Abstract. - Western Atlantic tonguefishes of the Symphurus plagusia (Schneider, in Bloch and Schneider 1801) complex are distinguished from other Atlantic Symphurus species by the possession of 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal-fin pterygiophores and neural spines, absence of a pupillary operculum, reduced or absent dentition on ocular-side jaws, and an unpigmented peritoneum. Considerable taxonomic uncertainty has been associated with nominal species of this complex, but the most common practice has been to recognize one widespread species (S. plagusia) with two subspecies ranging from the Caribbean southward to Uruguay, and a second species, S. civitatium Ginsburg 1951, occurring in inshore areas along the southeastern and Gulf of Mexico coasts of the United States and northern Mexico. The validity of S. civitatium is confirmed in this study. Examination of tonguefishes from the Caribbean and southward indicates that specimens previously identified as S. plagusia do not comprise one species with two allopatric subspecies, but rather four largely sympatric, albeit not necessarily syntopic, species. Symphurus plagusia, the first described species in this complex, occurs in inshore habitats ranging from the Caribbean to Rio de Janeiro. Symphurus tessellatus (Quoy and Gaimard 1824), removed from the synonymy of S. plagusia, occurs in nearshore, estuarine, and neritic waters throughout the Caribbean southwards to Uruguay. Two new species, S. oculellus occurring in neritic waters off northern South America (Guyana to northern Brazil), and S. caribbeanus (nearshore habitats throughout the Caribbean), are described and figured. A key to the western Atlantic species of this complex is provided.

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Western Atlantic Tonguefishes of the Symphurus plagusia Complex (Cynoglossidae: Pleuronectiformes), with Descriptions of Two New Species*

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Shallow-water symphurine tonguefishes possessing 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal pterygiophores and neural spines, with reduced or absent dentition on ocular-side jaws, an unpigmented peritoneum, and lacking a pupillary operculum comprise the Symphurus plagusia (Schneider, in Bloch and Schneider 1801) complex.** Five western Atlantic and several eastern Pacific species of tonguefishes are recognized in this complex. Throughout the western Atlantic, from North Carolina, U.S.A., to Uruguay (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987), these commonly collected tonguefishes are abundant locally in estuarine and nearshore habitats as well as on sandy or muddy substrates on the inner continental shelf (Meek and Hildebrand 1928, Ginsburg 1951, Lowe-McConnell 1962, Caldwell 1966, Cervigon 1966, Carvalho et al. 1968, Palacio 1974, Menezes and Benvegnú 1976, Lema and Oliveria 1977, Lema et al. 1980, Munroe 1987).

Nomenclatural uncertainty and questions regarding taxonomic validity have been associated with these western Atlantic tonguefishes since the first description of a species from Jamaica by Browne (1756). Much of the confusion centers on species collected in shallow waters of the Caribbean and coastal seas of Central America and much of South America. At least ten combinations of names have been used for these tropical western Atlantic, shallow-water tonguefishes.

Historically (Kaup 1858, Jordan and Evermann 1898, Chabanaud 1949), Atlantic members of this species complex were long regarded as comprising populations of a single widespread, polytypic species, Symphurus plagusia. This nomenclatural arrangement began with Kaup (1858) and has continued to the present (Jordan and Goss 1889, Jordan and Evermann 1898, Ginsburg 1951, Menezes and Benvegnú 1976, Rosa 1980, Lucena and Lucena 1982). Ginsburg considered the tropical western Atlantic members of this complex to represent two allopatric subspecies, and his newly-described S. civitatium with its disjunct northern distribution, perhaps representing a third subspecies of one wide-ranging polytypic species. However, the most recent review of Symphurus of southern South America (Menezes and Benvegnú 1976) questioned recog-

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^{**} There is another western Atlantic tonguefish, S. plagiusa (Linnaeus), completely allopatric from S. plagusia, which unfortunately has a nearly identical spelling for its specific epithet. It is emphasized that these are completely different and distinctive species that should not be confused because of similarities in their names.

nition of only one species in the tropical western Atlantic region.

My examination of approximately 1000 specimens of Symphurus possessing 12 caudal fin rays and a 1-4-3 interdigitation pattern, collected in inshore waters from North Carolina, throughout the Gulf of Mexico and Caribbean, to Uruguay, reveals that previous studies failed to recognize the presence of multiple sympatric species among their material. Neither the hypothesis of multiple populations within a single polytypic species, envisioned especially by Jordan and co-workers, nor Ginsburg's hypothesis of one widespread polytypic species comprised of allopatric subspecies, adequately explain the divergent morphological variation observed in the specimens and the sympatric (sometimes syntopic) occurrences of specimens with different morphological attributes. Instead, the present study recognizes not one, but rather five, western Atlantic members of the S. plagusia complex, which are somewhat phenetically similar species that differ in morphology and pigmentation. Four of these species have largely sympatric, but not necessarily syntopic, distributions. The fifth species, S. civitatium Ginsburg 1951, is completely allopatric to the others, occurring along the southeastern and Gulf coasts of the United States and northern Mexico.

Three species in this assemblage, *S. plagusia*, *S. tessellatus* (Quoy and Gaimard 1824), and *S. civitatium*, were described previously. Two additional species are described herein. Available taxonomic and ecological information is summarized, differential diagnoses are provided for each species, and a key to identification of the five species is included.

Materials and methods

Methods for counts and measurements and general terminology follow Munroe and Mahadeva (1989) and Munroe (1990). Meristic data, exclusive of scale counts, were taken from radiographs. ID pattern refers to the pattern of interdigitation of dorsal pterygiophores and neural spines. In species accounts, total ranges for meristic features are presented first, followed by modal counts when data were sufficient.

Measurements less than 150 mm were taken to the nearest 0.1 mm with dial calipers or ocular micrometer. Measurements over 150 mm were taken to the nearest mm with a steel ruler. Measurements are expressed either as thousandths of standard length (SL) or thousandths of head length (HL).

Morphometric abbreviations

ABL anal fin length

- BD body depth CD chin depth CFL caudal fin length DBL dorsal fin length ED eve diameter HL head length HW head width LHL lower head lobe width OPUL width of upper opercular lobe OPLL width of lower opercular lobe PA pelvic to anal fin length PAL
- PAL preanal length PDL predorsal lengt
- PDL predorsal length PL pelvic fin length
- POL postorbital length
- SNL snout length
- UHL upper head lobe width
- UJL upper jaw length

All descriptions of pigmentation are based on fishes fixed in formalin and stored in ethyl or isopropyl alcohol.

Maturity was estimated by macroscopic examination of stages of developing ova and extent of posterior elongation of the ovaries (ovaries of mature females are sometimes conspicuous through the body wall in transmitted light; in immature females and large females, ovaries are best observed by dissection). Since no obvious differences in male testicular size were apparent, estimates of maturity were based entirely on females. Immature females were those with nonelongate or only partially elongate ovaries. Mature females had fully elongate ovaries. Gravid females were those individuals with enlarged ovaries filled with large, macroscopically visible ova.

When available, depth-of-capture information (converted to the nearest meter) was recorded and summarized for specimens listed in the "Material examined" sections in each species account. If depth of capture included a range of depths over which the nets were towed, a mean depth for that particular trawl was calculated.

Synonomies are selective for *S. plagusia* and *S. tessellatus* because of the numerous locality citations; synonomies are presumed to be complete for the other species. Because of their common occurrence, *S. plagusia* and *S. tessellatus* are listed in numerous studies, beginning with the oldest literature dealing with shallow-water marine fish faunas of the Caribbean and temperate regions of eastern South America. Since little descriptive or ecological information was provided in most original accounts of these tonguefishes, it is often impossible, when reviewing the literature, to determine accurately the species studied. For example, in studies of tonguefishes occurring in the Caribbean and along the coasts of Central and northern

South America, the possibility exists of any combination of four species being considered in the accounts. Since many of these earliest studies of Caribbean fishes considered only shore-zone fishes, much of this literature is discussed under the account of *S. plagusia*, one of the more widely distributed shallow-water species, and the one first named in the complex. Most references from extreme southern South America pertaining to shallow-water tonguefishes possessing 12 caudal fin rays refer to *S. tessellatus* and are included in the synonymy of that species. Synonymies for the remaining species include only those studies from which I examined specimens.

Abbreviations of institutions

Institutions providing study material, or in which type material is deposited are:

ALA Museum of Natural History, University of Alabama, University

ANSP Academy of Natural Sciences, Philadelphia

BMNH British Museum of Natural History, London

- CAS-SU California Academy of Sciences, San Francisco
- **FMNH** Field Museum of Natural History, Chicago **GCRL** Gulf Coast Research Laboratory, Ocean
- Springs
- IMS Marine Sciences Institute, University of Texas

at Austin, Port Aransas

- LACM Natural History Museum of Los Angeles County, Los Angeles
- MCP Museu de Ciencias, Pontificia Universidade Catolica do Rio Grande do Sul, Porto Alegre
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge
- MHNN Musee d'Histoire Naturelle de Neuchâtel, Neuchâtel
- MNHN Museum National d'Histoire Naturelle, Paris
- **TCWC** Texas Cooperative Wildlife Collection, Texas A&M University, College Station
- TU Department of Zoology, Tulane University, New Orleans
- UF Florida State Museum, University of Florida, Gainesville
- **UFPB** Departamento de Sistematica e Ecologia, Universidade Federal da Paraiba, Joao Pessoa
- **UMML** Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami
- **UMMZ** Museum of Zoology, University of Michigan, Ann Arbor
- UPRM University of Puerto Rico at Mayaguez
- USA University of South Alabama, Mobile
- **USNM** National Museum of Natural History, Smithsonian Institution, Washington, DC
- ZMA Zoologisch Museum, Universiteit van Amsterdam

Artificial key to Western Atlantic members of the Symphurus plagusia complex

Large black spot on outer margin of ocular-side opercle; dorsal fin rays 91–107; anal fin rays 77–89; total vertebrae 50–55	2
No obvious black spot on ocular-side opercle; dorsal fin rays 86–97; anal fin rays 70–81; total vertebrae 46–51	3

- 2a 4-8 small ctenoid scales on blind side of posterior rays of dorsal and anal fins; ocular-side lower jaw without fleshy ridge on posterior portion; jaws reaching only to rear margin of pupil or rear margin of eye; crossbands wide, usually nine or less; posterior third of dorsal and anal fins without alternating series of pigment blotches and unpigmented areas, usually becoming increasingly darker posteriorly (black in mature males); dorsal fin rays 91-102; anal fin rays 77-86; total vertebrae usually 50-53. (Caribbean Sea to Uruguay) S. tessellatus (Quoy and Gaimard)

3a	Dorsal and anal fins with an alternating series of dark blotches and unpigmented areas; ocular-
	side lower jaw without fleshy ridge on posterior portion; snout pointed; distance between upper
	eye and dorsal fin base usually slightly smaller than twice eye diameter; body with 9–15, narrow,
	dark crossbands; eye usually 9.0-10.0% of HL. (Caribbean Sea) S. caribbeanus new species

- 4b Eye 7.0-11.0% HL, usually 8.0-10.0% HL; total vertebrae usually 47-49; dorsal fin rays 86-93; anal fin rays 70-78; longitudinal scales 66-83. (Gulf of Mexico and southeastern United States)

Frequency dis sal pterygioph Atlantic speci	ores and	neural s	pines (ID	patterns pattern)	observed		
			Ι	D patter	n		
Species	1-3-3	1-3-4	1-4-2	1-4-3	1-4-4	1-5-2	1-5-3
civitatium	8	6	19	127	_	7	3
plagusia	4	1	2	32	1	_	1
tessellatus	10	16	11	177	12	3	14
oculellus	1	2	1	33	_	_	1
caribbeanus	8	3	-	69	2	2	

Table 2

Frequency distributions of the numbers of caudal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

	(Caudal fin	n ray coun	t
Species	10	11	12	18
civitatium		8	163	
plagusia		2	39	1
tessellatus	4	11	216	2
oculellus		4	49	
caribbeanus	1	2	80	1

Table 3

Frequency distributions of the numbers of dorsal fin rays for five western Atlantic species of the Symphurus plagusia complex. Dorsal fin ray number Species 97 98 \overline{x} civitatium 90.1plagusia 93.2 tessellatus 96.9 oculellus 101.2 caribbeanus 93.5 1 13 29

Frequency	/ dist	ributi	ons o	f the	numb	ers o	f anal	fin r	ays fo		le 4 e west	tern 1	Atlant	ic spe	ecies o	of the	Sym	phuru	us pla	gusia	comp	lex.
										Ana	l fin 1	ray n	umber	•								
Species	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	\overline{x}
civitatium	1	2	6	34	49	57	20	3	1													74.3
olagusia				1	_	5	8	15	5	6	1	1										77.0
essellatus								5	24	36	45	45	37	26	18	3	1					80.8
culellus												1	2	5	17	17	5	5	1	2		84.8
caribbeanus					1	3	6	24	40	6	3											77.6

					Verte	ebrae n	umber				
Species	46	47	48	49	50	51	52	53	54	55	\overline{x}
civitatium	2	34	108	28	2						48.0
plagusia		1	4	20	12	5					49.4
tessellatus				3	47	87	71	32	2		51.
oculellus							2	23	11	1	53.
caribbeanus			1	43	33	4					49.

Table 6

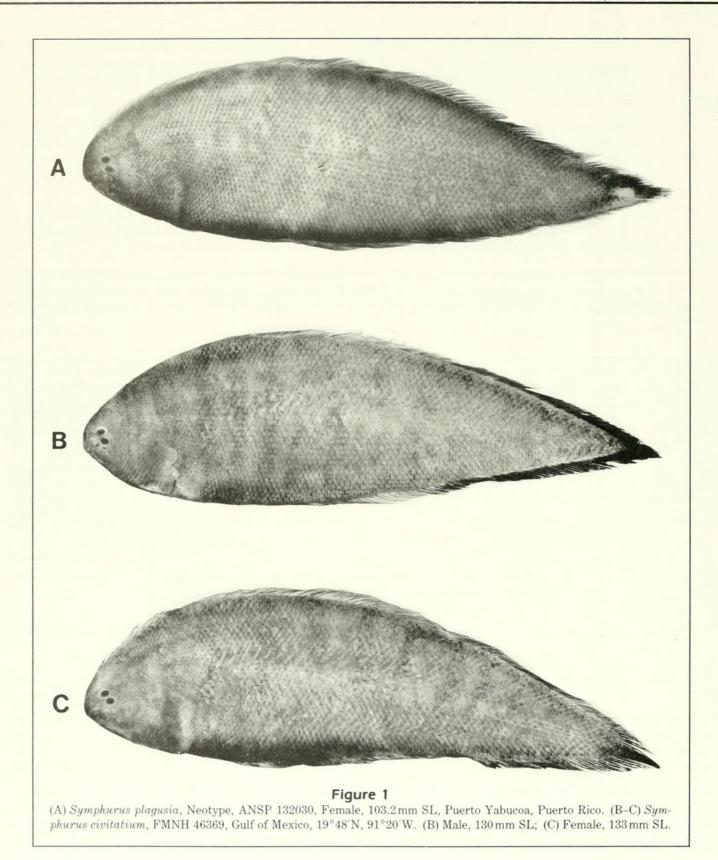
Frequency distributions of the numbers of longitudinal scale rows for five western Atlantic species of the Symphurus plagusia complex.

Scale rows																								
66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	\overline{x}
1	_	-	_	2	-	_	1	4	8	11	5	14	8	7	3	3	1							77.2
													1	3	2	3	2	2	1	3	_	_	2	83.3
												3	-	4	11	4	3	6	2	2	1	1	3	82.8
81	82	2	83	84	1	85	86	8	7	88	89		90	91	9	92	93	94	1	95	96	9	97	\overline{x}
2	2		8	10		10	11	2	1	31	21		21	14		5	4	2		_	1			87.9
				1		3	1.		7	5	2		6	4		2	_	1		_	_		1	89.
	1 81	1 – 81 82	$\begin{array}{cccc} 1 & - & - \\ \\ \hline 81 & 82 \end{array}$	1 81 82 83	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$														

Frequencies of the eyes Atlantic spe	to the m	idpoint	s of sc emarg	ginatio	ws betw n of th	e oper	cle for		-
		-		S	cale ro	ows			
Species	16	17	18	19	20	21	22	23	\overline{x}

Species	16	17	18	19	20	21	22	23	\overline{x}
civitatium	3	18	32	16	3				18.0
plagusia			8	4	8	2	1		19.3
tessellatus			1	_	8	9	4	1	20.8
oculellus				3	8	1	1	2	20.4
caribbeanus		1	1	9	16	8	3		20.0

Frequency di	istrib	utions	of th	e tran	svers	e scale	e coun	t obse					tlant	ic spec	cies of	the S	ymph	urus j	olagus	ria con	mplex
										50	cale co	ount									
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	\overline{x}
civitatium	2	1	2	_	2	5	4	6	2	11	5	6	6	1							33.
plagusia										1	-	-	2	3	7	3	3	1			40.
tessellatus													1	2	4	5	3	1	3	2	41.
oculellus											1	1	6	2	2	1	1				38.
caribbeanus										-	2	3	6	10	3	6	2	1	1		39.



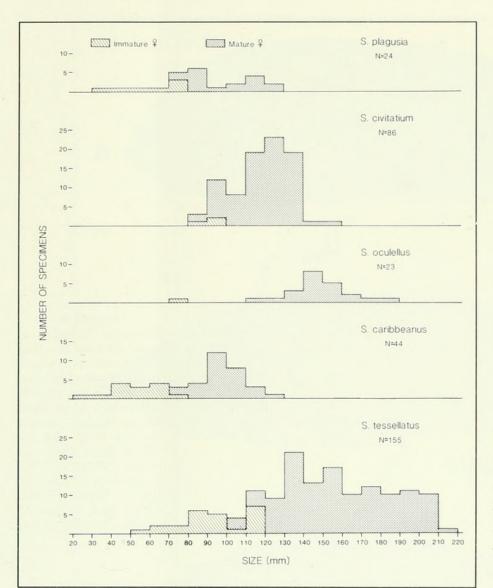


Figure 2

Frequency histogram of size distributions (standard length) and relative sizes at sexual maturity for females of five western Atlantic species of the *Symphurus plagusia* complex. Mature females were those with fully elongate ovaries. Immature females were those with non-elongate or only partially elongate ovaries.

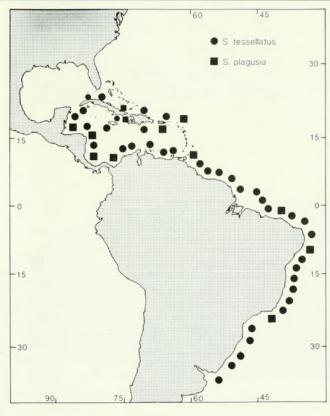
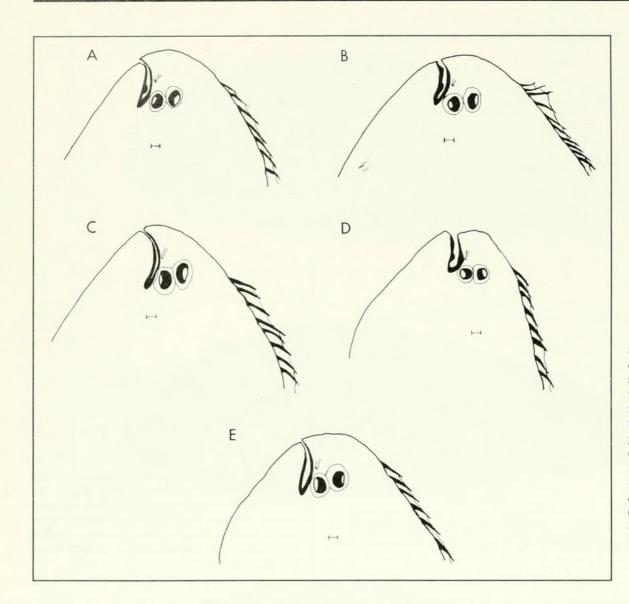


Figure 3 Geographic distributions of *Symphurus plagusia* and *S. tessellatus* based on material examined.



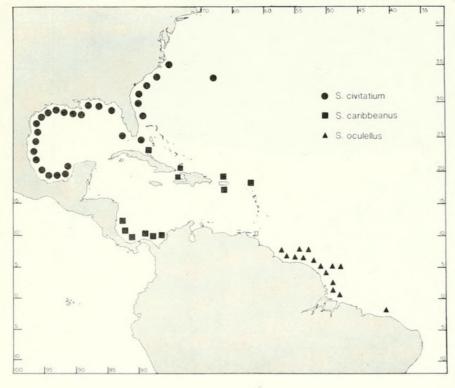


Figure 5

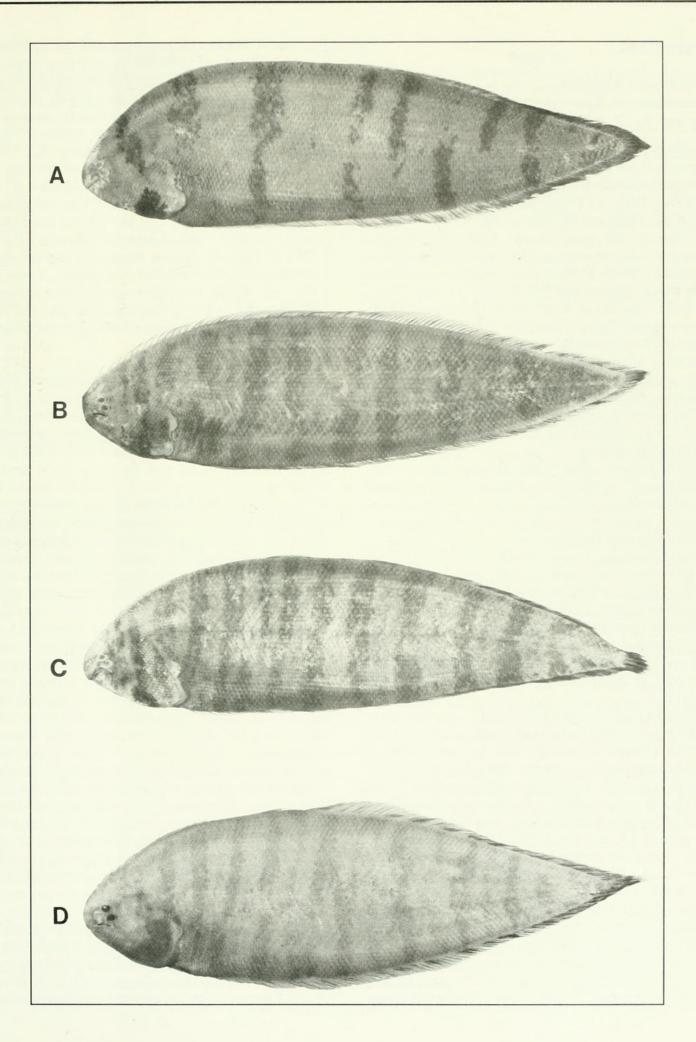
Geographic distributions of Symphurus civitatium, S. oculellus, and S. caribbeanus based on material examined.

