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A Review of the Western Atlantic *Starksia ocellata*-Complex (Pisces: Clinidae) with the Description of Two New Species and Proposal of Superspecies Status

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ABSTRACT

Starksia ocellata (*sensu* Böhlke and Springer, 1961) represents a species complex composed of five species, in addition to *S. guttata*. *S. ocellata* occurs on both coasts of Florida north to North Carolina, and questionably in the Bahama Islands; *S. culebrae* ranges from Haiti through Puerto Rico and down the Lesser Antilles to and including St. Vincent; *S. guttata* is found in the Tobago Cays and the Grenadines south to Trinidad and west to Curaçao; *S. brasiliensis* is known from southern Brazil; *S. variabilis* occurs at Santa Marta, Colombia; and *S. occidentalis* ranges from Panamá north to Yucatán, México, including certain offshore islands. Of the above species, two (*S. variabilis* and *S. occidentalis*) are described as new, and two others (*S. culebrae* and *S. brasiliensis*) are resurrected from the synonymy of *S. ocellata*.

The importance of head coloration in this complex is discussed and examples of character displacement in meristic and morphometric characters are presented. It is proposed that the *S. ocellata*-complex represents a superspecies composed of six allospecies. Zoogeographic implications of the superspecies are discussed in relation to formal provinces.

ABSTRACTO

Starksia ocellata (*sensu* Böhlke and Springer, 1961) representa un complejo de especies compuesto de cinco especies además de *S. guttata*: *S. ocellata* ocurre desde

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ambas costas de Florida, norte por la costa Atlántica a Norte Carolina, y dudosamente desde las Islas Bahama; *S. culebrae* ocurre desde Haiti a Puerto Rico y por los Antillas menor a St. Vincent; *S. guttata* ocurre desde los Cayos Tobago y los Grenadines hasta Trinidad al sur y hasta Curacao al oeste; *S. brasiliensis* ocurre en el sur de Brasil; *S. variabilis* ocurre en Santa Marta, Colombia; *S. occidentalis* ocurre desde Panamá norte a Yucatán, México. Las especies *S. occidentalis* y *S. variabilis* son nuevas, describas por la primera vez en este estudio. Las especies *S. culebrae* y *S. brasiliensis*, anteriormente consideradas como sinónimas de *S. ocellata*, son tratadas como especies distintas.

La importancia de la coloración de la cabeza se discute con respecto a las especies de este complejo, y se presentan ejemplos de la divergencia de característicos merísticos y morfométricos entre las poblaciones contiguas de unas especies. Se propone que este complejo de especies representa una "superespecie" compuesto de seis "allo-especies," y se discuten las implicaciones zoogeográficas.

INTRODUCTION

Recent collections in Belize and Honduras resulted in the capture of a series of clinids most closely resembling *Starksia ocellata*, a species not yet recorded from the area. Comparison of these specimens with material of *S. ocellata* from throughout its reported range demonstrated that not only did the material from Central America represent an undescribed species, but that *Starksia ocellata* (*sensu* Böhlke and Springer, 1961) represents a species complex.

The first Atlantic species of *Starksia* (*Clinus ocellatus*) was described by Steindachner in 1876 from the Bahama Islands (possibly Florida: see *S. ocellata*). Two additional species of *Starksia* were described in 1900: *Brannerella brasiliensis* Gilbert from near Maceió, Brazil, and *Malacoctenus culebrae* Evermann and Marsh from Puerto Rico. Longley and Hildebrand (1941, p. 258) synonymized both *S. brasiliensis* and *S. culebrae* with *S. ocellata*. Böhlke and Springer (1961, p. 51) listed *S. culebrae* in the synonymy of *S. ocellata* without comment and also retained *S. brasiliensis* in the synonymy of *S. ocellata* stating (p. 53), ". . . it (*S. brasiliensis*) may eventually be shown separable at the subspecific level." Fowler (1931) described *Brannerella guttata*, a species closely related to *S. ocellata*, from Trinidad. Böhlke and Springer (1961, p. 50) stated, "*S. guttata* is like *S. ocellata* in most regards and it is with some misgivings that we tentatively retain the two as distinct." Gilbert (1971) described two new species of *Starksia*, including *S. elongata* (which he believed to be most closely related to *S. ocellata*) and followed Böhlke and Springer (1961) in considering *S. culebrae* and *S. brasiliensis* to be synonyms of *S. ocellata*. Gilbert (1971, p. 204) recorded the distribution of *S. ocellata* as follows: "B & S, North

Carolina, South Carolina, Florida, Cuba, Haiti, Puerto Rico, Virgin Is., Grenadines (Lesser Antilles), Old Providence Is., Brazil, questionably from Bahamas; C, Venezuela. New record: Panama."

A comparison of the populations of *S. ocellata* (*sensu* Böhlke and Springer) from throughout its range with the material from Central America shows striking differences in the color pattern on the side of the head. The populations fall into six obviously different patterns: Pattern I—North and South Carolina, Atlantic Florida, Gulf of México, and Bahama Islands?; Pattern II—Haiti, south through the Lesser Antilles to and including St. Vincent; Pattern III—Togabo Cays, Grenadines, Tobago Island, Trinidad, and Curaçao; Pattern IV—north coast of South America at Santa Marta, Colombia; Pattern V—coast of Central America from Yucatén to Panamá including Providencia; Pattern VI—southern Brazil.

METHODS

Counts and measurements follow Böhlke and Springer (1961) and Gilbert (1971), with the exceptions of the method of counting the number of scales in the lateral line, and in measuring upper jaw length. All scales are included in the count whether pored or unpored, and the straight portion of the lateral line begins with the first scale whose posterior end is in line with the remainder of the

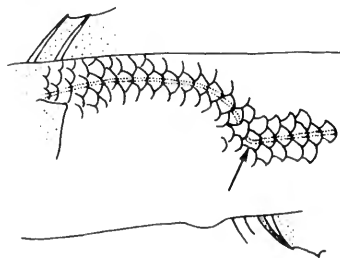


FIG. 1. Method of counting arched and straight portions of the lateral line. Arrow indicates location of first scale in straight portion.

lateral line, even if the anterior portion of the pore curves upward (fig. 1). Upper jaw length is measured by placing one point on the posterior end of the maxillary and the other on the midline of the premaxillary. All measurements were made with dial calipers to the nearest 0.1 mm. and presented as thousandths of standard length (SL). Vertebral and fin ray counts were taken from radiographs.

The following abbreviations of collections are used in listing material examined: ANSP, Academy of Natural Sciences of Philadelphia; CAS and CAS-SU, California Academy of Sciences; FMNH, Field Museum of Natural History; GCRL, Gulf Coast Research Laboratory Museum; LACM, Los Angeles County Museum of Natural History; MPM, Milwaukee Public Museum; RMNH, Rijksmuseum van Natuurlijke Historie; SIO, Scripps Institution of Oceanography; UF, University of Florida (Florida State Museum); UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

***Starksia ocellata* (Steindachner). Figures 2-4. Tables 1-3.**

Clinus ocellatus Steindachner, 1876, p. 230, pl. 12, fig. 5. Type locality: Bahama Islands.

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult male united along entire length (fig. 3), papilla projecting beyond tip of spine a distance equal to a little less than one-fifth length of spine; first anal-fin spine longer than second anal-fin spine; obvious pelvic-fin rays I,2; pectoral-fin rays 13-15 (usually 14); dorsal-fin elements XX-XXII,6-9 (usually XXI,8); anal-fin elements II,17-20 (usually II,18); lateral-line scales, 16-20 in arch (usually 17) and 20-22 in straight (usually 21), total 37-41 (usually 38); vertebrae 33-35 (usually 34); no dark diagonal bar on lower part of pectoral-fin base; body color pattern not consisting of well-defined, dark bands. May be distinguished from its closest congeners *S. culebrae*, *S. occidentalis*, and *S. variabilis* by lacking distinct black vertical bars on the lips, from *S. brasiliensis* in having two rows of infraorbital pores rather than a single row, and from *S. guttata* by the presence of small, dark, ring-like markings with light centers on the cheek and opercle

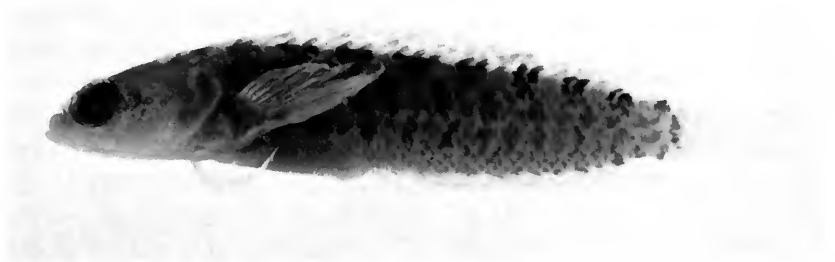


FIG. 2. *Starksia ocellata*, UF 10875, female, 31.3 mm. S.L., Florida.

TABLE 1. Meristic characters for six species in the *Starksia ocellata*-complex.

	Dorsal-fin spines	Dorsal-fin soft rays	Anal-fin soft rays	Pectoral-fin rays	Vertebrae
	XX XXI XXII	6 7 8 9	16 17 18 19 20	13 14 15	30 31 32 33 34 35
<i>S. ocellata</i>	7 60 10	1 5 52 19	9 43 23 1	1 30 2	9 52 8
<i>S. culebrae</i>	4 45 15	5 39 20	2 37 25	2 49	37 24
<i>S. guttata</i>	6 13	15 4	6 13	1 18	1 15
<i>S. brasiliensis</i>	1 3	3 1	1 3	4	1 3
<i>S. variabilis</i>	4 8	1 8 3	2 10	2 9 1	6 6
<i>S. occidentalis</i>	18 46	9 46 8	2 37 24 1	5 40	1 33 28 1
		Lateral-line scales			
		Arched	Straight	Total	
	15 16 17 18 19 20	19 20 21 22	34 35 36 37 38 39 40 41		
<i>S. ocellata</i>	1 20 8 1 1	11 19 1	7 17 6 1		
<i>S. culebrae</i>	8 33 4 1	12 25 9	2 10 7 1 1		
<i>S. guttata</i>	1 2 13 3	3 13 2	5 9 3		
<i>S. brasiliensis</i>	3 1	1 2	1 2 1		
<i>S. variabilis</i>	5 6 1	9 3	2 9 1		
<i>S. occidentalis</i>	10 23	16 16 2	3 17 12 2		

TABLE 2. Comparison of proportional measurements for six species in the *Starkisia ocellata*-complex. Means above, ranges below in parentheses, expressed as thousandths of the S.L.

