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TAXONOMY AND ECOLOGY OF THE GENUS
CHASMODES (PISCES: BLENNIIDAE)
WITH A DISCUSSION OF ITS ZOOGEOGRAPHY

JEFFREY T. WILLIAMS



UNIVERSITY OF FLORIDA

GAINESVILLE

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TAXONOMY AND ECOLOGY OF THE GENUS *CHASMODES* (PISCES: BLENNIIDAE) WITH A DISCUSSION OF ITS ZOOGEOGRAPHY

JEFFREY T. WILLIAMS¹

SYNOPSIS: The western Atlantic blennioid fish genus *Chasmodes* is represented by two species, *C. bosquianus* and *C. saburrae*. *C. saburrae* is the more tropical of the species and is found on Florida's east coast from Edgewater southward around the tip of Florida, northward and westward to the Chandeleur Islands, Louisiana. *C. bosquianus* is composed of two subspecies, *C. b. bosquianus* and *C. b. longimaxilla* new subspecies. *C. b. bosquianus* is distributed on the Atlantic seaboard from Maryland to Marineland, Florida, and *C. b. longimaxilla* occurs in the northern Gulf of Mexico from Pensacola, Florida, to Veracruz, Mexico.

Chasmodes bosquianus longimaxilla exhibits character displacement in the zone of sympatry with *C. saburrae* in the Gulf. Increased maxillary length in this area may be contributing to the divergence of the disjunct populations of *C. bosquianus*.

The zoogeography of the genus *Chasmodes* is discussed and recent geological information is used in a consideration of the events leading to its present distribution.

Experimental hybridization experiments were performed with *Chasmodes saburrae* and *C. b. longimaxilla*, but lack of adequate facilities prevented rearing the larvae.

RESUMEN: El género *Chasmodes* de peces blieniidos del Atlántico Occidental está representado por dos especies: *C. bosquianus* y *C. saburrae*. *C. saburrae* es la más tropical de las especies y se encuentra en la costa este de Florida, desde Edgewater hasta el extremo sur de Florida; y hacia el norte y este hasta las Islas Chandeleur, en Louisiana. *C. bosquianus* se compone de dos subespecies: *C. b. bosquianus* y *C. b. longimaxilla*.

C. b. bosquianus se distribuye cerca a las costas atlánticas desde Maryland a Marineland, en Florida; y *C. b. longimaxilla* se distribuye en la parte norte del Golfo de México, desde Pensacola en Florida, hasta Veracruz en México.

Chasmodes bosquianus longimaxilla exhibe desplazamiento de caracteres en la zona de simpatria con *C. saburrae* en el Golfo de México. El aumento de longitud maxilar en esta área podría contribuir a la divergencia observada en poblaciones disyuntivas de *C. bosquianus*.

Se discute la zoogeografía del género *Chasmodes*; así como información geológica reciente al considerar los eventos que conducen a su actual distribución.

Se llevaron a cabo experimentos de hibridación utilizando *Chasmodes saburrae* y *C. b. longimaxilla*, pero debido a la falta de facilidades adecuadas las larvas no pudieron ser criadas con éxito.

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¹The author is with the Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. The study was begun at the University of South Alabama, Mobile, and completed at the University of Florida, Gainesville, in partial fulfillment for the degree of Master of Science.

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INTRODUCTION

Chasmodes Valenciennes 1836 is a ditypic genus commonly encountered in bays and estuaries from Chesapeake Bay, Maryland, around the southern tip of Florida, and westward to Veracruz, Mexico. Although the species are usually found in salinities ranging from 15 to 25 ppt, one has been recorded from salinities as low as 5.5 ppt in Whitewater Bay, Florida (Springer 1959), and can survive salinities in excess of 35 ppt. They are usually found in grassbeds or over hard substrates permeated with small holes and crevices (such as oyster reefs and rock jetties) and have occasionally been collected over open mud or sand bottom (Springer 1959).

Springer (1959) reviewed the genus, but subsequent workers have experienced difficulty identifying specimens. The mandibular tooth and maxillary length characters Springer used permit identification of most adult specimens, but do not always provide a distinct separation when applied to young individuals or specimens from the eastern coast of Florida. My study describes several characters not discussed by Springer, which permit specific identification of any postlarval specimen of *Chasmodes* regardless of locality and presents a key to species and subspecies. Springer recognized the distinctness of the two species in the area of sympatry in the northern Gulf of Mexico, but offered no explanation for this phenomenon. A mechanism is proposed herein to explain how genetic integrity of the two species is maintained within this area. Springer's observation on the divergence of the Texas population of *C. bosquianus* is supported and, in addition, the northern Gulf of Mexico population is recognized as a distinct subspecies. Analysis of the Everglades population supports Springer's contention that this population is not taxonomically distinct from neighboring populations.

The two species of *Chasmodes* are of special interest from a zoogeographic point of view. Their distribution patterns coincide with those described for other fishes (e.g. Dawson 1964, Relyea 1965, Shipp and Yerger 1969, Hardy 1980) and help to define previously proposed faunal transition areas. In order to elucidate the zoogeographical implications of the distribution patterns, the evolutionary histories of the species are analyzed using geological and climatological evidence.

Since the original description of the genus *Chasmodes* in 1836, the only

comprehensive taxonomic treatment of the genus is that of Springer (1959), who recognized two species, *C. bosquianus* and *C. saburrae*. Bath (1977) assigned eastern Pacific species (*C. jenkinsi* and *C. maculipinna*) to *Hypsoblennius*. Springer and Gomon (1975) placed *C. herklotsi* in the synonymy of *Omobranchus fasciolatoceps*.

Norman (1943) provided a synopsis of the genera in the family Blenniidae. Included were three species in the genus *Chasmodes*: *C. bosquianus*, *C. novemlineatus*, and *C. maculipinna*. He apparently overlooked *C. saburrae*. Springer (1959) placed *C. novemlineatus* in the synonymy of *C. bosquianus*.

In an osteological analysis of the family Blenniidae, Spring (1968) mentioned *Chasmodes* several times, but only in regard to intergeneric relationships.

Bath (1977), in his review of the tribe Blenniini, analyzed phylogenetic relationships within the group. He suggested that *Chasmodes* serves as a link between the genera *Hypsoblennius* and *Hypleurochilus*, but he did not examine the relationship between the two species of *Chasmodes*.

In a review of the western Atlantic species of *Hypsoblennius*, Smith-Vaniz (1980) presented characters to distinguish *Chasmodes* from *Hypsoblennius* and *Hypleurochilus*.

Ecological studies dealing with *Chasmodes saburrae* appear in Reid (1954) and Springer and Woodburn (1960). Tavalga (1958) presented his results of studies on underwater sounds produced by specimens of *C. saburrae* (erroneously called *C. bosquianus*). Phillips (1971a, 1971b, 1974, 1977) reported on the social behavior and utilization of space by *C. bosquianus*.

Hildebrand and Cable (1938) presented information on the development and life history of *Chasmodes bosquianus*.

Additional references to the genus *Chasmodes* are in the form of geographical records and/or ecological notes (Weymouth [1910] for Louisiana; Baughman [1950] and Hoese [1958] for Texas; Tabb and Manning [1961] for Whitewater Bay, Florida; and Ogren and Brusher [1977] for northwest Florida).

In this paper, *Chasmodes bosquianus* (Lacépède 1800) and *C. saburrae* Jordan and Gilbert 1883 are considered valid species, and a new subspecies, *C. b. longimaxilla*, is described from the northern Gulf of Mexico.

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METHODS

Measurements were made with dial calipers and recorded to the nearest 0.1 mm. All counts and most measurements were made using a Wild M5 stereoscope. Meristic counts and morphometric measurements follow Hubbs and Lagler (1958) and Smith-Vaniz (1976). Maxillary length was measured from the tip of the snout to the posterior edge of the left maxilla. The edge was occluded from view by an opaque covering of skin. The posterior edge was located with a sharp probe or jewelers forceps. Counts of pores in the mandibular series (Fig. 1A, B) include all pores anterior to the narrow space between the preopercular and articular bones on each side of the head (Fig. 1). This space can usually be seen as a narrow translucent area immediately ventrad to the posterior edge of the maxilla. Caudal ray counts include all segmented rays. The branchiostegal membrane is broadly fused to the body and was cut on the right side to provide access to the branchial cavity. Counts of gill rakers and pseudobranchial filaments refer to those on the right side of the body. Gill raker counts include those rakers on the upper and lower limbs of the first arch (no rudiments were observed). Upper pharyngeal teeth are located by separating the second and third gill arches with jewelers forceps and, using illumination from beneath the specimen, are found in two small semicircular clusters on the posterodorsal roof of the branchial cavity. As the lower pharyngeal teeth must be dissected out of the specimen to be counted, my counts are based on examination of four specimens of each subspecies of *Chasmodes bosquianus* and eight specimens of *C. saburrae*. Vertebral counts were taken from radiographs and cleared and stained specimens. Precaudal vertebrae included vertebrae lacking a well-developed hemal spine. Caudal vertebrae include vertebrae with a well-developed hemal spine; posteriormost caudal vertebra bears the dorsal and ventral hypural plates.

Information regarding embryonic development and posthatching characters was obtained from eggs and larvae taken from experimental laboratory aquaria.

Numbers in parentheses in material examined sections refer to the number of specimens in that particular lot.

Linear regression equations and their correlation coefficients, and covariance comparisons (Sokal and Rohlf 1969) were computed using a covariance program written by Dr. S. A. Bloom (Zoology Department, University of Florida). Computations were made utilizing the facilities of the Northeast Regional Data Center of the State University System of Florida, located on the campus of the University of Florida. *F* values are not included for covariance comparisons presented in matrix form, but are available upon request.

Because of editorial problems, all the populations of each form are not differentiated in Figs. 3 and 4. Maxillary length as percent of SL is presented in tabular form for selected populations (Table 8). Graphs of the number of mandibular teeth vs. SL were prepared for each population to facilitate comparisons but are not included owing to space limitations.

Repositories, with abbreviations in parentheses, of specimens examined are: Academy of Natural Sciences of Philadelphia (ANSP), British Museum (Natural History) (BMNH), California Academy of Sciences (CAS-SU), Field Museum of Natural History (FMNH), Florida Department of Natural Resources, Marine Research Laboratory, St. Petersburg (FSBC),

Florida State Museum, University of Florida (UF), Florida State University (FSU), Grice Marine Biological Laboratory, College of Charleston, South Carolina (GMBL), Gulf Coast Research Laboratory, Ocean Springs, Mississippi (GCRL), Indian River Coastal Zone Study Reference Museum, Harbor Branch Foundation, Ft. Pierce, Florida (IRCZ), Museum National d'Histoire Naturelle, Paris (MNHN), Northeast Louisiana University, Baton Rouge, Louisiana (NLU), Texas Cooperative Wildlife Collection of Texas A&M University (TAMU), Tulane University (TU), University of Massachusetts (UMS), University of Miami Rosenstiel School of Marine and Atmosphere Sciences (UMML), University of Michigan Museum of Zoology (UMMZ), United States National Museum of Natural History (USNM), University of North Carolina, Morehead City (UNC), University of South Alabama Ichthyological Collection, Mobile (USAIC), University of Texas Institute of Marine Science (UTMSI), Virginia Institute of Marine Science (VIMS and CBL for specimens donated to VIMS by Chesapeake Biological Laboratory). The Florida fishes included in the GCRL material were from the Raney-Wang Collection donated to GCRL by the Mote Marine Laboratory.

