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A systematic review of the genus *Chasmodes* (Teleostei: Perciformes: Blenniidae)

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Abstract

A systematic review of the Atlantic blenniid genus *Chasmodes* was conducted. Principal components analysis (PCA) of 18 box-truss measurements revealed little variation in overall body shape among the three recognized *Chasmodes* species. In contrast, PCA of six more standard ichthyological measurements and the number of segmented dorsal-fin rays showed significant differences among the three. The species-level classification presented herein agrees with nomenclature in recently published works. Cladistic analysis of partial 12S rRNA gene sequences indicates *Chasmodes* is sister to a lineage comprising *Hypleurochilus*, *Scartella*, and *Hypsoblennius*. Based on our conclusions about phylogenetic relationships, we infer that sea-level fluctuations were likely associated with speciation in *Chasmodes*. Remarks on the critical habitats of these blennies are given.

Key words: morphometric analysis, taxonomy, Blennioidei, mtDNA

Introduction

The perciform suborder Blennioidei is a large group of fishes, representing over 800 species in 136 genera (Nelson 2006) and six families (Springer 1993): Dactyloscopidae (sand stargazers), Tripterygiidae (triplefin blennies), Labrisomidae (labrisomid blennies), Clinidae (kelp blennies), Chaenopsidae (tubeblennies), and Blenniidae (combtooth blennies). Most blennioids are relatively small and elongate in shape, occupying nearshore benthic habitats, with some involved in mimetic or symbiotic relationships with other species. Springer (1993) proposed blennioid monophyly by citing specializations in five character complexes: dorsal gill arches, caudal skeleton, pelvic girdle, anal-fin rays, and pectoral girdle. Stepien *et al.* (1997) obtained a concordant result with genetic sequence data. The present study addresses the taxonomic status, nomenclature, and relationships of a small subset of the Blennioidei: the genus *Chasmodes* Valenciennes and some other northwestern Atlantic blenniid species.

Blenniid fishes of the genus *Chasmodes* are encountered as part of the benthic fauna from New York, New York, to Veracruz, Mexico. They are typically collected in shallow, brackish (salinity ~20‰) habitats, including oyster reefs, mud, and grassy areas with shell and sand. Springer (1959) reviewed the genus and recognized two species, *C. bosquianus* (Lacepède) and *C. saburrae* Jordan and Gilbert. The Striped Blenny, *C. bosquianus*, was considered to consist of two disjunct populations: an eastern population ranging from Chesapeake Bay to Marineland, Florida, and a western population ranging from Pensacola, Florida, to southern Texas. The range of *C. saburrae*, the Florida Blenny, is situated between these two populations. A small area of sympatry was evidenced by the capture of "a few specimens" of *C. bosquianus* at Pensacola and one specimen of *C. saburrae* west of Florida, at Cat Island, Mississippi (Springer 1959). The shape of dentary teeth and the length of the upper jaw were used to discriminate the two species (Springer 1959).

The next taxonomic treatment of *Chasmodes* was that of Williams (1983), who noted difficulties in using Springer's characters to distinguish among the species. In particular, maxillary-length and mandibular-tooth

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characters were ineffective for immature individuals and those from eastern Florida. Williams (1983) used the number of pores on the ventral side of the head, presence or absence of prominent ventral lip flaps, and the shape of dentary teeth to distinguish between the two species of *Chasmodes*. Of further taxonomic significance was Williams' recognition and designation of subspecies for the disjunct populations of *C. bosquianus*. His bivariate analyses of covariance supported this distinction. The eastern population was designated *C. b. bosquianus* and the western population *C. b. longimaxilla*. The area of range overlap (sympatry) for the two species, *C. b. longimaxilla* and *C. saburrae*, was determined to be between Pensacola, Florida, and the Chandeleur Islands, Louisiana (Williams 1983). In this area, the species were observed to be allotopically distributed (Williams, 1983). There was no apparent area of recorded overlap between *C. b. bosquianus* and *C. saburrae*.