Figure 6 (facing page)

(A) Symphurus tessellatus, USNM 159536, Female, 177 mm SL, Surinam, 6°41'N, 54°17' W.
(B-C) Symphurus oculellus. (B) Holotype, USNM 159606, 144 mm SL, Male, 6°24'N, 55°00'W; (C) USNM 313515, 151 mm SL, Female, 6°21'N, 54°28'W. (D) Symphurus caribbeanus, Holotype, USNM 313487, 101 mm SL, Male, Mayaguez Bay, Puerto Rico.

Figure 4

Schematic illustration of ocular-side lower jaws, head shapes, and relative positions of the dorsal fin origin for five western Atlantic tonguefishes of the Symphurus plagusia species complex. (A) S. plagusia, ANSP 132030. (B) S. civitatium, USNM 274485. (C) S. tessellatus, UPRM 2859. (D) S. oculellus, UMML 34334. (E) S. caribbeanus, USNM 313487. Bar = 1 mm.



Systematics

Symphurus plagusia (Schneider, in Bloch and Schneider 1801) Figures 1a, 2, 3, 4a

Synonymy

- Plagusia Browne 1756 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9],
 Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956).
- Pleuronectes plagusia Browne 1789:445 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956). Cuvier 1816:224 (listed). Cuvier 1829:344 (listed).
- *Pleuronectes plagusia* Schneider, in Bloch and Schneider 1801:162 (after Browne; no original material examined, based strictly on description provided by Browne).
- ?Achirus ornata (nomen dubium) Lacepède 1802:659, 663 (vague description of a tonguefish donated to France by Holland but of uncertain identity and geographic origin).
- Aphoristia ornata. Kaup 1858:107 (in part) (new combination; synonymized with Plagusia tessellata Quoy and Gaimard 1824). Günther 1862:490 (in part) (synonymy; meristics; synonymized with Plagusia tessellata Quoy and Gaimard 1824). Poey 1868:409 (in part) (synonymy; listed, Cuba). Poey 1876:182 (in part) (synonymy; listed, Cuba). Goode and Bean 1885:196 (in part) (substitute name for Pleuronectes plagiusa Linnaeus 1766). Jordan 1885:395 (in part) (possible synonymy of A. ornata Lacepède 1802 with Pleuronectes plagiusa Linnaeus 1766; Aphoristia ornata Lacepède 1802 from Jamaica distinct from A. fasciata [= Plagusia fasciata] Holbrook in DeKay 1842).
- Aphoristia plagiusa (not of Linnaeus). Jordan 1886a: 31 (Cuba; equals A. ornata of Poey). Jordan 1886b: 603 (in part) (West Indies; equals A. ornata of Poey).
- Symphurus plagusia. Jordan and Goss 1889:100 (in part) (synonymy, nomenclature review; West Indies to Brazil; comparison with S. plagiusa; synonymized with Plagusia tessellata Quoy and Gaimard 1824). Jordan and Evermann 1898:2709 (in part) (synonymy, counts, measurements, description; after Jordan and Goss). Meek and Hildebrand 1928:1005 (in part) (synonymy; counts, measurements, description; summary of distribution records; listed, Panama). Chabanaud 1939:26 (listed, Antilles). Chabanaud 1940: 182 (descriptive osteology). Chabanaud 1949:82 (synonymy; description including counts, measurements, description of scales; figures; radiograph; mouth of Amazon, Brazil). Duarte-Bello and Buesa

1973:234 (in part) (synonymy; listed, Cuba). Menezes and Benvegnú 1976:142 (in part) (recommended reexamination of Ginsburg's diagnoses of two subspecies). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lema et al. 1980:44 (in part) (synonymy; listed, southern Brazil). Symphurus plagusia plagusia. Ginsburg 1951:199 (in part) (synonymized with Plagusia tessellata Quoy and Gaimard 1824; description and diagnoses of two subspecies; four species included in material studied). Carvalho et al. 1968:22 (in part) (brief description; in key; Antilles, Central America to Brazil). Palacio 1974:87 (in part) (counts; suggested reexamination of subspecies status; listed, Colombia). Lema and Oliveira 1977:6 (in key; suggested synonymy of Pleuronectes plagusia, Plagusia tessellata, and Symphurus civitatium). Soares 1978:23 (in part) (listed. northern Brazil).

Diagnosis A Symphurus with the following combination of characters: predominant ID pattern 1-4-3; 12 caudal fin rays; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; no pupillary operculum; relatively small, spherical eye (64–95 HL, \overline{x} 82); 89–97 dorsal fin rays; 73-81 anal fin rays; 47-51, usually 49-50, total vertebrae; 79-89 scales in longitudinal series; moderately long jaws, usually extending posteriorly to vertical line through posterior margin of lower eye, less frequently to vertical through rear margin of pupil or slightly posterior to rear margin of lower eye; dorsal fin origin placed far forward, usually at vertical through anterior margin of upper eye, or with first and sometimes second rays inserting anterior to vertical through anterior margin of upper eye; scales absent on blind sides of dorsal and anal fin rays; ocular surface usually uniformly light-brown or yellowish, occasionally with 8-14 narrow, faint crossbands; outer surface of ocular-side opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus dusky- to darkbrown, that of blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Dorsal and anal fins uniformly pigmented, without progressive darkening or alternating series of pigmented blotches and unpigmented areas posteriorly.

Description A medium-sized tonguefish attaining maximum known body sizes of approximately 130 mm SL. ID pattern usually 1-4-3 (32/42 individuals), less frequently 1-3-3 (4), 1-4-2 (2), or 1-3-4 (1) (Table 1). Caudal fin rays 12(39/42), infrequently 11 or 13 (Table

Table 9

Summary of morphometrics, expressed as thousandths of standard length (except SL in mm) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

Character	Neotype	Range	Mean	SD
SL	103.2	57.4-130.3	98.8	22.29
BD	304	278-319	292.1	13.05
PDL	30	23-50	32.9	6.87
PAL	222	166 - 244	209.3	18.60
DBL	970	950-977	967.1	6.87
ABL	776	758-802	785.6	15.38
PL	64	51-73	63.6	5.76
PA	48	38-60	50.0	7.00
CFL	98	88-111	100.3	7.13
HL	196	174 - 216	189.6	11.98
HW	239	218 - 256	236.4	13.25
POL	130	110 - 143	125.9	9.26
SNL	45	36 - 54	43.3	4.21
UJL	42	38-52	43.1	4.56
ED	16	12-18	15.3	2.02
CD	42	39-67	52.1	7.99
UHL	142	125-186	160.1	15.93
LHL	107	81-115	96.8	10.22

2). Dorsal fin rays 89–97 (Table 3). Anal fin rays 73–81 (Table 4). Total vertebrae 47–51, usually 49–50 (32/42 specimens) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 79–89 (Table 6). Scale rows on head posterior to lower orbit 18–22, usually 18–20 (Table 7). Transverse scales 35–43 (Table 8).

Proportional measurements appear in Tables 9 and 10. Body relatively deep (278-319 SL, \overline{x} 292); maximum depth in anterior one-third of body. Preanal length 166–244 SL, \bar{x} 209; shorter than body depth. Head relatively short (174–216 SL, \bar{x} 190) and wide (HW 218-256 SL, \bar{x} 236); usually much wider than long (HW/HL 1.2-1.3, \bar{x} 1.2); lower head lobe relatively narrow (81-115 SL, \overline{x} 97) considerably narrower than upper head lobe (125–186 SL, \bar{x} 160). Lower opercular lobe of ocular side considerably wider (250-346 HL, \bar{x} 297) than upper opercular lobe (169-272 HL, \overline{x} 212). Postorbital length 110–143 SL, \overline{x} 126. Snout moderately long (205-250 HL, \bar{x} 229), somewhat square (Fig. 4a), covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions. Jaws moderately long, upper jaw length 200-250 HL, \bar{x} 228; posterior extension of maxilla usually reaching to vertical line through posterior margin of lower eye, less frequently only to vertical through rear margin of pupil or slightly posterior to rear margin of

г	-	ь	1	0	1	n
	a	ν		C		v

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

Character	Neotype	Range	Mean	SD
HL/HW	1.2	1.2-1.3	1.2	0.38
POL	663	630-714	665.8	25.18
SNL	228	205-250	229.1	15.62
UJL	213	200 - 250	227.6	14.99
ED	79	64-95	81.9	9.57
CD	213	222-374	275.1	40.32
OPLL	272	250 - 346	296.9	29.10
OPUL	223	169 - 272	211.9	27.24
UHL	703	695-926	843.1	63.80
LHL	530	427-606	510.3	53.23

lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4a). Chin depth 222-374 HL, \overline{x} 275. Lower eye small (64-95 HL, \overline{x} 82), spherical; upper eye usually anterior to lower eye; eyes not covered with scales; usually 1-2 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 950-977 SL, \overline{x} 967. Dorsal fin origin placed far forward (Fig. 4a), usually at vertical through anterior margin of upper eye or with first and sometimes second fin rays inserting anterior to vertical through anterior margin of upper eye; predorsal length 23–50 SL, \bar{x} 33. Length of anal fin base 758-802 SL, \bar{x} 786. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin length 51–73 SL, \bar{x} 64; longest pelvic fin ray reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 38–60 SL, \bar{x} 50. Posterior pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in many specimens). Caudal fin length moderate $(88-111 \text{ SL}, \bar{x} 100).$

Teeth well developed on blind-side jaws. Ocular-side dentary without teeth or with short row of small teeth developed only on anterior one-half to one-third; premaxilla on ocular side usually with small, single, mostly incomplete row of slender teeth anterior to vertical equal with anterior nostril.

Scales large, ctenoid on both sides of body.

Pigmentation Ocular surface usually uniformly lightbrown or yellowish, occasionally with 8–14 narrow, faint crossbands. Crossbands not continued onto dorsal and anal fins; mostly complete in anterior trunk region; on remainder of body obvious only as vertical markings at body margin along dorsal and anal fin bases.

Bathymetric d cent occurrence			for five spe	cies of the	Table western Atl		hurus plagu	sia complex	. Numbers	represent tl	he per-
						Dep	oth				
Species	N	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	110
civitatium	216	2	26	34	26	5	5	0.5	0.5		
tessellatus	349	10	26	2	- 24	19	5	8	6	0.3	
oculellus	57	4	19	12	9	9	2	40	-	4	2
plagusia	25	80	_	_	16	_	_	4			
caribbeanus	94	51	32	17							

Blind side creamy-white. Peritoneum unpigmented. Pigmentation of outer surface of ocular-side opercle usually same as that of body; occasionally with dusky blotch on upper opercular lobe due to pigment on inner lining of ocular-side opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually dusky; some specimens with darkbrown pigmentation on inner opercular lining; inner opercle and isthmus on blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Usually with slight pigment band on ocular-side upper lip and diffuse pattern of melanophores on lower lip.

Dorsal and anal fins dusky; fin rays streaked with pigment darker brown than that of connecting membrane; sometimes with alternating series of darkerpigmented rays (usually 2–3 in succession) separated by about 4–5 successive, lighter-pigmented rays. Basal half (scale-covered) of caudal fin dark-brown; fin rays in distal half streaked with pigment.

Size and sexual maturation (Fig. 2) Symphurus plagusia is a medium-sized tonguefish. The largest of five males examined was 130 mm SL; the largest of 23 females was only slightly smaller (127 mm SL).

Sexual maturity occurs at a relatively large body size in this species. All females larger than 80 mm SL were mature. All but one female (79.3 mm SL) smaller than 80 mm SL were immature, with gonads undergoing elongation without ripening ova or with ovaries barely elongating.

Geographic distribution (Fig. 3) Widely distributed in shallow waters of the tropical western Atlantic. In the northern portion of its distribution, this species occurs in Puerto Rico, Haiti, and Hispaniola, but is unknown from the Bahamas (Böhlke and Chaplin 1968). Along the continental margin of Central America, *S. plagusia* has been collected at Belize, Nicaragua, Costa Rica, and Panama, while further south it ranges along the Atlantic coast of Colombia and coastal regions in Surinam, Tobago, and Brazil at least as far south as Rio de Janeiro.

Bathymetric distribution Symphurus plagusia is a shallow-water species (1–51m) most commonly inhabiting depths between the shoreline and 10m (Table 11), where (20/25, 80%) of specimens examined were taken. All life-history stages occur in these shallow areas and only occasionally were individuals taken at deeper locations (one specimen at 51m, three specimens at 40m, and one specimen at 37m).

Ecology Little is known concerning the biology of *S*. *plagusia*. Its general rarity in collections indicates that it occurs in rarely-sampled habitats.

Remarks The earliest description of a western Atlantic, shallow-water, 12-caudal-rayed tonguefish is of a specimen collected in Jamaica that Browne first described (1756) as *Plagusia* and later (1789) as *Pleuronectes plagusia*. He described this specimen as a small sinistral flatfish with dorsal, anal, and caudal fins united (tail ending in sharp point), lacking pectoral fins and lateral lines. His description was clearly that of a tonguefish, but he provided no figure or diagnostic characters to unequivocally identify his specimen. Browne's names were later suppressed under the plenary powers for nomenclatorial purposes in Opinion 89 of the Commission for Zoological Nomenclature (see Hemming and Noakes 1958).

In 1801, Schneider first made Browne's tonguefish *Pleuronectes plagusia* available as a binomial. Schneider's *Pleuronectes plagusia* was based entirely on the description of the tonguefish from Jamaica in Browne's works (1756, 1789). The description by Schneider (in Bloch and Schneider 1801) is identical to that provided by Browne and, in addition, all indications are that Schneider did not directly examine any specimens of this species. Dr. H.-J. Paepke (Mus. für Naturkunde der Humboldt-Universität zu Berlin, Zoologisches Mus., Invalidenstrasse 43, Berlin DDR 1040, pers. commun. 8 Nov. 1986) informs me that no remarks were made in Bloch's ledger to indicate that specimens were available for examination when Schneider wrote the description of *Pleuronectes plagusia*. Additionally, Paepke also stated that there are no specimens of this species in the Bloch and Schneider collection. Therefore, it appears that the description of *Pleuronectes plagusia* Schneider, in Bloch and Schneider 1801, was copied directly from Browne's work and that no type exists for this species.

Although quite vague, the original description of Pleuronectes plagusia by Schneider does refer to a species of Symphurus and is the oldest available name for a tropical, western Atlantic species in the genus. This name represents the oldest binomial generally considered to represent a member of this species group and has been the one name most consistently applied to any shallow-water tonguefish possessing 12 caudal fin rays. In order to stabilize the nomenclature for this species, it is necessary to designate a neotype. Since the original description is based on a specimen from Jamaica, a topotypic specimen would be the most appropriate neotype. Unfortunately, no specimens of S. plagusia from Jamaica were available to Munroe (1987) and several more recent attempts to procure a specimen during the present study have also been unsuccessful. All tonguefishes collected from Jamaican waters that I have examined are specimens of S. tessellatus trawled at depths generally exceeding those usually occupied by S. plagusia. Therefore, designation of a neotype for S. plagusia, based on a topotype specimen from Jamaica, is not possible. Instead, ANSP 132030, a mature female measuring 103.2 mm SL, collected by beach seine at Puerto Yabucoa, Puerto Rico, 24-27 July 1974, is selected as the neotype for this species. Meristic features for this specimen are: ID pattern 1-4-3; caudal fin rays 12; dorsal fin rays 93; anal fin rays 78; total vertebrae 50; longitudinal scales 79; transverse scale count 39; and 18 scale rows on head posterior to eyes.

Many authors have included Achirus ornatus Lacepède 1802 in the synonymy of Symphurus plagusia. The description of this species is very brief and does not include figures or locality data, and it is unknown if any type(s) exists. The information provided is that the fish was donated to France by Holland, and has the following characteristics: dorsal and anal fins joined, 95 dorsal fin rays, 82 anal fin rays, 8 or 9 dark transverse bands, and a lateral line on each side. Notably absent in Lacepède's account is the caudal-fin-ray count for this specimen. The lateral line referred to in the description may refer to the mid-lateral junction of the myomeres that is apparent on some tonguefish specimens (especially those partially dehydrated during preservation). Based on counts listed by Lacepède, it is possible his specimen is a S. plagusia (sensu strictu). However, the dark, transverse bands and meristic features listed in the description of Achirus ornatus could also apply to several other western Atlantic tonguefishes. Among shallow-water species possessing 12 caudal fin rays, the data fit at least three species: S. caribbeanus (described below), S. plagusia (Schneider, in Bloch and Schneider 1801), and S. tessellatus (Quoy and Gaimard 1824). Of these, the description is more typical of S. tessellatus, especially the reference to darkly-pigmented crossbands. Nonetheless, the exact identity of Achirus ornatus Lacepède cannot be determined from the vague original description, particularly given the unknown site of capture for the specimen on which this name is based. Achirus ornatus Lacepède 1802 is therefore regarded as a nomen dubium.

In 1824, Quoy and Gaimard described Plagusia tessellata from Rio de Janeiro Bay (= Guanabara Bay), Brazil. Although no figure of this specimen was provided, the descriptive account of meristic features, color pattern, and other characters leave little doubt as to the identity of the species. Quoy and Gaimard described the dorsal fin as originating above the eyes and consisting of 99 rays; the anal fin has 78 rays. The color is described as brown with small transverse bands of the same color. Although no type exists for this species (M.L. Bauchot, Ichtyologie Générale et Appliquée, 43 Cuvier, Mus. Natl. Hist. Nat., Paris Cedex 05 75231, pers. commun. 23 June 1982), the original description is sufficient to allow identification of this species. Unfortunately, most authors beginning with Kaup (1858) and continuing to Ginsburg (1951) regarded this species as a junior synonym of S. plagusia (Schneider, in Bloch and Schneider 1801). It is unlikely that the specimen described by Quoy and Gaimard belongs to S. plagusia (sensu strictu), because the S. tessellatus specimen has slightly higher meristic features, darker banding, and the dorsal fin origin is described as being above and not anterior to the eyes, which is the typical condition found in S. plagusia.

A second nominal species of tonguefish from Brazilian waters, *Plagusia brasiliensis*, described by Agassiz (in Spix and Agassiz 1829–1831), has also been placed in the synonymy of *S. plagusia*. The possible holotype or syntype (MHNN 691; see Kottelat 1984, 1988) was illustrated and an adequate description provided. The specimen has 99 dorsal fin rays, 83 anal fin rays, 12 caudal fin rays, 53 total vertebrae, several small ctenoid scales on the blind sides of the dorsal and anal fin rays, the dorsal fin origin at the vertical through the front margin of the pupil of the upper eye, and a relatively large eye (10.6% HL). It agrees in all these features with *S. tessellatus* and is removed from the synonymy of *S. plagusia* and placed in the synonymy of *S. tessellatus* (see below).

Beginning with Kaup (1858), all previously described species of western Atlantic, shallow-water tonguefishes possessing 12 caudal fin rays were regarded as a single species. Kaup placed Achirus ornatus Lacepède, Plagusia brasiliensis Agassiz, in Spix and Agassiz (Kaup cited authorship of this species as Cuvier, in Spix), and Plagusia tessellatus Quoy and Gaimard (Kaup listed Valenciennes as the author of this name) in synonymy and proposed the new combination Aphoristia ornata to accommodate a single, widespread species ranging from the Caribbean to southern South America. Günther (1862) regarded Aphoristia ornata as including the nominal species Pleuronectes plagusia Browne, Plagusia brasiliensis Agassiz, and Plagusia tessellatus Quoy and Gaimard.

Subsequent authors, including Jordan and Goss (1889) and Jordan and Evermann (1898), until Ginsburg (1951), continued to include three species in the synonymy of Symphurus (= Aphoristia) plagusia (Schneider, in Bloch and Schneider): P. tessellatus, P. brasiliensis, and A. ornatus. Jordan and his co-workers, and other researchers, still recognized only one widespread, polytypic species of shallow-water, 12-caudal-rayed Symphurus occurring in the western Atlantic. Ginsburg (1951), although continuing to regard all Caribbean and South American specimens as representing a single widespread, polytypic species, S. plagusia (Schneider, in Bloch and Schneider 1801), allocated his study specimens to two allopatric subspecies. He considered S. plagusia plagusia as a northern subspecies ranging from the West Indies to Central America that was characterized by somewhat lower meristic features. The second subspecies, S. p. tessellatus, with a more southern distribution along the coasts of Brazil and Uruguay had higher meristic features. In this revision, Ginsburg also described a second species (S. civitatum = civitatium, this study) of shallow-water, 12caudal-rayed tonguefish from continental seas off the southeastern United States and Gulf of Mexico. He equivocated in his description of this new species, stating that his S. civitatium could also be recognized as a third northern subspecies of a widespread, polytypic S. plagusia.