GENUS *CHASMODES* VALENCIENNES 1836

Chasmodes Valenciennes (in Cuvier and Valenciennes) 1836: 295. (Type species: *Blennius bosquianus* Lacépède 1800 by original designation).
Blennitrachus Swainson 1839: 78, 274. (Type species: *Pholis quadrifasciatus* Wood 1825, by original designation).

A genus of blennioid fish (*sensu* Springer 1968) characterized by dorsal elements X to XII, 16-20 (XI spines in 99% of specimens examined, usually 18 or 19 rays; Table 1), occasionally 2 or 3 rays bifurcate; anal elements II, 16-20 (usually 18 or 19 rays; Table 1); pectoral-fin rays 11 to 13 (99% of specimens examined have 12); segmented caudal-fin rays 10 to 13 (99% of those examined have 11, one specimen has 9 due to an anomalous condition); branched caudal-fin rays 0-10; dorsal procurrent caudal-fin rays 4-5; ventral procurrent caudal-fin rays 3-5; precaudal vertebrae 10; caudal vertebrae 24-26; epipleural ribs 12; branchiostegal rays 6; teeth in jaws typically uniserial and uniformly spaced; one specimen examined has two teeth immediately behind uniserial row of teeth in anterior portion of lower jaw. This is probably anomalous, as various anomalies were observed in other specimens. Mandibular teeth distributed over approximately anterior half of dentary; premaxillae toothed over anterior three-quarters; vomer and palatines toothless; upper pharyngeals each have 5-7 enlarged canines and 0 to 5 small canines; each lower pharyngeal has 4-6 enlarged canines and 4-6 small ones, number of enlarged canines on upper pharyngeals relatively constant, but count of small pharyngeal teeth highly variable (Table 1); gill openings restricted by broad fusion of branchiostegal membranes with body, opening never extends ventrad below ventral level of pectoral-fin base.

Chasmodes is, perhaps, unique in the blennioid tribe Blenniini, in having the ventral hypural plate fused to the complex urostylar centrum (Peters 1981; Springer, pers. comm.). Springer (1968) erroneously reported that the ventral plate was autogenous in *Chasmodes*.

Lateral line development is described by Bath (1977). He refers to the development of the lateral line as "type C," which is a reduced form of the lateral line consisting anteriorly of alternating narrow branches from the main canal. This branching pattern terminates immediately behind the pectoral-fin base, and the lateral line continues posteriorly in the form of short straight tubes to its terminus at about the middle of the body.

Primary sexual dimorphism is in the form of a greatly reduced first anal spine in females, and in nuptial males having enlarged, fleshy structures with many longitudinal folds present on both anal spines (see Smith-Vaniz 1980: Fig. 1b).

Secondary sexual dimorphism was found in color pattern (see discussion of coloration), maximum length, and maxillary length (in some populations of *Chasmodes saburrae*). The SL of the largest male in any given population of *Chasmodes* exceeds that of the largest female by 2 to as much as 25 mm. This difference in length may be related to territory maintenance by males.

Statistical analysis of the maxillary length character (Tables 2, 3) revealed a significant sexual difference in 4 of 7 populations of *Chasmodes saburrae*, but no significant sexual dimorphism was found in populations of *C. bosquianus*. A similar analysis of the number of mandibular teeth (Tables 2, 3) showed no sexual dimorphism for any population of *Chasmodes*. I am unable to explain the appearance of sexually dimorphic maxillary lengths in only 4 of the 7 populations of *C. saburrae* tested. The biological significance of this sexual dimorphism is unknown.

Coloration shows no variation among the species and subspecies. Coloration of males varies from light lines running longitudinally on a dark background to a mottled pattern. Females of all sizes are variously mottled. In life, territorial adult males have light longitudinal lines on an olivaceous background with an iridescent blue spot on the membrane between the first and second dorsal spines and an orange streak extending posteriorly from this spot to about the tenth dorsal spine. The chest and branchiostegal membranes of these males are orange. Females, immature males, and non-territorial males have dark brown and white mottled pigmentation. (Information on coloration is modified from Springer [1959].)

KEY TO THE SPECIES AND SUBSPECIES OF *CHASMODES*

- A. Pores in both mandibular series combined usually 6 or more (Figure 1B and Table 1), if less than 6, then lower jaw with prominent lip flaps (Figure 1B); mandibular teeth with broadly rounded tips (Figure 2A) in specimens over 35 mm SL *saburrae* (Edgewater, Florida, to Chandeleur Islands, Louisiana).
- AA. Pores in both mandibular series combined usually 4 (occasionally 5 or 6; Figure 1A and Table 1), if more than 4, then lower jaw without prominent lip flaps (Figure 1A); mandibular teeth with sharply pointed tips (Figure 2B) in specimens of any length ... B

- B. Maxillary length usually 13 to 16.5% SL (range 11-18.5%, \bar{X} = 14.9%; Table 4); gill rakers modally 12 (Table 1); total number of small upper pharyngeal teeth 1-6 (Table 1) *bosquianus bosquianus* (New York to Marineland, Florida).
- BB. Maxillary length usually 15.5 to 20% SL (range 14-22.5%, \bar{X} = 17.3%; Table 4); gill rakers modally 11 (Table 1); total number of small upper pharyngeal teeth usually 0-1 in specimens over 40 mm SL, 2-5 in those under 40 mm SL (Table 1) *bosquianus longimaxilla* new subspecies (Pensacola, Florida, to Veracruz, Mexico).

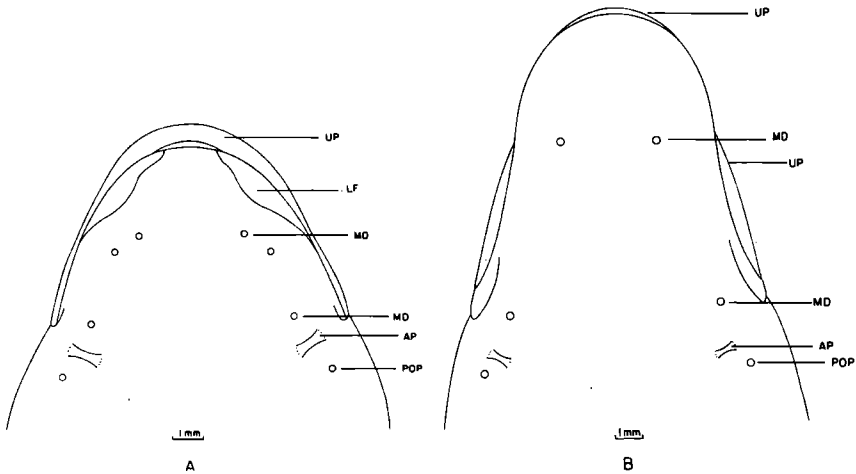


FIGURE 1.—Ventral aspect of lower jaw of *Chasmodes bosquianus* (A) and *C. saburrae* (B). Abbreviations are as follows: UP = upper lip, LF = lip flap, MD = mandibular pore (anterior and posterior pores are indicated on one side of the lower jaw), AP = space between the articular and preopercular bones, POP = preopercular pore.

CHASMODES BOSQUIANUS (LACÉPÈDE 1800)
 (See individual subspecies for synonymy)

DIAGNOSIS—*Chasmodes bosquianus* is readily distinguished from *C. saburrae* in usually having 4 (vs. 6) mandibular pores (83% of specimens examined of each species have these counts; Fig. 1A, B and Table 1). *C. bosquianus* typically lacks lip flaps, whereas *C. saburrae* has well-developed lip flaps (Fig. 1A, B). *C. bosquianus* can also be separated from *C. saburrae* by having 9-13 (vs. 12-14) gill rakers on the first arch (visible only upon dissection; Table 1). Dissected specimens of *C. bosquianus* have 4 enlarged canines on the lower pharyngeals, whereas *C. saburrae* has 6.

STATISTICAL COMPARISONS.—Pairwise covariance comparisons were made between regression equations (Table 2) for males of each population of *Chasmodes saburrae* and males of each population of *C. bosquianus*, and the same was done for females of each population. The resulting maxillary length comparisons showed statistically significant ($p < 0.001$)

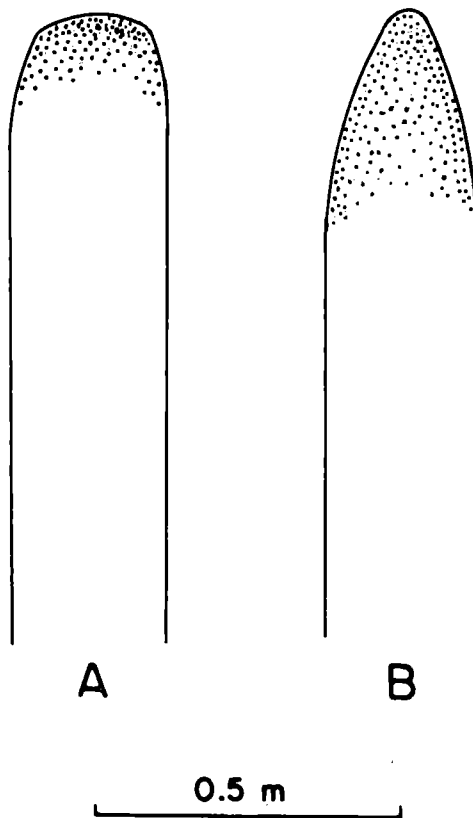


FIGURE 2.—Frontal view of an anterior mandibular tooth from *Chasmodes saburrae* (A) and *C. bosquianus* (B). Stippled area indicates curved portion of teeth.

differences in every interspecific comparison. The lack of statistically significant sexual dimorphism in the number of mandibular teeth (Table 3) enabled covariance comparisons of regression equations (Table 5) for entire populations (males and females). All populations of *C. saburrae* had significantly fewer mandibular teeth than populations of *C. bosquianus* (Table 6).

Chasmodes bosquianus bosquianus (LACÉPÈDE)

Blennius bosquianus Lacépède 1800: 495 (Type locality: South Carolina; holotype lost?).

Pholis novemlineatus Wood 1825:280 (Type locality: Charleston Harbor, South Carolina; holotype ANSP 10410).

Pholis quadrifasciatus Wood 1825:282 (Type locality: unknown; holotype lost?).

Table 1—Frequency distributions for certain characters in species and subspecies of *Chasmodes*. (Holotype of new subspecies is designated by a ° for characters not requiring dissection.)