Most recently, Williams (2003) recognized three species in the genus: *C. bosquianus*, *C. longimaxilla*, and *C. saburrae*. However, this elevation of *C. b. longimaxilla* to species status was without comment. We tested this new provisional classification, also recognized by Nelson *et al*. (2004), with morphometric and osteological data, and present taxonomic accounts. The intergeneric relationships and biogeography of *Chasmodes* were also examined. Tissue samples were not available for *C. b. longimaxilla*, which prevented our use of molecular data for further testing of species-level status. We comment upon the critical habitats for species in the genus.

Material and methods

Institutional abbreviations are listed as in Leviton *et al.* (1985). Meristic and morphometric data were taken from 283 specimens with the aid of a Wild M5 dissecting microscope. Methods were based on Hubbs and Lagler (1958), except as noted. Counts were made of dorsal, anal, pectoral (left side), pelvic (left side), and caudal-fin rays. Mandibular pores were counted following Williams (1983). Following Johnson and Patterson (1993), the term “epineurals” is used for the intermuscular bones that had been conventionally called “epipleurals” in perciform fishes. Osteological comparisons were made among specimens that had been cleared and stained for bone and cartilage, according to the method of Pothoff (1984). Except as noted, common names are those given by Nelson *et al.* (2004). In lists of material examined, entries follow a roughly geographic order along the coast from New York towards Mexico.

Two sets of measurements were made on specimens that were not severely distorted. The first set utilized a box truss network of homologous landmarks, identified by number, along the outline of the specimen that when connected yield three quadrilaterals with internal diagonals and an anterior triangle (Fig. 1). This method allows for quantification of overall body shape in the horizontal, vertical, and oblique directions (Bookstein *et al.* 1985). The following homologous points, referred by number, were used to make the box-truss network: tip of snout (1), dorsal-fin origin (2), insertion of lateralmost pelvic-fin ray (3), insertion of anteriormost segmented ray of dorsal fin (4), anal-fin origin (5), insertion of last segmented ray of dorsal fin (6), insertion of last segmented ray of anal fin (7), insertion of dorsalmost caudal-fin ray (8), and insertion of ventralmost caudal-fin ray (9). The following measurements were made: truss 1–2, truss 2–3, truss 1–3, truss 2–4, truss 4–5, truss 3–5, truss 2–5, truss 3–4, truss 4–6, truss 5–7, truss 6–7, truss 4–7, truss 5–6, truss 6–8, truss 8–9, truss 7–9, truss 6–9, truss 7–8 (Fig. 1). The second set consisted of standard ichthyological measurements: standard length (SL), head length (HL), snout length, upper-jaw length, fleshy orbit diameter, fleshy interorbital width, and length of posteriormost dorsal-fin spine. Measurements were made to the nearest 0.1 mm with Mitutoyo digital calipers. To facilitate accurate recording of measurement data, a foot-pedal device triggered automatic entry of measurements from the calipers to spreadsheet software.

Sheared principal-component analysis (sPCA) was used to assess the morphometric differences among species of *Chasmodes*. The computer program SHEAR (MacLeod 1990) was used to identify measurements that differed most among the nominal species and to calculate sPC scores, which were plotted in order to visualize spatial relationships among specimens with respect to shape vectors. The first (unsheared) principal component is not considered important for detecting interspecific differences in shape (Harold & Lancaster

2003). After inspecting sPC scores to identify which measurements accounted for most interspecific differences, raw measurements were used to calculate a discriminant function that provided the probability of a given specimen belonging to one species or another.

Genetic data were used to infer the relationships among the following blenniid genera: *Chasmodes*; *Hypsoblennius* Gill; *Hypleurochilus* Gill; *Parablennius* Miranda Ribeiro; and *Scartella* Jordan. Tissue samples (0.1–0.5 g) were taken from *C. bosquianus*, *C. saburrae*, *Hypsoblennius ionthas* (Jordan & Gilbert), *Hypsoblennius hentz* (Lesueur), and *Hypleurochilus geminatus* (Wood) that were either freshly caught or initially preserved, and maintained in 95% ethanol (Table 1). In most cases, the samples came from the right pectoral fin, but for small specimens (<~20 mm standard length) the portion of the body posterior to the anus was taken. Tissue samples were stored at room temperature in either 95% ethanol or a sarcosyl-urea solution (1% sarcosyl, 8 M urea, 20 mM sodium phosphate, 1 mM ethylene diamine tetraacetic acid [EDTA], pH 6.8) for later use. Additional tissue samples from the following species were supplied by the Division of Ichthyology, University of Kansas Natural History Museum: *Ophioblennius atlanticus* (Valenciennes), *Hypleurochilus springeri* Randall, and *Entomacrodus nigricans* Gill (Table 1).

