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Evidence of a Second Species of *Synbranchus* (Pisces, Teleostei) in South America

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ABSTRACT

A new species of *Synbranchus* from the Amazon Basin is described and compared with sympatric and allopatric populations of *Synbranchus marmoratus* and with the cavernicolous synbranchid, *Furmastix infernalis*, from Yucatán. The new species and *marmoratus* are found to differ in metameric, morphometric, pigmentary, and osteological features. Variation in *marmoratus* from throughout its range is analyzed and discussed in relation to local and global temperatures and latitude.

INTRODUCTION

As presently understood, the New World Synbranchidae include two forms. One, *Synbranchus marmoratus* Bloch, is epigeal and has a vast range that extends from Mexico south to Argentina and includes many of the Antillean islands. The second, *Furmastix infernalis* (Hubbs), is cavernicolous and confined to the cenotes of Yucatán. The current taxonomy in which all New World epigeal populations of *Synbranchus* are referred to *marmoratus* dates from Günther (1856) who stated that: "The varieties of this widely distributed species are numerous, especially with regard to the width of the snout and head, form of the gill-opening, width of the palatine band of teeth, and coloration; but it is evident, from an examination of a

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long series of examples, that the differences are not specific.” The varieties that Günther wrote of were the basis for no fewer than 13 nominal species, as follows¹: *Synbranchus marmoratus* and *S. immaculatus* of Bloch (1795), from Surinam and Surinam or Tranquebar, India respectively; *S. transversalis* of Bloch and Schneider (1801), from Guinea; *Unibranchapertura grisea* and *U. lineata* of Lacépède (1803), from Surinam (Lacépède considered *S. marmoratus* Bloch as the type of *Unibranchapertura*); *Synbranchus fuliginosus* of Ranzani (1840), from Brazil; *S. pardalis* of Valenciennes (1847), from Buenos Aires; *Muraena lumbricus* of Gronow (1854) from the Sea of Guinea; *Synbranchus vittata* of Castelnau (1855), from Rio de Janeiro; *S. hieronymi*, *S. doringii*, *S. tigrinus*, and *S. mercedarius* of Weyenbergh (1877), all from Argentina. There is an unresolved confusion concerning the origin of forms originally attributed to Guinea or Tranquebar. Bloch and Schneider’s and Gronow’s Guinea localities were interpreted as errors by Günther, and Bloch’s mixed locality for *immaculatus* (Surinam and Tranquebar) must certainly be one or the other and can be clarified only by examination of the type.² Previous workers have assumed that the Surinam locality is the correct one and have included *immaculatus* in the synonymy of *marmoratus*, largely, it appears, on the strength of Günther’s original synonymy and his brief comments quoted above. Nevertheless, it is significant that of the 10 nominal species definitely attributable to the New World, eight have been well illustrated (those of Bloch, Ranzani, Valenciennes, Castelnau, and Weyenbergh) and each of these illustrations depicts a spotted or marmorated synbranchid. Lacépède’s nominal forms, *grisea* and *lineata*, never were represented by type material, are not figured, and are described in vague and imprecise terms. Bloch’s description of *immaculatus* is accompanied by an excellent figure that shows this animal to be a uniform gray-brown, not mottled, at least not so that the artist was aware of any spotting or speckling. In Bloch’s description, *immaculatus* is distinguished from *marmoratus* by the absence of spotting and by the looser or less adherent skin. Perhaps Bloch’s specimen may have deteriorated somewhat before he first saw it, and a poor state of preservation, suggested by the loose skin, may have accounted for the absence of a definable pigment pattern.

Although the numerous color variants of *Synbranchus marmoratus* are well known, it was the discovery of a distinctive gray form with a high verte-

¹ For the basis of all current synonymies, see Gunther (1854) and Ringuélet et al. (1967).

² Dr. Kurt Deckert, of the Institut für Spezielle Zoologie und Zoologisches Museum, Berlin, informs us that both of Bloch’s types are now lost.

bral number living together with typically mottled *marmoratus* that prompted the present study. The significant material was collected by Sydney Anderson and Reeve M. Bailey during the American Museum-Bolivian Expeditions of 1964 and 1965 to the upper part of the Río Madeira system of the Bolivian Amazon. Anderson, in 1965, collected the first seven sympatric specimens, of which three were *marmoratus* and four, the gray form. In 1964, Bailey collected three individuals from within a few miles of Anderson's material (see Materials and Methods), of which two were *marmoratus*, and one, the gray form. All seven of Anderson's specimens were taken from pools within a single small stream, whereas Bailey's mottled and gray fish were not taken together. When all of these specimens were radiographed, the gray forms were found to have eight to 15 more vertebrae than the highest number in the mottled specimens. Subsequent study showed that the gray and mottled samples from these two small collections differed also in head and body proportions and in some osteological features. Further comparisons of the original 10 specimens with material of *Synbranchus* from throughout its range, and particularly with specimens taken earlier by Pearson on the Mulford Expedition in the Bolivian portion of the Río Madeira drainage, have clarified the biological status of the gray and mottled forms in the region where they occur together. Of the 15 specimens collected by Pearson in November, 1921, two are of the undescribed gray type.¹

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¹ Pearson (1924) reported only 14. On the basis of counts and measurements given below we conclude that all 15 specimens (CAS 11259, 13704, 13705 and UMMZ 66373) are attributable to the same locality.

in the collection of synbranchid samples in northern Central America.

MATERIALS AND METHODS

Specimens from more than a hundred localities from Argentina north to Mexico and Cuba were studied. Costa Rica is the only political unit from which no material was examined. In the list given below by numbered stations, the samples from South America are arranged by river system or broad geographical area. The Río Amazonas is subdivided so that samples from the Río Madeira Basin are listed separately. Within each hydrographic or other division the samples are noted by country and alphabetically by province or department within the country. Latitude and longitude are given for each specific locality that had been confirmed in an atlas or gazetteer. Middle American samples are listed by country and the countries are arranged south to north. Each sample for which there is precise locality data is plotted on the drainage map in figure 1.

Each of the 380 specimens was taped down on its side and radiographed. Orbit and snout length were measured from the radiographs as the horizontal distance across the interior of the bony orbit and as the distance from the posterior wall of the anterior orbital rim to the tip of the ethmoid bone. In making the vertebral counts, the first caudal vertebra was taken as the first element in which the parapophyses were joined ventrally to form a hemal canal. Post-anal length of body was measured from the anus to the tail tip. Other measurements were attempted, such as head length and width, interorbital bony width, and gill opening to tip of lower jaw, but, with the exception of head length, the results of these measurements were too variable to be useful, as were also orbit and snout length when made directly from the specimen. Usable measurements and counts could not be made on every specimen as a result of slight imperfections in some parts of many of the radiographs. Cleared and alizarin-stained preparations were made from specimens from stations 25 through 28 (see below) after these specimens had been measured, radiographed, and photographed.

Radiographs of the type of *Furmastix infernalis* (Hubbs) (UMMZ 116093) also were examined.

Río Paraná System (Río Paraná, Río Paraguay, Río Uruguay)

Argentina

1. Buenos Aires; Distrito Federal; Buenos Aires (34° S, 58° 30' W); 1 spec. 400 mm.; USNM 176020.
2. Córdoba Province; Capital; Río Primero, 1 km. E. Va. Warcalde (31° S, 64° 10' W); 2 specs. 208 and 216 mm.; Univ. of Texas uncatalogued. Birkhead Nov. 28, 1968.
3. Córdoba; Capital; La Carahna 1-2 km. E. Va. Warcalde (31° S, 64° W);

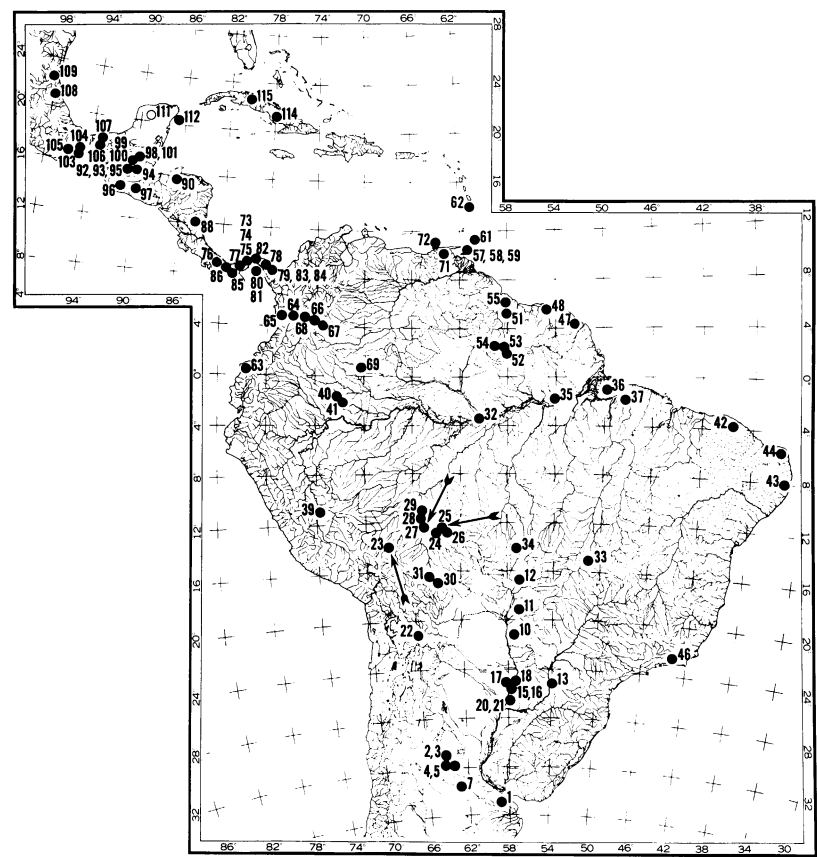


FIG. 1. Distribution by record stations of New World *Synbranchus*. Numbers correspond with those listed in Materials and Methods in text. Arrows indicate three localities from which *Synbranchus madeirae*, new species, was taken. Open circle in Yucatán Peninsula represents the single known locality (111) for the cavernicolous synbranchid, *Furmastix infernalis* (Hubbs). All other localities, except 25 where *S. madeirae* was taken alone, represent collections of *S. marmoratus* Bloch.

- 1 spec. 423 mm.; Univ. of Texas uncatalogued. Birkhead December 5, 1968.
4. Córdoba; Punilla; Río San Francisco at El Retiro (31° 11' S, 64° 29' W); 1 spec. 250 mm.; Univ. of Texas uncatalogued. Birkhead May 16, 1969.
5. Córdoba; Punilla; Río Cosquín at Bialet Massé (31° 19' S, 64° 28' W); 1 spec. 317 mm.; Univ. of Texas uncatalogued. R. Martori.
6. Córdoba; Santa María; Río Segundo at Despeñaderos (31° 45' S, 64° 15' W); 1 spec. 242 mm.; Univ. of Texas uncatalogued. Birkhead September 27, 1969.

7. Córdoba; Santa María; A° Los Quebrachos 2 km. E. Va. Serranita (33° 30' S, 63° W); 4 specs. in 3 lots 34 mm. to 252 mm.; Univ. of Texas uncatalogued. Birkhead Jan. 23, 1969, May 13, 1969.
8. Locality within country unknown; 1 spec. 485 mm.; BMNH 1922-5-23:11.

Uruguay

9. Locality within country unknown; 1 spec. 202 mm.; BMNH 1969-10-23:1.

Brazil

10. Mato Grosso; Río Branco, tributary of Río Paraguay (21° 20' S, 57° 30' W); 1 spec. 85 mm.; AMNH 1323.
11. Mato Grosso; Carandasinha, Río Taquari, tributary of Río Paraguay (19° S, 57° 15' W); 6 specs. 44 mm. to 97 mm.; BMNH 1900-4-14; 97-101.
12. Mato Grosso; Descalvado, Río Paraguay (17° S, 57° 30' W); 3 specs. 107 mm. to 182 mm.; BMNH 1895-5-17; 273-275.
13. Paraná; Foz do Iguaçu, near fork of Río Paraná and Río Iguaçu (25° 33' S, 54° 31' W); 1 spec. 89 mm.; USNM 179033.

Paraguay

14. Boquerón; swamp at Makthlawaiya, Paraguayan Chaco (coordinates unknown); 3 specs. 407 mm. to 605 mm.; BMNH 1927-11-23:69-71.
15. Central; Asunción (25° 15' S, 57° 40' W); 1 spec. 268 mm.; BMNH 1895-1-30:26.
16. Central; Asunción Bay, Río Paraguay, near Asunción (25° 15' S, 57° 40' W); 3 specs. 330 mm. to 667 mm.; USNM 181770.
17. Central; near Asunción (25° 15' S, 57° 50' W); 33 specs. 21.5 mm. to 152 mm.; BMNH 1935-6-4:474-492.
18. Central; Campo Grande (25° 13' S, 57° 35' W); 1 spec. 152 mm.; AMNH 1487.
19. Concepción; Estancia Samalday, 200 km. from Asunción (coordinates unknown); 1 spec. 317 mm.; BMNH uncatalogued (pres. by Stockholm Museum).
20. Paraguairí; Laguna Vera, Río Tebicuary drainage (26° 30' S, 58° 10' W); 1 spec. 476 mm.; USNM 181450.
21. Paraguairí; Arroyo Pachongo, Río Tebicuary drainage (26° 45' S, 58° W); 1 spec. 95 mm., USNM 181794.

Bolivia

22. Potosí; Caiza, Río Yura, tributary of Río Pilcomayo (22° S, 66° W); 2 specs. 362 mm. and 510 mm.; BMNH 1897-1-27; 104-105.

