.

No patterns could be seen in meristics between the populations. Specimens vary only in number of teeth; however tooth number varies ontogenetically (Fig. 1) and not geographically.

No patterns could be found in the morphometric data by examining the data univariately. In the principal components analysis, principal component 1 was strongly affected by standard length and was excluded from the analysis. The remaining principal components were not strongly affected by standard length. The plot of prin-

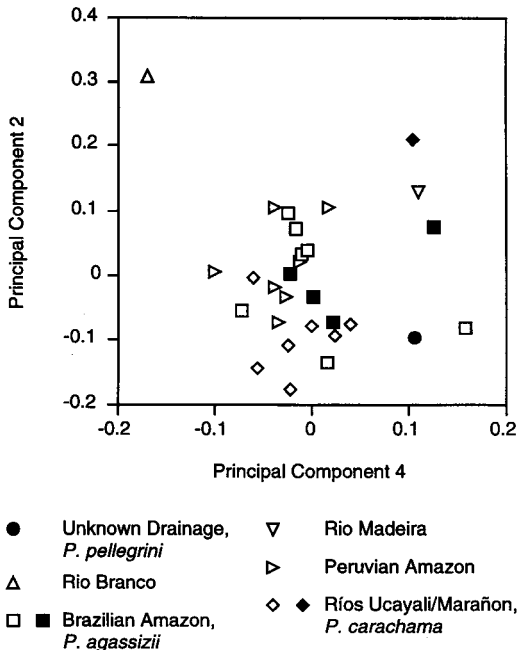


Fig. 2. Principal components analysis for specimens of *Pseudorinelepis* by drainage. Filled symbols are type specimens.

Principal component 2 and principal component 4 provided the most separation between the populations. Principal component 2 was affected most strongly and positively by snout-opercle length, snout length, and orbit diameter; and negatively by anal width and thorax length. Principal component 4 was affected most strongly and positively by abdominal length, pelvic spine length, and pectoral spine length; and negatively by anal width, snout-opercle length, and head depth. Specimens were coded by drainage and locality in the PCA (Fig. 2), but (excluding the Rio Branco specimen) there are no geographic patterns evident in the data and there are no relevant differences between type specimens. The Rio Branco is outside of the main cloud of points. This may be a significant difference, but little can be said at this time because the Rio Branco is represented only by a single, very large specimen. There are two other specimens from the Rio Branco available at MZUSP, but they are also of a very large size (> 300 mm; O. Oyakawa, pers. comm.). Before the specific status of the Rio Branco population can be assessed, more specimens from a wider variety of size classes must become avail-

able. We tentatively consider the Rio Branco population to be *P. genibarbis*.

With the exception of the Rio Branco specimen, no differences in gross morphology, color, meristics, or morphometrics were discernible in specimens from across the range of *Pseudorinelepis*. Given that there are no differences among the extant type specimens of *Pseudorinelepis* it is clear that the names *P. agassizii*, *P. carachama*, and *P. pellegrini* refer to the same species. The identity of *P. genibarbis* is confounded by the fact that the type specimen is lost. The drawing of *P. genibarbis* in Cuvier and Valenciennes (1840) is of an entirely brown fish of the morphotype expressed by *P. agassizii*, *P. carachama*, and *P. pellegrini*. We conclude that *P. agassizii*, *P. carachama*, and *P. pellegrini* are junior synonyms of *P. genibarbis*, and designate a neotype of *P. genibarbis*.

Pseudorinelepis Bleeker

Pseudorinelepis Bleeker, 1862: 3 (type species:

Rhinelepis genibarbis Valenciennes, 1840).

Canthopomus Eigenmann, 1910: 404 (type species:

Rhinelepis genibarbis Valenciennes, 1840).

Monistancistrus Fowler, 1939: 236 (type species:

Monistancistrus carachama Fowler, 1939).