Subsequent workers have utilized subspecies designations proposed by Ginsburg for Caribbean and South American shallow-water, 12-caudal-rayed tonguefishes and have used the name *S. civitatium* for specimens collected in the Gulf of Mexico and along the southeastern coast of the United States. More recently, however, several studies have noted that both nominal subspecies of *S. plagusia* occur sympatrically in northern South America. For example, Carvalho et al. (1968) found both subspecies in northern Brazil, and Palacio (1974) reported both subspecies from the Colombian Caribbean.

In their revision of western South Atlantic tonguefishes, Menezes and Benvegnú (1976) reported that all their specimens (collected mostly in offshore habitats by trawling) were quite similar, lacking variation reported for specimens collected in more northern regions. Using the name *S. plagusia*, they considered their specimens to represent a single taxon but also pointed out that the sympatric occurrence of both subspecies in other South American localities indicated that the subspecific status designated by Ginsburg should be reexamined.

In examining material of S. plagusia, I successfully located 19 of the 25 specimens listed by Ginsburg (1951) in his account of S. plagusia plagusia. These include representatives of four species: twelve S. tessellatus, one S. caribbeanus, one S. parvus Ginsburg 1951, with only five actually S. plagusia (sensu strictu). The twelve specimens of S. tessellatus incorrectly identified as S. p. plagusia by Ginsburg are small juveniles collected from shallow-water habitats. These, as well as many of the remaining 25 specimens that Ginsburg included in his account of S. p. plagusia, had been collected in the latter part of the last century and during the early 1920s. Most of these older specimens were completely devoid of any obvious pigmentation pattern. As a consequence, the specimens provided little clue that more than a single species was represented in these shallowwater collections. Additionally, since most of Ginsburg's Caribbean and Central American specimens came from shallow-water collections, very few adult S. tessellatus were available to his study. Therefore, he was unable to unravel size-related differences among the three sympatric species in this complex that occur in this region (the two smaller species, S. plagusia and S. caribbeanus, and the much larger S. tessellatus).

Ginsburg did not list catalog numbers for 34 specimens identified as S. p. tessellatus in his study, so that it is difficult to ascertain if more than one species was included in his account of this subspecies. Of the eight lots designated as S. p. tessellatus by Ginsburg that I have examined, all are one species, S. tessellatus (Quoy and Gaimard 1824). It is highly probable, therefore, that Ginsburg's S. p. tessellatus are equivalent to S. tessellatus (Quoy and Gaimard 1824) in the present study.

Comparisons Symphurus plagusia most closely resembles S. civitatium but differs from that species in its modally higher meristic features (total vertebrae modally 49–50 vs. 47–49 in S. civitatium; dorsal fin rays 89–97 vs. 86–93; anal fin rays 73–81 vs. 70–78); and degree of development of sexually dimorphic coloration. In S. plagusia, both sexes are more or less

uniformly pigmented with only slight evidence of banding on the body, and with vertical fins of both sexes uniformly colored with no darkening in the posterior portion of the body. In contrast, in *S. civitatium* there is considerably more pronounced sexual dimorphism in pigmentation. Females tend to have well-developed crossbands on the body whereas in males the crossbands are less conspicuous. In male *S. civitatium*, posterior portions of the dorsal and anal fins are noticeably darkened with black pigment (black pigment absent in females).

Symphurus plagusia of all sizes are usually collected with juveniles and small adults of S. tessellatus. Despite overall similarities in meristic features, the two species are quite distinctive. Symphurus plagusia is uniformly colored with only faint, narrow crossbands in some individuals, has a well-developed fleshy ridge on the ocular-side lower jaw (Fig. 4a), and this species lacks a striking black pigment spot on the outer opercle (some individuals have a diffuse blotch on the inner opercle where the pigmentation on the inner surface of the ocular-side opercle shows through). In S. tessellatus, in contrast, all individuals have a bold pattern of wide crossbands, a prominent black spot on the outer surface of the opercle, and lack a fleshy ridge on the ocular-side lower jaw (Fig. 4c). Symphurus plagusia also has a smaller eye (6.4-9.5, \overline{x} 8.2% HL vs. 7.9-11.4, \bar{x} 9.5% HL in S. tessellatus) and lacks the small ctenoid scales on the posterior fin rays on the blind side of the dorsal and anal fins that are present in S. tessellatus larger than about 70 mm SL. Symphurus plagusia also has modally lower meristic values (total vertebrae 49-50 vs. 50-53 in S. tessellatus; dorsal fin rays 89-97 vs. 91-102 (usually 93-101); anal fin rays 73-81 vs. 77-86 in S. tessellatus).

Symphurus plagusia differs further from S. tessellatus in the almost squarish snout of S. plagusia, which contrasts with the more pointed snout of S. tessellatus (compare Figs. 4a and 4c). Also, in S. plagusia the dorsal fin origin is usually anterior to the vertical through the eye, while in S. tessellatus the dorsal fin originates slightly more posteriorly, usually above the anterior margin of the pupil of the upper eye, or even as far back posteriorly as the mid-eye region. Viewed from the blind side, the more posterior location of the dorsal fin origin in S. tessellatus is apparent in the number of rays occurring along the dorsal margin of the body immediately above the space between the two nostrils. In S. tessellatus usually only the first dorsal fin ray occurs above the space between the nostrils, while the second dorsal fin ray lies immediately above the posterior nostril or the second dorsal fin ray is placed even slightly posterior to the rear nostril. In S. plagusia, usually the first two dorsal fin rays occur along the dorsal margin in the space between the nostrils, and in many specimens the first dorsal fin ray is actually situated anterior to the vertical equal with the anterior nostril. In *S. plagusia*, the jaws usually extend to the posterior margin of the lower eye or, in some cases, actually extend slightly posterior to the rear margin of the lower eye, while in *S. tessellatus* the jaws usually reach only to the middle, rarely to the posterior margin, of the lower eye.

These two species also differ significantly in overall body size and size at sexual maturation. *Symphurus plagusia* is a medium-sized tonguefish reaching a maximum known body size of about 130 mm SL and attaining sexual maturity as small as 80 mm SL. *Symphurus tessellatus* is a much larger species attaining maximum known lengths of 220 mm SL and does not attain sexual maturity until reaching approximately 120 mm SL.

Meristic values of S. plagusia overlap almost completely those of S. caribbeanus. The two species can be distinguished, however, by the absence in S. caribbeanus of the fleshy ridge on the ocular-side lower jaw (present in S. plagusia; see Figures 4a and 4e). Symphurus plagusia is generally uniformly colored with only slight evidence of crossbanding, and the fins are uniformly colored. In contrast, S. caribbeanus usually has numerous, prominent crossbands on the body, and the vertical fins have an alternating series of blotches and unpigmented areas, which are especially well developed posteriorly. Symphurus caribbeanus has a more pointed snout with a distance between upper eye and dorsal fin base usually slightly less than twice the eye diameter, versus a squarish snout with distance from upper eye to dorsal fin base usually larger than twice the eye diameter in S. plagusia (compare Figures 4a and 4e). The body shape of S. caribbeanus is rounded with a pronounced taper posterior to dorsal fin rays 25-35 (versus somewhat elongate in S. plagusia with a more gradual taper). Additionally, S. caribbeanus has a slightly larger eye (8.2-11.0% HL, usually 9.0-10.0% HL) when compared with that of S. plagusia (usually 7.0-9.0% HL).

Symphurus plagusia is also similar to S. oculellus with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much lower counts (47–51 total vertebrae vs. 52–55 in S. oculellus; dorsal fin rays 89–97 vs. 99–104; anal fin rays 73–81 vs. 82–88) and pigmentation pattern. Symphurus plagusia has a relatively uniform body color with faint crossbands, uniformly pigmented fins without blotches, and no pigment spot on the outer opercle (versus sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in the dorsal and anal fins, and a black spot on the outer opercle in S. oculellus). Furthermore, in S. plagusia the first, and occasionally the second, rays of the dorsal fin are usually located along a vertical line anterior to the upper eye, while in *S. oculellus* the dorsal fin origin usually extends anteriorly only to the vertical through the anterior margin or mideye region of the upper eye. Differences in morphometrics between the two species are that *S. oculellus* has a narrower body (231–297 SL vs. 278–319 SL in *S. plagusia*) and attains larger sizes (up to 190 mm SL vs. largest of only 131 mm SL in *S. plagusia*).

Some meristic values of *S. plagusia* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus plagusia* occurs sympatrically, and occasionally syntopically, with *S. diomedeanus* (Goode and Bean) but differs from this species in having 12 caudal fin rays (versus 10 in *S. diomedeanus*) and in lacking the series of dark spots on posterior rays of the dorsal and anal fins and the pupillary operculum that are present in *S. diomedeanus*.

Symphurus plagusia can be distinguished from S. plagiusa (Linnaeus), which has an allopatric distribution in the western North Atlantic, in having 12 versus 10 caudal fin rays, and S. plagusia also lacks the welldeveloped black pigment spot on the ocular-side outer opercle (present in S. plagiusa). In addition, only the ocular-side opercular lining is pigmented in S. plagusia whereas the inner opercular linings on both sides of the body are heavily pigmented in S. plagiusa. Symphurus plagiusa has larger eyes (83-126 HL vs. 64-95 HL in S. plagusia) that are usually equal in position (slightly subequal in S. plagusia). Also, in S. plagiusa the jaws reach only as far posteriorly as a vertical through the mid-eye region; in contrast, in S. plagusia the jaws reach a vertical through the rear margin of the pupil or the rear margin of the eye, or the jaws occasionally even extend slightly beyond the vertical through the posterior margin of the lower eye in S. plagusia. In larger (>60 mm SL) S. plagiusa, there are 4-8 ctenoid scales on the blind sides of the dorsal and anal fin rays (scales usually absent altogether, or occasionally 1-2 scales along bases of fin rays in S. plagusia).

Symphurus plagusia is not easily confused with other Atlantic species (S. kyaropterygium Menezes and Benvegnú, S. trewavasae Chabanaud, S. normani Chabanaud, S. piger (Goode and Bean), S. nigrescens Rafinesque, S. pusillus (Goode and Bean), S. lubbocki Munroe, and S. reticulatus Munroe) with which it overlaps in meristic features. Symphurus plagusia differs from all of these in its 1-4-3 ID pattern (versus 1-4-2 in S. kyaropterygium; 1-3-3 in S. trewavasae and S. normani; 1-3-2 in S. piger, S. nigrescens, S. pusillus, S. reticulatus, and S. lubbocki). In addition, S. plagusia differs from the South Atlantic S. kyaropterygium in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and dark pigment blotch on the caudal extremity that are present in S. kyaropterygium. It differs from the South Atlantic S. trewavasae

in its caudal-fin-ray count (12 vs. 10) and smaller eye (64-95 HL vs. 114-162 HL in S. trewavasae). Symphurus plagusia lacks scales on the blind sides of the dorsal and anal fin rays and the spotted peritoneum that are present in S. normani. Symphurus plagusia differs from the 1-3-2 species (except S. lubbocki and S. reticulatus) in lacking a black peritoneum. Symphurus plagusia differs from S. lubbocki and S. reticulatus in having no dentition or greatly reduced dentition on ocular-side jaws (versus ocular-side jaws with complete or nearly complete row of teeth in S. lubbocki and S. reticulatus), its much larger size (130 vs. <50 mm SL), and pigmentation (dark- or light-brown, usually without crossbands, and with uniformly-pigmented fins, versus light-brown or yellowish body with incomplete crossbands in S. lubbocki, and dark, chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in S. reticulatus).

Meristic values of S. plagusia overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including S. leei Jordan and Bollman, S. atricaudus (Jordan and Gilbert), S. melanurus Clark, S. williamsi Jordan and Culver, S. fasciolaris Gilbert, and S. melasmatotheca Munroe and Nizinski. Of these species, S. plagusia is most similar to S. melanurus in that both species possess a fleshy ridge on the ocularside lower jaw, and in both the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye. The two species are distinguished in that S. plagusia lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in S. melanurus), has fewer scales in a longitudinal series (79-89 vs. 89-108 in S. melanurus), has a lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blindside opercle in S. melanurus), and in S. plagusia the posterior dorsal and anal fins and the caudal fin are not darker than the anterior regions (versus progressive darkening in posterior dorsal and anal fins and darkly-pigmented caudal fin in S. melanurus). Symphurus plagusia differs from the remaining five eastern Pacific species with comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). Symphurus plagusia is further distinguished from S. fasciolaris and S. melasmatotheca in possessing 12 caudal fin rays (versus 10 and 11 in S. fasciolaris and S. melasmatotheca, respectively) and in lacking an ocellated spot on the caudal fin (present in S. fasciolaris) or pigmented peritoneum (present in S. melasmatotheca). Symphurus plagusia differs further from S. atricaudus and S. williamsi in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species).

From S. leei, S. plagusia is further distinguished in having the head length considerably smaller than the head width (versus head length usually equal to or greater than head width in S. leei), in having a smaller eye (12–18 SL vs. 22–27 SL in S. leei), and in having an unpigmented peritoneum (versus black or heavily spotted in S. leei).

Material examined 45 specimens (19.5–130 mm SL).

Counted and measured (15 specimens, 57.4–130.3 mm SL) **Puerto Rico**: ANSP 132030; Neotype; (102.9); Puerto Yabucoa, onehalf mile east of Playa de Guayanes, Municipio de Yabucoa; collected by J.J. Loos, 24–27 Jul 1973. FMNH 3286; (83.1); Mayaguez; 20 Jan 1899. FMNH 61572; (117.0); Allasco Bay; 10 Jan 1954. UF 12059; (127.1); beach at Mani, just N of Mayaguez; 16 Apr 1964. **Costa Rica**: UF 10762; (79.6); Tortuguero Lagoon, Limon Province; Aug 1963. **Panama**: GCRL 15694; (57.4); Canal Zone; 8 Feb 1977. **Trinidad**: UPRM 1828; (89.4); Icacos Bay; 4 May 1964. **Brazil**: FMNH 88853; 2(120.0–130.3); 2°09'S, 42°44'W; 40m; 10 Mar 1963. UFPB 884; (101.4); Praiade Jacare; 13 Nov 1981. UFPB 896; 3(79.3–87.5); Rio Paraiba do Norte; 30 Jul 1981. ANSP 121326; 2(112.9–118.3); Atafona (23°02'S, 44°01'W); Jul–Aug 1963.

Counted (27 specimens, 17 lots) Puerto Rico: ANSP 118542; (47.4); Puerto Yabucoa; 25 Jan 1971. ANSP 129952; (112.7); Puerto Yabucoa; 21 Jul 1973. ANSP 129985; (98.2); Puerto Yabucoa; 25 Jul 1973. USNM 50178; 4(61.9-83.1); Ponce; 31 Jan 1899. Haiti: UF 33896; 5(82.8-90.8); 2km NW of Port Salut; sandy beach near eelgrass bed; 7 Apr 1979. Belize: FMNH 97492; (49.3); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97493; 2(52.1-68.2); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97494; (25.1); Belize City, St. John's College Beach; 16 Apr 1973. FMNH 97495; (36.4); Belize City, St. John's College Beach, mangroves and beach; 3 Aug 1973. Honduras: FMNH 94818; (54.3); Brus Lagoon; 1m; 10 May 1975. FMNH 94822; (34.8); Roatan; 1m; 1 May 1975. FMNH 97490; 3(19.5-61.3); Stann Creek District, along Pelican Beach, 17-33 m N of Pelican Beach Motel; 30 Mar 1973. FMNH 97491; (40.0); Stann Creek District, along Pelican Beach, 17-33 m N of Pelican Beach Motel; 15 Apr 1973. Panama: UMML 34347; (121.5); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. USNM 81654; (54.9); Colon; 5 Jan 1911. French Guiana: USNM 236252; (110.5); 6°34'N, 54°28'W; 37 m; 28 Jun 1972. USNM 291331; (79.4); 5°30'N, 52°10'W; 51m; 12 Sep 1958.

Other material examined (3 specimens, 1 lot) **Tobago**: USNM 313648; 3(19.5–20.3); Bloody Bay, 11°18′14″N, 60°37′46″W; 3m; 13 Sep 1990.

Symphurus civitatium Ginsburg 1951 Figures 1b-c, 2, 4b

Synonymy

- Symphurus piger (not of Goode and Bean). Baughman 1950:137 (inner harbor, Freeport, Texas).
- Symphurus civitatum Ginsburg 1951:198 (counts, figure, included in key; Gulf of Mexico and southeastern coasts of the United States; see "Remarks" about emendation of specific name). Springer and Bullis 1956:65 (Gulf of Mexico; list of Oregon stations at which this species was collected). Reséndez 1979:646 (occurrence in lagunas El Carmen, La Machona, and Lagunade Terminos, northern Mexico).
- Symphurus civitatus. Briggs 1958:297 (summary of distribution records; North Carolina to Florida and widespread in Gulf of Mexico; see "Remarks" about emendation of specific name). Roithmayr 1965:22 (included in industrial bottomfish catch in northcentral Gulf of Mexico). Struhsaker 1969:298 (rarely occurring [<10% of the tows] in demersal fish community of continental shelf from North Carolina to central Florida). Swingle 1971:65 (listed, offshore waters of Alabama). Topp and Hoff 1972:78 (general absence from west Florida shelf). Miller and Jorgenson 1973:305 (meristic features reported for four specimens). Chittenden and McEachran 1976: 93; 99 (abundance on continental shelf of northwestern Gulf of Mexico). Walls 1976:390 (counts, figure, in key; suggested synonymy with S. plagiusa). Schwartz et al. 1981:32 (Cape Fear River, North Carolina). McCaffrey 1981:204 (in part) (abundance and distribution in northeastern Gulf of Mexico). Darcy and Gutherz 1984:104 (collected on west Florida continental shelf).

Diagnosis Symphurus civitatium is identified by the combination of: a predominant 1-4-3 ID pattern; 12 caudal fin rays; an unpigmented peritoneum; absence of a pupillary operculum; relatively small eye (70-110 HL, \overline{x} 88); a fleshy ridge on the ocular-side lower jaw; 86-93 dorsal fin rays; 70-78 anal fin rays; 46-50, usually 47-49 total vertebrae; 66-83, usually 74-82, scales in longitudinal series; relatively short jaws usually extending posteriorly to a vertical line through the middle of the pupil of the lower eye, or sometimes extending to the vertical line through the posterior margin of the pupil of the lower eye; dorsal fin origin usually situated at the vertical anterior to the front margin of the upper eye, or occasionally only reaching the vertical line through the front margin of the pupil of the upper eye; scales usually absent on the blind sides of the dorsal and anal fin rays (occasionally with 1-3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays); ocular surface

usually light- to dark-brown, occasionally with 6–14 narrow, dark-brown crossbands; outer surface of ocularside opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus usually heavily pigmented, that of blind side usually unpigmented. Dorsal and anal fins considerably darker posteriorly, without an alternating series of pigmented blotches and unpigmented areas.

Description A medium-sized tonguefish reaching maximum lengths of approximately 152mm SL. The usual ID pattern (Table 1) is 1-4-3 (127/177 specimens), less frequently 1-4-2 (19/177) and 1-5-2 (7/177). Caudal fin rays usually 12 (163/171), infrequently 11 (Table 2). Dorsal fin rays 86–93 (Table 3). Anal fin rays 70–78 (Table 4). Total vertebrae 46–50, usually 47–49 (170/174) (Table 5); abdominal vertebrae 3 + 6. Hypurals 4. Longitudinal scale rows 66–83, usually 74–82 (Table 6). Scale rows on head posterior to lower orbit 16–20, usually 17–19 (Table 7). Transverse scales 26–39, usually 31–38 (Table 8).

Proportional measurements appear in Tables 12 and 13. Body relatively deep (247-328 SL, \bar{x} 307) with greatest depth in anterior one-third of body. Preanal length 147–238 SL, \bar{x} 202. Head moderately short, 170-219 SL, \bar{x} 191; considerably shorter than body depth. Head wide (212-271 SL, \bar{x} 238); usually greater than head length (HW/HL 1.0-1.5, \bar{x} 1.2); lower head lobe (87-118 SL, \bar{x} 104) narrower than upper head lobe (139–184 SL, \bar{x} 159). Lower opercular lobe of ocular side (253–388 HL, \bar{x} 321) considerably wider than upper opercular lobe (178-329 HL, \bar{x} 230). Postorbital length 117–187 SL, \bar{x} 134. Snout relatively short (169–231 HL, \bar{x} 206), somewhat square (Fig. 4b); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions. Jaws relatively short; upper jaw length 181–289 HL, \bar{x} 228; posterior extension of maxilla usually reaching to vertical line through middle of pupil of lower eye or sometimes to vertical through posterior margin of pupil of lower eye. Chin depth 225–331 HL, \bar{x} 268. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4b). Lower eye relatively small (70–110 HL, \bar{x} 88); upper eye slightly anterior to lower eye; eyes not covered with scales; usually only 1-3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 925-982 SL, \overline{x} 963. Dorsal fin origin (Fig. 4b) usually situated at vertical line anterior to front margin of upper eye; occasionally dorsal fin origin only reaching vertical line

Table 12

Summary of morphometrics expressed in thousandths of standard length, except SL (in mm), for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

Character	Holotype	N	Range	Mean	SD
SL	110.3	30	48.8-149.3	108.6	24.96
BD	304	30	247-328	306.9	16.42
PDL	43	29	22-46	34.5	6.78
PAL	210	30	147 - 238	202.4	19.7
DBL	957	30	925-982	963.0	13.22
ABL	787	30	745-891	797.9	31.30
PL	68	30	49-85	63.0	8.8
PA	39	26	33 - 74	44.7	10.23
CFL	124	29	87-124	108.6	9.3
HL	200	30	170 - 219	191.3	11.5
HW	240	30	212-271	238.3	14.4
POL	134	30	117-187	134.3	13.64
SNL	41	30	31-47	39.5	3.5
UJL	54	30	37-54	43.5	4.8
ED	16	30	13 - 21	16.6	2.0
CD	62	29	39-68	50.6	7.3
UHL	159	30	139-184	158.9	11.6
LHL	103	30	87-118	103.9	6.8

through front margin of pupil of upper eye; predorsal length 22–46 SL, \bar{x} 34. Scales usually absent on blind sides of dorsal and anal fin rays; occasionally with 1–3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays. Pelvic fin length 49–85 SL, \bar{x} 63; longest pelvic fin ray usually reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 33–74 SL, \bar{x} 45. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–124 SL, \bar{x} 109.

