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REVIEW OF SOUTH AMERICAN FRESHWATER ANGELFISHES—GENUS *PTEROPHYLLUM*

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The illustration of the new *Plataxoides leopoldi* Gosse (1963, Inst. Roy. Sci. Nat. Belgique Bull., vol. 39, no. 35, pp. 4–6, pl. 1, fig. 2) so closely resembled the illustration of *Plataxoides dumerilii* Castelnau (1855, Animaux nouveaux ou rares . . . d'Amérique du Sud, p. 21, pl. 11, fig. 3) that I decided to review the taxonomic status of all the nominal species of *Pterophyllum*. I shall attempt (1) to clarify the nomenclatural validity of the generic names *Pterophyllum* and *Plataxoides*, (2) to review the species complexes of *Pterophyllum scalare* (= *P. eimekei*) and *Plataxoides dumerilii* (= *P. leopoldi*), and (3) to discuss the relationship between *Pterophyllum altum* Pellegrin and *P. scalare* (Lichtenstein).

I have studied all nonaquarium specimens of *Pterophyllum* available in the following museums: British Museum of Natural History (BMNH); California Academy of Sciences (CAS); Chicago Natural History Museum (CNHM); Museum of Comparative Zoology, Harvard (MCZ); Museum National Histoire Naturelle, Paris (MNHN); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRSNB); Stanford University (SU); U.S. National Museum (USNM). To the authorities of the above institutions, I wish to express my gratitude for their help and other courtesies.

In the "Tropical Fish Hobbyist" (1953, vol. 1, no. 5, pp. 5-7, 20) I attempted to distinguish three species of aquarium-bred *Pterophyllum*. Since then I have studied specimens collected from their natural habitat, the syntypes of *Pterophyllum altum* Pellegrin, a syntype of *P. eimekei* Ahl, 27 paratypes of *Plataxoides leopoldi* Gosse, and the holotype of *P. dumerilii* Castelnau.

In my 1953 study I recognized *Pterophyllum scalare*, *P. eimekei*, and *P. altum* as valid species; however, with additional material my conclusions have changed and in this review I now recognize as valid *P. scalare*, *P. altum*, and *P. dumerilii*. *P. eimekei* is a synonym of *P. scalare*.

In the synonymy for each species I have recorded only the most pertinent references, omitting those related to aquaria.

I have attempted to record each locality from which *Pterophyllum* has been reported by latitude and longitude as found in "The Times Atlas of the World," 1957, vol. 5 ("The Americas"); "U.S. Board of Geographic Names Gazetteer," no. 56 ("Venezuela") and no. 71 ("Brazil"); Eigenmann's "The American Characidae," 1917, pt. 1, pl. 1; and Eigenmann and Allen's "Fishes of Western South America," 1942, pp. 67-81. Since I was unable to find a few localities, specimens from such places are not included in the distributional map for the species (pl. 1). Some of the other records are so unspecific in locality, e.g., "Rio Orinoco," that these cannot be plotted on the map. I have studied the routes followed by the collectors; the latitude and longitude used represents the best estimate for the information available.

The specific localities from which specimens of *Pterophyllum* have been collected are as follows:

locality	longitude	latitude
Ambyiacu, Río, Peru	3°10' S	73°13' W
Araguaia, Rio, near Aruana, Brazil	14°54' S	51°05' W
Atabapo, Río, Colombia	4°03' N	67°45' W
Belém [= Pará], Brazil	1°30' S	48°55' W
Cacaul or Cacaoal [= Cacoal], Brazil	1°59' S	46°13' W
Cashiboya, Lago above Contamana, Peru	7°19' S	75°04' W
Casiquiare, Río, Venezuela	2°01' N	67°07' W
Coary, Brazil	4°08' S	63°07' W
Crab Falls, British Guiana	5°17' N	58°59' W
Cupai [probably Rio Cupari], Brazil	3°04' S	55°25' W
Demerara or Georgetown, British Guiana	6°46' N	58°10' W
Iquitos, Peru	3°51' S	73°13' W
Jutahy, Brazil	3° S	66°57' W
Manacapurú, Brazil	3°18' S	60°37' W
Manacapurú, Lago, Brazil	3°10' S	61°30' W
Manaus, Brazil	3°06' S	60°00' W
Marajó I, in Amazon, Brazil	1°45' S	49° W
Maximo, Lago, Brazil	(?)	(?)
Monte Alegre, Brazil	2°01' S	54°04' W

