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INTERDIGITATION PATTERN OF DORSAL-FIN PTERYGIOPHORES AND NEURAL SPINES, AN IMPORTANT DIAGNOSTIC CHARACTER FOR SYMPHURINE TONGUEFISHES (*SYMPHURUS*: CYNOGLOSSIDAE: PLEURONECTIFORMES)

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ABSTRACT

Numbers of proximal dorsal-fin pterygiophores in each of the anterior most five interneural spaces (ID patterns) were examined in 69 of 71 nominal species of symphurine (*Symphurus*) tonguefishes and were found to be of diagnostic value. All species of *Symphurus* typically have a single pterygiophore inserted into the first interneural space, a unique arrangement among the Cynoglossidae and related taxa that supports the monophyly of the genus. All but seven species in the genus usually have two pterygiophores inserted into interneural spaces four and five. Observed variation among species in ID patterns, therefore, results primarily from different numbers of pterygiophores inserting into interneural spaces two and three. Formulae for individual ID patterns listed below, with a single exception, are abbreviated to represent the pterygiophore arrangements in the first three interneural spaces. Nine different predominant ID patterns were discovered among 69 species examined. These patterns and the numbers of nominal species (in parentheses) possessing each are as follows: 1-2-2-1-2 (7); 1-2-2 (16); 1-2-3 (3); 1-3-2 (15); 1-3-3 (4); 1-3-4 (1); 1-4-2 (4); 1-4-3 (11); and 1-5-3 (8). Overall, average fidelity for the predominant ID pattern was approximately 78% per species, with values ranging from 37 to 100% per species. Forty-eight species had 70% or more of the individuals possessing the predominant ID pattern; seven had 60% or more with the predominant ID pattern; and only four of 69 species had 50% or fewer of the individuals with the predominant ID pattern. Less than 5% of the individuals per species had anomalous ID patterns that provided little or no useful information for identification of the specimens. Between 0 and 37% of the individuals for most species had variant ID patterns that were predominant patterns recorded for other species. Twenty of 24 New World species with 1-3-4, 1-4-2, 1-4-3, and 1-5-3 ID patterns had between 0 and 43% of the individuals per species with secondary ID patterns that occurred uniquely in species characterized by these predominant ID patterns. Intraspecific variation in ID patterns was limited and predictable for each species and was found to be largely non-overlapping among species with different predominant patterns. ID patterns are an important diagnostic character for *Symphurus*, especially when used in combination with caudal- and dorsal-fin ray counts. Geographical ranges of species characterized by each predominant ID pattern were plotted within four major marine faunal regions revealing interesting distributions for species with different predominant patterns. Species with 1-2-2-1-2 and 1-2-2 ID patterns occur predominantly, while those with a 1-2-3 occur exclusively, in deep-sea habitats throughout temperate and tropical regions of the Indo-Pacific. Only one species with a 1-2-2-1-2 ID pattern and two with the 1-2-2 pattern occur in the Atlantic, while no species with these three ID patterns is found in the eastern Pacific. Species characterized by other ID patterns are not found in the Indo-Pacific region. Those with the 1-3-2 and 1-3-3 ID pattern occur only in northern and southern hemispheres of the Atlantic Ocean and in the tropical eastern Pacific from the Gulf of California to northern Peru. Species with 1-3-4, 1-4-2, 1-4-3, and 1-5-3 ID patterns are found only in the New World. *Symphurus callopterus*, the only species with the 1-3-4 ID pattern, and all species with the 1-5-3 ID pattern occur in temperate and tropical regions of the eastern Pacific. Four species characterized by the 1-4-2 ID pattern occur entirely in the western Atlantic, while those with a 1-4-3 pattern occur in shallow-water environments of the western Atlantic and eastern Pacific Oceans.

The cynoglossid subfamily Symphurinae comprises a single genus *Symphurus*, which is the most speciose genus in the family with over 70 described nominal species (Munroe, 1987). Symphurine tonguefishes are small to medium-sized (ranging in adult sizes from 28–320 mm SL), sinistral flatfishes, occurring worldwide in all temperate and tropical oceans. The majority of species inhabit shallow continental seas of the New World (ca. 40 nominal species recorded from both sides of the Americas) and bathyal depths of the Indo-Pacific (ca. 23 nominal species reported). Species of *Symphurus* span a wide bathymetric range, inhabiting sandy and muddy substrates from shallow estuarine waters to deep bathyal depths on the outer continental shelf and slope. *Symphurus australis* (McCulloch, 1907) and *S. regani* (Chabanaud, 1955a), at 1,480 m and 1,489 m, respectively, are among the deepest-dwelling flatfishes. (Other deep-dwelling species of flatfishes include *Reinhardtius hippoglossoides* (Walbaum, 1792) and *Hippoglossus hippoglossus* (Linnaeus, 1758), which have been reported to occur at depths reaching 2,000 m (Nielsen, 1986); *Glyptocephalus cynoglossus* has been collected at depths of about 1,570 m (Scott and Scott, 1988); and *Bathysolea profundicola* (Vaillant, 1888), which reportedly has been taken (Quero et al., 1986) at depths of about 1,300 m.)

Of the pleuronectiforms, symphurine tonguefishes are among the most curious and divergent from the generalized fish form. The species share a similar morphology featuring many structural reductions and losses including a small mouth with strongly-curved and dentigerous blind-side jaws, and a caudal fin with reduced number of rays (10–14, including the last dorsal- and anal-fin rays) (Chapleau, 1988; Munroe and Mahadeva, 1989) that is continuous with the dorsal and anal fins. Furthermore, these flatfishes lack a lateral line, pectoral fins (in adults) on either side of the body, and the right pelvic fin. The greatly shortened left pelvic fin, consisting of four simple rays, is situated along the ventral midline and connected to the body near the anus or at the base of the anal fin by a short, delicate membrane. Additionally, in the most recent classification of cynoglossid genera, Chapleau (1988) found six osteological features that he considered autapomorphies of *Symphurus*.

Several revisionary studies have examined *Symphurus* from selected geographical regions (Chabanaud, 1949, 1955a, 1955b, 1955c, 1956; Ginsburg, 1951; Mahadeva, 1956; Ochiai, 1963; Menezes and Benvegnú, 1976; Munroe, 1987, 1990a); however, there has never been a comprehensive revision or detailed comparative osteological study of the entire genus. Therefore, despite these regional treatments, much confusion persists regarding the status of many nominal forms, especially those in the Indo-Pacific. Taxonomic uncertainty exists for many species because previous workers have relied almost exclusively on external characters, primarily fin-ray counts and morphometrics, to diagnose the species. Since *Symphurus* comprises morphologically-similar species that overlap considerably in traditional meristic and morphometric features, these characters are of limited value when used alone to delineate species. Additionally, many smaller-sized species are residents of the deep sea (especially in the Indo-Pacific) and are rarely captured by conventional sampling techniques. Deep-water taxa are scarce in museum collections and several nominal species including *S. fuscus* Brauer, *S. arabicus* Chabanaud, *S. macrophthalmus* Norman, *S. maldivensis* Chabanaud, *S. marmoratus* Fowler, *S. variegatus* (Gilchrist), *S. sayademalhensis* Chabanaud, *S. hondoensis* Hubbs, *S. holothuriae* Chabanaud, *S. fallax* Chabanaud, *S. diabolicus* Mahadeva and Munroe, and *S. microlepis* Garman are known only from the holotype or a small number of specimens ($N < 3$). Accordingly, the number of valid species of *Symphurus* and their interrelationships is still imprecisely known.

In revising Atlantic (Munroe, 1987, 1990a, 1991) and eastern Pacific symphurine tonguefishes (Munroe and Mahadeva, 1989; Munroe, 1990b; Mahadeva and Munroe, 1990; Munroe and Nizinski, 1990), I have had the opportunity to examine types and representative series of specimens for 69 of 71 nominal species presently assigned to *Symphurus* (Table 1). Comparisons of radiographs revealed that each species has a predominant pattern of interdigitation of proximal dorsal pterygiophores and neural spines (hereafter referred to as the ID pattern) and the species differ with respect to their predominant ID pattern. Since there is interspecific variation in ID patterns, it became evident that these patterns could be useful, either alone or in combination with other characters, in diagnosing species or groups of species in the genus.

Here I present information on interspecific variation in ID patterns observed in species of *Symphurus*, identify and discuss intraspecific variation in this character, and assess the utility of interdigitation patterns as a diagnostic character for identification of symphurine tonguefishes. Additionally, geographic and bathymetric distributions of species, grouped together by possession of a similar ID pattern, were compared in an attempt to identify patterns of zoogeographical distributions or areas of endemism for species with unique pattern types. The phylogenetic value of this character can not be evaluated until on-going osteological studies are completed.

Methods

A total of 4,251 specimens, representing 69 of 71 nominal species of *Symphurus* (Table 1), were radiographed and their ID patterns recorded (Tables 2–9). Holotypes of *S. fallax* Chabanaud, *S. orientalis* (Bleeker), *S. woodmasoni* (Alcock), *S. gilesii* (Alcock), *S. septemstriatus* (Alcock), and *S. novemfasciatus* Shen and Lin were unavailable for this study. ID patterns of related taxa, including species of the two genera of the subfamily Cynoglossinae, and selected representatives of the families Soleidae and Achiridae are listed in Table 12. All specimens examined in this study are listed in the Appendix, with collection acronyms following those provided by Leviton et al. (1985). Whenever possible, specimens examined represented the entire size range and geographic distribution for a species. Counts for a small number of specimens, including larvae as small as 7.5 mm SL, were made from specimens cleared and counter-stained for cartilage and bone following the method outlined in Dingerkus and Uhler (1977).

Vertebral and fin-ray counts follow methods outlined in Munroe and Mahadeva (1989) and Munroe (1990a). For each specimen, the number of dorsal pterygiophores inserting into the first five interneural spaces was recorded as the ID pattern (Figs. 1–3). Since the first neural spine abuts directly against the cranium, there is no obvious space between it and the cranium. All but seven species in the genus usually have two pterygiophores inserted into interneural spaces four and five. Observed variation among species in ID patterns, therefore, results primarily from different numbers of pterygiophores inserting into interneural spaces two and three. Except for the seven species noted above, the formulae designating the different ID patterns occurring in the remainder of the species were abbreviated for ease of reading. These ID pattern formulae reflect the numbers of pterygiophores inserting into each respective interneural space beginning with the first (posterior to the first neural spine) and continuing with each successive space to interneural space three or five. For example, the 1-2-2-1-2 formula indicates one pterygiophore inserts into interneural space one; two into interneural spaces two and three; one into interneural space four; and two pterygiophores insert into interneural space five. The 1-3-2 pattern indicates one pterygiophore inserts into interneural space one; three into interneural space two; and two into interneural spaces three, four, and five, respectively. Numbers of dorsal pterygiophores inserting into interneural spaces posterior to the fifth interneural space were not recorded because those spaces almost invariably contain two pterygiophores (at least until the posteriormost two or three interneural spaces).

The "predominant pattern" is defined as the pattern that occurs in the majority of specimens of a species. A "variant pattern" is defined as one that occurs less frequently than the predominant pattern (in approximately 5–15% of the individuals per species) and that corresponds to one of the predominant patterns recorded for other species. A "secondary pattern" is one that occurs less frequently than the predominant pattern but is unique to a particular group of species. "Anomalous patterns" are defined as those patterns that do not correspond to any predominant or secondary patterns observed in other species. Anomalous patterns were rarely observed and usually occurred in less than 5% of the specimens per species. The nine predominant ID patterns are illustrated in Figures 1–3.

Abbreviations for geographic regions discussed in text and tables and outlined in Figure 4 are: CAR Caribbean; EA eastern Atlantic including Mediterranean; EP eastern Pacific; IP Indo-West Pacific; WA western Atlantic; WNA western North Atlantic; WSA western South Atlantic.

Table 1. List of nominal species of *Symphurus* and species recognized in the present study (Species are arranged chronologically by date of publication of original description)

Nominal species	This study
Pleuronectes plagiusa Linnaeus 1766	*Symphurus plagiusa* (Linnaeus)
Pleuronectes plagusia Schneider, in Bloch & Schneider 1801	*S. plagusia* (Schneider, in Bloch & Schneider)
Symphurus nigrescens Rafinesque 1810	*S. nigrescens* Rafinesque
Plagusia tessellatus Quoy & Gaimard 1824	*S. tessellatus* (Quoy & Gaimard)
Plagusia brasiliensis Agassiz, in Spix & Agassiz 1831	=*S. tessellatus* (Quoy & Gaimard)
Plagusia lactea Bonaparte 1833	=*S. nigrescens* Rafinesque
Plagusia fasciata DeKay 1842	=*S. plagiusa* (Linnaeus)
Bibronia ligulata Cocco 1844	*S. ligulatus* (Cocco)
Aphoristia ornata Kaup 1858	=*S. plagusia* (Schneider, in Bloch & Schneider)
Plagusia picta Costa 1862	=*S. nigrescens* Rafinesque
Ammopleurops lacteus Günther 1862	=*S. nigrescens* Rafinesque
Aphoristia elongata Günther 1868	*S. elongatus* (Günther)
Aphoristia orientalis Bleeker 1879	*S. orientalis* (Bleeker)
Aphoristia atricauda Jordan & Gilbert 1880	*S. atricaudus* (Jordan & Gilbert)
Aphoristia nebulosa Goode & Bean 1883	*S. nebulosus* (Goode & Bean)
Aphoristia diomedeana Goode & Bean 1885	*S. diomedeanus* (Goode & Bean)
Aphoristia pusilla Goode & Bean 1885	*S. pusillus* (Goode & Bean)
Aphoristia marginata Goode & Bean 1886	*S. marginatus* (Goode & Bean)
Aphoristia pigra Goode & Bean 1886	*S. piger* (Goode & Bean)
Aphoristia gilesii Alcock 1889	*S. gilesii* (Alcock)
Aphoristia woodmasoni Alcock 1889	*S. woodmasoni* (Alcock)
Symphurus atramentatus Jordan & Bollman 1890	*S. atramentatus* Jordan & Bollman
Symphurus leei Jordan & Bollman 1890	*S. leei* Jordan & Bollman
Aphoristia septemstriata Alcock 1891	*S. septemstriatus* (Alcock)
Symphurus fasciolaris Gilbert 1892	*S. fasciolaris* Gilbert
Aphoristia trifasciata Alcock 1894	*S. trifasciatus* (Alcock)
Symphurus williamsi Jordan & Culver 1895	*S. williamsi* Jordan & Culver
Symphurus microlepis Garman 1899	*S. microlepis* Garman

Table 1. Continued

Nominal species	This study
Symphurus varius Garman 1899	*S. varius* Garman
Aphoristia variegata Gilchrist 1903	*S. variegatus* (Gilchrist)
Symphurus strictus Gilbert 1905	*S. strictus* Gilbert
Symphurus undatus Gilbert 1905	*S. undatus* Gilbert
Symphurus fuscus Brauer 1906	*S. fuscus* Brauer
Symphurus jenynsi Everman & Kendall 1906	*S. jenynsi* Evermann & Kendall
Symphurus australis McCulloch 1907	*S. australis* McCulloch
Aphoristia elongata Weber 1913	=*S. regani* Weber & de Beaufort
Aphoristia microrhynchus Weber 1913	*S. microrhynchus* (Weber)
Symphurus hondoensis Hubbs 1915	*S. hondoensis* Hubbs
Symphurus bergi Thompson 1916	*S. jenynsi* Evermann & Kendall
Symphurus ocellatus von Bonde 1922	*S. ocellatus* von Bonde
Symphurus regani Weber & de Beaufort 1929	*S. regani* Weber & de Beaufort
Symphurus marmoratus Fowler 1934	*S. marmoratus* Fowler
Symphurus melanurus Clark 1936	*S. melanurus* Clark
Symphurus macrophthalmus Norman 1939	*S. macrophthalmus* Norman
Symphurus sechurae Hildebrand 1946	=*S. melanurus* Clark
Symphurus paitensis Hildebrand 1946	=*S. williamsi* Jordan & Culver
Symphurus gorgonae Chabanaud 1948	*S. gorgonae* Chabanaud
Symphurus holothuriae Chabanaud 1948	*S. holothuriae* Chabanaud
Symphurus trewavasae Chabanaud 1948	*S. trewavasae* Chabanaud
Symphurus sumptuosus Chabanaud 1948	=*S. diomedeanus* (Goode & Bean)
Symphurus normani Chabanaud 1950	*S. normani* Chabanaud
Symphurus civitatum Ginsburg 1951	*S. civitatium* Ginsburg
Symphurus minor Ginsburg 1951	*S. minor* Ginsburg
Symphurus parvus Ginsburg 1951	*S. parvus* Ginsburg
Symphurus pelicanus Ginsburg 1951	*S. pelicanus* Ginsburg
Symphurus urospilus Ginsburg 1951	*S. urospilus* Ginsburg
Symphurus pterospilotus Ginsburg 1951	=*S. diomedeanus* (Goode & Bean)
Symphurus vanmelleae Chabanaud 1952	*S. vanmelleae* Chabanaud

Table 1. Continued

Nominal species	This study
Symphurus arabicus Chabanaud 1954	*S. arabicus* Chabanaud
Symphurus luzonensis Chabanaud 1955a	*S. luzonensis* Chabanaud
Symphurus schultzi Chabanaud 1955a	*S. schultzi* Chabanaud
Symphurus maldivensis Chabanaud 1955b	*S. maldivensis* Chabanaud
Symphurus seychellensis Chabanaud 1955b	=*S. melanurus* Clark
Symphurus sayademalhensis Chabanaud 1955b	*S. sayademalhensis* Chabanaud
Symphurus fallax Chabanaud 1957	*S. fallax* Chabanaud
Symphurus ommaspilus Böhlke 1961	*S. ommaspilus* Böhlke
Symphurus rhytisma Böhlke 1961	*S. rhytisma* Böhlke
Symphurus arawak Robins & Randall 1965	*S. arawak* Robins & Randall
Symphurus ginsburgi Menezes & Benvegnú 1976	*S. ginsburgi* Menezes & Benvegnú
Symphurus kyaropterygium Menezes & Benvegnú 1976	*S. kyaropterygium* Menezes & Benvegnú
Symphurus meridionalis Lema & Oliveira 1977	=*S. jenynsi* Evermann & Kendall
Symphurus novemfasciatus Shen & Lin 1984	*S. novemfasciatus* Shen & Lin
Symphurus callopterus Munroe & Mahadeva 1989	*S. callopterus* Munroe & Mahadeva
Symphurus lubbocki Munroe 1990	*S. lubbocki* Munroe
Symphurus reticulatus Munroe 1990	*S. reticulatus* Munroe
Symphurus melasmatotheca Munroe & Nizinski 1990	*S. melasmatotheca* Munroe & Nizinski
Symphurus undecimplerus Munroe & Nizinski 1990	*S. undecimplerus* Munroe & Nizinski
Symphurus chabanaudi Mahadeva & Munroe 1990	*S. chabanaudi* Mahadeva & Munroe
Symphurus diabolicus Mahadeva & Munroe 1990	*S. diabolicus* Mahadeva & Munroe
Symphurus oligomerus Mahadeva & Munroe 1990	*S. oligomerus* Mahadeva & Munroe
Symphurus oculellus Munroe 1991a	*S. oculellus* Munroe
Symphurus caribbeanus Munroe 1991a	*S. caribbeanus* Munroe
Symphurus prolatinaris Munroe, Nizinski & Mahadeva 1991	*S. prolatinaris* Munroe, Nizinski & Mahadeva
Symphurus species C Munroe 1987	*Symphurus* species C Munroe
Unidentified species New Guinea	New Guinea species

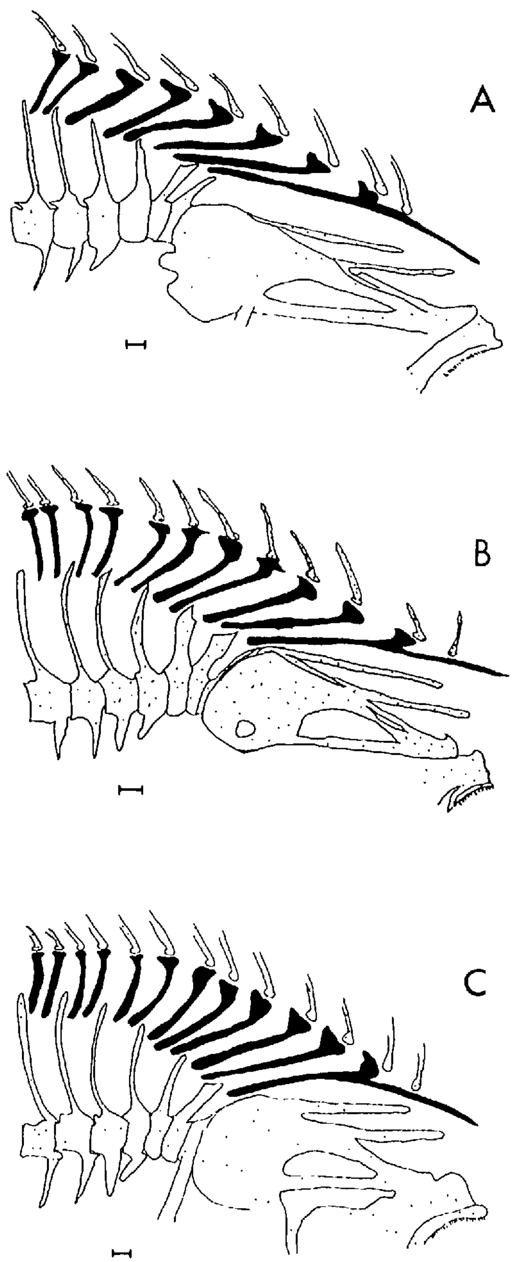

Figure 1. Interdigitation of proximal dorsal pterygiophores and neural spines in species of *Symphurus* representing three different ID patterns. A. *S. vanmelleae* (1-2-2-1-2 pattern). B. *S. nebulosus* (1-2-2-2-2 pattern). C. *S. undatus* (1-2-3-2-2 pattern). Scale bar equals 1 mm.