Species	Segmented dorsal-fin rays					Total dorsal-fin elements					Segmented anal-fin rays					Caudal vertebrae									
	16	17	18	19	20	27	28	29	30	31	16	17	18	19	20	24	25	26							
<i>saburrae</i>	1	1	14	5	1	1	1	13	6	1		1	14	3	2	15	7	2							
<i>bosquianus</i>			3	24	12	2		3	24	12	2		1	4	19	13	3								
<i>b. longimaxilla</i>	1	1	27°	5				9	27°	5		1	6	23°	9	1	6	5							
Species	Enlarged upper pharyngeal teeth (both sides included)					Small upper pharyngeal teeth (both sides included)										Specimens <40 mm SL					Dorsal + ventral procurrent caudal-fin rays				
	10	11	12	13	14	0	1	2	3	4	5	6	7	8	9	10	2	3	4	5	6	7	8	9	10
<i>saburrae</i>	3	4	17	6	1	1	1	—	7	7	3	2	1	—	1	2	—	3	2	1	6	10	2	1	
<i>bosquianus</i>			2	17	1				2	3	1	7	2	2		1	—	—	—	2	4	8	1		
<i>b. longimaxilla</i>	1	1	18	1	1	5	2	1	1	1	1					1	6	1	3		6	8	2		
Species	Pseudobranchial filaments							Gill rakers							Number of mandibular pores										
	8	9	10	11	12	13	14	9	10	11	12	13	14	4	5	6	7	8	X						
<i>saburrae</i>		6	15	5	—	2	1				8	13	10	5	33	560	69	6	6.0						
<i>bosquianus</i>											7	12	4	136	23	10			4.3						
<i>b. longimaxilla</i>	4	5	6	6	2			1	5	17	2			103°	13	1			4.1						

Table 2—Regression equations, correlation coefficients (r), and probability values ($P <$) for maxillary length and number of mandibular teeth (Y) versus standard length (X) for males and females within populations of *Chasmodes*.

Species, population, sex	N	Regression equation maxillary length	r	$P <$	Regression equation mandibular teeth	r	$P <$
<i>bosquianus bosquianus</i>							
Marineland, Florida							
males	16	$Y = -0.9520 + 0.1669X$	0.959	0.01	$Y = 20.3108 + 0.4950X$	0.920	0.01
females	21	$Y = 0.0840 + 0.1399X$	0.862	0.01	$Y = 22.5687 + 0.4458X$	0.718	0.01
N. E. Florida and Georgia							
males	8	$Y = -2.6378 + 0.2059X$	0.970	0.01	$Y = 21.1373 + 0.4911X$	0.773	0.05
females	7	$Y = -0.1528 + 0.1416X$	0.997	0.01	$Y = 24.9190 + 0.4209X$	0.789	0.05
South Carolina							
males	10	$Y = -1.4728 + 0.1842X$	0.962	0.01	$Y = 18.8009 + 0.5621X$	0.854	0.01
females	10	$Y = -0.1885 + 0.1528X$	0.918	0.01	$Y = 21.2808 + 0.5150X$	0.838	0.01
North Carolina							
males	22	$Y = -1.3193 + 0.1803X$	0.972	0.01	$Y = 21.6752 + 0.4948X$	0.808	0.01
females	11	$Y = -0.7484 + 0.1608X$	0.986	0.01	$Y = 14.7354 + 0.6340X$	0.913	0.01
Chesapeake Bay to New York							
males	51	$Y = -1.9534 + 0.1910X$	0.964	0.01	$Y = 18.4520 + 0.4753X$	0.867	0.01
females	48	$Y = -0.9159 + 0.1650X$	0.971	0.01	$Y = 18.8321 + 0.4779X$	0.911	0.01
<i>bosquianus longimaxilla</i>							
Pensacola, Florida to Louisiana							
males	20	$Y = -1.6030 + 0.2164X$	0.943	0.01	$Y = 25.5717 + 0.4622X$	0.921	0.01
females	11	$Y = -4.4562 + 0.2631X$	0.962	0.01	$Y = 27.0016 + 0.4493X$	0.770	0.02
Matagorda Bay area, Texas							
males	25	$Y = -1.2860 + 0.2072X$	0.928	0.01	$Y = 31.5014 + 0.3560X$	0.711	0.01
females	8	$Y = -0.7269 + 0.1830X$	0.984	0.01	$Y = 28.5067 + 0.4183X$	0.963	0.01

Aransas Bay area, Texas								
males	12	$Y = -1.3109 + 0.1928X$	0.948	0.01	$Y = 31.5834 + 0.3215X$	0.714	0.02	
females	16	$Y = -1.5726 + 0.2063X$	0.983	0.01	$Y = 26.2605 + 0.4383X$	0.915	0.01	
Southern Laguna Madre, Texas								
males	25	$Y = -1.2872 + 0.1950X$	0.970	0.01	$Y = 15.7722 + 0.6451X$	0.934	0.01	
females	21	$Y = -1.1026 + 0.1857X$	0.962	0.01	$Y = 17.7885 + 0.6597X$	0.828	0.01	
<i>saburrae</i>								
Louisiana to Pensacola, Florida								
males	43	$Y = -0.6861 + 0.1340X$	0.982	0.01	$Y = 16.7828 + 0.3289X$	0.894	0.01	
females	60	$Y = -0.0690 + 0.1116X$	0.966	0.01	$Y = 13.1644 + 0.4274X$	0.880	0.01	
Ft. Walton area to Cedar Key, Florida								
males	116	$Y = -0.7615 + 0.1339X$	0.984	0.01	$Y = 14.0077 + 0.3906X$	0.903	0.01	
females	82	$Y = -0.1677 + 0.1139X$	0.981	0.01	$Y = 14.4744 + 0.3773X$	0.926	0.01	
Tampa Bay area								
males	55	$Y = -0.8562 + 0.1395X$	0.986	0.01	$Y = 13.3902 + 0.4070X$	0.928	0.01	
females	45	$Y = -0.1698 + 0.1170X$	0.982	0.01	$Y = 13.4447 + 0.4362X$	0.924	0.01	
Charlotte Harbor								
males	18	$Y = -0.6510 + 0.1357X$	0.996	0.01	$Y = 16.8821 + 0.3266X$	0.939	0.01	
females	17	$Y = 0.4354 + 0.1257X$	0.990	0.01	$Y = 14.6048 + 0.4007X$	0.934	0.01	
Everglades								
males	28	$Y = -0.4289 + 0.1269X$	0.951	0.01	$Y = 15.0054 + 0.4161X$	0.844	0.01	
females	18	$Y = 0.1629 + 0.1086X$	0.966	0.01	$Y = 12.1411 + 0.5037X$	0.914	0.01	
Biscayne Bay area								
males	6	$Y = -0.9597 + 0.1428X$	0.982	0.01	$Y = 14.4144 + 0.3866X$	0.977	0.02	
females	9	$Y = 0.1289 + 0.1026X$	0.949	0.01	$Y = 15.1999 + 0.3449X$	0.907	0.01	
Indian River area								
males	29	$Y = -0.5455 + 0.1373X$	0.992	0.01	$Y = 13.6418 + 0.4745X$	0.966	0.01	
females	26	$Y = 0.1782 + 0.1082X$	0.991	0.01	$Y = 13.8857 + 0.4654X$	0.941	0.01	

Table 3—*F* values for covariance comparisons of regression equations (Table 2) of maxillary length and number of mandibular teeth between males and females within populations of *Chasmodes* (** = $P < .001$; NS = not significant). *F* values for testing parallelism of the regression lines are given only when the lines are not coincident.

Species, population	Abbreviation	<i>df</i>	<i>F</i> values coincidence	<i>df</i>	<i>F</i> values parallel
<i>bosquianus bosquianus</i>					
Marineland, Florida	BM				
maxillary length		2/35	1.16 NS		
mandibular teeth		2/35	0.10 NS		
N. E. Florida and Georgia	BF				
maxillary length		2/13	4.47 NS		
mandibular teeth		2/13	0.07 NS		
South Carolina	BS				
maxillary length		2/18	0.82 NS		
mandibular teeth		2/18	0.04 NS		
North Carolina	BN				
maxillary length		2/31	3.18 NS		
mandibular teeth		2/31	0.66 NS		
Chesapeake Bay to New York	BC				
maxillary length		2/97	6.16 NS		
mandibular teeth		2/97	0.32 NS		
<i>bosquianus longimaxilla</i>					
Pensacola, Florida to Louisiana	LS				
maxillary length		2/29	0.79 NS		
mandibular teeth		2/29	0.12 NS		
Matagorda Bay area, Texas	LM				
maxillary length		2/31	3.64 NS		
mandibular teeth		2/31	0.27 NS		
Aransas Bay area, Texas	LA				
maxillary length		2/26	1.38 NS		
mandibular teeth		2/26	0.62 NS		

Southern Laguna Madre Bay, Texas	LL				
maxillary length		2/44	0.99 NS		
mandibular teeth		2/44	3.43 NS		
<i>saburrae</i>					
Louisiana to Pensacola, Florida	SS				
maxillary length		2/101	16.71 **	1/101	15.85 **
mandibular teeth		2/101	3.33 NS		
Ft. Walton area to Cedar Key, Florida	SN				
maxillary length		2/196	33.72 **	1/196	30.68 **
mandibular teeth		2/196	0.19 NS		
Tampa Bay area	ST				
maxillary length		2/98	10.88 **	1/98	17.80 **
mandibular teeth		2/98	4.58 NS		
Charlotte Harbor	SC				
maxillary length		2/33	3.35 NS		
mandibular teeth		2/33	1.11 NS		
Everglades	SE				
maxillary length		2/44	4.18 NS		
mandibular teeth		2/44	2.03 NS		
Biscayne Bay area	SM				
maxillary length		2/13	4.37 NS		
mandibular teeth		2/13	0.51 NS		
Indian River area	SF				
maxillary length		2/53	25.39 **	1/53	34.99 **
mandibular teeth		2/53	0.03 NS		

Table 4—Frequency distribution of maxillary length expressed as percent of standard length in *Chasmodes bosquianus*.

Maxillary Length as % SL	<i>C. b. longimaxilla</i>		
	<i>C. b. bosquianus</i>	Florida, Mississippi, Louisiana	Texas
12.5	6		
13.0	9		
13.5	13		
14.0	28	1	1
14.5	32		4
15.0	34		3
15.5	29	1	13
16.0	15		11
16.5	11	1	9
17.0	5	1	12
17.5	3	3	11
18.0	2	2	13
18.5	2	2	4
19.0		3	9
19.5		3	1
20.0		2	6
20.5		3	1
21.0		1	
21.5		1	
22.0		1	
22.5		2*	

*indicates the holotype

DIAGNOSIS.—*Chasmodes bosquianus bosquianus* differs from *C. b. longimaxilla* in having a shorter maxillary length (\bar{X} = 14.9 vs. 17.3% SL; Fig. 3, Table 4), and in having a total of 1-6 small canines (Table 1) in addition to enlarged canines on upper pharyngeals, whereas *C. b. longimaxilla* has 0-5 (most specimens examined over 40 mm SL with 0-1). Gill rakers 11-13 (modally 12) for *C. b. bosquianus* vs. 9-12 (modally 11) for *C. b. longimaxilla* (Table 1).

