

Review of the loricariid catfish genus *Aphanotorulus* and redescription of *A. unicolor* (Teleostei: Siluriformes)

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Geographic variation within the loricariid genus *Aphanotorulus* was assessed and two species are considered valid, *A. ammophilus* and *A. unicolor*. *Aphanotorulus chaparae*, *A. frankei*, *A. madeirae*, *A. micropunctatus*, and *A. popoi* are synonyms of *A. unicolor*. *Aphanotorulus ammophilus* occurs in the Orinoco drainage while *A. unicolor* is found in the Ríos Japurá, Napo, Marañon, Ucayali, Jurua, Purus, and Madeira of the Amazon drainage and is variable across its range. It is hypothesized that the *A. ammophilus* and *A. unicolor* speciated allopatrically after Orinoco and Amazon became separated 5 MYA.

Variación geográfica en el genero loricariid *Aphanotorulus* fue valorada y dos especies son consideradas validas, *A. ammophilus* y *A. unicolor*. *Aphanotorulus chaparae*, *A. frankei*, *A. madeirae*, *A. micropunctatus*, y *A. popoi* son sinónimos de *A. unicolor*. *Aphanotorulus ammophilus* ocurre en la cuenca del Río Orinoco mientras *A. unicolor* se encuentra en Ríos Japurá, Napo, Marañon, Ucayali, Jurua, Purus, y Madeira de la cuenca del Río Amazonas y es variable a través de su extensión. La hipótesis es hecha que *A. ammophilus* y *A. unicolor* fueron separados por razones geográficas después que los Ríos Orinoco y Amazonas se separaron hace 5 millones de años.

Introduction

Aphanotorulus is a small genus of Loricariidae (the suckermouth armored catfishes) that is closely related to *Hypostomus emarginatus* and *Isorineloricaria* and probably makes *Hypostomus* paraphyletic (Armbruster & Page, 1996). Currently, seven species of *Aphanotorulus* are recognized and the genus is diagnosed by several traits including numerous enlarged papillae in the buccal cavity, elongated first basibranchials and first and second hypobranchials, and elongated, unicuspid teeth in breeding males (Isbrücker & Nijssen,

1982; Armbruster & Page, 1996). Breeding males have elongated odontodes on the lateral plates, a trait shared with some *Hypostomus* and *Isorineloricaria*. *Aphanotorulus* is often common in small to large, lower piedmont streams over sand (Armbruster & Page, 1996).

Recently, *A. ammophilus* was described from the Río Orinoco drainage of Venezuela and several described species were transferred to *Aphanotorulus* (Armbruster & Page 1996); however, no attempt was made to diagnose the Amazonian species. In this study, additional specimens of *Aphanotorulus* and most types of *Hypostomus* were

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examined so that a revision of the genus could be completed. *Hypostomus unicolor* (Steindachner 1908) was also found to be an *Aphanotorulus*. Based on the new data, it is suggested that only two species of *Aphanotorulus*, *A. ammophilus* and *A. unicolor*, should be recognized and that *A. chaparae* (Fowler 1940), *A. frankei* Isbrücker & Nijssen 1982, *A. madeirae* (Fowler 1913), *A. micropunctatus* (La Monte 1935), and *A. popoi* (Person 1924) are synonyms of *A. unicolor*. In this paper, *A. unicolor* is redescribed, a lectotype is designated, and the biogeography of *Aphanotorulus* is discussed.

Materials and methods

Measurements and counts are as in Armbruster & Page (1996). Institutional abbreviations are as in Leviton et al. (1985) and Leviton & Gibbs (1988) with the addition of MUSM for Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos Lima, Peru.

All measurements were natural log-transformed and a principal components analysis was performed using the covariance algorithm of SYSTAT (ver. 5.0, Systat Inc., 1992). No meristic characters were used in the principal components analysis and adipose spine length was excluded because of extreme variability due to the spine often being broken. Principal component scores were plotted against one another to identify shape differences. PCA was performed on the entire data set and a subset consisting only of those fish over 75 mm SL. Additionally, ANCOVA's were performed on natural log transformed measurements for putatively diagnostic characteristics holding the larger value as the covariate for all specimens over 75 mm SL.

Osteological examination was performed on specimens cleared and stained according to procedures modified from Taylor & Van Dyke (1984). Drawings were prepared with the aid of a camera lucida attached to a Wild MZ8 stereoscope.

Aphanotorulus unicolor (Steindachner) (Fig. 1)

Plecostomus unicolor Steindachner, 1908: 164.
Plecostomus madeirae Fowler, 1913: 81, figs. 38-40.
Plecostomus popoi Pearson, 1924: 20.
Plecostomus micropunctatus La Monte, 1935: 1.

Plecostomus chaparae Fowler, 1940: 81.
Aphanotorulus frankei Isbrücker & Nijssen, 1982: 105.

Material examined. NMW 44271:2, 113.1 mm SL, lectotype (present designation); Rio Purus (probably Brazil); Goeldi, 1908. – NMW 44271:1, 1 paralectotype, 115.7 mm SL; NMW 44271:3, 1 paralectotype, 76.0 mm SL; NMW 44272:1, 1 paralectotype, 115.7 mm SL; same data as lectotype.

