

Redescription of *Aphanotorulus* (Teleostei: Loricariidae) with Description of One New Species, *A. ammophilus*, from the Río Orinoco Basin

JONATHAN W. ARMBRUSTER AND LAWRENCE M. PAGE

Aphanotorulus is redescribed, and several described species are placed in *Aphanotorulus* based upon new information and examination of the type specimens. A new species is described from sandy, lower piedmont streams of the Río Orinoco Basin of Venezuela. *Aphanotorulus ammophilus* is distinguishable from other described species by a combination of characteristics including the presence of a relatively well-developed, angled ridge on the pterotic/supracleithrum, spots on the dorsal-fin interradiation membrane that are mostly free from the fin rays, a low caudal peduncle depth to standard length ratio, a low orbit diameter to head length ratio, and a pectoral-fin spine that reaches beyond the pelvic-fin rays when depressed. The phylogenetic relationships of *Aphanotorulus* and the paraphyly of *Hypostomus* are discussed.

Se redescrive *Aphanotorulus* basado en nueva información y varias especies descritas son puestas en *Aphanotorulus* basado en examinación de los ejemplares tipos. Una nueva especie se describe de los arroyos arenosos en las colinas bajas del Río Orinoco de Venezuela. *Aphanotorulus ammophilus* se puede distinguir de otras especies por una combinación de características incluyendo: la presencia de una relativamente bien desarrollada cresta angulada en el pterótico/supracleitro; manchas en la aleta dorsal cuyas están casi libres de las rayas; una proporción baja entre la profundidad del pedúnculo caudal y la longitud estándar; una proporción baja entre el diámetro orbital y la longitud cefálica; y una espina pectoral que alcanza más allá de los radios pélvicos cuando es sostenida. Las relaciones filogénicas de *Aphanotorulus* y el estado parafilético de *Hypostomus* son discutidos.

APHANOTORULUS is a small genus of loricariid catfishes of the subfamily Hypostominae that is closely related to *Hypostomus* (Isbrücker and Nijssen, 1982). Isbrücker and Nijssen (1982) described *Aphanotorulus* as a new genus because they felt that the autapomorphy of numerous papillae in the buccal cavity (Fig. 1) sufficiently distinguished it from *Hypostomus*. In the description of *Aphanotorulus*, the type species *A. frankei*, known only from the type locality in the Río Ucayali system of Peru, was described. However, like many taxa from South America, *Aphanotorulus* is much more widespread than the original description suggests. One species, described below as new, is quite common in sandy, lower piedmont streams of the middle Río Orinoco drainage. Discovery of this species led to a continuing revision of *Aphanotorulus*.

Few specimens have been available from the Río Ucayali, but they appear very similar to those from the Río Caquetá, Río Huallaga, Río Marañón, and Río Napo; therefore, all specimens from these drainages are considered by

us to be *A. frankei*. However, there are subtle differences in specimens from each of the river systems, and it is possible that several species may be present in these drainages.

Based on examination of types, it is clear that several species recently referred to by Isbrücker (1980) to be *Hypostomus* also belong in *Aphanotorulus*. *Plecostomus madeirae* Fowler (1913) from the Río Madeira and Río Marmoré of Bolivia and Brazil, *P. popoi* Pearson (1924) from the Río Beni and Río Madre de Dios systems of Bolivia and Peru, *P. micropunctatus* La Monte (1935) from the Río Purus and Río Jurua systems of Brazil, and *P. chaparae* Fowler (1940) from the Río Marmoré system of Bolivia all belong in *Aphanotorulus*. The holotype of *A. chaparae* is a juvenile with faded coloration. Fowler (1940) stated that *A. chaparae* differed from other species now in *Aphanotorulus* based on color; but color varies ontogenetically, and *A. chaparae* may be synonymous with *A. madeirae*. We have tentatively assigned species names to specimens based on overall similarity and drainage in which the specimens were collected. However, it is

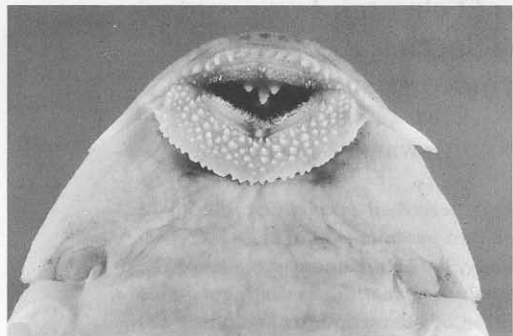


Fig. 1. *Aphanotorulus* is defined by the presence of numerous small papillae in the buccal cavity. INHS 28711, SL = 135.8 mm. Photo by K. S. Cummings.

likely that further information will support placing some of the described species into synonymy. We avoid placing species into synonymy until more material can be examined and a complete revision of the genus can be completed.

Two collections from the Río Guaviare (Río Orinoco Drainage) of Colombia are currently not easily assignable to species and are referred to as *Aphanotorulus* sp. throughout the manuscript.

Isbrücker and Nijssen (1992) placed *H. phrixosoma* (Fowler, 1939) in *Aphanotorulus*, but the species lacks the characters used below to diagnose *Aphanotorulus* and appears to belong in *Hypostomus* sensu lato. *Hypostomus phrixosoma* does share a derived characteristic with *Aphanotorulus*, the presence of elongated odontodes in breeding males, but several other species of *Hypostomus* and *Isorineloricaria* also possess the trait. In this paper, we rediagnose *Aphanotorulus*, identify all species examined that are currently assignable to *Aphanotorulus*, describe *A. amophilus* as new, and suggest that the recognition of *Aphanotorulus* renders *Hypostomus* paraphyletic.