TABLE 1. Specimens included in phylogenetic analysis of 12S DNA sequences.

Species	GenBank accession number	Voucher and/or tissue number
Chasmodes bosquianus	GQ865555	GMBL 01-22-E
C. bosquianus	EU447256	GMBL 01-22-F
C. bosquianus	GQ865549	GMBL 02-89-B
C. bosquianus	GQ865550	GMBL 02-89-E
C. bosquianus	GQ865551	GMBL 02-162-A
C. bosquianus	GQ865552	GMBL 02-162-B
C. bosquianus	GQ865553	GMBL 02-162-C
C. bosquianus	GQ865554	GMBL 02-162-D
C. saburrae	GQ865562	GMBL 02-122
C. saburrae	GQ865556	GMBL 02-175-A
C. saburrae	EU447255	GMBL 02-175-B
C. saburrae	GQ865557	GMBL 02-175-D
Entomacrodus nigricans	DQ143880	USNM 327613 (tissue KU 139)
Hypleurochilus geminatus	EU447258	GMBL 02-89-A
Hypl. geminatus	GQ865561	GMBL 02-89-D
Hypl. springeri	DQ143879	USNM 327614 (tissue KU 157)
Hypsoblennius hentz	GQ865558	GMBL 02-89-C
Hyps. hentz	GQ865559	GMBL 02-89-H
Hyps. hentz	EU447257	GMBL 02-89-I
Hyps. ionthas	DQ143878	GMBL 02-89-G
Hyps. ionthas	GQ865560	GMBL 02-89-J
Ophioblennius atlanticus	DQ143877	USNM 349074 (tissue KU 136)
Parablennius parvicornis	AF414712	
Scartella cristata	AY098803	

Genomic DNA was isolated from tissue samples using either a phenol-chloroform-isoamyl protocol (Ausubel *et al.* 1995) or a Qiagen DNeasy Tissue kit. A portion of the mitochondrial gene that codes for the 12S ribosomal subunit was amplified using the polymerase chain reaction (PCR). Each PCR was carried out in a 50 μL microcentrifuge tube with the following optimization values: 32.0 μL sterile H_2O, 5.0 μL Promega

(1x) buffer, 4.0 μL (0.2 mM each) deoxyribonucleoside triphosphates (dNTP's: dATP, dCTP, dGTP, dTTP), 4.0 μL $MgCl_2$ solution (2 mM), 1.0 μL Promega *Taq* polymerase (0.2 x), 1.0 μL sample DNA (1x), and 1.5 μL (0.3 μM) each of the L1091 and H1478 universal primers described by Kocher *et al.* (1989). Thermal conditions started at 94° C for 180 seconds (s), followed by 35 cycles of denaturation at 94° C for 45 s, primer annealing at 52° C for 45 s, primer extension at 72° C for 90 s, a final extension and annealing period at 72° C for 5 minutes, and storage at 4° C. A Qiagen QIAquick PCR Purification Kit was used to purify the PCR products, which were then sequenced in the forward and reverse directions with an ABI 377 DNA Sequencer at the Medical University of South Carolina's Biotechnology Resource Laboratory. The resulting sequences were edited using DNASIS 7.00 (Hitachi Software 1991). Sequences from homologous genes were retrieved from GenBank for *Scartella cristata* (Linnaeus) (accession number AY098803) and *Parablennius parvicornis* (Valenciennes) (accession number AF414712). CLUSTALX (v. 2.0, Larkin *et al.* 2007) was used to align sequences. The gap-opening penalty was 15 and the gap-extension penalty was 6.66 for pairwise alignments. For the multiple sequence alignment, the gap-opening penalty was 15, the gap-extension penalty was 6.66, and the delay-divergent-sequences parameter was 30%.