Pterygiophore patterns recorded in this study relate only to the numbers of pterygiophores inserting into successive interneural spaces. These formulae are not analagous to those adopted by other authors (Smith and Bailey, 1961) to demonstrate relationships and correspondence between neural spines and predorsal bones. Additionally, patterns do not reflect numbers of fin rays supported by the pterygiophores.

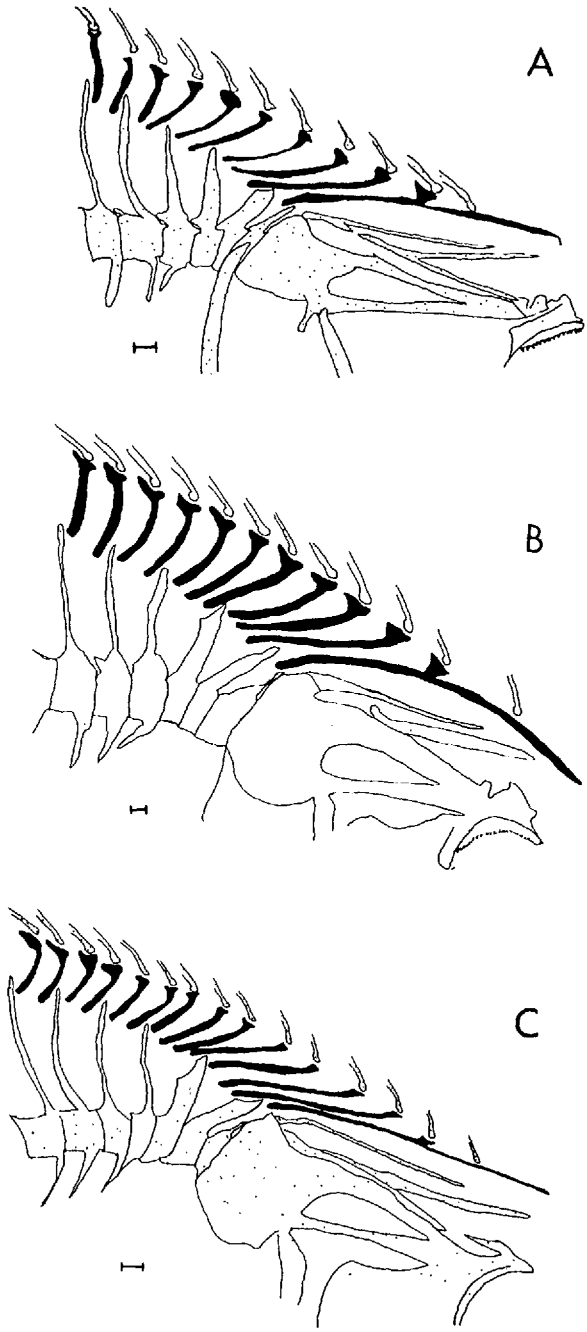

Figure 2. Interdigitation of proximal dorsal pterygiophores and neural spines in species of *Symphurus* representing three different ID patterns. A. *S. marginatus* (1-3-2-2-2 pattern). B. *S. trewavasae* (1-3-3-2-2 pattern). C. *S. callopterus* (1-3-4-2-2 pattern). Scale bar equals 1 mm.

Results

Nine different predominant ID patterns were discovered among the species examined. These patterns and their percent occurrence in species of *Symphurus*

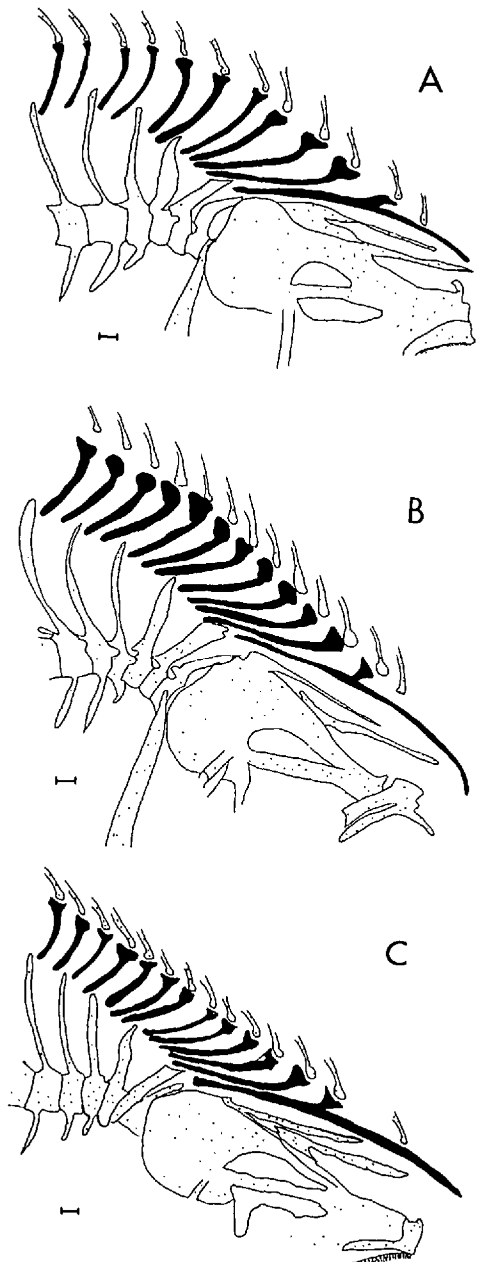

Figure 3. Interdigitation of proximal dorsal pterygiophores and neural spines in species of *Symphurus* representing three different ID patterns. A. *S. kyaropterygium* (1-4-2-2-2 pattern). B. *S. plagiusa* (1-4-3-2-2 pattern). C. *S. chabanaudi* (1-5-3-2-2 pattern). Scale bar equals 1 mm.

are listed in Tables 2–8. Comparisons of ID patterns occurring in 53 species (where N > 5 individuals examined), grouped by common ID pattern, appears in Table 9. Most frequently occurring ID patterns are 1-2-2 (16 species), 1-3-2 (15), 1-4-3 (11), 1-5-3 (8), and 1-2-2-1-2 (7 species) patterns. Other patterns occurring less frequently are 1-3-3 and 1-4-2 ID patterns (4 species with each

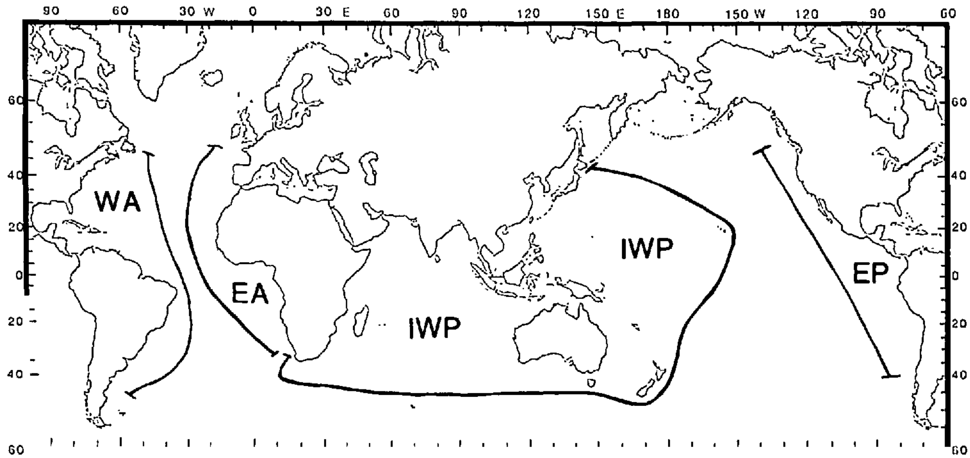

Figure 4. Generalized geographic regions referred to in text. Abbreviations for geographic regions outlined in figure are: WA Western Atlantic; EA Eastern Atlantic; IWP Indo-West Pacific; and EP Eastern Pacific.

pattern); 1-2-3 pattern (3 nominal species, but may actually be limited to only one species, see comments below); and 1-3-4 (one species). A smaller number of secondary patterns, such as 1-5-2, 1-4-4, and 1-6-3, occurred uniquely and less frequently in specimens of species characterized by 1-3-4, 1-4-2, 1-4-3, and 1-5-3 predominant ID patterns (Tables 5–8). The frequencies of secondary patterns occurring in these species are discussed under respective sections for each predominant pattern beginning with species characterized by the 1-3-4 pattern and continuing through those with the 1-5-3 pattern.

Several features of ID patterns are shared by most species of *Symphurus*. All species (where more than 10 specimens were examined), except three, are char-

Table 2. Frequency distributions (percent) of predominant, variant, and anomalous ID patterns for four species of *Symphurus* characterized by a 1-2-2-1-2 ID pattern (Abbreviations for geographic locations are defined in text)

	vanmelleae	*gilesii*	*regani*	*schultzi*
Location	EA	IP	IP	IP
Sample size	65	9	7	7
Predominant patterns				
1-2-2-1-2	45	—	28	28
1-2-2-2-1	31	78	28	28
1-2-1-2-1	9	—	14	—
1-2-1-2-2	5	—	—	—
1-2-2-1-1	5	—	14	—
Variant pattern				
1-2-2-2-2	—	22	14	28
Anomalous patterns				
1-1-2-2-1	—	—	—	14
1-1-3-2-2	2	—	—	—
1-3-1-2-1	2	—	—	—
1-3-1-2-2	2	—	—	—
New World patterns	0	0	0	0

Table 3. Frequency distributions (percent) of predominant, variant, and anomalous ID patterns for eight species of *Symphurus* characterized by a 1-2-2-2-2 ID pattern (Abbreviations for geographic locations are defined in text)

	ligulatus	*nebulosus*	*ocellatus*	*strictus*	*australis*	*wood-masoni*	*septem-striatus*	*trifas-ciatus*
Location	EA	WNA	IP	IP	IP	IP	IP	IP
Sample size	37	25	15	34	30	93	63	6
Predominant pattern								
1-2-2-2-2	73	84	80	76	87	80	89	100
Variant patterns								
1-2-1-2-2	—	—	—	3	3	1	—	—
1-2-2-1-2	8	—	20	9	—	10	3	—
1-2-2-2-1	—	—	—	—	3	6	—	—
1-2-3-2-2	3	4	—	6	7	—	5	—
Anomalous patterns								
1-1-2-2-2	—	—	—	—	—	—	2	—
1-1-3-1-2	—	—	—	—	—	1	—	—
1-1-3-2-2	3	—	—	—	—	—	—	—
1-2-1-3-2	—	—	—	—	—	1	—	—
1-2-2-3-2	5	—	—	6	—	—	—	—
1-2-3-1-2	5	—	—	—	—	—	—	—
1-3-2-2-1	—	—	—	—	—	1	—	—
2-1-2-2-2	—	4	—	—	—	—	—	—
2-2-2-1-2	3	—	—	—	—	—	—	—
2-2-2-2-2	—	8	—	—	—	—	2	—
New World patterns	0	0	0	0	0	0	0	0

acterized by a single predominant ID pattern (Tables 2–8). Frequency values for a predominant pattern ranged from 37–100%, but were usually greater than 70% (overall $\bar{x}$ = 77.8%) for 53 of 70 species with sufficient sample size. Only in three of the 70 species did two or more patterns occur with nearly equal frequencies. In *S. parvus* (Table 6), 43% of the specimens had a 1-5-2 pattern and 40% had a 1-4-2 pattern; in *S. williamsi* (Table 8), 42% had 1-5-3 and 36% had 1-4-3 patterns; while in *S. undecimplerus* (Table 8), 37% of the specimens had a 1-5-3 pattern, 21% were found with a 1-4-4 pattern, and 21% possessed a 1-5-4 secondary pattern.

Secondly, ID patterns were not found to vary intraspecifically with respect to sex, size, or geographic range of a given species. With rare exception, *Symphurus* have only one pterygiophore inserting into the first interneural space. Only 29 of 4,251 individuals (0.7%), distributed among 17 species, were found with two pterygiophores inserted into interneural space one, and only a single specimen (of *S. diomedeanus*) had three pterygiophores inserted into the first interneural space. Rarely did specimens lack pterygiophores in the first interneural space (one specimen each of *S. pelicanus* and *S. leei*).

Additionally, with the exception of seven species (i.e., those characterized by the 1-2-2-1-2 ID pattern), all *Symphurus* typically have two pterygiophores inserted into interneural spaces four and five. Therefore, interspecific variation in ID patterns of symphurine tonguefishes results almost exclusively from different numbers of pterygiophores inserting into interneural spaces two and three.

Interdigitation patterns in tonguefishes have not previously been studied or utilized in diagnosing species in this genus, except by Munroe and co-workers (1987; and subsequent publications). Therefore, prior to evaluating the importance

Table 4. Frequency distributions (percent) of predominant, variant, and anomalous ID patterns for eight species of *Symphurus* with a 1-3-2-2-2 predominant ID pattern (Abbreviations for geographic regions are defined in text)

	arawak	*rhytisma*	*reticulatus*	*ginsburgi*	*gorgonae*	*marginatus*	*nigrescens*	*pelicanus*	*piger*	*pusillus*	Species C	*oligomerus*
Location	CAR	CAR	EA	WSA	EP	WA	EA	WNA	WNA	WNA	WNA	EP
Sample size	41	5	5	56	73	94	161	62	142	24	82	205
Predominant pattern												
1-3-2-2-2	83	100	100	93	81	77	90	94	97	88	94	89
Variant patterns												
1-2-2-2-2	2	—	—	—	1	2	1	—	1	—	—	2
1-2-3-2-2	—	—	—	2	4	7	2	2	<1	4	—	2
1-3-3-2-2	2	—	—	2	6	13	1	2	<1	4	1	4
1-4-2-2-2	—	—	—	2	—	—	—	—	—	—	1	2
Anomalous patterns												
0-3-2-2-2	—	—	—	—	—	—	—	2	—	—	—	—
1-1-3-2-2	—	—	—	—	—	—	—	2	—	—	—	—
1-2-3-1-2	—	—	—	—	—	—	2	—	—	—	—	—
1-2-3-2-1	—	—	—	—	3	—	—	—	—	—	—	—
1-3-1-2-2	5	—	—	—	—	—	<1	—	—	4	—	—
1-3-2-1-2	—	—	—	—	—	—	2	—	—	—	3	—
1-3-2-2-1	2	—	—	—	—	—	—	—	—	—	—	—
1-3-2-3-1	—	—	—	—	1	—	—	—	—	—	—	—
1-3-3-1-2	—	—	—	—	—	—	—	—	—	—	—	—
2-2-2-2-2	—	—	—	2	1	—	<1	—	—	—	—	—
2-2-3-2-2	—	—	—	—	—	1	—	—	—	—	—	—
2-2-2-2-3	—	—	—	—	—	—	<1	—	—	—	—	—
2-3-2-2-2	5	—	—	—	3	—	—	—	—	—	—	<1
New World patterns	0	0	0	2	0	0	0	0	0	0	1	2

Table 5. Frequency distributions (percent) of predominant, variant, and anomalous ID patterns for species of *Symphurus* characterized by a 1-3-3-2-2 ID pattern (Abbreviations for geographic locations are defined in text)

	atramentatus	*normani*	*trewavasae*	*varius*
Location	EP	EA	WSA	EP
Sample size	151	35	58	49
Predominant pattern				
1-3-3-2-2	90	83	69	74
Variant patterns				
1-2-3-2-2	—	3	—	—
1-3-2-2-2	<1	3	5	—
1-3-4-2-2	5	3	3	—
1-4-2-2-2	1	—	16	20
1-4-3-2-2	2	3	2	2
Anomalous patterns				
1-2-3-3-2	—	—	2	—
1-2-4-2-2	—	—	2	—
1-3-2-3-1	1	—	—	—
1-3-2-3-2	—	3	2	—
1-3-3-3-2	—	—	—	2
1-4-2-3-2	—	—	—	2
2-3-2-2-2	—	3	—	—
New World patterns	8	6	21	24

of this character in species identifications, it was necessary to measure the level of intraspecific variation that occurs in this feature.

Although each species was found to have a predominant ID pattern (Tables 2–8), some level of intraspecific variation in this character was observed in all but a few of the species examined. Intraspecific variation in ID patterns, potentially limiting the usefulness of this character for identification purposes, occurs when specimens have patterns unlike the predominant pattern observed for that species. Additionally, variation in the form of anomalous patterns occurred in a few specimens of most species (usually <5%) and, unlike variant patterns, did not occur as a predominant pattern for any other species. For example, in the 53 species with sufficient data (those with N > 5 specimens), the occurrence of anomalous patterns averaged approximately 4.2% (0–17%) of the specimens per species. For those individuals with anomalous patterns, ID pattern has limited or no application in identification of the specimens.