Teeth well developed on blind-side jaws. Dentary on ocular side with single, mostly incomplete row of slender teeth on anterior one-third of jaw. Premaxilla on ocular side with only short row of teeth on anterior one-third; or occasionally lacking teeth altogether.

Scales large, ctenoid on both sides of body.

Pigmentation Body coloration generally similar for both sexes (dichromatic differences in pigmentation are discussed below). Ocular surface light- to dark-brown; sometimes with dark-brown crossbands continuous across the body. Crossbands, when developed, narrow, 6–14 in number, sometimes sharply contrasting (especially in mature females), otherwise faint and barely perceptible against dark body coloration. Crossbands not continued onto dorsal and anal fins. First band

Table 13

Summary of morphometrics expressed in thousandths of head length (except HW/HL) for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

Character	Holotype	N	Range	Mean	SD
HW/HL	1.2	30	1.0-1.5	1.2	0.10
POL	670	30	645-740	692.0	27.45
SNL	204	30	169 - 231	206.4	13.84
UJL	272	30	181-289	227.7	24.14
ED	81	30	70-110	87.8	10.26
CD	308	29	225-331	267.9	30.55
OPLL	371	29	253-388	321.3	34.80
OPUL	217	29	178-329	230.0	34.86
UHL	792	30	636-996	832.6	82.14
LHL	516	30	462-629	543.0	46.00

crossing head short distance anterior to opercular opening. Crossbands along trunk 3–6 scale rows wide. Two posteriormost bands immediately anterior to caudal fin base often conjoined. Blind side off-white. Peritoneum unpigmented. Dorsal margin of outer surface of ocularside opercle often with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually heavily pigmented; lining of blindside opercle and blind-side isthmus usually unpigmented. Band of pigmentation usually developed on ocular-side upper lip; lower lip on ocular side frequently spotted but usually without definite band.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. All dorsal and anal fin rays on anterior two-thirds of body streaked with brown pigment similar in shade and intensity to body color. Fin rays completely pigmented other than for extreme distal tips, which are unpigmented. Membranes of anterior three-fourths of fins unpigmented. Caudal fin and dorsal and anal fins on posterior one-third of body more heavily pigmented and considerably darker than anterior two-thirds of fin. Fin membranes on posterior quarter of body heavily pigmented. Basal one-third of caudal fin more lightly pigmented than posterior two-thirds of fin. Distal tips of middle caudal fin rays unpigmented, or with tips of middle caudal fin rays streaked with pigment but membrane unpigmented.

Size and sexual maturity (Fig. 2) The largest fish examined, a female (152 mm SL), was only slightly larger than the largest male (149 mm SL). Most specimens examined ranged in size from 80 to 140 mm SL.

Females mature at sizes usually larger than 90 mm SL. Of 86 females examined, only three (83–95 mm SL)

were immature. The two smallest gravid females were 80–90 mm SL, whereas the majority of gravid females were usually larger (91–140 mm SL).

Geographic distribution (Fig. 5) Western North Atlantic from Cape Hatteras, North Carolina, to the Yucatan Peninsula of Mexico. There is a single record for this species from Bermuda (ANSP 137573). In the Gulf of Mexico, S. civitatium occurs most commonly west of Apalachicola Bay in northern Florida (Springer and Bullis 1956, Chittenden and McEachran 1976, McCaffrey 1981). It is one of the most commonly collected tonguefishes on inner continental shelf regions in the central and western portions of the Gulf of Mexico from Alabama to Texas. Along northern Mexico, this species occurs coastally on sandy substrates at least as far south as coastal lagoons (lagunas El Carmen y La Machona, Laguna de Terminos) in Tabasco and Campeche, Mexico (Reséndez 1979) and on the continental shelf of the southern Gulf of Mexico (Cabo Rojo, Veracruz to Sabuncuy, Yucatan).

Collection data for 347 specimens from this study reveal a general absence of this species from the western Florida shelf. Only two collections record this species from the Tortugas region off southern Florida. Topp and Hoff (1972) also noted the general absence of this species along the west Florida shelf and found just a single record for S. civitatium in the eastern Gulf of Mexico (St. Joseph Bay; from Ginsburg 1951). Neither their efforts during the Hourglass cruises on the continental shelf off west Florida nor other studies (Moe and Martin 1965, Ogren and Brusher 1977, Naughton and Saloman 1978) have collected this species in coastal and continental shelf habitats off west Florida. Furthermore, Darcy and Gutherz (1984) reported taking only a single specimen during 338 10-minute bottom trawls in 9-193m on the west Florida shelf.

Symphurus civitatium occurs on sand or silt substrates throughout its range. The geographic and bathymetric distribution of this species apparently coincides with the distribution of terrigenous, quartzite sandy, and silty substrates on the inner continental shelf. The scarcity of this species on the west Florida shelf and Yucatan Peninsula may reflect the strikingly different substrate compositions there. Along the west Florida shelf, primarily in depths of 55-92m, Topp and Hoff (1972) reported that substrates consist of lithified sediments of cemented lime, including (1) nearshore deposits of cemented shell beachrock, (2) limestone, ranging from soft marl to conglomeritic and foraminiferal limestone, (3) small patches of living and dead coral, and (4) calcareous algae. They noted that substrates off the Yucatan Peninsula are similar in composition to those of the west Florida shelf. In

contrast, in the central and western Gulf of Mexico from the Mississippi Delta to Cabo Rojo, Veracruz, where *S. civitatium* is very abundant, substrates on the inner shelf consist largely of terrigenous quartzite sands, silts, and clays delivered primarily by Mississippi and Rio Grande rivers (van Andel 1960).

Substrate preference may also affect the distribution of S. civitatium in coastal seas off the southeastern United States. The depth of occurrence (11-40 m, seebelow) for S. civitatium apparently coincides with sandsilt substrates on the inner portions of the shelf, and this species is absent from live-bottom habitats occurring at similar depths (Struhsaker 1969).

The specimen of *S. civitatum* reported by Lazzaro (1977:69) from the continental shelf off Uruguay is neither this species nor any other of the *Symphurus plagusia* complex (those possessing 12 caudal fin rays, a 1-4-3 ID pattern, and an unpigmented peritoneum). The body shape evident in the photograph, meristic features, and great depth of occurrence (183 m) indicate the specimen is probably *S. ginsburgi* Menezes and Benvegnú.

Bathymetric distribution Although S. civitatium has been collected over a wide depth range of 1-73 m (Table 11), its center of abundance, based on overall frequency of capture and general abundance, occurs between 11 and 45m. Approximately 91% (199/216) of the specimens examined in the present study were captured at these depths. The deepest captures were at 73 and 62 m, where a single fish was taken each time. It is unusual for adult S. civitatium to occur in shallow, inshore regions. Of four fish collected shallower than 10m, three were small juveniles (<35mm SL). Recently, several small juveniles (22-24 mm SL) have been collected in the Cape Fear River estuary, North Carolina (S.W. Ross, Dep. Nat. Resour., Morehead City, NC, pers. commun. 24 July 1985). It is not known how regularly this species occurs in these inshore areas or whether the recent captures represent isolated occurrences; however, Schwartz et al. (1981) listed this species as rare in the Cape Fear River estuary. Seasonal occurrence and abundance of juveniles in nearshore waters need further investigation.

McCaffrey (1981) reported capture depths of 30-187m for 23 specimens purported to be *S. civitatium* taken on the continental shelf in the northeastern Gulf of Mexico between $84^{\circ}30'$ and $89^{\circ}00'$ W longitudes. Nineteen of these specimens were collected between 80 and 187m, depths considerably deeper than records for specimens I examined. Not all specimens identified as *S. civitatium* by McCaffrey were preserved and curated in collections (at least nine were indicated as having been discarded). One retained specimen (UF 70946) collected at 45m, is *S. civitatium*, but two other specimens (UF 70885) from *Tursiops* Station 7019-07 with an estimated depth of 187 m are, rather, *S. pusillus* (Goode and Bean) and an undescribed species (species C of Munroe 1987), which occur commonly at depths similar to that reported for this station (187 m). Given the complexity of the series identified as *S. civitatium* in McCaffrey's study, the very deep captures reported (80–187 m) for *S. civitatium* are probably erroneous.

Remarks In the original description of *S. civitatum*, Ginsburg (1951:198) stated that this species and *S. plagusia* differed enough to consider them distinct species but that it was possible that they represented subspecies of a more widespread polytypic species. It was shown earlier (see "Remarks" section in account of *S. plagusia*) that Ginsburg had more than one species in his account of *S. plagusia*, and therefore his subspecific designations for this species were unfounded. *Symphurus civitatium* is consequently recognized as a species within this complex of morphologically similar species of *Symphurus*.

The etymology of the name *civitatum*, applied by Ginsburg to this species, is unclear from the original description. The name may have been derived from the genitive plural of *civitas* (meaning "of the citizenry"). Following this assumption, the proper genitive plural is *civitatium*, not *civitatum* as indicated by Ginsburg (G.C. Steyskal, Dep. Entomology, Natl. Mus. Nat. Hist., Wash. DC, pers. commun. 1989). Thus, the spelling of the specific name for this species remains unchanged regardless of generic assignment of the species. Therefore, spelling changes such as *S. civitatus* (Bailey et al. 1960, and other checklists of common and scientific names) are incorrect.

Comparisons Symphurus civitatium is most similar to, but has a completely allopatric distribution from, the Caribbean and South Atlantic species S. plagusia. Differences between these two species were discussed in the "Comparisons" section under the account for S. plagusia.

Meristic features of *S. civitatium* overlap at least partially those of two other Atlantic species belonging to this complex (the Caribbean and South Atlantic species *S. caribbeanus* and *S. tessellatus*). There is almost complete overlap in several meristic features between *S. civitatium* and *S. caribbeanus*; however, *S. civitatium* has a fleshy ridge on the ocular-side lower jaw (absent in *S. caribbeanus*; see Figures 4b and 4e) and has lower modal counts for total vertebrae (47– 49 vs. 49–50 in *S. caribbeanus*), dorsal fin rays (86–93 vs. 89–96), and anal fin rays (70–78 vs. 74–80). *Symphurus civitatium* also has narrow crossbands with uniformly-colored fins (becoming progressively darker in the posterior portions of sexually mature males). In contrast, *S. caribbeanus* has numerous well-developed crossbands and vertical fins with an alternating series of blotches and unpigmented areas in individuals of both sexes. *Symphurus caribbeanus* also has a more pointed snout with only a narrow space between the upper eye and dorsal fin base (versus a square snout with a space between the upper eye and the dorsal fin base usually greater than twice the eye diameter in *S. civitatium*; compare Figures 4b and 4e).

Despite some overlap in certain meristic values, S. civitatium and S. tessellatus are guite distinctive. The easiest way to distinguish these species is that S. civitatium has a well-developed fleshy ridge on the ocularside lower jaw (absent in S. tessellatus; compare Figures 4b and 4c), lacks a black spot on the ocular-side opercle, and, when present on the body, crossbands are faint and narrow, whereas S. tessellatus has a bold pattern of wide crossbands and a well-developed black opercular spot. Other distinctions between these species include the absence of scales on the blind sides of the dorsal and anal fin rays of S. civitatium (present in S. tessellatus larger than about 60mm SL), fewer vertebrae (total vertebrae 47-49 vs. 50-53 in S. tessellatus), and modally lower meristic features: dorsal fin rays 86-93 vs. 91-102 (usually 93-101) in S. tessellatus; anal fin rays 70-78 vs. 77-86; scales in a longitudinal series 66-83 vs. 81-96.

Some meristic values of S. civitatium overlap those of 11 other species of Atlantic tonguefishes. Symphurus civitatium occurs sympatrically with S. diomedeanus and S. plagiusa and may be collected with these species. The suggestion by Walls (1976:390) to synonymize S. civitatium with S. plagiusa, based on partial overlaps in meristic features, pigmentation, and ecological co-occurrence, is not supported by results of this study. Symphurus civitatium differs from both these species primarily in caudal-fin-ray count (12 vs. 10 in the others) and by notable differences in pigmentation patterns. Symphurus diomedeanus usually has a series of black spots on posterior rays of the dorsal and anal fins and a well-developed pupillary operculum (both characters absent in S. civitatium). Symphurus civitatium can be distinguished from S. plagiusa in that S. plagiusa usually has a well-developed black spot on the outer surface of the ocular-side opercle (absent altogether or only a diffuse blotch resulting from pigment from the inner opercular lining showing to the outside in S. civitatium), and inner opercular linings on both sides are heavily pigmented (only the ocularside opercular lining is pigmented in S. civitatium). Symphurus plagiusa has larger eyes (83-126 HL) that are usually equal in position (versus smaller eyes 70-110 HL, which are slightly subequal in position in S. civitatium). Also, the jaws reach only as far posteriorly as a vertical through the mid-eye region in S. *plagiusa*, while in S. *civitatium* the jaws reach a vertical through the rear margin of the pupil, the rear margin of the eye, or may even extend slightly beyond a vertical equal with the posterior margin of the lower eye in S. *civitatium*. In larger S. *plagiusa*, there are 4–8 ctenoid scales on the blind sides of the dorsal and anal fin rays (absent or at most only 1–2 scales along bases of fin rays in S. *civitatium*).

Symphurus civitatium is not easily confused with other Atlantic species (S. kyaropterygium, S. trewavasae, S. normani, S. piger, S. nigrescens, S. pusillus, S. lubbocki, and S. reticulatus) with which it overlaps in some meristic features. Symphurus civitatium differs from all of these in ID pattern (1-4-3 versus other patterns: 1-4-2 in S. kyaropterygium; 1-3-3 in S. trewavasae and S. normani; 1-3-2 in S. piger, S. nigrescens, S. pusillus, S. reticulatus, and S. lubbocki). In addition to differences in ID pattern, S. civitatium differs from the South Atlantic S. kyaropterygium in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and darkly-pigmented blotch on the caudal extremity both present in S. kyaropterygium. Symphurus civitatium differs from the South Atlantic S. trewavasae principally in caudal-fin-ray count (12 vs. 10) and its smaller eye (70-110 HL vs. 114-162 HL in S. trewavasae). The eastern Atlantic S. normani possesses scales on the blind sides of the dorsal and anal fin rays, has a spotted peritoneum, and pepper-dot pigmentation on the blind side of the body (all absent in S. civitatium). Symphurus civitatium differs from the species with a 1-3-2 ID pattern (except S. lubbocki and S. reticulatus) in lacking a black peritoneum. Symphurus civitatium is further distinguished from S. lubbocki and S. reticulatus in having a fleshy ridge on the ocular-side lower jaw (absent in these others), in lacking complete dentition on ocular-side jaws (ocular-side jaws without dentition, or with only a partial row of teeth, versus ocular-side jaws with complete dentition in S. lubbocki and S. reticulatus), by its much larger size (152 vs. <50 mm SL), and by differences in pigmentation (dark-brown body with crossbands and uniformly-pigmented fins versus light-brown or yellowish body with incomplete crossbands in S. lubbocki and dark chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in S. reticulatus).

Meristic values of *S. civitatium* overlap those of five eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. Of these species, *S. civitatium* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocularside lower jaw, and in both the first dorsal fin ray reaches the vertical equal with or anterior to the anterior margin of the upper eye. The two species differ in that S. civitatium lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in S. melanurus), has fewer scales in a longitudinal series (66-83 vs. 89-108 in S. melanurus), and S. civitatium has an unpigmented or only lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in S. melanurus). Symphurus civitatium differs from the remaining four eastern Pacific species that have comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). Symphurus civitatium is further distinguished from S. fasciolaris and S. melasmatotheca in possessing 12 caudal fin rays (versus 10 and 11 in S. fasciolaris and S. melasmatotheca, respectively) and in lacking an ocellated spot on the caudal fin (present in S. fasciolaris) or pigmented peritoneum (present in S. melasmatotheca). Symphurus civitatium differs further from S. atricaudus and S. williamsi in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species). From S. leei, S. civitatium is further distinguished in having the head length considerably smaller than the body depth (versus head length nearly equal with body depth in S. leei), in having a smaller eye (13-21 SL vs. 22-27 SL in S. leei), and in having an unpigmented peritoneum (versus black in S. leei).

Material examined 298 specimens (22.0–149.0 mm SL).

Counted and measured (30 specimens, 48.8-149.0 mm SL). Southeastern United States. North Carolina: USNM 157403; Paratype (109); 35°21'10", 75°22'40"; 26m; 19 Oct 1884. Florida: TU 75907; 3(131-136); 27°35'04"N, 80°04'04"W; 26m; 5 Sep 1965. UF 13062; (130); 28°35.5'N, 80°08'W; 62m; 21 Feb 1965. USNM 154946; Paratype (139); Cape Canaveral; 18m; 4 Apr 1940. Gulf of Mexico. Alabama: ALA 3015; 3(75.5-85.2); to 30 m; 1968. Mississippi: ALA 606.29; (94.4); Horn Island; Jul-Aug 1958. FMNH 45979; (110); 29°22'N, 88°40'W; 51 m; 22 Oct 1953. Louisiana: USNM 155227; Holotype (110); 29°06'30"N, 89°40'W; 17m; 8 Jul 1938. USNM 313647; 2(48.8-72.2); Calcasieu Lake (ca. 30°N, 93°W); Feb 1982. Texas: FMNH 45109; 3(138-149); 27°43'N, 96°51'W; 27 m; 26 Sep 1950. USNM 313646; 9(88.6-108); 3 mi. offshore, Port Aransas (ca. 28°N, 97°W); 15m; 16 Sep 1982. Mexico: IMS 544; 3(121-130); W Campeche; 27 m; 22-29 Jul 1951. UMML 34365; (130); 20°12'N, 91°40'W; 37m; 11 Dec 1952.

Counted paratypes (148 specimens, 41 lots). Gulf of Mexico. Florida: USNM 86153; (120); St. Joseph's Bay; 27 Jan 1917. Alabama: USNM 157402; (117); Mobile; 13 m; 7 Feb 1917. Louisiana: USNM 86140; (120); Calcasieu Pass; 9 m; 15 Feb 1917. USNM 154945; 3(122–130); 28°54'N, 91°41.5'W; 18 m; 11 Jul 1938. USNM 154947; 5(110–123); 28°55.5'N, 91°46'W; 18 m; 11 Jul 1938. USNM 154948; 2(120–124); 28°58'N, 91°40.5'W; 16 m; 12 Nov 1938. USNM 154949; 2(105–129); 28°41.5'N, 91°10'W; 15 m; 11 Nov 1938. USNM 154950; 2(122–124); 28°47'N, 91°21.5'W; 11 Jul 1938. USNM 154951; (126); 29°12'N, 89°50.5'W; 13 m; 8 Jul 1938. USNM 154952; (117); 28°43'N, 91°13'W; 15 m; 11 Jul 1938. USNM 154953; 2(102–105); 29°12.5'N, 89°57'W; 7m; 10 Jul 1938. USNM 154954; 3(114–118); 28°35.5'N, 91°01.5'W; 22m; 13 Jul 1938. USNM 155226; (114); 28°45'N, 91°17.5'W; 16m; 11 Jul 1938. USNM 157399; 3(109–121); Grand Terre; 2 Jul 1930. USNM 157400; 3(99.7–118); Grand Terre; 27 Jun 1930. **Texas**: USNM 86139; 2(118–126); Aransas Pass; 15m; 5 Mar 1917. USNM 120081; (111); Galveston; 1941. USNM 120082; (81.5); Aransas Pass; 7 Aug 1941. USNM 157401; (117); Galveston; 10m; 26–27 Feb 1917.

Counted (non-type material). Southeastern United States. Florida: UMML 34342; 3(136-140); 28°34'N, 80°15'W; 42 m; 19 Nov 1964. USNM 274484; (117); 28°13.5'N, 80°21'W; 22 m; 14 Nov 1963. USNM 291316; (132.0); 28°13'N, 80°21'W; 22m; 14 Nov 1963. USNM 291317; 13(114-142); 28°13'N, 80°21'W; 22m; 14 Nov 1963. UMML 34343; (131); 28°12'N, 80°05'W; 60 m; 14 Mar 1965. UMML 34344; (118); 27°57 N, 80°03'W; 55 m; 28 Sep 1963. Gulf of Mexico. Alabama: ALA 301.17; 2(85.4-94.3); Dauphin Island; 28 Sep 1952. ALA 353.05; (108); Mobile Ship Channel; 6 Sep 1951. ALA 2385; 13(85.8-103); Dauphin Island; 15 Jul-20 Aug 1966. Texas: TCWC 4187.4; (100); 29°10'N, 94°30'W; 14m; 28 Sep 1973. TCWC 4189.21; 18(97.8-124); 28°26'N, 95°23'W; 28m; 29 Sep 1973. TCWC 4195.31; 9; 28°25N, 95°18'W; 35m; 31 Oct 1973. UMML 34345; (128); 28°07'N, 95°53'W; 37m; 26 Jan 1958. Mexico: FMNH 45427; 7(126-140); 20°18'N, 91°48'W; 42m; 7 Dec 1952. UMML 34366; (130); 20°12'N, 91°40'W; 37 m; 11 Dec 1952. USNM 157693; 5(117-126); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. USNM 157694; 3(128-132); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. USNM 291318; (127); Campeche, Yucatan, 20°05'N, 91°28'W; 31 m; 26 Aug 1951. FMNH 46369; 11(115-138); 19°48'N, 91°20'W; 25 Aug 1951. GCRL 16383; 2(76.0-86.5); Lagunas de Terminos, Punta Zachtal, Campeche; 17 Nov 1970. IMS 543; 16(126-142); Pta Frontera; 31 m; 29 Jul-6 Aug 1951. USNM 274485; (132); N of Soto La Marina; 15 Mar 1947.