Most specimens are listed in Armbruster & Page (1996) under the names of the synonymized species. In addition, the following specimens were examined: Huallaga drainage: UMMZ 179262 (2 examined); Peru, Yurimaguas, Río Paranapura; W. R. Allen, Nov. 1920. – UMMZ 179263 (2); Peru, Yurimaguas, Río Paranapura; W.R. Allen, Oct. 1920.

Jurua drainage: MCZ 33520 (1), USNM 94629 (1); Brasil, vicinity of mouth of Rio Embira, a tributary of the Rio Tarauaca, which is in turn a tributary of the Rio Jurua; B. A. Krukoff, 1934. – ZMA 120216 (1); Brasil, Acre, Rio Tarauacá, 8°06'S 70°45'W; M. Goulding, 1 Aug. 1984.

Madeira drainage: AMNH 77434 (33); Bolivia, Depto. Beni, Río Marmore, ca. 23 km W of San Javier; S. Anderson, 10 Sept. 1965. – UMMZ 203887 (1); Bolivia, Depto. La Paz, Río La Paz, Sararia, 2 hrs. by river NW of Punto Linares; G. K. Creighton, 17 June 1978. – UMMZ 205129 (8); Bolivia, Río Marmoré, at and near head of Isla Nicolar Suarez, between Guayaramerin and Guajara Mirim; R. M. Bailey & W. Villarael, 22 Oct. 1964. – ZMA 116845 (1); Bolivia, Depto. Cochabamba, Río Chaparé, about 16°45'S 65°15'W, left bank tributary to Río Marmoré; G. Loubens, 11 June 1982.

Madre de Diós drainage, Peru, Depto. Madre de Diós: MCZ 50970 (1); Parque Nacional Manu, Río Manu, Cashucocha, 12°14'S 70°50'W; Kiestev et al., 13 Aug. 1974. – MUSM 4990 (2); Pakitza, Río Manu; F. Chang, 9 July 1993. – STRI 464 (1), STRI 465 (1); Río Manu; E. Bermingham & A.P. Martin. – USNM 301642 (9), USNM 301646; Parque Nacional Manu, Pakitza and vicinity; H. Ortega, Oct. 1987. – USNM 319355 (5); Parque Nacional Manu, Pakitza, Caño Picaflor; H. Ortega, 23 Apr. 1991. – USNM 319356 (5); Parque Nacional Manu, Pakitza, Río Manu; H. Ortega & W. Valles, 9 May 1991. – USNM 319357 (5); Parque Nacional Manu, Pakitza, Río Manu; H. Ortega et al., 9 May 1991.

Napo drainage: FMNH 103285; Ecuador, Napo, Río Aguatico, about 1 km upstream from

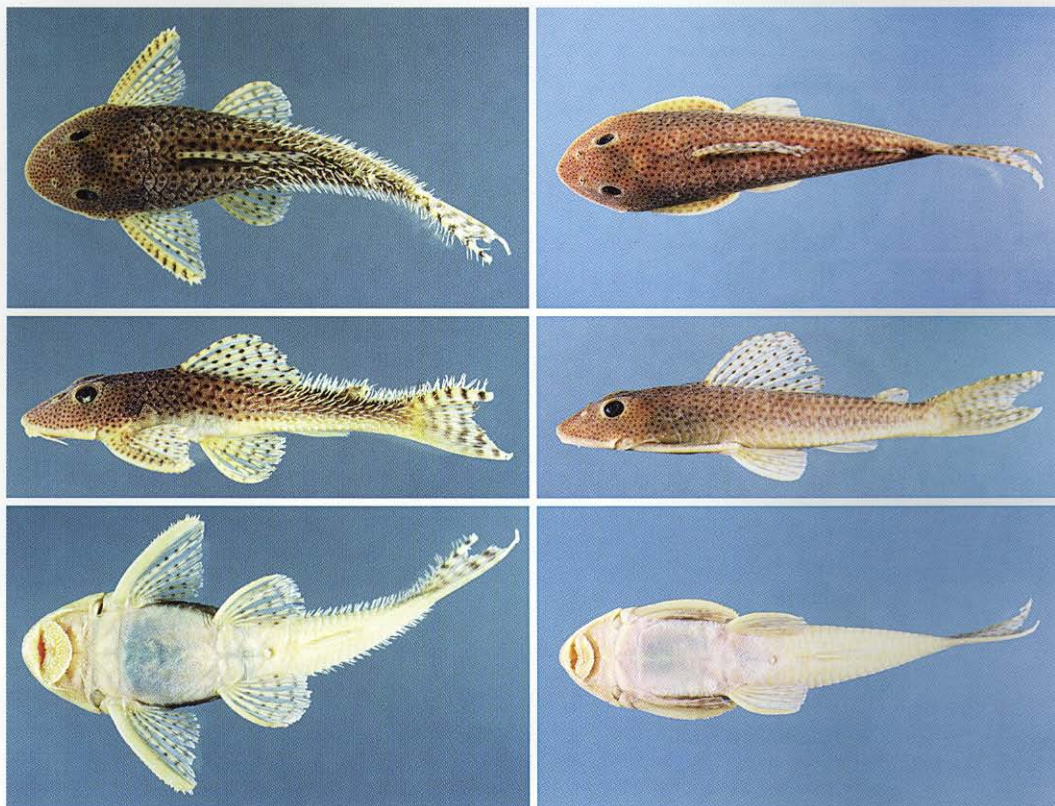


Fig. 1. Left: *Aphanotorulus ammophilus*, holotype, INHS 32035, 86.0 mm SL, Río Apure drainage; right: *A. unicolor*, FMNH 103279, 98.2 mm SL, Río Napo drainage. Photographs Kevin S. Cummings.