Diagnosis. *Pseudorinelepis* and, hence, *P. genibarbis* was diagnosed by the following synapomorphies by Armbruster (1998a): an enlarged posterior shelf of the fourth epibranchial; a well-developed lateral ridge on the quadrate; a wide, flat parasphenoid; well-developed ridges on the pterotic-supracleithrum (taller than in other loricariids); a wide ventrolateral strut of the coracoid that is wholly exposed (supporting odontodes directly); passage of the arrector ventralis muscle of the pectoral girdle through a channel; and elongate, non-evertible cheek odontodes. Of these, only the wide, flat parasphenoid is unique among loricariids to *Pseudorinelepis genibarbis*.

Pseudorinelepis genibarbis can be distinguished from all other hypostomines and ancintrines by a combination of the absence of an adipose fin, a simple eye without a dorsal flap of the iris (vs. dorsal flap of iris present making the eye appear bilobed); 5 branched anal-fin rays (vs. 4 in *Hypostomus* and *Pterygoplichthys*); a single medium-sized plate posterior to the pterotic-supracleithrum (vs. many small plates or no plates in some loricariids); a patch of non-evertible, elongate odontodes



Fig. 3. *Pseudorinelepis genibarbis*, about 100 mm SL, Ushpa Caño, in aquarium. Photograph by M. Hardman.

on the cheek, well-developed ridges on the pterotic-supracleithrum (vs. ridges not as well-developed); and well-keeled lateral plates. See also Armbruster & Page (1997).

Pseudorinelepis genibarbis differs from all other members of the *Rhinelepis* group 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 deeper head (20.0-26.0 % SL vs. 16.1-19.8); from *Pogonopomoides* by the presence of elongate cheek odontodes in adults, a completely plated abdomen, and the following morphometric features: a shorter snout (13.8-17.6 % SL vs. 17.6-19.3), a longer thorax (25.8-31.7 % SL vs. 18.9-23.3), a deeper head (20.0-26.0 % SL vs. 15.5-19.0), and a wider cleithral (27.5-32.1 % SL vs. 23.3-27.5); and from *Rhinelepis* by the presence of elongate cheek odontodes in adults, lack of a plate between the pterotic-supracleithrum and the exposed opercle, small (vs. large) gill openings, and the following morphometric features: a shorter snout (13.8-17.6 % SL vs. 21.0-24.3), a smaller interorbital width (12.4-16.6 % SL vs. 18.2-19.4), a longer thorax (25.8-31.7 % SL vs. 15.1-20.7), a larger postanal length (20.6-31.0 % SL vs. 20.3-24.1), and a longer dorsal-fin spine (23.6-34.2 % SL vs. 18.5-22.9). See also Armbruster (1998a).

Pseudorinelepis genibarbis (Valenciennes)
(Fig. 3)

Rhinelepis genibarbis Valenciennes, in Cuvier & Valenciennes, 1840: 484, pl. 453 (holotype lost; type locality: probably Brazil).

Rhinelepis Agassizii Steindachner, 1877: 12 (syntypes: NMW 44559 (3), NMW 44560 (1), NMW 44561 (1); type locality: Brazil, Amazonas, lago Manacapuru, Manacapuru [lago Grande de Manacapuru], 3°6'S 61°30'W).

Plecostomus pellegrini Regan, 1904: 218 (holotype: MNHN A.3956; type locality: Upper Amazon).

Monistancistrus carachama Fowler, 1939: 237, figs. 26-27 (holotype: ANSP 68654; type locality: Peru, Ucayali, Río Ucayali Basin, at Contamana).

Material examined. Brazil: Amazonas: MZUSP 52897, neotype, 202.0 mm SL; FMNH 95569, 1; FMNH 95570, 1cs; MZUSP 6339, 4 (1cs); ZMA 107.858, 3; lago Castro do Rio Purus; 7-8 Nov 1967, EPA. – NMW 44559, 3; NMW 44560, 1; NMW 44561, 1; syntypes of *P. agassizii*; lago Manacapuru, Manacapuru (lago Grande de Manacapuru), 3°6'S 61°30'W.