*Rio Madeira**Bolivia*

23. Beni; Reyes, Río Beni (14° 18' S, 67° 23' W); 8 specs. 79 mm. to 280 mm.; CAS 11259, 13704, 13705 and 7 specs. 79 mm. to 260 mm.; UMMZ 66373.¹
24. Beni; Río Baures, 400 meters above mouth in Río Itenez, 6 km. SW. of Costa Marques (12° 30' S, 64° 30' W); 1 spec. 340 mm.; UMMZ uncatalogued. Field no. B-64-49.²
25. Beni; Río Itenez and overflow pools along middle sand bar, 9 km. SE. of

¹ Specimens collected by N. E. Pearson, November, 1921, on the Mulford Expedition.

² Collected by R. M. Bailey and R. Reimos, October 3, 1964.

- Costa Marques (12° 30' S, 63° 30' W); 1 spec. 136 mm.; AMNH 30219.¹
26. Beni; pool in grassy swale on Pampa de Meio, *ca.* 12 km. SE. of Costa Marques (12° 30' S, 63° W); 1 spec. 75 mm.; UMMZ uncatalogued. Field no. B64-28.²
27. Beni; pools and riffles of small stream between Nuevo Berlin and Mayo Mayo, Río Mamoré (12° 26' S, 65° 10' W); 3 mottled specs. 110 mm. to 141 mm., AMNH 30213; 4 gray specs. 93 mm. to 142 mm., AMNH 30214.³
28. Beni; Santa Rosa, Río Mamoré (11° 41' S, 65° 17' W); 1 spec. 146 mm.; AMNH 20636.
29. Beni; Guajara-Mirim, Río Mamoré (11° S, 65° 30' W); 3 specs. 290 mm. to 530 mm.; USNM 133134.
30. Santa Cruz; Buena Vista, Río Palacios, tributary of Río Mamoré (17° 28' S, 63° 37' W); 1 spec. 197 mm.; BMNH 1927-10-4:45.
31. Santa Cruz; Sara, Río Grande, tributary of Río Mamoré (17° S, 64° W); 1 spec. 226 mm.; BMNH 1907-10-31:79.

Rio Amazonas Drainage excluding Río Madeira

Brazil

32. Amazonas; Manacapuru, Río Solimões Amazonas, left bank, (3° 16' S, 60° 37' W); 1 spec. 417 mm.; BMNH 1925-10-28:24.
33. Goiás; Río Araguaia, tributary of Río Tocantins, near Aruana (15° S, 51° W); 1 spec. 270 mm., USNM 191596.
34. Mato Grosso; Primavera, Alto Paraguay, Río Agua Verde, tributary of Río Arinos-Río Juruena, about 1500 km. upstream from confluence of Río Tapajos and Río Amazonas (14° 05' S, 56° 54' W); 6 specs. 75 mm. to 125 mm.; BMNH 1956-1-16:2-7; 1 spec. 135 mm.; BMNH 1956-1-16:1.
35. Pará; Monte Alegre, on Río Maicuru about 30 km. upstream from confluence of Río Maicuru and Río Amazonas (2° S, 54° 04' W); 1 spec. 78 mm.; BMNH 1926-10-27:412.
36. Pará; Ilha do Marajó (0-2° S; 49-51° W); 1 spec. 218 mm.; BMNH 1923-8-11:44-45.
37. Pará; Belém, where Río Capem empties into Río do Pará (1° 27' S, 48° 29' W); 1 spec. 171 mm., USNM 200300; 2 specs. 89 mm. to 121 mm., USNM 200302.
38. Pará; locality within state unknown; 1 spec. 485 mm.; BMNH uncatalogued, collector R. Graham.

Peru

39. Cuzco; Osherato, stream tributary to Río Tambo, about 900 km. upstream from confluence of Río Ucayali and Río Marañon (11° 12' S, 73° 56-57' W); 1 spec. 380 mm.; AMNH 20859.
40. Loreto; mouth of Río Ampiyacu (3° S, 72° W); 1 spec. 311 mm.; USNM 124881.
41. Loreto; Pébas, Río Amazonas, left bank (3° S, 71° 30' W); 2 specs. 450 mm. to 760 mm.; BMNH 1867-9-7:34-35.

East Coastal Brazil (Atlantic Drainage)

42. Ceará; Reservoir at Pentecoste (3° 49' S, 39° 18' W); 44 specs. in 4 collections

¹ Same collectors as in station 24, September 15-16, 1964.

² Collected by R. M. Bailey, September 14, 1964.

³ Collected by S. Anderson, October 9, 1965.

54 mm. to 607 mm.; USNM uncatalogued. Collector J. S. Dendy and V. Fronca, collecting station nos. P-2, P-3, P-4, P-5.

43. Pernambuco; Recife (8° S, 35° W); 3 specs. 380 mm. to 435 mm.; BMNH uncatalogued. (J. P. G. Smith.)
44. Río Grande do Norte; Ceará Mirim, Río Ceará Mirim (5° 30' S, 35° 25' W); 2 specs. 352 mm. and 435 mm.; AMNH 3780.
45. Río Grande do Norte; locality within state unknown, 1 spec. 226 mm.; USNM 126666.
46. Rio de Janeiro; Rio de Janeiro (22° 53' S, 43° 17' W); 1 spec. 125 mm.; USNM 129916.

Northern South America

French Guiana

47. Guyane; Cayenne, Cayenne River (5° N, 52° 18' W); 1 spec. 335 mm.; BMNH 1846-2-16.

Surinam

48. Marowine; Moengo (5° 36' N, 54° 25' W); 1 spec. 635 mm.; USNM 86319.
49. Locality within country unknown (2-6° N, 54-58° W); 1 spec. 810 mm.; BMNH 1870-3-10:45.

Guyana

50. Berbice; locality within department unknown; 2 specs. 273 mm. and 550 mm.; BMNH 1853-4-6:80-82.
51. Demerara; Wismar, on Demerara River, 50 mi. S. of Georgetown (5° 58' N, 58° 36' W); 2 specs. 112 mm. and 115 mm.; AMNH 30216.
52. Essequibo; Marudi, on tributary of Kwitaro River (2° 10' N, 59° 10' W); 1 spec. 285 mm.; AMNH 17638.
53. Essequibo; Marudi Mountains, drained by tributaries of Kwitaro River (2° 20' N, 59° 20' W); 1 spec. 108 mm.; AMNH 17628.
54. Essequibo; Upper Rupununi River (3° N, 59° 30' W); 1 spec. 350 mm.; AMNH 17604.
55. Essequibo; Rockstone, Essequibo River (6° N, 58° 30' W); 1 spec. 215 mm.; AMNH 16878.
56. Locality within country unknown; 1 spec. 260 mm.; BMNH 1862-12-15:82; 1 spec. 565 mm.; AMNH 4571.

Trinidad

57. Nariva; boat canal leading into Nariva swamp (10° 20' N, 61° 05' W); 1 spec. 69 mm.; AMNH 26386.
58. St. George; Simla, Arima Valley (10° 50' N, 61° 20' W); 2 specs. 222 mm. and 550 mm.; AMNH 30218.
59. Province unknown; Tucker Valley; 9 specs. 76 mm. to 552 mm.; USNM 136042.
60. Locality on island unknown; 1 spec. 570 mm., BMNH 1891-7-3:12; 1 spec. 500 mm., BMNH 1866-4-25:9; 2 specs. 435 mm. and 503 mm., BMNH 1906-6-23:1-2.

Tobago

61. Locality on island unknown (11°-11° 20' N, 60° 30'-61° W); 1 spec. 400 mm.; BMNH 1922-6-22:2.

St. Lucia

62. Locality on island unknown (13° 45'-14° 10' N, 61°-61° 20' W); 1 spec. 376 mm.; BMNH 1852-8-12:30.

*Northwestern South America**Ecuador*

63. Esmeraldas; Esmeraldas, mouth of Río Esmeraldas (0° 56' N, 79° 40' W); 1 spec. 253 mm.; BMNH 1924-4-17:4.

Colombia

64. Caldas; Río Condoto (5° N, 76° W); 8 specs. 115 mm. to 635 mm.; BMNH 1914-5-18:112-113 and BMNH 1913-10-1:98-99.
65. Choco; Andagoya, Río San Juan (5° N, 77° W); 1 spec. 305 mm.; BMNH 1915-10-1:20.
66. Cundinamarca; Bogotá (4° 38' N, 74° 05' W); 1 spec. 386 mm.; BMNH 1868-3-4:3.
67. Meta; Villavicencio (4° 09' N, 73° 38' W); 1 spec. 235 mm.; USNM 120528.
68. Tolima; Ibagué (4° 35' N, 75° 30' W); 1 spec. 102 mm.; USNM 120528.
69. Vaupés; Mitu (1° 07' N, 70° 05' W); 1 spec. 156 mm.; USNM 257403.
70. Locality within country unknown; 1 spec. 359 mm.; USNM 120526.

Venezuela

71. Monagas; Caicara, small feeder brook into Río Guarapiche (9° 52' N, 63° 38' W) 1 spec. 289 mm.; USNM 163183 (broken tail).
72. Nueva Esparta; stream of Río Matasiete near La Asunción (11° 06' N, 63° 53' W) 1 spec. 451 mm.; USNM uncatalogued, collected January 21, 1967 by Smith, Venezuela project.

Panama

73. Canal Zone; Barro Colorado Island in Gatun Lake (9° 10' N, 79° 50' W); 1 spec. 260 mm.; AMNH 30215.
74. Canal Zone; near Cocoli (8° 58' N, 79° 36' W); 1 spec. 264 mm.; USNM uncatalogued, collected Mar. 5, 1967 (no collector).
75. Canal Zone; Río Corderas (8° 58' N, 79° 36' W); 1 spec. 105 mm.; USNM uncatalogued, collected April 16, 1962 by Loftin and Tyson.
76. Chiriquí; creek into Río Jaques near San Lorenzo; 1 spec. 163 mm.; USNM uncatalogued, collected by Loftin, Tyson, Gale, Roquebert, December 9, 1961.
77. Colon; Río Coclé del Norte (9° 06' N, 80° 45' W); 1 spec. 203 mm.; USNM 112564.
78. El Darien; Río Subcuti, tributary of Río Chucunaque-Río Tuira into Gulf of Panama (8° 45' N, 78° W); 8 specs. 67 mm. to 405 mm.; AMNH 11370, AMNH 11374, AMNH 11373.
79. El Darien; Río Tapia, tributary of Río Subcuti (see above, Gulf of Panama drainage) (8° 30' N, 77° 45' W); 3 specs. 94 mm. to 440 mm.; AMNH 11234, AMNH 8305.
80. Pearl Islands; San Jose Island, headwaters of WNW stream (8° 20' N, 79° 10' W); 5 specs. 83 mm. to 425 mm.; USNM 128477.
81. Pearl Islands; San Jose Island; Olive Road Crossing (8° 20' N, 79° 10' W); 61 specs. 76 mm. to 603 mm.; USNM 128514.
82. San Blas, Río Acle (8° 40' N, 77° 23' W); 1 spec. 873 mm.; USNM uncata-

logged, collector and date unknown.

83. San Blas, Arnila (8° 40' N, 77° 23' W); 1 spec. 225 mm.; USNM 197920.
84. San Blas; Caledonia Bay, Atlantic coast (8° 50' N, 77° 40' W); 1 spec. 245 mm.; AMNH 11190.
85. Veraguas; Río Martin Chiquita, 7 mi. S of Santiago on Montigo Rd.; 2 specs. 114 mm. to 197 mm.; USNM uncatalogued, coll. by Loftin et al. Jan. 1962.
86. Veraguas; creek 13 mi. W of ocean rd. on Inter-American Highway; 1 spec. 314 mm.; USNM uncatalogued, collected by Loftin and Tyson October 21, 1961.
87. Locality within country unknown; 1 spec. 210 mm.; USNM 2923.

Nicaragua

88. Bluefields; Río Escondido, 50 mi. from Bluefields (12° N, 84° 30' W); 3 specs. 222 mm. to 267 mm.; USNM 44310, USNM 44309, USNM 44308.
89. Locality within country unknown; 5 specs. 76 mm. to 102 mm.; USNM 6970.

Honduras

90. Colon; Balfate, Gulf of Honduras drainage (15° 46' N, 86° 21' W); 1 spec. 660 mm.; AMNH 17870.
91. Olancho; Río Segovia, Atlantic drainage; 1 spec. 460 mm.; USNM 39390.

Guatemala

92. Alta Verapaz; Arroyo Batzulup about 200 meters above mouth in Río Chixoy, 2 km. upstream from Rubelolom (15° 51' N, 90° 43' W); 2 specs. 81 mm. and 279 mm.; AMNH 25470.
93. Alta Verapaz; Río Dolores along shore at Yaxcabnal (16° N, 90° 10' W); 1 spec. 148 mm.; AMNH 30217.
94. Alta Verapaz; Río de la Pasión and creek mouth 4 km. downstream from Sebol (16° N, 90° W); 1 spec. 90 mm.; AMNH 24515.
95. El Quiché; Arroyo de Dante into upper Río Chixoy (16° 01' N, 90° 41' W); 2 specs. 89 mm. and 172 mm.; AMNH 25403.
96. Escuintla; Laguna Encantada, 9 km. E. of Escuintla on Finca El Salto (14° 15' N, 91° W); 5 specs. 412 mm. to 660 mm.; AMNH 24465.
97. Jutiapa; Laguna Atescatempa (14° 12' N, 89° 42' W); 8 specs. in 2 lots, 175 mm. to 349 mm.; USNM 134646, USNM 134647.
98. Petén; Tikal Reservoir at Tikal Ruins near Río Folmui, tributary of Río Bravo (17° 15' N, 89° 40' W); 2 specs. 205 mm. and 333 mm.; Univ. Minn. uncatalogued. (Collector D. Puleston, August, 1968.)
99. Petén; Sulphur spring entering west into lower end of Laguna Petexbatún (16° 27' N, 90° 12' W); 1 spec. 265 mm.; AMNH 25145.
100. Petén; Arroyo Yaxtunilá 8 km. from Río de la Pasión; (16° 36' N, 90° 16' W); 1 spec. 310 mm.; AMNH 25187.
101. Petén; Lago Petén Itza (17° N, 89° 45'-90° W); 1 spec. 520 mm.; BMNH 1864-1-26:370.
102. Locality within country unknown; 1 spec. 172 mm.; AMNH 24651; 1 spec. 475 mm.; BMNH 1864-1-26:329.