MATERIALS AND METHODS

Morphological measurements were made to the nearest 0.01 mm with the use of dial calipers. Measurements were made according to Boeseman (1968) with the addition of three new measurements: anal width is the body width at the insertion of the first anal-fin ray; folded dorsal-fin length is the length of the depressed dorsal fin, measured from the posterior edge of the nuchal plate (the scute just anterior to the first spine of the dorsal fin) to the tip of the most posteriorly extending dorsal-fin ray; snout-opercle length is the distance from the tip of

the snout to the postero-dorsal edge of the bony opercle. Head height was not used.

All measurements were natural log-transformed, and a principal components analysis was performed using the covariance algorithm of SYSTAT (version 5.0, for Macintosh, Evanston, IL, 1992). No meristic characters were used in the principal components analysis. Principal component scores were plotted against one another to identify shape differences. Additionally, ANCOVAs were performed on natural log-transformed measurements holding the larger value as the covariate. Tukey tests were then utilized to determine pairwise differences. Results for comparisons with *A. chaparae* are not reported because *A. chaparae* is represented only by one specimen.

Lateral-line scutes were counted on the left side of the body and excluded the elongated scute at the anterior margin of the caudal fin. Other counts include the following: predorsal scutes (number of scutes from the tip of the supraoccipital process up to and including the nuchal plate); scutes within the base of the dorsal fin; scutes between the posterior ray of the dorsal fin and the adipose spine (excluding any scutes in contact with the adipose spine); scutes within the membrane of the adipose fin; scutes within the anal-fin interradiation membrane; scutes from the end of the anal fin to the caudal-fin membrane; scutes within the depressed pectoral-fin spine (includes only those scutes in the row proceeding posteriorly from the cleithrum, not the scutes that form the abdominal row); number of dorsal, pectoral, pelvic, and anal-fin rays; and number of teeth per jaw ramus. For tooth counts, only the jaw ramus with the maximum number of teeth was compared between species (referred to as "maximum number of teeth").

Osteological examination was performed on specimens that were cleared and double-stained according to procedures modified from Taylor and Van Dyke (1984). Drawings were prepared with the aid of a camera lucida attached to a Wild M5 stereoscope. Institutional abbreviations are as listed in Leviton et al. (1985) and Leviton and Gibbs (1988). In lists of specimens, "cs" refers to cleared and stained specimens, and numbers in parentheses indicate only the specimens for which measurements and counts were taken. Catalog numbers for *Aphanotorulus* sp. are FMNH 73406 (2) and USNM 181367 (2). Comparisons of external and internal characteristics of *Aphanotorulus* were made on whole and cleared and stained specimens of other loriciariids, including phenetically similar species of *Hypostomus* and *Isorineloricaria*.

DESCRIPTIONS

Aphanotorulus Isbrücker and Nijssen
Figures 1–2

Type species: *Aphanotorulus frankei* Isbrücker and Nijssen, 1982. Rev. fr. Aquariol. 9(4): 105–110.

Diagnosis.—Medium-sized species of the subfamily Hypostominae as diagnosed by Schaefer (1986, 1987). Autapomorphies for the genus are as follows: numerous small papillae inside the buccal cavity (Fig. 1); extremely elongate 1st and 2nd hypobranchials (Fig. 3); extremely elongate 1st basibranchials (Fig. 3); and elongate, unicuspid teeth in the jaws of breeding males (Fig. 4). Elongate hypobranchials and 1st basibranchials are also found in astroblepids, considered to be the sister family of Loricariidae (Schaefer 1986, 1987); however, these characteristics are found nowhere else in Hypostominae, and we consider them to have been independently evolved in *Aphanotorulus*.

Several species of *Hypostomus* are very similar in color to *Aphanotorulus* but can be separated based on the generic characteristics listed above. Many *Hypostomus* species have a single large papilla in the buccal cavity instead of the multiple small papillae of *Aphanotorulus*. Similar *Hypostomus* also usually have a longer, more pointed head.

Description.—Body strongly bicolored, belly white, upper sides above first lateral row of scutes light tan with numerous, moderately sized dark spots arranged in 4–5 longitudinal rows. Head with numerous small black spots. In life, the head appears iridescent gold in bright sunlight. Dorsal, pectoral, pelvic, and adipose fins spotted. Caudal-fin rays with dark rectangular spots that appear to coalesce and form bands when the caudal fin is folded.

Juvenile coloration similar to that of adult. Smallest specimens have four brown dorsal saddles, a brown midlateral stripe, and a mottled head. As the fish grow, the saddles and stripe disappear and are replaced with spots that are, as in species of *Hypostomus* (Boeseman, 1968), proportionately larger in juveniles than in adults.

Head is short with a rounded snout, occasionally with a small, circular, scuteless patch at the tip. Eyes moderate in size, laterally placed. Dorsal-fin spine thin and weak. Dorsal fin set well forward of adipose fin such that when the dorsal fin is depressed, the posterior tip falls short of the origin of the adipose-fin spine. Pelvic-fin origin set slightly posterior in vertical from the dorsal fin origin. Caudal fin forked,

its lower lobe longer than the upper. Gill openings small, mainly ventral. Abdomen and ventral surface of head completely covered with small scutelets.

Dorsal fin with two spines and seven rays. Pectoral fin with one spine and six rays. Pelvic fin with one spine and five rays. Anal fin with five rays. Lateral scutes 28–31 (modally 29). All specimens have three predorsal scutes. Usually eight (occasionally seven or nine) dorsal scutes between the posterior ray of the dorsal fin and the adipose spine and usually seven (occasionally six) dorsal scutes within the base of the dorsal fin. Three to four scutes within the adipose fin membrane and 2–3 within the anal fin. Thirteen to 15 (modally 14) scutes from the anal fin to the caudal fin. Teeth few, usually about 12–15 (Table 1) per jaw ramus, each with a small lateral cusp in all but males in breeding condition.