From the aligned sequences, the program TNT (Goloboff *et al.* 2008) was used to construct phylogenetic trees based on the maximum parsimony criterion. The salariine blenny *Entomacrodus nigricans* was designated as the outgroup taxon. Parsimony-informative characters were treated as unordered and equally weighted. Gaps were treated as missing data. A heuristic search began with 100 Wagner trees and proceeded with the tree bisection-reconnection algorithm of branch swapping to recover the most parsimonious topology. Nodal support was quantified with bootstrap (1,000 pseudoreplicates) and Bremer support values (Bremer 1994), the latter calculated by retaining 10,000 suboptimal trees of up to 20 steps longer than the single most parsimonious tree.

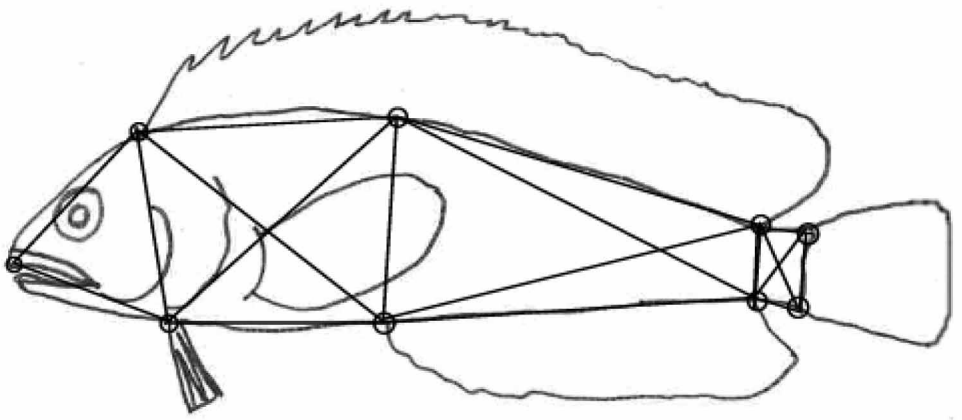

FIGURE 1. Schematic of *Chasmodes* specimen with box-truss network superimposed. Landmarks defined in text.

Results

The mean number of segmented rays in the dorsal fin differed significantly among species of *Chasmodes* ($F_{2,281} = 10.78$, $p < 0.0001$). All pairwise comparisons using the Tukey-Kramer HSD procedure ($\alpha = 0.05$) revealed that the mean number of segmented dorsal-fin rays is higher in *C. bosquianus* (n = 73, mean = 18.5) than in both *C. longimaxilla* (n = 51, mean = 18.0) and *C. saburrae* (n = 160, mean = 18.1). The most variable meristic data are reported in Table 2 and morphometric characters are summarized in Table 3. The extensive overlap among the three species of *Chasmodes* with respect to the PC score values plotted against principal axes PC 1, sPC 2, and sPC 3 indicated that the truss measurements were unlikely to yield any diagnostic morphometric characters. The truss measurements were therefore not used in any subsequent analyses, but are reported to quantify body proportions (Table 3).

TABLE 2. Frequency distributions of counts from species of *Chasmodes*. Counts of gill rakers from Williams (1983).

	Mandibular pores						Spines in dorsal fin			
Species	4	5	6	7	8	mean	10	11	12	mean
C. bosquianus	63	8	5			4.2	3	69	1	11.0
C. longimaxilla	41	6	1			4.2	1	40	4	11.1
C. saburrae	4	18	131	5	2	5.9	4	156	6	11.0

	Segmented rays in dorsal fin						Pectoral-fin rays					
Species	16	17	18	19	20	mean	9	10	11	12	13	mean
C. bosquianus		6	32	29	6	18.5			2	67	5	12.0
C. longimaxilla	1	13	25	11	1	18.0			3	46	1	12.0
C. saburrae		32	89	38	1	18.1	1		5	149	4	12.0

	Segmented rays in anal fin							Segmented caudal-fin rays				
Species	16	17	18	19	20	21	mean	9	10	11	12	mean
C. bosquianus	1	4	30	32	5		18.5			71	2	11.0
C. longimaxilla	1	7	23	17	1	1	18.3	1	4	44	1	10.9
C. saburrae	1	14	86	56	4		18.3		7	137	7	11.0