Mexico

103. Oaxaca; Tehuantepec (16° 21' N, 95° 13' W); 2 specs. 95 mm. and 191 mm.; USNM 120367.
104. Oaxaca; Santo Domingo (also called Petapa), 500-600 ft. elevation, drained

- by tributaries of Río Sarabia, tributary of Río Coatzacoalcos (17° N, 95° W); 1 spec. 252 mm.; AMNH 20305.
105. Oaxaca; Juquila Mixes, 4000 ft. elevation, drained by tributaries of Río Trinidad, tributary of Río San Juan (17° N, 96° W); 1 spec. 266 mm.; AMNH 26271.
106. Tabasco; Teapa, Río Teapa (17° 30' N, 93° W); 1 spec. 430 mm.; BMNH 1913-6-21:225.
107. Tabasco; Tapijulapa (18° 30' N, 92° 45' W); 1 spec. 337 mm.; USNM 4415.
108. Vera Cruz; Santa Maria (21° N, 98° W); 1 spec. 476 mm.; USNM 45481.
109. Vera Cruz; San Lorenzon on Río Chiquita, from marshy pool at Potrero Nuevo (22° 30' N, 98° W); 1 spec. 175 mm.; USNM 132417.
110. Vera Cruz; locality within state unknown; 3 specs. 216 mm. to 605 mm.; USNM 163604, BMNH 1864-1-26:106, BMNH uncatalogued (collected by Cuming).
111. Yucatán; Hoctun, Hoctun Cave in subterranean pool (21° N, 89° W); 1 spec. 325 mm.; UMMZ 116093, *Furmastix infernalis* (originally *Pluto infernalis*) holotype.
112. Yucatán; Cozumel Island (20° 45' N, 87° W); 3 specs. 270 mm. to 318 mm.; USNM 127047.
113. Locality within country unknown; 7 specs. 228 mm. to 675 mm.; BMNH 1856-3-17:37, BMNH 1869-12-5:1-2, USNM 86210.

Cuba

114. Camagüey; 9 km. W. of Camagüey (21° N, 78° W); 1 spec. 510 mm.; AMNH 19584.
115. Las Villas; Santa Clara, Baños de Ciego Montero, note with AMNH 8817 collection that water temperature was 98° F. (22° 45' N, 80° W); 15 specs. 131 mm. to 462 mm.; AMNH 8817, AMNH 3286, AMNH 18683.
116. Locality within country unknown; 1 spec. 702 mm.; USNM 43105.

Synbranchus madeirae, NEW SPECIES

Figures 2-8, 12-18, 21-26, 28, 29; table 1

Synbranchus marmoratus: PEARSON, 1924, p. 50 (material from Reyes, in part; individuals 212 mm. and 280 mm. only).

MATERIAL: Holotype, a presumed adult¹ 280 mm. in total length, CAS 13704, from locality 23, above. From the same locality, taken with the holotype, a fish 212 mm., CAS 13705. Five additional specimens 93 mm. to 142 mm. from localities 25 and 27, AMNH 30219, 30214.

DIAGNOSIS: A gray or clouded *Synbranchus* with a broad pale band middorsally, bordered by slender, dark lines and a series of whitish spots; with a relatively large orbit (16 or 17 percent of head length in adults), long caudal peduncle (35 to 37 percent of total length), and numerous

¹ Breder (1927) noted that, in Panamanian *Synbranchus*, the examples available to him in excess of 240 mm. were either ripe or spent adults, and he inferred from growth curves that all individuals of more than about 200 mm. are sexually mature.

TABLE 1
MERISTIC AND MORPHOMETRIC DATA ON *Synbranchus madeirae*, NEW SPECIES
FROM THE RIO MADEIRA SYSTEM, BOLIVIA

	Measurements			Proportional Measurements								Number of		
	Mm.			Percent								Vertebrae		
	TL	CL	HL	CL/TL	HL/TL	HL/PL	HL/CL	OL/HL	PO/HL	OL/PO		A	C	T
Río Beni														
CAS 13704	280	100	20.5	36	7.3	11.4	20.5	16.0	16.0	100.0		89	65	154
CAS 13705	212	75	16.5	35	7.8	12.0	22.0	16.8	16.8	100.0		91	70	161
Río Mamoré														
AMNH 30214	142	52	11.0	37	7.7	12.2	21.1	18.9	18.0	104.8		86	71	157
	134	50	10.4	37	7.8	12.4	20.8	19.5	17.8	109.2		89	73	162
	114	40	8.5	35	7.4	11.5	21.2	19.5	18.8	103.4		89	72	161
	93	34	7.5	37	8.1	12.7	22.0	18.0	16.4	110.0		91	72	163
AMNH 30219	136	48	10.0	35	7.3	11.2	20.8	19.6	17.4	112.9		90	72	162

Symbols: TL = total length; CL = caudal length; HL = head length; PL = precaudal length (the difference between TL and CL); OL = orbit length in arbitrary units; PO = preorbital length in arbitrary units; measurements for ratios OL/HL, PO/HL, and OL/PO based on same arbitrary units derived from comparably enlarged radiographs of head; A = abdominal vertebrae; C = caudal vertebrae; T = total vertebrae.

vertebrae (154 to 163); dorsal tip of cleithrum at level of fifth or sixth vertebra; neural spines of the abdominal region long and slender, longer than the distance between any two succeeding spines, and the parietal bones rounded anteriorly, never rectangular. Snout pointed in dorsal profile; fleshy upper lip not expanded; nuchal region not elevated.

DESCRIPTION AND COMPARISONS: Detailed meristic and morphometric data are given in table 1 and figures 2-8, 12-14, 28, 29. In coloration, the holotype (figs. 15, 16), and the 212 mm. individual taken with it at Reyes are similar. The sides of the body and head are covered with small, close-set, punctate melanophores that are interrupted by vaguely delimited clear areas here and there irregularly to produce a clouded, rather than marbled or mottled, pattern. Dorsally on the head the wash of dark pigment is also interrupted by unpigmented areas in the form of stripes or spots corresponding with the positions of cephalic lateral line sense organs or canals. A post-ocular streak of deep-lying dark pigment extends backward and slightly downward to a point beyond the angle of the jaw. Ventrally on the head there is a sparse scattering of melanophores, two narrow concentrations of dark pigment in the gular region, and another at the tip of the lower jaw. Ventrally on the body, pigment is present only as a fine open stippling of tiny punctate melanophores. Dorsally there is a pale band passing backward from just behind the head nearly to the tail tip (figs. 16, 17B). The dorsal band is made up of fine, evenly distributed melanophores that are simply less concentrated than are those on the sides. The band is bordered by dark lines of deeper pigment, apparently in the myosepta, and is divided in half anteriorly by a fainter central line of deep, dusky pigment. A series of pale spots or ocelli lie just over the inner edge of the dark pigment border. In the smaller examples of *madeirae* from the Río Mamoré, body pigment is uniform dark gray that fades to pale gray ventrally and the dorsal band is set off more strongly. Only on the tail of the largest specimen from the Río Mamoré (142 mm.) is the clouded pattern at all evident. In both large and small individuals there is a thin, exceedingly delicate line of deep pigment midlaterally, presumably in the horizontal septum. In two individuals from the Río Mamoré the middorsal pigment on the head is present as a darker band from snout tip to occiput (figs. 17B, 18B).

Synbranchus marmoratus of more than 80 mm., in contrast is invariably speckled, spotted, or blotched on some part of the body, most consistently on the side and underpart of the head (figs. 17A, 18A, 19, 20). Even when *marmoratus* occurs in its dark phase (fig. 20), occasionally in samples from Panama south and uniformly in northern Central American and Mexican populations, the spotting is still present along with the darker ground

TABLE 2
MERISTIC AND MORPHOMETRIC DATA ON *Synbranchus marmoratus*
FROM THE RIO MADEIRA SYSTEM, BOLIVIA

	Measurements			Proportional Measurements										Number of		
	Mm.			Percent										Vertebrae		
	TL	CL	HL	TL	HL	TL	HL	PL	HL	CL	OL	HL	PO	HL	OL	PO
Río Beni																
UMMZ 66373	260	81	19.0	31	7.3	10.6	23.4	12.2	16.4	74.3	77	65	142			
	169	52	11.5	31	6.8	9.8	22.1	16.4	17.0	96.4	75	63	138			
	138	42	9.0	30	6.5	9.4	21.4	15.7	19.4	81.3	79	65	144			
	97	32	7.0	33	7.2	10.8	21.9	15.8	16.9	93.4	79	66	145			
	86	27.5	6.5	33	7.5	11.1	23.6	17.3	17.9	96.7	76	63	139			
	85	27.5	6.5	32	7.6	11.3	23.6	15.6	18.0	86.7	79	69	148			
	79	26.5	6.0	34	7.6	11.4	22.6	17.6	18.6	94.8	77	66	143			
CAS 11259	140	44	10.5	31	7.5	10.9	23.9	17.6	18.0	97.9	79	60	139			
	130	44	9.5	34	7.3	11.0	21.6	17.4	17.4	100.0	80	61	141			
	86	28	6.5	33	7.5	11.2	23.2	15.7	19.8	79.4	80	62	142			
	83	27.5	6.2	33	7.5	11.2	22.5	17.3	18.6	93.2	80	64	144			
	80	27	6.0	34	7.5	11.3	22.2	16.4	18.4	89.3	81	63	144			
	79	27	6.0	34	7.6	11.5	22.2	15.8	19.9	79.4	79	65	144			

TABLE 2—(Continued)

	Measurements			Proportional Measurements							Number of		
	Mm.			Percent							Vertebrae		
	TL	CL	HL	CL/TL	HL/TL	HL/PL	HL/CL	OL/HL	PO/HL	OL/PO	A	C	T
Río Mamoré													
AMNH 20636	146	45	10.0	31	6.8	9.9	22.2	12.6	18.2	69.5	88	60	148
AMNH 30213	141	45	9.5	32	6.7	9.9	21.1	12.1	18.3	66.3	84	62	146
	113	36	8.2	32	7.2	10.6	22.8	14.3	17.4	82.7	84	62	146
	110	34	—	31	—	—	—	—	—	67.0	83	63	146
USNM 133134	530	112	—	21	—	—	—	—	—	—	96	49	145
	430	108	—	25	—	—	—	—	—	—	92	57	149
	290	73	19.1	25	6.6	8.8	26.2	13.4	20.0	67.0	92	45	137
BMNH													
1927-10-4:45	197	50	—	25	—	—	—	—	—	—	92	55	147
BMNH													
1907-10-31:79	226	52	15.5	23	6.8	8.9	29.8	13.6	19.8	68.9	89	37	126

Symbols: TL = total length; CL = caudal length; HL = head length; PL = precaudal length (the difference between TL and CL); OL = orbit length in arbitrary units; PO = preorbital length in arbitrary units; measurements for ratios OL/HL, PO/HL, and OL/PO based on same arbitrary units derived from comparably enlarged radiographs of head; A = abdominal vertebrae; C = caudal vertebrae; T = total vertebrae.

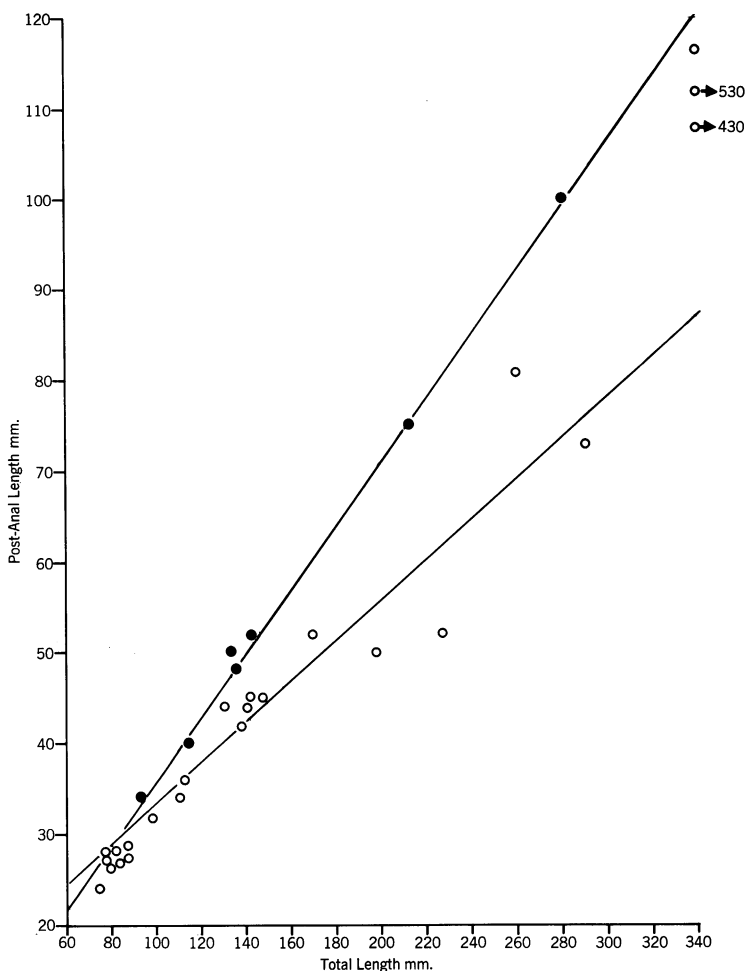


FIG. 2. Graph of relationships of post-anal length of body and total length in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from the Rio Madeira system in Bolivia. Plotted regressions intersect at a total length of 75 mm. Post-anal length of two large individuals of *S. marmoratus* (430 and 530 mm.) fall beyond limits of graph and are identified by open circles and arrows at upper right.