Sexual dimorphism.—Males in breeding condition are endowed with extremely elongate, bristle-like odontodes (Fig. 2). The bristles cover the entire back and sides behind the dorsal fin, including the adipose-fin spine and the dorsal caudal-fin spine. The bristles are thin and flexible, similar to those on species of the *Peckoltia vittata* species group (Isbrücker and Nijssen, 1992) and not like the stout, sharp odontodes found in loricariids such as *Acanthicus* and *Pseudacanthicus* (Burgess, 1989).

In *A. frankei* (Isbrücker and Nijssen, 1992) and *A. ammophilus*, there are usually three to four bristles per scute, and the bristles begin approximately middorsally, becoming denser posteriorly. In *A. madeirae*, there is usually only one bristle per scute, and a few bristles can be found forward of the dorsal fin. Breeding males of *A. chaparai*, *A. micropunctatus*, and *A. popoi* have not been examined.

Male *Aphanotorulus* in breeding condition also possess elongate, unicuspid teeth whereas most other specimens have teeth with a small, lateral cusp (Fig. 4). Lateral teeth of breeding males occasionally are bicuspid, but the lateral cusp is usually smaller than in specimens lacking bristles.

In *A. ammophilus*, three specimens examined (INHS 32035 holotype, MCNG 14566, MBUCV V-7405) possess bristles on the posterior half of the body and unicuspid teeth. Another male specimen (MCNG 9501) does not have the elongate odontodes but has unicuspid teeth. The standard length of this specimen (148.5 mm) in comparison with that of the holotype (86.0 mm) suggests that the bristles may be deciduous. A paratype (INHS 34738, SL = 102.2 mm) has a

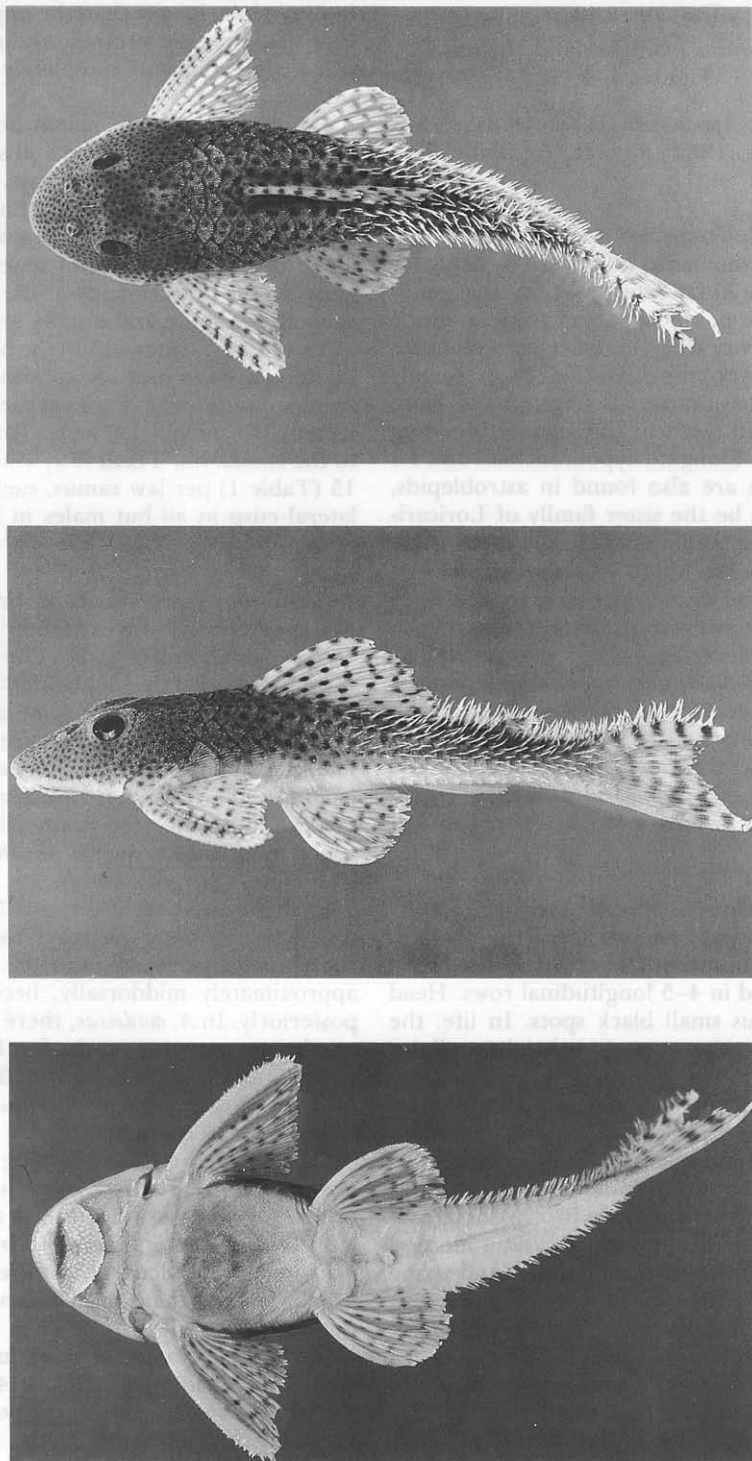


Fig. 2. Holotype of *Aphanotorulus ammophilus* (INHS 32035, SL = 86.0 mm); dorsal, lateral, and ventral views. Photos by K. S. Cummings.