Destacamento Lagartococha; D. Stewart et al., 1 Nov. 1983. – MUSM 4784 (2), USNM 32981 (1); Peru, Depto, Loreto, P.V. Arcadia, Río Napo, Queb. Isla; F. Chang, 3 Nov. 1993. – USNM 329611 (1); Peru, Depto. Loreto, P. V. Arcadia, Río Napo, Padre Isla; F. Chang & M. Hasedorn, 8 Nov. 1993. – USNM 362763 (1), Río Manu at Pakitza; H. Ortega and D. Siebert, 20 Sept. 1988.

Purus drainage: AMNH 77429 (7), USNM 94654 (4); Brasil, Amazonas, mouth of Río Macaú, a tributary of Río Iaco, which is a tributary of the Río Purus near Sena Maduiera, 9°20'S ca. 68°45'W; B. A. Krukoff, 1934.

Ucayali drainage: MUSM 1339 (1); Peru, Depto. Ucayali, Río Tahuaya; H. Ortega, 19 Nov. 1983. – ZMA 107869 (2); Peru, Depto. Huanaco, Río Pachitéa, Pacanasi, Tournavista; H. Ortega, 30 Aug. 1973. – ZMA 116640 (1, holotype of *A. frankei*), ZMA 116641 (1, paratype of *A. frankei*); Peru, Depto. Ucayali, Río Aguaytia drainage, Río

Neshuya, 8°36'S 74°50'W, 60 km SW of Pucallpa on road to Tingo Maria.

Diagnosis. A member of *Aphanotorulus* as diagnosed by Armbruster & Page (1996), *A. unicolor* lacks an angled ridge on the pterotic-supracleithrum (versus present in *A. ammophilus*, Fig. 2) and has a pectoral fin spine that, when depressed ventral to the base of the pelvic fin, extends maximally to the origin of the last pelvic fin ray (versus well beyond the origin of the last pelvic fin ray). *Aphanotorulus unicolor* has a unique modification of the urohyal (Fig. 3). In most loricariids, the lateral arms of the urohyal are fairly short and do not overlap with the anterohyal, but in *A. unicolor* the lateral arms are thin and elongate and often overlap the anterohyal. The lateral arms of the urohyal in *A. ammophilus* are more elongate than those of most loricariids, but not to the extent seen in *A. unicolor*.

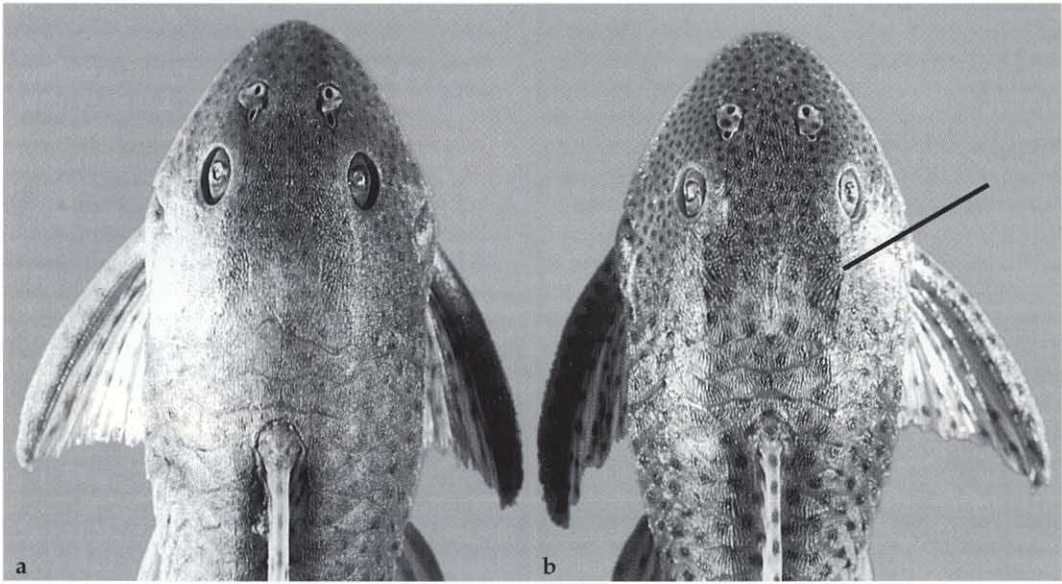


Fig. 2. Dorsal view of head of: a, *Aphanotorulus unicolor*, FMNH 103284, 98.7 mm SL; and b, *A. ammophilus*, MCNG 27678, 79.8 mm SL. Line shows ridge of the pterotic-supracleithrum.