Other material examined (120 specimens, 22 lots). Bermuda: ANSP 137573; (79.3); washed onto shore. Southeastern United States. North Carolina: 3(22-24); Cape Fear River; Aug 1981; (uncatalogued reference specimens, CP&L Biol. Lab., Southport, NC 28461). Florida: UF 35486; (125); 29°58.1'N, 81°16.9'W; 14m. TU 92501; 25(82.0-120); 29°11'05"N, 80°53'05"W; 12m; 24 Feb 1970. UMML 34346; 3(118-134); 28°22'N, 80°05'W; 60 m; 14 Mar 1965. Gulf of Mexico. Florida: ANSP 94305; (25.0); Key West; 1m; 21 Mar 1958. Mississippi: FMNH 45980; 2(110-120); 28°45'N, 89° 15'W; 60 m; 23 Oct 1953. FMNH 86369; (113); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. TU 5374; 18(113-137); 29°14.4'N, 88°52.4'W; 32m; 11 Aug 1952. TCWC 2251.1; (126); 29°09'N, 88°52'W; 73m; 10-16 Dec 1963. Alabama: FMNH 89568; 2(119-121); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. ALA 798.14; 2(108-110); Gulf Shores, Breton Island; 3 Aug 1959. UF 70946; (115); 29°41'N, 88°14.5'W; 45m; 22 Jul 1971. USA 1905; 25(91.9-122); 29°57'N, 87°54'W; 26 m; 20 Apr 1975. Louisiana: ANSP 55825; (125); Breton Island; Nov 1930. BMNH 1931.11.5:75; 1; Reversed Specimen; Breton Island. FMNH 45981; 2(109-119); 28°56'N, 89°09'W; 59 m; 25 Oct 1953. Texas: CAS-SU 40556; (133.4); Freeport; 28 Apr 1940. FMNH 79851; 3(139-152); 27°43'N, 96°53'W; 26m; 14 Dec 1950. UMMZ 199071; 5(46.0-57.3); 8-9 Apr 1939. USA 4070; 20(111-127); 10 mi. SSE Port Aransas; 3 Dec 1975. Mexico: GCRL 16384; (32.7); Laguna el Carmen, Tabasco; 2 Mar 1978.

Symphurus tessellatus (Quoy and Gaimard 1824) Figures 2, 3, 4c, 6a

Synonymy

Plagusia tessellata Quoy and Gaimard 1824:240 (counts and color description; Rio de Janeiro Bay [= Guanabara Bay], Brazil).

- Plagusia brasiliensis Agassiz, in Spix and Agassiz 1831:89 (counts, color description, and figure; Bahia, Brazil). Castelnau 1855:79 (brief description and figure). Whitehead and Myers 1971:495 (nomenclature and dating of Spix and Agassiz's Brazilian Fishes). Kottelat 1984:150 (listed in type catalogue of MHNN). Kottelat 1988:79 (nomenclature and type status of species described in Spix and Agassiz's Brazilian Fishes).
- Aphoristia ornata. Kaup 1858:106 (in part) (synonymy; listed, South America). Günther 1862:490 (in part) (synonymized with S. plagusia Schneider, in Bloch and Schneider 1801; brief description; counts; Atlantic coasts of tropical America). Kner 1865-67: 292 (listed, Rio de Janeiro, Brazil).
- Symphurus plagusia (not of Schneider, in Bloch and Schneider). Jordan and Goss 1889:324 (in part) (synonymy; in key; brief description; nomenclature; West Indies to Rio de Janeiro, Brazil). Jordan and Evermann 1898:2709 (in part) (after Jordan and Goss 1989). Berg 1895:79 (in part) (Mar del Plata-Montevideo; counts include those for S. jenynsi). Thompson 1916:416 (in part) (after Jordan and Goss; counts, measurements, brief color description). Devincenzi 1920:135 (Río de la Plata; distinguished from S. jenynsi). Devincenzi 1924-26:281 (listed, Uruguay; counts). Meek and Hildebrand 1928:1005 (in part) (color description; counts; Panama). Puyo 1949:178 (in part) (French Guyana; figure, counts, color description). Lowe-McConnell 1962:694 (in part) (listed, British Guiana). Caldwell 1966:84 (collections from offshore localities, Jamaica). Menezes and Benvegnú 1976:142 (synonymized with S. plagusia). Soares 1978:23 (listed, Rio Grande do Norte, Brazil; counts, color description, and figure). Lema et al. 1980:44 (Río de la Plata region, Rio Grande do Sul, Brazil; synonymy). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lucena and Lucena 1982:56 (listed, collections in southern Brazil). Matsuura in Aizawa et al. 1983:463 (listed, French Guiana and Surinam; counts, measurements, color photograph).
- Aphoristia fasciata (not of DeKay). Goode and Bean 1896:458 (in key and figured; Jamaica).
- Symphurus plagusia tessellata. Ginsburg 1951:199 (diagnosis and description of subspecies from Brazil-Uruguay). Ringuelet and Aramburu 1960:91 (in

key; figure; synonymy; listed, Argentina). Carvalho et al. 1968:22 (in part) (synonymy; in key; brief description; occurrence in northern Brazil). Lazzaro 1973: 247 (in key; distribution in southern Brazil and Uruguay). Palacio 1974:87 (listed, north of Puerto, Colombia). Lazzaro 1977:70 (in key). Lema and Oliveira 1977:7 (recorded from Santa Catarina, Brazil; in key; suggested that *S. civitatium*, *S. tessellatus*, and *S. plagusia* are geographic races of the same species).

- Symphurus plagusia plagusia (not of Schneider, in Bloch and Schneider). Cervigon 1966:816 (listed, Venezuela; probably S. tessellatus based on high meristic features, color description, and large sizes reported). Palacio 1974:87 (in part) (Colombia; specimens listed as S. p. plagusia were misidentified).
 Symphurus pterospilotus (not of Ginsburg). Lema and
- Oliveira 1977:7 (in part) (specimens misidentified).

Diagnosis A Symphurus with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; distinct, dark-brown or black, almost spherical blotch on the outer surface of the ocular-side opercle; 4-8 small ctenoid scales on the blind sides of the dorsal and anal fin rays (best developed on fin rays in posterior onethird of body in specimens >70 mm SL); lacking a fleshy ridge on the ocular-side lower jaw; 91-102 dorsal fin rays; 77-86, usually 78-84, anal fin rays; 49-54, usually 50-53, total vertebrae; 81-96, usually 83-93, scales in a longitudinal series; moderately long jaws usually extending to the vertical line through the middle or posterior margin of pupil of lower eye; moderatelysized eye (79-114 HL, \bar{x} 95) without pupillary operculum; dorsal fin origin reaching the vertical line through the anterior margin of the upper eye, or occasionally only reaching the vertical through the middle of the upper eye; ocular surface dark- to light-brown, with 5-9 well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk; inner lining of opercle and isthmus heavily pigmented on both sides of body; dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas; anterior dorsal and anal fin rays usually streaked with brown pigment; fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming progressively darker posteriorly; males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

Description A large tonguefish, attaining adult sizes to 220 mm SL. ID pattern (Table 1) usually 1-4-3 (170/231 specimens), less frequently 1-5-3 (14), 1-4-2

Table 14

Summary of morphometrics expressed as thousandths of standard length (except SL in mm) for *Symphurus tessellatus* (N 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

Character	Range	Mean	SD	P. brasiliensis
SL	97.9-203	145.0	27.66	140.3
BD	247-312	280.2	18.82	262
PDL	32-48	41.7	4.48	32
PAL	181-227	204.7	10.58	217
DBL	952-968	958.3	4.48	968
ABL	771-876	798.0	22.90	793
PL	44-73	59.0	6.47	43
PA	27-56	41.5	6.01	-
CFL	72-118	90.9	10.36	88
HL	170 - 199	186.6	7.37	175
HW	193 - 247	218.6	15.58	209
POL	117-135	125.9	5.38	117
SNL	35 - 46	40.3	2.55	32
UJL	41-52	46.3	3.12	41
ED	15-21	17.6	2.04	18
CD	33-63	46.4	6.51	36
UHL	113 - 163	143.3	12.03	120
LHL	80-114	97.8	10.56	94

(10), or 1-3-3 (8). Caudal fin rays usually 12 (207/224), less frequently 10,11, or 13 (Table 2). Dorsal fin rays 91–102 (Table 3). Anal fin rays 77–86, usually 78–84 (Table 4). Total vertebrae 49–54, usually 50–53 (228/ 233) (Table 5). Hypurals 4. Longitudinal scale rows 81–96, usually 83–93 (Table 6). Scale rows on head posterior to lower orbit 18–23, usually 20–22 (Table 7). Transverse scales 38–45 (Table 8).

Proportional measurements appear in Tables 14 and 15. Body relatively elongate, only moderately deep $(247-312 \text{ SL}, \overline{x} 280)$; greatest depth usually occurring in anterior third of body. Preanal length 181-227 SL, \overline{x} 205. Head relatively short (170–199 SL, \overline{x} 187); considerably shorter than body depth. Head relatively wide (193–247 SL, \overline{x} 219), wider than head length (HW/HL 1.1–1.4, \bar{x} 1.2); lower head lobe (80–114 SL, \bar{x} 98) narrower in width than upper head lobe (113-163 SL, \overline{x} 143). Lower opercular lobe on ocular side (243–359 HL, \bar{x} 307) greater in width than upper opercular lobe (161–252, \overline{x} 206). Postorbital length 117–135 SL, \overline{x} 126. Snout (Fig. 4c) moderately long and somewhat pointed (196–231 HL, \bar{x} 216); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws moderately long; upper-jaw length 222–278 HL, \bar{x} 248; posterior exten-

Table 15

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for *Symphurus tessellatus* (N 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

Character	Range	Mean	SD	P. brasiliensis
HL/HW	1.1-1.4	1.2	0.08	1.2
POL	593-723	674.9	25.07	669
SNL	196 - 231	215.7	9.25	184
UJL	222-278	248.1	15.58	237
ED	79-114	95.2	10.06	106
CD	173 - 322	245.0	31.85	204
OPLL	243-359	306.8	31.68	-
OPUL	161 - 252	205.7	24.03	-
UHL	682-891	774.2	56.18	690
LHL	422-593	523.1	46.26	539

sion of maxilla usually reaching to the vertical through the middle or posterior margin of pupil of lower eye. Ocular-side lower jaw lacking a fleshy ridge near posterior margin (Fig. 4c). Chin depth 173-322 HL, \bar{x} 245. Lower eye moderate in size (79–114 HL, \bar{x} 95); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1-3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952–968 SL, \overline{x} 958. Dorsal fin origin (Fig. 4c) usually reaching to vertical line through anterior margin of upper eye, or occasionally only reaching vertical line through middle of upper eye; predorsal length 32-48 SL, \bar{x} 42. Length of anal fin base 771-876 SL, \bar{x} 798. Four to eight scales present on blind sides of dorsal and anal fin rays (best developed on fin rays in posterior third of body of specimens >70 mm SL). Pelvic fin length 44-73 SL, \overline{x} 59; longest pelvic fin ray usually reaching base of first anal fin ray or occasionally falling short of that point; pelvic to anal fin distance 27-56 SL, \overline{x} 42. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 72–118 SL, \bar{x} 91.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either with very short row of teeth anterior to vertical line equal with anterior nostril or lacking teeth altogether.

Scales large, strongly ctenoid on both sides of body.

Pigmentation General pattern of body pigmentation similar in both sexes at all sizes but usually more intense in sexually mature males. Males, especially those in breeding condition (collected with gravid females), usually with more intense banding, dark-black fins, dark-black spot on ocular-side opercle, and, additionally, some specimens with irregularly-shaped, black pigment patches on posterior one-half of blind side of body. In contrast, mature females also with crossbands but less conspicuous than in males and with posterior portions of fins dark-brown but usually not black. Females lack black pigment patches on blind side observed in males.

Ocular-surface background pigmentation ranging from dark- to light-brown. Body usually with 5-9 (usually 5-7) well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk. First two bands relatively consistent in position; first crossing head immediately posterior to eyes; second crossing body immediately behind opercular opening. Crossbands on trunk variable in number and degree of completeness, especially those between opercular opening and point about equal to two-thirds of trunk length. Males usually with 3-4 well-developed and lesser number of incomplete bands along trunk. Two posteriormost bands, just anterior to caudal fin base, slightly arched and usually darker than others on body. Blind side usually uniformly creamy-white; some mature males with irregular patches of black pigment on caudal one-third of blind side. Peritoneum unpigmented.

Outer surface of ocular-side opercle usually with distinct, dark-brown or black spot on ventral margin slightly forward of posterior margin of opercle. Opercular spot ranging from almost spherical to dorsoventrally-elongate black blotch covering most of lower opercle. Intensity of pigmentation in spot maximally developed in sexually mature adults. Inner linings of opercles and isthmus heavily pigmented on both sides of body. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined band.

Anterior dorsal and anal fin rays usually streaked with brown pigment, more heavily pigmented than connecting membranes. Fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming increasingly darker posteriorly. Males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

Size and sexual maturity Symphurus tessellatus is one of the largest species in the genus and is the second largest Atlantic tonguefish species after *S. jenynsi* Evermann and Kendall (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987). Size-related life-history information is based on data from 385 fish. Males and females attain nearly similar sizes, but females are somewhat larger. The largest fish measured in this study was a female of 220 mm SL; the largest male measured 205 mm SL.

There were 214 males, 155 females, and 16 immature fish among material examined. There were 119 mature females ranging in size from 104 to 220 mm SL (Fig. 2). Based on reproductive stages for females, sexual maturity in this species occurs at sizes of 104–120 mm SL, but usually larger than 115 mm SL. Most mature females exceeded 140 mm SL, with only six smaller than 125 mm SL and two smaller than 110 mm SL present among fish examined. Twenty-six females of 49.5–119 mm SL were immature. The smallest of these, measuring 49.5 and 62.8 mm SL, had ovaries that were scarcely elongate. Other immature females, ranging from 68.6 to 119 mm SL, had only partially elongate ovaries with no indications of developing ova.

Geographic distribution (Fig. 3) A widespread tropical species, ranging in the north from the larger Caribbean Islands such as Cuba, Hispaniola, and Puerto Rico, southward to Uruguay. In the West Indies, adults and juveniles have frequently been taken in abundance at several localities, but the distribution of this species appears limited by the location of soft silt and mud sediments. These bottom types are more common on the larger islands that support river and estuarine habitats. The species has been taken at several inshore locations in Puerto Rico, Cuba, and Haiti, and a large number of adults were collected by the RV *Oregon* on the shelf area southwest of Jamaica (Caldwell 1966). Juveniles of this species have been taken from several inshore areas in Jamaica as well.

Along the continental margin it has been frequently captured on muddy bottoms from Belize and Nicaragua south to southern Brazil and Uruguay (ca. 37°S). In the northern part of its range along Central America, it has been collected as far north as Belize (17°12'N), but thus far is unknown from the Yucatan Peninsula or Campeche Bay. The absence of this species in the Yucatan region may be explained by upwelling (Rivas 1968) or by changes in the sediments of this region. The Yucatan Shelf is a broad limestone plateau with a minimum of land-derived detrital sediments (Harding 1964, Topp and Hoff 1972). Instead of soft silt and mud sediments typical of more southern locations, sediments on the inner shelf off the Yucatan Peninsula are firmer, consisting of skeletal remains of various planktonic and benthonic organisms, ooids, calcareous pellets, lithic fragments, and grapestone aggregates. This dramatic change from soft, mud substrates to firmer sediments in the Yucatan region may account for the absence of S. tessellatus in the waters off southern Mexico.

Symphurus tessellatus is one of the most abundant and frequently collected tonguefish species, especially in trawls, from Belize and Honduras south to Venezuela and along the entire coastline of northern South America from the Guianas to about southern Brazil (Meek and Hildebrand 1928, Cervigon 1966, Palacio 1974, Carvalho et al. 1968, Menezes and Benvegnú 1976). Menezes and Benvegnú (1976) described S. tessellatus as the most abundant tonguefish collected along the Brazilian coast from about 26°49'S to 4°S in northern Brazil. South of 28°S, it appears to be much rarer, and all specimens I examined from Rio Grande do Sul and south are juveniles. The small size of these specimens suggests that adult S. tessellatus may not be regular components of the ichthyofauna of Uruguay and northern Argentina, but that juvenile S. tessellatus either seasonally migrate, or are expatriated by passive transport, into waters along the continental shelf and coastline of Uruguay and northern Argentina. Thus it appears that the region south of Rio Grande do Sul, which comes under periodic influence from the cold Falkland Current, does not harbor large populations of this essentially tropical species so common in warmer waters further north.

The specimen from the inner continental shelf of Argentina described by Lazzaro (1973) as *S. plagiusa* and cited in the distribution section for *S. plagusia* (= *S. tessellatus* in the present study) by Menezes and Benvegnú (1976) is probably not a specimen of *S. tessellatus*. Based on the counts and figure provided by Lazzaro, it more closely matches meristic features and has the general body shape of *S. trewavasae*.

Bathymetric distribution Throughout its range, juvenile S. tessellatus are commonly taken by beach seine in nearshore habitats, and larger adults are frequently captured by trawl in deeper waters. Individuals have been collected from a depth range of 1-86m (Table 11). There is an ontogenetic migration offshore. Juveniles occur commonly in medium- to high-salinity regions of estuaries and in high-salinity, soft-bottom habitats in nearshore mudflats. Adults generally range into deeper water, although a few large fishes I examined were taken in relatively shallow water. Most of the 349 S. tessellatus examined in this study were collected between 1 and 70 m (Table 11), but the majority of captures, and the center of abundance for this species, occurs in depths of 1-50m (81% of the individuals in this study). The deepest captures are for a single specimen taken at 86m and 21 individuals at 73m. The majority of shallow-water captures were specimens smaller than 130mm SL.

Interestingly, Menezes and Benvegnú (1976) reported that in southern Brazil, *S. tessellatus* (misidentified as *S. plagusia*) occurs only in shallow water

 $(<12 \mathrm{m})$, though it is known to occur deeper in northern Brazil. They suggested that the presence of S. jenunsi off southern Brazil, which generally occurs on the continental shelf at depths greater than 12m, somehow prevented the occurrence of S. tessellatus at these depths. Another explanation is that S. tessellatus is primarily a tropical species reaching its southern limit of distribution in southern Brazil south of Rio de Janeiro. Its bathymetric distribution in these waters may be limited not by competitive interaction from S. jenynsi; rather, the offshore distribution of S. tessellatus may be restricted by cooler water temperatures on the shelf. The appearance of S. jenynsi, a temperatewater species (Menezes and Benvegnú 1976), in these regions indicates that temperature may strongly influence the offshore distribution of S. tessellatus in southern Brazil.

Throughout its range to at least Rio de Janeiro, juvenile S. tessellatus occur in similar habitats and are often collected with a complete size range of S. plagusia. In the Caribbean, juvenile S. tessellatus are also taken with a complete size range of S. caribbeanus. Along the northeastern coast of South America from Surinam to eastern Brazil, large adults of this species are collected in deeper areas with a wide size range of specimens of S. oculellus and S. diomedeanus.

Remarks Comments regarding the nomenclatorial history of this species were reviewed under the "Remarks" section in the account of *S. plagusia*. All authors since Kaup (1858) have considered *S. tessellatus* and *S. plagusia* as conspecific. However, results of this study indicate that *S. plagusia* and *S. tessellatus* are both valid species.

The original description of *Plagusia tessellata* by Quoy and Gaimard (1824) provides sufficient information to clearly identify their specimen. This is the earliest name applied to a tonguefish collected from the southern Brazil region and, therefore, has priority over Plagusia brasiliensis Agassiz, in Spix and Agassiz 1831. Plagusia brasiliensis was collected at "Bahia," Brazil. The type specimen was thought to have been destroyed during the Second World War (Whitehead and Myers 1971). However, in two recent publications concerning authorship and existence of type specimens described in Spix and Agassiz's "Brazilian Fishes" (1829-31), Kottelat (1984) listed a specimen (MHNN 691) first as the holotype, and later (Kottelat 1988) as a possible syntype of P. brasiliensis, thus indicating the existence of at least one specimen from the original account of this nominal species. My examination of this specimen reveals that meristic features lie completely within the range of counts typical for S. tessellatus (ID pattern 1-4-3, caudal fin rays 12, dorsal fin rays 99, anal fin rays 83, total vertebrae 53, longitudinal scales 90,

scale rows on head 21, transverse scale count 42). Additionally, the specimen has small ctenoid scales on the blind sides of the dorsal and anal fin rays and a relatively large eye (10.6% HL), features characteristic of *S. tessellatus. Plagusia brasiliensis* is therefore regarded as a junior subjective synonym of *Symphurus tessellatus* (Quoy and Gaimard 1824).