color. The ground color of the southern light phase is typically pale cream or yellow. Young *marmoratus* of less than 80 mm. are lightly to heavily pigmented with fine, punctate melanophores and closely resemble the young of *madeirae*. Unlike *madeirae*, however, they do not have a distinct

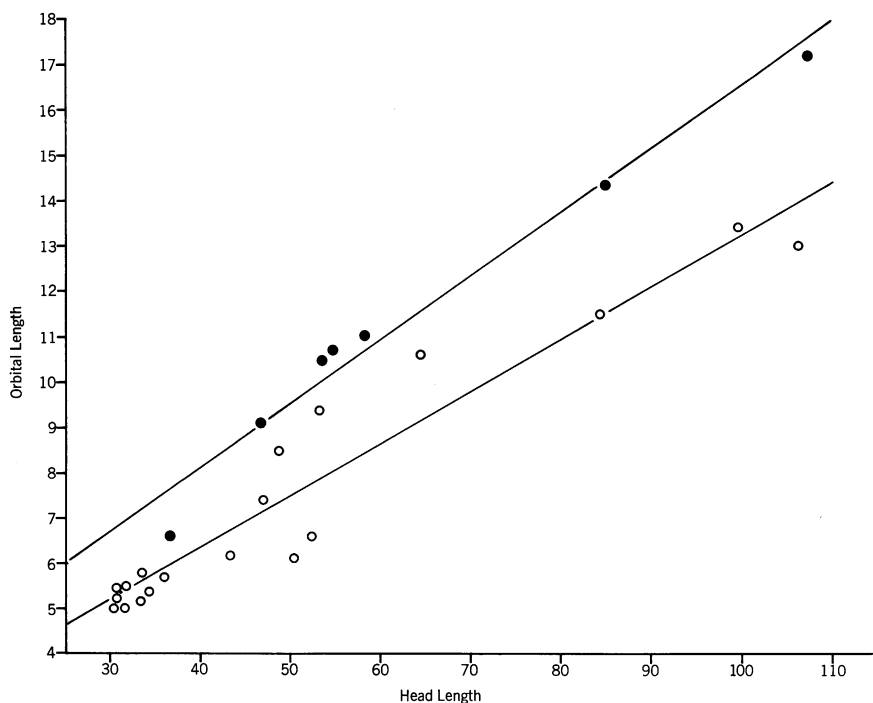


FIG. 3. Graph of relationships of orbital length and head length measured in arbitrary units from enlarged radiographs in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

light middorsal band. Many *marmoratus* also lack the post-ocular streak that is present in each specimen of *madeiraae*.

Although the sample of *madeiraae* is small, and it is unwise to make too many generalizations, there are numerous other differences between *madeiraae* and *marmoratus* from the Río Madeira Basin that may prove to be constant. For example, no specimen of *madeiraae* has a nuchal hump, although this hump (figs. 19, 20) is present in most examples of *marmoratus* of more than 200 mm. The upper lip in *marmoratus* of more than 100 mm. is enlarged anterolaterally to give the tip of the snout a blunt aspect in dorsal view, whereas the upper lip in all of our *madeiraae* is not greatly enlarged or noticeably swollen and the snout is slender (fig. 18). The dorsal tip of the cleithrum in *marmoratus* extends upward at the level of the fourth or fifth vertebra, rather than at the level of the fifth or sixth as in *madeiraae* (fig. 21). The posterior cone of the central ossification in the vertebrae of *marmoratus* is much longer than wide, whereas in *madeiraae* the two dimen-

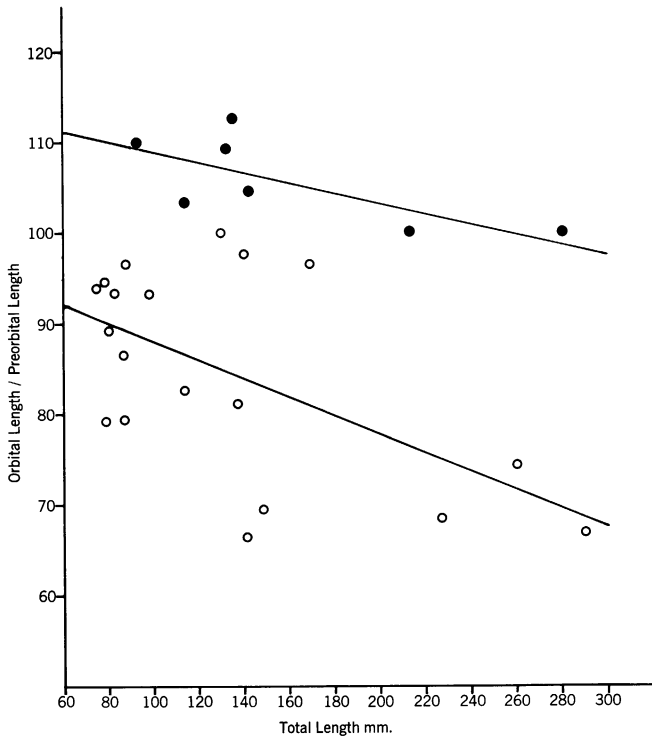


FIG. 4. Graph of relationships of ratio, orbital length/preorbital length, and total body length in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

sions are subequal, and the shorter and stouter neural spines of *marmoratus* are relatively more widely spaced in consequence (figs. 21, 22). Another correlate of difference in vertebral length is that southern and central South American *marmoratus* have a relatively longer abdominal region although they have modally fewer abdominal vertebrae than does *madeirae*. The two species appear to differ also in the shape and size of the prezygapophyses on the vertebrae of the abdominal region: they are short and blunt in *marmoratus* and longer, more slender, and with upturned, sharply tapering distal ends in *madeirae* (fig. 22).

In addition, the two forms differ in the shape and development of the parietals and to a lesser extent in the form of many of the roofing and other bones of the skull and branchial skeleton, and in a variety of morphometric and meristic traits (see figs. 23–26, tables 1, 2, and discussion

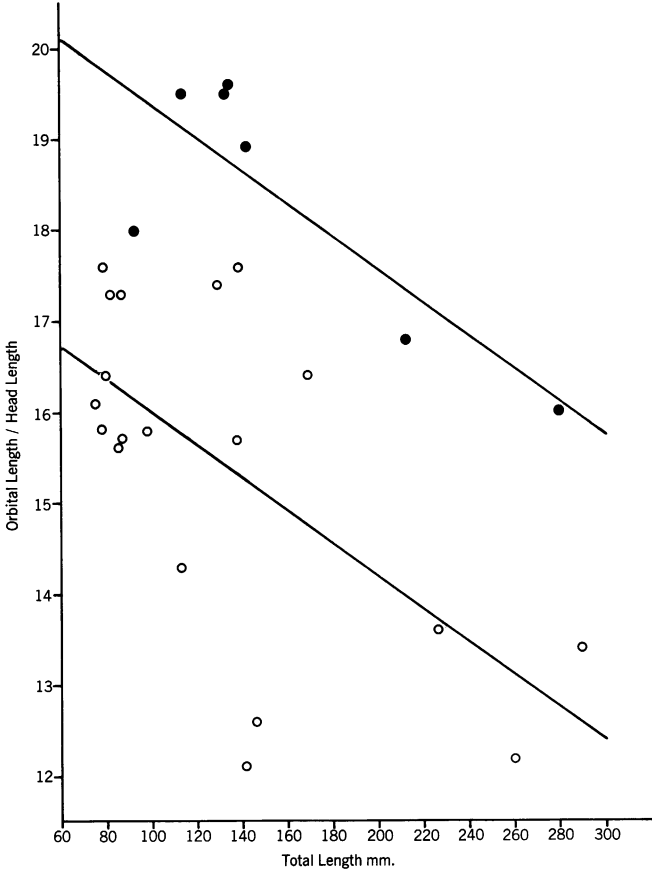


FIG. 5. Graph of relationships of ratio, orbital length/head length, and total body length in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

below). The sum of the more trenchant contrasting characters are incorporated in the diagnosis of *madeirae*, above, and in the following rediagnosis of *marmoratus*:

A speckled or blotched *Synbranchus* of dusky or pale ground color without a distinct pale band middorsally; with a relatively small orbit (12 to 14 percent of head length in adults), short caudal peduncle (23 to 34 percent of total length), and 126 to 148 vertebrae (where sympatric with *madeirae*); dorsal tip of cleithrum at level of fourth or fifth vertebra; neural spines of the abdominal region short and stout, not longer than the distance

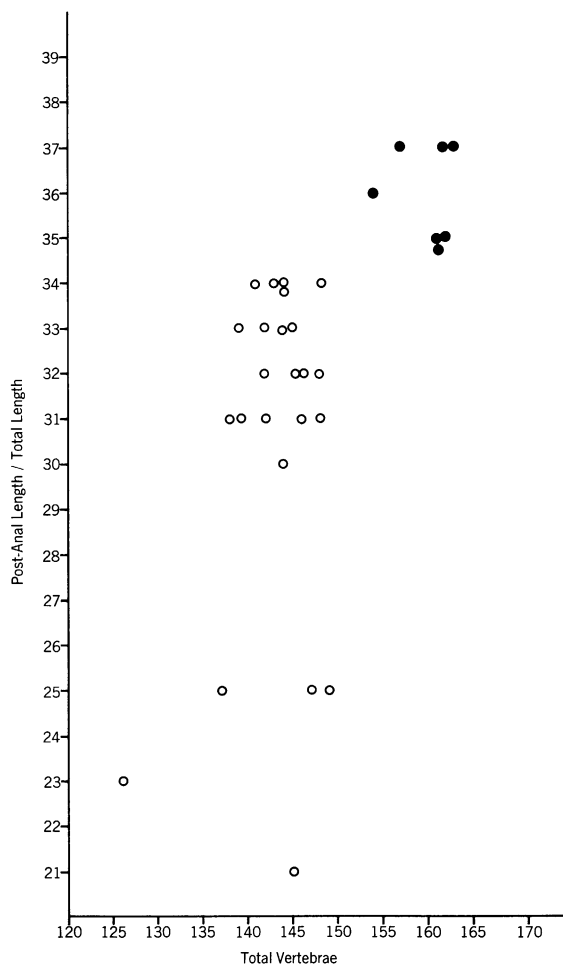


FIG. 6. Graph of relationships of ratio, post-anal length/total length, and total vertebrae in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

between any two succeeding spines, and the parietal bones rectangular anteriorly, or distinctly squared off in examples of more than 200 mm. Fleshy upper lip expanded, giving snout a blunt or squarish aspect in dorsal profile, nuchal region elevated in adults.

ETYMOLOGY: The genitive *madeirae* refers to the Río Madeira.

DISCUSSION: In pigmentation all individuals of *madeirae* differ from all

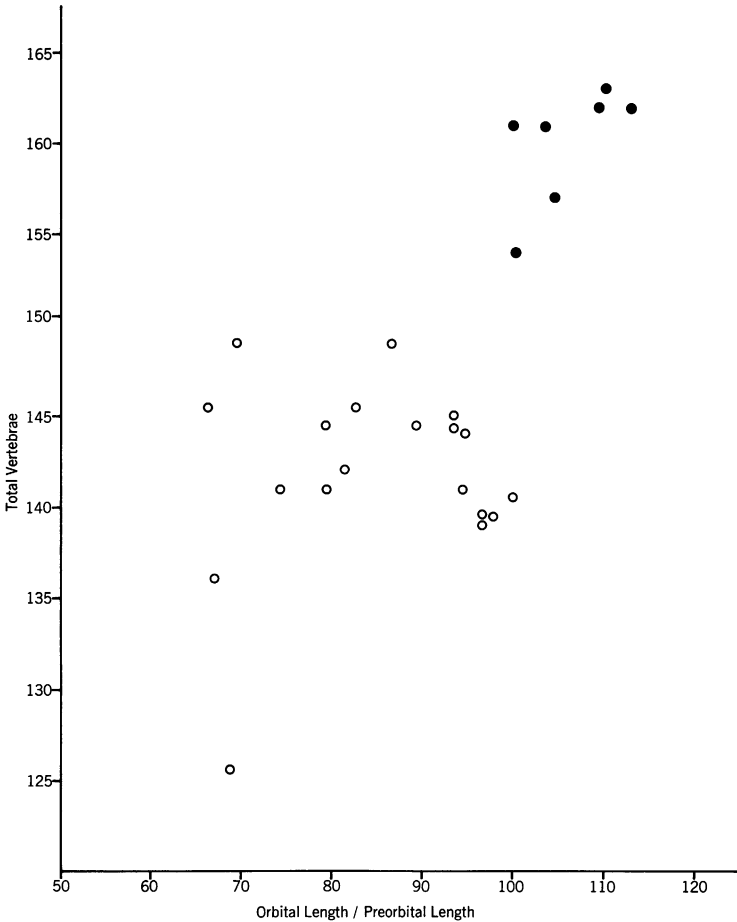


FIG. 7. Graph of relationships of total vertebrae and ratio, orbital length/preorbital length, in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

specimens of *marmoratus* within the Río Madeira Basin. In this region *marmoratus* has the typically mottled appearance of this species from elsewhere in South America. The ground color, in preservative, is pale cream or yellow, over which are distributed many large, widely spaced dark blotches (fig. 17A). The blotches, which are made up of generally large isolated or clustered stellate melanophores, are heaviest on the sides. The ventral surface of the body anterior to the anus has fewer, scattered blotches, and ventrally on the head blotching and other dark pigment