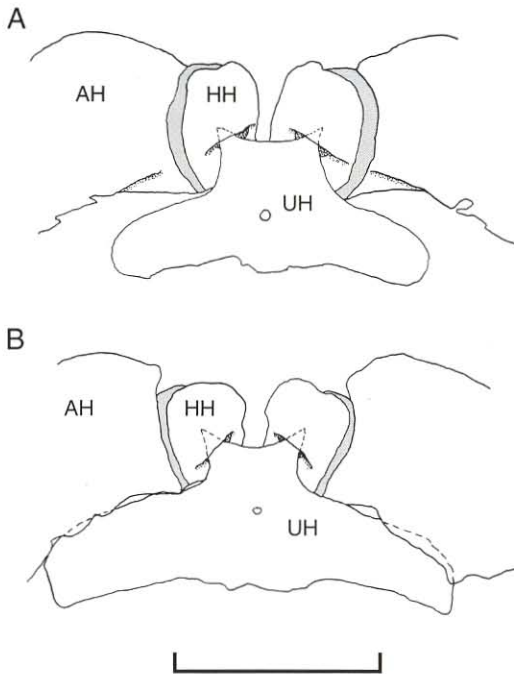


Fig. 3. Ventral view of urohyal of: A, *Aphanotorulus ammophilus*, MCNG 13504; and B, *A. unicolor*, USNM 318357. AH, anterohyal; HH, hypohyal; UH, urohyal. Scale bar: 5 mm.

Description. The largest known specimen is 139.0 mm (USNM 324257). Morphometrics are given in Table 1 and by population in Table 2. 28-30 (usually 29) lateral-line plates, 3 predorsal plates, 10-13 plates in the depressed dorsal fin, 13-16 postanal plates, 4-6 plates in the depressed pectoral fin, and 8-16 teeth per jaw ramus. Dorsal fin with 1 spinelet, 1 spine, and 7 rays. Pectoral fin with 1 spine and 6 rays. Pelvic fins with 1 spine and 5 rays. Anal fin with 5 rays (4 branched, 1 unbranched).

Color pattern as described for *Aphanotorulus* by Armbruster & Page (1996). Spot size varies between populations with specimens from the Río Napo having relatively large spots and those from the Madeira, Purus, and Jurua having small spots. Specimens from the Japurá, Madre de Diós, and Ucayali are intermediate in spot size and specimens from the Marañon vary between both extremes.

Sexual dimorphism. During the breeding season, males possess elongate, unicuspid teeth and elongate odontodes on the adipose fin spine, the upper caudal spine, and the posterior lateral and dorsal plates.

Distribution. *Aphanotorulus unicolor* is found in the upper Amazon tributaries of Bolivia, Brazil, Colombia, Ecuador, and Peru (Fig. 4).

Comparisons. *Aphanotorulus unicolor* can be distinguished from *A. ammophilus* mainly by the absence of an angled ridge on the pterotic-supracleithrum (Fig. 2). Also, the pectoral spine of *A. unicolor* when depressed ventral to the base of the pelvic fin extends maximally to the origin of the most posterior pelvic fin ray while in *A. ammophilus* the pectoral spine extends well beyond the origin of the last pelvic fin ray. Three morphometric ratios separate the majority of specimens (Fig. 5; Table 1). *Aphanotorulus unicolor* has a larger orbit diameter to snout length ratio ($\bar{x} = 0.336, 0.280-0.422$ vs. $\bar{x} = 0.252, 0.185-0.279$; $p < 0.00001$), a larger caudal depth to pectoral spine length ratio ($\bar{x} = 0.295, \text{range} = 0.256-0.351$ vs. $\bar{x} = 0.241, \text{range} = 0.198-0.255$; $p < 0.00001$), and a

smaller pectoral spine length to thorax length ratio ($\bar{x} = 1.121, \text{range} = 0.993-1.169$ vs. $\bar{x} = 1.243, \text{range} = 1.170-1.363$; $p < 0.00001$). The ranges given separate at least 75 % (pectoral spine/thorax) or 80 % (orbit/snout and caudal peduncle depth/pectoral spine) of the specimens over 75 mm SL and work best with the largest specimens; complete ranges for the ratios are given in Table 1. *Aphanotorulus ammophilus* and *A. unicolor* are apparently allopatric; *A. ammophilus* is in the Orinoco basin and *A. unicolor* is in the Amazon basin.

Results and discussion

Specimens listed as *Aphanotorulus* sp. in Armbruster & Page (1996) from the Río Guaviare (Río Orinoco Drainage) are here identified as *A. ammophilus* because of the presence of an angled ridge on the pterotic-supracleithrum and pecto-

Table 1. Selected morphometric features of *Aphanotorulus*. Only fishes greater than 75 mm SL are reported. Information on the type of *A. ammophilus* is available in Armbruster & Page (1996).