locality	longitude	latitude
Nazareth, Brazil	1°13' N	67°51' W [probably]
Óbidos, Brazil	1°52' S	55°30' W
Pacaya, Río [see Yarinacocha]		
Pévas [= Pébas] Caño, Peru	3°10' S	71°46' W
Pôrto Alegre, Brazil	4°23' S	52°45' W
Pôrto do Móz, Brazil	1°45' S	52°10' W
Pôrto Negro [probably near Manaus], Brazil		
Purus, Río, Brazil	3°42' S	61°28' W
Rockstone, British Guiana	6°00' N	58°30' W
Rupununi River, British Guiana	3°55' N	59°06' W
Santarém, Brazil	2°26' S	54°41' W
Solimões, Rio, at Manacapurú, Brazil	3°18' S	60°37' W
Tabatinga, near Leticia, Brazil	4°14' S	69°44' W
Tefé [= Teffé], Rio, Brazil	3°24' S	64°45' W
Tonantins, Brazil	2°46' S	67°45' W
Ueranduba, Brazil	(?)	(?)
Urubu Rio, Brazil	2°55' S	58°25' W
Villa Bella [Rio Ramos], Brazil	2°36' S	56°39' W
Xingu, Rio [Pôrto Alegre], Brazil	4°23' S	52°45' W
Yarinacocha [Río Pacaya], Peru	5°10' S	74° W

Pterophyllum Heckel

Pterophyllum Heckel, 1840, Ann. Wien. Mus., vol. 2, no. 12, p. 334 [type species:

P. scalare Heckel = *Platax scalaris* Cuvier and Valenciennes].—Ahl, 1928, Zool. Anz., vol. 76, p. 252 [revision of 3 species].

Plataxoides Castelnau, 1855, Animaux nouveaux ou rares . . . de l'Amerique du Sud . . . , p. 21, pl. 11, fig. 3 [type species: *P. dumerilii* Castelnau].

TABLE 1.—Number of vertebrae in *Pterophyllum*

Species and localities	Abdominal			Caudal					Total				
	12	13	14	14	15	16	17	18	27	28	29	30	31
<i>dumerilii</i>													
British Guiana			1			1					1		
Rio Negro-Amazon		2	1	1	2						2		
Rio Negro, types of <i>leopoldi</i>	5	21		7	16	3			10	15	1		
Belém and Marajó Island	1						1				1		
<i>altum</i>													
Upper Orinoco		2					2					2	
<i>scalare</i>													
British Guiana	26			1	8	13	4		1	8	13	4	
Middle and lower Amazon	13					6	6	1			6	6	1
Belém and Marajó Island	7						7					7	
Peruvian Amazon	7				2	4	1			2	4	1	

The validity of the generic name *Pterophyllum* Heckel, long in use by ichthyologists and aquarists, needs to be clarified because Gosse (1963, p. 4) used the generic name *Plataxoides* Castelnau instead of *Pterophyllum*. Gosse (loc. cit.) and Whitley (1951, Proc. Roy. Zool.

Soc. New South Wales, p. 68) were in error in considering that *Pterophyllum* Heckel is not available as a generic name with the type species *Pterophyllum scalare* Heckel (= *Zeus scalaris* Lichtenstein). Myers (1940, Stanford Ichthy. Bull., vol. 2, no. 1, p. 36) pointed out that Neave (1940, Nomenclator zoologicus, vol. 3, p. 1028) was in error in the following statement: "*Pteropyhllum* (pro-Ila, Kirby 1825), Harris 1833, in Hitchcock, Rept. Geol. Min. Bot. Zool. Massach., 582-Orth." I have checked Harris (1833, 1835, Rep. Geol. Mineral. Bot. Zool. Massachusetts) and can verify Myers' observation that Harris consistently used *Pterophylla*, leaving *Pterophyllum* available.