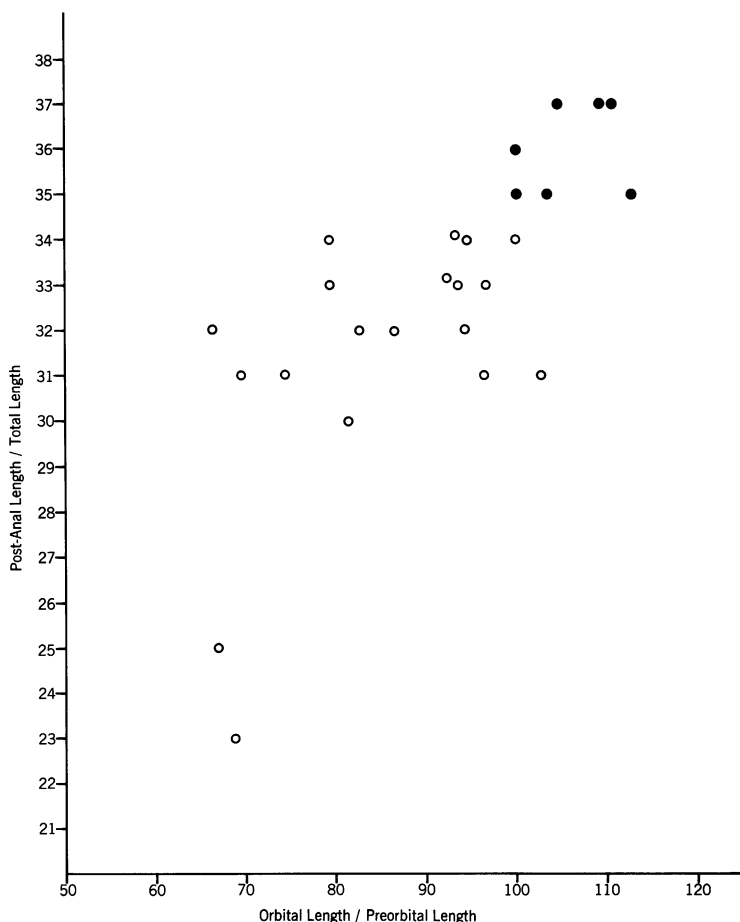


FIG. 8. Graph of relationships of ratios, post-anal length/total length and orbital length/preorbital length, in *Synbranchus madeirae* (black dots) and *Synbranchus marmoratus* (open circles) from Río Madeira system, Bolivia.

extends forward from the single gill opening, along the folded gular region to the tip of the lower jaw (fig. 20B). A diffuse dark streak of dermal pigment extends obliquely backward from the eye in many individuals (fig. 20A), and a thin dark pigment line extends backward from behind the head to the tail tip along the horizontal septum. Despite the obvious differences in pigmentation between the two forms, each individual aspect of pigmentation in *madeirasae* occurs in some examples of *marmoratus*. For example the post-ocular streak, which occurs in each specimen of *madeirasae*,

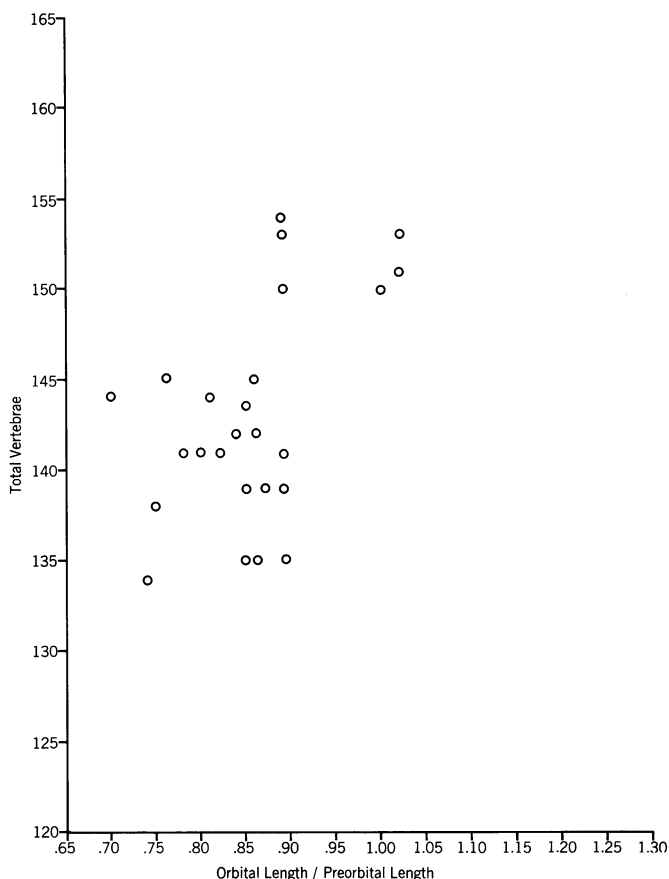


FIG. 10. Graph of relationship of total vertebrae, and the ratio, orbital length/preorbital length, in *Synbranchus marmoratus* from the Río Paraná-Río Paraguay system.

pared with the blotched or marbled pattern of larger *marmoratus*. On the other hand, no individual of *madeirae* has a blotched pattern or any pattern made up of large, clustered, stellate melanophores. The finely punctate melanophores of juveniles apparently are modified in larger *marmoratus* by reduction in cell number and by cell enlargement to form the characteristic irregular blotching, and in *madeirae* only by the development of a scattering of clear interspaces among the otherwise unmodified punctate melanophores. Panamanian and some South American populations of *marmoratus*, however, have a dark color phase, in addition to the pale

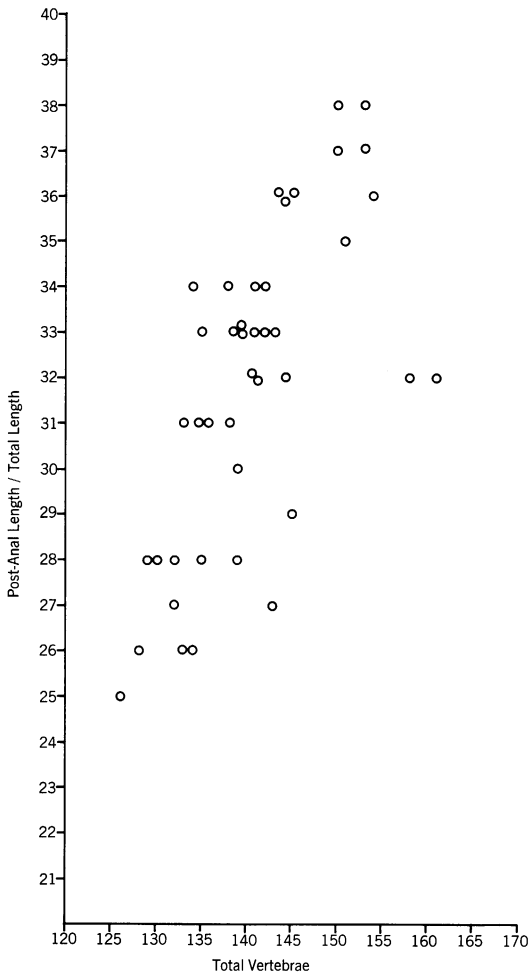


FIG. 11. Graph of relationship of ratio, post-anal length/total length, and total vertebrae in *Synbranchus marmoratus* from Río Paraná-Río Paraguay system.

blotched phase, in which an even wash of dark pigment is superimposed on the typical blotched pattern. Northern Central American and Mexican *marmoratus* all appear to exist in this darker phase, and these may be so dark that the blotched pattern is difficult to observe in many cases. It is therefore possible that the blotching in *marmoratus* is a distinct pattern of separate origin and that the *madeirae* pigmentation and the dark phase superimposed pigment in some *marmoratus* arise from the same basic pig-

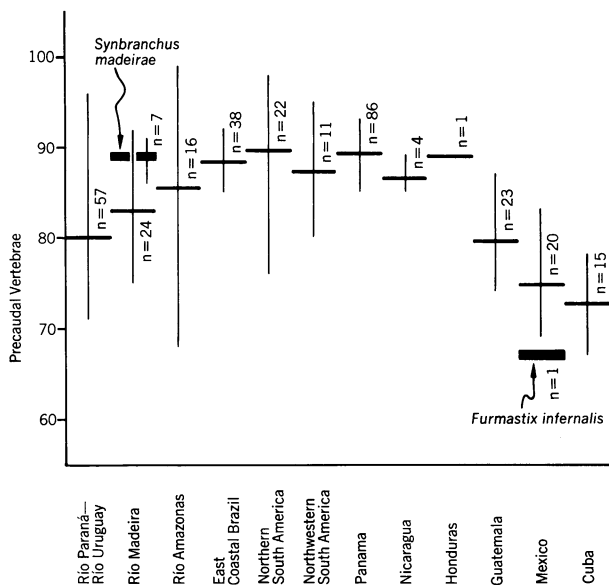


FIG. 12. Number of precaudal vertebrae in *Synbranchus madeirae*, *Furmastix infernalis*, and in consolidated samples of *Synbranchus marmoratus*, showing ranges of values (vertical lines), arithmetic means (horizontal lines), and sample size (n).

mentary system found in the juveniles of both species. Some of the individuals of *marmoratus* taken with *madeirae* in the Rio Beni show both patterns (fig. 20).

In general, pigmentation in *marmoratus* is more variable than in *madeirae* and resembles it more closely at the smaller sizes, and such size-related similarities are found consistently with respect to all characters analyzed except vertebral number. When post-anal length is plotted against total length, for example, within a comparable size range the values for *madeirae* have an exceedingly linear distribution and show little scatter around the computed regression, whereas the values for *marmoratus* show an increasing variability with increase in body size. The calculated regressions of post-anal length on total length for the two species converge at a body size of about 75 mm. (fig. 2). A plot of orbit length against head length gives similar results (fig. 3), as do the distributions of ratios of orbit length/preorbital length or orbit length/head length when plotted against total body length (figs. 4, 5). Nevertheless, for any part of the size range, the values for *madeirae* are higher than those for *marmoratus* and this difference, which is barely apparent at the smaller sizes, is greatly magni-

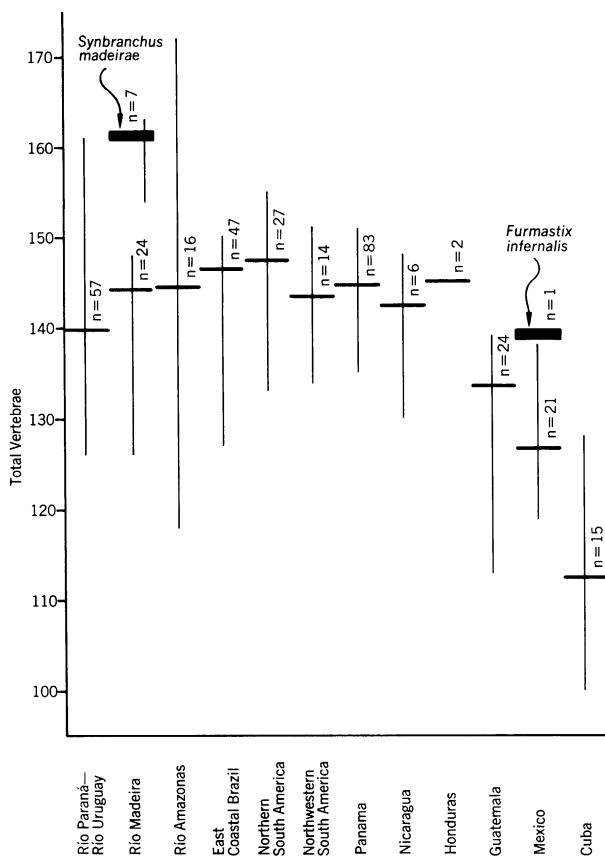


FIG. 13. Total number of vertebrae in *Synbranchus madeirae*, *Furmastix infernalis*, and in consolidated samples of *Synbranchus marmoratus*, showing ranges of values (vertical lines), arithmetic means (horizontal lines), and sample size (n).

fied at the larger sizes—even though the variability of *marmoratus* increases tremendously at the larger sizes. The estimates of the differences between the two species as expressed in the plots of the two ratios against body length are conservative as other analyses show (see tables for data) that mean preorbital length (snout length) in *madeira* is smaller (17.3 percent of head length) and mean head length slightly larger (7.6 percent of body length) than comparable mean values for *marmoratus* (18.3 percent and 7.2 percent). By eliminating the independent variable, body size, and comparing total number of vertebrae with the ratios post-anal length/total length (fig. 6) and orbit length/preorbital length (fig. 7), and the

two ratios with each other (fig. 8), the two species are seen to be clearly separated and their considerable difference in variability is further documented. These comparisons show that when size factors are eliminated there is a slight overlap between the two species only in the ratio of orbit length to preorbital length in spite of the great variability of *marmoratus*.