	lectotype	<i>A. unicolor</i>				<i>A. ammophilus</i>			
		n	mean	SD	range	n	mean	SD	range
Standard length (SL), mm	113.1	224	92.3	11.2	75.0-139.0	44	104.2	22.5	75.3-160.9
Percent of SL									
Predorsal length	37.9	223	38.1	0.9	35.6-40.1	44	38.3	1.1	36.1-40.8
Head length	29.9	223	26.2	1.3	19.0-34.1	44	32.0	1.3	29.2-34.8
Cleithral width	27.8	223	26.2	1.1	23.2-31.6	44	26.6	0.9	24.4-28.2
Snout length	16.5	222	16.2	0.9	14.0-18.6	44	16.9	0.6	15.6-18.5
Interorbital width	11.7	224	10.9	0.9	9.2-12.9	44	11.4	0.5	10.5-12.3
Dorsal fin spine length	26.7	190	28.1	1.8	22.4-32.0	35	26.5	1.8	21.6-28.9
Folded dorsal fin length	34.2	221	33.6	1.2	29.4-37.6	43	34.0	1.1	31.8-36.9
Base of dorsal fin length	21.2	224	19.5	1.0	16.5-22.9	44	20.1	1.1	17.7-22.8
Interdorsal length	25.5	223	23.6	1.3	20.2-26.5	44	21.9	1.4	18.1-24.1
Thorax length	23.1	223	25.3	1.1	22.0-27.8	44	24.0	1.2	21.3-26.6
Pectoral fin spine length	27.5	223	28.3	1.1	25.0-31.4	44	29.8	1.5	26.0-33.0
Abdomen length	23.4	223	23.4	0.8	21.1-25.5	44	22.2	0.8	20.5-24.4
Pelvic fin spine length	20.2	223	20.8	1.1	16.4-24.2	44	19.5	0.9	17.6-22.5
Postanal length	28.6	223	30.2	1.2	26.8-33.4	44	30.1	0.9	28.4-31.8
Caudal peduncle depth	8.8	224	8.3	0.4	7.0-9.6	44	7.2	0.4	6.0-8.3
Adipose fin spine length	6.8	221	8.1	0.7	6.6-10.3	42	8.1	0.9	5.7-10.6
Anal width	17.9	223	15.2	1.1	12.1-17.9	44	13.5	0.8	11.8-16.1
Snout-opercle length	21.1	223	21.6	1.3	17.6-24.2	44	22.4	0.8	20.2-23.6
Head width	26.5	222	25.3	1.3	22.3-28.3	44	26.1	0.8	24.3-27.8
Percent of snout length									
Orbital diameter	32.2	222	33.6	2.9	26.4-42.2	44	25.2	2.7	18.5-32.5
Percent of thorax length									
Pectoral length	119.3	223	112.1	5.8	99.3-132.8	44	124.3	8.0	106.6-136.3
Percent of pectoral spine length									
Caudal peduncle depth	32.1	224	29.5	1.9	24.3-35.1	44	24.1	2.1	19.8-30.7

Table 2. Selected morphometric features of populations of *Aphanotorulus unicolor*. Only fishes greater than 75 mm SL are reported. Species described from the populations are given in parentheses.

	Huallaga				Japurá				Jurua/Purus (<i>A. micropunctatus</i> and <i>A. unicolor</i>)				Marañon			
	n	mean	SD	range	n	mean	SD	range	n	mean	SD	range	n	mean	SD	range
Standard length (SL), mm	14	93.4	7.2	85.9-110.6	12	84.0	7.0	76.3-102.1	25	100.6	14.2	76.0-126.7	51	92.6	9.5	75.0-110.8
Percent of SL																
Predorsal length	14	37.8	0.8	35.6-38.9	12	38.7	0.8	37.4-39.8	25	38.2	0.7	36.8-39.6	51	37.3	0.7	35.8-38.9
Head length	14	30.7	0.8	29.6-32.2	12	31.7	0.8	30.2-32.8	25	31.4	1.0	29.1-33.0	51	30.4	0.8	28.9-32.2
Cleithral width	14	25.9	0.7	24.9-27.8	12	25.8	0.5	24.9-26.6	25	26.5	0.6	25.4-28.1	51	25.5	0.7	23.2-26.9
Snout length	14	15.7	0.3	15.0-16.2	12	16.0	0.4	15.5-16.4	25	16.9	0.5	16.1-18.0	51	15.0	0.5	14.0-16.0
Interorbital width	14	10.3	0.3	9.9-11.0	12	10.0	0.3	9.5-10.3	25	11.6	0.4	10.8-12.5	51	10.0	0.4	9.2-11.2
Dorsal fin spine length	13	28.5	1.3	26.5-30.5	10	28.5	1.4	26.8-30.6	21	28.9	1.5	24.9-31.6	38	27.5	1.7	24.0-31.7
Folded dorsal fin length	14	33.7	0.8	32.1-35.2	12	34.4	1.1	32.1-36.4	24	34.5	1.1	32.7-37.6	51	33.8	0.9	31.2-35.4
Base of dorsal fin length	14	19.0	1.1	16.8-20.5	12	18.9	0.4	18.0-19.4	25	20.5	1.0	19.0-22.9	51	19.1	0.9	17.2-20.8
Interdorsal length	14	24.0	1.0	22.2-25.5	12	22.6	1.2	20.2-24.1	25	23.1	1.3	20.7-25.8	51	23.5	1.1	20.5-25.4
Thorax length	14	25.5	1.1	23.3-27.5	12	25.9	0.9	24.8-27.4	25	24.6	1.0	22.8-26.8	51	25.8	1.0	23.5-27.8
Pectoral spine length	14	28.9	1.0	27.4-30.5	12	29.1	0.7	27.7-30.5	24	28.0	0.9	26.0-29.2	51	28.5	1.2	25.6-31.4
Abdomen length	14	23.9	0.8	21.9-25.0	12	23.6	0.8	21.9-24.8	25	23.1	1.0	21.1-25.5	51	23.3	0.8	21.1-24.6
Pelvic spine length	14	21.2	0.9	19.7-22.5	12	20.6	0.7	19.7-21.8	25	20.5	0.9	18.9-22.3	51	20.5	0.9	18.3-22.4
Postanal length	14	30.8	0.7	29.6-31.9	12	29.0	0.6	27.7-30.0	25	30.5	1.1	28.6-32.5	51	29.5	1.0	26.8-32.2
Caudal peduncle depth	14	8.2	0.3	7.7-8.6	12	8.0	0.3	7.6-8.5	25	8.5	0.5	7.7-9.4	51	8.2	0.4	7.0-8.9
Adipose fin spine length	13	8.6	0.6	7.4-9.7	12	7.9	0.6	6.6-8.7	25	8.0	0.8	6.8-9.5	50	8.0	0.7	6.7-10.3
Anal width	14	15.1	0.6	14.6-17.0	12	13.5	0.7	12.6-15.5	25	14.9	1.3	12.5-17.9	51	15.1	0.9	13.4-16.8
Snout–opercle length	14	20.6	0.7	19.6-22.0	12	21.2	0.8	19.7-22.5	25	22.5	0.8	21.1-24.1	51	20.2	0.8	17.6-21.6
Head width	14	24.8	0.8	23.6-26.2	12	24.3	1.0	22.9-26.6	25	26.3	0.8	25.2-28.0	50	24.2	0.8	22.3-25.9
Percent of snout length																
Orbital diameter	14	35.3	3.0	30.0-39.6	12	35.2	2.3	30.9-39.3	25	33.4	2.2	28.8-37.6	51	30.4	1.7	26.4-35.1
Percent of thorax length																
Pectoral length	14	113.9	5.9	102.8-125.4	12	112.2	5.0	104.9-122.4	24	113.6	5.5	102.1-123.4	51	110.6	5.5	99.3-120.9
Percent of pectoral spine length																
Caudal peduncle depth	14	28.4	1.4	24.3-32.7	12	27.6	0.9	26.0-29.0	24	30.2	2.0	27.7-34.3	51	28.7	2.0	24.3-32.7