For most species, the highest level (0–37% of the specimens) of intraspecific variation was the occurrence of specimens with variant ID patterns (Tables 2–9). These variant patterns averaged about 13% ($\bar{x}$ = 13.1%) per species. Of the 53 species surveyed in detail, 23 had 10% or less of the specimens with variant patterns, 17 species had values of variant patterns ranging between 11 and 20%, and 13 species (almost all New World with 1-4-2, 1-4-3, and 1-5-3 ID patterns) had variant patterns in more than 20% of the specimens examined (Table 9). Individual species values for the occurrence of variant patterns (Tables 2–8) ranged from 0% in five species (*S. vanmelleae, S. trifasciatus, S. rhytisma, S. reticulatus,* and *S. ommaspilus*) to 37% in *S. plagiusa* and *S. williamsi.*

Although variant patterns were observed in approximately 13% of the individuals per species, this intraspecific variation did not necessarily detract from the overall value of ID patterns as a diagnostic character in identifying specimens

Table 6. Frequency distributions (percent) of predominant, variant, secondary, and anomalous ID patterns for *Symphurus callopterus* (with a 1-3-4-2-2 ID pattern) and four species with a 1-4-2-2-2 ID pattern (Abbreviations for geographic locations are defined in text)

	callopterus	*kyaropterygium*	*minor*	*ommaspilus*	*parvus*
Location	EP	WSA	WNA	CAR	WNA
Sample size	191	14	78	28	82
Predominant pattern					
1-3-4-2-2	64				
1-4-2-2-2		93	95	100	40
Secondary patterns					
1-4-4-2-2	5	—	—	—	—
1-5-2-2-2	—	—	—	—	43
Variant patterns					
1-3-2-2-2	—	—	3	—	1
1-3-3-2-2	3	7	—	—	—
1-4-3-2-2	14	—	—	—	10
Anomalous patterns					
1-2-4-2-2	<1	—	—	—	—
1-3-2-3-2	—	—	1	—	—
1-3-3-3-2	5	—	—	—	—
1-3-4-2-3	<1	—	—	—	—
1-3-4-3-2	3	—	—	—	—
1-4-1-2-2	—	—	—	—	1
1-4-3-1-2	—	—	1	—	—
1-4-3-3-2	4	—	—	—	—
1-5-1-2-2	—	—	—	—	5
2-3-4-3-2	<1	—	—	—	—
New World patterns	91	93	96	100	99

since the range of variant patterns encountered in a species was limited and predictable. Therefore, the range in variation of variant patterns itself was informative, especially in preliminary stages of identification. Species possessing different predominant ID patterns, often, also differed with respect to the range of possible variant ID patterns as well. For example, individuals of species characterized by 1-5-3 (Table 8) or 1-4-3 ID patterns (Table 7) were never found with the following ID patterns: 1-2-2-1-2, 1-2-2, 1-2-3, or 1-3-2. The converse is also true; species with ID patterns featuring three or fewer pterygiophores inserting into the second interneural space (Tables 2–5) never had specimens with a 1-5-3 ID pattern. Nor were there specimens with variant ID patterns between species with1-2-2-1-2, 1-2-2, 1-2-3, or 1-3-2 patterns and those possessing the 1-4-3 pattern. Thus, the occurrence of variant ID patterns in these specimens, although limiting the application of this character somewhat, does not eliminate entirely the value of ID patterns as a diagnostic character. Even when possessing variant patterns, the range of possible species groups an individual specimen can be assigned to in preliminary stages of identification is considerably narrowed when ID patterns are examined.

The following sections discuss the occurrence of the nine predominant and several secondary ID patterns featured in the species; examines the levels of intraspecific variation (specimens with anomalous and variant patterns) for species with each predominant pattern; and summarizes geographic distributions of species possessing each predominant pattern.

Table 7. Frequency distributions (percent) of predominant, variant, secondary, and anomalous ID patterns for eight species of *Symphurus* characterized by a 1-4-3-2-2 ID pattern (Abbreviations for geographic locations are defined in text)

	diomedeanus	*fasciolaris*	*jenynsi*	*plagiusa*	*urospilus*	*civitatium*	*leei*	*plagusia*	*tessellatus*	*oculellus*	*caribbeanus*
Location	WA	EP	WSA	WNA	WNA	WNA	EP	WA	WA	WA	CAR
Sample size	204	39	85	138	110	170	198	42	241	45	83
Predominant pattern											
1-4-3-2-2	74	69	72	60	67	75	62	76	73	89	82
Variant patterns											
1-3-3-2-2	3	8	4	17	4	5	1	10	4	2	10
1-3-4-2-2	6	3	6	<1	<1	4	7	2	7	4	4
1-4-2-2-2	6	8	2	18	7	11	<1	5	5	2	—
1-5-3-2-2	6	8	7	<1	4	2	6	2	5	2	—
Secondary patterns											
1-4-4-2-2	1	—	2	<1	<1	—	11	2	5	—	2
1-5-2-2-2	3	3	2	3	14	4	2	—	<1	—	2
Anomalous patterns											
0-6-3-2-2	—	—	—	—	—	—	<1	—	—	—	—
1-3-3-3-2	—	—	1	—	—	—	—	—	—	—	—
1-3-4-3-2	—	—	—	—	—	—	<1	—	—	—	—
1-4-2-3-1	—	—	—	—	<1	—	—	—	—	—	—
1-4-2-3-2	—	—	—	—	—	—	1	—	—	—	—
1-4-3-1-2	—	—	—	—	<1	—	—	—	—	—	—
1-4-3-2-1	—	—	—	<1	—	—	—	—	—	—	—
1-4-3-3-2	—	3	—	1	—	—	5	2	—	—	—
1-4-4-3-2	—	—	—	—	—	—	<1	—	—	—	—
1-5-2-3-2	—	—	—	—	<1	—	<1	—	—	—	—
2-3-3-2-2	—	—	1	—	—	—	<1	—	—	—	—
2-3-3-3-2	—	—	—	—	—	—	<1	—	—	—	—
2-3-4-2-2	—	—	—	—	—	—	<1	—	—	—	—
2-4-3-2-2	—	—	2	—	—	—	1	—	—	—	—
3-3-2-2-2	<1	—	—	—	—	—	—	—	—	—	—
New World patterns	97	94	91	86	97	96	97	89	96	97	90

Table 8. Frequency distributions (percent) of predominant, variant, and secondary ID patterns for eight eastern Pacific species of *Symphurus* characterized by a 1-5-3-2-2 ID pattern

	atri-caudus	*chaba-naudi*	*elongatus*	*mela-nurus*	*melasma-totheca*	*prola-tinaris*	*undecim-plerus*	*williamsi*
Sample size	85	132	91	120	107	108	43	135
Predominant pattern								
1-5-3-2-2	53	59	72	75	62	80	37	42
Variant patterns								
1-3-4-2-2	—	—	—	—	—	—	—	<1
1-4-2-2-2	—	<1	—	—	—	—	—	—
1-4-3-2-2	14	24	10	5	21	4	7	36
Secondary patterns								
1-4-4-2-2	5	11	3	3	4	<1	21	4
1-5-2-2-2	16	2	1	7	8	2	—	5
1-5-4-2-2	5	<1	1	<1	<1	4	21	—
1-6-2-2-2	—	—	2	—	—	3	—	—
1-6-3-2-2	4	—	9	5	2	5	2	2
Anomalous patterns								
1-4-3-2-3	—	—	—	<1	—	—	—	—
1-4-3-3-2	—	2	1	2	<1	—	5	4
1-4-4-3-2	—	—	—	—	<1	—	—	—
1-5-3-1-2	—	—	—	—	—	—	—	<1
1-5-2-3-2	2	—	—	—	—	—	—	4
1-5-3-3-2	—	2	—	—	—	3	7	—
1-6-2-3-2	1	—	—	—	—	—	—	—
2-3-2-2-2	—	—	—	—	—	—	—	—
2-3-3-2-2	—	—	—	—	—	—	—	<1
2-4-2-2-2	—	—	—	—	<1	—	—	—
2-4-3-2-2	—	—	—	—	—	—	—	<1
2-5-3-2-2	—	—	—	<1	—	—	—	—
New World patterns	100	100	100	99	99	100	100	98

1-2-2-1-2 ID Pattern.—Among the seven species with a predominant ID pattern of 1-2-2-1-2, fidelity of this pattern ranged from 57% (4/7 individuals) in *S. schultzi,* 78% (7/9) in *S. gilesii,* 86% (6/7) in *S. regani,* to 96% in *S. vanmelleae* (62/65). Both the holotype and paratype of *S. macrophthalmus* and the holotypes of *S. arabicus* and *S. fuscus* also featured this pattern.

Of species with this ID pattern, only *S. vanmelleae* was available in sufficient sample size (N = 65) to detail intraspecific variation in pterygiophore patterns. At first observation (Table 2), there appeared to be little evidence toward characterization of *S. vanmelleae* by a single ID pattern because five ID patterns, which differed only in the placement of a single pterygiophore in either interneural space 3, 4, or 5, were observed. In *S. vanmelleae,* 45% (29/65) of the individuals had a 1-2-2-1-2 pattern, 31% (20 individuals) had a 1-2-2-2-1 pattern, while 9% had a 1-2-1-2-1 pattern. Another 10% of the specimens had either a 1-2-1-2-2 or 1-2-2-1-1 pattern. Justification for grouping these specimens under a single predominant pterygiophore pattern is that all patterns occurring in this species, with three exceptions (one specimen each with a 1-1-3-2-2, 1-3-1-2-2, and a 1-3-1-2-1 pattern), have two pterygiophores inserting into interneural space two and only a single pterygiophore inserting into at least one of the next three interneural spaces (3, 4, or 5). No other species (other than those with the 1-2-2-1-2 pattern) exhibit this particular arrangement of pterygiophores. Therefore, I consider all

Table 9. Frequency of occurrence for predominant ID patterns, variant patterns, and ID patterns unique to New World species, occurring in 53 species of *Symphurus* (data summarized for species with N > 5 individuals) grouped by common ID pattern (Abbreviations defined in text)

ID Pattern	Species (No)	Geographic location	Specimens with predominant pattern (%)		Specimens with variant patterns (%)		Specimens with New World patterns (%)	
			Range	Mean	Range	Mean	Range	Mean
1-2-2-1-2	4	IP, EA	56–95	78.2	0–28	16.0	0	0
1-2-2-2-2	8	IP, EA, WA	73–100	83.6	0–20	11.4	0	0
1-2-3-2-2	1	IP	69.6	—	20	—	0	—
1-3-2-2-2	12	EA, WA, EP	77–100	90.5	0–22	5.8	0–2	0.6
1-3-3-2-2	4	EA, WA, EP	69–90	79.0	9–26	17.2	6–24	14.7
1-3-4-2-2	1	EP	64	—	17	—	91	—
1-4-2-2-2	4	WA	40–100	82.0*	0–11	5.2	93–100	97.0
1-4-3-2-2	11	WA, EP	60–89	72.6	10–37	20.1	86–97	93.6
1-5-3-2-2	8	EP	37–80	60.0	4–37	15.4	98–100	99.5
Totals	53		37–100	77.8	0–37	13.1		

* 96.0% when *S. parvus* is excluded from the calculations.

patterns where two pterygiophores insert into interneural space 2, a single pterygiophore inserts into either interneural space 3, 4, or 5, and no more than two pterygiophores insert into the remaining spaces, to represent variations on a single pattern type. With this modification (Table 2), the fidelity in *S. vanmelleae* for ID patterns with these arrangements of pterygiophores is approximately 95% (62 of 65 specimens).

Symphurus vanmelleae was unusual in that none of the 65 specimens examined had variant ID patterns, but three specimens had anomalous patterns (1-1-3-2-2, 1-3-1-2-1, and 1-3-1-2-2, respectively). For other species with a 1-2-2-1-2 pattern, data are generally limited by small sample size, however, variant patterns were noted in several species. Two of seven *S. schultzi* specimens had a 1-2-2 ID pattern as did one of nine *S. gilesii* and one of seven *S. regani.*

Six of the seven species with a 1-2-2-1-2 ID pattern occur in the Indo-West Pacific region and *S. vanmelleae* occurs in the tropical eastern Atlantic Ocean (Fig. 5A). All seven species inhabit deep areas on the outer continental shelf and upper continental slope and are generally rare in collections. *Symphurus arabicus* is known only from the holotype captured along the south Arabian coast (21°50'N, 59°52'E, 1,046 m), while *S. macrophthalmus,* collected in the Gulf of Aden (13°14'24"N, 46°14'12"E, 457–549 m), and *S. fuscus,* from off the east coast of Africa (0°27'04"S, 42°47'30"E, 638 m), are known from only two specimens each. Likewise, limited material of *S. schultzi* (7), *S. gilesii* (9), and *S. regani* (7) could be located for inclusion in this study.

1-2-2 ID Pattern.—Sixteen species are characterized by the 1-2-2 ID pattern. For several of these species, the holotype (or a small type series) is the only specimen known. For others, such as *S. trifasciatus,* much more material exists in fish collections in India, but fewer than 10 specimens were available from collections outside India for inclusion in this study. In addition to the eight species listed below, holotypes of *S. maldivensis, S. marmoratus, S. sayademalhensis, S. variegatus, S. luzonensis, S. microrhynchus,* two specimens of *S. orientalis,* and 4/5 specimens of an unidentified species from New Guinea also have a 1-2-2 ID pattern. A paratype of *S. sayademalhensis* has a variant 1-2-3 ID pattern.

Of the species possessing this ID pattern, eight were abundant enough to detail intraspecific variation in ID pattern (Table 3). For these eight species, the mean value for the frequency of occurrence of the 1-2-2 ID pattern was approximately 84% (Table 9), with values for individual species ranging from 73% in *S. ligulatus* (27/37), 89% in *S. septemstriatus* (56/63), and 100% of the *S. trifasciatus* (6/6). In *S. woodmasoni, S. ocellatus, S. nebulosus,* and *S. australis* with values of 80, 80, 84, and 86%, respectively, the number of specimens per species possessing the 1-2-2 ID pattern was also relatively high.

For eight species, variant patterns averaged 11.4% per species for the group (Table 9), with individual values ranging from 0–20% (Table 3). Most frequently observed variant patterns were specimens with 1-2-2-1-2 and 1-2-3 patterns. Only a single specimen of the 318 specimens representing 16 species characterized by a 1-2-2 pattern had an ID pattern with more than two pterygiophores inserting into interneural space two (one *S. woodmasoni* with a 1-3-2 ID pattern). The lowest frequency of variant patterns occurred in *S. nebulosus* where only 1 of 23 specimens (4%) possessed a pattern (the 1-2-3 pattern) other than the 1-2-2 pattern. In *S. septemstriatus, S. ligulatus,* and *S. australis,* 8%, 11%, and 13%, respectively, of the individuals had variant patterns nearly equally divided between the 1-2-2-1-2 and 1-2-3 patterns. For other species with the 1-2-2 ID pattern, such as *S. woodmasoni* (14/83, 17%), *S. ocellatus* (3/15, 20%), and *S. strictus* (4/34, 12%),

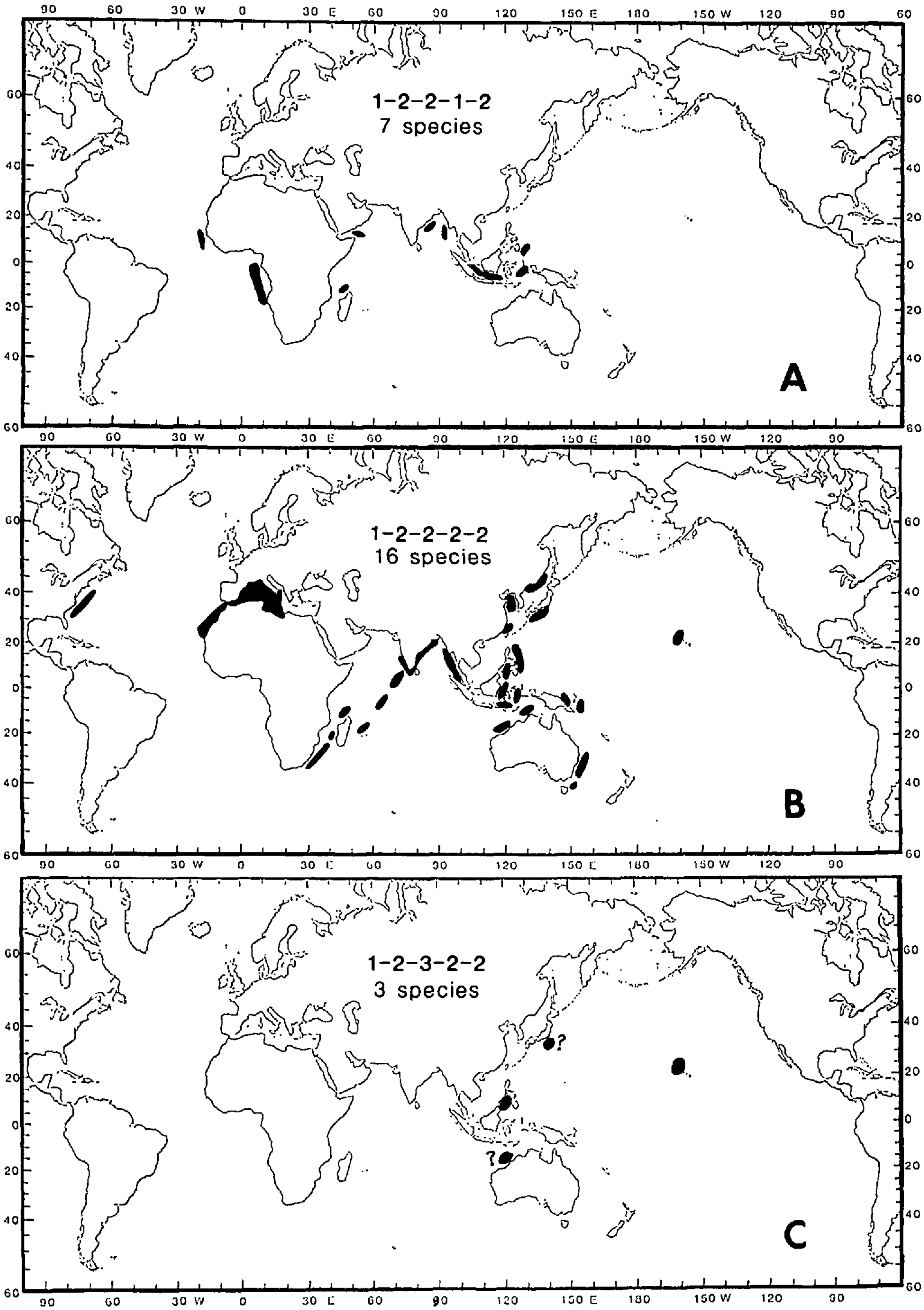

Figure 5. Geographic distribution of *Symphurus* species characterized by different ID patterns. A. 1-2-2-1-2 ID pattern (7 nominal species). B. 1-2-2-2-2 ID pattern (16 nominal species). C. 1-2-3-2-2 ID pattern (3 nominal species).

more individuals had the 1-2-2-1-2 ID pattern as the most frequently occurring variant pattern with fewer individuals possessing the 1-2-3 ID pattern.

Compared with species bearing other ID patterns, those *Symphurus* with a 1-2-2 predominant ID pattern have the most widespread geographic distribution of any group examined. Collectively, these species occur in all temperate and tropical oceans, with notable absences in the eastern Pacific and western South Atlantic (Fig. 5B), but most are found primarily in the Old World. All, except two, of the 16 nominal species possessing this ID pattern are deep-sea inhabitants. As a group, these species are generally rarely collected, undoubtedly because of their small size and great depth of occurrence. Most species with a 1-2-2 ID pattern have been collected only at a single, or several adjoining localities. Whether these distributions reflect actual restricted ranges for these species, or result merely from the lack of adequate sampling in appropriate habitats, is presently unknown.

Except for *S. ligulatus* and *S. nebulosus*, all others with the 1-2-2 pattern have been collected in the western and central Pacific and Indian oceans. Only one deepwater species (*S. strictus*) is known from the central Pacific (Hawaiian Islands), while 14 species occur in the western Pacific and Indian oceans. Collections of these species range from the Sea of Japan and Yellow Sea, off southern Japan, throughout the Philippine Archipelago to southern Australia, and throughout the Indian Ocean, ranging as far westward as South Africa.

1-2-3 ID Pattern.—This pattern is rare among symphurine tonguefishes, occurring in only three nominal species, *S. undatus, S. hondoensis,* and *S. holothuriae*. However, this pattern may be typical only for *S. undatus* (see discussion below). *Symphurus hondoensis,* described from a single specimen (Hubbs, 1915) and placed into the synonymy of *S. strictus* by Ochiai (1963), may not be a valid species. If *S. hondoensis* and *S. strictus* are conspecific, then the ID pattern observed in the holotype of *S. hondoensis* (1-2-3) is only an unusual variant from the more typical 1-2-2 pattern characteristic of *S. strictus*. This is plausible since in the present study 6% (2/34) of the *S. strictus* examined had a 1-2-3 pattern (Table 3).