***Pterophyllum dumerilii* (Castelnau)**

PLATE 2

Plataxoides dumerilii Castelnau, 1855, Animaux nouveaux ou rares . . . de l'Amérique du Sud . . . , p. 21, pl. 11, fig. 3 [Pará=Belém].

Plataxoides leopoldi Gosse, 1963, Inst. Roy. Sci. Nat. Belgique Bull., vol. 39, no. 35, p. 4, pl. 1, fig. 2 [mouth of Rio Solimões, about 90 km above Manacapurú].

Specimens studied (see page 2 for more precise locality): BMNH 1902-11-4-10-12, Marajó, 3 (27 to 40 mm); BMNH 1902-2-11-4-9, Tonantins, 1 (41 mm); MCZ (out of 14992), Tefé, 2 (33 and 37 mm); CNHM (out of 15254); Santarém, 1 (40 mm); CNHM 53846 Rupununi River, 2 (33 and 54 mm); CNHM (out of 54370), Santarém, 1 (37 mm.); USNM 167772, Rupununi River, 1 (40 mm.); USNM 198177, Rio Urubu, 1 (45 mm.); USNM 198178, Rio Purús, 2 (29 and 31 mm.); IRSNB 460, Rio Solimões. 90 km above Manacapurú, 27 paratypes of *P. leopoldi*, (34 to 61 mm); MNHN A 254, Pará, Brazil, holotype of *P. dumerilii* (49 mm); MNHN 221-61-3-7, Cacaual, 1 (37 mm); MNHN 221-61-3-6, Caldron, 2 (42 and 51 mm).

I examined the holotype of *Plataxoides dumerilii* Castelnau at the Museum National Histoire Naturelle, Paris, and found that Castelnau's illustration (1855, pl. 11) is in error. In his illustration, a black spot is shown behind the prominent black vertical bar that extends from the middle of the dorsal fin across body to the middle of the anal fin, whereas in the holotype this spot now shows as a trace in front of that dark bar, not behind it. Also, the dark vertical bars anteriorly on the illustration are incorrectly portrayed. On the holotype a short bar extends from the spiny dorsal origin ventrally to the lateral line, another short bar occurs halfway between the eye and the spiny dorsal origin; there is also a dorsoventral bar through the eye and across the cheek. These bars are prominent in well-preserved specimens and their positions differ notably from those of *Pterophyllum scalare* and *P. altum*. On the latter two species, the black bar through the eye extends dorso-posteriorly to the origin

of the spiny dorsal fin, replacing the two middle predorsal vertical bars on *P. dumerilii*. Thus, on the basis of coloration *P. dumerilii* can always be distinguished from *P. scalare* and *P. altum*. The number of vertebrae averages slightly fewer in *P. dumerilii* than in the other two species (table 1) and there are also slightly fewer soft dorsal and soft anal rays and fewer oblique scale rows (from rear of head to midbase of caudal fin) (table 2) than in *P. scalare* and

TABLE 2.—Counts recorded for *Pterophyllum dumerilii*

Localities	Dorsal fin rays										Pectoral fin rays	
	XI	XII	XIII	18	19	20	21	22	23	24	10	11
British Guiana		3		1	1	1					2	
Rio Negro-Amazon	1	8	1		3	1	2	1	1	2	2	10
Rio Negro (types of <i>leopoldi</i>)	4	20	2		7	14	5				2	24
Mouth of Amazon		3	1						4		1	3
Holotype of <i>dumerilii</i>		1							1			1

Localities	Anal fin rays												Oblique scale rows							
	VI	19	20	21	22	23	24	25	26	27	28		26	27	28	29	30	31	32	33
British Guiana	3		2	1											1	1				
Rio Negro-Amazon	10		2	2	2		1	3					1	2	2		3	1		1
Rio Negro (types of <i>leopoldi</i>)	26	1	8	11	5	1							1	3	9	8	4	1		
Mouth of Amazon	4						1		2		1						1	3		
Holotype of <i>dumerilii</i>	1						1										1			

P. altum (table 3); however, these differences are not great enough to enable me to identify all specimens on the basis of fin ray and scale counts, even if the dorsal and anal rays are added to the oblique scale rows to form a character index (table 4).