	Gill rakers						
Species	9	10	11	12	13	14	mean
C. bosquianus			7	12	4		11.9
C. longimaxilla	1	5	17	2			10.8
C. saburrae				8	13	10	13.1

Similar treatment of the sPC scores that were derived from the six standard ichthyological measurements, however, demonstrated morphological divergence among *Chasmodes* species (Fig. 2). PC 1 (size) accounted for 96.3% of the variation among species, while sPC 2 and sPC 3 accounted for 1.9% and 0.8%, respectively (Table 4). The sPC loadings of three standard measurements (upper-jaw length, interorbital distance, and length of posteriormost dorsal-fin spine) were relatively high, each with a magnitude greater than 0.40 on sPC 2 or sPC 3. Upper-jaw length and interorbital distance loaded at –0.83 and 0.49, respectively, on sPC 2. Interorbital distance also loaded highly on sPC 3 at –0.64, as did length of posteriormost dorsal-fin spine at 0.73. Statistical comparisons show that *C. saburrae* (n = 100), *C. bosquianus* (n = 65), and *C. longimaxilla* (n = 49) are distinct from one another based on the standard measurement data (MANOVA Pillai's Trace Approximate $F_{4,422} = 97.6$, $p < 0.0001$). An overall difference in mean sPC2 scores was detected (ANOVA $F_{2,211} = 561.9$, $p < 0.0001$), as were differences in all pairwise contrasts (*C. bosquianus* vs. *C. longimaxilla*: $F_{1,211} = 43.6$, $p < 0.0001$; *C. bosquianus* vs. *C. saburrae*: $F_{1,211} = 619.6$, $p < 0.0001$; *C. longimaxilla* vs. *C. saburrae*: $F_{1,211} = 894.6$, $p < 0.0001$). Univariate ANOVA of sPC 3 scores was also significant ($F_{2,211} = 14.9$, $p < 0.0001$), as were all pairwise contrasts (*C. bosquianus* vs. *C. longimaxilla*: $F_{1,211} = 29.8$, $p < 0.0001$; *C. bosquianus* vs. *C. saburrae*: $F_{1,211} = 6.7$, $p = 0.0102$; *C. longimaxilla* vs. *C. saburrae*: $F_{1,211} = 12.7$, $p = 0.0005$). Thus, all three species of *Chasmodes* exhibited significant morphometric differences from each other along both shape components (sPC 2 and sPC 3).

TABLE 3. Summary of morphometric characters for species of *Chasmodes*.

Character		*C. bosquianus*	*C. longimaxilla*	*C. saburrae*
		n = 65	n = 49	n = 100
		19.2–76.9 mm standard length	21.2–86.8 mm standard length	14.0–72.6 mm standard length
In % head length				
	Snout length	23.9–30.7	23.0–31.3	24.0–35.3
	Upper-jaw length	35.8–56.2	40.0–60.6	28.0–43.3
	Orbit diameter	19.3–31.1	20.2–31.3	18.0–40.5
	Interorbital distance	9.7–15.5	10.7–15.9	11.5–18.4
In % standard length				
	Head length	27.9–32.7	28.7–34.5	27.0–36.1
	Last dorsal-fin spine	10.9–15.8	10.0–16.8	9.3–16.0
	Truss 1–2	22.5–29.4	21.2–27.7	22.6–30.8
	Truss 2–3	23.9–30.4	24.1–28.9	23.7–28.9
	Truss 1–3	22.4–32.0	24.2–34.2	21.5–30.6
	Truss 2–4	27.2–38.1	29.6–39.0	25.8–35.8
	Truss 4–5	21.9–28.0	22.2–29.5	22.8–28.0
	Truss 3–5	25.8–39.3	25.0–39.5	26.6–37.4
	Truss 2–5	39.6–47.0	39.4–45.7	38.3–46.1
	Truss 3–4	35.4–42.6	34.8–42.4	35.2–44.4
	Truss 4–6	36.2–44.4	31.3–41.8	35.9–43.8
	Truss 5–7	36.7–45.9	35.9–46.5	36.9–46.5
	Truss 6–7	7.3–9.6	7.0–9.2	6.1–8.9
	Truss 4–7	38.2–48.3	38.8–43.4	38.2–45.3
	Truss 5–6	40.4–47.5	39.3–47.2	39.7–49.1
	Truss 6–8	4.7–8.1	5.2–7.8	5.0–8.0
	Truss 8–9	4.7–6.2	4.5–6.1	4.4–6.6
	Truss 7–9	6.2–11.0	6.8–8.9	6.0–9.5
	Truss 6–9	7.6–10.3	8.4–10.3	7.9–10.0
	Truss 7–8	9.1–11.4	9.0–11.6	8.8–11.6