Symphurus holothuriae is a small-sized species also of uncertain taxonomic status (Nielsen, 1961). This nominal species was described from a single specimen collected off Holothuria Bank, northwestern Australia (Chabanaud, 1948). The holotype of *S. holothuriae,* although possessing a 1-2-3 ID pattern, is otherwise quite unlike *S. undatus* (Table 10), differing in many characteristics including caudal-fin ray count (12 versus 14 in *S. undatus*), dorsal-fin rays (84 versus 99–102), anal-fin rays (70 versus 88-89), vertebral number (46 versus 54–55), hypural number (4 versus 5), and pigmentation (uniform pigmentation on ocular side versus marbled or freckled ocular surface). Except for differences in ID patterns (1-2-3 in *S. holothuriae* versus 1-2-2 in the others), *S. holothuriae* is otherwise morphologically similar to, and has comparable caudal-, dorsal-, and anal-fin ray counts and vertebral counts, to those of at least three other poorly-known Indo-Pacific species (*S. microrhynchus, S. trifasciatus,* and *S. luzonensis*). The hypothesis that the holotype of the nominal species, *S. holothuriae,* represents a variant specimen (with respect to ID pattern) of one of these other species characterized by a 1-2-2 pattern is presently under investigation as part of a general revision of Indo-Pacific symphurine tonguefishes (Munroe and Nizinski, in progress).

Symphurus undatus, therefore, appears to be the only species examined in the present study that is characterized by the 1-2-3 ID pattern. Of the *S. undatus* examined, 70% (16/23) possessed a 1-2-3 pattern; four others had anomalous patterns (two with a 1-2-4-2-2 pattern and one each with a 1-2-2-3-2 and a

1-3-2-3-2 ID pattern). Of three specimens (13%) with variant patterns, one had a 1-3-3 pattern and two had a 1-3-2 ID pattern.

All but one of the known specimens of *S. undatus* have been collected off Hawaii (Fig. 5C). A single specimen, mistakenly identified as a paratype of *S. marmoratus* by Fowler (1934) in his original description of that species (Chabanaud, 1955b), was collected in 1909 by the ALBATROSS near Tulayan Island, Philippines (6°06′48″N, 121°20′32″E). *Symphurus undatus* is only one of two species of *Symphurus* (*S. strictus* being the other) known to occur in the central Pacific near Hawaii.

1-3-2 ID Pattern.—Fifteen species are characterized by the 1-3-2 ID pattern. Of these, 12 species were available in sufficient sample sizes for detailed comparisons (Table 4). In addition to these 12 species, the holotype and only known specimens of *S. microlepis* and *S. diabolicus,* and holotype and paratype of *S. lubbocki,* also have a 1-3-2 ID pattern.

Frequency values for the predominant pattern in 12 species with sufficient sample size ranged from 77-100% (Table 9). Overall, the frequency of occurrence ($\bar{x}$ = 90.5%) for this pattern was one of the highest noted in any pattern group. For individual species, the frequencies of occurrence of specimens with this pattern ranged from values of 77% in *S. marginatus,* 94% in *Symphurus* species C and *S. pelicanus,* respectively, 97% in *S. piger,* and 100% in *S. rhytisma* and *S. reticulatus* (Table 4).

Variant patterns in species with the 1-3-2 ID pattern usually were among the lowest encountered in the study (Tables 4 and 9). Seven species, including *S. arawak, S. ginsburgi, S. nigrescens, S. pelicanus, S. pusillus, Symphurus* species C, and *S. piger,* never had variant patterns greater than 8% (Table 4). For *S. oligomerus* and *S. gorgonae,* variant patterns were 10 and 11%, respectively, while the highest level of variant patterns (22%) was observed in specimens of *S. marginatus.*

Variant patterns in species characterized by the 1-3-2 ID pattern were usually either a 1-3-3 (3.4% of the individuals examined) or 1-2-3 pattern (2.2%). Smaller numbers of specimens of several species were recorded with a 1-2-2 ID pattern (0–3% per species), and only six (four *S. oligomerus,* and a single specimen each of *S. ginsburgi* and *Symphurus* species C) of 951 specimens examined had a pattern (1-4-2) featuring more than three pterygiophores in the second interneural space (Table 4).

The geographic distribution of species possessing a 1-3-2 pattern is distinctively different and comparatively restricted when compared to that of the 1-2-2 species (compare Figs. 6A with 5B). Species with the 1-3-2 pattern occur in northern and southern hemispheres in both eastern and western portions of the Atlantic Ocean, as well as in the tropical eastern Pacific Ocean from the Gulf of California, along Central and South America, extending westward to the Galapagos Islands. The 1-3-2 ID predominant pattern is unknown from species of *Symphurus* inhabiting Indo-West Pacific localities.

Of 15 species with this pattern, 11 occur in the Atlantic, 3 in eastern Atlantic locations and 8 in western Atlantic waters. Four eastern Pacific species occur in relatively deep waters ranging from the Gulf of California to northern Peru (about 30°N to 10°S) and the Galapagos Islands.

1-3-3 ID Pattern.—Four species have a 1-3-3 ID pattern (Table 5). Overall, the fidelity for this predominant pattern was relatively high ($\bar{x}$ = 79.0%) in these species. For individual species, frequency values for the 1-3-3 pattern ranged from

Table 10. Meristic information for nominal species of *Symphurus* grouped by geographic location, interdigitation pattern, and caudal-fin ray count. Species marked with an asterisk (*) were unavailable to this study (data taken from the literature)

Species	Caudal-fin rays	Dorsal-fin rays	Anal-fin rays	Vertebrae		Hypurals	ID Pattern
				Abdominal	Total		
Eastern Pacific							
gorgonae	12	80–89	63–74	(3+6)	46–49	4	1-3-2-2-2
oligomerus	12	87-97	72–83	(3+6)	48–52	5	1-3-2-2-2
microlepis	12	106	92	(3+6)	57	5	1-3-2-2-2
diabolicus	12	109	94	(3+6)	58	5	1-3-2-2-2
atramentatus	12	89–98	75–82	(3+6)	49–53	4	1-3-3-2-2
varius	12	90–97	77–81	(3+6)	50–52	5	1-3-3-2-2
callopterus	12	105–114	91–98	(3+6)	57–61	4	1-3-4-2-2
fasciolaris	10	90–97	75–80	(3+6)	48–52	4	1-4-3-2-2
leei	12	93–104	78–88	(3+6)	51–56	4	1-4-3-2-2
melasmatotheca	11	90–98	74–80	(3+6)	49–52	4	1-5-3-2-2
undecimplerus	11	97–105	80–87	(3+6)	52–56	4	1-5-3-2-2
williamsi	12	89–95	73–79	(3+6)	47–51	4	1-5-3-2-2
atricaudus	12	94–102	77–83	(3+6)	50–53	4	1-5-3-2-2
melanurus	12	96–104	79–87	(3+6)	50–54	4	1-5-3-2-2
chabanaudi	12	98–109	82–92	(3+6)	52–57	4	1-5-3-2-2
elongatus	12	99–107	83–90	(3+6)	53–56	4	1-5-3-2-2
prolatinaris	12	103–110	86–93	(3+6)	54–58	4	1-5-3-2-2
Western Atlantic							
nebulosus	14	105–113	91–98	(3+6)	57–60	4–5	1-2-2-2-2
arawak	12	70–76	55–61	(3+6)	39–42	4	1-3-2-2-2
pelicanus	12	77–85	61–70	(3+6)	43–46	4	1-3-2-2-2
rhytisma	12	83–85	68–71	(3+6)	47–48	4	1-3-2-2-2
pusillus	12	83–88	71–75	(3+6)	47–49	4	1-3-2-2-2
ginsburgi	12	87–95	74–81	(3+6)	50–52	4	1-3-2-2-2
Species C	12	89–95	76–84	(3+6)	50–53	4	1-3-2-2-2
piger	12	80–88	68–74	(3+6)	45–49	5	1-3-2-2-2
marginatus	12	91–104	80–89	(3+6)	51–56	4–5	1-3-2-2-2
trewavasae	10	88–94	73–79	(3+6)	47–51	4	1-3-3-2-2
minor	10	69–81	55–64	(3+6)	41–44	4	1-4-2-2-2
ommaspilus	10	75–79	60–64	(3+6)	43–44	4	1-4-2-2-2
parvus	10	75–86	60–70	(3+6)	43–47	4	1-4-2-2-2
kyaropterygium	10	80–87	67–72	(3+6)	46–49	4	1-4-2-2-2
plagiusa	10	81–91	66–75	(3+6)	44–49	4	1-4-3-2-2
diomedeanus	10	86–96	69–80	(3+6)	47–50	4	1-4-3-2-2
jenynsi	10	107–115	91–99	(3+6)	57–60	4	1-4-3-2-2
urospilus	11	82–90	64–74	(3+6)	44–48	4	1-4-3-2-2
civitatium	12	86–93	70–78	(3+6)	46–50	4	1-4-3-2-2
caribbeanus	12	89–96	74–80	(3+6)	48–51	4	1-4-3-2-2
plagusia	12	89–98	73–81	(3+6)	47–51	4	1-4-3-2-2
tessellatus	12	91–102	74–86	(3+6)	48–54	4	1-4-3-2-2
oculellus	12	99–104	82–88	(3+6)	52–55	4	1-4-3-2-2
Indo-Pacific							
macrophthalmus	14	87	75	(3+6)	48	5	1-2-2-1-2
schultzi	14	85–88	72–75	(3+6)	48–50	5	1-2-2-1-2
fuscus	14	105	93	(3+6)	58	5	1-2-2-1-2
gilesii	14	95–99	79–84	(3+7)	53–54	5	1-2-2-1-2
arabicus	14	97	84	(3+7)	53	5	1-2-2-1-2
regani	14	103–105	89–91	(3+7)	56–58	5	1-2-2-1-2
microrhynchus	12?	87	73	(3+6)	48	4	1-2-2-2-2
trifasciatus	12	87–91	74–80	(3+6)	46–51	4	1-2-2-2-2
New Guinea sp.	12	88–92	75–78	(3+6)	48–50	4	1-2-2-2-2
septemstriatus	12	94–104	81–91	(3+6)	52–56	4	1-2-2-2-2
**fallax*	12	95	82	?	?	?	?

Table 10. Continued

Species	Caudal-fin rays	Dorsal-fin rays	Anal-fin rays	Vertebrae Abdominal	Vertebrae Total	Hypurals	ID Pattern
orientalis	12	96	82–83	(3+6)	53	4	1-2-2-2-2
luzonensis	12	99	85	(3+6)	53	4	1-2-2-2-2
**novemfasciatus*	12	100–101	88	?	?	?	?
woodmasoni	14	88–100	77–87	(3+6)	49–55	5	1-2-2-2-2
ocellatus	14	97–103	85–89	(3+6)	54–56	5	1-2-2-2-2
sayademalhensis	14	101	87	(3+6)	54	5	1-2-2-2-2
variegatus	14	104	91	(3+6)	56	5	1-2-2-2-2
strictus	14	109–121	95–108	(3+6)	59–65	5	1-2-2-2-2
australis	14	111–119	98–104	(3+6)	60–64	5	1-2-2-2-2
marmoratus	14	119	106	(3+6)	63	5	1-2-2-2-2
holothuriae	12	84	70	(3+6)	46	4	1-2-3-2-2
undatus	14	101–105	87–91	(3+6)	54–57	5	1-2-3-2-2
hondoensis	14	113	95	(3+7)	59	5	1-2-3-2-2
maldivensis	6+†	107	96	(3+6)	58	5	1-2-2-2-2
Eastern Atlantic							
vanmelleae	12	101–108	86–93	(3+7)	55–59	4–5	1-2-2-1-2
ligulatus	14	102–113	90–102	(3+6)	56–61	4–5	1-2-2-2-2
nigrescens	12	82–92	69–80	(3+6)	47–51	4	1-3-2-2-2
lubbocki	12	87–88	74	(3+6)	48–49	4	1-3-2-2-2
reticulatus	12	88–89	74–75	(3+6)	48–49	4	1-3-2-2-2
normani	12	87–92	71–77	(3+6)	48–50	4–5	1-3-3-2-2

† Probably 14 caudal-fin rays supported by the five hypurals.

69% in *S. trewavasae,* 74% in *S. varius,* 83% in *S. normani,* to 90% in *S. atramentatus* (Table 5).

Variant patterns in species with the 1-3-3 ID pattern (Table 5) ranged from approximately 8% in *S. atramentatus* to 26% in *S. trewavasae.* Unlike those species characterized by other patterns discussed earlier, variant patterns in species with the 1-3-3 predominant pattern usually featured patterns with three or more pterygiophores inserted into the second and third interneural spaces, such as the 1-4-2, 1-3-4, or 1-4-3 ID patterns. Variant patterns were infrequent with patterns featuring three or fewer pterygiophores inserted into the second interneural space. For example, none of the specimens examined had variant patterns with either the 1-2-2-1-2 or 1-2-2 ID patterns. One specimen of *S. normani* had a 1-2-3 ID pattern. Three of the species characterized by a 1-3-3 predominant ID pattern had specimens with variant 1-3-2 patterns (representing only 1 to 3 individuals per species).

The highest levels of variant patterns occurred in *S. trewavasae* and *S. varius,* where 26% (15/58) and 22% (11/49), respectively, of the specimens examined had either a 1-4-2 or 1-4-3 ID pattern (Table 5). Frequencies of variant patterns observed in *S. atramentatus* and *S. normani* were somewhat lower (ca. 9 and 12%, respectively), with no more than 5% of the specimens (eight specimens of *S. atramentatus* with a 1-3-4 ID pattern) overlapping with any one other pattern.

Species with a 1-3-3 ID pattern (Fig. 6B) occur on both sides of the Atlantic Ocean (north and south of the equator) and in the eastern Pacific from the Gulf of California to northern Peru, including the Galapagos Islands. This distribution is similar to that observed for species with a 1-3-2 ID pattern. *Symphurus atramentatus* and *S. varius* occur in the tropical eastern Pacific, including the Galapagos Islands; *S. trewavasae* occurs in the South Atlantic along the coast of temperate Brazil; and *S. normani* inhabits inner continental shelf waters in the eastern

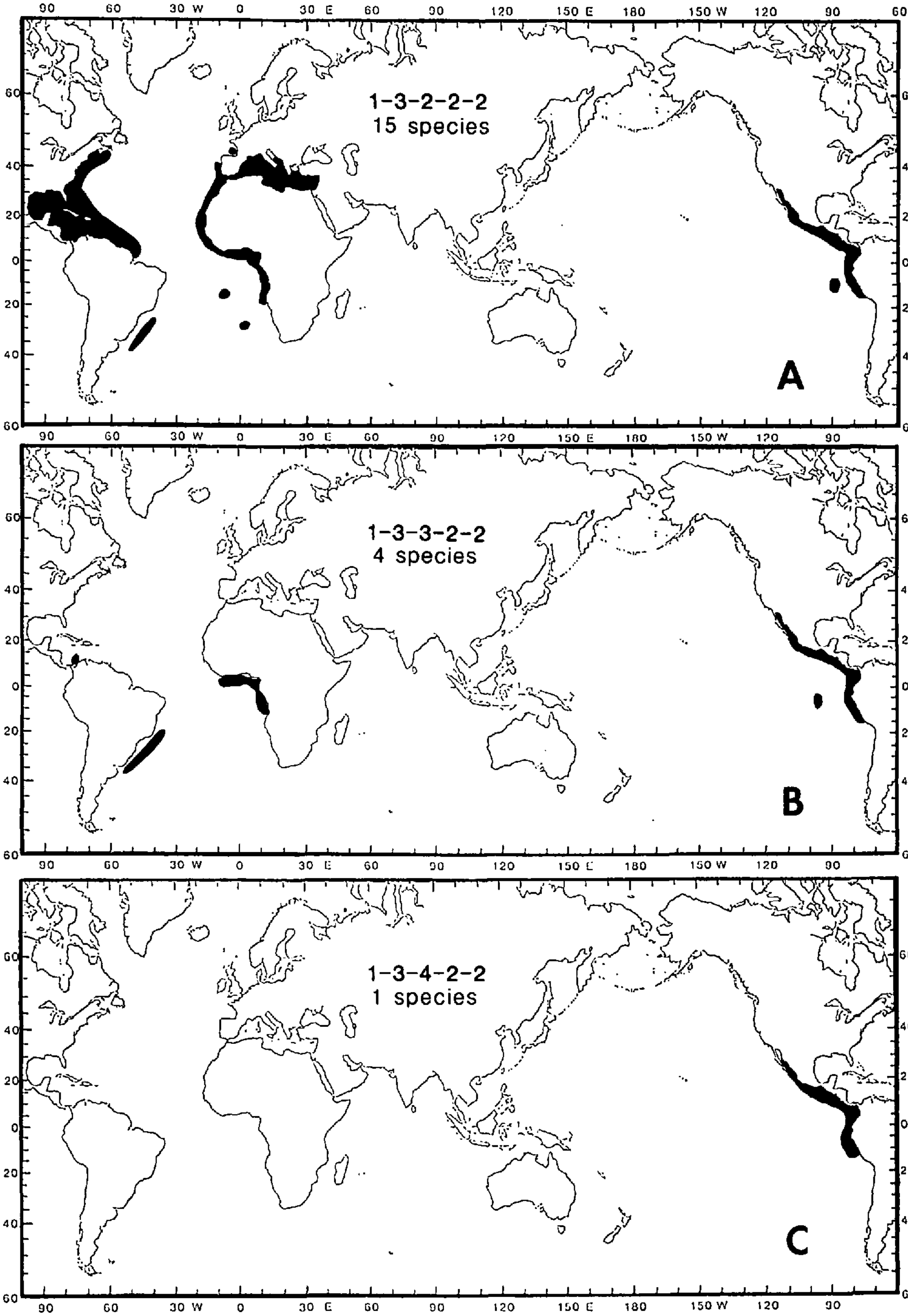

Figure 6. Geographic distribution of *Symphurus* species characterized by different ID patterns. A. 1-3-2-2-2 ID pattern (15 species). B. 1-3-3-2-2 ID pattern (4 species). C. Distribution of *S. callopterus* characterized by the 1-3-4-2-2 ID pattern.

Atlantic off tropical west Africa. No species possessing this pattern are known from Indo-West Pacific locations.

1-3-4 ID Pattern.—This pattern is extremely rare in the genus, apparently limited to a single species, *S. callopterus* (Table 6). A total of 64% of 191 specimens of *S. callopterus* had this arrangement of pterygiophores.

Seventeen percent of the *S. callopterus* examined had variant patterns (Table 7). Of these, 14% had a 1-4-3 pattern, while 3% had a 1-3-3 ID pattern. Additionally, a small number of specimens (5%) had a 1-4-4 secondary ID pattern.

The rarity of the 1-3-4 pterygiophore arrangement in the genus is further evidenced by the fact that it was rarely observed as a variant pattern in species characterized by other ID patterns (compare Tables 2–8). For example, no specimens of species characterized by 1-2-2-1-2, 1-2-2, 1-2-3, and 1-3-2 ID patterns had a 1-3-4 ID pattern. In three of four species with a 1-3-3 ID pattern, specimens with a 1-3-4 variant pattern ranged from 3% in *S. normani* (1/35) and *S. trewavasae* (2/58), to 5% (8/152) in *S. atramentatus*. Even among species of *Symphurus* with 1-4-2, 1-4-3, or 1-5-3 patterns (Tables 6–8), there was little overlap with the 1-3-4 pterygiophore arrangement. No individuals of the four species with a 1-4-2 ID pattern, for example, had this pattern (Table 6). Although a few specimens of each of the 11 species characterized by a 1-4-3 predominant ID pattern had variant 1-3-4 ID patterns, the frequency was never very large, ranging from <1% in *S. plagiusa* to 7% in *S. leei* and *S. tessellatus*. Additionally, only one *S. williamsi*, of 714 specimens representing eight species that are characterized by the 1-5-3 ID pattern (Table 8) and that occur sympatrically with *S. callopterus*, had a variant 1-3-4 ID pattern.