	N	Head length	Body depth	Eye diam.	Snout length	U. jaw length	Pectoral-fin length	Ventral fin length	1st D. spine length
<i>S. ocellata</i>	10	325 (306-355)	197 (186-218)	80 (73-89)	56 (48-65)	134 (124-147)	254 (220-285)	216 (163-252)	79 (52-112)
<i>S. culebrae</i>	20	326 (298-361)	182 (161-201)	82 (71-97)	58 (46-72)	131 (120-146)	254 (201-278)	214 (155-247)	75 (51-96)
<i>S. guttata</i>	17	316 (295-338)	207 (180-228)	78 (66-105)	58 (48-74)	139 (122-161)	241 (224-282)	198 (156-233)	70 (56-79)
<i>S. brasiliensis</i>	4	320 (300-360)	198 (188-211)	88 (81-101)	59 (49-77)	138 (136-142)	244 (236-250)	204 (192-221)	77 (67-89)
<i>S. variabilis</i>	12	304 (289-316)	192 (174-210)	83 (76-90)	48 (36-58)	138 (127-151)	233 (212-258)	193 (145-211)	75 (62-82)
<i>S. occidentalis</i>	20	310 (286-335)	195 (165-213)	85 (74-105)	49 (37-61)	135 (116-147)	237 (203-294)	212 (174-281)	83 (65-112)

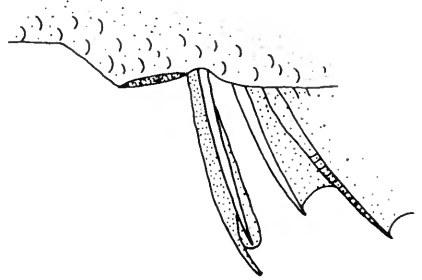
TABLE 3. Meristic characters for *Starksia ocellata* from various localities.

	Dorsal-fin spines	Dorsal-fin soft rays	Anal-fin soft rays	Pectoral-fin rays	Vertebrae
XX XXI XXII	6 7 8 9	17 18 19 20	13 14 15	33 34 35	
North & South Carolina	2 3	1 1 3	3 2	5	4 1
Florida	4 49	2 42 17	4 34 21 1	1 14 2	2 44 7
G. Mexico	1 8 2	2 7 2	2 7 2	11	3 7 1
TOTAL	7 60 10	1 5 52 19	9 43 23 1	1 30 2	9 52 8

Lateral-line scales

	Arched	Straight	Total
	16 17 18 19 20	20 21 22	37 38 39 40 41
North & South Carolina	1 2 1 1	2 3	2 2 1
Florida	10 6 1	5 11 1	2 9 6
G. Mexico	8 1	4 5	3 6
TOTAL	1 20 8 1 1	11 19 1	7 17 6 1

FIG. 3. Gonopodium of *Starksia ocellata*, UF 10875, 24.1 mm. S.L. Line equals 1 mm.



falling mostly within a horizontal pale area running from the orbit posteriorly to the edge of the preopercle. *Starksia ocellata* has a longer snout (mean 56) than either *S. occidentalis* (mean 49) or *S. variabilis* (mean 48).

Description.—Meristics are presented in the diagnosis. Measurements are presented in Table 2 and are based on 10 specimens, 17.2-33.4 mm., USNM 116831 and UF 16187.

Color pattern of head.—*Starksia ocellata* is clearly separable from other members of the species complex by the presence of small ring-like markings on the cheek and opercle. These rings are dark with light centers and fall mostly within a horizontal pale area running from the orbit posteriorly to the edge of the preopercle (figs. 2, 4). The anterior portion of the lips have a scattering of melanophores; however, there are no distinct black vertical bars on the lips. This color pattern is clearly illustrated in Böhlke and Springer (1961, fig. 15) and in Böhlke and Chaplin (1968, p. 525).

Remarks.—As restricted herein, *S. ocellata* occurs only along the Gulf and Atlantic coasts of Florida, the Florida Keys including the Dry Tortugas and north along the Atlantic coast of the United States to N. Carolina. Böhlke and Springer (1961) have discussed the problem of the type locality of *S. ocellata*. Although listed as "Bahama-Inseln," this species has not since been collected in the

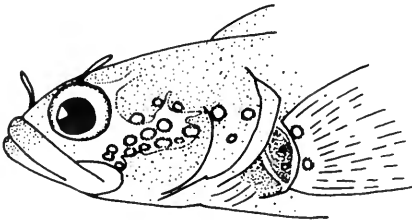


FIG. 4. Typical head color pattern of *Starksia ocellata*.

Bahamas and it is likely that the type locality may actually be Florida.

Material examined.—N. Carolina—USNM 120131(1). S. Carolina—UF 7270(2); GCRL 189(2). Gulf of México—UF 7858(2); UF 7859(9). Florida (Monroe Co.)—UF 10875(9); UF 11876(9); UF 16187(34); USNM 116831(6); SIO-67-86(3). Florida (Indian R. Co.) UF 12040(1). Florida (Palm Beach Co.) UF 16018(1). Standard length of specimens examined 17.2-33.8 mm.

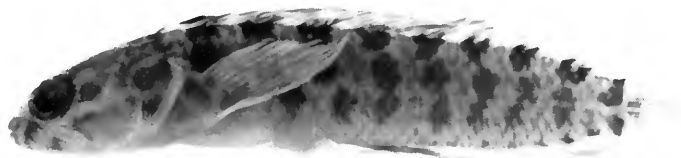


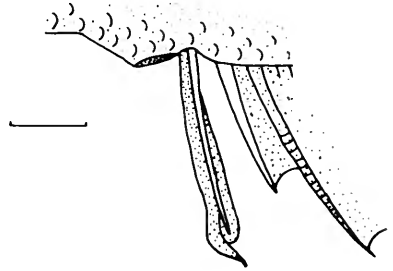
FIG. 5. *Starksia culebrae*, ANSP 124681, male, 27.9 mm. S.L., St. Lucia.

Starksia culebrae (Evermann and Marsh). Figures 5-7. Tables 1, 2, 4.

Malacoctenus culebrae Evermann and Marsh, 1900a, p. 357. Type locality: reefs outside the harbor of Culebra, Puerto Rico.

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult male united along entire length (fig. 6), papilla projecting beyond tip of spine a distance equal to one-fifth length of spine; first anal-fin spine longer than second anal-fin spine; obvious pelvic-fin rays I,2; pectoral-fin rays 13-14 (usually 14); dorsal-fin elements XX-XXII,7-9 (usually XXI,8); anal-fin elements II,17-19 (usually II,18); lateral-line scales 16-19 in arch (usually 17) and 20-22 in straight (usually 21), total 37-41 (usually 38); vertebrae 34-35 (usually 34); no dark diagonal bar on lower part of pectoral-fin base; body color pattern not consisting of well-defined, dark bands. May be distinguished from its closest congeners *S. ocellata*, *S. guttata*, and *S. brasiliensis* by the presence of distinct black vertical bars on the lips and from *S. occidentalis* and *S. variabilis* by possessing a pale horizontal bar running from the orbit posteriorly past the edge of the preopercle onto the opercle. The horizontal bar does not branch into a Y, and

FIG. 6. Gonopodium of *Starksia culebrae*, ANSP 124679, 25.8 mm. S.L. Line equals 1 mm.



dark ring-like markings are almost always absent. It may further be distinguished from *S. brasiliensis* in having two rows of infraorbital pores rather than a single row. *Starksia culebrae* has a longer snout (mean 58) than *S. occidentalis* (mean 49) or *S. variabilis* (mean 48).

Description.—Meristics are presented in the diagnosis. Measurements are presented in Table 2 and are based on 20 specimens, 15.9-27.3 mm., ANSP 134946, ANSP 134945, ANSP 113248, ANSP 124674, ANSP 124679, ANSP 112981, ANSP 124687, and ANSP 124685.

Color pattern of head.—*Starksia culebrae* is clearly separable from other members of the species complex by the combination of distinct black vertical bars on the lips and a pale horizontal bar running from the orbit posteriorly past the edge of the preopercle onto the opercle (fig. 7). The horizontal bar does not branch into a Y and dark ring-like markings are almost always absent. Specimens from Martinique occasionally have one or two small ring-like markings, which are located ventral to the horizontal bar. The only other species with bars on the lips are *S. occidentalis* from the coast of Central America and *S. variabilis* from Colombia, but the pale patterns on the side of the cheek are different. This color pattern is clearly illustrated in Evermann and Marsh (1900b, fig. 96) and in Beebe and Tee-Van (1928, p. 236).

Remarks.—*Starksia culebrae* ranges from Haiti through Puerto Rico and down the Lesser Antilles to and including St. Vincent.

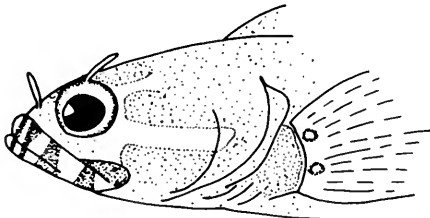


FIG. 7. Typical head color pattern of *Starksia culebrae*.

TABLE 4. Meristic characters for *Starksia culebrae* from various localities.

	Dorsal-fin spines			Dorsal-fin soft rays			Anal-fin soft rays			Pectoral-fin rays		Vertebrae	
	XX	XXI	XXII	7	8	9	17	18	19	13	14	34	35
Haiti	1	8	2	10	1		10	1		11		9	2
Puerto Rico		1				1			1	1			
St. Barthelemy		4	5	1	6	2	1	6	2	1	4	5	5
Antigua		4	2		3	3		2	4		6	3	3
Dominica		1				1			1	1			1
Martinique	1	9	2	3	8	1	1	9	2		10	8	1
St. Lucia	2	8	2	1	8	3		9	3		7	9	3
St. Vincent		10	2		4	8		1	11		10	3	9
Total	4	45	15	5	39	20	2	37	25	2	49	37	24

Lateral-line scales

	Arched				Straight			Total						
	16	17	18	19	20	21	22	36	37	38	39	40	41	
Haiti			9		5	4		5	4					
Puerto Rico			1		1			1						
St. Barthelemy	1	4			1	4		2	3					
Antigua			6			4	2			4	2			
Dominica				1			1						1	
Martinique	4	4	1		4	4	1	2	3	3	1			
St. Lucia	3	2			1	4		1	2	2				
St. Vincent			7	2	1		4	6			3	5	1	1
Total	8	33	4	1	12	25	9	3	13	19	9	1	1	

Whether this species occurs in Cuba is not known. The specimen, USNM 82548, listed by Böhlke and Springer (1961) from Cuba as *S. ocellata* is *S. fasciata* (Longley). Although *S. culebrae* is 100 per cent separable from *S. ocellata* on the basis of coloration, counts and measurements cannot be used for separation inasmuch as the only noticeable difference is an upward shift in the number of vertebrae in *S. culebrae*. To the south of St. Vincent *S. culebrae* is replaced by *S. guttata*, which lacks bars on the lips.