DESCRIPTION.—(See also Table 1). Maxillary length expressed as percent of SL 12.5-18.5 (\bar{X} = 14.9%, number [n] = 189; Table 4); number of mandibular teeth varies ontogenetically, number increasing with increased size (Fig. 4); mandibular pores 4 to 6 (\bar{X} = 4.3, n = 169; Table 1); enlarged upper pharyngeal teeth 6 or 7 on each side; branched caudal-fin rays 0-10; small upper pharyngeal teeth 0-4 on each side (Table 1); enlarged lower pharyngeal teeth 4 (n = 4); maximum size approximately 80 mm SL.

Twelve larvae (5.4 to 7.3 mm SL) have 5 to 7 spines radiating posteriorly from preopercle, with spine at angle of preopercle enlarged. Small mandibular teeth range in number from approximately 8 to 12. Maxillary length

Table 5—Regression equations, correlation coefficients (r), and probability values ($P <$) for maxillary length and number of mandibular teeth (Y) versus standard length (X) for those populations (males and females combined) of *Chasmodes* in Table 3 showing no significant sexual dimorphism in these characters. (Species and populations are designated using the abbreviation in Table 3.)

Species, population	N	Regression equation maxillary length	r	$P <$	Regression equation mandibular teeth	r	$P <$
BM	37	$Y = -0.9274 + 0.1648X$	0.950	0.01	$Y = 21.0121 + 0.4817X$	0.887	0.01
BF	15	$Y = -1.9437 + 0.1924X$	0.985	0.01	$Y = 23.8910 + 0.4453X$	0.882	0.01
BS	20	$Y = -1.0009 + 0.1735X$	0.950	0.01	$Y = 20.2408 + 0.5368X$	0.865	0.01
BN	33	$Y = -1.3681 + 0.1796X$	0.980	0.01	$Y = 18.0279 + 0.5608X$	0.886	0.01
BC	99	$Y = -1.6662 + 0.1838X$	0.969	0.01	$Y = 19.0285 + 0.4688X$	0.896	0.01
LS	31	$Y = -2.1628 + 0.2253X$	0.945	0.01	$Y = 26.0300 + 0.4585X$	0.886	0.01
LM	33	$Y = -1.7690 + 0.2126X$	0.963	0.01	$Y = 30.3805 + 0.3748X$	0.859	0.01
LA	28	$Y = -1.3976 + 0.1987X$	0.970	0.01	$Y = 27.8290 + 0.4008X$	0.859	0.01
LL	46	$Y = -1.5185 + 0.1980X$	0.976	0.01	$Y = 19.6115 + 0.5889X$	0.901	0.01
SS	103				$Y = 15.5021 + 0.3599X$	0.894	0.01
SN	198				$Y = 14.1252 + 0.3874X$	0.920	0.01
ST	100				$Y = 14.0308 + 0.4022X$	0.921	0.01
SC	35				$Y = 16.3956 + 0.3416X$	0.938	0.01
SE	46				$Y = 14.9886 + 0.4242X$	0.871	0.01
SM	15				$Y = 13.9553 + 0.3857X$	0.963	0.01
SF	55				$Y = 13.7037 + 0.4722X$	0.961	0.01

varies from 8.5 to 10% SL ($\bar{X} = 9.1\%$, $n = 12$). Twelve pectoral-fin rays present in all larvae.

Larvae exhibit the following pigment pattern in alcohol: membrane between lower 6 pectoral rays pigmented to tips, membranes between sixth-seventh and seventh-eighth rays pigmented only on inner half and fourth respectively, with outer portion of membrane transparent; membrane covering brain with several large pigment spots; two pigment spots on either side of tip of upper jaw, immediately anterior to orbital margin; a pigment spot at dorsal edge of each opercle at upper angle of gill opening.

Table 6—Matrix of covariance comparisons of regression equations (Table 5) for number of mandibular teeth between different populations of *Chasmodes* ($P < 0.001$; see Table 3 for explanation of abbreviations). 0 = coincident regression lines; - = noncoincident but parallel lines; + = noncoincident and nonparallel lines.

	BM	BF	BS	BN	BC	LS	LM	LA	LL	SS	SN	ST	SC	SE	SM	SF
BM		0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
BF			0	0	-	0	0	0	0	-	-	-	-	-	-	-
BS				0	-	0	0	0	0	+	-	-	-	-	-	-
BN					-	0	0	0	-	+	+	+	+	-	-	-
BC						-	-	-	-	+	+	-	-	-	-	-
LS							0	0	0	-	-	-	-	-	-	-
LM								0	0	-	-	-	-	-	-	-
LA									0	-	-	-	-	-	-	-
LL										+	+	+	+	-	-	-
SS											0	0	0	-	0	+
SN												0	0	-	0	+
ST													0	-	0	-
SC														-	0	+
SE															-	0
SM																-
SF																

STATISTICAL COMPARISONS.—The results of statistical comparisons of the populations of *Chasmodes bosquianus* are summarized in Tables 6 and 7. Populations of *C. b. bosquianus* have significantly shorter maxillary lengths than populations of *C. b. longimaxilla* (Table 7). No consistent statistical differences were obtained for the number of mandibular teeth between *C. b. bosquianus* and *C. b. longimaxilla* populations (Table 6). Two populations of *C. b. bosquianus* (Chesapeake Bay area and Marineland) have significantly fewer mandibular teeth than all populations of *C. b. longimaxilla*. The North Carolina population of *C. b. bosquianus* significantly differs in number of mandibular teeth from only one population (Laguna Madre) of *C. b. longimaxilla*. Comparisons of the number of mandibular teeth between other populations of the two subspecies did not show significantly different regression equations for number of mandibular

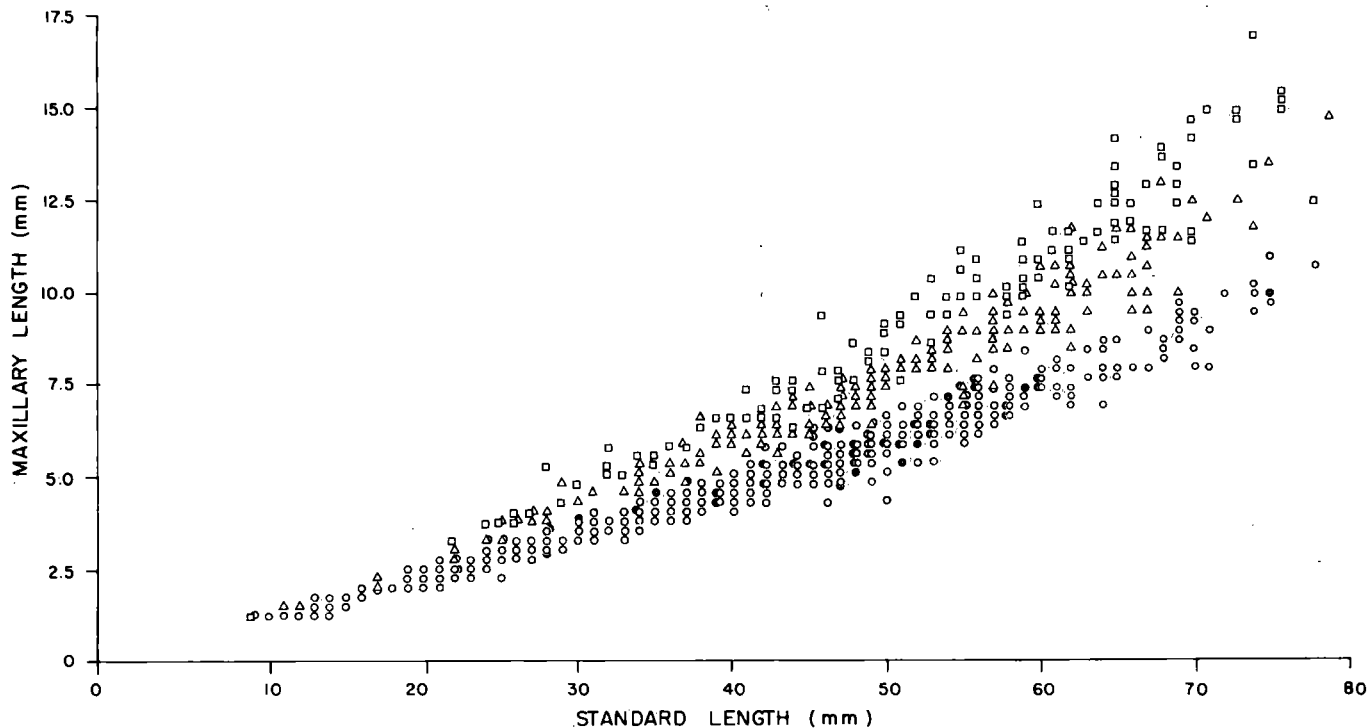


FIGURE 3.—Graph of maxillary length vs. standard length for *Chasmodes*: *C. saburrae*, circles, closed circles represent Everglades specimens; *C. bosquianus bosquianus*, triangles; *C. b. longimaxilla*, squares.