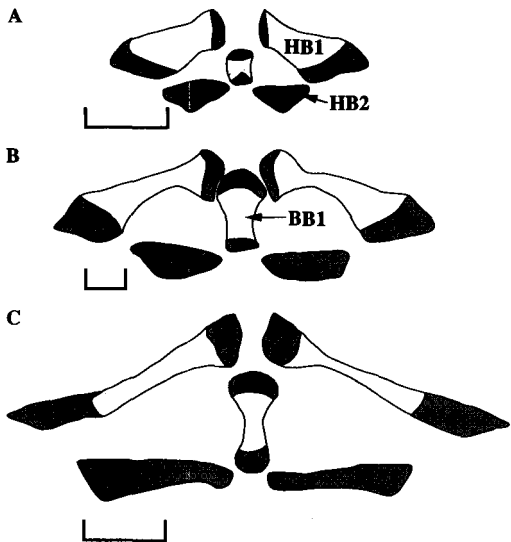


Fig. 3. Hypobranchials 1–2 (HB) and Basibranchial 1 (BB), dorsal view; shaded areas are cartilage. (A) *Hypostomus* sp. (INHS 31414), (B) *H. emarginatus* (INHS 29085), (C) *Aphanotorulus ammophilus* (IHS 29001). Scales = 1 mm.

few bristles, but the teeth are all bicuspid. However, the teeth appear to be new (no teeth are worn or broken) suggesting that the fish may have been collected just after the end of the breeding season. These specimens suggest that males first develop unicuspid teeth, then the bristles. At the end of the breeding season, males regain bicuspid teeth and then lose the bristles. Of the hypostomines and ancistrines we have examined, none has a similar change in teeth during the breeding season.

Similar bristles occur in other loricariids (Burgess, 1989; Isbrücker and Nijssen, 1992); however, they are generally found only on the forward half of the body. Among hypostomines examined, bristles are most extensive in *H.*

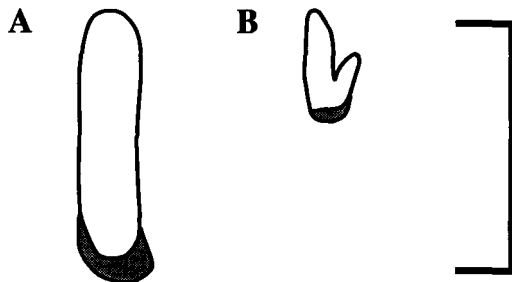


Fig. 4. Third dentary teeth, left side, dorsal view of two similarly sized *Aphanotorulus ammophilus*. Unshaded area is the crown; shaded area is the stalk. (A) Breeding male (MCNG 14566, SL = 134.5 mm). (B) Female (INHS 28711, SL = 135.8 mm). Scale = 1 mm.

phrixosoma, covering the entire body from head to tail.

Ecology.—Based on collections of *A. ammophilus* and *A. popoi*, adults inhabit sandy, slow to moderately fast runs of small to large, turbid rivers. Most adults were collected over sand; however, some were collected over sand covered with a thin layer of mud. Juveniles were found in habitats similar to that of adults but were also common in pools and backwaters over a sand/mud substrate.

Distribution.—Most collections are from the lower piedmont regions of Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. However, the holotype of *A. madeirae* is from the lowlands of the Amazon, suggesting that the range of *Aphanotorulus* may include much of the Amazon basin (Fig. 5).

Etymology.—*Aphano*, from the Greek *aphanes* meaning overlooked, and *torulus* from the Latin meaning a small expansion, in reference to the

TABLE 1. FREQUENCY DISTRIBUTION OF THE MAXIMUM NUMBER OF TEETH FOR SPECIES OF *Aphanotorulus*.

Species	No. teeth													n	Mode
	8	9	10	11	12	13	14	15	16	17	18	19	20		
<i>A. ammophilus</i>					3	14	15	19	21	7	5	—	3	87	15
<i>A. chaparae</i>					1									1	12
<i>A. frankei</i>		2	2	4	23	39	43	23	6	4	1			147	14
<i>A. madeirae</i>	1	2	3	15	6	1	1	1	2	1				33	11
<i>A. micropunctatus</i>			1	1	5									7	12
<i>A. popoi</i>					2	6	8	4	6	1				27	14
<i>Aphanotorulus</i> sp.					1	1	—	1	—	—	1			4	14



- *A. ammophilus*
- ◆ *A. chaparae*
- ▲ *A. frankei*
- ▲ *A. madeirae*
- ▼ *A. micropunctatus*
- *A. popoi*
- *Aphanotorulus* sp.

Fig. 5. Distribution of species of *Aphanotorulus*.

numerous, small buccal papillae (gender masculine).

Aphanotorulus chaparae (Fowler)

Plecostomus chaparae Fowler, 1940. Proc. Acad. Nat. Sci. Phila. 92:81. figs. 38–40.

Hypostomus chaparae Isbrücker, 1980. Versl. Techn. Gegevens, Univ. van Amsterdam. No. 22:21.

Holotype.—ANSP 69067, 37.0 mm SL. Bolivia: Cochabamba, Boca Chapare, Río Chimore; M. Carriker and G. Howes, 28 Aug. 1937.

Aphanotorulus frankei Isbrücker and Nijssen

Aphanotorulus frankei Isbrücker and Nijssen, 1982. Rev. fr. Aquariol. 9(4):105–110. figs. 1–2.

Holotype.—ZMA 116640, 105.4 mm SL. Peru: Ucayali Department, Coronel Portillo Province, Río Neshua, Río Aguaytia/Río Ucayali drainage; 60 km southeast Pucallpa on the road to Tingo Maria; 8°36'S, 74°50'W; P. de Rham, H. Nijssen, H.-J. Franke, and C. Villanueva, 21 Aug. 1981. Not examined.

Paratype.—ZMA 116641, 92.5 mm SL. Same locality as holotype. Not examined.