An examination of table 2, shows that the specimens of *P. dumerilii* collected near Belém, at the mouth of the Amazon have a slightly greater number of fin rays and scales than do specimens further up the Amazon—Río Negro systems.

The counts made on the holotype of *P. dumerilii* from Pará (now Belém) with XII,23 dorsal, VI,24 anal, 11 pectoral fin rays, and 30 scale rows along the side, fit into the higher end of the frequency distributions (table 2) for *P. dumerilii*; however, since the frequency distributions partly overlap for the various localities and the number of specimens are not sufficient to establish the extent of variability among populations, if such exist, I am recognizing only a single species, *P. dumerilii*.

P. dumerilii has been collected in the Amazon basin and in the Rupununi River of British Guiana (see open circles in map, pl. 1).

Pterophyllum altum Pellegrin

PLATE 3

Pterophyllum altum Pellegrin, 1903a, Bull. Mus. Hist. Nat. Paris, vol. 9, p. 125 [Rio Atabapo, Orinoco]; 1903b, Mem. Soc. Zool. France, vol. 16, p. 252, pl. 4, fig. 4 [Atabapo].—Regan, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 16, p. 442 [Rio Orinoco].—Eigenmann, 1910, Rep. Princeton Univ. Exped. Patagonia 1896–1899, vol. 3 (Zool.), pt. 4, p. 479 [Orinoco].—Ahl, 1928, Zool. Anz., vol. 76, p. 255 [Orinoco].—Schultz, 1949, Proc. U.S. Nat. Mus., vol. 99, p. 167 [Rio Atabapo]; 1953, Tropical Fish Hobbyist, vol. 1, no. 5, pp. 5–7, 20 [key to aquarium-bred angelfish].

Specimens studied (see page 2 for more precise locality): BMNH 1904–6–28–2–3, Rio Orinoco, 2 (59 and 60 mm); MNHN 221–61–1–3, Chaffanjon (Rio Atabapo), 5 syntypes of *P. altum* (42 to 62 mm); MNHN 221–61–1–1, Chaffanjon, 4 syntypes of *P. altum* (63 to 75 mm); MNHN 221–61–1–2, Chaffanjon, 5 syntypes of *P. altum* (59 to 65 mm); USNM 163204, Venezuela, 1 (79 mm); USNM 196007, Colombia, 1 (67 mm); CAS [no number], Rio Casiquiare, 1 (53 mm).