Symphurus callopterus ranges throughout the tropical eastern Pacific (Fig. 6C) from Mazatlan and southern Baja California, Mexico, to northern Peru (10°36′S).

1-4-2 ID Pattern.—Four species, including *S. parvus* (discussed below), are characterized by the 1-4-2 ID pattern (Table 6). The frequency of occurrence of this pattern (Table 9) was quite high in these species ($\bar{x}$ = 96.0 excluding *S. parvus*; overall $\bar{x}$ = 82.0% including *S. parvus*). Frequency values of the 1-4-2 ID pattern for the individual species ranged from 40% in *S. parvus*, to 93% in *S. kyaropterygium*, 95% in *S. minor*, and 100% in *S. ommaspilus* (Table 6).

Three of the four species possessing this pattern had few or no variant patterns (Table 6), and overall, the fidelity (96%) for the predominant ID pattern in these three species was among the highest observed in the study (Table 9). Little intraspecific variation in ID pattern was evident for *S. minor* with 74/78 (95%) individuals possessing a 1-4-2 ID pattern. In *S. kyaropterygium*, 13 of 14 specimens had a 1-4-2 ID pattern, while all specimens (N = 28) of *S. ommaspilus* had this pattern. Overall, variant patterns, when present in these species (Table 6), were primarily the 1-4-3 pattern (10% of *S. parvus*) and less frequently the 1-3-2 pattern (3% of the *S. minor* and 1% of *S. parvus*).

The most unusual frequencies of pterygiophore patterns in this group of species were found in *S. parvus* where two patterns occurred with almost equal frequencies in the specimens examined (Table 6). Thirty-three of 82 (40%) specimens had a 1-4-2 pattern, while 35/82 (43%) had a 1-5-2 pattern. No correlations between geography, sex, or size and the observed bimodal distribution of pattern types in this species were found. This species is included in the 1-4-2 ID pattern group since it shares a combination of characters with the other species of the group that are found nowhere else in the genus (Munroe, 1987). *Symphurus parvus* is one of only three species studied in which two ID patterns occurred in nearly equal frequencies in the specimens.

Species with a 1-4-2 ID pattern have one of the most restricted geographic distributions of any pattern group studied. Species characterized by this pattern occur entirely in the western Atlantic (Fig. 7A) ranging from the inner continental shelf off Nova Scotia (a few expatriated individuals of *S. minor*), off the southeastern coast of the United States south of Cape Hatteras, throughout the Gulf of Mexico and Caribbean to Trinidad, south to about Rio Grande do Sul, Brazil. *Symphurus minor* occasionally ranges north of Cape Hatteras to Long Island and the Scotian shelf (Ginsburg, 1951; Markle et al., 1980), but this species and *S. parvus* more commonly occur from Cape Hatteras, North Carolina, southward along eastern Florida, and into the Gulf of Mexico. *Symphurus minor* extends into the Gulf only as far westward as the region near DeSoto Canyon (Munroe, 1987). The range of *S. parvus* encompasses the entire Gulf of Mexico and the Caribbean Sea southward and eastward to Trinidad. *Symphurus kyaropterygium* is the only species with a 1-4-2 pattern found outside the western North Atlantic. This species occurs on the inner continental shelf along southern Brazil from Baia da Ilha Grande, Rio de Janeiro (23°S) to about Rio Grande do Sul (31°S) (Menezes and Benvegnú, 1976). The fourth species, *S. ommaspilus*, is a widespread Caribbean species recorded from the Bahamas, Puerto Rico, the Virgin Islands, and Glovers Reef in Belize. *Symphurus ommaspilus*, unlike the other species with a 1-4-2 ID pattern, is found in shallow-water sandy habitats adjacent to coral reefs.

1-4-3 ID Pattern.—Eleven species are characterized by the 1-4-3 ID pattern (Table 7). Overall, the fidelity of this pattern was generally high ($\bar{x}$ = 72.6%), with values for individual species ranging from 60% in *S. plagiusa* and 62% in *S. leei*, to 82% and 89% in *S. caribbeanus* and *S. oculellus*, respectively.

Among species characterized by the 1-4-3 predominant pattern, individuals with variant patterns usually had the 1-3-3, 1-4-2, and 1-3-4 patterns, with the 1-5-3 ID pattern occurring less frequently. There were no specimens among these species with 1-2-2-1-2, 1-2-2, 1-2-3, or 1-3-2 patterns. No single variant pattern occurred consistently with the highest frequency among all of the species with the 1-4-3 predominant pattern. For two species (*S. caribbeanus* and *S. plagusia*), their most common (10% of the specimens of each species) variant pattern was the 1-3-3 ID pattern, while for *S. plagiusa* and *S. fasciolaris*, this variant pattern was the second most frequent of the variant patterns observed in these species. Five species (*S. plagiusa, S. civitatium, S. diomedeanus, S. urospilus,* and *S. fasciolaris*) had the 1-4-2 ID pattern as their most frequent variant pattern (6–18%).

Symphurus leei, among species with the 1-4-3 ID pattern, was the most unusual with respect to the total number, variety, and occurrence of secondary ID patterns in the specimens. The majority of individuals (122/198) of this species had a 1-4-3 ID pattern; however, the fidelity (62%) for this predominant pattern was among the lowest of the 11 species characterized by this pattern. The range of ID patterns varied more among specimens of *S. leei* than for any other species with this pattern with no less than 17 different ID patterns occurring among individuals of this species (Table 7). Variant patterns in this species were also different from those observed for most other species characterized by the 1-4-3 ID pattern. In *S. leei*, the most frequent variant pattern (7%) was the 1-3-4 pattern, while the 1-5-3 pattern was the next most frequently occurring variant pattern (6% of the individuals). Other variant patterns occurred in fewer than 2% of the *S. leei* examined (Table 7).

Particularly interesting among species characterized by a 1-4-3 pattern is the generally low frequency of occurrence (0–8%, $\bar{x}$ = 4.0%) of specimens with a variant 1-5-3 pattern (Table 7). Six of 11 species had less than 5% of the specimens

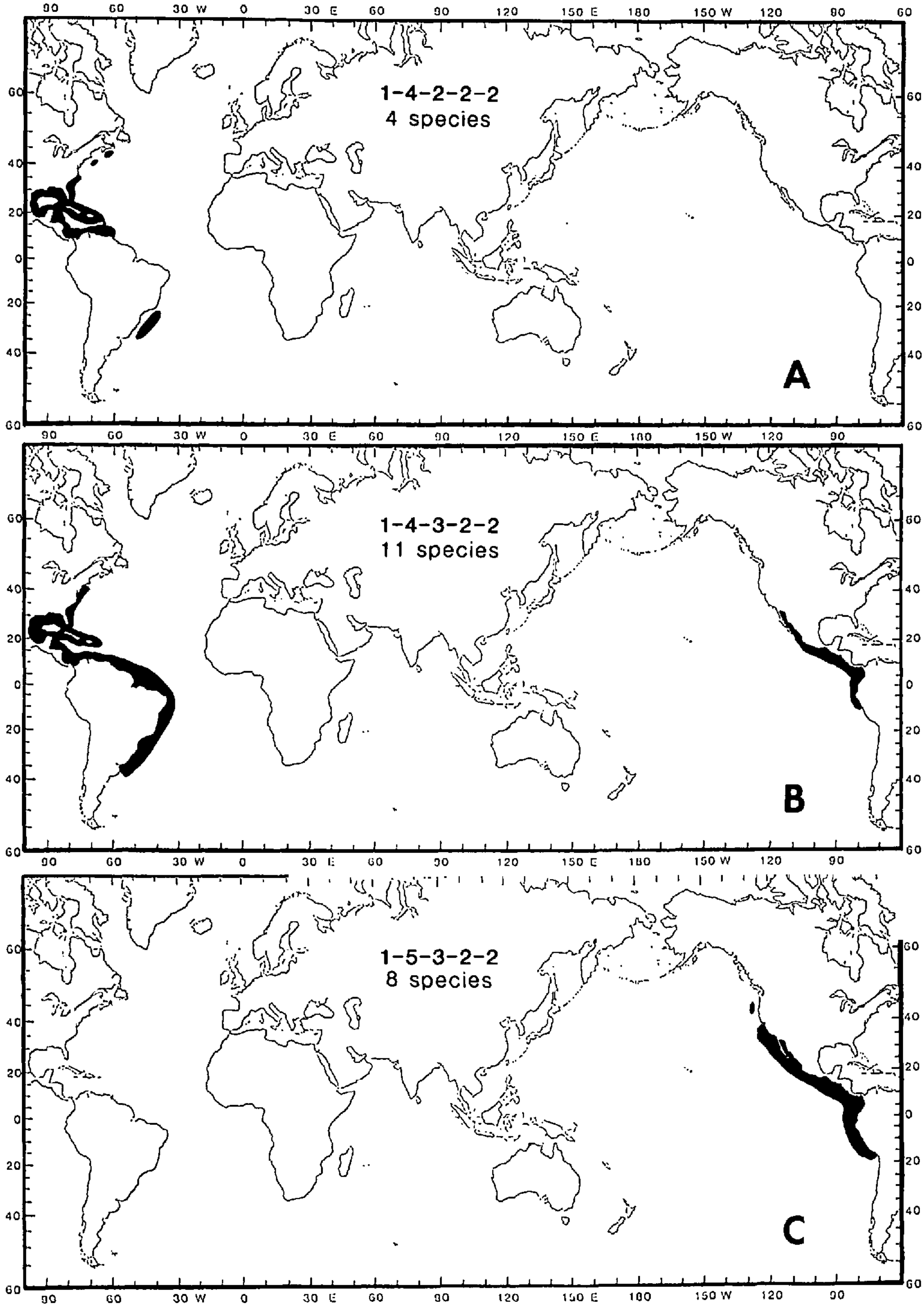

Figure 7. Geographic distribution of *Symphurus* species characterized by different ID patterns. A. 1-4-2-2-2 ID pattern (4 species). B. 1-4-3-2-2 ID pattern (11 species). C. 1-5-3-2-2 ID pattern (8 species).

with a 1-5-3 ID pattern. None of the 83 *S. caribbeanus* and only 1/136 *S. plagiusa* had a 1-5-3 pattern, while just over 7% of the *S. fasciolaris* and *S. jenynsi* had a 1-5-3 ID pattern. This contrasts with the situation found in species characterized by a 1-5-3 predominant pattern (see below) where the frequency of occurrence of specimens with a variant 1-4-3 ID pattern ranged from 5-36% ($\bar{x}$ = 15.1%; see Table 8).

Species characterized by a predominant 1-4-3 ID pattern had from 0–15% ($\bar{x}$ = 5.4% per species) of the individuals possessing secondary patterns. Most frequently occurring of these secondary patterns in five of the species was the 1-5-2 pattern. Of these five, *S. urospilus* was distinctive in that 14% of the specimens examined had this secondary pattern (Table 7). For two others (*S. jenynsi* and *S. caribbeanus*), the number of specimens with secondary patterns was equally divided between the 1-5-2 and 1-4-2 patterns. Of the 11 species with a predominant 1-4-3 pattern, *S. leei* (11%) and *S. tessellatus* (5%) had distinctly more individuals with the 1-4-4 secondary pattern than with the 1-5-2 secondary pattern (2 and 0.9%, respectively).

Species with the 1-4-3 ID pattern occur primarily in coastal habitats of the New World (Fig. 7B). Nine of 11 species with this ID pattern are found in the western Atlantic Ocean ranging from approximately 45°N–35°S. A single species (*S. plagiusa*) ranges north of Cape Hatteras along the eastern coast of the United States; four species (*S. plagiusa, S. diomedeanus, S. urospilus,* and *S. civitatium*) occur in the Gulf of Mexico; five species (*S. plagusia, S. diomedeanus, S. carribeanus, S. oculellus,* and *S. tessellatus*) occur in the Caribbean Sea; and four species (*S. plagusia, S. diomedeanus, S. tessellatus,* and *S. jenynsi*) extend to southern Brazil, with *S. jenynsi* ranging somewhat further south to northern Argentina (Menezes and Benvegnú, 1976). The remaining two species, *S. fasciolaris* and *S. leei,* occur in the eastern Pacific from the Gulf of California to northern Peru (ca. 32°N–15°S).

1-5-3 ID Pattern.—Eight species are characterized by this predominant ID pattern (Table 8). As a group, fidelity of the predominant pattern is the lowest observed (60%) for any pattern group (Table 9). Frequency values for individual species with the 1-5-3 ID pattern ranged from 37% and 42% in *S. undecimplerus* and *S. williamsi* (which represent the lowest frequencies of a predominant pattern for any species examined in the study); to 53% in *S. atricaudus*; 72% in *S. elongatus*; and 80% in *S. prolatinaris.* The much lower occurrence of a predominant pattern in five of the eight species with the 1-5-3 ID pattern results from the greater frequency of occurrence of secondary patterns in these species. These secondary patterns usually featured four or more pterygiophores inserting into the second interneural space and three or more pterygiophores in the third interneural space. In addition, *S. williamsi* was unique among those with a 1-5-3 pattern in that nearly as many specimens (36%) had a 1-4-3 ID pattern as had the 1-5-3 pattern (43%). *Symphurus undecimplerus* also differed from other species with a 1-5-3 ID pattern in that nearly 21% of the specimens examined had either 1-4-4 or 1-5-4 ID patterns, which are secondary patterns rarely appearing in other symphurine tonguefishes. However, even when frequency of occurrence of a predominant pattern is estimated for species with the 1-5-3 pattern exclusive of *S. williamsi* and *S. undecimplerus,* the mean value ($\bar{x}$ = 67.0%) for the predominant pattern is still the lowest observed for species with other predominant ID patterns.

Although the predominant ID pattern occurs with much less frequency in species characterized by the 1-5-3 ID pattern than noted for species with other predominant patterns (Table 8), it should be emphasized that most intraspecific variation in species characterized by the 1-5-3 pattern occurs as variants with patterns found only in other New World species (those with 1-3-4, 1-4-3, and 1-5-3 patterns). The same is also true for species possessing the 1-4-3 ID pattern (Tables 7–8).

Variant patterns for species with a 1-5-3 ID pattern were almost exclusively the 1-4-3 pattern ($\bar{x}$ = 15.4% for eight species combined). Frequency of the 1-4-3 variant pattern ranged from 4% in *S. prolatinaris,* to 21% in *S. melasmatotheca,* 24% in *S. chabanaudi,* and 36% in *S. williamsi* (which was among the highest variant values observed for any species in the study; Tables 2–8). No specimens of species with a 1-5-3 ID pattern had 1-2-2-1-2, 1-2-2, 1-2-3, 1-3-2, or 1-3-3 variant patterns, and only a single specimen of *S. williamsi* and one *S. chabanaudi* were found with a 1-3-4 or 1-4-2 variant pattern, respectively.

Occurring considerably less frequently among species with the predominant 1-5-3 ID pattern were specimens with the following secondary patterns: 1-4-4, 1-5-2, 1-5-4, 1-6-3, and 1-6-2 patterns. Among the eight species with a 1-5-3 pattern, specimens with a secondary 1-4-4 pattern ranged in frequency from <1% (*S. prolatinaris*) to 11% and 21% in *S. chabanaudi* and *S. undecimplerus,* respectively. The highest occurrences of specimens with the 1-5-2 secondary pattern were for *S. atricaudus* (16%) and *S. melasmatotheca* (8%). Fewer specimens per species were found with the 1-5-4 secondary pattern ($\bar{x}$ = 4.2% for eight species), the 1-6-3 secondary pattern ($\bar{x}$ = 3.6% for eight species), and the 1-6-2 secondary pattern ($\bar{x}$ < 1%, and occurring in only two species). Exceptional to this was *S. undecimplerus,* in which 21% of the specimens possessed the 1-5-4 secondary pattern. It is noteworthy that only in species (seven of the eight) characterized by the 1-5-3 predominant pattern were specimens found with six pterygiophores inserted into the second interneural space. Even among these species, however, the frequency of specimens with six pterygiophores in the second interneural space was generally low ($\bar{x}$ = 4.3%; range 0–11%) with the highest frequencies registered in *S. prolatinaris* and *S. elongatus* (8 and 11%, respectively).

Species with a 1-5-3 ID pattern occur entirely in coastal seas of the eastern Pacific from about 44°N–20°S (Fig. 7C) and have one of the most restricted geographic distributions compared with species possessing other predominant patterns. Seven species have largely sympatric distributions encompassing shallow water habitats from the Gulf of California to northern Peru. *Symphurus atricaudus* occurs northward from the Gulf of California, coastally along the Baja Peninsula and southern California, occasionally ranging into waters off northern California and southern Oregon (Krygier et al., 1973).

Discussion

This study describes the types of intra- and interspecific variation encountered when examining interdigitation patterns of dorsal pterygiophores and neural spines in cynoglossid tonguefishes of the genus *Symphurus.* The present study expands upon an earlier study by Munroe (1987) and represents the first detailed reports on the occurrence of ID patterns in *Symphurus* or for any other cynoglossid fishes. Interdigitation patterns of dorsal-fin pterygiophores and neural spines have previously been shown to be important in distinguishing scombrid fishes (Matsui, 1967; Potthoff, 1974, 1975), temperate basses (*Morone* species; Fritzsche and Johnson, 1980; Olney et al., 1983; but not hybrids of these species, see Harrell and Dean, 1987) and gobioid fishes (Birdsong, 1975; Akihito et al., 1984; Birdsong et al., 1988). More recently, Chapleau (1989) discussed the arrangement of supracranial dorsal-fin pterygiophores in 96 specimens representing 41 species in 26 genera of soleid fishes.

Among 69 nominal species of *Symphurus* examined, nine different predominant interdigitation patterns were discovered. A smaller number of secondary patterns were also noted, occurring almost exclusively in New World species with 1-4-3 and 1-5-3 predominant ID patterns. On average, approximately 78% of the individuals of a species shared a predominant ID pattern (Table 9). The frequency of occurrence for a predominant pattern was highest in species with a 1-3-2 pattern, averaging ca. 90% for 12 species. Frequency values for the predominant pattern were also high in species with 1-2-2-1-2 (78.2%), 1-2-2 (83.6%), and 1-4-2 (82.0%) ID patterns. Approximately 79% of the specimens of species possessing a 1-3-3 ID pattern shared this pattern, while an average of 72.6% of the individuals of species characterized by a 1-4-3 pattern had the same predominant pattern. For *S. undatus* and *S. callopterus,* the only species characterized by 1-2-3 and 1-3-4 ID patterns, respectively, 69% and 64% of the specimens shared the predominant pattern characteristic for that species.

Of all the species studied, those characterized by a 1-5-3 ID pattern had the lowest occurrence (60.0%) of a predominant pattern for any group studied. Correspondingly, in these species intraspecific variation in ID pattern was generally greater when compared with other species characterized by predominant patterns featuring less than four pterygiophores in interneural space two.

New World species, i.e., those with 1-3-4, 1-4-2, 1-4-3, or 1-5-3 patterns, also differed distinctly from species characterized by other patterns. Although characterized by a predominant ID pattern, these species usually had a small proportion of specimens featuring secondary ID patterns. These secondary patterns were unique to species with ID patterns featuring three or more pterygiophores inserted into interneural spaces two and three, and rarely, if ever, occurred in species characterized by 1-2-2-1-2, 1-2-2, 1-2-3, and 1-3-2 ID patterns (Tables 2–5).

The species of *Symphurus* also differed with respect to the levels and types of intraspecific variation occurring in ID patterns. Anomalous ID patterns, providing little or no useful information for identification, preclude the usefulness of this character in identifications of less than 5% of the specimens per species. The frequency of variant patterns ranged from approximately 0–37% in the specimens per species. Although variant patterns represent variation from the predominant pattern recorded for each species, they nevertheless provide useful information for identification purposes because, unlike anomalous variation, the range of variant patterns encountered in a species is predictable and mostly non-overlapping, especially for species with different predominant ID patterns (compare Tables 2–8). This predictability in variation considerably narrows the range of possibilities necessary for comparison, at least in preliminary stages of identification.