Brazil: Rondônia: ZMA 119.401, 1; small pool on Rio Jamari near confluence with Rio Madeira just below Samuel Hydroelectric.

Table 1. Selected morphometric features of *Pseudorinelepis genibarbis*.

	neotype	n	mean	SD	range
Standard length (mm)	202.0	41	150.5	51.8	72.2-356.2
% standard length					
Predorsal length	39.4	41	41.0	1.5	37.9-43.9
Head length	28.8	41	31.1	1.8	27.8-35.1
Cleithral width	28.1	41	29.4	1.2	27.5-32.1
Snout length	14.7	41	15.8	1.0	13.8-17.6
Interorbital width	12.6	41	14.0	0.8	12.4-16.6
Dorsal spine length	25.6	32	26.7	2.3	23.6-34.2
Folded dorsal fin length	40.7	39	42.4	2.5	35.4-49.3
Dorsal fin base length	25.3	41	25.0	1.5	21.6-28.8
Dorsal-caudal length	34.0	40	34.2	2.3	27.3-38.0
Thorax length	27.1	41	28.6	1.6	25.8-31.7
Pectoral spine length	29.9	41	27.9	1.7	24.2-31.5
Abdomen length	23.8	41	22.5	1.0	20.4-25.1
Pelvic spine length	25.6	39	23.1	1.4	20.6-26.9
Postanal length	24.6	41	25.2	1.8	20.6-31.0
Caudal peduncle depth	9.3	41	10.0	0.6	8.1-10.9
Anal width	15.9	41	16.7	1.7	12.0-20.9
Snout-opercle length	22.1	41	21.7	1.5	15.8-24.2
Head width	28.6	41	27.6	1.3	24.9-30.3
% head length					
Head depth	76.7	41	72.6	3.7	59.1-78.0
% snout length					
Orbit diameter	33.6	36	32.0	2.7	24.3-38.1

Brazil: Roraima: ZMA 120.102, 1; Rio Branco, Marará, floodplain lake (Lago Central).

Peru: Loreto: BMNH 18035, 1; Cashiboya. – CAS 42325, 1; Quebrada Yaguas Yacu near Pebas. – CAS 58801, 1; Iquitos. – IIAP 114, 6; Río Samiria (Caño Ungurahui). – IIAP uncat., 2; Tachacocho, Río Samiria, Río Marañon drainage. – INHS 36938, 5 (1cs); Río Amazonas, at Pueblo Gallito. – INHS 36941, 1; Felipe Cocha (Río Itaya), 12 km S Iquitos on road to Quistococha near the community of 29 Enero 1995. – INHS 39730, 5 (1cs); Ushpa and Moena Caños, Río Itaya – Río Amazonas drainage, 1.73 miles NNE Iquitos.

Peru: Ucayali: ANSP 68654, holotype of *P. carachama*; Río Ucayali Basin, at Contamana. – ZMA 107.867, 1; Coronel Portillo Prov., Río Ucayali basin, Cashiba Cocha. – IIAP uncat., 1; Cocha Vainilla, Supay, Río Ucayali drainage.

MNHN A.3956, holotype of *P. pellegrini*; Upper Amazon.

Description. Largest specimen examined male, 356.2 mm SL (ZMA 120.102). A large, bulky loricariid with strongly keeled lateral plates that have well-developed ridges of bone and odontodes above and below the keels. Head relatively