The only noticeable instance of geographic variation in populations of *S. culebrae* is found in the St. Vincent population, which, when compared to populations to the north of St. Lucia and Martinique, shows a modal increase in dorsal-fin soft rays, anal-fin soft rays, vertebrae, and lateral-line scales. The St. Vincent population is located at the southernmost limit of the range of *S. culebrae*, and thus is geographically closest to populations of *S. guttata*. These shifts in certain modal values in *S. culebrae* result in modal differences between the two species that are not observed between their geographically more distant populations, and thus possibly represent a case of character displacement, a phenomenon supporting genetic differences between these two species.

Material examined.—Haiti—USNM 178297(5); ANSP 134946(1); ANSP 134945(5). Puerto Rico—USNM 125973(1), (paratype of *M. culebrae*). St. Barthelemy—ANSP 113248(1); ANSP 124674(4); ANSP 124677(4). Antigua—ANSP 117907(5); UF 11404(1). Dominica—USNM 198272(1). Martinique—ANSP 112981(1); ANSP 113012(2); ANSP 113060(5); ANSP 124679(2); ANSP 124687(2). St. Lucia—ANSP 124661(1); ANSP 124666(6); ANSP 124681(5). St. Vincent—ANSP 124623(1); ANSP 124685(12). Standard length of specimens examined 13.4–31.2 mm.

***Starksia guttata* (Fowler).** Figures 8, 9a, b, 10a-c. Tables 1, 2, 5.

Brannerella guttata Fowler, 1931, p. 401, text-fig. 3. Type locality: Monas Island, Trinidad.

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult male united along entire length (fig. 9a, b), papilla projecting beyond tip of spine a distance equal to one-sixth to one-third length of spine; first anal-fin spine longer than second anal-fin spine; obvious pelvic-fin rays I,2; pectoral-fin rays 13-14 (almost always 14); dorsal-fin elements XX-XXI,8-9 (usually XXI,8); anal-fin elements II,17-18 (usually II,18); lateral-line scales, 15-18 in arch (usually 17) and

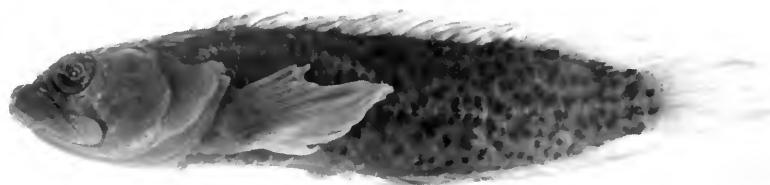


FIG. 8. *Starksia guttata*, ANSP 53327-30 (paratype), male, 37.8 mm. S.L., Trinidad.

20-22 in straight (usually 21), total 37-39 (usually 38); vertebrae 33-34 (almost always 34); no dark diagonal bar on lower part of pectoral-fin base; body color pattern not consisting of well-defined, dark bands. May be distinguished from its closest congeners *S. culebrae*, *S. occidentalis*, and *S. variabilis* by lacking distinct black vertical bars on the lips; from *S. brasiliensis* in having two rows of infraorbital pores rather than a single row; and from *S. ocellata* by usually having a pale horizontal bar which branches into a definite Y posteriorly, and often lacking dark ring-like markings, or having solid dark spots overlaying the pale horizontal bar. *Starksia guttata* has a longer snout (mean 58) than either *S. occidentalis* (mean 49) or *S. variabilis* (mean 48).

Description.—Meristics are presented in the diagnosis. Measurements are presented in Table 2 and are based on all material listed except for a bent specimen from LACM 22682 and one from USNM 170202.

Color pattern of head.—Lips dusky anteriorly or evenly peppered with melanophores, without distinct black vertical bars; cheek dusky with a pale horizontal bar, equal to or greater than half the

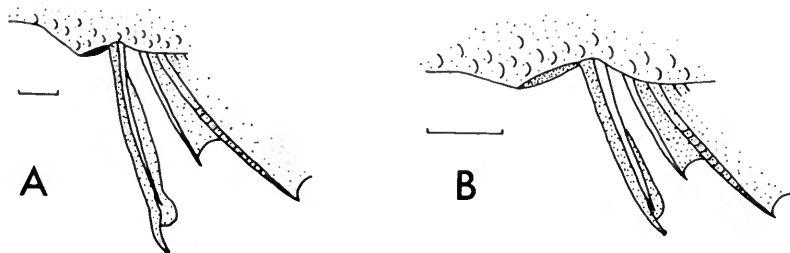


FIG. 9. Gonopodium of *Starksia guttata*. a, ANSP 53325, 36 mm. S.L., Trinidad; b, ANSP 124624, 23.3 mm. S.L., Union Is. Line equals 1 mm.

TABLE 5. Meristic characters for *Starksia guttata* from various localities.

	Dorsal-fin spines		Dorsal-fin soft rays		Anal-fin soft rays		Pectoral- fin rays		Vertebrae	
	XX	XXI	8	9	17	18	13	14	33	34
Tobago Cays	4		1	3	3	1		4		2
Grenadines	2	3	5		2	3	1	4	1	4
Tobago Is.		3	3		1	2		3		2
Trinidad		6	5	1		6		6		6
Curaçao		1	1			1		1		1
Total	6	13	15	4	6	13	1	18	1	15

Lateral-line scales

	Arched				Straight			Total		
	15	16	17	18	20	21	22	37	38	39
Tobago Cays			1	2	1		3		2	1
Grenadines			4	1		1	4	1	3	1
Tobago Is.	1		1			1	1	1	1	
Trinidad			1	5	1	1	5	1	2	3
Curaçao			1			1			1	
Total	1	2	13	3		3	13	2	5	9

pupil diameter above the maxillary, running from the orbit posteriorly, usually branching into a definite Y posteriorly and often lacking dark ring-like markings (fig. 10a, b). Several of the paratypes have dark spots overlaying the pale horizontal bar, but this pattern has not been observed outside of Trinidad (fig. 10c). The Y-shaped pale bar on the side of the head is clearly illustrated in Randall (1968, fig. 273) (a specimen from Tobago).

Remarks.—The determination of the species limits for *S. guttata* has posed a difficult problem. When Böhlke and Springer (1961) reviewed the genus they had available only the type material of *S.*

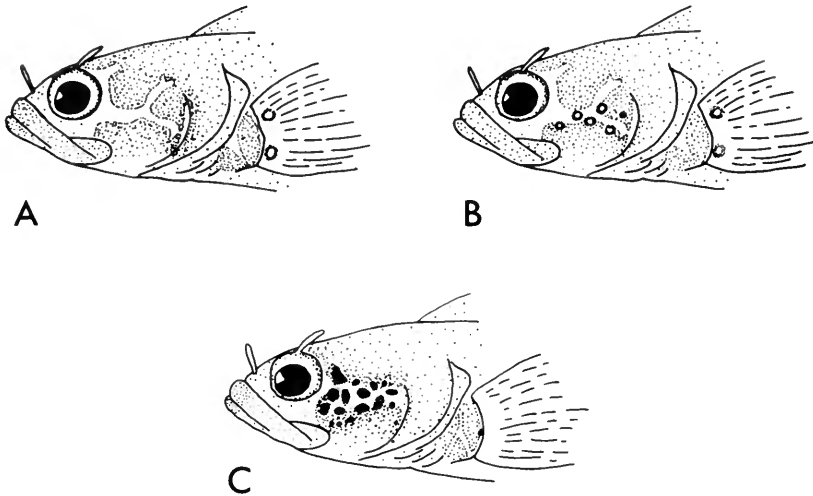


FIG. 10. Three head color patterns of *Starksia guttata*: a, b, typical patterns; c, paratype from Trinidad exhibiting spotted pattern.

guttata. On the basis of the distinctive color pattern of the body and supposed slight differences in two body proportions they recognized this species as valid. Böhlke and Springer (1961) and later Gilbert (1971) used the following characters to separate *S. guttata* from *S. ocellata* (*sensu* Böhlke and Springer): head length 280-314 SL and upper jaw length 133-144 SL in *S. ocellata* vs. head length 328-351 SL and upper jaw length 147-168 SL in *S. guttata*. Allometric growth is a factor in the supposed differences in upper jaw length (fig. 11) and no differences in head length are evident (fig. 12). Thus, part of the problem in locating additional specimens of *S. guttata* was related to the validity of these characters. Further, additional specimens having the distinctive round black spots on the body were not located. The color pattern of the body is variable and may show some clinal variation. Specimens from Trinidad (paratype, fig. 8) and Tobago (fig. 13) have the body covered with distinct round black spots on a light background. One small specimen (16.1 mm.) from Tobago is barred and lacks spots, which is perhaps a juvenile color phase. To the north this spotting pattern becomes less distinct and blotches more typical of other species in the *S. ocellata*-complex begin to appear. At Union Island the pattern of blotches is indistinct and the background color dark; however, the round black spots are still evident (fig. 14). At Little St. Vincent Island the