Species of *Symphurus* possessing the 1-5-3 and 1-4-3 predominant patterns were similar to each other, but differed from other species with respect to the type of intraspecific variation occurring in their ID patterns. Species possessing 1-5-3 and 1-4-3 predominant patterns were generally similar in that they overlapped to a large extent with respect to their variant patterns and species with both of these predominant patterns featured individuals with secondary ID patterns (1-4-4, 1-5-2, and others), which were found almost exclusively in these species. The relatively frequent occurrence of variant and secondary patterns lowered the frequency of occurrence for the predominant pattern in these species. For example, less than 80% of the individuals of 9/11 species possessing the 1-4-3 pattern and seven of eight species with the 1-5-3 pattern had the predominant pattern. The low frequencies for a predominant pattern in species with the 1-4-3 pattern, and particularly those with the 1-5-3 pattern, might raise questions concerning the value of ID patterns as a diagnostic character for these species. However, when combinations of uniquely-occurring patterns (predominant, variant, and secondary patterns) in these New World species are considered (Tables 7–8), the frequency of patterns diagnostic for these species is more apparent. For example, in 11 species with the 1-4-3 ID pattern, the frequency of the predominant pattern averaged 72.6%, whereas the combined total for individuals with uniquely-occurring New World ID patterns (the predominant pattern, the 1-5-3 variant pattern, and secondary patterns) averaged 93.6%. For individual species characterized by the 1-4-3 predominant pattern, frequency values for these combined data ranged from 86 (*S. plagiusa*) to 97% (four species). These combined frequencies compare with frequency values for the 1-4-3 pattern alone of 60–89% for the individual species.

For species characterized by the 1-5-3 pattern, the frequency of occurrence for the combination of uniquely-occurring New World patterns is substantially greater than for the predominant pattern. For eight species with the 1-5-3 pattern, the predominant pattern averaged only 60.0% (range 37–80%) in occurrence. In contrast, the average value for combined pattern data is 99.5%, with combined values for individual species ranging from 98% in *S. williamsi* to 100% in five species.

Based on this information, it is evident that when compared with most other species, individuals of species characterized by 1-4-3 and 1-5-3 patterns have a lower percentage of the predominant ID pattern typical for that species. However, combined frequencies for uniquely-occurring predominant and secondary New World patterns (86–100%) are comparable to those values observed for species characterized by other predominant ID patterns. Admittedly, the predominant pattern occurs less frequently and there is more intraspecific variation in species characterized by 1-4-3 and 1-5-3 ID patterns than noted in congeners with other ID patterns. However, these species, nonetheless, have distinctly different pterygiophore arrangements from those occurring in congeners and the combinations of uniquely-occurring patterns are useful in identification of these specimens.

Overall, how good is interdigitation pattern as a diagnostic character when compared with more traditional characters used to identify symphurine tonguefishes? Like other meristic characters examined in these fishes, interdigitation pattern, except in rare instances, when used as a single diagnostic character will not allow for identification of an individual specimen to the species level. When ID patterns are used as a single diagnostic character the 69 species for which information is available can be sorted into nine groups, with the largest containing only 16 species, which is only slightly more than one-third that attained when caudal-fin ray counts alone were used (41 species in the largest group) and less than one-half as many resulting from using dorsal-fin ray counts (34 of 69 species have overlapping counts). Identification of the species, therefore, is improved when ID patterns are used compared with using only caudal- or dorsal-fin ray counts.

The best resolution of the species is attained when ID pattern information is used in combination with fin-ray counts (Table 10). Including this character with more traditional counts of caudal- or dorsal-fin rays immediately eliminates certain species and even groups of species from consideration because neither their predominant ID patterns nor their range of variant patterns overlap those of the specimen being identified. Inclusion of ID patterns in a suite of diagnostic characters quickly reduces the range of possible species with which a specimen need be compared. Using combined information from ID pattern and caudal-fin ray counts, the 69 species sort into 16 groups, the two largest still containing 15 and 10 species, but with all others having six or fewer species. Including ID pattern information with caudal- and dorsal-fin ray counts greatly reduces the number of possible comparisons required in the identification of a specimen than was possible previously based on fin-ray counts alone. Therefore, ID pattern, when used in combination with either caudal- or dorsal-fin ray counts, greatly facilitates the identification of symphurine tonguefishes compared to using either caudal- or dorsal-fin ray counts alone or in combination.

Since species of *Symphurus* characterized by different predominant ID patterns have sympatric distributions (within the broad geographic areas outlined in Fig. 4) and not all species of *Symphurus* overlap in geographic distribution, identification of specimens is further facilitated when the species are compared on a geographic basis (Table 10). Seventeen nominal species occur in the eastern Pacific, 14 of which overlap in caudal- or dorsal-fin ray counts. However, when ID pattern is examined together with caudal-fin ray counts, much less overlap among these species is evident, and the species can be identified much more easily. For example, four species have a 1-3-2 ID pattern and 12 caudal-fin rays; two have a 1-3-3 pattern and 12 caudal-fin rays; one species is characterized by a 1-3-4 pattern and 12 caudal-fin rays; two species, one with 10 and the other with 12 caudal-fin rays, possess the 1-4-3 pattern; and eight species, two with 11 and six with 12 caudal-fin rays, have the 1-5-3 pattern.

Western Atlantic *Symphurus,* although somewhat more variable with respect to caudal-fin ray counts than their eastern Pacific counterparts, also have a large overlap in dorsal-fin ray counts. In this region, eight species have 10 caudal-fin rays; one has 11 finrays; 13 species have 12 caudal-fin rays; and one species possesses 14 caudal-fin rays. However, when ID patterns are used in combination with caudal-fin ray counts these species are more readily identified. Of the eight species possessing 10 caudal-fin rays, four are characterized by a 1-4-2 ID pattern, three have a 1-4-3 pattern, and one species has a 1-3-3 pattern. For 13 species with 12 caudal-fin rays, eight are characterized by the 1-3-2 ID pattern and five species possess the 1-4-3 pattern.

Caudal-fin ray counts are less variable among the species of *Symphurus* inhabiting the Indo-Pacific region. Sixteen of 24 nominal species have 14 caudal-fin rays, while 10 species have 12 caudal-fin rays. When ID pattern information is combined with caudal-fin ray counts, the species sort into five groups. Six species share a combination of 14 caudal-fin rays and a 1-2-2-1-2 ID pattern; eight nominal species plus an unidentified form possess 14 caudal-fin rays and a 1-2-2 ID pattern; two nominal species have 14 caudal-fin rays and a 1-2-3 pattern; seven nominal species plus one unidentified form have 12 caudal-fin rays and a 1-2-2 ID pattern; and one nominal species has 12 caudal-fin rays and a 1-2-3 ID pattern.

Among eastern Atlantic *Symphurus,* identifications are also greatly facilitated by combining ID pattern information with other meristic features (Table 10). Six species occur in the eastern Atlantic, St. Helena, and Ascension Island (Munroe, 1990a). Although only two different caudal-fin ray counts (12 and 14) are represented in the six species, four different predominant ID patterns are evident among these species. *Symphurus vanmelleae, S. ligulatus,* and *S. normani* feature ID patterns not found in other sympatric species, while the remaining three species possess the 1-3-2 ID pattern.

Interdigitation patterns as a sorting and diagnostic character may prove to be just as important, if not more so, for identifying early life history stages as it is in identifying adult specimens of *Symphurus.* Olney and Grant (1976) and Matarese et al. (1989) noted that in larval *S. plagiusa* and *S. atricaudus* the anterior dorsal-fin rays first develop in larvae ranging from about 3–6 mm notochord length, followed by fin-ray development in the other fins. If this sequence of fin development exists for other species of *Symphurus,* then the appearance and patterns of dorsal-fin pterygiophores should prove informative in identification of early life history stages of members of this genus. Nomenclatural confusion and lack of adequate diagnostic characters for adult *Symphurus* have also hampered efforts in identifying early life history stages of members of this taxon. Despite the fact that larval stages of *Symphurus* were first described over 100 years ago (Cocco, 1844; Raffaele, 1888) and their larvae are expected to be abundant in ichthyoplankton collections, especially in the western Atlantic and eastern Pacific where a large number of species occur, very few ontogenetic series have been described to date. Of 71 nominal species listed in Table 1, for example, larval stages have been adequately described for only four, all of which occur in geographic or ecological regions containing an extremely low diversity of symphurine tonguefishes. Thus far, ontogenetic series have been described for the two species (*S. nigrescens* and *S. ligulatus*) occurring in the Mediterranean Sea (Cocco, 1844; Raffaele, 1888; Kyle, 1913; Padoa, 1956); for *S. atricaudus* (Matarese et al., 1989), the only species occurring in southern Californian waters (Mahadeva, 1956; Eschmeyer et al., 1983); and *S. plagiusa,* the only species occurring within estuarine waters of Chesapeake Bay (Olney and Grant, 1976; Munroe, 1987).

As is the case with adult stages of *Symphurus,* ID pattern alone will not allow identification of larvae to the species level. Nonetheless, utilizing this character will reduce the number of species necessary for consideration in the identification process. Facilitating identification of larval stages of *Symphurus* is especially important particularly in areas with large numbers of species, such as the Indo-West Pacific and warm-temperate and tropical regions of the western Atlantic and eastern Pacific, where approximately 77% of the described species are known to occur. Although these regions contain the majority of described species, the species inhabiting these areas exhibit variety in their ID patterns, which may facilitate identifications of early life history stages. For example, three different predominant patterns are represented among the 24 nominal species occurring in the Indo-Pacific (Table 11), while six different predominant patterns occur in the 40 species known to inhabit warm temperate and tropical regions in the New World.

Geographic distributions of species with similar ID patterns were plotted revealing some interesting zoogeographical distributions (Figs. 5–7). Distinctly different geographic distributions were apparent for species possessing different ID patterns. Only three (1-2-2-1-2, 1-2-2, and 1-2-3 ID patterns) of nine predominant pattern types identified in this study are represented in species occurring in the Indo-West Pacific region (Fig. 5). The 1-2-2-1-2 ID pattern is found only in six species occurring in western Pacific and Indian Ocean locations and in *S. vanmelleae,* which occurs in the tropical eastern Atlantic ocean. The majority (14/16) of species with a 1-2-2 pattern are also found only in Indo-West Pacific localities, ranging from Hawaii to South Africa. Only two species with this pattern occur beyond this region (continental slopes on opposite sides of the North Atlantic including the Mediterranean). Thus far, no species with the 1-2-2 pattern are known to occur in either the western South Atlantic or eastern Pacific Oceans. Three nominal species (but probably only one valid species), known only from collections in Hawaii, the Phillipines, and southern Japan, have the 1-2-3 ID pattern.

Table 11. Predominant interdigitation patterns of species of *Symphurus* occurring in the Indo-Pacific and on both coasts of the Americas

	ID Pattern						
Indo-Pacific	1-2-2-1-2	1-2-2-2-2	1-2-3-2-2	Unknown			
No. of Species	6	13	3	2			
New World	1-2-2-2-2	1-3-2-2-2	1-3-3-2-2	1-3-4-2-2	1-4-2-2-2	1-4-3-2-2	1-5-3-2-2
No. Species	1	12	3	1	4	11	8

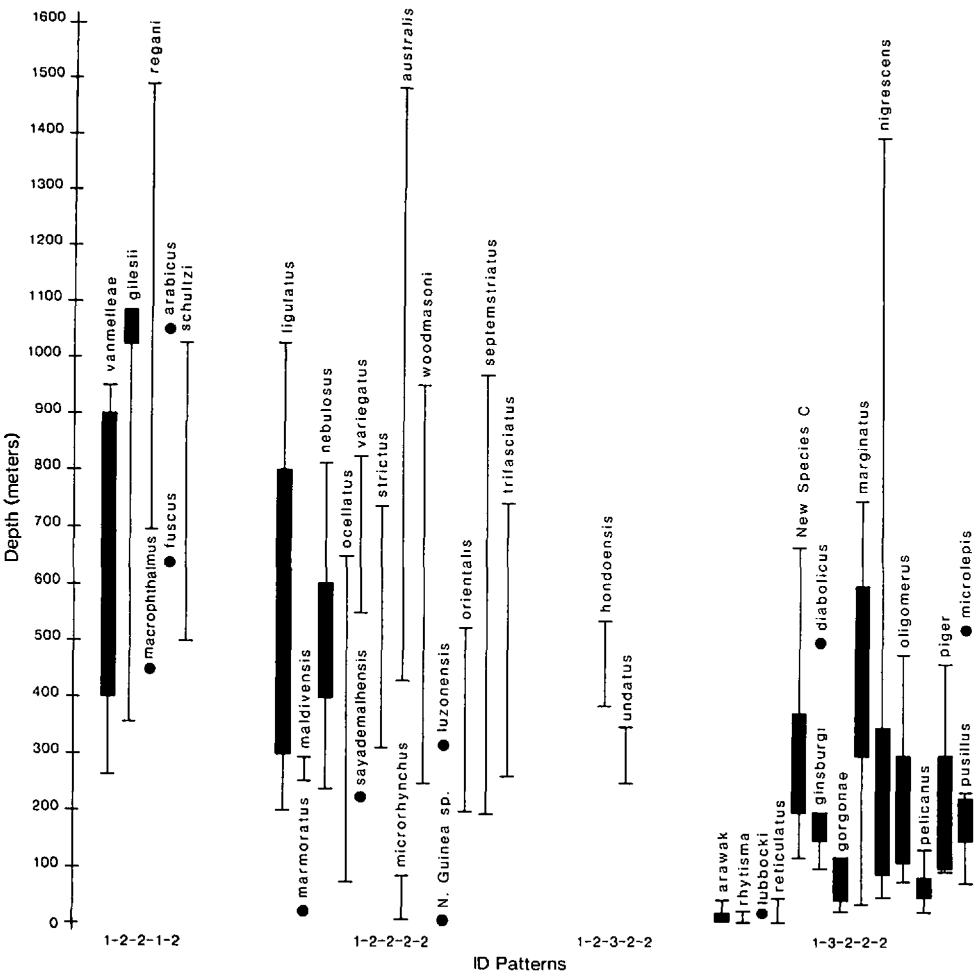

Figure 8. Bathymetric distribution (in meters) of *Symphurus* species characterized by different ID patterns. Species are grouped by ID pattern. Vertical lines represent the depth range over which a species has been collected (lines do not necessarily indicate a continuous vertical distribution). Expanded and darkened segments added to the vertical distribution lines of some species reflect the estimated centers of abundance for the species (based on both frequency of occurrence and numerical abundance).

Exclusive of three species with 1-2-2-1-2 (N = 1) and 1-2-2 patterns (N = 2), all other patterns occurring in Atlantic and eastern Pacific *Symphurus* are unique to species inhabiting these regions. In terms of number of species, 26 of 29 Atlantic species (Munroe, 1987) and all 17 eastern Pacific species have patterns not found in species occurring in Indo-Pacific waters. Seven of the nine predominant ID patterns (exclusive of the 1-2-3 and 1-3-4 patterns) occur in species inhabiting Atlantic locations, while only five patterns are represented among species occurring in the eastern Pacific. The 1-3-2 and 1-3-3 ID patterns occur in 15 and four species, respectively, which have largely similar geographic distributions on both sides of the North and South Atlantic and in the warm temperate and tropical regions of the eastern Pacific. Of 15 species with a 1-3-2 ID pattern, eight occur in the western Atlantic, three in the eastern Atlantic, and four in the eastern Pacific. The single species characterized by a 1-3-4 pattern and all eight species

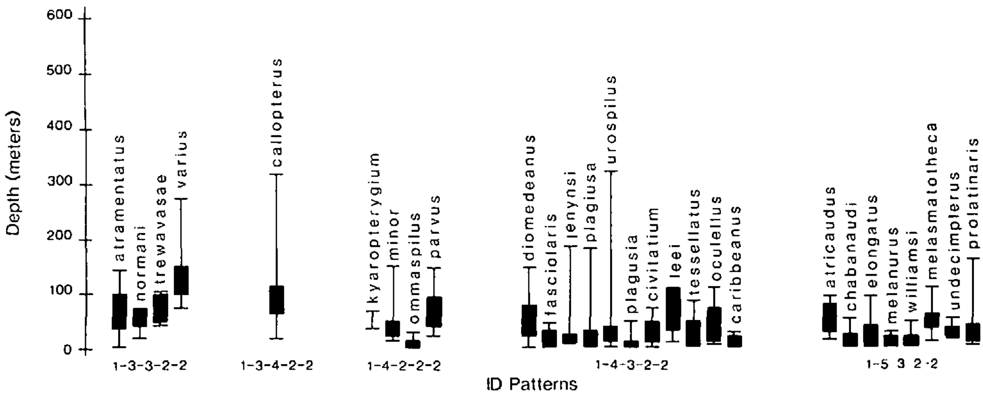

Figure 9. Bathymetric distribution (in meters) of *Symphurus* species characterized by different ID patterns. Species are grouped by ID pattern. Vertical lines represent the depth range over which a species has been collected (lines do not necessarily indicate a continuous vertical distribution). Expanded and darkened segments added to the vertical distribution lines of some species reflect the estimated centers of abundance for the species (based on both frequency of occurrence and numerical abundance).

with a 1-5-3 ID pattern also occur in the warm temperate and tropical eastern Pacific. All four species with the 1-4-2 ID pattern and all but two of 11 species characterized by the 1-4-3 ID patterns are restricted to the western Atlantic. Of 11 species with the 1-4-3 pattern, nine occur in the western Atlantic and two are present in the eastern Pacific.

Also of interest is that species possessing the same predominant ID pattern have somewhat similar bathymetric distributions, which are usually distinctly different from the vertical distributions of species characterized by other predominant ID patterns. Bathymetric ranges plotted for New World species characterized by 1-3-4, 1-4-2, 1-4-3, and 1-5-3 patterns (Figs. 8–9) reveal that these are primarily shallow-water inhabitants with most species commonly inhabiting depths shallower than 50 m. In fact, several of these species occur within estuarine and extremely shallow (<1 m) coastal environments. The deepest record of common occurrence for any of these New World species is only about 110 m (*S. callopterus* and *S. leei*).

Two groups of species, those characterized by the 1-3-3 ID pattern and those with the 1-3-2 pattern, are usually found in moderately deeper waters on the continental shelf in contrast to the depths typically occupied by species with 1-4-3 and 1-5-3 ID patterns. Species with the 1-3-3 ID pattern typically occupy substrates ranging from about 30 to 100 m, while the majority of species with the 1-3-2 ID pattern occur in deeper waters (between 30 and 200 m) on the continental shelf. Several of these species have vertical ranges extending to approximately 500–600 m, depths more typically inhabited by *Symphurus* with 1-2-2-1-2 or 1-2-2 ID patterns (see below). Interestingly, species with the 1-3-2 ID pattern that occur in depths typically occupied by species with the 1-2-2-1-2 or 1-2-2 patterns, do so only in geographic areas where species with these patterns are absent such as in the eastern Pacific (*S. oligomerus* from 50–481 m; *S. microlepis* and *S. diabolicus* between 300–600 m), and Gulf of Mexico and Caribbean Sea (*S. piger* and *S. marginatus* from 100–300 and 300–700 m, respectively). Exceptional among species with the 1-3-2 ID pattern are four diminutive species (*S. arawak, S. rhytisma, S. lubbocki,* and *S. reticulatus*), which inhabit relatively shallow (1–40 m) sandy areas adjacent to coral reefs.