Nontype material examined.—Río Orteguzza (Río Caquet drainage) of Colombia: FMNH 84125 (2); SU 50694 (12); SU 50697 (1). Río Maraon drainage of Peru: CAS 64530 (1), Río Puran-

apura; CAS 77252 (8), Río Puranapura; CAS 13195 (1), Río Hullaga basin; LACM 39851-13 (27), Río Santiago; LACM 39873-7 (1), Río Santiago; LACM 39879-6 (1), Río Santiago; LACM 39883-12 (12), Río Santiago; LACM 39884-12 (1), Río Santiago; LACM 39890-7 (1), Río Santiago; LACM 39898-2 (1), Río Santiago; LACM 39901-2 (4), Río Santiago; LACM 39936-4 (1), Río Santiago; LACM 39940-5 (1), Río Santiago; LACM 41721-3 (1), Río Santiago; LACM 41724-18 (1), Río Santiago; LACM 41729-41 (7), Río Santiago; LACM 41738-9 (15), Río Maraon; LACM 41740-21 (6), Río Maraon; LACM 41741-34 (2), Río Maraon; USNM 086834 (1), Río Paranapura; USNM 167886 (1), Río Hualaga; USNM 167888 (3), Río Paranapura. Río Napo drainage of Ecuador: FMNH 103280 (1), Río Napo; FMNH 103281 (2), Río Jivino; FMNH 103282 (30), Río Tiputini; FMNH 103283 (1), Río Napo; FMNH 103284 (1), Río Aguarico; LACM 36338-2 (1). Río Ucayali drainage of Peru: AMNH 20863 (1), Río Tambo; FMNH 103279 (2), Río San Alejandro. Unknown localities: FMNH 84145 (6 cs); FMNH 101120 (2 cs), Peru.

Aphanotorulus madeirae (Fowler)

Plecostomus madeirae Fowler, 1913. Proc. Acad. Nat. Sci. Phila. 65:81. figs. 38–40.

Hypostomus madeirae Isbrücker, 1980. Versl. Techn. Gegevens, Univ. van Amsterdam. No. 22:27.

Holotype.—ANSP 69067, 79.9 mm SL. Brazil: Estado Amazonas, Río Madeira, about 200 miles east of W. Long. 63°54'; M. Carriker and G. Howes, 28 Aug. 1937.

Nontype material examined.—Río Madeira drainage of Bolivia: AMNH 40166 (1), Río Marmoré; AMNH 77386 (5), Río Marmoré; AMNH 77434 (15), Río Marmoré; FMNH 59739 (8), Villa Bella (river not stated). Brazil: FMNH 59738 (1), Río Madeira. Unknown localities, listed as "Brazil?": FMNH 77299 (3); FMNH 96280 (1).

Aphanotorulus micropunctatus (La Monte)

Plecostomus micropunctatus La Monte, 1935. Amer. Mus. Novitates. No. 784:1. fig. 1.

Hypostomus micropunctatus Isbrücker, 1980. Versl. Techn. Gegevens, Univ. van Amsterdam. No. 22:28.

Holotype.—AMNH 12598, 150.6 mm SL. Brazil, Estado Amazonas; Vicinity of mouth of Río

Macaua, a trib. of Río Iaco, which is a tributary of the Río Purus near Sena Madureira; 9°20'S, approximately 68°45'W; B. Krukoff, 1934.

Paratypes.—AMNH 26943 (4), 77.3–97.4 mm SL. Same data as holotype.

Nontype material examined.—Río Jurua drainage of Brazil: AMNH 12608 (2), Río Embira.

Aphanotorulus popoi (Pearson)

Plecostomus popoi Pearson, 1924. Indiana Univ. Studies. 11:20–21, Plate III, figs. 2–3.

Hypostomus popoi Isbrücker, 1980. Versl. Techn. Gegevens, Univ. van Amsterdam. No. 22:32.

Holotype.—CAS 77346 (IU 17010), 98.8 mm SL. Bolivia: Popoi River, Río Beni drainage; N. Pearson, Sept. 1921.

Paratypes.—CAS 81231 (IU 17010) (2), 31.3–55.7 mm SL. Same data as holotype. One specimen has been lost.

Nontype material examined.—Río Madre de Dios drainage of Peru: ANSP 143894 (2), Río Manu; ANSP 143897 (2), Río Pinquen; USNM 301646 (1), Río Manu; USNM 302645 (2), Quebrada Pachija; USNM 302656 (1), Río Manu; USNM 302657 (1), Río Manu; USNM 302726 (1), Quebrada Panahua; USNM 319354 (3), oxbow lake of Río Manu; USNM 319360 (4), Caño Fortaleza; USNM 324257 (3), Río Manu; USNM 327337 (2), Quebrada Panahua; USNM 302763 (1), Río Manu.

Aphanotorulus ammophilus n. sp.

Armbruster and Page

Sand Corroncho, Corroncho de Arena

Figures 1–2

Holotype.—INHS 32035, 86.0 mm SL. Venezuela: Estado Cojedes, Río San Carlos, Río Portuguesa drainage; at Caño Hondo, 2 km west of Las Vegas on road from Las Vegas to Campo Alegre; 9°31'51"N, 68°39'39"W; captured over sand with seine in an approximately 60 cm deep run along edge, J. Armbruster, M. Sabaj, K. Cummings, and C. Mayer; 14 Jan. 1994.

Paratypes.—ANSP 173089 (ex. INHS 34784) (2), 66.9–72.4 mm SL; FMNH 105064 (ex. INHS 29001) (2) 66.5–93.6 mm SL; INHS 29001 (1 cs), 69.7 mm SL, Venezuela: Estado Cojedes, Río San Carlos, Río Portuguesa drain-

age, WNW Las Vegas; 9°33'40"N, 68°38'89"W; D. Taphorn, L. Page, K. Cummings, C. Mayer, P. Ceas, J. Armbruster, and M. Sabaj; 9 Jan. 1993; INHS 34738 (2), 89.4–102.2 mm SL, same locality as holotype, 28 Jan. 1995, J. Armbruster, P. Ceas, K. Cummings, C. Mayer; INHS 34784 (31 juveniles, not analyzed), 18.3–38.8 mm SL, same data as holotype; MBUCV V-26460 (ex. INHS 34738) (1), 89.5 mm SL; MCNG 27678 (2), 65.8–79.8 mm SL, same data as INHS 29001; SIUC 23936 (ex. INHS 34738) (1), 90.6 mm SL; TU 173803 (ex. INHS 34784) (3 juveniles, not analyzed), 27.9–40.5 mm SL; UAIC 11126.01 (ex. INHS 34738) (1), 92.8 mm SL; USNM 335171 (ex. INHS 34738) (2), 41.4–96.1 mm SL.