In their revision of the tonguefishes occurring in the western South Atlantic, Menezes and Benvegnú (1976) reported that the species they identified as S. plagusia had high counts and that the pigmentation consisted of sharply contrasting crossbands with dorsal and anal fins becoming almost black in their posterior portions. These authors found little variation in their material and believed that only a single species was present on the inner continental shelf of southern South America. Menezes and Benvegnú (1976) used the oldest available name, Symphurus plagusia (Schneider, in Bloch and Schneider 1801), for their species. These authors also suggested that the subspecific designation for S. plagusia, as proposed by Ginsburg (1951), should be reexamined. Based on the high counts and color description of their specimens (strongly banded with fins becoming black posteriorly) and the capture location (open-shelf region where S. plagusia [sensu strictu] is rare), it is probable that Menezes and Benvegnú had studied only S. tessellatus.

Comparisons Symphurus tessellatus most closely resembles and is completely sympatric throughout the Caribbean and warmer waters of the western South Atlantic with S. oculellus, S. caribbeanus, and S. plagusia. Symphurus tessellatus differs from S. oculellus in having 4-8 small but well-developed scales on the blind sides of the dorsal and anal fin rays (especially evident in specimens >70 mm SL), a larger eye (79-114, \overline{x} 95 HL in S. tessellatus vs. 68–104, \overline{x} 84 HL), and lower meristic values (dorsal fin rays 91-102 vs. 99-106 in S. oculellus; anal fin rays 77-86 vs. 81-88; total vertebrae usually 50-53 versus 53-54). Symphurus tessellatus lacks a fleshy ridge on the ocularside lower jaw that is usually present and well developed in S. oculellus (compare Figures 4c and 4d). Also, the posterior extension of the jaws is slightly less extensive in S. tessellatus, reaching only to about the vertical line through the rear margin of the pupil or rear margin of the lower eye. In S. oculellus, the jaws extend further backwards reaching a vertical line through the posterior margin of the eye, and in many specimens the jaws extend slightly posterior to the vertical line through the posterior margin of the lower eye.

Symphurus tessellatus generally has about nine wide, dark-brown crossbands; S. oculellus has 10-14 (usually 10-12) narrower crossbands. In S. tessellatus the caudal fin and the posterior one-third of the dorsal and

anal fins are usually dark-brown or black and without an alternating series of blotches and unpigmented areas. In *S. oculellus*, the dorsal and anal fins are not uniformly dark-brown or black; instead, in the posterior two-thirds of the dorsal and anal fins there is an alternating series of blotches and unpigmented areas.

Symphurus tessellatus, especially juveniles and small adults (to $\sim 150 \,\mathrm{mm}$ SL), are superficially similar in overall body shape, relative eye size, and body pigmentation (crossbanding) to S. caribbeanus. However, S. tessellatus is easily distinguished from S. caribbeanus by the black spot on the outer surface of the ocular-side opercle and presence of scales on the blind sides of the dorsal and anal fin rays (both absent in S. caribbeanus), and S. tessellatus has the posterior dorsal and anal fins, as well as the caudal fin, uniformly darkly-pigmented without alternating blotches and unpigmented areas, and often has black pigment patches on the blind side of the body. In contrast, in S. caribbeanus, posterior regions of the vertical fins have alternating dark blotches and unpigmented areas without a progressive darkening in coloration posteriorly in these fins, and the blind side of the body lacks black pigment patches. Symphurus tessellatus also has modally higher counts than S. caribbeanus (total vertebrae 50-53 vs. 49-50 in S. caribbeanus; dorsal fin rays 91-102 vs. 89-96; anal fin rays 77-86 vs. 74-80; 81-96 scales in a longitudinal series vs. 78-89).

Symphurus tessellatus can readily be distinguished from S. plagusia and S. civitatium, and differences between these species were discussed in the "Comparisons" sections under the accounts for S. plagusia and S. civitatium, respectively.

Symphurus tessellatus is quite distinct from other Atlantic tonguefishes. Some meristic values of this species overlap those of *S. marginatus* (Goode and Bean) and *S. diomedeanus*, a species sometimes collected with *S. tessellatus*. Additionally, in the southern extent of its range *S. tessellatus* sometimes co-occurs with *S. jenynsi*.

Although S. tessellatus and S. marginatus have nearly complete overlap in fin-ray and vertebral counts, such similarities are the only ones between these otherwise distinctive species. Important differences between these species occur in ID pattern (1-4-3 vs. 1-3-2 in S. marginatus), hypural number (4 vs. 5), presence of scales on the blind sides of the dorsal and anal fin rays in S. tessellatus (absent in S. marginatus), and pigmentation features including an unpigmented peritoneum (black in S. marginatus), crossbanding on the body, and a black spot on the ocular-side opercle (vs. no crossbanding on body; instead, body with a dark blotch in the caudal region and no opercular spot in S. marginatus). Despite co-occurrence and some morphological similarities, S. tessellatus is readily distinguished from S. diomedeanus and S. jenynsi in caudal-fin-ray number (12 in S. tessellatus vs. 10 in the others), and presence of scales on the blind sides of the dorsal and anal fin rays and presence of a black spot on the ocular-side opercle (absent in the others). Symphurus tessellatus differs further in lacking a pupillary operculum and the large pigmented spots in the dorsal and anal fins characteristic of S. diomedeanus. From S. jenynsi, S. tessellatus is further distinguished by its much lower meristic values, including 91–102 dorsal fin rays (vs. 107–115), 77–86 anal fin rays (vs. 91–99), and 49–54 total vertebrae (vs. 57–60 in S. jenynsi).

There are nine eastern Pacific Symphurus with somewhat similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in S. tessellatus. Of these nine, only S. chabanaudi Mahadeva and Munroe and S. elongatus (Günther) are similar to S. tessellatus in that they lack a pupillary operculum. Of all species in the genus, S. tessellatus is most similar in form, size, and pigmentation pattern to S. chabanaudi. However, S. tessellatus is distinguished from S. chabanaudi primarily by modal differences in the number of dorsal (91-102 vs. 98-109 in S. chabanaudi) and anal fin rays (74-86 vs. 82-92); total vertebrae (48-54, usually 50-53 vs. 52-57, usually 53-56); and scales in a longitudinal series (81-96 vs. 92-102 in S. chabanaudi). The two species also differ in relative frequencies of occurrence of particular ID patterns. In S. chabanaudi, 50% (49/95) of the individuals had a 1-5-3 ID pattern while only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 173 of 233 (74%) S. tessellatus possessed a 1-4-3 ID pattern. while only 6% (13 specimens) had a 1-5-3 pattern.

There is some overlap in fin-ray and vertebral counts between S. tessellatus and S. elongatus; however, these overlaps are the only similarities between these otherwise distinctive species. Symphurus tessellatus has a pattern of crossbands on the body and a large black blotch on the ocular-side opercle, whereas in S. elongatus the body is uniformly pigmented without crossbands and this species lacks the prominent black blotch on the ocular-side opercle. Further differences include the presence of small ctenoid scales on blind sides of the dorsal and anal fin rays in S. tessellatus (absent in S. elongatus) and absence of a fleshy ridge on the ocular-side lower jaw in S. tessellatus (a well-developed ridge present in S. elongatus). Symphurus tessellatus also has a much larger eye (15-21 SL) compared with that of S. elongatus (9–15 SL).

The remaining seven eastern Pacific species with meristics comparable to those observed in S. tessellatus include S. fasciolaris, S. leei, S. atricaudus, S. melanurus, S. williamsi, S. melasmatotheca, and S. undecimplerus Munroe and Nizinski. As mentioned above, all of these species, in contrast to S. tessellatus, possess a pupillary operculum, and none have the black spot on the ocular-side opercle characteristic of S. tessellatus. Symphurus tessellatus differs further in caudal-fin-ray number (12) from S. fasciolaris (10) and S. melasmatotheca and S. undecimplerus (each with 11 caudal fin rays). Symphurus tessellatus is distinguished from S. melanurus in lacking a fleshy ridge on the ocular-side lower jaw (present in S. melanurus), in having small ctenoid scales on the blind sides of the dorsal and anal fin rays (usually none or occasionally 1-3 small scales at bases of fin rays in S. melanurus), and in having the first dorsal fin ray placed posterior to a vertical through the front margin of the upper eye (versus first dorsal fin ray placed anteriorly to a vertical through front margin of upper eye in S. melanurus). Symphurus tessellatus is further distinguished from S. williamsi in having crossbanding on the body with the posterior portions of the dorsal and anal fins considerably darker than the anterior portions (versus uniform body color without prominent crossbanding and no posterior darkening of dorsal and anal fins in S. williamsi). Symphurus tessellatus differs from S. leei in having an unpigmented peritoneum (versus black in S. leei), and the length of the head is smaller than the body depth in S. tessellatus (nearly equal to body depth in S. leei). Symphurus tessellatus is further distinguished from S. atricaudus in that it lacks the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

Material examined 454 specimens (13.4–220 mm SL).

Counted and measured (23 specimens, 96.6–203 mm SL). **Puerto Rico**: UPRM 2717; (142); Puerto Rico; 8 m; 14 Mar 1966. UPRM 2760; (142); Mayaguez; 12 m; 15 Mar 1966. UPRM 2859; (111); Mayaguez; 9 m; 29 Apr 1966. UPRM 3758; (130); Anasco River; 1–2 Jul 1953. UPRM 3759; 2 (130–133); Mayaguez Bay; 1966. **French Guiana**: UF 35275; (172); 5°14'N, 52°06'W; 45 m; 11 Dec 1977. **Brazil**: UFPB 143; 5(96.6–135); Rio Paraiba do Norte; 27 Apr 1978. MHNN 691; (140.3); Bahia (possible holotype or syntype of *Plagusia brasiliensis*). ANSP 121549; 10(108–203); Rio de Janeiro; Jul–Aug 1963.

Counted (234 specimens, 64 lots). **Puerto Rico**: MCZ 28843; (91.8); Puerto Rico; 1898–99. UF 83996; (146); beach at Mani, just N of Mayaguez; 16 Apr 1964. UPRM 1590; 2(159–173); Mayaguez; 3 Mar 1962. UPRM 2743; 15(114–172); Mayaguez; 6 m; 15 Mar 1966. UPRM 3760; 2(128–143); Rio Anasco; 17 Aug 1951. UPRM 3761; 3(126–158); Mayaguez Bay; 1966. USNM 126448; (132); Mayaguez; 1899. **Cuba**: MCZ 11269; (111); Cuba. USNM 35108; (81.3); Havana. USNM 37750; (68.6); Havana. USNM 154857; (131); Cuba. **Dominican Republic**: USNM 108369; (123). USNM 108372; (126). **Haiti**: ANSP 81861; (97.7); Port-au-Prince; Nov 1949. ANSP 83626; 8(83.3–113); Port-au-Prince; 1949. ANSP 97661; 6(114–146); Port-au-Prince; 1936. UMMZ 142422; (127); Haiti; 15 Apr 1983. USNM 133671; 3(109–124); Port-au-Prince; 1–4 Jan 1947. USNM 164849; 2(87.7–133); Haiti; 1927. **Jamaica**: LACM 6215; (142); 17°52'N, 77°53'W; 40 m; 15 May 1962. LACM 6217; 10(123–

152); 17°46'N, 77°30'W; 16m; 15 May 1962. UMML 4831; (115); Hunts Bay; 3 Aug 1958. UMML 34367; 3(118-160); 17°45'N, 77°38'W; 35m; 15 May 1962. UMML 34368; (144); 17°55'N, 77°51'W; 39m; 18 May 1965. USNM 37348; (79.9); Jamaica. USNM 291333; 6(128-161); 17°55'N, 77°51'W; 40m; 18 May 1965. USNM 291347; 2(130-146); 17°53'N, 77°50'W; 42 m; 18 May 1965. USNM 291346; 2(128-138); 17°51'N, 77°49.5'W; 49m; 18 May 1965. Belize: UMML 34354; 4(132-160); 17°12'N, 88°11.2'W; 19m; 9 May 1967. UMML 34355; 9(134-160); 17°12'N, 88°11.2'W; 19m; 18 May 1967. Honduras: FMNH 100384; 5(38.1-56.0); Brus Lagoon; 10 May 1975. FMNH 94819; 5(37.7-49.5); Brus Lagoon; 10 May 1975. UMML 34348; 2(130-134); 15°49.15'N, 83°44'W; 31 m; 7 Apr 1967. UMML 34349; 2(126-141); 15°48'N, 83°54'W; 24m; 7 Apr 1967. UMML 34350; 5(111-164); 15°49.5'N, 83°44'W; 31m; 7 Apr 1967. UMML 34351; 3(130-148); 15°54'N, 83°40'W; 37m; 8 Apr 1967. UMML 34352; 3(132-155); 15°54'N, 83°40'W; 37m; 8 Apr 1967. UMML 34353; 2(138-147); 15°45'N, 83°32'W; 35m; 9 Apr 1967. Panama: GCRL 12698; 2(13.4-65.8); Canal Zone; 5 Mar 1974. FMNH 18251-57; 7(50.3-73.3); Panama. Colombia: UMML 34369; 4(145-155); 10°53'N, 75°22'W; 42m; 23 May 1964. UMML 34356; (148); 9°30'N, 76°07.5'W; 41 m; 26 May 1964. USNM 291332; (147); 8°59'N, 76°27'W; 26 m; 29 Nov 1968. Venezuela: ANSP 121394; 7(67.9-152); Venezuela; 15 Mar 1962. FMNH 88650; 16(155-200); 12°19'N, 70°34'W; 73m; 27 Sep 1963. UMML 34370; (173); 11° 52'N, 70°22'W; 35 m; 27 Jun 1968. UMML 34357; (171); 12°19'N, 70°34'W; 73m; 27 Sep 1963. UMML 34358; (145); 10°29'N, 62° 30'W; 9m; 24 Oct 1963. Trinidad: UPRM 3762; (142); Trinidad; 4 May 1964. Guyana: FMNH 86364; (162); 8°09'N, 58°23'W; 42 m; 29 Aug 1958. FMNH 90546; 23(152-204); 8°32'N, 59°10'W; 43 m; 28 Oct 1958. GCRL 3835; (196); 8°13'N, 58°40'W; 37 m; 27 Apr 1969. GCRL 3838; 3(192-202); 9°14'N, 60°19'W; 44 m; 25 Apr 1969. Surinam: FMNH 86459; (161); Surinam; Coquette 1957. GCRL 23512; 6(164-196); 6°56'N, 54°05'W; 59m; 2 May 1969. USNM 291335; (168); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. Brazil: FMNH 90544; 3(183-196); 1°57'N, 48°12'W; 55m; 14 Nov 1957. FMNH 91129; (197); 2°29'N, 48°54'W; 86m; 15 Nov 1957. MCZ 11381; 14(93.9-202); Rio de Janeiro; 1865. MCZ 24939; (174); Rio de Janeiro; 1865. UFPB 1120; 5(51.5-115); Rio Paraiba do Norte; 30 Aug 1981. UFPB uncat.; 9(55.7-123); Rio Paraiba do Norte; 13 Nov 1981. UFPB uncat.; 2(100-110); Rio Paraiba do Norte; 30 Jul 1981. USNM 159225; 2(182-187); 1°57'N, 48°12'W; 55m; 17 Nov 1957.

Other material examined (197 specimens, 70 lots). Cuba: MCZ 91961; (89.9); Cuba. Honduras: UF 33892; 4(138-154); 15°45'N, 83°32'W; 35 m; 9 Apr 1967. USNM 291345; 6(136-161); 15°56'N, 83°55'W; 47 m; 2 Feb 1967. Nicaragua: UMML 34359; 2(126-140); 11°51'N, 83°35'W; 20 m; 28 Jan 1971. UMML 34360; 9(56.4-142); 12°16'N, 83°31'W; 12m; 28 Jan 1971. Panama: GCRL 14930; 2(173-177); Colon; Apr 1974. MCZ 58656; (31.1); Panama; 9 Sep 1964. UF 75622; (57.5); Canal Zone; 1974. UF 76003; (62.8); Canal Zone; Aug 1974. UMML 26664; 2(123-141); 9°18.2-18.4'N, 80°03.3-04'W; 24 m; 20 Jul 1966. USNM 81652; (89.4); Porto Bello; 24-28 Apr 1911. USNM 81653; 2(61.1-67.6); Fox Bay; 11 Jan 1911. USNM 81655; 2(38.1-43.5); Fox Bay; 27 Jan 1912. USNM 144792; (65.1); Canal Zone; 4 Mar 1937. USNM 291351; 3(170-208); 8°25'N, 79°56'W; 10m; 19 Dec 1963. USNM 291354; 5(189-220); 8°25'N, 79°56'W; 10m; 19 Dec 1963. Colombia: UMML 22247; 22(84-148); 8°48-46.8'N, 76°39.7-42.8'W; 20m; 12 Jul 1966. UMML 31320; (133); 8°51.9-53.9'N, 76°37.2'W; 12 Jul 1966. USNM 291350; (152); 8°50'N, 76°48'W; 49 m; 2 Nov 1970. USNM 291353; (194); 6°46'N, 54°27'W; 49m; 28 Jun 1972. USNM 291356; 9(191-207); 6°54'N, 53°58'W; 64 m; 30 Jun 1972. USNM 291352; 3(162-173); 6°34'N, 54°28'W; 37m; 28 Jun 1972. Venezuela: ANSP 120209; (133); Venezuela; 23 Jul 1960-17 Mar 1962. GCRL 3837; (163); 8°52'N, 59°58'W; 29m; 26 Apr 1969. MCZ 41081; (104); 10°17'N, 69°45'W; 1958. UMML 30197; 30(84-183); 11°25.1-25.8'N, 70°52.1-50'W; 18 m; 27 Jul 1968. UMML 30223; (160); 11°55-55.3'

N, 70°59.9'-71°00'W; 11m; 28 Jul 1968. UMML 34361; 2(138-185); 10°49'N, 63°13'W; 48 m; 19 Jul 1968. UMML 34362; (187); 10°36'N, 68°12'W; 24 m; 25 Jul 1968. UMML 34363; 6(158-201); 10°11'N, 64°48'W; 35 m; 19 Oct 1963. USNM 291355; 10(144-197); 12°17'N, 70°34'W; 73 m; 27 Sep 1963. USNM 291348; 4(161-185); 11°50'N, 70°40'W; 59m; 10 May 1965. Trinidad: USNM 113251; (124); 10°37'N, 61°42'W; 60m; 3 Feb 1884. USNM 123112; (179); Gulf of Paria. French Guiana: UF 44365; (168); 5°05'N, 51°58'W; 45m; 11 Dec 1977. Surinam: UMML 12251; (162); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. USNM 159536; (177); 6°41'N, 54°17'W; 46 m; 14 Jun 1957. USNM 159567; (205); 6°42'N, 54°12.5'W; 44m; 14 Jun 1951. USNM 159612; (204); 6°41.5'N, 54°14.5'W; 44 m; 14 Jun 1957. USNM 159618; (194); 6°42.5'N, 54°10'W; 42m; 14 Jun 1957. USNM 291349; (82.3); 5°30'N, 52°10'W; 51m; 12 Sep 1958. USNM 291358; 5(126-142); 9°33'N, 76°02'W; 49 m; 28 Nov 1968. Brazil: USNM 159237; 6(165-191); 2°00'N, 48°19'W; 46 m; 16 Nov 1957. FMNH 88193; (160); Bahia; 13 Apr 1908. MCP 1198; (116); Florianopolis; 30 Oct 1968. MCP 1199; (114); Florianopolis; 30 Oct 1968. MCP 1200; (118); Florianopolis; 30 Oct 1968. MCP 1202; (116); Florianopolis; 30 Oct 1968. MCP 2193; (156); Florianopolis; Oct 1968. MCP 2194; (112); Florianopolis; Oct 1968. MCP 3139; (126); Florianopolis; Oct 1968. MCP 5663; (180); Port Belo, Santa Catarina. MCP 7270; (128); Port Belo, Santa Catarina; 3-4 Nov 1973. MCP 7327; (126); Porto Belo, Santa Catarina; 1 Aug 1973. MCP 7345; (130); Porto Belo, Santa Catarina; 31 Jul-1 Aug 1973. MCZ 889; 2(123-139); Rio de Janeiro. MCZ 11149; (160); Rio de Janeiro. MCZ 11323; (105); Pernambuco. MCZ 11378; 3(68.7-96.1); Pernambuco. MCZ 11379; (147); Santos. MCZ 11380; (91.7); Curuca. MCZ 11382; (137); Rio de Janeiro. UF 19938; 3(109-133); Sao Paulo; 13 Jul 1961. UFPB 882; 5(36.0-115); Cabedelo; 29 Oct 1981. UFPB uncat.; 5(57.8-107); Ilha da Restinga, Rio Paraiba do Norte. UMML 13292; (186); 4°38'N, 51°05'W; 59 m; 26 Feb 1963. UMML 13977; (157); 2°10'S, 42°24'W; 48 m; 11 Mar 1963. USNM 83172; (94.4); Rio de Janeiro. Uruguay: USNM 87772; (119); Montevideo. USNM 87773; (113); Montevideo.

Symphurus oculellus, new species Figures 2, 4d, 5, 6b-c

Synonymy

Symphurus atricaudus (not of Jordan and Gilbert 1880). Puyo 1949:179 (French Guyana; counts, color description, poor figure; distinguished from S. plagusia).

Diagnosis A Symphurus characterized by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays; prominent fleshy ridge on ocular-side lower jaw; no pupillary operculum; 99-106 dorsal fin rays; 81-88, usually 83-88, anal fin rays; 52-55, usually 53-54, total vertebrae; 85-98, usually 86-93, scales in longitudinal series; relatively long jaws with posterior extension of maxilla usually reaching to the vertical through posterior margin of pupil of lower eye, occasionally extending to or slightly beyond the vertical through posterior margin of lower eye; relatively small eye (68-104 HL, \overline{x} 84); dorsal fin origin usually at or occasionally slightly anterior to the vertical line through the anterior margin of upper eye; ocular surface dark- to light-brown with 10-14 welldeveloped, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle with dark melanophores in diffuse circular pattern or with melanophores coalesced into somewhat rounded pigment spot; inner lining of opercle and isthmus more heavily pigmented on ocular surface than blind side; and dorsal, anal, and caudal fins with an alternating series of pigmented blotches and unpigmented areas.