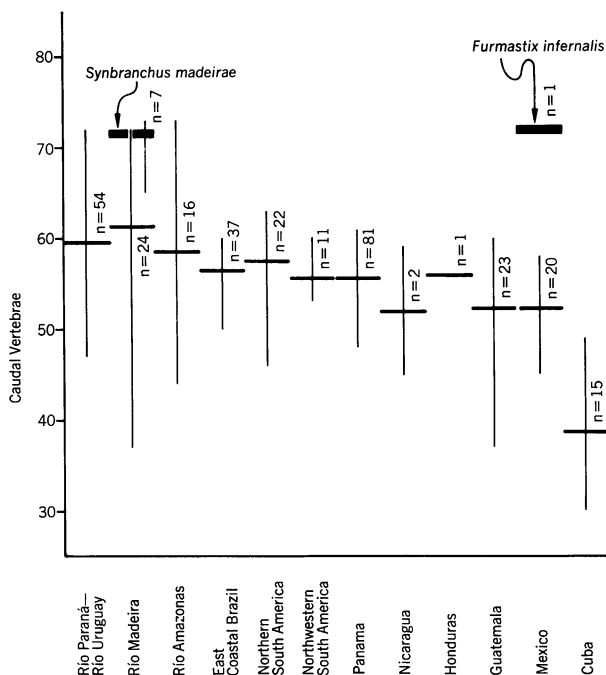


FIG. 14. Number of caudal vertebrae in *Synbranchus madeirae*, *Furmastix infernalis*, and in consolidated samples of *Synbranchus marmoratus*, showing ranges of values (vertical lines), arithmetic means (horizontal lines), and sample size (n).

In fact, the bulk of the extremes of variation in *marmoratus* appears to be toward the lower values, away from the mean value of *madeirae* in each of the three non-size-related comparisons.

Within the Rio Madeira system *madeirae* and *marmoratus* differ significantly in at least one and probably several osteological features, and here again the differences are most evident at the larger sizes. A comparison of small individuals of each species of almost the same length (*madeirae*, 114 mm. total length, 74 mm. preanal length; *marmoratus*, 110 mm. total length, 76 mm. preanal length) shows differences in the shape of the orbit

and snout, the palatopterygoid arch and vomer, shape and relative size of the frontal and parietal bones and of the bones in the otic, occipital, and ethmoid regions, size of the eyeball, and size, shape, and dentition of the fifth ceratobranchial element (figs. 23–25). Because of an insufficient number of large specimens of *madeirae*, little can be said about the comparative osteology in adults of the two species, but a careful incision along the dorsal midline near the back of the neurocranium in the two largest specimens of *madeirae* (from the Ríó Beni) reveals even more striking differences in the form of the parietal than are evident in the smaller skeletons. In the large *madeirae* the anterior border of the parietals (actually those portions of the bones not covered by the frontals) is slightly rounded or somewhat triangular, as in the smaller individual illustrated, whereas in large examples of *marmoratus*, the anterior margin of the parietal is squared off as a result of the backward growth of the frontals in the midline (fig. 26). Differences in the form of the parietal are constant for all individuals of *madeirae* and *marmoratus* examined from the Ríó Madeira system.

A comparison of *madeirae* with samples of *Synbranchus* from throughout its range in the New World suggests that *madeirae* may be endemic to the Ríó Madeira system, and that all other New World synbranchids except for the blind Mexican cavernicole, *Furmastix infernalis*, can be provisionally assigned to *marmoratus*. Because of the occurrence in the Ríó Paraná-Ríó Paraguay samples of some eels with exceptionally high vertebral counts, we thought originally that examples of *madeirae* might be present also in those samples. A comparable analysis of the non-size-related variables that most sharply separate *madeirae* from Ríó Madeira *marmoratus* shows that the values for the Ríó Paraná-Ríó Paraguay *Synbranchus* fall entirely outside of the *madeirae* distribution of plots of post-anal length/total length against orbit length/preorbital length (figs. 8, 9) and total vertebrae against orbit length/preorbital length (figs. 7, 10), and to overlap the distribution of *madeirae* values of post-anal length/total length against total vertebrae at only one point representing a single individual (figs. 6, 11). A majority of the Ríó Paraná-Ríó Paraguay specimens are from a few collections (localities 14 to 21) from Paraguay, and some of the individuals are exceedingly small and others relatively small in comparison with those in the Ríó Madeira samples. Our largest collection from this region (locality 17) is of 33 specimens ranging in size from 21.5 mm. to 152 mm. As with Ríó Madeira *marmoratus*, it is the smallest specimens that have values most closely approximating those of *madeirae*. For example, two of the 13 individuals from locality 17 less than 90 mm. in total length have orbit lengths that are 100.0 and 101.9 percent of preorbital length, and

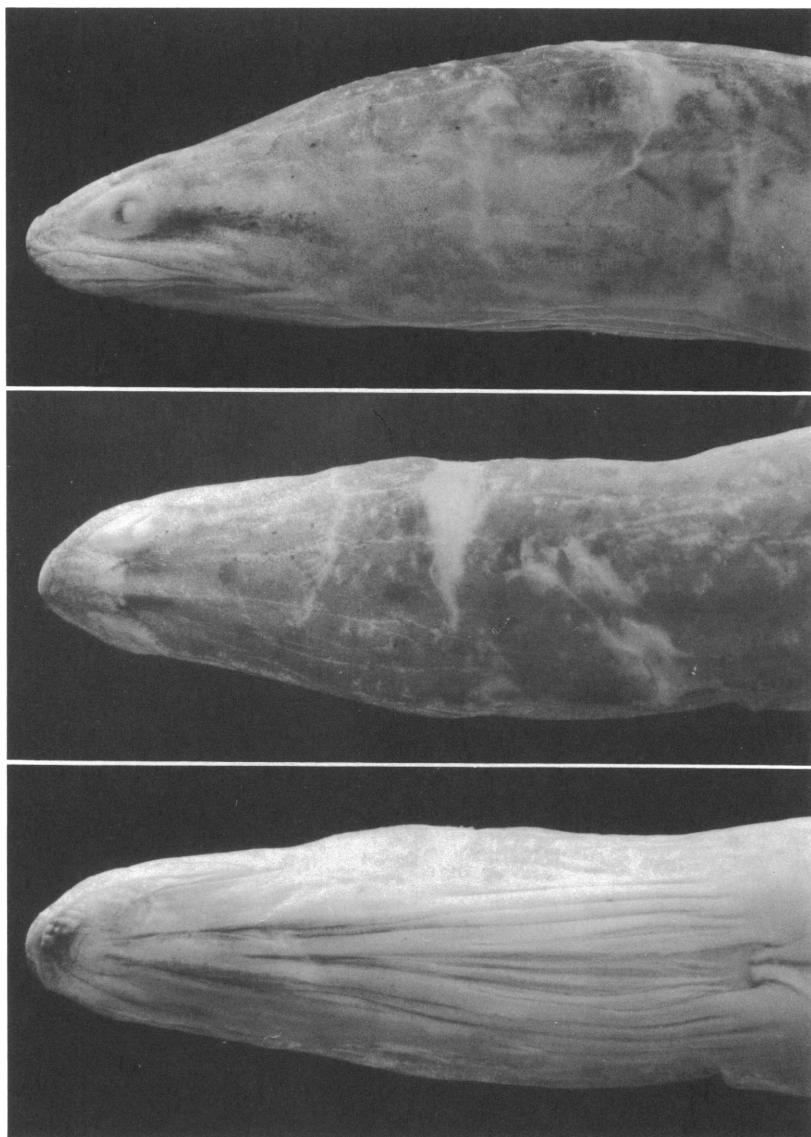


FIG. 15. *Synbranchus madeirae*, holotype, 280 mm. total length, CAS 13704; head in side view (top), dorsal view (middle), and ventral view (bottom).

five of these same 13 individuals have caudal lengths that are 35 to 37 percent of total length.

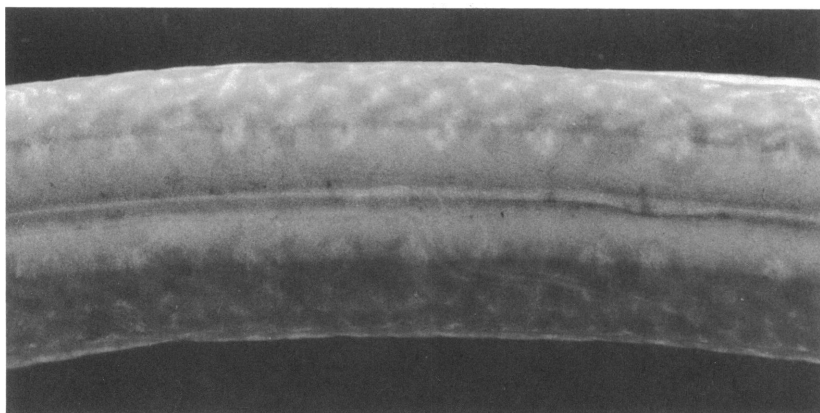


FIG. 16. *Synbranchus madeirae*, holotype, 280 mm. total length, CAS 13704; dorsal view of mid-section of body.



FIG. 17. Sympatric representatives of *Synbranchus marmoratus* AMNH 30213 (A) and *Synbranchus madeirae* AMNH 30214 (B) from Río Mamoré (Río Madeira system), Department of Beni, Bolivia (locality 27). Note differences in snout shape which result from the development in *S. marmoratus* of expanded lip fold. Compare with figure 18.

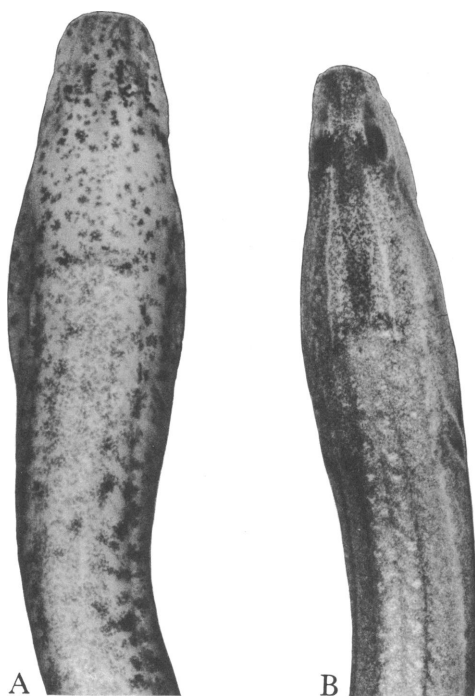


FIG. 18. A. *Synbranchus marmoratus*. B. *Synbranchus madeirae*. Enlargement of head region of specimens from figure 17 to show cephalic pigmentation.

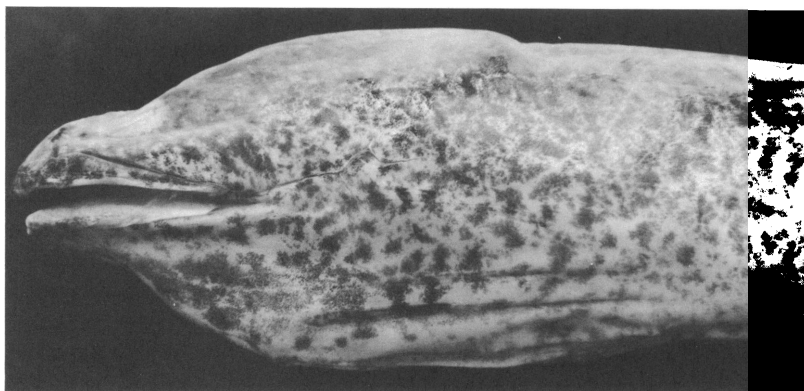


FIG. 19. Lateral view of head of *Synbranchus marmoratus* (AMNH 17638) from Essequibo, Guyana, showing pigment pattern typical of most South American representatives of this species.

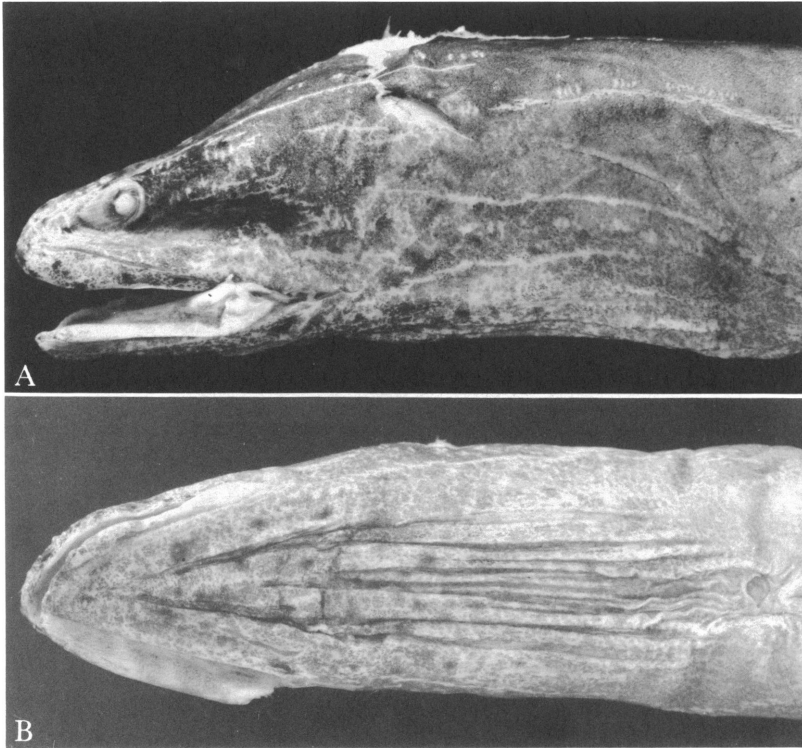


FIG. 20. *Synbranchus marmoratus* (UMMZ 66373) from Reyes, Río Beni, Bolivia, taken with the holotype (CAS 13704) and a paratype (CAS 13705) of *Synbranchus madeirae*. A. Lateral. B. Ventral. Note dark phase pigment overlying blotched pattern, most evident in B.