Table 12. Patterns of dorsal pterygiophores in selected representatives of Cynoglossidae, Achiridae, and Soleidae

	N	Supra-cranial pterygiophores*	Pterygiophores inserted in interneural space 1
Family Cynoglossidae			
Subfamily Symphurinae			
Symphurus	4,251	0	1
Subfamily Cynoglossinae			
Cynoglossus sp.	4	5–6	3–4
Paraplagusia sp.	4	9–10	3–4
Family Soleidae			
Heteromycteris sp.	1	16	8
Aseraggodes sp.	1	1	6
Liachirus sp.	1	2	6
Parachirus sp.	2	10	3
Pardachirus sp.	1	1	7
Solea sp.	2	4	2
Zebrias sp.	1	3	4
Family Achiridae			
Trinectes sp.	1	5	2
Gymnachirus sp.	1	8	2
Achirus sp.	73	3–7	1–2

* In addition to erisma.

The deepest-dwelling species in the genus are those with the 1-2-2-1-2, 1-2-2, and 1-2-3 ID patterns (Fig. 8). Except for two shallow-water species with the 1-2-2 ID pattern, most are bathyal species occurring in outer continental shelf and upper continental slope waters at depths greater than 200 m. In fact, the deepest recorded captures for members of this genus (ca. 1,470 m for *S. australis* and 1,480 m for *S. arabicus*) are for species characterized by the 1-2-2 and 1-2-2-1-2 ID patterns.

For comparative purposes, interdigitation patterns for a small number of species representative of the Cynoglossinae, Achiridae, and Soleidae were also examined (Table 12). In *Cynoglossus, Paraplagusia,* soleid, and achirid species, ID patterns are quite different than those observed in *Symphurus.* All of these taxa differ from *Symphurus* in having the first pterygiophore usually completely overlying the cranium with its posterior end lying anterior to the first neural spine and there are usually between one and 16 supra-cranial proximal pterygiophores that overlie the first pterygiophore. In contrast, in species of *Symphurus,* although the first pterygiophore overlies the cranium, its posteriormost end extends rearward beyond the first neural spine and inserts into the first interneural space. Also, *Symphurus* does not have any supra-cranial proximal pterygiophores overlying the first dorsal-fin pterygiophore.

Symphurus also differs from these other taxa in having only a single pterygiophore inserting into the first interneural space. In the Cynoglossinae (*Cynoglossus* and *Paraplagusia*) there are 3–4 proximal pterygiophores inserting into the first obvious interneural space. Some achirids have only a single pterygiophore in the first interneural space as does *Symphurus,* however, in these species (*Achirus*) there are also 3–7 supra-cranial pterygiophores as well. In *Gymnachirus* there are two pterygiophores inserting into the first interneural space, while *Parachirus* has three, and *Aseraggodes* has six pterygiophores inserting into the first interneural space.

The occurrence of two or more pterygiophores inserting into or preceding the first interneural space appears to be an anomalous condition for members of *Symphurus*. Only 29 of 4,251 specimens, distributed among 17 species of *Symphurus*, were found with two pterygiophores inserted into interneural space one, and only a single specimen of *S. diomedeanus* had three proximal pterygiophores inserted into the first interneural space.

Chapleau (1988) presented osteological evidence supporting recognition of the monophyletic subfamily Symphurinae within the Cynoglossidae. He listed six synapomorphies defining the clade including a greatly reduced ocular-side lateral ethmoid lacking an osseous attachment dorsally to the interorbital complex or to the ventral portions of the ocular-side lateral ethmoid and vomer; a blind-side lateral ethmoid with a long posterodorsal arm in contact with the anterior process of the supraoccipital; fused portions of the ocular- and blind-side anterior arms of the frontals (interorbital complex); anterior portion of the supraoccipital bone replaced by a cranial fontanelle; and all proximal radials anterior to the first hemal spine are equally long and in contact with this spine. Chapleau did not comment on interdigitation patterns of dorsal-fin proximal pterygiophores in his study of the Cynoglossidae. Insertion of the posteriormost end of the first pterygiophore into the first interneural space is unique to *Symphurus* among the pleuronectiform families Cynoglossidae, Soleidae, and Achiridae (see Chapleau, 1989, for information on Soleidae). Therefore, among these pleuronectiform fishes, this condition is not only diagnostic for the subfamily Symphurinae, but may be added to the list of synapomorphies provided by Chapleau (1988) further supporting recognition of this taxon as a monophyletic clade within the Cynoglossidae.

Although the primary intent of this paper is to present data demonstrating the importance of ID patterns as a diagnostic character for identification of symphurine tonguefishes, it is evident both from the morphological similarity (for more detail see Munroe, 1987, 1990a, 1991), geographical distributions, and ecological occurrences of species bearing similar ID patterns, that these patterns may also be useful in formulating hypotheses regarding interrelationships of the species. However, applicability and importance of interdigitation patterns as a phylogenetic character remains to be tested and evaluated through a detailed osteological study of the symphurine tonguefishes using phylogenetic analysis and outgroup comparisons. Only in this way can monophyletic assemblages within the genus be identified and their relationships understood. Such a study is underway and will be completed following alpha-level taxonomic revisions within major zoogeographic regions—eastern Atlantic (Munroe, 1990a), eastern Pacific (Munroe and Mahadeva, 1989; Munroe, 1990b; Munroe and Nizinski, 1990; Mahadeva and Munroe, 1990; Munroe et al., 1991; plus subsequent papers), western Atlantic (Munroe, 1987, 1991, in preparation), and Indo-Pacific (Munroe and Nizinski, in preparation).

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APPENDIX

Material Examined:

FAMILY CYNOGLOSSIDAE: SUBFAMILY SYMPHURINAE: *Symphurus* (4,251 specimens).

arabicus (1 specimen).—BMNH 1939.5.24.1839 (holotype).

arawak (41 specimens).—ANSP 101985 (holotype); 111378 (1); 111924 (3); 119056 (1); 119057 (1). AMNH 27327 (1); 27706 (1); 29214 (1); 34603 (1). FMNH 94817 (1); 97496–99 (4). UF 12269 (1); 13455 (2); 17054 (1); 25721 (1); 25876 (1). UMML 15491 (2); 15492 (2); 19274 (1); 21421 (1); 31430 (1); UMML 34385 (2); UMML 34386 (1); UMML Uncat. (1); USNM 198200 (2); 265177 (2); 265178 (1); 265182 (2); 267784 (1).

atramentatus (151 specimens).—BMNH 1913.7.10:69 (1). CAS 24074 (1); 24182 (13); 24183 (2); 24184 (1); 24954 (1); CAS 24955 (2); 24956 (2). CAS-SU 3 (7); 8483 (1); 46250 (1). MCZ 35922 (syntype, 1). UMML 26035 (10); 26144 (27); 26151 (6); 26158 (3); UNCAT. FROM UMML 27031 (2); UNCAT. P-553 (24); UNCAT. FROM UMML 27288 (1); UNCAT. ARGOSY 55 (2). USNM 41157 (syntype); USNM 41471 (syntypes, 4). USNM 41367 (syntype, 1). USNM 41368 (syntype, 1). USNM 46354 (1); 93992 (1); 101981 (1); 101982 (3); 101986 (1); 116207 (1); 117645 (2); 121970 (2); 126740 (4); 183988 (19).

atricaudus (85 specimens).—ANSP 85363 (1). LACM 31761-3 (5); 32042-4 (12). SIO 64-879 (5); 64-881 (4); 84-91 (20); 85-155 (2); 85-139 (3). UCLA W67-149A (5). USNM 27396 (syntypes 3); 34771 (9); 41866 (7); 54494 (2); 126742 (2). VIMS 7770 (5).

australis (30 specimens).—IAMS I.7898 (1) holotype. AMS 22817-024 (2); IAMS 23458-001 (2); IAMS 24367-005 (1); IAMS 24457-002 (1); IAMS 25932-003 (2); IAMS 26824-003 (19); IAMS I.27041-002 (2).

Symphurus species C (82 specimens).—AMNH 40834 (1). FMNH 88819 (1). MCZ 27968 (1); 39205 (2). NMC 82-0332 (1). UF UNCAT. TURSIOPS (1). UMML 13917 (1); 15642 (5); 16314 (1); 27173 (4); UNCAT. G-893 (1); UNCAT. G-898 (3); UNCAT. OR 4834 (1). USNM 158310 (1). VIMS 1600 (3); 1601 (1); 1900 (5); 1905 (4); 3070 (2); 3071 (1); 3073 (1); 5511 (3); 5564 (2); 5570 (3); 5572 (6); 5574 (1); 5575 (1); 5579 (2); 5581 (1); UNCAT. ALB IV 73-8 STA. 44 (3); UNCAT. ALB IV 84-02 STA. 21 (1); UNCAT. ALB IV STA. 166 (2); UNCAT. DEL 75-15 STA. 76.3.6 (1); UNCAT. DEL 76-5 STA. 8.1.44 (1); UNCAT. DEL 82 STA. 8 (1); UNCAT. GI 74-04 STA. 68 (6); UNCAT. GI 74-04 STA. 69 (1); UNCAT. GI 74-04 STA. 79 (1); UNCAT. GI 74-04 STA. 91 (3); UNCAT. GI 76-01 STA. 63 (2).

callopterus (191 specimens).—BMNH 1956.3.1:3–4 (2). CAS 4785 (1); 4786 (1); 5304 (1); 11710 (1); 24188 (10); 24189 (11); 24190 (1); 24191 (3); 24192 (2); 24194 (2); 24195 (3); 24198 (1); 24957 (1); 64023 (holotype). LACM 33590-2 (2); 33827-55 (4). SIO 63-518 (9); 63-521 (2); 73-279 (3); 79-5 (43). UCLA W56-80 (1); W58-395 (3); W61-198 (2). UF 47590 (1). UMML 26003 (11); 26069 (33); 34317 (2); 34318 (30); 34319 (1); UNCAT. FROM UMML 31935 (1). USNM 164492 (2).

caribbeanus (83 specimens).—ANSP 115601 (7); 118553 (1). FMNH 61574 (1). MCZ 11200 (1). UF 83998 (10). UMML 30087 (6); 34337 (3); 34338 (2); 34339 (1); 34340 (27). UPRM 736 (1); 740 (10); 1588 (1); 2926 (8). USNM 313513 (2); 313514 (1); 313487 (holotype).

chabanaudi (132 specimens).—ANSP 123572 (2); 123579 (1). BMNH 1956.3.1:6–14 (9). CAS 24199 (5); CAS-SU 5571 (2). SIO 80-23 (5). UMML 34330 (2); UNCAT. FROM UMML 25049 (1). UMMZ 194670 (2). USNM 50333 (1); 81032 (1); 119742 (1); 126741 (2); 144788 (12); 144789 (3); 144790 (10); USNM 144791 (2); 164493 (1); 164494 (9); 220701 (4); 220804 (7); USNM 236606 (2); 291339 (1); 291340 (18); 291357 (1); 305717 (holotype); 305725 (3); 305728 (3). YPM 4369 (8); YPM UNCAT. PAWNEE 630–631 (11). YPM UNCAT. PAWNEE 632, 633 (2).

civitatium (170 specimens).—ALA 301.17 (2); 353.05 (1); 606.29 (1); 2385 (12); 3015 (3). ANSP 137573 (1). FMNH 45109 (3); 45427 (7); 45979 (1); 46369 (11). GCRL 16383 (2). IMS 543 (16); 544 (3). TCWC 4187.4 (1); 4189.21 (14); 4195.31 (9). TU 75907 (3). UF 13062 (1). UMML 1784 (1); 34342 (3); UMML 34345 (1). USNM 86139 (2); 86140 (1); 86153 (1); 120081 (1); 120082 (1); 154945 (3); 154946 (1); 154947 (5); 154948 (2); 154949 (2); 154950 (2); 154951 (1); 154952

(1); 154953 (2); 154954 (3); 155226 (1); 155227 (holotype); 157399 (3); 157400 (3); 157401 (1); 157402 (1); 157403 (1); 157693 (5); 157694 (3); 274484 (1); 274485 (1); 291316 (1); 291317 (13); 291318 (1); 313646 (8); 313647 (2).

diabolicus (1 specimen).—USNM 135653 (holotype).

diomedeanus (204 specimens).—ALA 5871.21 (3); 5959 (3). ANSP 101294 (2). BMNH 1923.7.30:345 (holotype of *S. sumptuosus*). FMNH 45428 (1); 45429 (6); 46370 (6); 61301 (3); 86363 (1); 86415 (1); 88848 (1); 88853 (1); 90083 (1); 90541 (1); 90942 (3); 91115 (1); UNCAT. FROM FMNH 90085 (1). IMS 548 (4). MCZ 11377 (2); 39982 (5); 40943 (2); 58654 (24). MNHN 1975-269 (9). TU 10594 (2); 12956 (1); 82932 (1); 82989 (1); 83888 (1). UF 12785 (1); 17018 (1); UF 21434 (1); UF 30333 (2); 35415 (2). UMML 7746 (1); 10551 (1); 10552 (1); 10580 (1); 11153 (1); 11160 (1); 11226 (1); 17441 (2); 23893 (1); 26697 (1); 30188 (1); 34374 (5); 34375 (2); 34376 (1); 34377 (1); 34378 (1); 34379 (2); 34380 (1); 34381 (1); 34382 (1); 34383 (3); 34384 (3); UNCAT. OR 4866 (1). UNC 1552 (3); 1563 (3); 1565 (1); 4031 (1); 14920 (2). USA 3563 (6); 5748 (6). USNM 37347 (holotype); 113251 (1); 133935 (1); 157692 (1); 158306 (2); 159610 (1); 159617 (2); 159619 (2); 274483 (4); 87770 (holotype of *S. pterospilotus*); UNCAT. OR 4875 (1); UNCAT. OR 5354 (1); UNCAT. OR 5621 (4); UNCAT. OR 5697 (1); UNCAT. OR 5699 (1); UNCAT. OR 5703 (1); UNCAT. SB 5320 (1); UNCAT. ATLANTIS G. VENEZUELA (2). UWF 3230 (2). VIMS 1137 (8); 1599 (1); 2503 (13); UNCAT. DEL 82-02 STA 58 (1).

elongatus (91 specimens).—CAS 3419 (1); 3420 (1); 3421 (1); 3422 (1); 3423 (1); 3424 (1). CAS-SU 391 (10). FMNH 61575 (2). SIO 64-363 (2). UMML 25049 (11); 26214 (2); 26265 (56). USNM 291338 (2).

fasciolaris (39 specimens).—CAS 2848 (1); 30847 (1). CAS-SU 15 (syntypes, 3). UAZ 68-35-1 (1); 71-74-37 (1); 71-91-35 (2); 71-94-24 (1); 71-95-25 (2); 72-42-28 (5); 75-84-3 (1); 78-1-2 (5); 78-2-4 (2); 80-11-1 (1). UCLA W49-55 (1); W50-57 (7); W51-56 (1); W53-93 (1); W55-96 (1). USNM 44406 (syntype); 150430 (1).

fuscus (1 specimen).—ZMB 17686 (holotype).

gilesii (9 specimens).—BMNH 1939.5.24:1835–38 (syntypes, 4). BMNH 1939.5.24:1827–1834 (5).

ginsburgi (56 specimens).—MNHN 1975-270 (3). MZUSP 12314–19 (6); 12320 (1); 12327 (1); 12328–333 (6); 12335–338 (4); 12339 (holotype); 12340–12342 (3); 123444–448 (5); 12370–375 (6); 12377 (1); 12378–389 (11); 12391–93 (3); 12899–901 (3); 12902–903 (2).

gorgonae (73 specimens).—BMNH 1926.7.12:81 (holotype); 1926.7.12:82–83 (2); 1956.3.1.16–20 (5). CAS 20714 (1). SIO 60-90 (12); 68-92 (4); 84-69 (3). UMML 26002 (3); 26233 (7); UNCAT. GS-12 (9); UNCAT. ARGOSY 26 (12); UNCAT. from UMML 26003 (6); UNCAT from UMML 26009 (1); UNCAT. P-495 (2). USNM 164498 (1); USNM 164499 (4).

holothuriae (1 specimen).—BMNH 1892.1.14:34 (holotype).

hondoensis (1 specimen).—USNM 75675 (holotype).

jenynsi (85 specimens).—CAS-SU 22725 (13). FURG 3040 (1). MCN 2399–2400 (2); 2401 (holotype of *S. meridionalis*). MCP 8009 (1). MCZ 11384 (2). MZUSP 12555–560 (3); 12843 (10); 12849 (8); 12886 (3). UMMZ 95496 (1). USNM 55573 (holotype); 76852 (holotype of *S. bergi*); 76892 (9); 86170 (3); 86683 (1); 87771 (1); USNM 316768 (6); 316769 (9); 316770 (4); 316772 (6).

kyaropterygium (14 specimens).—MNHN 1975-264 (2); 1975-265 (2); 1975-266 (1); 1975-267 (1); 1975-268 (2). MZUSP 12425 (holotype); 12783 (1); 12784 (1); 12913–15 (3).

leei (198 specimens).—CAS 24974 (1). CAS-SU 39 (syntypes, 21); 6060 (6). LACM 30123-10 (1). MCZ 35906 (syntype, 1); 35916 (syntype, 1). UMML 25024 (10); 26009 (77); 26193 (12); 26196 (20); 29126 (12); UNCAT. P-495 (13). USNM 41270 (1); 41485 (syntypes, 7); 124318 (1); 131433 (14).

ligulatus (37 specimens).—ANSP 123249 (1). IRSNB 16576 (3). MSNG 45458 (4). MMF 22492 (28). UAB 15/III/85 (1).

lubbocki (2 specimens).—BMNH 1979.1.5:237–238 (holotype and paratype).

luzonensis (1 specimen).—USNM 138043 (holotype).

macrophthalmus (2 specimens).—BMNH 1939.5.24:1825–1826 (holotype and paratype).

maldivensis (1 specimen).—BMNH 1939.5.24:1815 (holotype).

marmoratus (1 specimen).—USNM 93092 (holotype).

marginatus (94 specimens).—AMNH 40249 (1). FDNR 6751 (1). FMNH 47908 (1); 86366 (1); 86396 (1); 88815 (2); 88817 (1); 88818 (1); 88820 (1); 88847 (1); 90533 (1); 90534 (1); 90539 (1); 94462 (1); 94468 (6); 94486 (1). MCZ 27967 (holotype); 51900 (1); 58657 (1). TU 11024 (1). UF 33894 (1); 33889 (2). UF/FSU 22224 (1). UMML 10519 (1); 10565 (1); 10569 (1); 10587 (1); 10589 (1); 10590 (2); 17440 (1); 20536 (1); 20569 (1); 23248 (1); 30106 (3); UNCAT. OR 3653 (1); UNCAT. OR 4860 (2); UNCAT. OR 5028 (1); UNCAT. OR 5030 (1); UNCAT. OR 5092 (1); UNCAT. OR 5093 (2); UNCAT. OR 5097 (1); UNCAT. OR 5101 (2); UNCAT. OR 5105 (1); UNCAT. OR 5106 (2); UNCAT. OR 5113 (6); UNCAT. SB 1611 (1); UNCAT. SB 3711 (5); UNCAT. SB 3752 (1); UNCAT. SB 4225 (1). UNC 12175 (1); UNC 12179 (1). USA 4665 (1). USNM 47658 (1); 108416 (1); 131634 (1); 159236 (1); 159607 (1); 159891 (1); 186042

(2); 236603 (1); 236609 (2); 47658 (1); UNCAT. OR 5240 (2); UNCAT. OR 5690 (1); UNCAT. OR 5782 (2). VIMS 4302 (1); 5510 (1); UNCAT. GI 74-07 STA 69 (1).

melanurus (120 specimens).—BMNH 1936.10.6:11 (holotype of *S. seychellensis*). CAS 3417 (1); 3418 (1); 3879 (1); 4401 (holotype); 4423–25 (3); 6135 (1); 24969 (2); 24976–78 (3); 30848 (7). CAS-SU 32247 (1); 47232 (1). LACM 20269 (1); 20310 (1). SIO 60-87 (2); 62-39 (2); 64-363 (2); 65-167 (9); 73-276 (1). UAZ 68-135-13 (1). UCLA W52-50 (9); W53-273 (1); W53-275 (3); W53-283 (3); W53-289 (3); W56-113 (3); W58-304 (10); UCLA W58-305 (14). UMML 8971 (1); UNCAT. FROM UMML 26214 (1). UMMZ UNCAT. FROM UMMZ 194670 (1). USNM 88832 (1); 128170 (holotype of *S. sechurae*); 128171 (2); 220702 (2); 220758 (1); 305726 (1); 305730–33 (7); USNM UNCAT. (11). YPM UNCAT. (1). ZMUC 86255–56 (2).

microlepis (1 specimen).—MCZ 28535 (holotype).

microrhynchus (1 specimen).—ZMA 108.193 (holotype).

melasmatotheca (107 specimens).—CAS 4806 (1); 24949 (1). LACM 42893-1 (1). SIO 60-90 (5); 62-51 (2); 62-52 (5); 62-75 (7); 63-504 (1); 63-518 (2); 63-521 (1); 63-523 (2); 65-158 (13); 65-166 (27); 73-232 (3); 73-256 (2); 73-278 (13); 73-283 (3); UNCAT. (4). UMML 34325 (1); 34326 (1); 34327 (1); 34328 (4); 34329 (6). USNM 101985 (1).

minor (78 specimens).—FDNR 2977 (1); 5144 (2); 6540 (1); 6542 (1); UNCAT. MOTE 310.11 STA 16A (2); UNCAT. MOTE 310.93 STA 8 (2). GCRL 17370 (1); 14893 (3). GMBL 79-106 (2). MCZ 58655 (2). UF 20442 (2); 20904 (2); 20918 (4); 20937 (1); 21066 (1); 21419 (2); 21511 (3); 24577 (1). UF/FSU 21385 (2); 24577 (1). UMML UNCAT. G-1237 (1); UNCAT. G-1089 (2); UNCAT. ORII 10740 (2); UNCAT. SB 3182 (1); UNCAT. SB 3183 (2). UNC 3913 (1). USA 1786 (1); 1864 (2); 1907 (1); 2140 (1); 2185 (1); 2989 (3); 3727 (1); 3733 (2). USNM 92614 (3); 131590 (1); 131591 (3); 131593 (1); 131643 (holotype); 134272 (1); 152734 (2); 155230 (1); 155231 (1); 155232 (1); 155233 (1); UNCAT. ORII 21868 (1). UWF 1321 (1); 1468 (1); 2964 (1); 3714 (1).

nebulosus (25 specimens).—MCZ 27966 (holotype); MCZ 39480 (1). UMML 20746 (2); 27439 (1). UMO 311.8 (1). UNC 4951 (10). USNM 84490 (1); 152842 (1); 265179 (1); UNCAT. ORII 11715 (1); UNCAT. ORII 11720 (2). VIMS 5577 (2); UNCAT. CI 80077 (1).