Description Symphurus oculellus is a relatively large tonguefish attaining maximum lengths of approximately 189 mm SL. ID pattern usually 1-4-3 (33/38), infrequently 1-3-4 (2), 1-5-3 (1), 1-4-2 (1), or 1-3-3 (1) (Table 1). Caudal fin rays 12 (49/53 specimens), less frequently 11 (Table 2). Dorsal fin rays 99–106 (Table 3). Anal fin rays 81–88, usually 83–88 (Table 4). Total vertebrae 52–55, usually 53–54 (34/37) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 85–98, usually 86–93 (Table 6). Scale rows on head posterior to lower orbit 19–23, usually 19–20 (Table 7). Transverse scales 36–42, usually 38–40 (Table 8).

Proportional measurements appear in Tables 16 and 17. Body relatively elongate with gradual taper posteriorly; body depth relatively narrow (231–297 SL, \bar{x} 274), and nearly uniform from vertical through anal fin rays 10–15 and extending posteriorly to mid-point of body. Preanal length 189–243 SL, \bar{x} 206; somewhat shorter than body depth. Head relatively short (168–218 SL, \bar{x} 182), shorter than body depth. Head Table 16

Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

	Holotype		Parat	ypes	
Character	(USNM 159606)	Ν	Range	Mean	SD
SL	144.1	14	75.8-164	142.5	21.09
BD	271	14	231-297	274.5	17.19
PDL	32	13	32-47	38.6	4.13
PAL	199	14	189-243	205.6	13.32
DBL	968	13	953-968	961.4	4.13
ABL	795	14	765-837	793.7	18.74
PL	53	12	40-64	54.3	6.08
PA	37	12	20-60	41.2	12.62
CFL	90	14	80-99	88.9	5.53
HL	180	14	168-218	182.3	11.58
HW	209	14	198-281	216.8	21.37
POL	126	14	112-153	124.8	9.38
SNL	37	14	34-46	38.0	3.21
UJL	46	14	37-50	43.3	3.24
ED	12	14	12-19	15.4	1.95
CD	50	14	39-63	45.4	6.39
UHL	140	14	126-151	139.4	6.81
LHL	98	14	79-111	92.9	8.13

relatively wide (198-281 SL, \overline{x} 217); usually greater than head length (HW/HL 1.1-1.5, \overline{x} 1.2); lower head lobe (79-111 SL, \bar{x} 93) considerably narrower than upper head lobe (126–151 SL, \overline{x} 139). Lower opercular lobe of ocular side (264-341 HL, \overline{x} 292) wider than upper opercular lobe (174-246 HL, \overline{x} 211). Postorbital length 112–153 SL, \overline{x} 125. Snout (Fig. 4d) moderately long (190-227 HL, \bar{x} 209), slightly rounded or truncate, covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind-side snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws relatively long; upper jaw length 221-258 HL, \overline{x} 238; posterior extension of maxilla usually reaching to vertical through posterior margin of pupil of lower eye, occasionally to or slightly beyond vertical through posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4d). Chin depth 214-291 HL, \bar{x} 248. Lower eye relatively small (68-104 HL, \overline{x} 84); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually only 1-3 small, ctenoid scales in narrow interorbital space. Interorbital space sometimes equaling half the diameter of the lower eye. Pupillary operculum absent. Length of dorsal fin base 953-968 SL, \overline{x} 961. Dorsal fin origin (Fig. 4d) usually at, or occasionally slightly anterior to, vertical line through an-

Table 17

Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes			
Character	(USNM 159606)	Range	Mean	SD	
HW/HL	1.2	1.08-1.53	1.2	0.11	
POL	700	651-722	683.8	20.64	
SNL	204	190 - 227	209.0	11.67	
UJL	254	221-258	238.3	11.74	
ED	69	68-104	84.3	10.52	
CD	277	214-291	248.4	23.62	
OPLL	308	264 - 341	292.3	23.77	
OPUL	200	174 - 246	210.6	20.39	
UHL	777	661-814	767.4	44.73	
LHL	542	464-556	510.3	28.01	

terior margin of upper eye; predorsal length 32–47 SL, \bar{x} 39. Length of anal fin base 765–837 SL, \bar{x} 794. Scales absent from distal two-thirds of blind-side dorsal and anal fin rays. Occasionally with one or two scales occurring sporadically on some blind-side dorsal and anal fin-ray bases. Pelvic fin relatively short, 40–64 SL, \bar{x} 54; longest pelvic fin ray extending posteriorly to base of first or occasionally second anal fin ray; pelvic to anal fin distance 20–60 SL, \bar{x} 41. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 80–99 SL, \bar{x} 89.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either lacking teeth altogether, or with very short row of teeth covering no more than one-third of premaxilla anterior to the vertical equal with the anterior nostril.

Scales large, ctenoid on both sides of body.

Pigmentation Ocular surface ranging from dark- to light-brown with 10–14 (usually 10–12) well-developed, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk. Anteriormost crossband on head immediately posterior to eyes; second band situated short distance (usually only 3–4 scales) posteriorly. Throughout most of their vertical extent, two anteriormost bands separate; several specimens with first two crossbands coalesced on ventral portion of opercle forming wide, somewhat circular spot. Crossbands on head somewhat narrower than those on midand posterior portions of body. Number of crossbands on trunk variable, differing in degree of completeness, especially in region between opercular opening to point about two-thirds of trunk length. Some bands on body complete, continuous on dorsal and anal fins as darkbrown blotches. Posteriormost crossband situated short distance from caudal fin base, somewhat expanded and slightly arched. Blind side creamy-white. Peritoneum unpigmented. Membrane on blind-side ovary with diffuse pattern of small melanophores (visible only by dissection).

Outer surface of ocular-side opercle with dark melanophores in diffuse pattern or with melanophores sometimes coalesced into somewhat rounded pigment spot. Inner lining of opercle and isthmus more heavily pigmented on ocular surface; blind-side inner opercle with pigmentation restricted to small band of pepperdot melanophores along ventral margin. Isthmus on blind side not heavily pigmented, but often with pepperdot pattern of melanophores. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined pigment band.

Dorsal, anal, and caudal fins with alternating series of blotches and unpigmented areas. Dorsal fin scarcely pigmented in anterior one-half of body; with series of alternating blotches and unpigmented areas beginning at approximately body mid-point and continuing to posteriormost extent of fin. Anterior one-fourth of anal fin without blotches; posterior three-fourths with pattern of alternating blotches and unpigmented areas as in dorsal fin. Blotches on dorsal and anal fins 3-5 fin rays wide including adjoining membrane. Both dorsal and anal fins with blotches coalescing in posterior one-sixth of fins and forming continuous pigmentation band on fins. Posterior portions of fins becoming gradually darker; blotches, although still present, much more difficult to discern. Distal two-thirds of caudal fin heavily pigmented; proximal one-third relatively lightly pigmented. Caudal fin of most specimens not uniformly pigmented; small cluster of rays (usually 2-4) more lightly pigmented giving appearance of alternating darkly- and lightly-pigmented areas. Smaller number of specimens with entire caudal fin heavily pigmented without pattern of alternating dark and light pigmentation.

Size and sexual maturity Among material examined, there were 39 males, 23 females, and five specimens of unknown sex. No significant differences were found between the sexes in overall size; males ranged from 82.2 to 189 mm SL, females were 75.8–180 mm SL. Based on reproductive stages of females, this species attains sexual maturity at about 110 mm SL (Fig. 2). All females larger than 111 mm SL had elongate ovaries. The smallest female, an immature fish of 75.8 mm SL, had only partially elongate ovaries. The next smallest female was 111mm SL and had small developing ova in the gonads. All other females were larger than 130mm SL, had elongate ovaries, and were considered sexually mature.

Etymology From the latin "oculus" (eye), plus "ellus" (little), in reference to the relatively small size of the eye in this species compared with that of *S. tessellatus*.

Geographic distribution (Fig. 5) A tropical species with a fairly restricted distribution along the inner continental shelf of northeastern South America from Guyana ($57^{\circ}W$) to northeastern Brazil ($2^{\circ}S$, $40^{\circ}W$) where the majority of specimens have been collected. All but one specimen (UMML 12265; $2^{\circ}20'S$) were collected north of the Amazon outflow. Since little systematic sampling has been conducted on the inner continental shelf off equatorial Brazil, it is not known whether the new species occurs more frequently in areas immediately south of the outflow from the Amazon River.

Bathymetric distribution Symphurus oculellus occurs at moderate shelf depths (7-110 m) and does not appear to utilize nearshore habitats or estuarine environments as nursery areas as do *S. plagusia* and *S. tessellatus*. Specimens ranging from 76 to 189 mm SL have been collected in offshore habitats, with most (52/57, or 91%) being collected between 11 and 70 m (Table 10). At these depths, it is occasionally collected with adult *S. tessellatus*; however, size differences between the two species in these collections are quite striking. All *S. tessellatus* collected with *S. oculellus* were large adults (>130 mm SL), while the *S. oculellus* were a mixture of sizes, with juveniles as small as 78 and 82 mm SL.

Remarks Not all specimens that are the basis of citations in the synonymies of *S. plagusia* and *S. tessellatus* could be examined, so it is impossible to determine if any specimens of *S. oculellus* were included among material listed in earlier accounts on *Symphurus* from northern South America. It is possible that specimens of *S. oculellus* were included in the study by Lowe-McConnell (1962), since some of the trawl stations in that study were at appropriate depths to capture *S. oculellus*. Lowe-McConnell listed all tonguefish captured as *S. plagusia* but did not include descriptive accounts for the specimens, thus preventing positive identification.

The fish described by Puyo as S. atricaudus (Jordan and Gilbert) is clearly S. oculellus. Symphurus oculellus may be distinguished from the eastern Pacific S. atricaudus by the following characters: dorsal fin rays 99–106 vs. 94–101 in S. atricaudus; anal fin rays 81–88 vs. 77–84; scales 85–98 vs. 104–115. Additionally, S. *oculellus* lacks a pupillary operculum and scales on the blind-side posterior rays of the dorsal and anal fins (both present in S. *atricaudus*).

Comparisons Among Atlantic members of the *S. plagusia* complex, *S. oculellus* most closely resembles and is largely sympatric with *S. tessellatus* and *S. plagusia*. Characteristics distinguishing *S. oculellus* from these species were discussed in the "Comparisons" sections under the accounts for *S. plagusia* and *S. tessellatus*, respectively. *Symphurus oculellus* is most easily distinguished from the two remaining Atlantic species belonging to this complex (*S. civitatium* and *S. caribbeanus*) by differences in counts for dorsal fin rays (99–106 vs. 96 or fewer in *S. caribbeanus* and *S. civitatium*), anal fin rays (81–89 vs. 80 or fewer), and total vertebrae (52–55 versus 51 or fewer in *S. caribbeanus* and *S. civitatium*).

Among other Atlantic Symphurus, some meristic values of S. oculellus overlap those of three relatively deep-water species: the eastern Atlantic S. vanmelleae Chabanaud and S. ligulatus Cocco, and the western Atlantic S. marginatus. Additionally, S. oculellus has pigmented dorsal and anal fins reminiscent of those of the sympatrically occurring S. diomedeanus. Comparable fin-ray or vertebral counts are the only similarities between S. oculellus and the deep-water species. Symphurus oculellus is otherwise distinctive from all three species in ID pattern (1-4-3-2-2 vs. 1-2-2-1-2 in S. vanmelleae, 1-2-2-2 in S. ligulatus, and 1-3-2-2-2 in S. marginatus), peritoneal pigmentation (unpigmented versus black in the others), and pigmentation of the dorsal and anal fins (alternating series of blotches and unpigmented areas in S. oculellus versus uniformly pigmented fins in the other species). From S. diomedeanus, S. oculellus differs in caudal-fin-ray count (12 vs. 10 in S. diomedeanus), and lacks a pupillary operculum (present in S. diomedeanus). In S. oculellus, the dorsal and anal fins have an alternating series of somewhat rectangular-shaped, pigmented blotches and unpigmented areas beginning in the mid-body region and continuing posteriorly inclusive of the caudal fin, whereas in S. diomedeanus the dorsal and anal fins have fewer, nearly spherical spots only in the posteriormost portions of these fins, and the caudal fin usually lacks pigmented spots completely (only rare specimens have a spot present on the caudal fin).

There are seven eastern Pacific Symphurus with similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in S. oculellus. Of these seven species, only S. chabanaudi and S. elongatus are similar to S. oculellus in lacking a pupillary operculum. Many meristic features of S. oculellus completely overlap those of the eastern Pacific

S. chabanaudi. Symphurus oculellus differs from S. chabanaudi, however, in lacking the 4-8 small but welldeveloped scales on the blind sides of the dorsal and anal fin rays prominent in S. chabanaudi specimens, especially those larger than 60 mm; in having a somewhat smaller eye $(1.2-1.9, \overline{x} \ 1.5 \ \text{SL} \text{ in } S. \text{ oculellus vs.}$ 1.7-2.3, \overline{x} 1.9 SL), and S. oculellus has a well-developed fleshy ridge on the ocular-side lower jaw (absent in S. chabanaudi). The posterior extension of the jaws in S. oculellus extends to the vertical line through the posterior margin of the eye, and in many specimens the jaws actually extend slightly beyond the posterior margin of the eves, whereas in S. chabanaudi the posterior extension of the jaws reaches only to a vertical line through the rear margin of the pupil or the rear margin of the lower eye. Symphurus oculellus also differs from S. chabanaudi in the relative frequencies of specimens possessing 1-5-3 and 1-4-3 ID patterns. Symphurus chabanaudi has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 40 of 45 (89%) of the S. oculellus examined had a 1-4-3 pattern and only one specimen possessed a 1-5-3 pattern.

Symphurus chabanaudi also differs from S. oculellus in that this species generally has about nine wide, dark-brown crossbands compared with the more numerous (10–14, usually 10–12), narrower bands in S. oculellus. In addition, in S. oculellus the posterior twothirds of the dorsal and anal fins usually have an alternating series of blotches and unpigmented areas, whereas in S. chabanaudi the posterior one-third of the dorsal and anal fins, and the caudal fin, are usually uniformly dark-brown or black without alternating blotches and unpigmented areas.

There is almost complete overlap in fin-ray and vertebral counts between those of *S. oculellus* and those of *S. elongatus*; however, these species are otherwise distinct. *Symphurus oculellus* has prominent crossbands on the body and a dark blotch on the ocularside opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands, and a prominent blotch on the ocular-side opercle is wanting.

The remaining five eastern Pacific species with meristics comparable to those observed in *S. oculellus* include *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, and *S. undecimplerus*. These species, in contrast to *S. oculellus*, possess a pupillary operculum, and none features the pigmented blotch found on the ocular-side opercle in *S. oculellus*. *Symphurus oculellus* differs further from *S. undecimplerus* in caudal-fin-ray number (12 vs. 11); is distinguished from *S. melanurus* and *S. williamsi* in having the dorsal and anal fins with an alternating series of pigmented blotches and unpigmented areas (versus dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas in these other species); is readily distinguished from *S. leei* in having an unpigmented peritoneum (versus black in *S. leei*) and in having the head length smaller than body depth (nearly equal to body depth in *S. leei*); and differs from *S. atricaudus* in lacking the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

Material examined 69 specimens (75.8–189 mm SL).

Counted and measured (14 specimens, 75.8–164 mm SL). **Holotype**: USNM 159606; female, 144 mm SL; Surinam (6°24'N, 55°00'W); 27 m; 11 May 1957. **Paratypes. Guyana**: BMNH 1950.5.15: 51; (139); off Georgetown. FMNH 86365; (148); 7°05'N, 57°12'W; 33 m; 1 Sep 1958. FMNH 88846; (132); 6°54'N, 57°47'W; 18 m; 25 Mar 1963. **Surinam**: USNM 159559; (75.8); 6°04'N, 54°51'W; 70 m; 13 May 1951. ZMA 111.212; (158); 5°15'N, 55°15'W; 12 m; 13 Oct 1969. **French Guiana**: UMML 12254; (141); 6°17'N, 53°35'W; 40 m; 21 Feb 1963. USNM 313518; 2(143–151); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. UMML 11549; (156); 5°57'N, 52°18'W; 70 m; 22 Feb 1963. UMML 12262; (148); 5°24'N, 51°34'W; 64 m; 23 Feb 1963. ZMA 111.234; (140); 3°45'N, 51°45'W; 40 m; 16 Nov 1969. **Brazil:** FMNH 86362; (155); 1°57'N, 48°15'W; 48 m; 17 Nov 1957. FMNH 100385; (164); 1°57'N, 48°12'W; 55 m; 14 Nov 1957.

Counted (30 paratypes, 14 lots). **Guyana**: BMNH 1961.9.4:117; (189). BMNH 1961.9.4:118; (163). UMML 34335; (136); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. **Surinam**: GCRL 3836; 5(130–165); 6°56'N, 54°05'W; 2 May 1969. UMML 12249; (143); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. ZMA 111.228; 1; 5°15'N, 55°15'W; 12 m; 10 Oct 1969. FMNH 90552; 2(142–147); Surinam; 18 m; 1957. FMNH 90553; (144); Surinam; 110 m; 3 May 1957. FMNH 91368; (141); Surinam; 1957. French Guiana: FMNH 100386; 7(154–180); 6°03'N, 52°22'W; 65 m; 13 Sep 1958. FMNH 90085; 5(163–180); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. FMNH 86397; (130); 5°05'N, 52°14.5'W; 20 m; 23 May 1957. Brazil: FMNH 100387; 2(140–155); 2°29'N, 48°54'W; 86 m; 15 Nov 1957. USNM 159541; (150); 2°29'N, 48°55'W; 42 m; 15 Nov 1957.

Other non-type material examined (25 specimens, 14 lots). Guyana: UMML 34364; (152); $7^{\circ}00'N$, $57^{\circ}08'W$; 26 m; 15 Jul 1968. Surinam: UMML 12498; (158); $7^{\circ}01'N$, $54^{\circ}21'W$; 64 m; 21 Feb 1963. FMNH 90223; (135); $6^{\circ}54'N$, $54^{\circ}47'W$; 18 m; 25 Mar 1953. UMML 34334; 2(104–140); $6^{\circ}25'N$, $55^{\circ}04'W$; 7 m; 10 Jul 1968. FMNH 91109; (151); $6^{\circ}24.5'N$, $55^{\circ}02.5'W$; 27 m; 11 May 1957. USNM 159602; 2(82.2–94.8); $6^{\circ}23'N$, $55^{\circ}05.5'W$; 27 m; 11 May 1957. USNM 313515; 3(136–152); $6^{\circ}21'N$, $54^{\circ}28'W$; 28 m; 29 Jun 1972. UMML 12310; 3(139–142); $6^{\circ}11'N$, $55^{\circ}39'W$; 15 m; 19 Feb 1963. French Guiana: UMML 13301; 6(111-175); $6^{\circ}00'N$, $52^{\circ}27'W$; 64 m; 22 Feb 1963. UMML 13307; (166); $5^{\circ}29'N$, $51^{\circ}37'W$; 64 m; 23 Feb 1963. UF 83997; (143); $5^{\circ}05'N$, $51^{\circ}58'W$; 45 m; 11 Dec 1977. USNM 313516; (147); $4^{\circ}47'N$, $51^{\circ}37'W$; 33 m; 5 May 1975. UMML 34336; (160); off Cayenne; F. Berry, Station 10, 12. **Brazil**: UMML 12265; (150); $2^{\circ}20'S$, $40^{\circ}24'W$; 40 m; 12 Mar 1963.

Symphurus caribbeanus, new species Figures 2, 4e, 5, 6d

Synonymy

- Symphurus plagusia plagusia. Ginsburg 1951:220 (in part) (Fox Bay, Panama; specimens in USNM 81654 included in account of S. p. plagusia).
- Symphurus plagusia. Austin and Austin 1971:38 (in part) (Guayanilla, Puerto Rico; food habits; nine specimens from UPRM 2926 belong to the new species).

Diagnosis A Symphurus with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; relatively large eye (82-110 HL); no fleshy ridge on ocular-side lower jaw; without a pupillary operculum; no small ctenoid scales on the blind sides of the dorsal and anal fin rays; dorsal fin rays 89-96, usually 92-96; anal fin rays 74-80; total vertebrae 48-51, usually 49-50; 78-89 scales in longitudinal series; relatively short jaws usually extending to the vertical line through the posterior margin of pupil of lower eye or occasionally extending to the vertical through posterior margin of lower eye; dorsal fin origin usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; ocular surface dark-brown to almost yellow; usually with 10-15 narrow, irregularly complete, sharply contrasting, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle without dark blotch; inner lining of opercle and isthmus heavily pigmented on ocular side, unpigmented on blind side; entire dorsal and anal fins with alternating series of blotches and unpigmented areas.

Description A medium-sized tonguefish attaining maximum lengths of approximately 122 mm SL. ID pattern usually 1-4-3 (67/82), less frequently 1-3-3 (8), 1-3-4 (23), or 1-4-4 (2) (Table 1). Caudal fin rays usually 12 (78/82), less frequently 11, 10, or 13 (Table 2). Dorsal fin rays 89–96, usually 92–96 (Table 3). Anal fin rays 74–80 (Table 4). Total vertebrae 48–51, usually 49–50 (75/79) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 78–89 (Table 6). Scale rows on head posterior to lower orbit 17–22, usually 19–21 (Table 7). Transverse scales 36–44 (Table 8).