Within the Amazon Basin itself (but outside the Río Madeira system) there have been collected a few individuals with very high vertebral counts, three of which are comparable with those of *madeirae* [one at 156 (locality 34), two at 161 and 162 (locality 41)], and one of which exceeds the known counts for *madeirae* (one at 172 from locality 33). Each of these four individuals is distinctly mottled and within the range of *marmoratus* morphometrically. Radiographs from which head measurements could be made were obtained for the first three individuals. Both specimens from locality 41 are large adults of 450 mm. and 760 mm., have exceedingly low orbit to preorbital ratios (76.9 and 79.2 percent), and caudal length to total length ratios (21 and 28 percent). In the case of the single individual from locality 34, a juvenile of only 138 mm., the orbit to preorbital

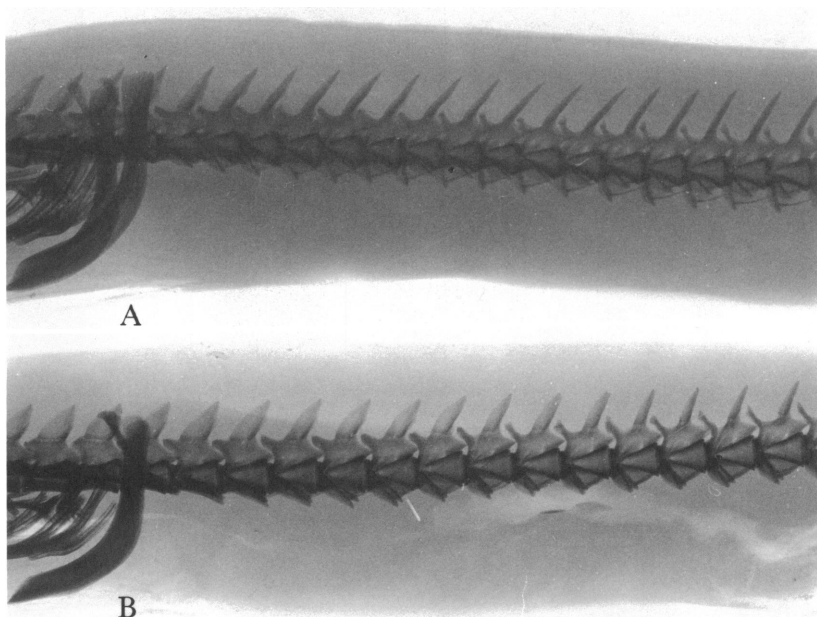


FIG. 21. Radiographs of anterior abdominal region of sympatric representatives of *Synbranchus madeirae* AMNH 30214 (A) and *Synbranchus marmoratus* AMNH 30213 (B) from Río Mamoré (Río Maderia system), Beni, Bolivia. Shoulder girdle and gill arches are at left.

ratio is high (95.8 percent), although well within the range of small *marmoratus* (table 2), but its ratio of caudal length to total length is typical of *marmoratus* (33 percent).

The considerable overlap in vertebral number between *madeirae* and Amazonian *marmoratus* is understandable if one examines vertebral number in *marmoratus* over its entire range. From Argentina northward to northern South America there is a gradual increase in the mean number of precaudal vertebrae, and from there northward to Mexico and Cuba the mean number declines to its lowest value for the species (fig. 12). The curve for total vertebrae (fig. 13) represents a damped version of the precaudal one because caudal vertebrae show a slight, steady decline in individuals from Argentina to Mexico, and a more sudden drop in those from Cuba (fig. 14). An examination of the distribution of mean minimum surface isotherms for the New World shows that the region including the Amazon Basin experiences the consistently highest temperatures during the year throughout the range of *marmoratus* (fig. 27). One might therefore not only expect geographic variation in precaudal vertebral number to be

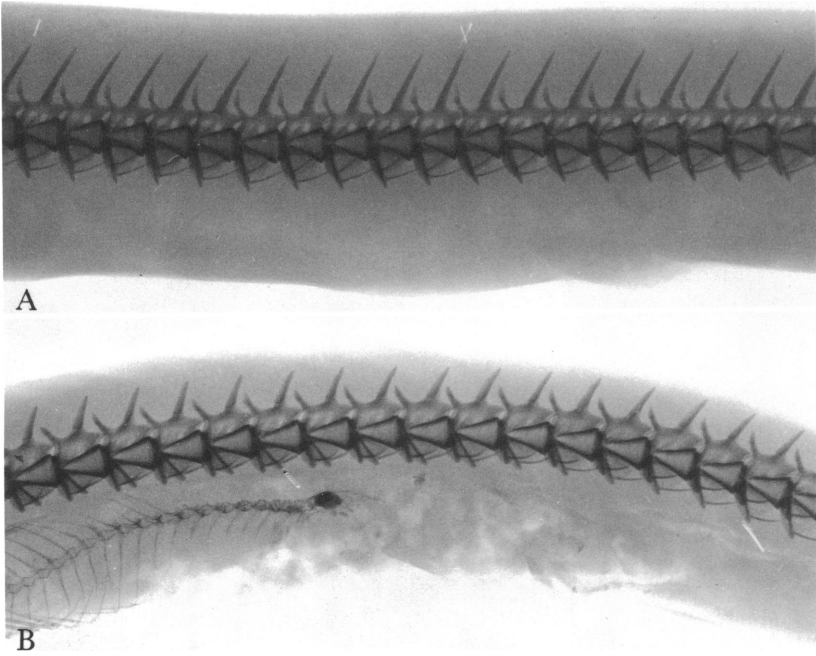


FIG. 22. Radiographs of posterior abdominal region of specimens as in figure 21. A. *Synbranchus madeirae*. B. *Synbranchus marmoratus*. Note small fish in gut at left in B.

somehow related to wide areas of different mean annual temperatures, but also to find the highest counts (or lowest ones, as in most fishes) within the Amazon Basin.

Two sets of data indicate that the view of a temperature-dependent variation in vertebral number on a global scale is an oversimplification. In the first place the number of caudal vertebrae steadily declines from south to north, and in the second, Cuban *marmoratus* taken from streams have counts similar to those in Mexico, whereas fish taken from thermal springs have exceedingly low (rather than high) counts. In other words, with respect to temperature-related effects on vertebral number Cuban *marmoratus* behave as do most fishes, and *marmoratus* from everywhere else within the range of the species behave in an exceptional manner. It is significant that the vertebrae most strongly correlated with known differences in water temperature in Cuba are the caudal vertebrae, and it is the caudal vertebrae that, within the range of the species, show no relationship to global isotherms. Unlike precaudal vertebrae, but like the

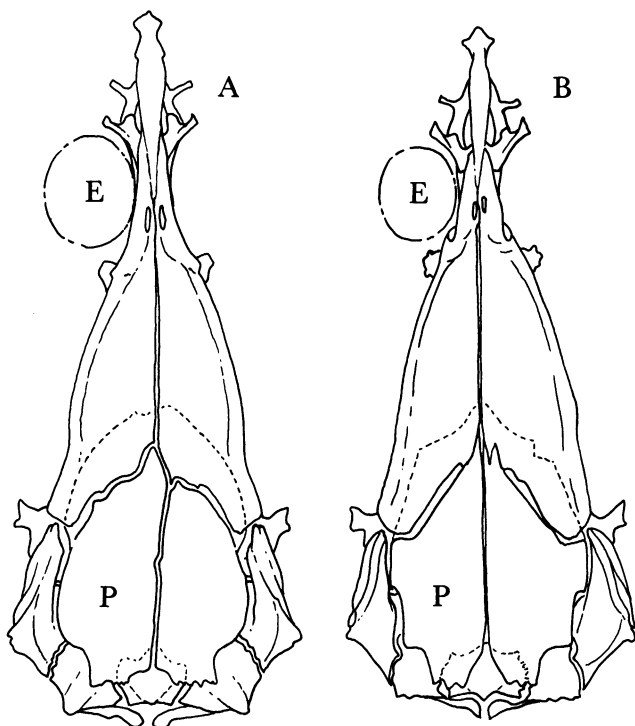


FIG. 23. Dorsicrania in *Synbranchus*. A. *S. madeirae*, AMNH 30214, 114 mm. total length. B. *S. marmoratus*, AMNH 30213, 110 mm. total length. Note differences in size of eye and shape of frontoparietal suture. E = eye; P = parietal.

caudal elements, the ratios of post-anal length to total length of body (fig. 28) and of orbit to preorbital length (fig. 29) also show a northward decline in values, although that decline is not very evident or well-documented for the latter ratio.

Some factor or combination of factors, however, has brought about the exceptional geographic behavior of precaudal vertebral number such that *madeirae*, as it is presently understood, would be impossible to identify on vertebral number alone if it were taken outside the confines of the R o Madeira Basin. This observation is to be reckoned with when one recalls that at the smallest sizes *madeirae* is difficult to tell apart from *marmoratus* on pigmentary or morphometric criteria.

Still further complicating the picture of variation within *marmoratus* is the possibility, suggested in figure 30, that mean vertebral number may also be correlated with distance upstream either in a major river system

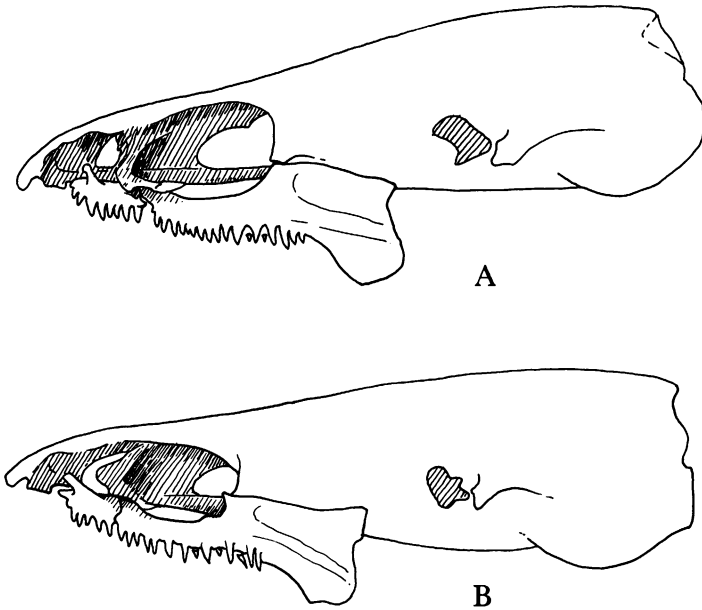


FIG. 24. Lateral view of neurocranium and palatine in *Synbranchus*. A. *S. madeirae*, AMNH 30214, 114 mm. total length. B. *S. marmoratus*, AMNH 30213, 110 mm. total length. Note differences in length and height of orbit.

(the Río Paraná-Río Paraguay) or in the tributaries of a system (the upper Río Solimões Amazonas and the Río Tocantins). Although the samples are meager, for synbranchids in most cases are collected only one or two per locality, and in the Amazon Basin the available samples being compared are from localities separated by vast distances, it appears as though the highest vertebral counts are in fish farthest from the river mouth. The existence of a lowland-headwater cline in vertebral number is suggested particularly by the material from the Río Paraná-Río Paraguay Basin where the 10 vertebral counts from the lowermost third of the system have a range of 126 to 133 and a mean of 131.5, and the 43 counts from the upper two-thirds of the system, a range of 127 to 161 and a mean of 142.3. The headwaters of the Río Paraguay extend northward toward the region of consistently high mean annual temperatures (fig. 27), although these upland tributaries also are at significantly higher elevations. For example, the Río Paraná Basin downstream from Asunción in Argentina, to its mouth in the Río de la Plata, is entirely below the 100-meter contour, whereas from Asunción upstream in the Río Paraguay it is entirely above

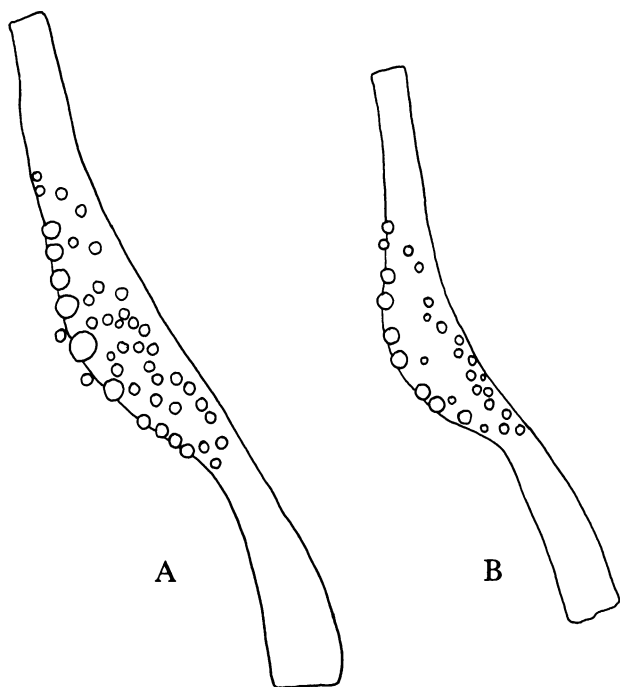


FIG. 25. Right fifth ceratobranchial element in *Synbranchus*. A. *S. madeirae*, AMNH 30214, 114 mm. total length. B. *S. marmoratus*, AMNH 30213, 110 mm. total length. Note differences in length and development of dentition.

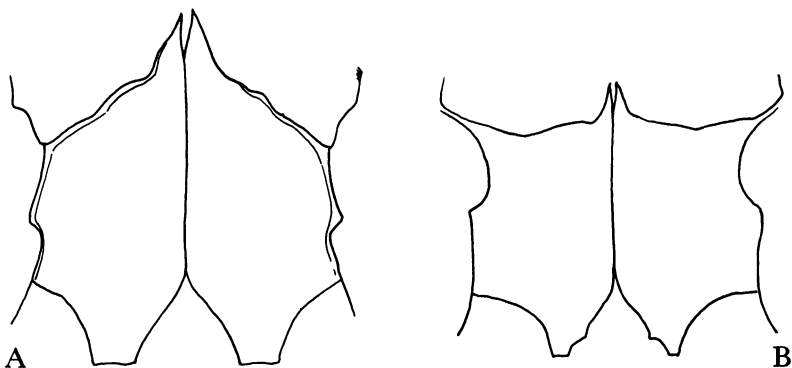


FIG. 26. Shape of parietal bone visible behind frontal in *Synbranchus* of over 200 mm. total length. A. *S. madeirae*, CAS 13705, 212 mm. total length. B. *S. marmoratus*, UMMZ 66373, 260 mm. total length. Both specimens taken together at Reyes, Río Beni, Bolivia.