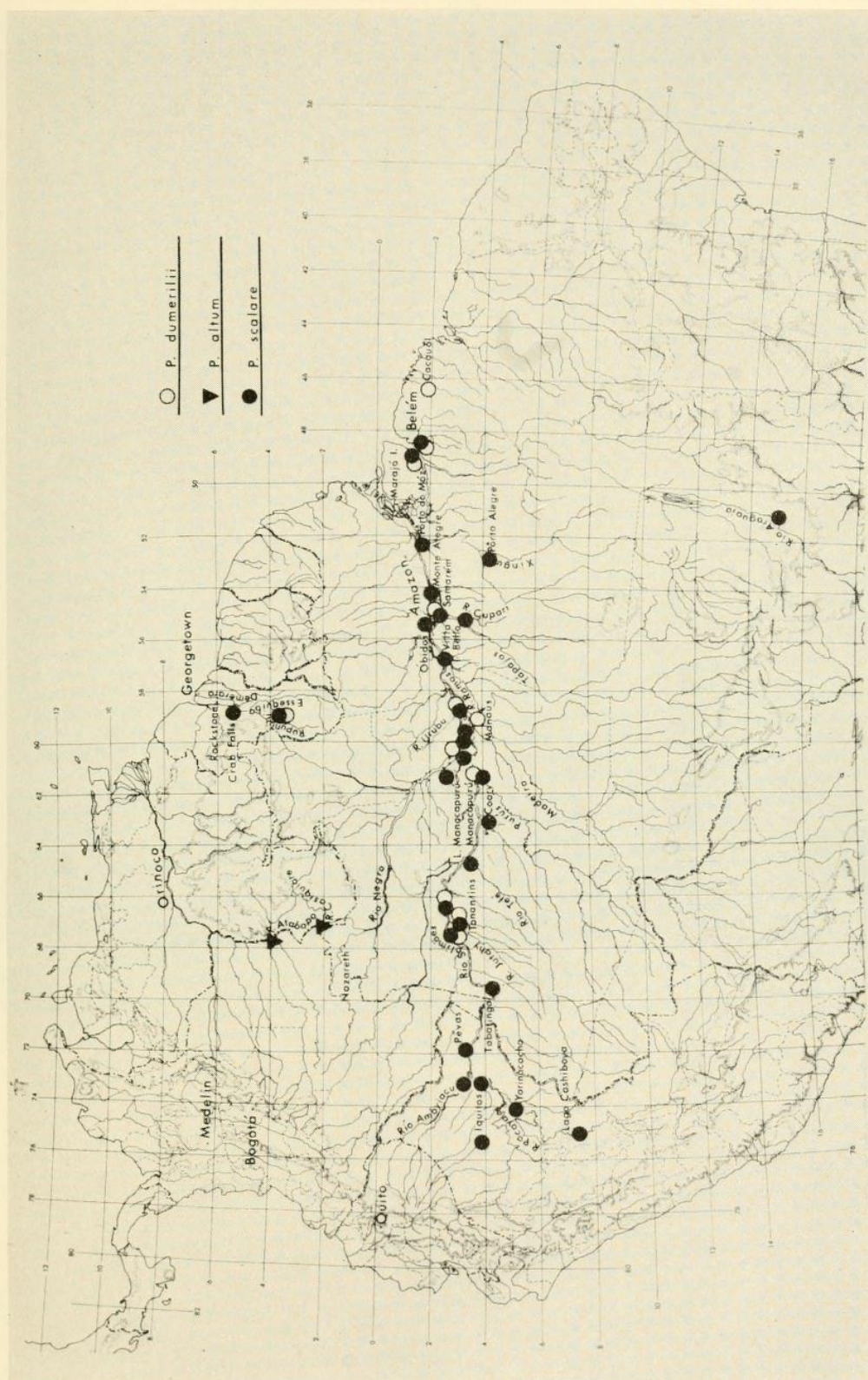
Pterophyllum altum Pellegrin has a color pattern identical with that of *P. scalare*; however, no black spot occurs on the upper midside as in *P. dumerilii*. The black bar through the eye curves dorso-posteriorly to the origin of the spiny dorsal and is not broken into three separate bars as in *P. dumerilii*.

This species is best recognized from *P. scalare* by the greater average number of median fin rays, oblique scale rows, and vertebrae (tables 1–4). Undoubtedly *P. altum* represents the *P. scalare* type of angelfish in the upper Orinoco, and in having a higher average number of dorsal, anal, oblique scale rows and vertebrae than *P. scalare*, it might be considered to represent only a subspecies of *P. scalare*; however, since *P. altum* has been taken so far only in the upper Orinoco basin, I prefer tentatively to recognize it as a distinct species.