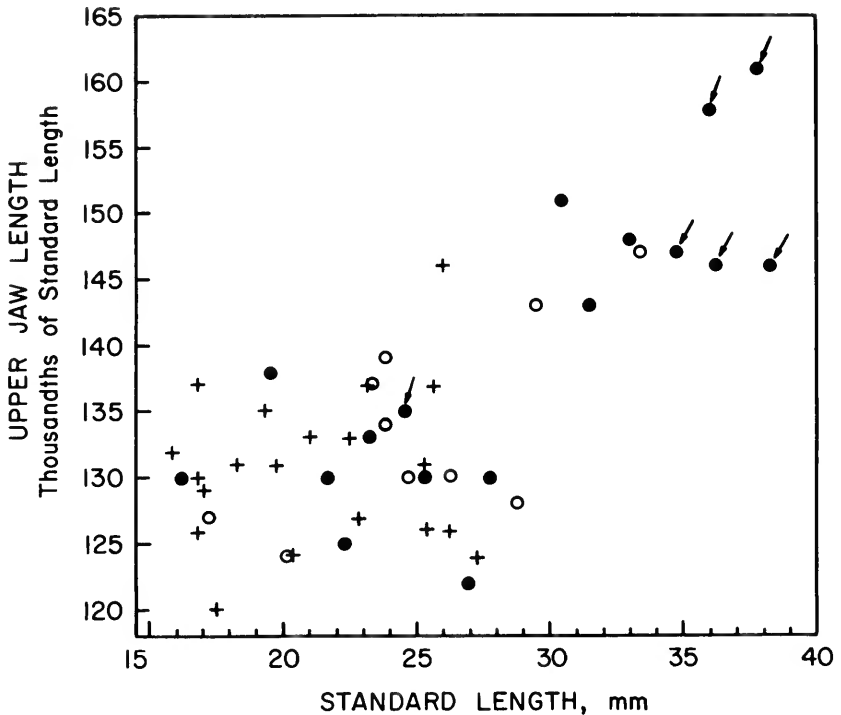


FIG. 11. Length of upper jaw in thousandths of standard length vs. standard length in millimeters for *Starksia guttata* (solid circles), *S. ocellata* (open circles), and *S. culebrae* (crosses). Arrows indicate paratypes of *S. guttata*.

background color is cream with distinct blotches; however, large black spots are present around the edges of the blotches and the central portions of the blotches are pale, thus approaching a spotted pattern (fig. 15). This clinal explanation is confounded, however, by the pattern illustrated by Randall (1968, fig. 273) of a specimen from Tobago that is very similar to the Little St. Vincent Island pattern. No significant differences in counts or measurements could be found between the spotted individuals from Trinidad and Tobago and other specimens here considered to be *S. guttata*, and thus they are treated as a single species.

The integrity of this species is demonstrated by comparing it to the geographically adjacent species. *Starksia guttata* occurs as far north as the Tobago Cays in the Grenadines. A single specimen from Bequia Island, just south of St. Vincent Island (ANSP 124663) is totally bleached and no color characters are available. *Starksia*

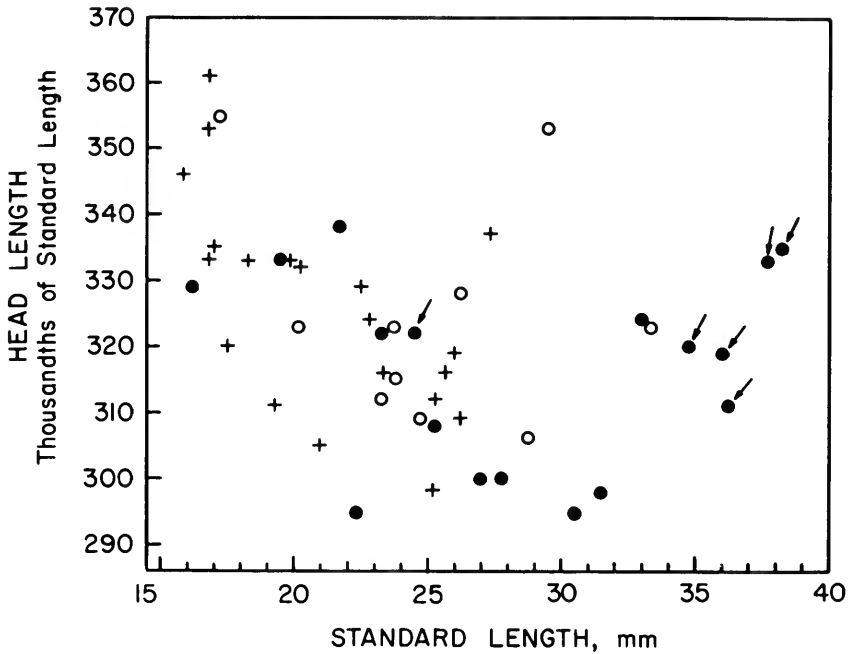


FIG. 12. Head length in thousandths of standard length vs. standard length in millimeters for *Starksia guttata* (solid circles), *S. ocellata* (open circles), and *S. culebrae* (crosses). Arrows indicate paratypes of *S. guttata*.



FIG. 13. *Starksia guttata*, LACM 22682, female, 33.4 mm. S.L., Tobago Is.



FIG. 14. *Starksia guttata*, ANSP 124624, male, 23.3 mm. S.L., Union Is.

culebrae is present at St. Vincent Island where it can be easily distinguished from *S. guttata* by the combination of distinct black vertical bars on the lips and the pale horizontal bar running from the orbit posteriorly past the edge of the preopercle onto the opercle. To the south of Trinidad along the southern coast of Brazil, *S. brasiliensis* is present. This species differs from *S. guttata* in having one, instead of two, rows of infraorbital pores, a lower total number of lateral-line scales, fewer vertebrae, fewer anal-fin and dorsal-fin rays, and a distinctive color pattern on the side of the head.

A single specimen from Curacao appears to be *S. guttata*. This specimen lacks black vertical bars on the lips and has a typical Y-shaped bar with light spots on the side of the head (similar to ANSP 117893 from Little St. Vincent Island). The body coloration is faded (it was collected in 1917), but some distinct black spots are evident on the body. To the west, two other species of the *S. ocellata*-complex occur: *S. variabilis* and *S. occidentalis*. Both of these species have distinct black vertical bars on the lips, different color

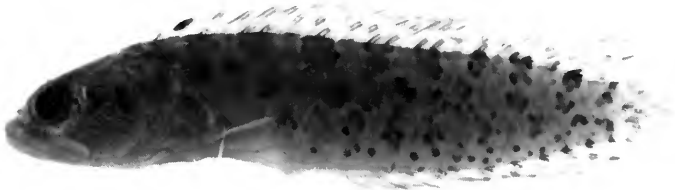


FIG. 15. *Starksia guttata*, ANSP 117893, male, 30.5 mm. S.L., Little St. Vincent Is.

patterns on the sides of the heads, shorter snouts, and fewer total lateral-line scales, vertebrae, and anal-fin rays.

Material examined.—TRINIDAD (paratypes) ANSP 53325(1); ANSP 53326(1); ANSP 53327-30(4). TOBAGO ISLAND—LACM 22682(2); ANSP 98488(1). GRENADINES (B.W.I.)—Tobago Cays USNM 170202(2); Little St. Vincent Island ANSP 114377(2), ANSP 117893(1), ANSP 124658(1); Union Island ANSP 124624(1). CURAÇAO—RMNH 9822(1). Standard length of specimens examined 16.1-38.2 mm.



FIG. 16. *Starksia occidentalis*, FMNH 83716 (holotype), female, 29.6 mm. S.L., Belize.

Starksia occidentalis new species. Figures 16-18. Tables 1, 2, 6.

Holotype.—FMNH 83716, adult female 29.6 mm. SL., Belize, Tarpon Cay (about 16° 10' N. lat., 88° 40' W. long.), depth 0-1 m., 19 July 1974, D. W. Greenfield, T. Greenfield, R. L. Woods, R. Williamson (field no. G-74-15).

Paratypes.—BELIZE—FMNH 84388 (3 females, 16.0-26.3 mm.), taken with holotype; FMNH 84386 (1 female, 27.8 mm.), Bugle Cays, depth 0-1.2 m., 16 July 1974, D. W. Greenfield, T. Greenfield, R. L. Woods, R. Williamson; UF 23348 (1 female, 28.5 mm.), Frenchman's Cay, depth 0-1.2m., 19 July 1974, D. W. Greenfield, T. Greenfield; FMNH 84385 (1 male, 26.9 mm.), Barrier Reef, Gallows Point, depth .9 m., 15 April 1973, D. W. Greenfield, T. Greenfield, A. Drew, M. Drew, J. Russo, D. Wildrick, R. Woods; FMNH 84389 (1 female, 25.0 mm.), Middle Snake Cay, depth 1.5 m., 20 July 1974, D. W. Greenfield.

HONDURAS—FMNH 84377 (1 male 25.8, 4 females 17.0-28.0

mm.), Hog Islands, Big Hog Island, depth .9 m., 20 May 1974, D. W. Greenfield, T. Greenfield, R. K. Johnson; UMMZ 200204 (1 male 20.5, 5 females 17.5-20.3 mm.), Hog Islands, Big Hog Island, depth 0-9 m., 21 May 1975, R. K. Johnson, R. R. Miller, F. Miller, G. Glodek; FMNH 84379 (1 male, 22.0, 1 female 20.2 mm), Hog Islands, Little Hog Island, depth .6 m., 19 May 1975, R. K. Johnson; FMNH 84380 (1 female 23.3 mm.), Hog Islands, Little Hog Island, depth 4.6 m., 18 May 1975, D. W. Greenfield, T. Greenfield, R. K. Johnson, G. Glodek, N. Hylton; FMNH 84381 (1 male, 17.1, 5 females 9.4-16.2 mm.), Hog Islands, N.W. Cay, depth 15.2 m., 20 May 1975, D. W. Greenfield, T. Greenfield, R. K. Johnson, R. R. Miller, F. Miller, G. Glodek, N. Hylton; FMNH 84382 (1 female 20.2, 4 males, 16.6 - 23.0 mm.), Roatán, Cow Island in Bay of Port Royal, depth 1.5 m., 2 May 1975, D. W. Greenfield, T. Greenfield, R. K. Johnson, R. R. Miller, F. Miller, G. Glodek; FMNH 84383 (1 male 24.2, 6 females 16.7-25.2 mm.), Hog Islands, Little Hog Island, depth 4.6 m., 19 May 1975, D. W. Greenfield, T. Greenfield, R. K. Johnson, G. Glodek; FMNH 84384 (2 males both 21.4, 7 females 15.9-25.6 mm.), Hog Islands, Big Hog Island, depth 1.8 m., 21 May 1975, D. W. Greenfield, T. Greenfield, R. K. Johnson, R. R. Miller, F. Miller, G. Glodek.