Because it is relatively easy to distinguish *C. saburrae* from both *C. bosquianus* and *C. longimaxilla* on the basis of morphological characters used by Williams (1983), the remainder of this section more explicitly addresses the distinction between *C. bosquianus* and *C. longimaxilla*. A discriminant functions analysis (DFA) was performed on various combinations of the standard measurements that loaded most highly in the sPCA. Although snout length did not load highly in the PCA, it differed significantly between species (ANCOVA with head length as covariate $F_{2,111} = 1514.7$, $p < 0.0001$) and was therefore incorporated into the discriminant analysis. Various linear combinations of the three high-loading standard measurements and snout length were used to find the combination that best discriminated between *C. bosquianus* and *C. longimaxilla*.

The following ratios were assigned as the predictor variables because they were found by trial and error to maximize discriminating power: upper-jaw length ÷ head length, snout length ÷ upper- jaw length, and fleshy interorbital distance ÷ length of posteriormost dorsal-fin spine, and fleshy interorbital distance ÷ snout length. The probability equation derived was:

$$\text{Prob}[\textit{bosquianus} \text{ or } \textit{longimaxilla}] = e^{(-0.5 * \text{Dist}[\textit{bosquianus} \text{ or } \textit{longimaxilla}])} \div \text{Prob}[0]$$

where

$$\text{Prob}[0] = e^{(-0.5 * \text{Dist}[\textit{bosquianus}])} + e^{(-0.5 * \text{Dist}[\textit{longimaxilla}])}$$

Dist[*bosquianus*] = Dist[0] - 3388.81(upper-jaw length ÷ head length) - 1612.70(interorbital distance ÷ snout length) + 750.67(interorbital distance ÷ length of posteriormost dorsal-fin spine) - 3050.44(snout length ÷ upper-jaw length) + 1973.10

Dist[*longimaxilla*] = Dist[0] - 3413.82(upper-jaw length ÷ head length) -1614.44(interorbital distance ÷ snout length) + 712.41(interorbital distance ÷ length of posteriormost dorsal-fin spine) - 2989.97(snout length ÷ upper-jaw length) + 1962.28

Dist[0] = 1686.77(upper-jaw length ÷ head length)(upper-jaw length ÷ head length) + 1103.79(interorbital distance ÷ snout length)(upper-jaw length ÷ head length) + 962.08(interorbital distance ÷ snout length)(interorbital distance ÷ snout length) – 632.72(interorbital distance ÷ length of posteriormost dorsal-fin spine)(upper-jaw length ÷ head length) – 1620.33(interorbital distance ÷ length of posteriormost dorsal-fin spine)(interorbital distance ÷ snout length) + 1449.66(interorbital distance ÷ length of posteriormost dorsal-fin spine)(interorbital distance ÷ length of posteriormost dorsal-fin spine) + 2499.68(snout length ÷ upper-jaw length)(upper-jaw length ÷ head length) + 1133.43(snout length ÷ upper-jaw length)(interorbital distance ÷ snout length) – 931.16(snout length ÷ upper-jaw length)(interorbital distance ÷ length of posteriormost dorsal-fin spine) + 1345.84(snout length ÷ upper-jaw length)(snout length ÷ upper-jaw length)

e = 2.718

In order to determine the efficacy of species prediction, a contingency analysis was performed. Fifty-four of 65 (83.1%) *Chasmodes bosquianus* specimens and 45 of 49 (91.8%) *C. longimaxilla* specimens were correctly identified using the discriminant function. Thus, using only the above set of equations 99 of 114 specimens (86.8%) were correctly identified as either *C. bosquianus* or *C. longimaxilla*.