short when compared to the related *Rhinelepis* (head depth to head length ratio 59.1-78.0 % vs. 47.0-59.0 %; Armbruster & Page, 1997). Pectoral fins relatively short (spine when folded ventral to pelvic fin extending from just prior to pelvic spine to slightly overlapping it). In large juveniles and adults, abdomen completely encased in plates as is small area just above pelvic fins. Lateral plates thick. Adipose fin and raised, median pre-adipose plate absent. Caudal peduncle roughly circular in cross-section. Teeth bifid; long and thin with small cusps. Tooth number increases with body size (Fig. 1). Small papilla present in middle of buccal cavity. As in other members of *Rhinelepis* group, anus close to anal fin, separated only by small plate; eye simple, lacking dorsal flap of iris that makes eye appear bilobed in most other loricariids. Dorsal fin II 7 (one specimen has additional, incomplete ray between posterior two complete rays), pectoral fin I 6, pelvic fin I 5, anal fin I 5, caudal fin I 14 I. Lateral line plates 23-26 (25), plates under base of dorsal fin 6-7 (7), plates in depressed dorsal fin 11-14 (12), postdorsal plates 12-15 (14), postanal plates 8-12 (12), teeth 23-62 per jaw ramus.

Coloration. Color patterns are variable and *P. genibarbis* can change color to match substrate. Most specimens preserved in alcohol are brown to charcoal gray with few if any spots (generally restricted to dorsal-fin membranes). In life, *Pseudorinelepis* may be completely dark brown to black; mottled with tan to dark brown background and black streaks; or light tan with large, sparse spots located at base of lateral plates, on fin membranes, and on abdomen. Armbruster & Page (1997) suggest that breeding males develop orange coloration along cheek margin and dorsal- and caudal-fin spines, but the orange coloration may be restricted to specimens from the Rio Branco.

Sexual dimorphism. Males have longer odontodes on the cheek that are more dense and numerous than in females; males may also have orange on the cheeks and dorsal- and caudal-fin spines.

Distribution. From Brazil and Peru, in the Amazon River and its major tributaries (Rios Madeira and Negro in Brazil and Ríos Marañón, Napo, and Ucayali in Peru) (Fig. 4).

Habitat notes. Based on specimens examined and personal observation, *Pseudorinelepis genibarbis* is typically found in small sluggish streams, floodplain lakes, and large rivers. Water quality measurements from Ushpa Caño indicated that the water was very low in oxygen ($2.5 \text{ mg}\cdot\text{l}^{-1}$), but neutral (pH 7.0). Other measurements included temperature (27°C), conductivity ($205.0 \mu\text{S}$), and total dissolved solids ($133.0 \text{ mg}\cdot\text{l}^{-1}$).

Comments. In Iquitos, Peru, *P. genibarbis* is often referred to as carachama sin costilla, which means loricariid without ribs. This refers to one of the diagnostic characters of the *Rhinelepis* group, a lack of ribs beyond the enlarged rib of the sixth vertebral centrum (Armbruster, 1998a).

Behavior. Air breathing in *P. genibarbis* was confirmed by field observations. When collected, the Ushpa Caño *P. genibarbis* were placed in a plastic bag and the fish immediately began to gulp air. Specimens would release a large air bubble from the exhalant aperture of the branchial cavity prior to surfacing. The fish would then gulp air and return to the bottom. The specimens were later temporarily kept in a small container (approximately 4 l) without aeration and they continued

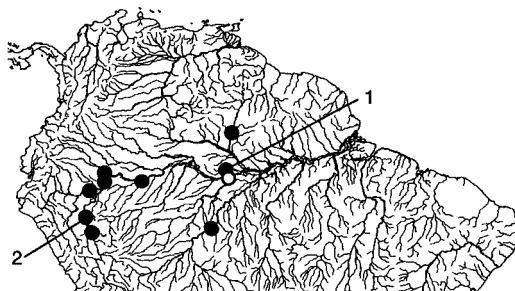


Fig. 4. Distribution of *Pseudorinelepis genibarbis*; open circle represents the locality of the neotype. Symbols may represent more than one locality. 1, type locality of *Rhinelepis agassizii*; 2, type locality of *Monistiancistrus carachama*. Base map by M. Weitzman.

to ingest air and did not show signs of distress. Given the low oxygen level in Ushpa Caño ($2.5 \text{ mg}\cdot\text{l}^{-1}$); the presence in that locality of known air-breathers such as callichthyid catfishes (*Hoplosternum*, *Dianema*, *Brochis*), electric eel (*Electrophorus electricus*), lungfish (*Lepidosiren paradoxa*), and synbranchid eel (*Synbranchus marmoratus*) which were actively engaged in air-breathing and the fact that the *P. genibarbis* does gulp air, it is probable that *P. genibarbis* is an air-breather. *Pseudorinelepis genibarbis* is not an obligate air-breather and does not routinely gulp air in well-oxygenated aquaria.