OLD PROVIDENCE-USNM 107110 (2 males 17.6-24.6 mm.), shore, 6 August 1938, W. L. Schmitt and presidential party; UF 24303 (1 female 25.6 mm.), S.W. Coast, Santa Catalina, 26 August 1968, Tyler, Tyler, Faunce, Perdew, Londono, Freidenberg, Anderson.

MÉXICO-MPM 11369 (1 female 24.1 mm.), Yucatán, Quintana Roo, Ascension Bay, 16 June 1976, Spieler, Yeo, Noeske; MPM 11577 (1 female 10.8 mm.), Yucatán, Quintana Roo, Ascension Bay, Cayo Culebra, 17 June 1976, Spieler, Noeske, Yeo; USNM 192388 (1 female 20.5 mm.), Yucatán, Quintana Roo, Ascension Bay, Nichaabin Reef, 14 April 1960, Smithsonian-Bredin Caribbean Expedition IV; USNM 192399 (1 male 19.4 mm.), Yucatán, 1960, Smithsonian-Bredin Caribbean Expedition IV; USNM 192401 (1 male 27.8 mm.), Yucatán, Quintana Roo, Ascension Bay, 16 April 1960, Smithsonian-Bredin Caribbean Expedition IV; USNM 192416 (1 male 17.0 mm.), Yucatán, 1960, Smithsonian-Bredin Caribbean Expedition IV.

PANAMÁ-S10 67-45 (1 female 24.5 mm.), Toro Point, depth 0-4.6 m., 23 March 1967, R. Rosenblatt, I. and R. Rubinoff; CAS 31610 (2

TABLE 6. Meristic characters for *Starksia occidentalis* from various localities.

	Dorsal-fin spines		Dorsal-fin soft rays			Anal-fin soft rays				Pectoral- fin rays		Vertebrae			
	XX	XXI	7	8	9	16	17	18	19	13	14	32	33	34	35
Yucatán	2	4		4	2	1	1	4			6		1	4	
Belize	2	6	3	4	1	1	5	2		1	7		3	5	
Honduras	9	28	5	27	5		22	14	1	2	17		22	15	1
Providencia		3		2	1		1	2			3				1
Panamá	5	5	1	9			8	2		2	7	1	7	3	
Total	18	46	9	46	9	2	37	24	1	5	40	1	33	28	1

Lateral-line scales

	Arched		Straight			Total						
	16	17	19	20	21	35	36	37	38			
Yucatán	3	2	2	3		2	1	2				
Belize	3	5	2	4	2		4	3	1			
Honduras	4	8	7	6		1	7	4	1			
Providencia		2	1	1			1	1				
Panamá		6	4	2			4	2				
Total		10	23		16	16	2		3	17	12	2

males 21.2-26.3, 3 females 16.2-26.5 mm.), San Blas Archipelago, Morbetupo, depth 10 m., 13 May 1974, J. E. McCosker, D. Diener; CAS 31661 (1 male 23.7 mm.), San Blas Archipelago, Río Tigre, depth 10 m., 14 May 1974, J. E. McCosker, D. Diener, R. Warner; CAS 31727 (1 male 16.8, 1 female 13.7 mm.), San Blas Archipelago, Cocos-Banderas Cays, depth 5 m., 15 May 1974, J. E. McCosker, S. McCosker, D. Diener; GCRL 3611 (1 immature 13.1 mm.), Devils Beach, Fort Sherman, depth to 9.1 m., 28 July 1968, C. E. Dawson.

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult

male united along entire length (fig. 17), papilla projecting beyond tip of spine a distance equal to a little less than one-third length of spine; first anal-fin spine longer than second anal-fin spine; obvious

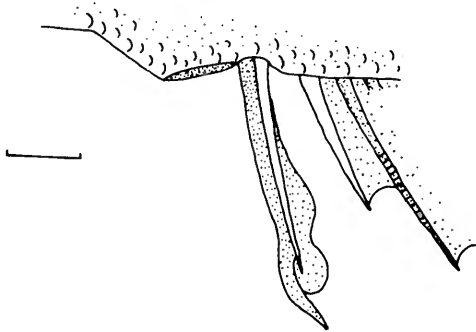


FIG. 17. Gonopodium of *Starksia occidentalis*, UF 10875, 24.1 mm. S.L. Line equals 1 mm.

pelvic-fin rays I,2; pectoral-fin rays 13-14 (usually 14); dorsal-fin elements XX-XXI,7-9 (usually XXI,8); anal-fin elements II,16-19 (usually II,17); lateral-line scales, 16-17 in arch (usually 17) and 19-21 in straight (usually 19), total 35-38 (usually 36); no dark diagonal bar on lower part of pectoral-fin base; body color pattern not consisting of well-defined, dark bands. May be distinguished from its closest congeners *S. guttata*, *S. brasiliensis*, and *S. ocellata* by the presence of distinct black vertical bars on the lips, and from *S. culebrae* by a Y-shaped pale bar running posteriorly from the orbit with distinct, dark, ring-like markings usually present under the ventralmost portion of the Y. It may further be distinguished from *S. ocellata*, *S. culebrae*, and *S. guttata* by possessing a lower number of vertebrae (mode 33 in *occidentalis* vs. 34 in others), a lower number of anal-fin soft rays (mode 17 in *occidentalis* vs. 18 in others), and a lower number of lateral-line scales in the straight portion (mode 19 or 20 in *occidentalis* vs. 21 in others). *Starksia occidentalis* also has a shorter snout than other species except *S. variabilis* (mean 49 in *occidentalis* vs. 56 in *ocellata*, 58 in *culebrae*, 58 in *guttata*, and 59 in *brasiliensis*). It also differs from *S. brasiliensis* in having two rows of infraorbital pores rather than a single row. *Starksia occidentalis* differs from its closest congener, *S. variabilis*, by having fewer anal-fin soft rays (mode 17 in *S. occidentalis* vs. 18), fewer total lateral-line scales (mode 36 in *S. occidentalis* vs. 37), a longer head (mean 310 in *S. occidentalis* vs. 304), and by its post-

orbital Y-shaped pale bar bordered ventrally (usually) with distinct dark ring-like markings.

Description.—Data for the holotype are presented first, followed in parentheses by the range for the paratypes, plus the mean for morphometric data and mode for meristics. Dorsal-fin elements XXI,7 (XX-XXI,7-9, usually XXI,8); anal-fin elements II,17 (II,16-19, usually II,17); pectoral-fin rays 14 (13-14, usually 14); vertebrae 33 (32-35, usually 33); lateral-line scales 17 in arch (16-17, usually 17) and 21 in straight (19-21, usually 19 or 20), total 38 (35-38, usually 36).

Measurements are based on 20 specimens, FMNH 83716, FMNH 84377, FMNH 84385, FMNH 84386, FMNH 84387, FMNH 84388, FMNH 84389, USNM 192401, USNM 192399, CAS 31610. Length of head 290 (286-355, 310); depth of body 209 (165-213, 195); diameter of eye 81 (74-105, 85); length of snout 37 (37-61, 49); length of upper jaw 132 (116-147, 135); length of pectoral fin 226 (203-294, 237); length of ventral fin 223 (174-281, 212); length of first dorsal-fin spine 71 (65-112, 83).

Narrow simple cirri present on nape, top of eyeball and rear margin of anterior nostril, orbital cirrus the longest, nostril cirrus three-fourths of orbital cirrus and cirrus on nape slightly shorter than nostril cirrus; teeth present on vomer and palatine bones; most or all scales of posterior part of lateral line with tubes and pores, scales of anterior arched portion with tubes and pores except usually the last one or two, which curve down to meet the straight portion; third pelvic ray greatly reduced and not obvious; pectoral fin extending posteriorly to between bases of 1st and 2nd soft anal-fin rays; belly mostly naked except for four or five scale rows immediately anterior to anus.

Color pattern of head.—Lips with distinct black vertical bars, anteriormost bar begins on upper lip just below nostril and runs ventrally onto lower lip, second bar begins on upper lip slightly posterior to first bar, third bar begins on upper lip under suborbital pore under eye, and fourth begins on maxillary and narrows ventrally toward lower jaw; cheek dusky with a pale Y-shaped horizontal marking running posteriorly from the orbit onto the opercle, its ventral margin with distinct, dark, ring-like markings with pale centers; top of head with brown band running between dorsal edges of opercle. Color pattern of body: background cream overlaid by three longitudinal rows of brown blotches, each blotch slightly smaller

than eye; dorsalmost row of 10 blotches located along base of dorsal fin, extending up onto bases of fin rays and membrane, first blotch located at base of first dorsal-fin spine, last blotch over hypural

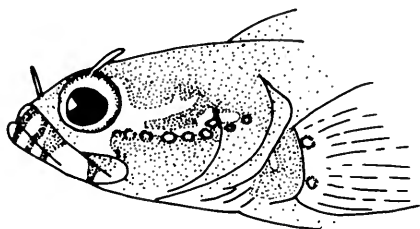


FIG. 18. Typical head color pattern of *Starksia occidentalis*.

(forming upper hypural marking); second row slightly dorsal to midline of body, each blotch slightly posterior to blotch above; third row slightly below midline of body and each blotch slightly posterior to blotch above and thus midway between blotches in dorsalmost row; distinctness of blotches variable, but usually well defined; pelvic fins cream; pectoral fins cream except for two dark, ring-like markings with cream centers located on basal portion of rays, one dorsally and one ventrally, dorsal fin with distinct dark brown spot on membrane between 1st and 2nd dorsal-fin spines in males, remainder of fin with scattered brown spots on fin rays, melanophores form spots running onto membranes; anal fin similar to dorsal fin; caudal fin crossed by a series of four or five light brown bars.

Etymology.—The name *occidentalis* refers to the fact that this species has the westernmost distribution of any species in the *S. ocellata*-complex.

Remarks.—*Starksia occidentalis* ranges from the east side of the Yucatán peninsula, México, south along the coast of Central America to Panamá. It is also present on the island of Old Providence off Nicaragua. With the exception of the southern species, *S. brasiliensis*, *S. occidentalis* exhibits the greatest divergence of all the *Starksia* species in the *S. ocellata*-complex. In addition to the distinctive color pattern, it has a shorter snout length and lower counts for lateral-line scales, vertebrae, and anal-fin soft rays. In Belize, where the most thorough collections have been made, it appears to be restricted to areas near continental influence. It has been taken on the Barrier Reef and around cays inside of the reef, but never on the atolls outside of the Barrier Reef. It appears to be most common in shallow waters, 1.5 m. or less; however, six individuals (FMNH 84381) were taken at a depth of 15.2 m. off Honduras. A discussion



FIG. 19. *Starksia variabilis*, FMNH 83717 (holotype), male 29.8 mm. S.L., Santa Marta, Colombia.

of the ecological relationships of *S. occidentalis* to other species in the genus is presented by Greenfield and Johnson (MS).