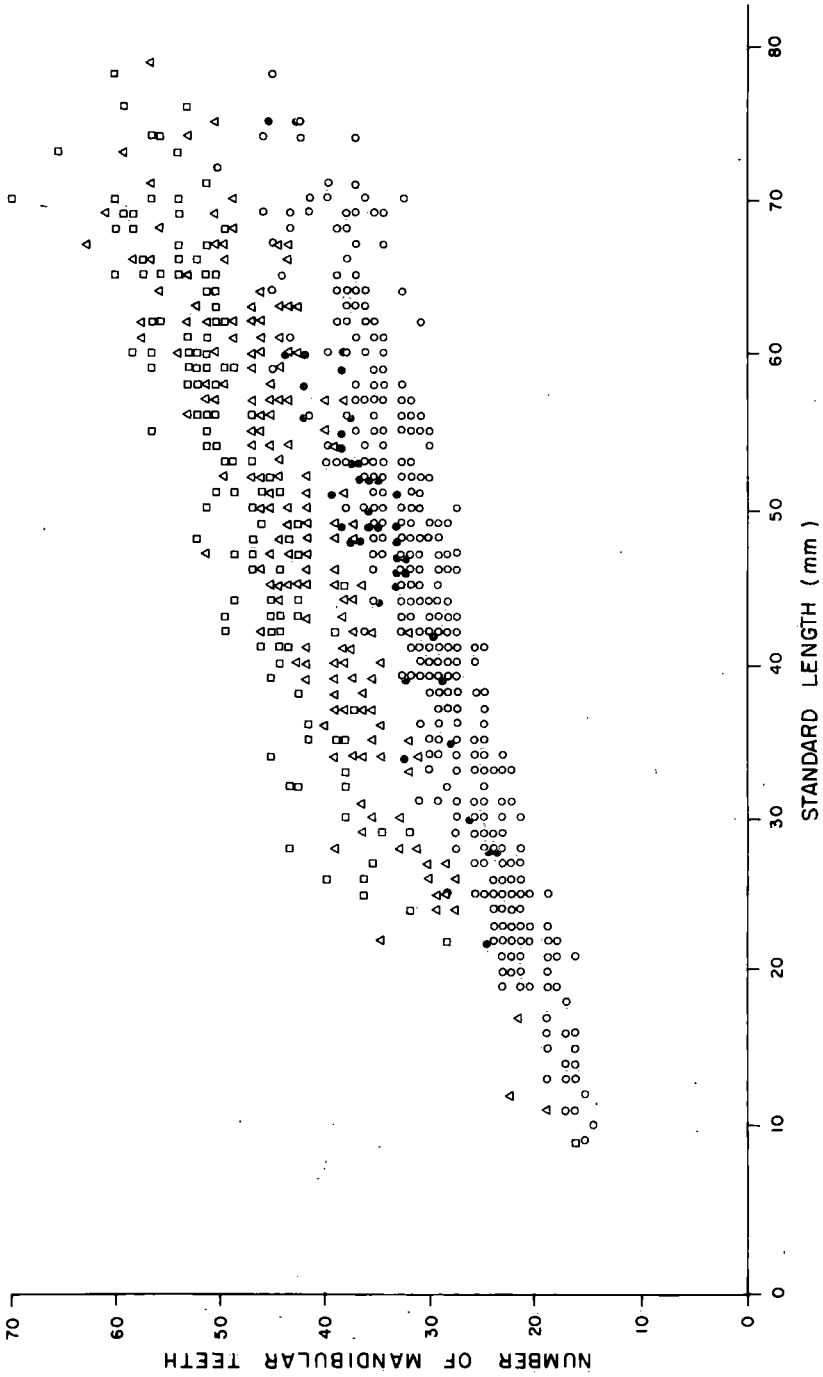


FIGURE 4.—Graph of number of mandibular teeth vs. standard length for *Chasmodes*: (symbols as in Fig. 3).

Table 7—Matrix of covariance comparisons of maxillary length regression equations (Table 5) for populations of *Chasmodes bosquianus bosquianus* and *C. b. longimaxilla* ($P < 0.001$). 0 = coincident lines; - = noncoincident but parallel lines; + = noncoincident and nonparallel lines. (Population abbreviations defined in Table 3.)

	BM	BF	BS	BN	BC	LS	LM	LA	LL
BM		0	0	0	0	-	-	-	-
BF			0	0	0	-	-	-	-
BS				0	0	-	-	-	-
BN					0	-	-	-	-
BC						+	-	-	-
LS							0	0	-
LM								0	0
LA									0
LL									

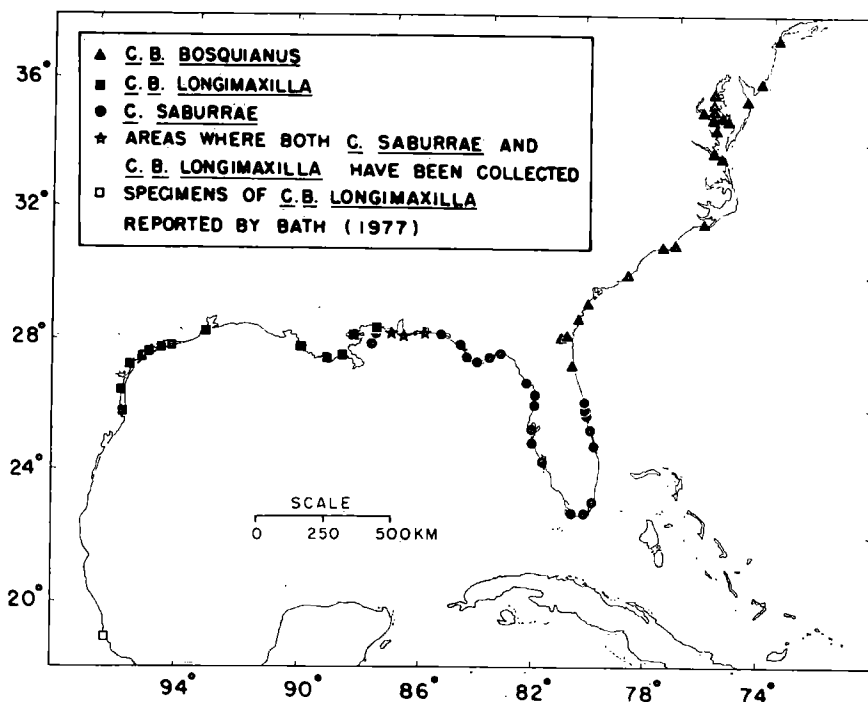


FIGURE 5.—Distributional records for species and subspecies of *Chasmodes*. Grand Terre, Louisiana, record based on University of Southwestern Louisiana specimen (cat. no. 3496) not included in material examined.

teeth.

Comparisons of regression equations for maxillary length (Table 5) show no statistically significant differences between populations of *C. b. bosquianus* (Table 7). Significant differences were found for comparisons

of regression equations for number of mandibular teeth between populations of *C. b. bosquianus* (Table 6). The Chesapeake Bay area population has significantly fewer mandibular teeth (Tables 5, 6) than other populations of this subspecies. I believe that this difference is due to a collecting bias. I was unable to locate specimens of *Chasmodes* from the Cape Hatteras area (Fig. 5), but the fact that *C. b. bosquianus* usually is found in an estuarine habitat, makes it probable that the extensive estuaries of the Cape Hatteras area support this form. An analysis of specimens from this area is needed to determine the nature of the relationship of the Chesapeake Bay area population to the other populations of *C. b. bosquianus*.

DISCUSSION OF SYNONYMY.—Examination of the holotype of *Pholis novemlineatus* Wood 1825 substantiates Springer's (1959) conclusion that this species is a synonym of *Chasmodes bosquianus*. Based on the maxillary length, the mandibular tooth count, and the type locality, I identify this form as *C. b. bosquianus*.

The holotype of *Pholis quadrifasciatus* Wood 1825 is missing (lost?). Only two meristic characters (caudal and anal ray counts) given in the original description vary from those of *C. bosquianus*. The count of 9 caudal-fin rays and 15 anal-fin rays for *P. quadrifasciatus* are below the minimum for *Chasmodes*, but it is not uncommon for specimens of *Chasmodes* to have anomalous fin ray counts. If Wood included only branched rays in his caudal-fin ray count, the count of 9 lies within the observed range (0-10) for the genus *Chasmodes*. Inasmuch as all other characters, including color pattern, agree with those of *C. b. bosquianus*, I believe that the original anal-fin count for *P. quadrifasciatus* was either in error or anomalous. The original description and illustration of *P. quadrifasciatus* leave no doubt that this is a specimen of *C. bosquianus*. I tentatively place *P. quadrifasciatus* in the synonymy of *C. b. bosquianus*, because it is probable that the holotype was collected on the Atlantic coast (Wood having obtained it from a museum in Baltimore).

ECOLOGY AND DISTRIBUTION.—*Chasmodes bosquianus bosquianus* is found primarily in bays and estuaries of the Atlantic seaboard. As is true of the genus as a whole, it usually inhabits waters with salinities between 15 and 25 ppt. The only reliable record of its capture in lower salinities is that of Dr. William D. Anderson, Jr. Two specimens (27 and 35 mm SL) were collected in Charleston Harbor 4 May 1971 in water with a salinity of 9.7 ppt.

Hildebrand and Cable (1938) stated that the spawning season extends from May to August. Acquisition of several 5-7 mm larval *Chasmodes bosquianus bosquianus* collected in Boque Sound, North Carolina, on 23 April 1957 indicates that the spawning season begins much earlier, probably in mid-March.

I have examined only five specimens of *Chasmodes bosquianus bos-*

quianus from waters north of Chesapeake Bay, Maryland: three from Delaware, one from New Jersey, and one from New York. The last is the northernmost record. All likely are stragglers to these areas, as they were collected either in late summer or early fall, which would have allowed sufficient time at sufficiently high temperature for migration or passive larval transport to these northern waters. *C. b. bosquianus* is primarily distributed from Chesapeake Bay, Maryland, south to Marineland, Florida. I have identified, as *C. b. bosquianus*, one specimen from a series of *C. saburrae* (USNM 48783) from Indian River, Florida. If this specimen was not erroneously mixed with this lot (collection date: 14 January 1896), it is the only record of sympatric occurrence of *C. b. bosquianus* with *C. saburrae*, and is the only record of *C. b. bosquianus* south of Marineland, Florida.

MATERIAL EXAMINED.—TYPES: ANSP 10410 (1), Charleston Harbor, South Carolina, holotype of *Pholis novemlineatus* Wood. NEW YORK: MNHN A-2206 (1). NEW JERSEY: UMMZ 109932 (1). DELAWARE: USNM 187154 (1), UMS 24-598-5-1 (1), 24-589-5-3 (1). MARYLAND: FSU 17747 (4), USNM uncatalogued (2), 68180 (1), 74857 (1), 91140 (1), 91149 (5), 91150 (17), 100728 (1), 116659 (1), 201352 (8), 205137 (1), CBL 1952 (2), 1971 (2), 1990 (4), 2320 (2), 2387 (12), 2390 (4), 2501 (26), 3601 (1), 4043 (3). VIRGINIA: USNM 91141 (2), 91146 (4), 91151 (1), 116660 (1), 156651 (6), VIMS 559 (1), 879 (1), 881 (3), 2694 (2). NORTH CAROLINA: USNM 198245 (2), UF 28282 (1), 28283 (1), 28284 (1), 28285 (1), 28286 (4), 28287 (3), 28288 (1), 28296 (1), UNC 36 (1), 1114 (3), 1472 (1), 1817 (2), 2065 (4), 2154 (2), 3846 (3), 6262 (3), 6279 (1), 6348 (2), 8510 (1), 8562 (2), 8558 (1), 9630 (1), 10430 (1). SOUTH CAROLINA: USNM 195819 (1), GMBL 70-23 (1), 70-157 (1), 71-67 (2), 71-85 (1), 71-110 (5), 74-173 (9), 152-FB-69 (1). GEORGIA: UF 23684 (3), USNM 91976 (1), 127459 (1), UMML uncatalogued (3), uncatalogued (1), uncatalogued (4). FLORIDA: ANSP 106142 (12), FSBC 15 (1), 17 (19), 21 (2), 22 (15), UF 11795 (2), 11797 (1).

Chasmodes bosquianus longimaxilla NEW SUBSPECIES

FIGURE 6

DIAGNOSIS.—*Chasmodes bosquianus longimaxilla* differs from *C. b. bosquianus* and *C. saburrae* in having 0-1 (range 0-5) total small upper pharyngeal teeth in most specimens over 40 mm SL (2-5 in specimens under 40 mm SL) vs. 1-10 in its congeners (Table 1), and in having a significantly longer maxillary length (17.3% SL versus 14.9 and 11.3% SL, respectively; Fig. 3, Tables 4, 8). Gill rakers 9-12 (modally 11) vs. 11-13 (modally 12) for *C. b. longimaxilla* and *C. b. bosquianus* respectively.