Nontype material examined.—All localities from the Río Orinoco drainage of Venezuela: ANSP 165832, Río Matiyure; FMNH 105065 (2), Río Suripa; FMNH 105066 (3), Río Anaro; FMNH 105067 (3), Río Suripa; FMNH 105068 (11), Río Suripa; INHS 28711 (1), Río Santo Domingo; INHS 34776 (1), Río Masparro; MBUCV V-7405 (1), Río Bocono; MBUCV V-16784 (3), Río Arauca; MBUCV V-16815, Río Pao; MCNG 508 (1), Río Tucupido; MCNG 894 (2), Río Apure; MCNG 2969 (2), zona inundada NE Puerto Bruzual; MCNG 3409 (1), 100 mt. del puente Bruzual; MCNG 3434 (2), Río Guanare Viejo; MCNG 3458 (2), Río Tucupido; MCNG 7238 (1), Río Masparro; MCNG 7388 (4), Río Suripa; MCNG 8960 (2), Río Tucupido; MCNG 9501 (1), Río Sarare; MCNG 9560 (1), Río Apure; MCNG 12836 (1), Río Guanare; MCNG 13015 (5), Río Guanare; MCNG 13504 (9, 2 cs), Río Suripa; MCNG 13773 (8, 1 cs), Río Tinaco; MCNG 14566 (1), Río Orituco; MCNG 17557 (1), Río Caparo; MCNG 19841 (1), Río Apure; UF 80360 (6, 1 cs) Río Guanare.

Diagnosis.—*Aphanotorulus ammophilus* is distinguishable from all other *Aphanotorulus* by several morphological measurements. In particular, *A. ammophilus* differs from all other species in the ratios of orbit diameter to head length (mean = $13.6 \pm 1.4\%$ vs $16.7 \pm 1.8\%$, $P < 0.0001$), and *A. ammophilus* differs from all but Río Guaviare specimens in the ratio of caudal peduncle depth to standard length (mean = $7.0 \pm 0.4\%$ vs $8.0 \pm 0.6\%$, $P < 0.0001$). *Aphanotorulus ammophilus* also differs from all other species by the presence of a moderately well-developed, angled ridge on the pterotic/supracleithrum (the ridge is poorly developed and rounded in other species) and a slightly more pronounced supraoccipital crest. Also, in *A. ammophilus* the pectoral-fin spine, when depressed

TABLE 2. FREQUENCY DISTRIBUTION OF NUMBER OF SCUTES IN THE DEPRESSED PECTORAL FIN FOR SPECIES OF *Aphanotorulus*.

Species	No. Scutes					Mode
	4	5	6	7	n	
<i>A. ammophilus</i>		32	46	11	89	6
<i>A. chaparae</i>		1			1	5
<i>A. frankei</i>	1	132	13		146	5
<i>A. madeirae</i>	3	25	5		33	5
<i>A. micropunctatus</i>		7			7	5
<i>A. popoi</i>	1	22	2		25	5
<i>Aphanotorulus</i> sp.		2	1	1	4	5

along the ventral surface of the body ventral to the pelvic fin, extends beyond the rays of the pelvic fin and modally includes six scutes (Table 2); in other species, the tip of the pectoral fin passes maximally to the origin of the posterior pelvic-fin ray and modally includes five scutes. In species other than *A. ammophilus*, if the pectoral fin includes six scutes, it is usually because a scute that is normally whole is split into two and the contralateral scutes will usually number five scutes; in *A. ammophilus*, the pectoral fin spine usually includes six whole scutes on both sides of the body.

Aphanotorulus ammophilus can be further distinguished from *A. frankei* by the placement of spots on the dorsal fin. In *A. ammophilus*, the melanophores forming the spots are mostly absent from the rays, and the spots are rounded; in *A. frankei*, the melanophores are split nearly evenly between the rays and the membrane, and the spots appear oblong. *Aphanotorulus ammophilus* has larger spots on the head than do *A. madeirae*, *A. micropunctatus*, and *A. popoi*. *Aphanotorulus ammophilus* can be separated from *A. madeirae* by the presence of 3–4, rather than 1–2, elongate odontodes per lateral scute on breeding males and by never having elongate odontodes further forward than the dorsal fin. *Aphanotorulus ammophilus* also differs from *A. madeirae* and *A. micropunctatus* in the modal number of maximum number of teeth (Table 1). No comparisons were made to *A. chaparae* because the holotype is a juvenile with its color faded, and the species is most likely synonymous with *A. madeirae*.

Description.—Morphometrics given in Table 3. See genus description for detailed information. Body distinctly tapered from head to tail, caudal peduncle narrow and short. Caudal peduncle height is short compared to other species. Spots

TABLE 3. SELECTED MORPHOMETRIC FEATURES OF *Aphanotorulus ammophilus*. Ratios expressed as percents.