***Starksia variabilis* new species. Figures 19-21. Tables 1, 2.**

Holotype—FMNH 83717, adult male 29.8 mm. SL., Colombia, northeast of Bahía de Nenquange, Parque Nacional Tayrona, Santa Marta (about 11°40'N. lat., 74°30'W. long), depth 1 m. (\pm .2 m.), August, 1976, Arturo Acero P.

Paratypes.—All collected with the holotype. FMNH 83718 (5 males, 23.7-32.9 mm. and 2 females, 25.1-27.6 mm.); USNM 217832 (1 female, 28.9 mm.); GCRL 15739 (1 male, 24.8 mm.); UF 23349 (1 male, 23.3 mm.); CAS 40229 (1 female, 21.7 mm.).

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult male united along entire length (fig. 20), the papilla projecting a short distance beyond tip of spine; first anal-fin spine longer than second anal-fin spine; obvious pelvic-fin rays I,2; pectoral-fin rays 13-15 (usually 14); dorsal-fin elements XX-XXI,7-9 (usually XXI,8); anal-fin elements II,17-18 (usually II,18); lateral-line scales, 16-18 in arch (usually 17) and 20-21 in straight (usually 20), total 36-37 (usually 37); no dark diagonal bar on lower part of pectoral-fin base;

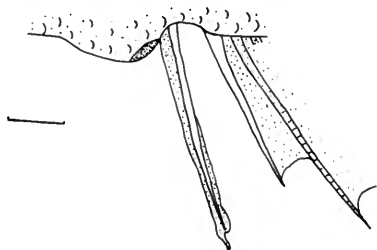


FIG. 20. Gonopodium of *Starksia variabilis*, FMNH 83718 (paratype), male, 32.9 mm. S.L., Santa Marta, Colombia.

body color pattern not consisting of well-defined, narrow, dark bands. May be distinguished from its closest congeners *S. guttata*, *S. brasiliensis*, and *S. ocellata* by the presence of distinct black vertical bars on the lips, from *S. culebrae* by a reticulated pale pattern on the side of the head, but never with a single horizontal pale bar. It may further be distinguished from *S. ocellata*, *S. culebrae*, and *S. guttata* by possessing a lower number of lateral-line scales in the straight portion (mode 20 in *S. variabilis* vs. 21 in others). *Starksia variabilis* has a shorter snout than all other species in the complex except *S. occidentalis* (mean 48 in *S. variabilis* vs. 56 in *S. ocellata*, 58 in *S. culebrae*, 58 in *S. guttata*, and 59 in *S. brasiliensis*). It also differs from *S. brasiliensis* in having two rows of infraorbital pores rather than a single row. *Starksia variabilis* differs from its most closely-related species, *S. occidentalis*, by having more anal-fin soft rays (mode 18 in *S. variabilis* vs. 17), more total lateral-line scales (mode 37 in *S. variabilis* vs. 36), a shorter head (mean 304 in *S. variabilis* vs. 310), and by the distinctive color pattern on the side of the head. *S. occidentalis* has a Y-shaped pale bar running posteriorly from the orbit with distinct, dark ring-like markings usually present under the ventralmost portion of the Y. In *S. variabilis* the pale pattern on the side of the head is more complex and variable (fig. 21). None of the individuals have the simple Y patterns, but rather have a more reticulated pattern with the pale area enclosing dark blotches. Occasionally dark ring-like markings are present within the pale area, ventral to it, or both.

Description.—Data for the holotype are presented first, followed in parentheses by the range for the paratypes, plus the mean for morphometric data and mode for meristics. Dorsal-fin elements XXI,8 (XX-XXI,7-9, usually XXI,8); anal-fin elements II,18 (II,17-18, usually II,18); pectoral-fin rays 14 (13-15, usually 14); vertebrae 34 (33-34, usually 33 or 34); lateral-line scales 17 in arch (16-18, usually 17) and 20 in straight (20-21, usually 20), total 37 (36-38, usually 37).

Measurements are based on all 12 specimens in the type series. Length of head 302 (289-316, 304); depth of body 201 (174-210, 192); diameter of eye 80 (76-90, 83); length of snout 57 (36-58, 48); length of upper jaw 151 (127-151, 138); length of pectoral fin 228 (212-258, 233); length of ventral fin 178 (145-211, 193); length of first dorsal-fin spine 74 (62-82, 75).

Narrow simple cirri present on nape, top of eyeball and rear margin of anterior nostril, nostril cirrus the longest, orbital slightly

shorter and nape slightly shorter than orbital cirrus; teeth present on vomer and palatine bones; most or all scales of posterior part of lateral line with tubes and pores, scales of anterior arched portion with tubes and pores except usually the last one or two which curve down to meet the straight portion; third pelvic ray greatly reduced and not obvious; pectoral fin extending posteriorly to base of 1st soft anal-fin ray; belly mostly naked except for five or six scale rows immediately anterior to anus.

Color pattern of head.—Lips with distinct black vertical bars, anteriormost bar beginning on upper lip just below nostril and running ventrally onto lower lip, second bar beginning on upper lip slightly posterior to first bar, third bar beginning on upper lip under suborbital pore under eye, fourth bar beginning on anterior portion of maxillary and running ventrally onto lower jaw either as a solid bar or as separated blotches, occasionally isolated blotches present between third and fourth bar, a distinct black blotch on posterior margin of maxillary; cheek dusky brown with variable pale pat-

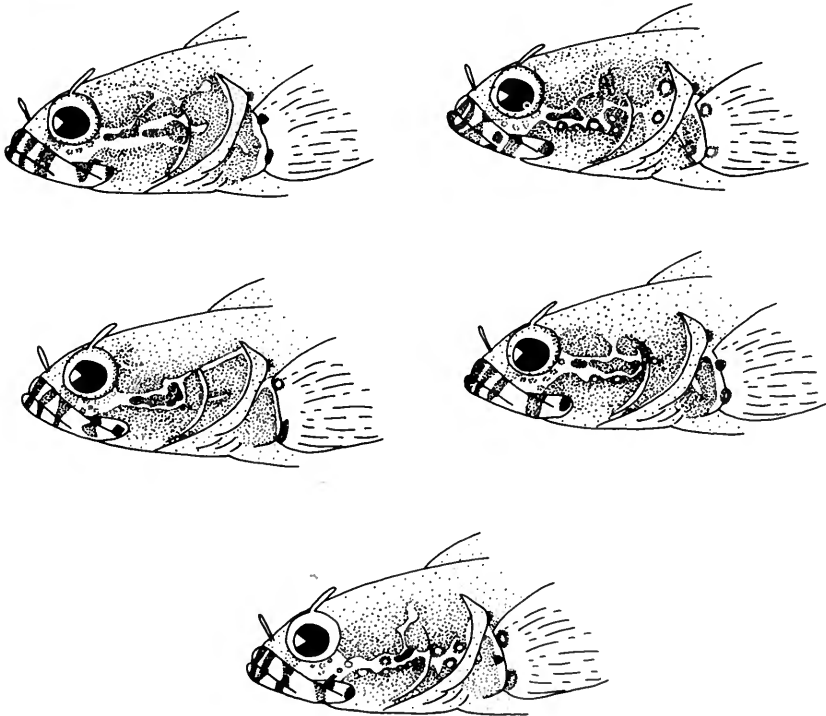


FIG. 21. Typical head color patterns of *Starksia variabilis*.

terns, beginning as a single pale bar at the posterior margin of the eye and branching into two or more portions posteriorly across the cheek, the pale areas enclosing dark brown blotches, occasionally with dark ring-like markings present either within the pale area, ventral to it or both; interorbital white with a black blotch in the center; top of head with a dark brown rectangular blotch in area between posterior margin of eye and posterior margin of preopercle, a white band posterior to the rectangular blotch, followed posteriorly by a white chevron anterior to the 1st dorsal-fin spine. Color pattern of body: background cream or white overlaid by three longitudinal rows of brown blotches, each blotch slightly smaller than eye; dorsalmost row of 10 blotches located along base of dorsal fin extending up onto bases of fin rays and membranes, first blotch located at base of first dorsal-fin spine, last blotch over hypural (forming upper hypural marking); second row slightly dorsal to midline of body, each blotch slightly posterior to blotch above; third row slightly below midline of body and each blotch slightly posterior to blotch above and thus midway between blotches in dorsalmost row; distinctness of blotches variable, but usually well defined, distinct black or dark brown dots often present around edges of blotches; pelvic fins cream; pectoral-fin rays dusky, membranes cream, two dark-brown markings, either solid or ring-like with cream centers located on basal portion of rays, one dorsally and one ventrally; dorsal fin with distinct, dark brown spot on membrane between 1st and 2nd dorsal-fin spines in males, remainder of fin with alternating dark brown and white areas corresponding to the dorsalmost row of blotches on body, each spine and soft ray with alternating white and dark brown bars. Anal fin similar to dorsal fin; caudal fin dusky with scattered black melanophores.

Etymology.—The name *variabilis* refers to the unusual variation of the coloration on the side of the head when compared to other members of the *S. ocellata*-complex.

Remarks.—*Starksia variabilis* is known only from the type series collected at Santa Marta, Colombia. This species is clearly most closely related to *S. occidentalis* which occurs along the Atlantic coast of Central America, based on the presence of barred lips in both species, a shared short snout (mean = 48 in *S. variabilis* and 49 in *S. occidentalis* whereas all other species in the complex have means of 56 or greater), and the variable, somewhat reticulated color pattern on the side of the head of *S. variabilis* which could be derived from the basic Y-shaped pattern present in *S. occidentalis*.