DESCRIPTION (See also Table 1).—Characters appearing in the generic description and subspecies diagnoses are not repeated here. In addition, the maxillary length varies from 14 to 22.5% SL (\bar{X} = 17.3% SL, n = 125;

Table 8—Frequency distribution with respect to maxillary length expressed as percent of standard length (specimens >30 mm SL) for selected populations of *Chasmodes*. *C. b. l.* = *Chasmodes bosquianus longimaxilla*; *C. b. b.* = *C. b. bosquianus*; *C. s.* = *C. saburrae*.

Maxillary Length as % SL	Southern Texas coast		Central Texas coast		Area of Sympatry								Allopatric East Coast Populations					
					Miss. Sd. & Mobile Bay				Pensacola, Fl.				N. W. Fl.		Indian River area, Fl.		Marineland, Fl.	
	<i>C. b. l.</i>		<i>C. b. l.</i>		<i>C. b. l.</i>		<i>C. s.</i>		<i>C. b. l.</i>		<i>C. s.</i>		<i>C. s.</i>		<i>C. s.</i>		<i>C. b. b.</i>	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
9.0										-	1							
9.5										-	-			-	2			
10.0							-	1		-	1	2	7	-		1		
10.5							-	1		1	8	10	30	-		1		
11.0							4	13		2	5	33	32	3		8		
11.5							4	6		5	3	49	14	2		4		
12.0							3	3		4	2	29	7	3		1		
12.5							2	-		4*	-	19	2	4		-		3
13.0							1	-		1	-	12	-	5		-	1	2
13.5												2	-	1		-	1	2
14.0			1	-					-	1				1		-	2	2
14.5		3	1	-					-	-						-	3	6
15.0	1	-	-	2					-	-						-	2	3
15.5	3	4	2	4					1	-						-	3	2
16.0	2	5	2	2												-	2	-
16.5	2	4	2	1	1	-										-	-	1
17.0	5	2	2	3	1	-										-	1	-
17.5	3	-	5	3	-	3										-	-	-
18.0	4	1	6	2	2	-										-	-	-
18.5	1	-	3	-	2	-										-	-	-
19.0	1	-	6	2	1	2										-	-	-
19.5			1	-	3	-										-	-	-
20.0			5	1	1	1										-	-	-
20.5			1	-	2	1										-	-	-
21.0					-	1										-	-	-
21.5					-	1										-	-	-
22.0					1	-										-	-	-
22.5					2*	-										-	-	-

*indicates a holotype value.

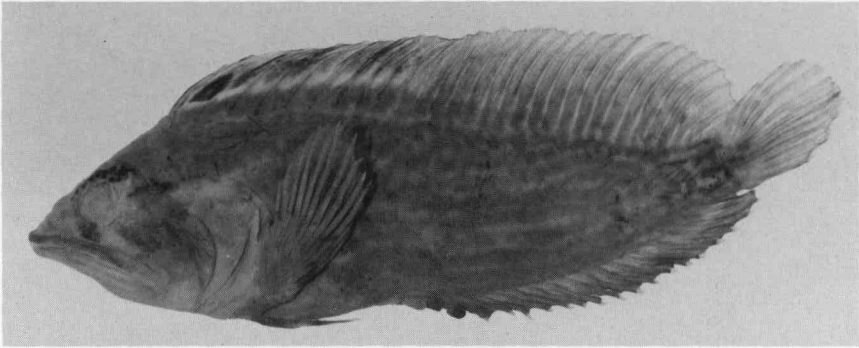


FIGURE 6.—Holotype of *Chasmodes bosquianus longimaxilla* new subspecies. Adult male, 86 mm SL, from Dauphin Island, Alabama (USNM 219830).

Table 4); like *C. b. bosquianus*, number of mandibular teeth increases with increased size (Fig. 4); pores in both mandibular series combined 4 to 5 (rarely 6; \bar{X} = 4.1, n = 115; Table 1). Of the three taxa referable to *Chasmodes*, *C. b. longimaxilla* alone shows a difference in number of small upper pharyngeal teeth between size classes (Table 1). Enlarged upper pharyngeal teeth 5-7 on each side (Table 1); each lower pharyngeal with 4-5 small teeth anterior to 4 large, recurved canines; maximum size approximately 85 mm SL.

Pigmentation and other characters of larvae immediately after hatching are similar to those described by Hildebrand and Cable (1938) for *C. bosquianus* (= *C. b. bosquianus*) from Chesapeake Bay.

The only small (<10 mm) posthatching, wild-caught specimen of *C. b. longimaxilla* examined measures 8.9 mm SL, and has the following characters: maxillary length 11% SL, 11 mandibular teeth, 4 pores in mandibular series, and no developed lip flaps on lower jaw. The 5 to 7 preopercular spines present in larval specimens of *C. b. bosquianus* are represented by 5 serrations in this specimen.

Pigmentation of this small individual is consistent with that described previously for adult female *Chasmodes*. All young of this subspecies, as well as other members of the genus, have the mottled pigmentation pattern until they attain a length of 35 to 40 mm SL, at which time the males begin to show the characteristic adult color pattern (described previously).

STATISTICAL COMPARISONS.—Statistical comparisons of populations of *Chasmodes bosquianus longimaxilla* with populations of *C. saburrae* and *C. b. bosquianus* are discussed in the generic and the other subspecies accounts, respectively. A statistically significant difference in comparison of regression equations (Table 5) for maxillary length and number of mandibular teeth between populations of *C. b. longimaxilla* was found in only one comparison (Tables 6, 7). A significant difference in maxillary

Table 9—Matrix of covariance comparisons of maxillary length regression equations (Table 2) for populations of *Chasmodes saburrae* ($P < 0.001$). Comparisons above the diagonal are between males in the different populations, and those below the diagonal between females (see Table 3 for explanation of abbreviations). 0 = coincident regression lines; - = noncoincident but parallel lines; + = noncoincident and nonparallel lines.

	SS	SN	ST	SC	SE	SM	SF
SS		0	0	0	0	0	0
SN	0		0	0	0	0	-
ST	0	0		0	0	0	0
SC	0	0	0		0	0	0
SE	0	0	0	0		0	-
SM	0	0	0	0	0		0
SF	0	0	0	0	0	0	

length comparisons is shown (Table 7) between the population in the southern Laguna Madre Bay (LL) and the population in the area of sympatry (LS). The lack of significant difference between any of the adjacent populations, coupled with the difference between LL and LS, suggests the existence of an east-west cline within this subspecies (see Table 8). This type of variation in maxillary length is not found in *C. b. bosquianus* or *C. saburrae* (Tables 7, 9) and may be related to character displacement in the area of sympatry (discussed later).

ECOLOGY AND DISTRIBUTION.—Like *Chasmodes bosquianus bosquianus*, *C. b. longimaxilla* typically inhabits the estuarine areas that have either a rock-shell bottom or a grassbed habitat. Unlike *C. b. bosquianus*, this subspecies has not been collected in salinities less than 10 ppt. It is usually captured in salinities ranging from 18 to 28 ppt.

Based on my observations, together with information from preserved specimens, the spawning season of *Chasmodes bosquianus longimaxilla* begins in March and extends over the summer months into October or early November. The longer spawning season may be attributable to water temperature. Water temperature in the northern Gulf of Mexico often remains warm until October or November (Bault 1972).

Male *Chasmodes bosquianus longimaxilla* over 35 mm SL are highly aggressive and maintain territories year-round. Females seek shelter among rocks and shells, but normally do not actively defend a territory. Females are constantly on the move during the spawning season. At their reproductive peak in early summer, I have noted one female spawning with more than one male. On several occasions, I have seen different females spawning with the same male. Each female laid a number of eggs on the inner surfaces of the shell being defended by the male, where he would then fertilize them. Thus, neither male nor female shows a preference for one partner during the spawning season.

The fish's pigmentation pattern renders it practically invisible against a

background of oyster shell or aquatic grasses. The greenish color of adult males blends with the algae covering the oyster shells and aquatic grasses. This cryptic coloration probably helps to protect the male from predation, and thus indirectly protects the eggs being guarded during the spawning season. The dark and light mottled color pattern of the females and younger fishes is also cryptic and aids in concealment.

Chasmodes bosquianus longimaxilla is known from Pensacola, Florida, westward to the Texas coast and southward to Veracruz, Mexico. Very few specimens of *C. b. longimaxilla* are known from Pensacola, and I believe these are stragglers to the area. Large aggregations of *C. b. longimaxilla* are encountered around oyster shell laden regions in Mobile Bay, Alabama, where very few *C. saburrae* occur. The zone of sympatry of *C. b. longimaxilla* and *C. saburrae* extends from Pensacola, Florida, where *C. saburrae* predominates, to the Chandeleur Islands, Louisiana. Individuals found in this zone exhibit no overlap in diagnostic characters and show almost exclusive segregation by habitat. Based on my collections in Mobile Bay and ecological data on preserved specimens, *C. saburrae* appears to be restricted to the grassbeds, whereas *C. b. longimaxilla* is associated with the oyster reef community. This habitat specificity does not seem to hold outside the zone of sympatry, allopatric populations of both species being found in either of the two communities.

The habitat specificity in the zone of sympatry is coupled with character displacement in *Chasmodes bosquianus longimaxilla*. The populations of *C. b. longimaxilla* in the zone of sympatry, although exhibiting a wide range of maxillary lengths (14 to 22.5% SL), tend to have longer maxillary lengths than other populations of this subspecies (Table 8). This difference may be due to habitat segregation in the zone of sympatry. There is a tendency for the maxillary length to decrease with increasing geographic distance from the zone of sympatry (Table 8). This decrease is not statistically significant until the populations at either end of the geographic range (excluding Veracruz) are compared (Table 7). This type of variation provides support for the existence of an east-west cline in the northern Gulf of Mexico. One possible explanation for this cline is that it is the result of the effect of character displacement on the gene pool in the zone of sympatry, together with a decreasing impact of this gene pool on increasingly distant populations. Biochemical studies of these populations are needed to either confirm or refute this hypothesis.

Bath's (1977) report of two specimens of *Chasmodes bosquianus* (= *C. b. longimaxilla*) from Veracruz, Mexico, constitutes the only record from waters south of Laguna Madre, Texas. It is likely that additional specimens will be collected from the northeastern coast of Mexico when these areas are more intensively sampled. Although not reported in the few ichthyofaunal studies done in this region (*e.g.* Reséndez 1970, 1973), it should be

noted that collecting was done mostly with trawls. Since *C. b. longimaxilla* is rarely captured in trawls, its absence is not surprising.

A specimen (FMNH 80505) supposedly collected at Key Largo, Florida, on 10 April 1968, and identified as *Chasmodes saburrae*, proves upon re-examination to be *C. bosquianus* (probably *C. b. longimaxilla*). As this record, if valid, would be the only instance of occurrence of *C. bosquianus* within the exclusive range of *C. saburrae*, I assume this to have resulted from a transposition of locality data.