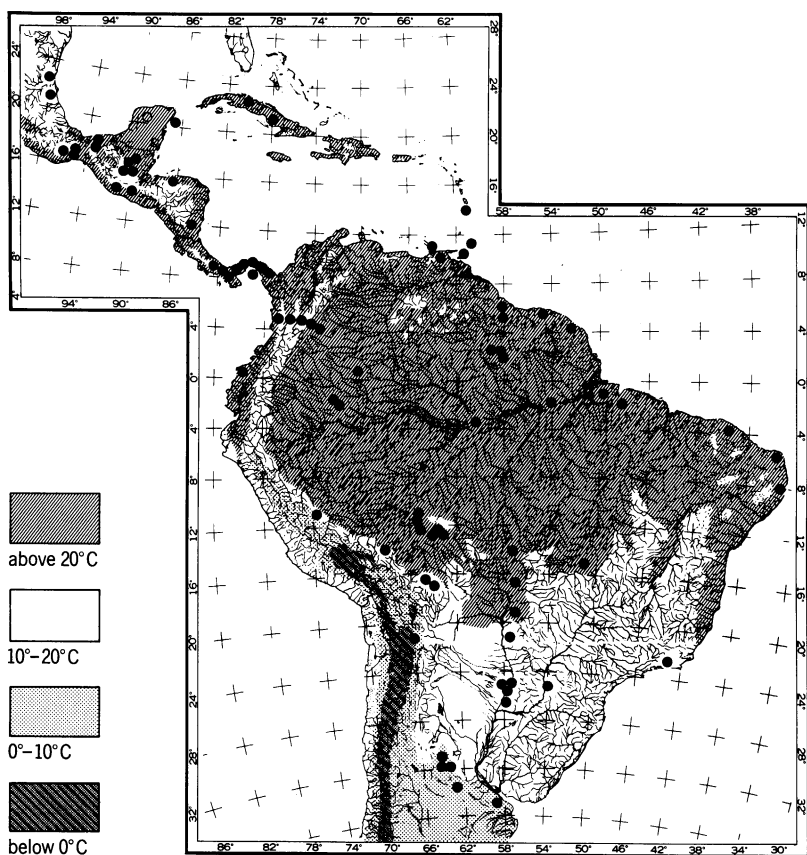


FIG. 27. Composite mean minimum temperatures for southern North America, Middle America, and South America in relation to record stations of *Synbranchus marmoratus* (black dots). South American mean minimum temperatures are for July, except for the January 10° C. to 20° C. isotherms south and north of the Orinoco. Simplified, from "Atlas of mean monthly temperatures" of U. S. Army Natick Laboratories.

the 100-meter contour and closely approached by the 200-meter contour along the Bolivian and Brazilian frontiers. Nevertheless, a detailed analysis of isotherms for the Río Paraná-Río Paraguay Basin (Republica Argentina, Atlas climatico, 1960) shows that at all times of the year surface temperatures are consistently lower toward the river mouth (below Asunción) than they are upriver. If the suspected variation in vertebral number from low counts in the cool lowlands to higher counts in the

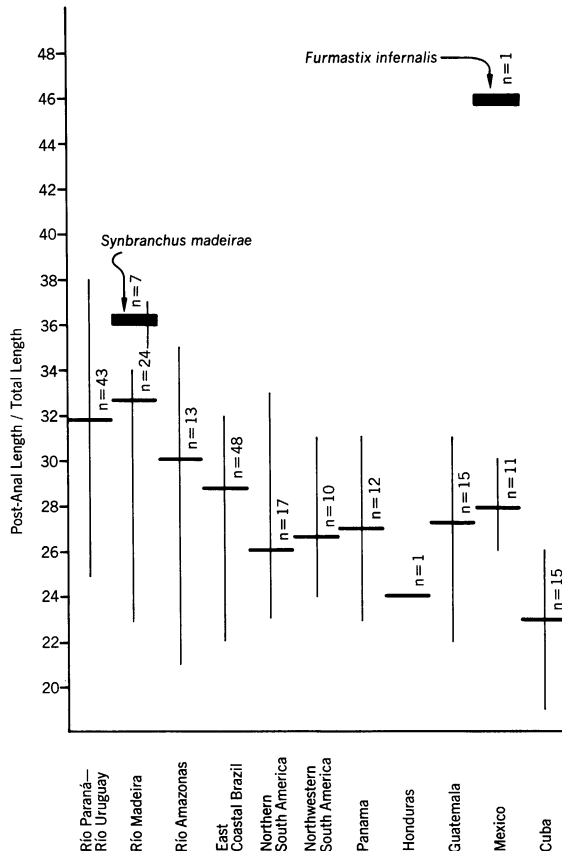


FIG. 28. Relative post-anal length of body in *Synbranchus madeirae*, *Furmastix infernalis*, and in consolidated samples of *Synbranchus marmoratus*, showing ranges of values (vertical lines), arithmetic means (horizontal lines), and sample size (n). Data not available for Nicaraguan material.

warmer uplands is confirmed, then local clinal variation (that is, within a single river system) in relation to temperature and altitude seems to follow the pattern of such variation in *marmoratus* generally, and is inconsistent with the findings in vertebral number of Cuban *marmoratus* from streams and thermal springs. The point should not be pressed further considering the small sample size, except to note that there is much local variation in vertebral number in *marmoratus* superimposed on overriding global clines in abdominal and caudal vertebrae (figs. 12–14, 30, 31). It is therefore evident that the significance of the difference between verte-

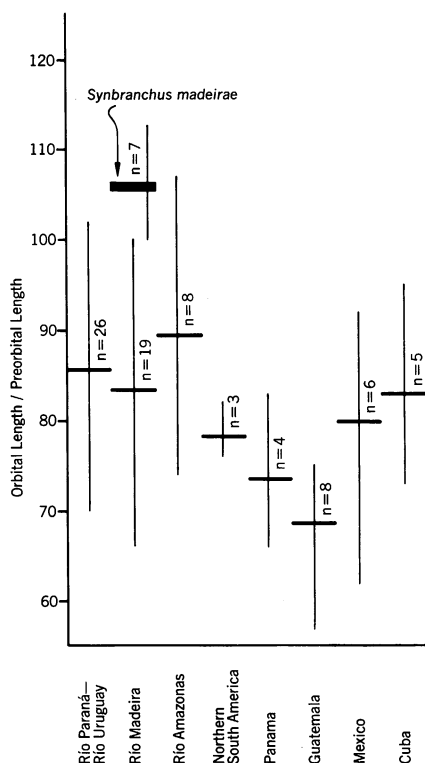


FIG. 29. Ratio of orbital length to preorbital length in *Synbranchus madeirae* and in consolidated samples of *Synbranchus marmoratus*, showing ranges of values (vertical lines), arithmetic means (horizontal lines), and sample size (n). Data not available for east coastal Brazilian, northwestern South American, Nicaraguan, and Honduran material.

bral number in *madeira* and *marmoratus* can only be judged fairly in comparisons of the two species from the same relatively localized geographical area—in this case, the upper Río Madeira system in Bolivia. One might expect that if *madeira* is found to occur in other parts of the Madeira system or in other tributaries of the Amazon Basin that it too would show geographic and ecophenotypic variations in vertebral number and that this number would be higher than that for any sympatric or nearby *marmoratus*.

Finally, some remarks concerning the relationships among the two epigeal and one cavernicolous species of New World synbranchids. The blind and depigmented *Furmastix infernalis* is known only from the holo-

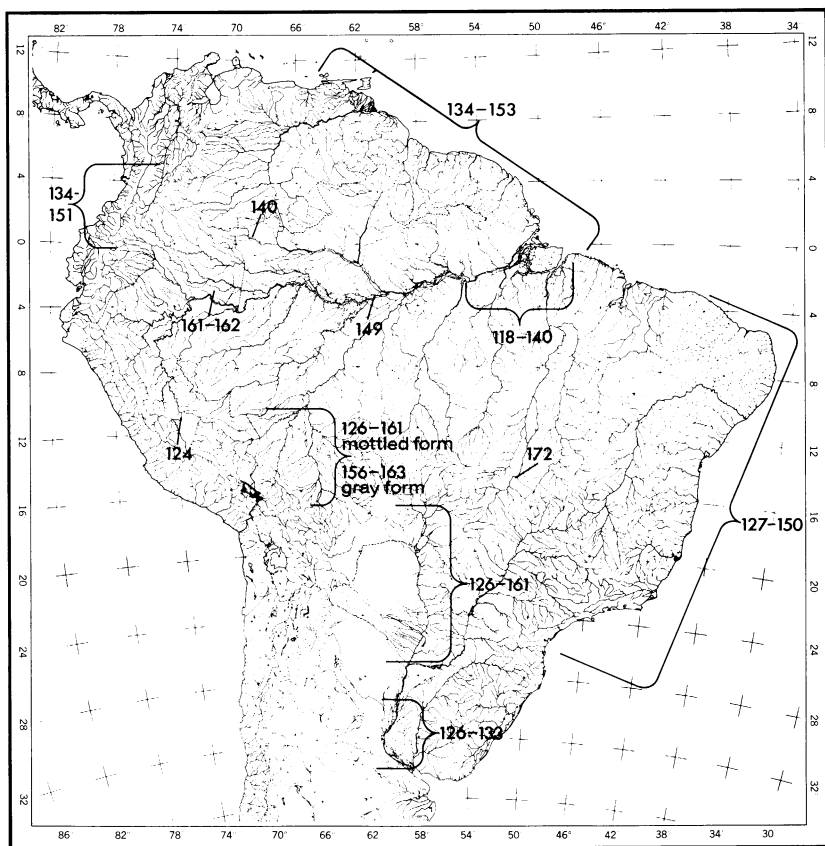


FIG. 30. Geographical distribution of vertebral number of *Synbranchus* in South America. Counts identified as those of mottled form (*Synbranchus marmoratus*) or gray form (*Synbranchus madeirae*) are from region in Bolivia where the two species are sympatric.

type, but we have been able to gather a few bits of information on its structure from the original description by Hubbs (1938) and from a series of radiographs. These data may be summarized as follows: *infernalis* has a total vertebral count of 139, which is comparable with the highest count for any Guatemalan *marmoratus*. The number of its abdominal vertebrae is low, 67, as low as the lowest abdominal count for any *marmoratus* and comparable with the lowest count in Cuban *marmoratus* from thermal springs. The caudal count is high, 72, and comparable with the caudal count in *madeirae* and southern and central South American *marmoratus*. The large number of caudal vertebrae is related to the relatively great

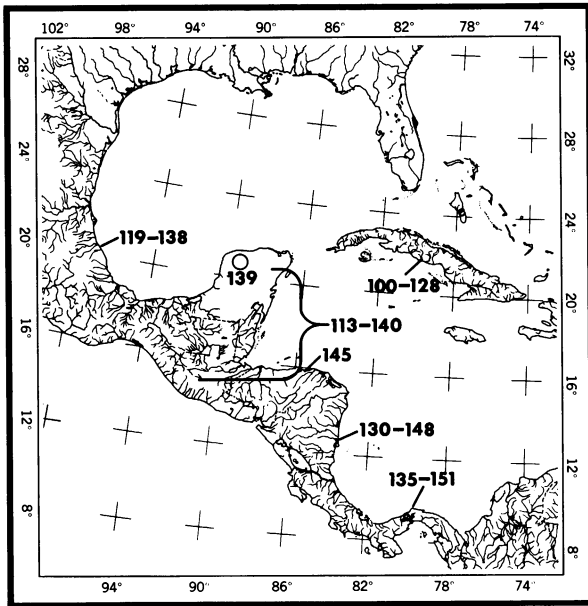


FIG. 31. Geographical distribution of vertebral number of *Synbranchus marmoratus* and *Furmastix infernalis* (open circle) in Middle America and Cuba.

length of the body posterior to the anus, 46.5 percent of total length (325 mm.), as compared with mean relative caudal length for *madeirae* (about 36 percent) or *marmoratus* (23 percent, in Cuba, to 32.5 percent, in the Río Madeira). Head length in *infernalis* (6.2 percent of total length) is less than for either epigeal species (7.2 percent in *marmoratus*, and 7.6 percent in *madeirae*). These few bits of comparative data obviously do not permit any decision as to the relationships of *infernalis* to *marmoratus* or *madeirae*. One would probably need to examine the skull and branchial structure of *infernalis* for more critical comparisons and this will require additional specimens. Nor are we assisted by the geographic position of *infernalis* in Yucatán, far from *madeirae* and within the range of *marmoratus*, as phylogenetic inferences are drawn from the structure and other biological attributes of the animals, not from their present distributions. In other words, the phylogenetic inferences must precede zoogeographic analysis to avoid circularity in reasoning. In concluding, we note that if *infernalis* and *marmoratus* had a more recent common ancestor than did either with *madeirae*, then maintaining *infernalis* in a separate genus, *Furmastix*, does not serve the needs of a phylogenetic taxonomy in which

the hierarchy should reflect genealogical relationship. If future study should show *infernalis* to be the sister group of both *madeirae* and *mar-moratus*, its separate generic status would, however, be an appropriate expression of its phylogeny.

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