Proportional measurements appear in Tables 18 and 19. Body relatively deep (277–320 SL, \bar{x} 301); with greatest depth in anterior one-third of body followed by relatively rapid taper posteriorly. Preanal length 191–261 SL, \bar{x} 223; somewhat shorter than body depth. Head relatively short (185–224 SL, \bar{x} 199); considerably shorter than body depth. Head relatively wide (220–268 SL, \bar{x} 240); greater than head length (HW/HL 1.1–1.3, \bar{x} 1.2); lower head lobe (84–111 SL,

Table 18

Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

	Holotype	Par	atypes	
Character	(USNM 313487)	Range	Mean	SD
SL	100.5	40.1-121.9	84.5	22.40
BD	317	277-320	300.6	12.14
PDL	34	29-48	36.2	5.45
PAL	219	191-261	223.0	15.89
DBL	966	952-972	964.3	5.70
ABL	792	751-820	781.0	18.89
PL	62	51-75	63.2	6.5
PA	45	35-63	47.6	6.6
CFL	106	87-116	102.4	7.5
HL	194	185-224	199.2	10.9
HW	239	220-268	240.0	11.03
POL	123	119-143	133.6	6.7
SNL	45	36 - 54	43.5	4.9
UJL	49	37-56	46.2	4.8
ED	20	17-22	19.4	1.5
CD	52	43-64	51.8	5.0
UHL	141	152 - 184	164.6	32.2
LHL	112	84-111	98.6	26.5

 \overline{x} 99) considerably narrower than upper head lobe (152–184 SL, \overline{x} 165). Lower opercular lobe of ocular side (241-348 HL, \bar{x} 292) considerably wider than upper opercular lobe (162-277 HL, \overline{x} 199). Postorbital length 119-143 SL, \bar{x} 134. Snout moderately long (193-255 HL, \bar{x} 218) and pointed (Fig. 4e), covered with small ctenoid scales. Anterior nostril usually not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense. Jaws relatively short; upper jaw length 195-253 HL, \bar{x} 231; posterior extension of maxilla usually reaching to vertical line through posterior margin of pupil or occasionally posterior margin of lower eye. Ocular-side lower jaw without distinct, fleshy ridge near posterior margin (Fig. 4e). Chin depth 227-305 HL, \bar{x} 260. Lower eye moderately large (82-110 HL, \overline{x} 97); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1-3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952-972 SL, \bar{x} 964. Dorsal fin origin (Fig. 4e) usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; predorsal length 29-48 SL, \overline{x} 36. Length of anal fin base 751-820 SL, \overline{x} 781. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin relatively short, 51-75 SL, \bar{x} 63; longest pelvic fin ray usually reaching base of first or

Table 19

Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes		
Character	(USNM 313487)	Range	Mean	SD
HW/HL	1.2	1.1-1.3	1.2	0.06
POL	636	632-744	671.6	28.72
SNL	231	193 - 255	218.4	18.47
UJL	251	195 - 253	231.3	15.96
ED	103	82-110	97.4	7.18
CD	267	227 - 305	259.8	19.74
OPLL	359	241 - 359	291.8	32.23
OPUL	236	162 - 274	199.4	27.34
UHL	728	725-973	828.0	57.84
LHL	580	437-592	495.7	39.42

occasionally second anal fin ray; pelvic to anal fin distance 35–63 SL, \bar{x} 48. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–116 SL, \bar{x} 102.

Teeth well developed on blind-side jaws. Upper and lower jaws on ocular side usually with small patch of teeth covering only anterior one-third of jaw, or lacking teeth altogether.

Scales moderate in size, strongly ctenoid on both sides of body.

Pigmentation Pattern of body pigmentation generally similar for both sexes at all sizes, but mature males with more intense pigmentation on body and posterior portions of dorsal and anal fins. Ocular surface darkbrown to almost yellow; usually with 10-15 narrow, irregularly complete, sharply contrasting, darker-brown crossbands on head and trunk. Crossbands not continued onto dorsal and anal fins. Anteriormost band on head immediately posterior to eyes. Second band crossing head just anterior to opercular opening. Crossbands on trunk variable in number, usually 3-6 scale rows in width. First band crossing body immediately posterior to opercular opening. Posteriormost band slightly anterior to caudal fin base, irregularly complete. Blind side off-white. Peritoneum unpigmented. Outer surface of ocular-side opercle with general background pigmentation. Dorsal margin of ocular-side opercle sometimes with dusky blotch due to dark pigmentation of inner lining of operculum showing through to outer surface. Inner lining of opercle and isthmus heavily pigmented on ocular side; unpigmented

on blind side. Slight band of pigment on ocular-side upper lip; ocular-side lower lip frequently spotted but without definite band of pigment.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Except for anteriormost portion of dorsal fin, entire dorsal and anal fin with alternating series of dark blotches and unpigmented areas. Blotches variable in shape, most frequently nearly rectangular; extending from base almost to distal tip of fin rays; blotches usually covering 2–5 fin rays alternating with 2–4 lightlypigmented fin rays. Caudal fin either uniformly darklypigmented, or with alternating series of pigmented blotches and unpigmented areas throughout length of fin.

Size and sexual maturity Adult S. caribbeanus range in size from approximately 71 to 122 mm SL, and this species is one of the smallest members of the S. *plagusia* complex. Size-related life-history information is derived from data taken from 89 specimens. Males and females attain similar sizes. The largest fish measured was a gravid female (122 mm SL); largest male was (120 mm SL).

There were 44 males (52.9–122 mm SL), 39 females (55.6–122 mm SL), and 6 immature fish (24.4–43.8 mm SL) among material examined. Based on reproductive stages of females, this species matures at 70–80 mm SL (Fig. 2). There were 30 mature females ranging in size from 71.8 to 122 mm SL. All females larger than 80 mm SL were mature. The smallest mature female (71.8 mm SL) was unusual because six of seven others in this size range had undeveloped gonads.

Of 39 females, nine, ranging from 55.6 to 79.1 mm SL, were immature with only partially elongate ovaries. The smallest immature females (55.6, 56.9 mm SL) had only partially elongate ovaries, whereas some larger immature females (58.1–79.1 mm SL) had more developed ovaries but were without obviously developing ova.

Etymology This species is named after its area of occurrence in reference to its common but apparently restricted distribution to habitats within the Caribbean Sea.

Geographic distribution (Fig. 5) Widely distributed in the Caribbean Sea. *Symphurus caribbeanus* has been collected along coastal margins of central and northern South America and off islands fringing the Caribbean Sea. Islands where this species has been collected include St. Martin and Cuba, but most specimens examined were taken at Puerto Rico and Haiti. This species has been collected at coastal locations in Nicaragua, Costa Rica, and Panama along 282

Central America, and also along the Caribbean coast of Colombia.

Bathymetric distribution Symphurus caribbeanus inhabits shallow water. Of 94 specimens for which depth information was available, the majority (78/94, 83%) were collected in 20 m or less (Table 11), and approximately half were collected in waters shallower than 10 m. All life stages are represented among the shallowest collections. The deepest capture (29 m) is for one lot (UMML 34341) comprising 16 individuals.

Ecology Other than depth of occurrence and geographic distribution, little is known about ecological requirements of this species. Austin and Austin (1971) included nine specimens of *S. caribbeanus* in their survey of feeding habits of fishes inhabiting mangrove areas in southwestern Puerto Rico. These specimens, ranging in size from 30 to 104 mm SL, had fed mostly on polychaetes and small, benthic crustaceans, and individuals collected at night had undigested food in their stomachs, suggesting nocturnal feeding.

Comparisons Among Atlantic members of the *S. plagusia* complex, *S. caribbeanus* most closely resembles and occurs sympatrically with *S. plagusia* and juvenile and subadult *S. tessellatus*. There is overlap also in some meristic features of *S. caribbeanus* and *S. civitatium*, but these species are otherwise quite distinct. *Symphurus caribbeanus* differs considerably from *S. oculellus*. Differences between *S. caribbeanus* and these other species were discussed previously in "Comparisons" sections under the accounts for *S. plagusia*, *S. civitatium*, *S. tessellatus*, and *S. oculellus*.

Meristic values of S. caribbeanus overlap those of 11 other Atlantic species of Symphurus. Symphurus caribbeanus is readily distinguished from six deepwater Atlantic species with similar meristic values (S. marginatus (Goode and Bean) and S. piger, occurring in the Gulf of Mexico and Caribbean; two western North Atlantic species, S. pusillus and undescribed species C of Munroe (1987); the western South Atlantic S. ginsburgi Menezes and Benvegnú; and the eastern Atlantic S. nigrescens) in ID pattern (1-4-3 vs. 1-3-2 in the others) and peritoneal pigmentation (unpigmented versus dark-black, visible through both sides of abdominal wall in the others). Symphurus caribbeanus differs from two diminutive eastern Atlantic species, S. lubbocki and S. reticulatus, in ID pattern (1-4-3 vs. 1-3-2), dentition on ocular-side jaws (absent or reduced in S. caribbeanus versus complete row in the others), and longitudinal scale counts (78-89 in S. caribbeanus versus 95 or more in S. lubbocki and S. reticulatus). Symphurus caribbeanus differs from the eastern Atlantic S. normani in ID pattern (1-4-3 vs. 1-3-3), peritoneal pigmentation (unpigmented versus spotted in *S. normani*), and *S. caribbeanus* lacks the small ctenoid scales on the blind sides of the dorsal and anal fin rays that are present in *S. normani. Symphurus caribbeanus* differs further from the western South Atlantic *S. trewavasae* and *S. kyaropterygium* Menezes and Benvegnú, in caudal-fin-ray count (12 vs. 10) and ID pattern (1-4-3 vs. 1-3-3 in *S. trewavasae*, 1-4-2 in *S. kyaropterygium*). Symphurus caribbeanus also lacks the pupillary operculum and fin membrane ostia characteristic of *S. kyaropterygium*.

Three shallow-water, western Atlantic species-S. diomedeanus, which occurs in sympatry with S. caribbeanus, and the allopatric S. plagiusa and S. urospilus Ginsburg-have meristic features similar to those of S. caribbeanus. Symphurus caribbeanus differs from these species in caudal-fin-ray count (12 vs. 10 in S. diomedeanus and S. plagiusa, 11 in S. urospilus) and pigmentation of the vertical fins. The vertical fins of S. caribbeanus have an alternating series of blotches and unpigmented areas and the caudal fin lacks an ocellated spot, unlike the vertical fins in S. diomedeanus which have fewer, nearly spherical spots; or those of S. plagiusa and S. urospilus, that are uniformly pigmented without darkly-pigmented blotches throughout their lengths; or the caudal fin in S. urospilus that has an ocellated spot. From S. plagiusa, S. caribbeanus further differs in the absence of a black opercular spot and the small ctenoid scales on the blind-side dorsal and anal fins characteristic of S. plagiusa. Symphurus caribbeanus is further distinguished from S. diomedeanus and S. urospilus in lacking a pupillary operculum (present in the others).

Meristic values of S. caribbeanus overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including S. leei, S. atricaudus, S. melanurus, S. williamsi, S. fasciolaris, and S. melasmatotheca. Symphurus caribbeanus differs from all of these species in lacking a pupillary operculum (present in the others). Of all these species, S. caribbeanus appears most similar to S. williamsi but differs in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in S. williamsi) and in having pigmented blotches in the dorsal and anal fins (versus dorsal and anal fins without blotches in S. williamsi). Symphurus caribbeanus also differs from S. atricaudus in lacking small ctenoid scales on the ocular-side dorsal and anal fin rays and in having an alternating series of pigmented blotches in the dorsal and anal fins (scales present and fins uniformly pigmented in S. atricaudus). From S. melanurus, S. caribbeanus differs in that S. melanurus possesses a fleshy ridge on the ocular-side lower jaw and the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye, whereas S. caribbeanus lacks a fleshy

283

ridge on the ocular-side lower jaw and the first dorsal fin ray is usually placed posterior to the vertical through the front margin of the upper eye. These two species are further distinguished by the fewer scales in a longitudinal series (78-89 in S. caribbeanus vs. 89-108 in S. melanurus), the lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in S. melanurus), and because the posterior dorsal and anal fins and the caudal fin of S. caribbeanus have an alternating series of pigmented blotches and unpigmented areas (versus progressive darkening in posterior dorsal and anal fins without alternating series of blotches and unpigmented areas in S. melanurus). Symphurus caribbeanus differs from S. fasciolaris and S. melasmatotheca in possessing 12 caudal fin rays (versus 10 and 11 in S. fasciolaris and S. melasmatotheca, respectively) and in lacking an ocellated spot on the caudal fin (present in S. fasciolaris) or pigmented peritoneum (present in S. melasmatotheca). From S. leei, S. caribbeanus is further distinguished in having the head length considerably smaller than the body depth (head length nearly equal with body depth in S. leei), in its smaller eye (17-22 SL vs. 22-27 SL in S. leei), and in having an unpigmented peritoneum (black in S. leei).

Material examined 100 specimens (24.4–122 mm SL).

Counted and measured (21 specimens, 40.1–122 mm SL). Holotype: USNM 313487; male, 100.5 mm SL; Mayaguez Bay, Puerto Rico; 1966; Collected by J.S. Ramsey. Paratypes. Haiti: FMNH 61574; (40.7); Port-au-Prince Bay; 12 Sep 1953. Netherlands Antilles: UMML 5297; (40.1); St. Martin; 1 m; 2 Jul 1959. Puerto Rico: UPRM 740; 2(120–122); Río Anasco; 1–2 Jul 1953. UPRM 1588; (98.0); Mayaguez; Mar 1962. UPRM 2926; 8(58.1–97.9); Guayanilla; 23 Jul 1968. ANSP 118553; (69.8); Puerto Rico; 25 Jan 1971. Colombia: UMML 30087; 6(88.7–98.1); 8°44.5–45.6'N, 76°52.71'W; 4m; 12 Jul 1966.

Counted (2 paratypes, 1 lot)—**Colombia**: USNM 313513; 2(102.8–116.7); Bajo-Sabanilla, off Barranquilla; 8 Sep 1969. (60 non-type specimens, 10 lots)—**Puerto Rico**: ANSP 115601; 7(43.3–82.5); Puerto Yabucoa; 12–13 Jul 1969. UPRM 736; (95.8); Río Anasco; 17 Aug 1951. UPRM 740; 8(90.0–122); Río Anasco; 1–2 Jul 1953. **Cuba**: MCZ 11200; (71.8); 1851. **Haiti**: UF 83998; 10(80.7–95.4); 2km NW of Port Salut; sandy beach near eelgrass bed; 1 m; 7 Apr 1979. UMML 34337; 3(95.8–110). **Nicaragua**: UMML 34338; 2(79.1–94.3); 12°16'N, 83°31'W; 12m; 28 Jan 1971. **Panama**: UMML 34339; (115); 8°49'N, 81°13'W; 18 m; 21 Jul 1966. UMML 34340; 26(24.4–117); 9°48'N, 82°50'W; 19 m; 26 Jan 1971. USNM 313514; (46.2); Colon; 5 Jan 1911.

Other non-type material examined (17 specimens, 2 lots). Cuba: MCZ 25982; (108.7). Costa Rica: UMML 34341; 16(52.9-117); 10°40'N, 83°29'W; 29 m; 27 Jan 1971.

Comparative life histories and distributions

In addition to morphological and pigmentation differences among Atlantic members of the S. plagusia complex, significant differences among members of this species complex are evident in geographic ranges, ecologies (primarily bathymetric occurrence), and lifehistory traits, including adult sizes and minimal sizes at sexual maturity. With the exception of S. civitatium, which occurs allopatrically in coastal seas off the southeastern United States and northern Mexico, these species occur in the Caribbean Sea and South Atlantic Ocean. Two species, S. plagusia and S. tessellatus, have extensive and sympatric distributions, ranging throughout insular and coastal locations from the northern Caribbean Sea to as far south as Rio de Janeiro, Brazil, for S. plagusia and to northern Uruguay for S. tessellatus. The geographic ranges of both S. plagusia and S. tessellatus completely overlap those of S. caribbeanus and S. oculellus, species with more restricted distributions. Symphurus caribbeanus occurs throughout insular and coastal areas in the Caribbean, with its southernmost occurrence in the western Caribbean off Colombia. Symphurus oculellus has the most restricted distribution of the species complex, occurring on the continental shelf along the northern coast of tropical South America north of 5°S from approximately 40°-60°W longitude.

Overall, members of the *S. plagusia* complex are generally shallow-water species, inhabiting nearshore and coastal seas usually shallower than 80 m (Table 11). Only rarely have individuals been collected deeper than 80 m, and none have been taken at depths greater than 110 m. In contrast, of the other eleven Atlantic species possessing 12 caudal fin rays (all have a 1-3-2 ID pattern), seven species usually inhabit much deeper waters on the continental shelf and upper continental slope, ranging from 35 to 700 m, with centers of abundance usually between 100 and 350 m (Munroe 1987). Exceptional to this observation are four diminutive species (*S. arawak* Robins and Randall, *S. rhytisma* Böhlke, *S. lubbocki*, and *S. reticulatus*), which occur on shallow substrates adjacent to coral reefs.

Although three of the five Atlantic species of the S. plagusia complex are known to have overlapping geographic ranges, the species do not occur syntopically at all life-history stages, especially with respect to bathymetric occurrences (Table 11). Three of the five Atlantic members of the S. plagusia complex, S. plagusia, S. tessellatus, and S. caribbeanus, occur syntopically at some stage in their life history in shallow waters of the Caribbean. Juveniles of all three species have been taken exclusively in beach seine and otter trawl collections in shallow-water (<10m) estuarine and mudflat habitats. However, striking differences are apparent in how these species utilize inshore habitats. In these habitats, juvenile S. tessellatus are collected with all life history stages of S. plagusia and S. caribbeanus. Adult S. tessellatus, however, apparently undergo an ontogenetic migration from shallow, nearshore habitats to deeper waters further offshore (11-80m) on the continental shelf. In contrast, although a small number of S. caribbeanus and S. plagusia have been taken as deep as 30-40 m on the continental shelf, these were isolated captures of large adults (>110 mm SL). The majority of S. plagusia and S. caribbeanus (80% and 83%, respectively), including all juveniles examined, were collected in waters shallower than 20 m. Most specimens were taken by beach seine and small otter trawls at depths shallower than 10m in nearshore mudflats, mangrove habitats, and estuarine locations.

Symphurus oculellus, although occurring sympatrically with S. plagusia and S. tessellatus (see Figures 3 and 5), apparently has a different life history than these other species. Symphurus oculellus inhabits deeper waters than the others (Table 11), spanning an overall bathymetric range of 7-110 m, but being captured most frequently in waters deeper than 20m (78% collected deeper than 20m). Symphurus oculellus, including juveniles as small as 76 mm SL, have been collected in neritic waters deeper than 7m and none have been taken from estuarine habitats, contrary to S. plagusia and S. tessellatus. However, estuarine environments in the geographic range of S. oculellus along northeastern South America have not been as thoroughly sampled as have those nearshore habitats occupied by S. plagusia and juvenile S. tessellatus in the northern Caribbean and southern Brazilian areas. Symphurus civitatium, the northernmost-occurring species, is the only Atlantic species with a distribution allopatric to those of other members of this species group. Adult S. civitatium are very abundant in collections and, although inhabiting a wide depth range (1-73m), are more commonly captured between 11 and 45m on the inner continental shelf where approximately 91% (199/216) of the specimens examined in the present study were collected (Table 11). It is unusual for adult S. civitatium to occur in habitats deeper or shallower than this depth range. For example, the deepest captures of this species were made at 73 and 62m, where a single fish was taken each time, and of four fish collected in waters shallower than 10m, only one was an adult and three others were small juveniles (<35mm SL). Little is known concerning early-life-history stages of S. civitatium. Few juveniles have been collected, but all of these were taken at inshore locations. The occurrence of early-life-history stages in nearshore waters suggests a life-history pattern similar to that of S.

tessellatus, where adults occur in deeper waters on the inner continental shelf and juveniles inhabit estuarine or nearshore nurseries. However, distribution data for this species, especially for early juveniles, are too incomplete to estimate how regularly this species utilizes inshore waters as nurseries. Further investigation is needed on whether recent captures of early juveniles in estuarine environments represent isolated occurrences of this species or its normal life-history pattern.

Among Symphurus, members of the S. plagusia complex are medium- to large-sized tonguefishes, ranging in maximum lengths from 122mm SL for S. caribbeanus to 220mm SL for S. tessellatus, the second largest species of tonguefish in the Atlantic (only S. jenunsi from the southern South Atlantic exceeds these sizes) and third largest in the genus (Fig. 2). Symphurus caribbeanus and S. plagusia are the smallest of the five Atlantic species of this complex (122 and 130 mm SL, respectively), and also mature at the smallest sizes (70-80mm SL for S. caribbeanus; 80mm SL for S. plagusia). Symphurus civitatium is only slightly larger, attaining maximum lengths of ~152 mm SL and maturing at sizes slightly greater than 90 mm SL. Symphurus oculellus and S. tessellatus are the largest Atlantic species in this complex, attaining maximum sizes of 189 and 220mm SL, respectively. Not surprisingly, these larger-sized species also mature at somewhat larger sizes. Female S. oculellus mature at about 110 mm SL and female S. tessellatus at 104-120 mm SL.

Comparisons of ecological and life-history parameters, like those above, supplement and corroborate systematic determinations based on morphological evidence. However, in the absence of a cladistic hypothesis, the value of these ecological comparisons, especially concerning historical relationships, either of the species complex within the genus or of the individual species comprising the *S. plagusia* complex, cannot be fully assessed. Further study, based on shared derived characters using outgroup comparisons or ontogeny, is needed before intrageneric relationships of the species complex and interrelationships of its members can be determined to better understand trends in the evolution of life-history attributes of these tonguefishes.

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285

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