REMARKS.—Although *Chasmodes bosquianus longimaxilla* may in fact be specifically distinct from *C. b. bosquianus*, I do not feel that specific recognition can be justified based on the information presented herein. Based on its allopatric distribution, statistical differences in maxillary length comparisons, modally different gill raker counts, and differences in pharyngeal tooth counts, I believe that the Gulf of Mexico population of *C. bosquianus* warrants subspecific recognition.

ETYMOLOGY.—The Latin name, a combination of *longus* (long) and *maxilla* (jawbone), refers to the long maxillary bones. The name is to be treated as a noun in apposition.

MATERIAL EXAMINED.—HOLOTYPE: USNM 219830, male, 86 mm, 30°15'30"N, 88°05'W, rock jetties on northeast side of Dauphin Island, Mobile County, Alabama; 20 October 1977; collected by Douglas Clarke. PARATYPES: FLORIDA: FMNH 57043 (1), Pensacola. ALABAMA: USNM 219831 (1), female taken with holotype; UF 31478 (1; *ex* USAIC 3980), 31479 (1; *ex* USAIC 4267), USNM 5721 (1), USAIC 3160 (2), 3164 (1), 4059 (1), 4268 (1), 4269 (2), 6003 (2), 6004 (1), 6274 (1), 6275 (1), 6276 (1), Mobile Bay; USAIC 3163 (1), Mississippi Sound. MISSISSIPPI: GCRL V61:514 (1), V67:2061 (1), V68:2903 (1) Mississippi Sound; GCRL V76:15103 (1), Davis Bayou; FMNH 62465 (1), Ocean Springs; USNM 72333 (1), Three Mile Bayou. LOUISIANA: GCRL V68:2711 (1), TU 91945 (1), Lake Pontchartrain; TU 5244 (1), 5564 (1), Oyster Bayou; USNM 162591 (1), off Schriever and Houma. TEXAS: TU 21596 (1), Galveston Bay; TAMU 690.1 (1), near Matagorda; USNM 69338 (3), Matagorda Bay; USNM 217325 (1), Port Lavaca; UMMZ 114470 (5), 114474 (1), 145880 (1), 145892 (3), 145976 (3), 170295 (3), Lavaca Bay; UMMZ 145885 (7), 145934 (3), Tres Palacios Bay; UMMZ 112925 (1), Kellen's Bay; TAMU 919.7 (1), Mustang Island; UTMSI 289 (1), Ransom Island; UMMZ 111743 (3), TU 21665 (2) near Rockport; ANSP 129692 (1), near Ingleside; FMNH 62464 (9), TAMU 187.3 (1), 700.1 (1), Aransas Bay; FMNH 40311 (2), USNM 156556 (5), 156557 (1), 156611 (1), 188252 (1), near Corpus Christi; ANSP 71181-2 (2), NLU 34793 (1), Laguna Madre; TAMU 468.3 (1), 784.1 (5), 898.2 (19), 929.6 (16), UF 4233 (1), UTMSI 1358 (1), Redfish Bay; NLU uncatalogued (5), Texas (exact locality unknown).

Chasmodes saburrae JORDAN AND GILBERT

Chasmodes saburrae Jordan and Gilbert 1883: 298 (Type locality: Pensacola, Florida; lectotype USNM 30824).

Blennius fabbri Nichols 1910: 161 (Type locality: Miami, Florida; holotype AMNH 2537).

DIAGNOSIS.—*Chasmodes saburrae* is distinguished from *C. bosquianus* in the diagnosis of the latter.

DESCRIPTION. (See also Table 1).—Characters appearing in generic and *Chasmodes bosquianus* descriptions are not repeated here. In addition, enlarged upper pharyngeal teeth 5-7 (each side); small upper pharyngeal teeth total 1-10 (Table 1); lower pharyngeals each with 5 to 6 small teeth immediately anterior to 6 enlarged canines ($n = 8$); number of mandibular teeth increases with increasing size (Fig. 4); maximum length about 80 mm SL.

Peters (1981) discussed the developmental osteology and reproductive biology of *Chasmodes saburrae*.

STATISTICAL COMPARISONS.—Secondary sexual dimorphism and comparisons of *Chasmodes saburrae* populations with *C. bosquianus* populations are discussed in the generic and *C. bosquianus* accounts, respectively. Two populations of *C. saburrae* (Everglades [SE] and Indian River area [SF]) were found to show statistically significant differences when compared with other populations of *C. saburrae*. Results of comparisons of regression equations for the number of mandibular teeth (Table 6) show that the SE and SF populations differ from other populations, but not from themselves. Both the SE and SF populations differ from the geographically intermediate Biscayne Bay area population (SM), but this may be due to the relatively small sample size for SM ($n = 15$). Springer (1959) suggested that the relatively high number of mandibular teeth found in some specimens from Whitewater Bay, Everglades, may be related to low salinity (5.5 ppt), but this explanation does not hold for the Indian River area population (specimens collected in 15-25 ppt).

Analysis of the maxillary length character between populations of *C. saburrae* (Table 9) revealed no significant differences between regression equations for females. Comparisons between the males in these different populations show a statistical difference in maxillary length (Table 9) between the Indian River area population (SF) and the populations in the Everglades (SE) and in the waters between Ft. Walton and Cedar Key (SN). It is interesting to note that the SF and the SE populations differ in maxillary length, but not in number of mandibular teeth (Tables 6, 9). I can offer no explanation for these differences.

ECOLOGY AND DISTRIBUTION.—Individuals of *Chasmodes saburrae* are sometimes found associated with oyster reef communities, but they appear to prefer grassbed habitats (Springer and Woodburn 1960). Like their

congeners, they are inclined toward places where small enclosures abound.

A population of *Chasmodes saburrae* in the Everglades inhabits waters that become less saline (down to 5.5 ppt) than those inhabited by the other populations. The combination of this and other environmental factors yet to be determined has apparently resulted in a slight increase in number of mandibular teeth in this population (Table 6). This slightly higher number of mandibular teeth (Fig. 4) than most other populations (Table 6) is the only character that shows measurable differences (statistical or otherwise). In addition, I have not examined specimens from the area between the southern tip of peninsular Florida and Charlotte Harbor (Fig. 5). This suggests the possibility that the Everglades population is isolated (*i.e.* no gene flow) from the Charlotte Harbor population. Although possible, the existence of estuarine habitat, suitable for *Chasmodes*, between these areas argues against this type of isolation. I believe that this disjunction is a collecting artifact, since most of this area is accessible only by boat and has apparently not been well sampled.

This difference of the Everglades population from the others is not unique to the genus *Chasmodes*. Weinstein and Yerger (1976) commented on the disparity between the Everglades "subpopulation" of *Cynoscion nebulosus* and other "subpopulations" of that species. In an attempt to explain this difference, they suggested that it results from environmental factors unique to that area.

Relyea (1967) presented data on an Everglades population of *Fundulus confluentus* that clearly show a trend toward an increase in number of elements in numerous meristic characters, although Relyea made no comment on this disparity.

Life history and reproductive strategies of *Chasmodes saburrae* are discussed by Peters (1981), and thus are not treated in this work.

Chasmodes saburrae occurs from Edgewater, Volusia County, Florida, southward around the southern tip of the state, northward and westward as far as the Chandeleur Islands, Louisiana. I have examined three young specimens (8.9 to 9.8 mm SL, collected on 27 May 1935, USNM 188254) from Matanzas River, Florida. Based on their small size and the fact that no other *C. saburrae* have been collected this far north on the east coast of Florida, I believe that these three specimens were wafted northward during their planktonic larval stage. Kevin Peters (pers. comm.) has informed me that *C. saburrae* larvae settled out of the plankton in three weeks under ideal conditions. This length of time would be sufficient to allow the larvae to drift from more southerly waters to Matanzas River, assuming a drift rate of approximately 3 to 4 miles a day. The absence of sexually mature *C. saburrae* in the Matanzas River indicates that this species does not normally occur this far north, and this region is therefore not considered to comprise a normal part of the range of the species. In

addition to these, there are three specimens of *C. saburrae* (USNM 4307, 4308, 4309) from the "Coast of South Carolina," collected in the late 1800's. Dr. Victor G. Springer has informed me that it is likely these locality data are in error, a conclusion with which I agree.

Between Pensacola, Florida, and Chandeleur Islands, Louisiana, *Chasmodes saburrae* is sympatric with *C. b. longimaxilla*. Within this region, the two species are allotopic (as defined by Rivas 1964), with *C. saburrae* almost exclusively inhabiting the grassbeds and *C. b. longimaxilla* restricted to the oyster shell areas, thus accounting for the genetic integrity of the two species over the area of sympatry.

The distinctness of the sympatric Gulf of Mexico populations can be contrasted with the overlapping characters of the allopatric populations on the Atlantic coast of Florida. This may be seen in Table 8, which shows a relatively high degree of overlap in maxillary length between *Chasmodes saburrae* and *C. bosquianus bosquianus*, and no overlap between sympatric *C. saburrae* and *C. b. longimaxilla*. The phenomenon of character displacement (see *C. b. longimaxilla* account) appears to be contributing to the divergence of the disjunct populations of *C. bosquianus*. It is interesting to note that maxillary length is one of the few morphological characters showing a significant difference between the disjunct populations (see Tables 4, 7).

DISCUSSION OF SYNONYMY.—Dr. C. Lavett Smith (American Museum of Natural History) has been unable to locate the holotype of *Blennius fabbri*, but I concur with Springer (1959) in assuming that this specimen, because of its type locality, must be a young specimen of *Chasmodes saburrae* and not *C. bosquianus*, as suggested by Nichols (1911).

REMARKS.—Bath (1977:181) designated a specimen from the British Museum (BMNH 1887.5.14.141) as a paratype of *Chasmodes saburrae*. This was apparently the first mention of this specimen as a type. Bath (1977) does not explain his reason for this action. I have examined this specimen and, although it belongs to *C. saburrae*, found nothing in the jar with the specimen to indicate that it was designated as a paratype by Jordan or Gilbert. Mr. Alwyne Wheeler, at the British Museum, informed me that he could find nothing in their records to indicate that this specimen was ever designated as a paratype. It is possible that this specimen was one of the 14 mentioned in the original description (Jordan and Gilbert 1883: 299), but I do not feel that there is any basis for its being designated as a paratype.

Another problem exists with regard to the number of paratypes. Springer (1959) pointed out that there are 9 type specimens of *Chasmodes saburrae* catalogued in the National Museum of Natural History, and 12 paratypes (now at the California Academy of Sciences) listed by Böhkle (1953). I have examined the latter series and confirm their identification as

C. saburrae. These specimens are clearly labeled as paratypes. The fact that 21 type specimens are known to exist, 7 more than the 14 mentioned by Jordan and Gilbert (1883), suggests to me that more than 14 specimens were actually used by Jordan and Gilbert in compiling the original description. Those specimens that are clearly labeled as types (*i.e.* USNM 1779448 [8], and CAS-SU 440 [12]) are recognized as paratypes in this work.