New Guinea species (5 specimens).—USNM 236607 (2); 245733 (1); 265183 (2).

nigrescens (161 specimens).—BMNH 1890.6.16:46 (1). IOS DISCOVERY Sta. 7810 (9); IOS DISCOVERY Sta. 8020 (29). IRSNB 23724-16576 (1); 16808-14787 (1). ISH 194177 (14). MCZ 26397 (1); 58645 (18); 58646 (1); 58647 (1); 58648 (1); 58649 (1); 58650 (2). MNHN 58-157 (2); 59-183 (3); 59-606 (1); 59-608 (4); 1967-539 (1); 1975-412 (2); 1989-1208 (neotype). MSNG 41890 (5); 47614 (1). UF 33890 (1). UMML 34324 (5). UAB 30/XI/84 (1); 14/II/74 (4). USNM 10092 (2); 48292 (1); 49333 (1); 300120 (2); USNM 304446 (11); USNM 304447 (32). ZMUC 86219 (1).

normani (35 specimens).—BMNH 1930.5.6:46–50 (4); 1930.5.6:51 (holotype); 1930.5.6:52–55 (4); 1935.5.11:230 (1). IRSNB 14788-105–106 (2); 16808-404–407 (4). MNHN 1967-540 (1). MRAC 140377 (1); 140379–381 (3). UMML 15244 (1); 15262 (1); 15291 (2); 16847 (1); 16982 (3); 21502 (2); 34323 (2). ZMUC 86224–25 (2).

ocellatus (15 specimens).—BMNH 1922.3.27:10 (holotype); 1922.3.27:24 (1). SAM 28814 (1). USNM 236604 (1); 236608 (1). ZMUC 86103–05 (3); ZMUC 86106–112 (7).

oculellus (45 specimens).—BMNH 1950.5.15:51 (1); 1961.9.4:117–118 (2). FMNH 86362 (1); 86365 (1); 86397 (1); 88846 (1); 90552 (2); 90553 (1); 90085 (4); 91109 (1); 91368 (1); 100385 (1); 100386 (7); 100387 (2). GCRL 3836 (5). UMML 11549 (1); 12249 (1); 12254 (1); 12310 (3); 34335 (1). USNM 159606 (holotype); 159541 (1); 159559 (1); 159615 (2); USNM 313518 (2).

oligomerus (205 specimens).—CAS 24200 (1); 24201 (6); 24979 (1); 43872 (1); 44104 (1); 57858 (1). LACM 20407 (19); 21719 (1). MCZ 28537 (1). SIO 68-94 (15); 73-281 (24); 84-70 (holotype); 84-80 (3); 84-81 (7). UF 33932 (3). UMML 31935 (19); 31947 (7); 26051 (16); 26179 (2); 27031 (73). USNM 57882 (2); 57883 (1).

ommaspilus (28 specimens).—AMNH 26260 (1); 29196 (5); 30969 (2). ANSP 93810 (holotype); 93811 (1); 103419 (1); 143267 (1). FMNH 94820 (1). UMML 12813 (1); 34387 (1). UPRM 2660 (7). USNM UNCAT. (3). ZMA 116.187 (1); 119.422 (1): ZMUC 8652 (1).

orientalis (2 specimens).—MNHN 1984-633 (1); USNM 77066 (1).

parvus (81 specimens).—AMNH 18887 (2). FDNR 6537 (1); 6543 (1); 6615 (1); 18029 (3); 18025 (2); 18026 (1). FMNH 46371 (1); 88816 (5). GMBL 78-159 (1). MCZ 50863 (1). TCWC 3321.1 (1); 3406.2 (6); 6191.7 (2); 6193.15 (1). UF 20586 (3); 20762 (1); 21280 (1); 21834 (1). UF/FSU 20769 (2); 21301 (1). UMML 3680 (1); 10737 (1); 15589 (1); 17406 (1); 20911 (1); 26658 (1); 26744 (1); 26769 (1); 29281 (1); 30081 (2); 30114 (1); 30123 (1); UNCAT. OR 5098 (1); UNCAT: P-371 (5); UNCAT. P-723 (1); UNCAT. P-1336 (1). USA 4906 (2); 4915 (1); 6361 (1). USNM 47657 (1); 74330 (4); 84491 (holotype); (1); 152733 (1); 153087 (1); 153088 (1); 153090 (1); 153097 (1); 153098 (1); 161351 (1); UNCAT. OR 5680 (1); UNCAT. DEL II STA 21 (1); UNCAT. ORII 5739 (1). UWF 1484 (1); 2670 (1).

pelicanus (62 specimens).—FMNH 45980 (1); 46372 (1); 88821 (1); 94460 (1). TCWC 6248.2 (3).

UF 15662 (1). UMML 1328 (1); 22282 (1); 26544 (2); 26616 (4); 26762 (1); 26780 (1); 30132 (4); 30181 (3); 34371 (1); UNCAT. FROM 26658 (1); UNCAT. FROM 26744 (1); UNCAT. FROM UMML 30081 (2); UNCAT. GS-53 (2); UNCAT. P-371 (3); UNCAT. P-402 (1); UNCAT. P-618 (5); UNCAT. P-696 (1); UNCAT. P-723 (10); UNCAT. P-731 (1); UNCAT. P-836 (5). USNM 74331 (1); 113252 (1); 155234 (holotype); USNM 155235 (1).

piger (142 specimens).—ANSP 144936 (1). FDNR 12566 (2). FMNH 86398 (4); 86414 (1); 90536 (1); 90538 (2); 90540 (1); 91116 (9); 94461 (5); 94463 (1); 94469 (1). GCRL 3817 (1). MCZ 27965 (holotype); 39395 (1). TCWC 4468.11 (9); 6097.14 (11); 6207.17 (1). UF 15637 (3); 33888 (11). UMML 11175 (1); 14146 (1); 17635 (7); 30166 (5); UNCAT. FROM UMML 30181 (3); UNCAT. GERDA 1329 (2); UNCAT. OR 2633 (3); UNCAT. OR 3587 (1); UNCAT. OR 3636 (7); UNCAT. OR 5021 (1); UNCAT. SB 3752 (2). USNM 159211 (23); 159605 (2); 159609 (7); UNCAT. OR 2468 (3); UNCAT. OR 5913 (3); UNCAT. SB 2464 (6).

plagiusa (138 specimens).—ANSP 101977 (1); 111567 (3). FDNR 5197 (1); 10772 (1); 18030 (2). IMS 553 (10); 554 (10); 555 (4). TCWC 461.3 (2); 528.1 (2); 547.4 (5). UF 35425 (1); 35435 (1). UMML 5217 (1); 20825 (6); 31721 (1); UNCAT. OR 713 (2); UNCAT. SB 5320 (1); UNCAT. TABL 67-283 (1). USNM 158222 (3); 187151 (1); 187180 (2); 265181 (1); 274481 (4); 274482 (3); 316748 (16); 316749 (1); 316755 (7); 316756 (5); 316758 (7); 316784 (2); 316786 (1); 316787 (1). VIMS 1315 (26); 1598 (3).

plagusia (42 specimens).—ANSP 118542 (1); 121326 (2); 129952 (1); 129985 (1); 132030 (neotype). FMNH 3286 (1); 61572 (1); 88853 (2); 94818 (1); 94822 (1); 97490 (3); 97491 (1); 97492 (1); 97493 (2); 97494 (1); 97495 (1). GCRL 15694 (1). UF 10762 (1); 12059 (1); 38896 (5). UFPB 884 (1); 896 (3). UMML 34347 (1). UPRM 1828 (1). USNM 50178 (4); 81654 (1); 236252 (1); 291331 (1).

prolatinaris (108 specimens).—CAS 24942 (6); 24944 (1); 24945 (1). IMARPE 66-2146 (1). LACM 20406 (1); UNCAT. FROM LACM 42893-1 (1). SIO 60-87 (2); 62-50 (1); 62-70 (1); 62-707 (1); 63-501 (12); 63-502 (7); 63-503 (3); 63-504 (1); 63-507 (1); 63-517 (1); 63-521 (1); 64-877 (4); 65-158 (2); 65-160 (2); 65-167 (11); 73-276 (1); 73-297 (1); 73-298 (30). UAZ 67-71-9 (2). UCLA W58-3 (1); W59-63 (1); W62-45 (4). UCR 1286-10 (1). USNM UNCAT. FROM 236606 (5); UNCAT. (1).

pusillus (24 specimens).—AMNH 19426 (1). UF 22139 (1). UF/FSU 20885 (2); 32430 (1). UMML 17387 (1); UNCAT. GERDA 1083 (2); UNCAT. GILLIS 10 (3). UNC 12180 (1). USA 4822 (1). USNM 28730 (holotype); 28778 (2); 153089 (1); 153099 (1). VIMS 1129 (2); 5571 (2); 5573 (2).

regani (7 specimens).—USNM 138045 (1); 138053 (1); 138054 (1). ZMA 100.246 (lectotype); 100.247–249 (3).

reticulatus (5 specimens).—BMNH 1984.7.16:246 (holotype). MMF 22999 (1). ZMUC 86220 (1); 86222 (1); 86223 (1).

rhytisma (5 specimens).—ANSP 93812 (holotype); 124854 (2). UF 1345 (1). FMNH 94821 (1).

sayademalhensis (2 specimens).—BMNH 1908.3.23:157–158 (holotype and paratype).

schultzi (7 specimens).—USNM 138025 (1); 138033 (1); 138044 (holotype); 138046 (1); 138057 (1). ZMUC 86117–18 (2).

septemstriatus (63 specimens).—USNM 138023 (2); 138028 (1); 138029 (1); 138037 (1); 138026 (4); 138031 (1); 138032 (2); 138040 (2); 138041 (1); 138042 (16); 138043 (2); 138060 (1); 163655 (1); 163657 (1). ZMUC 86360 (1); 86362 (1); 86363 (1); 86364 (1); 86368–82 (14); 86383–89 (7); 86390 (1); 86392 (1).

strictus (34 specimens).—BMNH 1939.5.24:1816–1824 (11); 1922.3.27:11 (1). BPBM 24730 (1). BSKU 13250 (1); 13464 (1); 13465 (1); 13466 (1); 13470 (1). CAS-SU 8614 (2). SIO 70-347 (1). USNM 51624 (holotype); 51673 (2); 113180 (1); 138022 (1); 138024 (1); 138027 (1); 138030 (1); 138050 (1); 138055 (1); 152779 (1). ZMUC 86357–58 (2).

tessellatus (241 specimens).—ANSP 81861 (1); 83626 (8); 97661 (6); 121394 (7); 121549 (9). FMNH 86364 (1); 86459 (1); 88650 (16); 90544 (3); 90546 (22); 91129 (1); 94819 (5); UNCAT. FROM FMNH 94818 (5). GCRL 3835 (1); 3836 (6); 3838 (3); 12698 (1). LACM 6215 (1); 6217 (7). MCZ 11269 (1); 11381 (14); 24939 (1). MHNN 691 (possible holotype of *Plagusia brasiliensis*). UF 35275 (1); UNCAT. FROM 12059 (1). UFPB 882 (4); 993 (5); 1120 (5); UNCAT. FROM UFPB 884 (9); UNCAT. FROM UFPB 896 (2). UMML 4831 (1); 34348 (2); 34349 (2); 34350 (5); 34351 (3); 34352 (3); 34353 (2); 34354 (4); 34355 (9); 34356 (1); 34357 (1); 34358 (1); 34367 (2); 34368 (1); 34369 (4); 34370 (1). UMMZ 142422 (1). UPRM 1590 (2); 2717 (1); 2743 (15); UPRM 3761 (3); UPRM 3760 (2); UPRM 3758 (2); UPRM 3762 (1). USNM 35108 (1); 37348 (1); 108369 (1); 108372 (1); 126448 (1); 133671 (3); 154857 (1); 159225 (2); 28843 (1); 291332 (1); 291333 (6); 291335 (1); 291346 (2); 291347 (2).

trewavasae (58 specimens).—BMNH 1913.12.4.264 (holotype); 1913.12.4:265–273 (14). MNHN 50-69 (1); 1975-271 (6); 1975-272 (4). MZUSP 12457–468 (12); 12476–477 (2); 12485–489 (5); 12498–500 (3); 12829 (8). USNM 314774 (2).

trifasciatus (7 specimens).—ANSP 122498 (2). USNM 46758 (syntype). ZMUC 86365 (1); 86393 (1); 86394 (1).
undatus (23 specimens).—BPBM 24982 (20). CAS-SU 8630 (1). USNM 51619 (holotype); USNM 93208 (1).
undecimplerus (43 specimens).—CAS 24943 (6); 24948 (2); 24950 (2); 24951 (1); 24952 (7); 67235 (holotype). LACM 44299-1 (1). SIO 63-523 (1). UMML 26233 (1); 34331–33 (19). USNM 199953 (1); 304450 (1).
urospilus (110 specimens).—FDNR 800 (1); 1595 (1); 2144 (1); 2460 (1); 4448 (2); 4880 (2); 4995 (1); 5059 (4); 9857 (1); 10155 (1); 10206 (1); 10231 (1); 10771 (2); 10932 (1); 11533 (1); 12849 (1); 14632 (1); 14670 (1); 18031 (2). FMNH 45430 (9). GCRL 14878 (1). GMBL 74-11 (1); 74-183 (1); 75-154 (1); 76-266 (1); 76-273 (1). IMS 559 (3); 560 (8). MCZ 58651 (2); 58652 (1). TCWC 3303.1 (1); 3307.1 (1). TU 14789 (2). UF 13238 (1); 21903 (10); 28318 (1); 30363 (1); 35443 (1); 43331 (1). UMML 2914 (1); 3083 (13); 4699 (3); UMML UNCAT. (1). USNM 73262 (1); 155225 (holotype); 156068 (1); 158315 (2); 267315 (5). UWF 2323 (6); 2406 (1); 2356 (1).
vanmelleae (65 specimens).—BMNH 1962.6.18:138–139 (2). IOS 10873 (30). IRSNB 16808-430 (holotype); 16808-440 (1). UF 33891 (4). UMML 21422 (2); 21682 (1); 34320 (2); 34321 (1); 34322 (1). USNM 300117 (3); 300118 (11); 300119 (1). ZMUC 86226–28 (3); 86230 (1); 86233 (1).
variegatus (2 specimens).—BMNH 1904.11.4:2 (paratype?). SAM 15399 (holotype).
varius (49 specimens).—CAS 30889 (2); 50570 (1); 57852 (1). CAS-SU 37622 (1); 37624 (1); 37625 (1). LACM 33646-10 (7); 33648-5 (1); LACM 33649-1 (27). MCZ 28536 (syntypes, 5). SIO 55-265 (1). USNM 153592 (syntype).
williamsi (135 specimens).—BMNH 1895.5.27:224 (1). CAS 24980 (1); CAS UNCAT. FROM CAS 30848 (1). CAS-SU 2943 (holotype); 46264 (1); 69110 (1); UNCAT. FROM CAS-SU 32247 (1). UAZ 67-29-10 (10); 67-31-13 (6); 73-42-2 (1); 77-14-2 (1); 75-112-4 (2). UCLA W50-57 (39); W50-190 (2); W51-36 (15); W52-16 (18); W78-11 (5). UMML 25085 (6); UMML UNCAT. ARGOSY 55 (1). USNM 101984 (1); 128172 (holotype of *S. paitensis*); 128173 (paratype of *S. paitensis*); USNM 291344 (19).
woodmasoni (93 specimens).—AMS I22825-024 (1). BMNH 1928.3.20:73 (1). MNHN 50-1 (1); 50-3 (1). UMMZ 159738 (1). USNM 113183–85 (3); 138021 (1); 138034 (1); 138035 (2); 138036 (1); 138039 (1); 138047 (1); 138048 (1); 138049 (2); 138051 (1); 138052 (1); 138056 (2); 138059 (13); 138060 (27); 138061 (19); 138062 (7); 163656 (1). ZMA 100.252 (1). ZMUC 86361 (1); 86366–86367 (2).
FAMILY CYNOGLOSSIDAE: SUBFAMILY CYNOGLOSSINAE: *Paraplagusia* sp. (4). USNM 106821 (1). ZMUC CN 2-4 (3). *Cynoglossus* sp. (4). USNM 72022 (2). ZMUC CN 5-6 (2).
FAMILY SOLEIDAE (9 specimens).—*Parachirus xenicus* USNM 218768 (2). *Solea solea* USNM 197589 (2). *Zebrias zebrinus* USNM 137383 (1). The following specimens are based on photographs of radiographs in Ochiai (1963). *Heteromycteris matsubarai* (p. 14; 1 specimen). *Liachirus melanospilus* (p. 22; 1 specimen). *Aseraggodes kaianus* (p. 30; 1 specimen). *Pardachirus pavoninus* (p. 35; 1 specimen).
FAMILY ACHIRIDAE (75 specimens).—*Gymnachirus melas* USNM 163509 (1). *Achirus fluviatilis* USNM UNCAT. (1). *Achirus scutum* USNM UNCAT. (2). *Trinectes maculatum* USNM 25657 (1). *Achirus* sp. USNM UNCAT. (70).