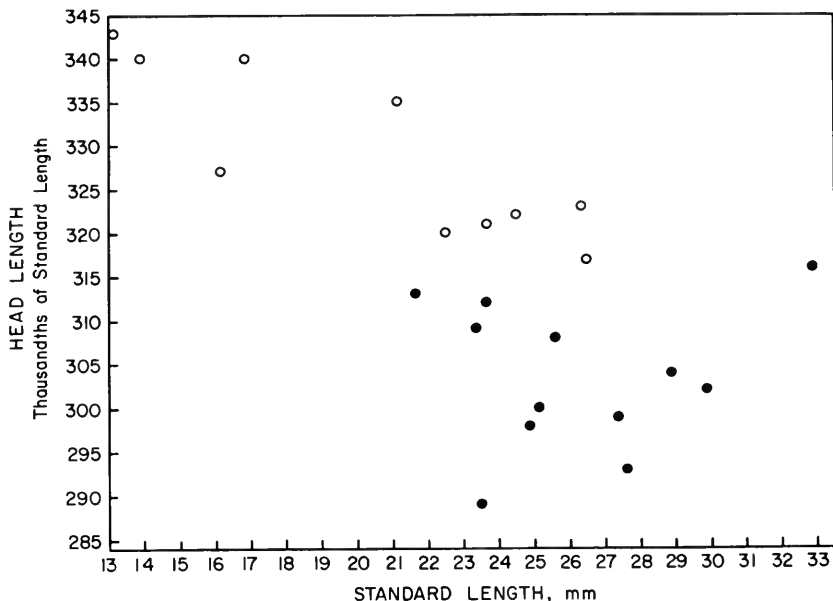


FIG. 22. Head length in thousandths of standard length vs. standard length in millimeters for *Starksia variabilis* (solid circles) and *S. occidentalis* from Panamá (open circles).

It can be argued that *S. variabilis* is simply a geographic variant of *S. occidentalis*; however, I have decided to recognize it as a distinct species for several reasons. *Starksia variabilis* exhibits modal differences in counts for anal-fin soft rays and total number of lateral-line scales that are greater than the differences exhibited between other species in the complex (i.e., *S. ocellata* and *S. culebrae*) and also greater than those exhibited by other species pairs in this morphologically conservative genus (i.e., *S. sluiteri*, *S. fasciata*, and *S. y-lineata*). In other members of the species complex, coloration on the side of the head has been considered to be a significant character and *S. variabilis* exhibits a pattern that despite its variability is clearly different from *S. occidentalis*. This variability in itself may serve as an additional indication of genetic distinctness, since in *S. occidentalis* there is little variation in coloration of the side of the head. In addition, when the freshly-caught specimens of *S. variabilis* were received they still retained some of their live coloration, which revealed that the ring-like markings under the eye and cheek were lemon yellow. In contrast, live specimens from Belize have white markings and no yellow: *Starksia variabilis* has a shorter head

length (mean = 304) than *S. occidentalis* (mean = 310). This character exhibits allometric growth, with smaller individuals having longer heads; however, specimens of comparable size are separable. When values for individuals from the total range of *S. occidentalis* are plotted against the values for *S. variabilis*, considerable overlap occurs; however, when only the Panamá population (which is geographically closest to *S. variabilis*) is plotted, 100 per cent separation is possible. The Panamá population of *S. occidentalis* exhibits values of 317 or greater, whereas *S. variabilis* exhibits values of 316 or less (fig. 22). This shift in values in adjacent populations of *S. occidentalis* can be interpreted as character displacement, a feature indicating genetic divergence.

The lack of collections from the area between Santa Marta, Colombia, and Panamá is indeed unfortunate, since this is a straight-line distance of at least 500 km. and the coastline distance would be even greater. It is recognized that clinal variation between these locations is possible; however, until further collections are obtained I recognize these two species as distinct.

***Starksia brasiliensis* (Gilbert). Figures 23-25. Tables 1, 2.**

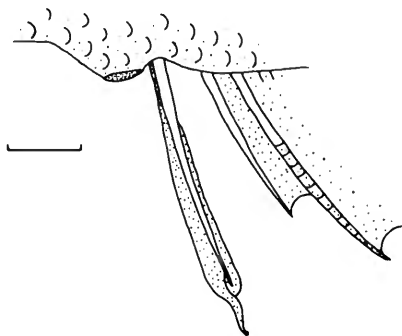
Brannerella brasiliensis Gilbert 1900, p. 180, pl. 9, fig. 1 Type locality: coral reef near Maceió, Brazil.

Diagnosis.—A species of *Starksia* with essentially naked belly; simple orbital cirrus; genital papilla and first anal-fin spine in adult male united along entire length (fig. 24), papilla projecting beyond tip of spine a distance equal to one-fourth length of spine; first anal-fin spine longer than second anal-fin spine; obvious pelvic-fin rays I,2; pectoral-fin rays 14; dorsal-fin elements XX-XXI,7-8 (usually XXI,7); anal-fin elements II,16-17 (usually II,17); lateral-line scales, 15-16 in arch (usually 15) and 19-20 in straight (usually 20), total



FIG. 23. *Starksia brasiliensis*, GCRL 9476, male, 24.6 mm. S.L., Brazil.

FIG. 24. Gonopodium of *Starksia brasiliensis*. GCRL 9476, 24.6 mm. S.L. Line equals 1 mm.



34-36 (usually 35); no dark diagonal bar on lower part of pectoral-fin base; vertebrae 30(1), 33(3); body color pattern not consisting of well-defined, dark bands. May be distinguished from its closest congeners *S. ocellata*, *S. guttata*, *S. culebrae*, *S. occidentalis*, and *S. variabilis* in having a single row of infraorbital pores rather than two rows. It may be further separated from *S. culebrae*, *S. occidentalis*, and *S. variabilis* by lacking distinct black vertical bars on the lips. *Starksia brasiliensis* is clearly separable from *S. guttata* and *S. ocellata* in having a very narrow Y-shaped pale bar extending from the orbit posteriorly to the preopercular margin.

Description.—Meristics are presented in the diagnosis. Measurements are presented in Table 2 and are based on the four specimens listed on p. 32.

Color pattern of head.—*Starksia brasiliensis* is clearly separable from other members of the species complex by the presence of a very narrow, Y-shaped pale bar that extends from the orbit posteriorly to the preopercular margin. The diameter of the bar directly above the maxillary is considerably less than one-half of the pupil diameter, whereas in *S. guttata* the diameter of the bar is equal to or greater than half of the pupil diameter. A few small, distinct, dark ring-like markings with pale centers are present under the ventralmost por-

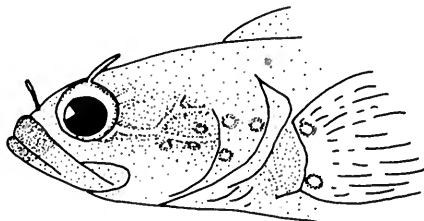


FIG. 25. Typical head color pattern of *Starksia brasiliensis*.

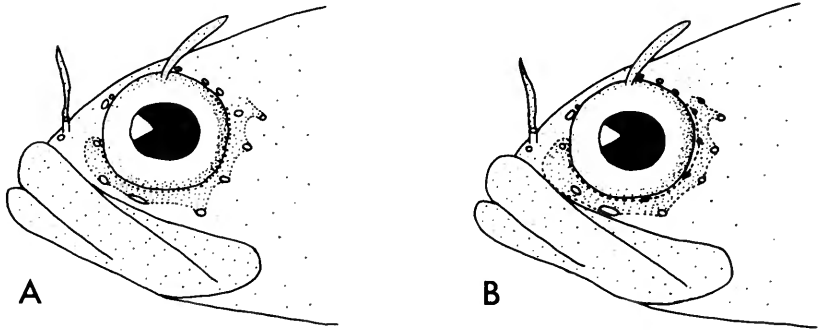


FIG. 26. Head pore patterns for (a) *Starksia brasiliensis*, GCRL 9476 and (b) *S. guttata*, ANSP 117893.

tion of the Y. An additional dark ring-like marking may be present inside the Y, as well as three larger ring-like markings on the opercle. The lips lack distinct black vertical bars, but are peppered with black pigment that is more heavily concentrated anteriorly (fig. 25). The lack of distinct vertical bars on the lips separates this species from *S. culebrae*, *S. variabilis*, and *S. occidentalis*. This color pattern is clearly illustrated in Gilbert (1900, pl. 9, fig. 1).

Remarks.—*Starksia brasiliensis* is known only from Brazil, south of Recife. It is possible that the mouth of the Amazon forms a barrier to its northward dispersal; however, shallow-water marine collections from the mouth of the Amazon north to Trinidad are not available. In addition to the distinctive color pattern, *S. brasiliensis* has fewer scales in the lateral line and a lower number of soft dorsal-fin rays. In addition, *S. brasiliensis* may be separated from all other species in the complex by having a single series of infraorbital pores rather than two series (fig. 26). This species bears the closest resemblance to *S. guttata*, which is geographically closest. In addition to the similarities of the Y-shaped pattern on the head, the body of *S. brasiliensis* tends to approach a spotted pattern as in *S. guttata*, but not distinctly so.

Material examined.—Brazil—CAS-SU 7750(1) 25.0 mm. SL, holotype; CAS-SU 53510(1) 20.8 mm., paratype; GCRL 9476(2) 24.6 and 26.0 mm.; Bahía, Isla Itaparica, Barra do Gil, 13°00'S lat., -38°37'W. long.

DISCUSSION

The recognition of five separate species within the currently rec-

ognized species limits of *S. ocellata* (*sensu* Böhlke and Springer, 1961), in addition to *S. guttata*, presents another example of the importance of color patterns within the genus *Starksia*. Gilbert (1965) discussed the fact that three species, *S. y-lineata*, *S. fasciata*, and *S. sluiteri*, can only be distinguished by color pattern, exhibiting no differences in meristics or morphometrics. Meristic and morphometric differences between other species pairs is often only modal. I believe that the color pattern on the lips and side of the head are particularly important as possible mechanisms of species recognition. Breder (1941) stated that when a gravid female of the clinid *Paraclinus marmoratus* approached a nesting site guarded by a male, the male underwent a striking color change, “. . . an intense purple coloration which was nearly black and dotted with brilliant metallic blue.” In addition, a head-on, open-mouth threat display was observed in the male. In the closely related family Chaenopsidae, Wickler (1967) has shown that *Emblemaria pandionis* has a head-on display that includes opening the mouth and swaying the head from side to side. Greenfield and Johnson (MS) have reported similar displays for *Acanthemblemaria spinosa*. Wickler (1967, p. 541) noted the following for blennioid fishes: “Nodding in blennies can be either a courtship or a threat movement, depending on the particular species. Since these fishes usually lie within a hole, with only the head and sometimes the forepart of the body visible, colour patterns underlining the nodding movements are mainly confined to these parts of the body. *Head and face colourations are, therefore, characteristic for the species and/or sex or motivational state of the fish*” (italics mine).