Morphometric feature	Holotype	n*	Mean	SD	Range
Standard length (SL), mm	86.0	89	81.9	28.1	36.0–160.9
Predorsal length/SL	40.1	89	39.4	1.6	36.1–44.0
Head length/SL	32.1	89	33.3	1.9	29.2–38.5
Cleithral width/SL	28.3	89	26.7	1.1	24.4–29.6
Snout length/SL	17.1	89	17.0	0.8	15.6–20.4
Interorbital width/SL	11.3	89	11.3	0.6	9.4–12.5
Dorsal-fin spine length/SL	28.1	68	26.5	1.6	21.6–29.5
Folded dorsal-fin length/SL	34.4	88	33.8	1.1	30.9–36.9
Base of dorsal-fin length/SL	18.8	89	19.6	1.2	17.2–22.8
Interdorsal length/SL	22.1	89	21.0	1.6	16.8–24.1
Thorax length/SL	23.1	89	24.5	1.2	21.3–26.8
Pectoral-fin spine length/SL	28.4	89	29.8	1.6	26.0–33.8
Abdomen length/SL	21.5	89	21.7	1.0	19.2–24.4
Pelvic-fin spine length/SL	20.0	89	19.3	1.0	17.1–22.5
Postanal length/SL	29.4	89	29.6	1.1	26.2–31.8
Caudal peduncle depth/SL	6.9	89	7.0	0.4	5.7–8.3
Adipose-fin spine length/SL	7.1	88	8.5	0.9	5.7–10.6
Anal width/SL	13.4	88	12.9	1.0	9.7–16.1
Snout–opercle length/SL	22.8	89	23.1	1.3	20.2–26.8
Head width/SL	25.9	88	26.3	0.9	24.3–28.7
Snout length/Head length	50.6	89	51.1	2.9	43.4–56.8
Orbital diameter/Head length	15.1	89	13.6	1.4	10.2–16.9
Anal width/Cleithral width	24.7	89	26.6	2.2	22.3–35.8

* Includes the holotype.

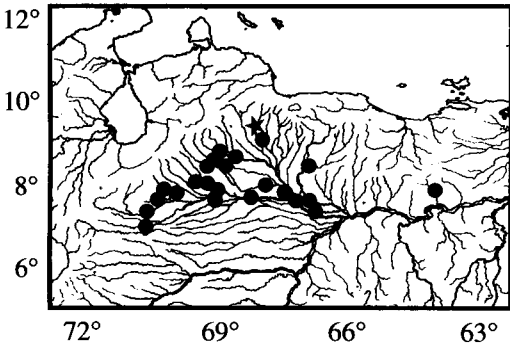


Fig. 6. Distribution of *Aphanotorulus ammophilus* in Venezuela. Star indicates type locality.

on dorsal-fin membrane rounded, mostly separate from fin rays. Spots on head large for *Aphanotorulus*. Pterotic/supracleithral ridge passing posteriorly from eye is relatively large and angled so that the head appears squared, odontodes on the ridge are larger than those in surrounding areas. Supraoccipital crest pronounced.

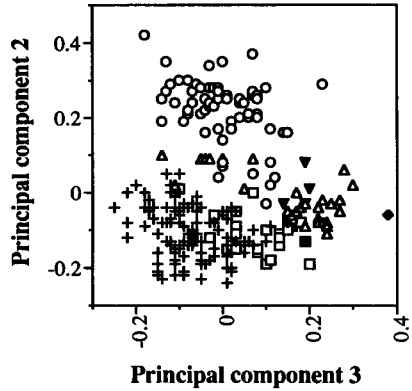
Sexual dimorphism.—See genus description. Collection dates for breeding males suggest a breeding season that begins no earlier than mid-March and continues no later than mid-Jan. Also in support of this hypothesis are a female collected in Nov. (ANSP 165832) with ripe eggs in her ovaries and the fact that juveniles are abundant in collections from Jan.

Distribution.—Río Orinoco drainage of Venezuela (Fig. 6); mainly known from the Río Apure system. Distribution probably includes parts of Colombia, although four specimens from the Río Guaviare (Fig. 5) probably represent a different species.

Etymology.—*Ammo* from the Latin for sand, and *philus* from the Latin for loving (gender, masculine). Specific and common names refer to the preference of the species for sandy habitats.

DISCUSSION

Principal components analysis supports the conclusion that specimens of *Aphanotorulus* from the Río Orinoco drainage of Venezuela are distinct from all other specimens and, thus, represent a separate species (Fig. 7). There was only slight overlap between *A. ammophilus* and other species; and given the unique characteristics of *A. ammophilus*, we considered the overlap to be



- *A. ammophilus*
- ◆ *A. chaparae*
- + *A. frankei*
- *A. micropunctatus*
- *A. popoi*
- *Aphanotorulus* sp.
- ▲ *A. madeirae*

Fig. 7. Results of multivariate analysis, plot of principal components 2 and 3.

insignificant. Principal component 1 mainly represented size and was excluded from further analysis. Other factors were relatively free from size differences and represented shape. Principal component 2 was strongly effected positively by interorbital width, snout length, and snout-opercle length and negatively by orbit diameter, caudal depth, and interdorsal length. Principal component 3 was strongly affected positively by orbit diameter, interorbital width, and snout length and negatively by adipose-fin spine length, dorsal fin spine length, and pectoral-fin spine length.

Principal component 2 best separated *A. ammophilus* from the Amazonian species (including *Aphanotorulus* sp.). Interorbital width and orbit diameter both loaded strongly and oppositely on PC2 suggesting a correlation between the two characters. Snout length and snout-opercle length are significantly longer in *A. ammophilus* than in *Aphanotorulus* sp., *A. frankei*, and *A. popoi* but not in *A. madeirae* and *A. micropunctatus*. Similarities in head shape have led to the intermediacy of *A. madeirae* and *A. micropunctatus* to *A. ammophilus* and *Aphanotorulus* sp., *A. frankei*, and *A. popoi* in Figure 7. PC3 served only to weakly separate *A. frankei* and *A. popoi* based mainly on differences in pectoral-fin spine length, snout length, interorbital width, and orbit diameter. Comparison of other principal components with PC2 showed similar distributions to that of Figure 7. No differences between species were apparent if PC2 was not used.