Casual observations of *P. genibarbis* in aquaria revealed somewhat more mid-water behavior than seen in most other loricariids. This behavior was particularly obvious when the fish were disturbed. Generally, when loricariids are disturbed, they will react by swimming close to the substrate or lift off the substrate temporarily while having to actively maintain forward thrust, i.e. swim vigorously to avoid sinking. *Pseudorinelepis genibarbis* appears to be able to maintain a position raised from the substrate without having to generate lift by the conventional mechanism of converting thrust into lift via orientation of the pectoral-fin foils. *Pseudorinelepis genibarbis* were collected only from large logs near the surface of the water, a habitat similar to that of *Otocinclus* which also has an esophageal diverticulum (Schaefer, 1997).

Liem (1988) suggests that the lung originally evolved in fishes for a dual purpose of air breathing and buoyancy control, just as is suggested above for the diverticulum of *Pseudorinelepis*. If *Pogonopoma* and *Pogonopomoides* do use the di-

verticulum solely as a hydrostatic organ (Armbruster, 1998b), then the diverticulum in the *Rhinelepis* group would represent a good model for testing theories on the physiological, structural, and functional evolution of the lung/swim bladder complex. Examining the evolution of the lung/swim bladder in lungfishes and basal actinopterygians involves comparing between distantly related fishes that have unique life-history characteristics. In contrast, the species of the *Rhinelepis* group are closely related and probably have very similar life-history characteristics, and, thus, may more accurately reflect the morphological, physiological, and behavioral changes of fishes as the lung evolved into a swim bladder. *Pseudorinelepis* is probably the most heavily armored loricariid, and the fact that it is neutrally buoyant seems extraordinary. However, the first fossil evidence of lungs is in the armored placoderm fish *Bothriolepis* (Denison, 1941) which, according to Liem's (1988) hypothesis on the function of early lungs, was probably also a somewhat mid-water fish.

Acknowledgments

We would like to thank R. Vari and S. Weitzman for comments and suggestions on improving the manuscript. We would also like to thank B. Burr, C. C. Guardia, M. Littman, L. Lozano, L. Isuiza, L. Page, R. Powell, H. Sanchez, M. Sabaj, and R. Weitzell for help in collecting fishes in Peru; H. Sanchez for the gift of two *Pseudorinelepis* to INHS; E. Isern, N. Flores, the Universidad Nacional Amazonia Peruana, and L. Verde for help and hospitality while in Peru; L. Page, D. Siebert, the Illinois Natural History Survey, and the Museum of Natural History for supporting us during this work; and O. Oyakawa for providing information on Rio Negro specimens. Special thanks to the following people for according the first author hospitality and help while visiting their museums and for the loan of specimens: W. Saul, S. Schaefer (ANSP), D. Catania, W. Eschmeyer, T. Iwamoto (CAS), B. Chernoff, M. Rogers, K. Swagel (FMNH), H. Sanchez (IIAP), K. Hartel (MCZ), S. Müller, C. Weber (MHNG), H. Britski, O. Oyakawa (MZUSP), I. Isbrücker and H. Nijsen (ZMA). This research was partially funded by the following grants and awards to JWA: Francis M. and Harlie M. Clark Research Support Grants (University of Illinois), Ernst Mayr Grant

(Harvard University), Edward C. Raney Memorial Fund Award (American Society of Ichthyologists and Herpetologists), Philip W. Smith Memorial Fund Award (Illinois Natural History Survey), and the University of Illinois – Department of Ecology, Ethology, and Evolution Graduate Student Research Award.

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Received 23 December 1997

Revised 23 June 1998

Accepted 26 August 1998