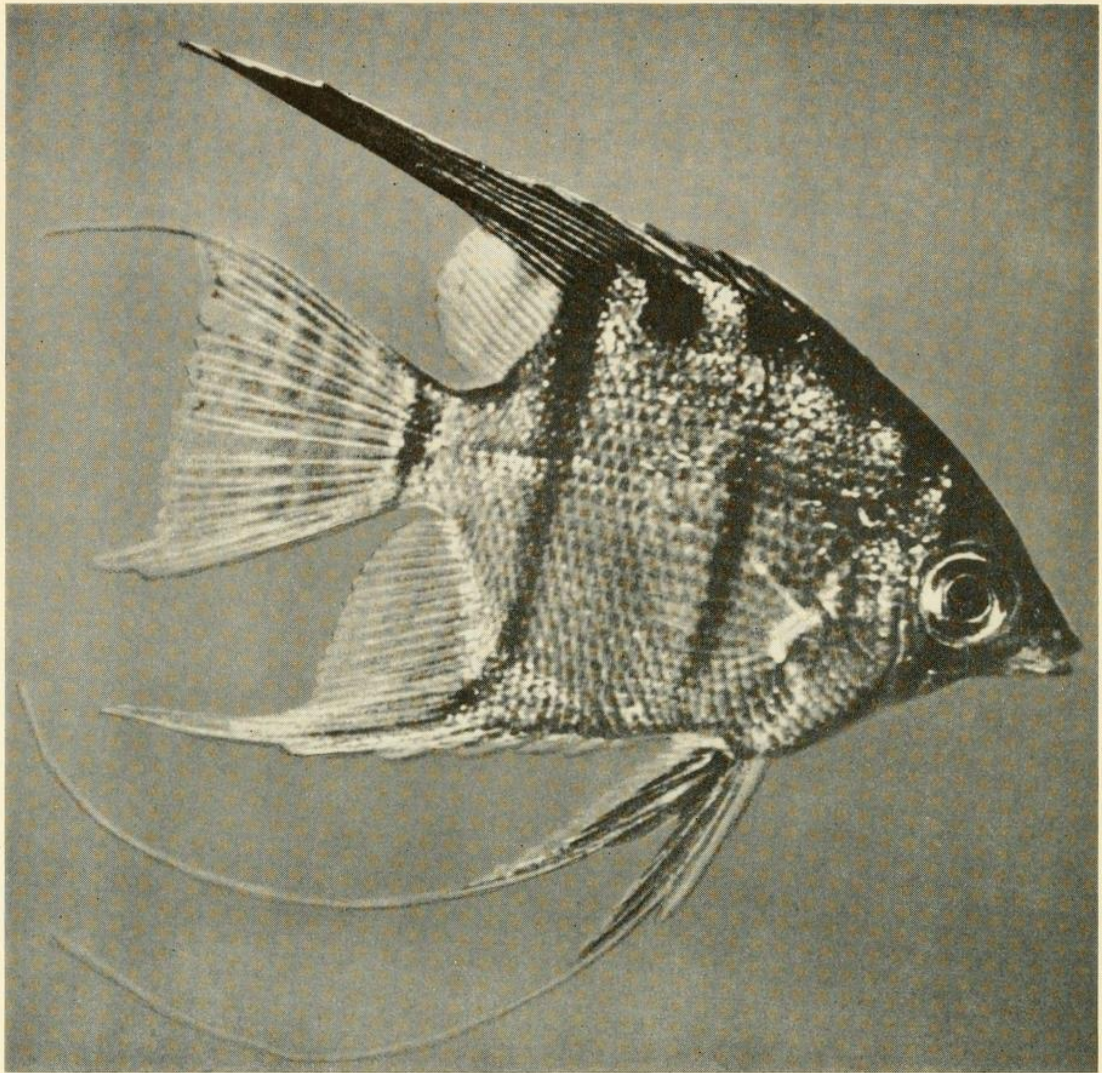
Pterophyllum scalare (Lichtenstein)