Table 2. (cont.)

morphometric feature	Madeira (<i>A. chaparae</i> , <i>A. madeirae</i> , and <i>A. popoi</i>)				Madre de Díos				Napo				Ucayali (<i>A. frankei</i>)			
	n	mean	SD	range	n	mean	SD	range	n	mean	SD	range	n	mean	SD	range
Standard length (SL), mm	49	86.0	7.3	75.8-110.2	53	96.4	12.2	77.2-139.0	12	88.7	8.8	75.5-105.1	6	93.1	9.2	79.4-106.1
Percent of SL																
Predorsal length	48	38.8	0.8	36.8-40.1	53	38.1	0.8	35.6-39.7	12	37.6	0.7	36.8-39.2	6	38.9	0.8	37.7-39.9
Head length	49	31.2	2.0	19.0-33.0	52	31.1	1.0	28.6-32.8	12	31.0	1.3	29.2-32.8	6	32.0	1.1	31.2-34.1
Cleithral width	48	27.4	1.0	25.4-31.6	53	26.0	0.7	24.4-27.3	12	24.9	0.4	24.4-25.7	6	27.0	0.8	25.7-27.8
Snout length	49	17.1	0.5	15.7-18.6	51	16.4	0.5	15.4-17.5	12	15.3	0.5	14.4-15.8	6	16.8	0.5	16.1-17.6
Interorbital width	49	11.9	0.5	10.4-12.9	53	11.0	0.4	10.1-11.8	12	10.2	0.5	9.4-11.1	6	11.0	0.3	10.6-11.3
Dorsal fin spine length	40	26.5	1.6	22.4-28.9	49	29.2	1.3	26.7-32.0	11	28.8	1.6	25.9-31.2	6	28.5	1.0	27.3-29.9
Folded dorsal fin length	47	33.0	1.3	30.5-35.9	53	33.4	1.1	29.4-35.6	12	33.7	0.9	32.0-35.0	6	34.2	1.1	32.7-36.0
Base of dorsal fin length	49	19.6	0.8	17.5-21.5	53	19.5	0.9	16.5-21.3	12	19.2	0.6	18.4-20.0	6	20.1	0.7	18.9-20.6
Interdorsal length	49	24.2	1.4	20.6-26.5	53	23.8	1.3	21.3-26.3	11	23.2	1.7	20.4-26.0	6	22.6	1.1	20.6-23.8
Thorax length	48	24.6	1.1	22.0-27.3	53	25.4	1.0	22.9-27.3	12	25.4	0.9	23.7-26.8	6	25.0	0.6	24.2-25.6
Pectoral spine length	49	27.6	0.9	25.8-30.1	53	28.5	1.2	25.0-30.6	12	28.5	0.9	27.3-29.9	6	27.7	1.2	25.7-29.0
Abdomen length	48	23.7	0.8	21.6-25.4	53	23.0	0.7	21.4-24.6	12	23.8	0.8	22.6-25.3	6	22.8	0.7	21.7-23.8
Pelvic spine length	48	20.5	1.0	18.8-24.2	53	21.5	0.9	18.8-23.1	12	20.7	1.3	17.2-21.9	6	20.2	1.9	16.4-21.5
Postanal length	48	29.9	1.3	26.8-33.4	53	30.9	1.1	28.9-33.4	12	30.7	0.9	29.3-32.0	6	30.3	1.3	28.5-32.2
Caudal peduncle depth	49	8.5	0.3	7.7-9.2	53	8.5	0.4	7.6-9.6	12	8.2	0.3	7.6-8.4	6	8.3	0.3	7.9-8.6
Adipose fin spine length	49	8.1	0.5	7.1-9.1	53	8.1	0.6	6.9-10.1	11	8.6	0.6	7.4-10.0	6	8.5	1.0	7.5-10.0
Anal width	48	16.0	0.8	14.6-17.5	53	15.2	0.9	12.1-16.8	12	15.1	1.0	13.5-16.8	6	15.3	0.7	14.4-15.9
Snout–opercle length	48	22.7	0.8	19.8-24.2	53	21.9	0.7	20.3-23.3	12	20.4	0.7	19.3-21.5	6	22.1	0.6	21.4-23.2
Head width	48	26.7	0.8	25.0-28.3	53	25.4	0.8	23.1-27.2	12	24.3	0.5	23.6-24.9	6	26.0	1.0	25.1-27.6
Percent of snout length																
Orbital diameter	49	34.0	1.9	27.4-38.3	51	34.6	2.1	29.9-39.4	12	36.6	3.4	31.3-42.2	6	35.8	0.8	34.8-36.7
Percent of thorax length																
Pectoral length	48	112.2	5.6	102.0-123.0	53	112.5	6.6	100.9-115.1	12	112.3	6.4	103.0-122.7	6	110.7	5.4	102.8-125.4
Percent of pectoral spine length																
Caudal peduncle depth	49	30.6	1.4	27.8-35.1	53	30.0	1.7	27.2-31.7	12	28.6	1.1	26.7-30.6	6	29.9	1.5	26.2-30.3