MATERIAL EXAMINED.—**TYPES:** USNM 30824 (1), Pensacola, Florida, lectotype of *Chasmodes saburrae* (designated by Springer 1959); USNM 1779448 (8), CAS-SU 440 (12), Pensacola, Florida, paratypes of *C. saburrae*. **FLORIDA:** IRCZ 107:1739 (1) and UMML 5385 (1), Edgewater; USNM 1908 (1), Mosquito Lagoon; UMML 457 (1), vicinity of Titusville; UMML 958 (2), 3245 (5), FSU 19159 (1), 19164 (2), vicinity of Cocoa; IRCZ 107:2409 (1), 107:4338 (5), 107:4809 (2), FSU 4312 (4), 19174 (1), UF 23685 (1), 23686 (5), 23687 (2), 23688 (21), 23689 (1), 24052 (1), UMML 1555 (3), 3875 (5), USNM 48035 (17), 48783 (11), Indian River; UMML 3132 (3), Jewfish Creek; UMML 40 (1), 44 (2), 50 (1), 776 (1), 2728 (1), 4467 (1), 5391 (1), 8183 (1), Biscayne Bay; UMML 5378 (1), Key Largo; UMML 24278 (2), Shark River Delta; UMML 3953 (2), 4171 (17), 4541 (11), 5211 (6), 5478 (1), 6872 (2), 7059 (1), 7636 (3), 10739 (1), 15496 (1), 17360 (2), Everglades; FMNH 50554 (4), 50555 (2), FSU 4108 (10), 15583 (1), 20644 (6), UMMZ 113268 (1), USNM uncatalogued (1), GCRL V60:144 (1), V71:7126 (1), V71:7410 (1), V72:8362 (1), V72:8363 (2), V73:10067 (1), V74:13333 (2), V74:13334 (1), V74:13356 (1), Charlotte Harbor; FSBC 154 (13), 183 (3), 436 (1), 931 (5), 932 (3), 933 (4), 943 (5), 944 (14), 953 (16), 1421 (14), 3177 (2), 3194 (1), 3204 (7), 3260 (37), 3315 (1), 3859 (7), 6186 (13), 7769 (1), USNM 184240 (50), 184242 (12), Tampa Bay; UF 2576 (1), Bayport; FSBC 3843 (1), 7776 (1), 7877 (1), 7915 (1), 9239 (3), 9558 (1), 9657 (2), Crystal River; FMNH 62461 (3), 62462 (2), FSBC 3 (2), 4 (3), 11 (13), UF 1084 (1), 1889 (2), 2577 (6), 2578 (8), 2579 (11), 2580 (1), 2581 (23), 2582 (20), 3342 (7), 7827 (2), 8634 (1), 8657 (1), 24015 (1), 24016 (1), 24017 (1), 24019 (7), 24020 (2), 24022 (1), 24023 (1), 24024 (3), 24026 (1), 24027 (2), 24028 (6), 24029 (4), 24030 (4), 24031 (8), 24032 (4), 24033 (4), 24034 (7), 24035 (2), 24036 (1), 24037 (3), 24038 (1), 24039 (1), 24040 (5), 24049 (1), 24050 (1), 24051 (2), USNM 39371 (1), Cedar Key; FSU 2467 (1), 2640 (1), 2642 (1), 4179 (1), 14640 (6), 19816 (2), 25175 (3), UTMSI 290 (1), Apalachee Bay; FSU 388 (1), 765 (1), 1672 (6), 1921 (3), 3215 (1), 4693 (1), 7791 (2), 14057 (1), 18271 (26), 18420 (1), 18657 (9), 23509 (3), 25127 (1), Alligator Harbor; USNM 101078 (1), Apalachicola; UF 4174 (1), St. Joseph's Bay; FSU 15642 (2), 17247 (3), 17258 (1), 17285 (2), 17346 (3), 17351 (1), 17403 (2), 17468 (2), St. Andrews Bay; FSU 1529 (1), 1536 (1), 14019 (2), UNC 4132 (1), Ft. Walton; BMNH 1887.5.14.141 (1), FSU 14167 (16), 14651 (9), USAIC 6135 (1), USNM 31934 (17), 44871 (1), Pensacola. **ALABAMA:** USAIC 3161 (1), Mobile Bay. **MISSISSIPPI:** FMNH 46657 (1), GCRL V61:505 (52), USNM 188248 (18), Mississippi

Sound. LOUISIANA: TU 12832 (1), 67392 (17), 67648 (2), 68315 (1), 69569 (1), 76615 (1), 76601 (10), 77611 (1), 77736 (2), 77751 (1), 77880 (5), 77918 (1), 77939 (5), 77995 (1), 78008 (1), 78298 (3).

ZOOGEOGRAPHY

Springer (1959) presented a hypothetical scenario of the evolutionary history of the genus *Chasmodes*. This hypothesis suggests that a single Pliocene species of *Chasmodes*, inhabiting the present range of the genus, was divided into continental and insular populations by rising sea level in the Pleistocene. The geographic isolation of the insular population eventually led to genetic divergence from the continental population. By the end of the Pleistocene, the insular population presumably had reached the specific level. The islands were then reunited with the mainland as the sea level receded to its present height, resulting in the disjunction of the mainland species, *C. bosquianus*. After the islands were reunited with the mainland, *C. saburrae* has excluded *C. bosquianus* from the peninsula. Springer (1959) further suggested that the disjunct populations of *C. bosquianus* have been diverging from each other since the emergence of the Florida peninsula.

This scenario has been used to describe the evolutionary history of a broad range of terrestrial and aquatic organisms in the southeastern U.S. (Ginsburg 1952, Relyea 1965, Zug 1968, Shipp and Yerger 1969, Shipp 1974, and Burgess and Franz 1978). In view of the number of different forms exhibiting this distributional pattern this pattern can be considered a generalized track *sensu* Croizat et al. (1974).

Only two aspects of this hypothetical scenario have been seriously criticized, the time frame for the events and the nature of the highest terrace (*i.e.* whether or not it is due to high sea level). Deevey (1950) questioned the marine origin of the high terraces of Cooke (1939) and suggested that they may be constructional rather than erosional. Zug (1968) chose to recognize five Pleistocene marine terraces, including the high terraces. Robertson (1976) confirmed the marine nature of the "90-100 foot" terrace of Alt and Brooks (1965), but suggested a late Pliocene age. This leads to the controversy over the timing of the events. Cooke (1935, 1939, 1954) and MacNeil (1950) suggest a Pleistocene age while other geologists prefer a Pliocene or even Miocene age for the terraces higher than the 10 m terrace (Alt and Brooks 1965; Osmond *et al.* 1965, 1970; Bender *et al.* 1979). Bender *et al.* (1979, and references therein) provide data that argue strongly against sea level rising higher than 10 m above the present level in approximately the last 500,000 years before present (BP), and probably not in the last one to two million years BP.

Although the timing of the hypothesized events has little effect on the mechanism, proposed by Springer (1959), for the evolution of *Chasmodes*

saburrae, it is very important to the understanding of the relationship between the disjunct populations of *C. bosquianus*. The slight morphological and meristic divergence of the disjunct populations (discussed previously) suggests either a relatively short period of isolation, parallel evolution, or a slow evolutionary rate. Although each of these mechanisms is possible, I believe the simplest explanation is that the two populations have only been isolated since the last glaciation, about 14,000 years BP (Brookes 1977).

The two populations of *Chasmodes bosquianus* could have come in contact with each other and interbred in the southern part of Florida by dispersing southward in response to decreased water temperature. This dispersal in response to decreased water temperature hypothesis was proposed by Walters and Robins (1961) and has been used by Smith-Vaniz (1980) to explain the lack of divergence between populations of *Hypso-blennius*. As water temperature rose following the end of the last glacial period, the *C. bosquianus* populations would disperse northward until reaching their present geographic positions.

EXPERIMENTAL HYBRIDIZATION

A hybridization experiment was performed using specimens of *Chasmodes saburrae* and *C. bosquianus longimaxilla* collected in Mobile Bay. Hybridization was observed between a male *C. saburrae* and a female *C. b. longimaxilla* in a 76-liter saltwater aquarium supplied with empty oyster and gastropod shells. In addition to the two specimens mentioned above, there was also one adult male *C. b. longimaxilla* in the aquarium. The three specimens were introduced into the aquarium simultaneously. Once introduced into the aquarium, the male *C. b. longimaxilla* established a territory in one of the empty oyster shells while the *C. saburrae* male chose a gastropod shell. This is interesting since the choices correspond to the types of shells found in their respective habitats. The female spawned indiscriminately with both males, although she also chose the oyster shells for protection. The eggs were tended by the males until hatching. The newly hatched conspecific and hybrid larvae were active, but due to a lack of suitable food or some other factor, they did not survive more than a few days.

Due to the extreme artificiality of the enclosure in which the interspecific spawning occurred, I do not feel that these results can justifiably be used to draw taxonomic conclusions regarding the validity of the two species, but it does at least prove that natural production of hybrids is possible. Hybridization in marine fish species is a comparatively rare phenomenon.

In the areas where these species are sympatric, they appear to be allotopically distributed. This segregation was indicated in the choice of

territories by the two males after introduction into the aquarium. In my experiment I did not have the facilities to simulate their natural habitat properly. Forcing them together in the confinement of a small aquarium could have altered any natural isolating mechanisms that might effectuate genetic isolation in their natural environment.

A more extensive analysis of this problem using large saltwater pools with both grassbed and oyster reef habitats should provide additional insight toward an understanding of the natural isolating mechanisms maintaining the genetic integrity of these species.

SUMMARY

Two valid species are included in the genus *Chasmodes* and a new subspecies is described from the northern Gulf of Mexico. *C. saburrae* is found from Edgewater, Florida, southward around the tip of Florida, northward and westward to the Chandeleur Islands, Louisiana. The second species, *C. bosquianus*, consists of two allopatric subspecies, *C. b. bosquianus* inhabits the Atlantic seaboard from Maryland to Marineland, Florida, and *C. b. longimaxilla* subsp. nov. is found from Pensacola, Florida, to Veracruz, Mexico. The new subspecies is differentiated from the Atlantic form by its decreased number of small upper pharyngeal canines in adults, a longer maxillary length, and a modally lower number of gill rakers.

Character displacement in the area of sympatry in the Gulf appears to be contributing to the divergence of the two populations of *Chasmodes bosquianus*.

Zoogeography of the genus *Chasmodes* is discussed and Springer's (1959) hypothesis is summarized. This hypothesis provides the simplest explanation for the evolution of *C. saburrae*, suggesting that it evolved as an island endemic. Geological views on the timing of the submergence and emergence of peninsular Florida are discussed in relation to the disjunct populations of *C. bosquianus*. The simplest explanation is that the disjunction originated with the emergence of peninsular Florida, but gene flow between the disjunct populations has occurred as recently as the last glacial period by means of southward dispersal due to lowered water temperatures (Walters and Robins 1961).

Results from hybridization experiments were inconclusive with regard to determination of the taxonomic status of the species currently recognized in the genus *Chasmodes*. Additional hybridization experiments combined with an experimental analysis of habitat partitioning should provide further insight into the relationship between the sympatric populations.

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