PLATE 4

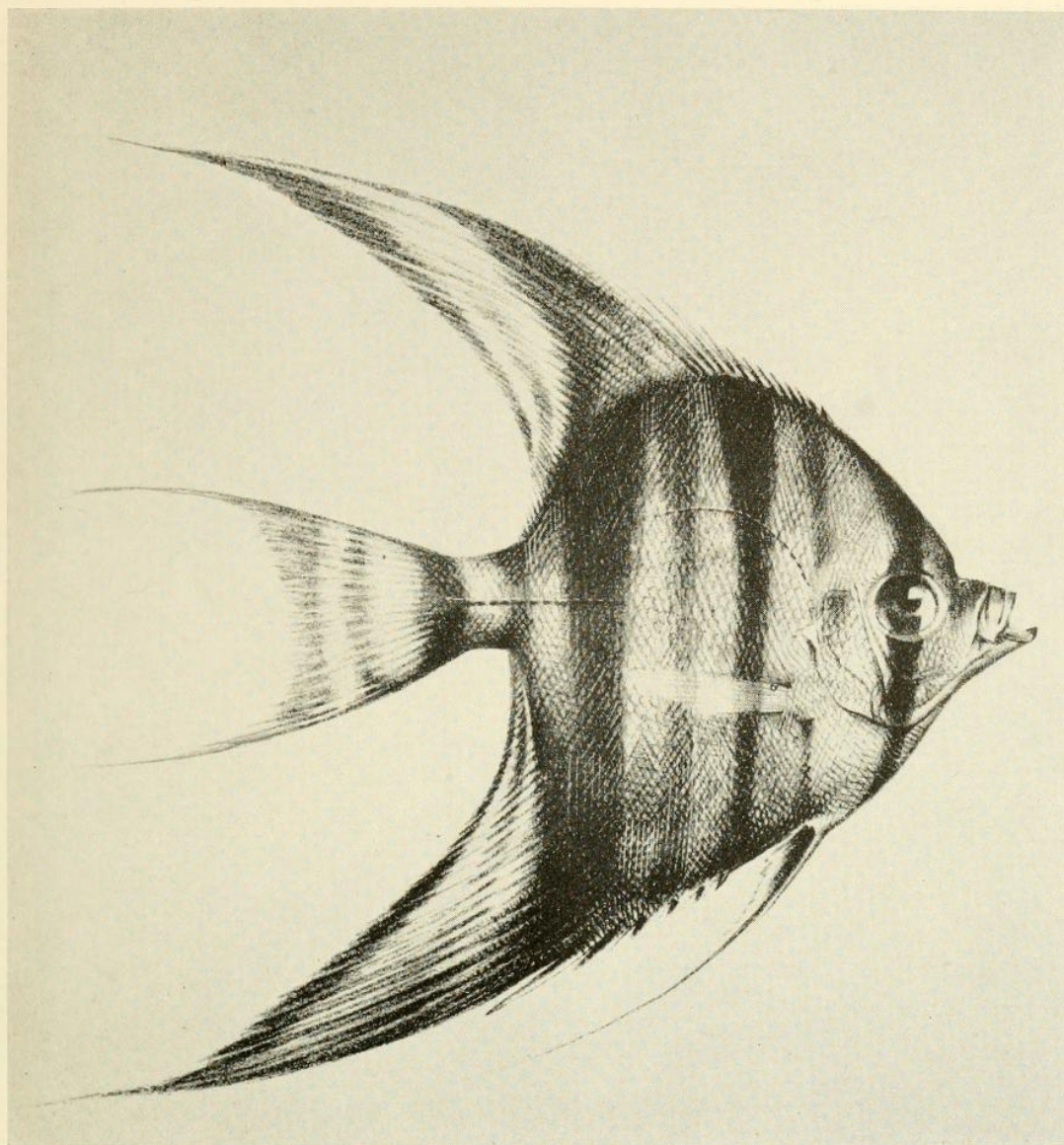
Zeus scalaris Lichtenstein, 1823, Verz. Doubl. Zool. Univ. Berlin, p. 114 [Brazil].
Platax scalaris Cuvier and Valenciennes, 1831, Histoire naturelle des poissons, vol. 7, p. 237 [Brazil, in "Collection de Bloch, au Musée de Berlin"].
Pterophyllum scalaris Heckel, 1840, Ann. Wien. Mus., vol. 2, p. 335, pl. 30, figs. 5, 6, 7–7a, 8–8b [Reo Negro].
Pterophyllum scalare Günther, 1862, Catalogue of the fishes in the British Museum, vol. 4, p. 316 [Rio Cupai; Brazil].—Kner, 1862, Sitz. Akad. Wiss. Wien., vol. 46, p. 295, pl. 1, figs. 1–1a.—Cope, 1872, Proc. Acad. Nat. Sci. Philadelphia, p. 250 [Rio Ambyiacu].—Steindachner, 1875, Sitz. Akad. Wiss. Wien., vol. 71, p. 76 [Amazon at Santarém, Monte Alegre, Villa Bella, Óbidos, Coary, Ueranduba, Tonantins, Tabatinga, Rio Jutahy, Xingu, Lago Manacapurú, Lago Maximo, Pará, Rio Ambyiacu; ?Barra do Rio Negro].—Eigenmann and Eigenmann, 1891, Proc. U.S. Nat. Mus., vol. 14, p. 71



Distributional map for species of *Pterophyllum*.



Pterophyllum dumerilii (Castelnau).



Pterophyllum altum Pellegrin.