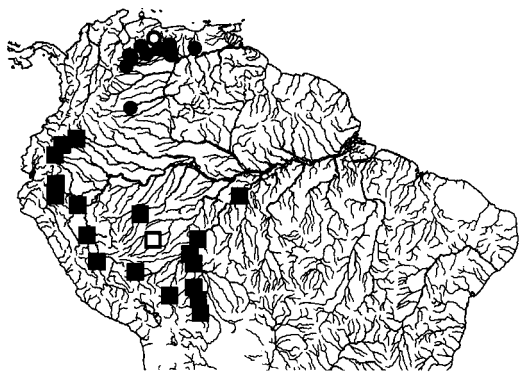


Fig. 4. Distribution of *Aphanotorulus* species. Circles: *A. ammophilus*; squares: *A. unicolor*. Open symbols represent the type localities.

ral fins that extend beyond the origin of the last pelvic fin ray when depressed. Ambiguity in the previous study was caused mainly by the tendency for the smaller specimens of *A. ammophilus* and *A. unicolor* to group in an intermediate position in the PCA. Because of the intermediate position of juveniles, subsequent analysis was limited to those fishes greater than 75 mm (a size that corresponds to a sub-adult). The one specimen over 75 mm from the Río Guaviare grouped with the remainder of *A. ammophilus*.

For specimens greater than 75 mm SL, there was 100 % separation in the PCA between *Aphanotorulus* from the Orinoco and the Amazon basins (Fig. 6). Principal component 1 loaded strongly on standard length and was excluded from further analysis. Other principal components were relatively free from the effects of size. On principal component 2, orbit diameter, caudal peduncle depth, and anal width loaded heavily and negatively, and pectoral spine length loaded heavily and positively. On principal component 3, interorbital width, snout length, and snout-opercle length loaded heavily and negatively, and thorax length, dorsal spine length, and inters dorsal length loaded heavily and positively.

For the PCA, Amazonian *Aphanotorulus* were grouped according to drainage into eight populations. Although most populations of *A. unicolor* formed tight clusters in the PCA, the clusters overlapped significantly with those of other populations. There was slight variation in spot size between populations of *A. unicolor* with specimens from the Napo having the largest spots and those from the Juruá, Madeira, and Purus, hav-

ing the smallest; however, specimens from the Río Marañon varied between the extremes of spot size and no distinct characters could be found to separate the populations of the Amazon drainage. With no distinct morphological or morphometric characters to separate the Amazonian populations of *Aphanotorulus*, it is most reasonable to suggest that all of the populations represent the same species.

Other than in Armbruster & Page (1996) and Fowler (1940), the species of *Aphanotorulus* have not been compared. Fowler (1940) compared *A. chaparae* to *A. madeirae* and *A. popoi* stating that *A. chaparae* differed in color pattern from the other species; however, this difference is due to the fact that the type of *A. chaparae* is a juvenile and color pattern varies with ontogeny in *Aphanotorulus* (Armbruster & Page, 1996). Armbruster & Page (1996) suggest that there might be differences between the species in morphometry (the number of plates under the depressed pectoral fin spine and tooth number); however, variation in tooth number and plates under the pectoral fin spine did not hold under further scrutiny. Variation in morphometry of the Amazonian species is apparent in the PCA (Fig. 6). In particular, specimens from the Marañon have smaller eyes than other *A. unicolor* and, thus, scored highly along PC2. PCA also suggests that specimens from the northern Amazon tributaries (Huallaga, Japurá, Marañon, and Napo) are morphometrically more similar to each other than they are to those from the southern tributaries (Juruá, Madeira, Purus, and Ucayali); however, the specimens from the Madre de Diós broadly overlap both groups and no consistent differences could be found to delineate any of the populations.

Armbruster and Page (1996) further suggest that there may be a difference in the pattern of elongate odontodes on the plates of breeding males with specimens from the Madeira having fewer elongated odontodes per plate; however, this difference was based on a few poorly preserved specimens that may have lost some of the odontodes due to poor preservation. It is possible that once breeding males from all of the populations become available, there may be significant differences between the populations; however, no distinct differences are currently known, and it is best to recognize only a single species, *A. unicolor*, at this time.