There is considerable overlap in Figure 7 among specimens attributed to Amazonian species; however, the species are considered to be distinct until a revision of *Aphanotorulus* can be completed. Thus far, no characters have been found to separate Amazonian species of *Aphanotorulus*.

Although *Aphanotorulus* is a well-defined monophyletic group, the recognition of the genus places serious doubt on the validity of *Hypostomus*. Elongate odontodes on breeding males represent a synapomorphy for *Aphanotorulus*, *Isorineloricaria*, and species allied with *Hypostomus commersoni*, *H. emarginatus*, and *H. phrixosoma*. Another synapomorphy for *Aphanotorulus*, *Isorineloricaria*, and species allied with *Hypostomus commersoni*, *H. emarginatus*, and *H. phrixosoma* are elongate first hypobranchials (Fig. 3B) which are evolutionarily intermediate between the stout bones of other *Hypostomus* (Fig. 3A) and the extremely elongate bones of *Aphanotorulus* (Fig. 3C). In addition, *H. emarginatus* possesses first basibranchials that are intermediate between those of other *Hypostomus* and *Aphanotorulus*. Unfortunately, no specimens of *H. phrixosoma* have been available for osteological examination, but we believe that *H. phrixosoma* is the sister to *Aphanotorulus* based on the extensiveness of the breeding odontodes and small adult size. These characters support the contention of Schaefer (1986, 1987) that *Hypostomus* is paraphyletic. Clearly, the description and continuing recognition of *Aphanotorulus* is one of the reasons for the paraphyly of *Hypostomus*; however, we choose to continue to recognize *Aphanotorulus* until a thorough investigation into the interrelationships of hypostomine genera and species groups can be completed.

ACKNOWLEDGMENTS

We would like to thank J. Lundberg, W. Fink, P. Ceas, and C. Laird for comments and suggestions on improving the manuscript. We would also like to thank P. Ceas, K. Cummings, C. Johnston, C. Laird, M. Manrique, C. Mayer, G. Mottesi, S. Phelps, M. Sabaj, and especially D. Taphorn for help in collecting specimens. Special thanks to the following people for invaluable help while visiting institutions, for the loan of specimens, and for permission to clear and stain specimens: R. Arrindell, N. Feinberg, G. Nelson, M. Stiassny, W. Saul, S. Schaefer, D. Catania, W. Eschmeyer, T. Iwamoto, E. Bermingham, M. Rogers, K. Swagel, B. Chernoff, J. Siegel, H. Ortega, F. Provenzano, D. Taphorn, K. Hartel, P. Buckup, H. Britski, O.

Oyakawa, G. Burgess, R. Vari, and J. Williams. 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.

LITERATURE CITED

- BOESEMAN, M. 1968. The genus *Hypostomus* Lacépède, 1803, and its Surinam representatives (Siluriformes, Loricariidae). *Zoologische Verhandlungen* 99:1-89.
- BURGESS, W. E. 1989. An atlas of freshwater and marine catfishes, a preliminary survey of the Siluriformes. T.F.H. Publications, Neptune City, NJ.
- FOWLER, H. W. 1913. Fishes from the Madeira River, Brazil. *Proc. Acad. Nat. Sci. Phila.* 65:517-579.
- . 1939. A collection of fishes obtained by Mr. William C. Morrow in the Ucayali River basin, Peru. *Ibid.* 99:219-289.
- . 1940. Zoological results of the second Bolivian expedition for the Academy of Natural Sciences of Philadelphia, 1936-1937. Part 1-The fishes. *Ibid.* 92:43-103.
- ISBRÜCKER, I. J. H. 1980. Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). *Versl. Techn. Gegevens, Univ. van Amsterdam* 22: 1-181.
- , AND H. NIJSSEN. 1982. *Aphanotorulus frankei*, une espece et un genre nouveaux de poissons—chats cuirasses du bassin du Rio Ucayali au Perou (Pisces, Siluriformes, Loricariidae). *Rev. fr. Aquariol.* 9:105-110.
- , AND ———. 1992. Sexualdimorphism bei Harnischwelsen (Loricariidae). *Harnischewelse*. Sept. 1992:19-33.
- LA MONTE, F. R. 1935. Fishes from the Rio Jurua and Rio Purus, Brazilian Amazonas. *Amer. Mus. Nov. No.* 784:1-8.
- LEVITON, A. E., AND R. H. GIBBS JR. 1988. Standards in herpetology and ichthyology standard symbolic codes for institutional resource collections in herpetology and ichthyology: Supplement No. 1: additions and corrections. *Copeia* 1988:280-282.
- , ———, E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Ibid.* 1985:802-832.
- PEARSON, N. E. 1924. The fishes of the eastern slope of the Andes. I. The fishes of the Rio Beni basin, Bolivia, collected by the Mulford Expedition. *Ind. Univ. Stud.* 11:1-83.
- SCHAEFER, S. A. 1986. Historical biology of the loricariid catfishes: phylogenetics and functional mor-

phology. Unpubl. Ph.D. diss. Univ. of Chicago, Chicago.

———. 1987. Osteology of *Hypostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). Contributions in science, Natural History Museum of Los Angeles County 394:1–31.

TAYLOR, W. R., AND G. C. VAN DYKE. 1984. Revised procedures for staining and clearing small fishes

and other vertebrates for bone and cartilage study. *Cybium* 9:107–119.

ILLINOIS NATURAL HISTORY SURVEY, 607 EAST PEABODY, CHAMPAIGN, ILLINOIS 61820. Send reprint requests to JWA. Submitted: 1 June 1995. Accepted: 22 Sept. 1995. Section editor: R. Winterbottom.