The importance of head coloration in species recognition is further supported by the fact that within the *S. ocellata*-complex, species with and without bars on the lips have alternating ranges (fig. 27). *Starksia ocellata* from Florida lacks bars on the lips, whereas the species to the south, *S. culebrae*, has distinct black bars on the lips. *Starksia guttata*, which occurs to the south of *S. culebrae* and reaches west along the coast of South America at least to Curaçao, lacks bars on the lips. Farther west in Colombia *S. guttata* is replaced by *S. variabilis*, which has very prominent black bars on the lips. *Starksia brasiliensis* lacks bars on the lips, as does *S. guttata*; however, it occurs (as far as is known) far to the south of *S. guttata*, south of Recife in Brazil. The only pair of species for which this correlation does not hold includes *S. variabilis* from Colombia and *S. occidentalis* from the coast of Central America. Both of these species

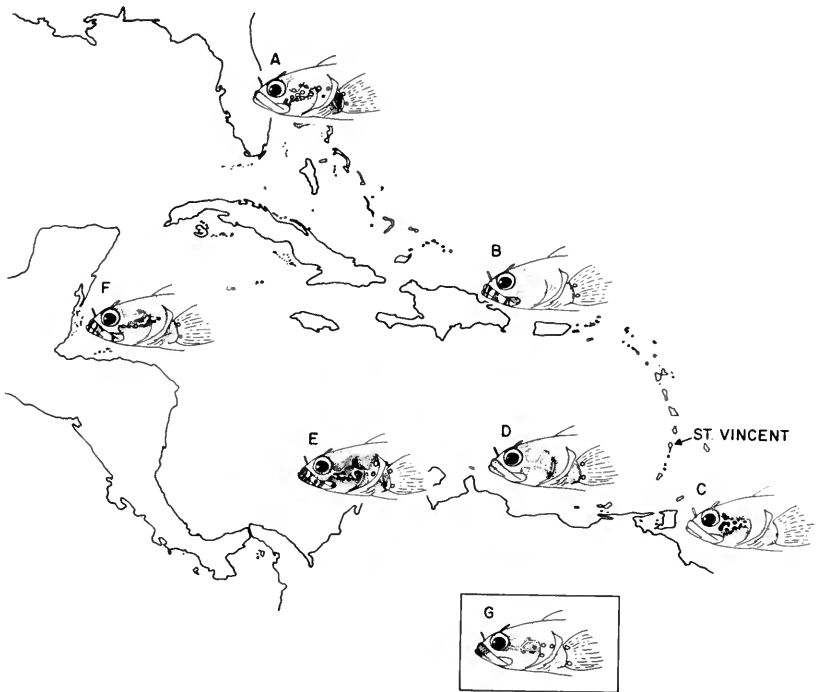


FIG. 27. Distribution of the *Starksia ocellata* superspecies: A, *S. ocellata*; B, *S. culebrae*; C, D, *S. guttata*; E, *S. variabilis*; F, *S. occidentalis*; G, *S. brasiliensis*.

have bars on the lips; however, they differ in the coloration of the sides of the head, in addition to which *S. variabilis* has lemon yellow spots under the eye and on the cheek, whereas *S. occidentalis* has white spots.

As far as is known, all of the species within the *S. ocellata*-complex have allopatric distributions. In fact, in the case of *S. culebrae* and *S. guttata*, there appears to be a rather sharp break between these two forms at St. Vincent Island. However, the possibility of past or present parapatry is suggested by the two cases of apparent character displacement (*S. occidentalis* and *S. variabilis*; *S. culebrae* and *S. guttata*), which usually develops as a result of interactions while in contact. The allopatric distribution of these species could be considered evidence that the observed variation is at the subspecific level. However, on the basis of coloration, and in some cases meristics and morphometrics, it is possible to identify all individuals without knowledge of the locality from which they were obtained.

Thus, the morphological differentiation is above that normally observed at the subspecific level. This complex of entirely allopatric species seems to fit well into the superspecies category proposed by Amadon (1966, p. 245). Amadon defined the superspecies as follows, "A group of entirely or essentially allopatric taxa that were once races of a single species but which now have achieved species status." Mayr (1963, p. 499) has defined the category as "... a monophyletic group of entirely or essentially allopatric species that are too distinct to be included in a single species." Following the terminology proposed by Amadon, each of the species within the *S. ocellata* superspecies would be termed an allospecies. As summarized by Amadon (1966, p. 247), the use of the superspecies concept "... will remove the temptation to treat as subspecies various allopatric forms which are so distinct as to make such a procedure questionable."

The discovery of this superspecies with its six allospecies poses some interesting zoogeographical questions. Briggs (1974) has divided the tropical western Atlantic into three zoogeographical provinces, Caribbean, Brazilian, and West Indian. The recognition of *Starksia braziliensis* as a distinct species adds to the level of endemism for the Brazilian Province. In an example from another family, investigation of the *Eupomacentrus fuscus*-complex showed that *E. fuscus* is present only off Brazil, whereas *E. dorsopunicans* (previously called *E. fuscus*) replaces it to the north (Greenfield and Woods, 1974). Gilbert (1977) has shown that *Apogon maculatus* is replaced by *A. americanus* in Brazil. Thus it is likely that further investigations of widespread species may show that levels of endemism in the Brazilian Province are greater than has previously been recognized.

Briggs has also recognized the West Indian Province (Bahamas to Grenada) as being distinct from the Caribbean Province (including Florida, Central America, and the northern coast of South America), based mainly on the level of endemism. For the fishes, this decision was based in part on work on the fishes of the Bahama Islands (Böhlke and Chaplin, 1968), and work on the seven-spined gobies (Böhlke and Robins, 1968). Briggs states that for the gobies, of the 24 species occurring in the West Indies, only 11 appear to be shared with the mainland (Caribbean Province). Our collections from Belize (of which only a portion of the gobies have been identified) and the records from Colombia presented by Palacio (1974) reduce the number of species occurring only at the Bahama Islands, Antilles,

or both to only five. Briggs also states that of the 466 shore species treated by Böhlke and Chaplin (1968), 87, or about 19 per cent, have not been taken outside the West Indies. Examining just the blennioid fishes collected from Belize and Honduras shows that 14 of the species considered to be in the group of 87 also occur along the coast of Central America (Greenfield and Johnson, MS). In addition, three more species of blennioids described since Böhlke's and Chaplin's treatment, and considered to occur only in the West Indies, have been taken along the Central American coast. If unpublished records from other families were considered, the 77 species left in this category would be further reduced. Thus, additional collecting along the coast of Central and South America has shown that the distributions of many reef-fish species in the tropical Western Atlantic are wider than was once believed, and that the levels of endemism cited for a particular locality may simply be a function of the intensity of the collecting.

The separation of the *Starksia ocellata* superspecies into six allo-species presents a paradox. Whereas other reef species are being shown to have widespread distributions throughout the tropical Western Atlantic, the species of *Starksia* exhibit distinct, restricted distributions. Although this pattern is unusual, it is not unique. Collette (1974) reviewed the toadfish genus *Sanopus*, recognizing two species from Yucatán, México (*S. splendidus* and *S. johnsoni*), one species from Belize (*S. astrifer*), and a fourth (*S. barbatus*) from Honduras south to Panamá. The two Yucatán species are sympatric; however, this pair and all other species appear to have allopatric distributions. Intensive collections throughout Belize and Honduras have emphasized this separation: the only species of *Sanopus* we have collected at Belize is *S. astrifer* (Greenfield and Greenfield, 1973), and a month of intensive collecting in Honduras yielded only specimens of *S. barbatus*. *Sanopus astrifer* and *S. barbatus* appear to occupy very similar habitats, caves or hollows underneath coral heads, usually with sand bottoms. Collette (1974) indicates similar habitats for *S. splendidus* and *S. johnsoni*.

It would thus appear that attempts to divide the fish fauna of the tropical Western Atlantic into provinces is premature. Although recent strides have been made in investigating the fish faunas of Central America and the northern coast of South America, many areas lack proper coverage. Until such surveys have been completed, the use of levels of endemism to designate fish faunal provinces will be meaningless.

A KEY TO THE ALLOSPECIES OF THE SUPERSPECIES *Starksia ocellata*

1. Infraorbital pores in a single series (fig. 26a); narrow Y-shaped pale bar extending from orbit posteriorly to preopercular margin, diameter of bar directly above maxillary considerably less than one-half pupil diameter; lips lacking distinct vertical bars *S. brasiliensis* (Gilbert)
Brazil
Infraorbital pores in two rows (fig. 26b); no Y-shaped pale bar on side of head or, if present, equal to or greater than one-half pupil diameter; distinct black vertical bars on lips either present or absent. 2
2. Lips with distinct black vertical bars. 3
Lips lacking distinct black vertical bars. 4
3. Side of head with a pale horizontal bar running from orbit posteriorly past edge of preopercle onto opercle, not branching into a Y (fig. 7); snout length 46-72, mean 58 *S. culebrae* (Evermann and Marsh)
Greater Antilles and south to St. Vincent
Side of head without a simple pale horizontal bar; pale area either Y-shaped or reticulated and enclosing dark blotches; snout length 36-61, mean 48 or 49. 5
4. Side of head with small, dark ring-like markings with light centers, most included within a horizontal pale area running from the orbit posteriorly to the edge of the preopercle (fig. 4). *S. ocellata* (Steindachner)
Florida north to North Carolina
Side of head usually with a pale horizontal bar originating from the orbit and branching into a definite Y posteriorly, occasionally with dark ring-like markings, or overlaid with solid dark spots (fig. 10a,b,c). *S. guttata* (Fowler)
Curaçao to Trinidad and north up Lesser Antilles
to Tobago Cays in the Grenadines.
5. Side of head with a Y-shaped pale bar usually bordered ventrally with distinct dark ring-like markings (fig. 18); anal-fin soft rays 16-19, usually 17.
S. occidentalis n. sp.
Atlantic coast of Central America
Side of head without a simple Y pattern, pale area reticulated and enclosing dark blotches (fig. 21); anal-fin soft rays 17-18, usually 18. *S. variabilis* n. sp.
Colombia

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