As a further note, all of the species of *Aphanotorulus* described from the Amazon are from the

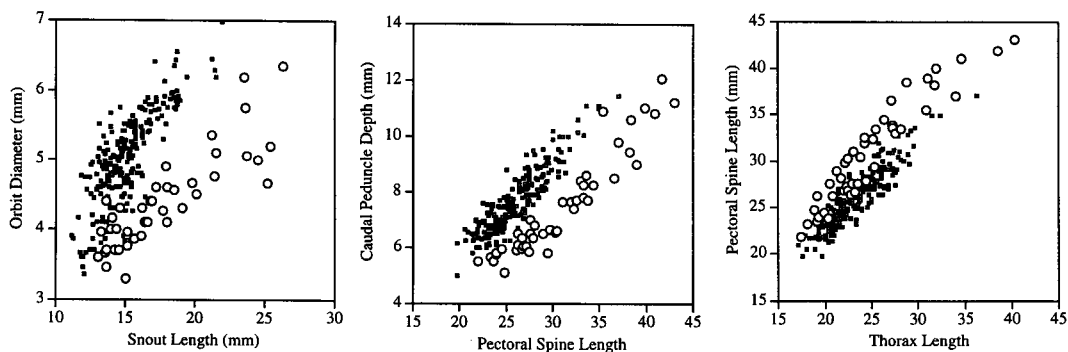


Fig. 5. Plot of morphometrics useful in separating species of *Aphanotorulus*. Circles: *A. ammophilus*; squares: *A. unicolor*.

Juruá, Madeira, Purus, and Ucayali systems and these populations showed no differences in the PCA (Fig. 6) or in color pattern and there is currently no evidence to suggest that more than one species is involved. At best, it could be argued that populations in the Huallaga, Japurá, Madre de Dios, Marañón, and Napo, or some combination of these populations, represent separate species, but the differences are minor and not significant enough to warrant the description of new species at this time.

Aphanotorulus is found only in whitewater rivers, and the blackwater Rio Negro probably provides an effective barrier to gene flow between *A. ammophilus* in the Orinoco and *A. unicolor* in the Amazon. Lack of dispersal through the Rio Negro would suggest that the two species of *Aphanotorulus* arrived at their current distributions through stream capture or through ancient river systems. An Orinoco outlet of the Amazon is hypothesized to have occurred between five and thirteen million years ago (Lundberg et al., 1988; Hoorn, 1993; Retzer, 1994), and this outlet could have allowed the dispersal of *Aphanotorulus* between the two drainages. The eventual separation of the Amazon and Orinoco could have led to the allopatric speciation of *Aphanotorulus*.

Continued analysis of the osteology of *Aphanotorulus* further supports the monophyly of the genus. Synapomorphies for *Aphanotorulus* in addition to those in Armbruster & Page (1996) include: an anterior surface of the hyomandibula that is perpendicular to the dorsal surface of the

metapterygoid (versus straight to slightly angled in other loricariids), a fourth infraorbital canal plate that does not contact the orbit except in rare instances where there is slight contact (the 4th infraorbital canal plate has a wide border with the anterior margin of the orbit in most loricariids), and a third basibranchial that is small and nearly square (vs. elongate in most other loricariids).

In addition to the synapomorphies given by Armbruster & Page (1996), further evidence suggests a close relationship between *Aphanotorulus*, *Isorineloricaria*, *Hypostomus squalinus* (called *H. commersoni* in Armbruster & Page, 1996), and *H. emarginatus*. These taxa possess a lateral line that continues onto the elongate plate that covers the base of the caudal fin rays (in most loricariids, including *Isorineloricaria*, the lateral line ends prior to this plate), 7 infraorbital canal plates (vs. usually 5-6), elongated anterolateral processes on the eighth vertebral centrum (vs. short or no processes), a forward shift of the metapterygoid condyle on the ventral surface of the lateral ethmoid such that the posterior edge of the condyle does not contact the posterior margin of the lateral ethmoid (vs. contacting the posterior of the lateral ethmoid), and a large medial papilla in the buccal cavity (vs. no or a small papilla). The strength of the relationships of *Aphanotorulus*, *Isorineloricaria*, *H. emarginatus*, and *H. squalinus* certainly indicates that the current taxonomy of *Hypostomus* and its allies is in need of revision, but I reserve modification of the taxonomy until a phylogeny can be produced from which an objective decision for generic placement can be made.

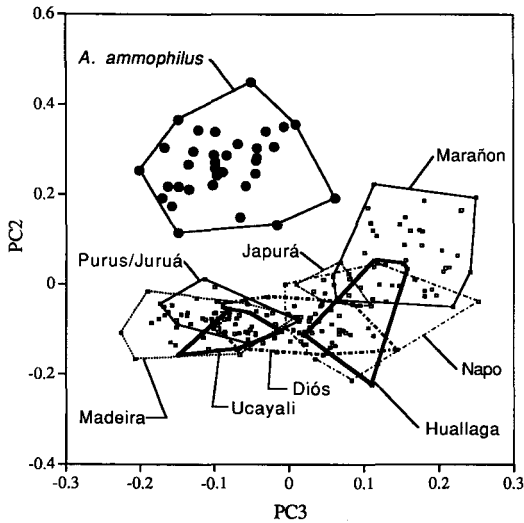


Fig. 6. Results of principal components analysis of populations of *Aphanotorulus unicolor*. Specimens are grouped according to drainage.

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