TABLE 4. Variable loadings from sheared principal components analysis for morphometric characters of *Chasmodes* species.

Principal Component	PC 1	sPC 2	sPC 3
Percentage of variance	96.256	1.895	0.813
Variables			
Head length	0.384	0.070	0.024
Snout length	0.398	0.163	0.051
Upper-jaw length	0.545	-0.826	-0.219
Orbit diameter	0.257	0.125	-0.052
Interorbital distance	0.363	0.486	-0.639
Length of last dorsal-fin spine	0.446	0.173	0.732

Given the demonstration of significant differences in the mean number of segmented dorsal-fin rays and body proportions between *C. bosquianus* and *C. longimaxilla*, and that those differences are large enough to enable significant discrimination between the two, we follow Williams (2003) and recognize *C. longimaxilla* as a distinct species. Taxonomic treatments follow.

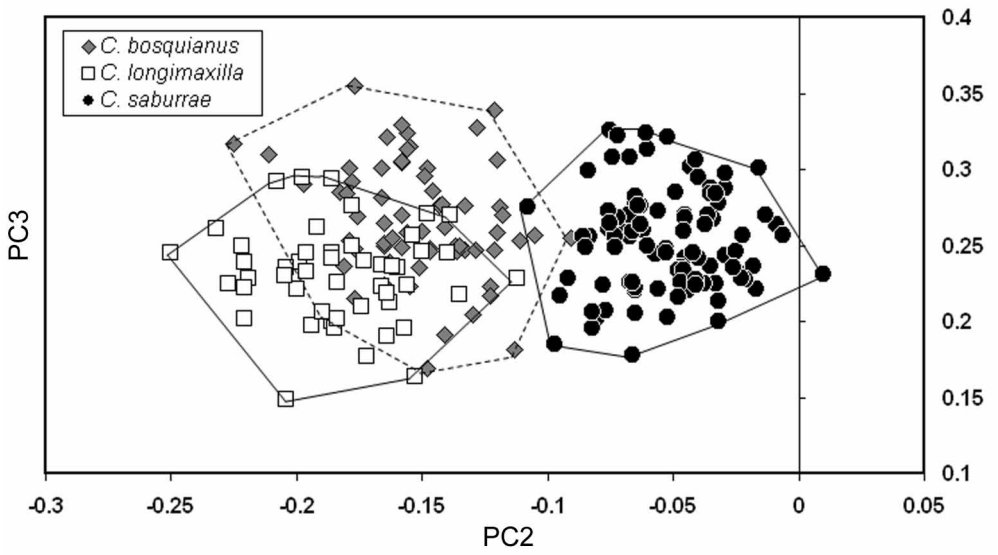

FIGURE 2. Plot of principal component scores for *Chasmodes* with respect to the first two sheared (shape) principal components. The size axis, PC 1, is not shown. Shaded diamonds: *C. bosquianus*, open squares: *C. longimaxilla*, black circles: *C. saburrae*.

Chasmodes

Chasmodes Valenciennes 1836: 295. Type species: *Blennius bosquianus* Lacepède 1800: 493 by subsequent designation of Jordan and Evermann (1898) and Eigenmann (1910).

Blennitrachus Swainson 1839: 78. Spelled *Blenitrachus* on pp. 182, 274 (Swainson 1839). Type species: *Pholis quadrifasciatus* Wood 1825: 282 by monotopy.

Diagnosis. Characters, in combination, which serve to distinguish *Chasmodes* from other blenniid genera: dentary and premaxillary canines absent; vomerine teeth absent; hypural 5 absent; orbital cirri absent or small and unbranched; interorbital region flattened; gill opening small and dorsal to ventralmost portion of pectoral-fin base; anterior portion of lateral line continuous, without regular pattern of side branches, and terminating at a point immediately posterior to pectoral fin; posterior portion of lateral line composed of short single tubes to about mid-length of body; in lateral view, first basibranchial shaped like a broad shallow U. No autapomorphies known.

Description. Dorsal-fin rays X–XII,16–20 (modally XI,18); anal-fin rays II,16–20 (modally 18); pelvic-fin rays I,3; pectoral-fin rays 11–13 (usually 12); segmented caudal-fin rays 9–12 (modally 11); branched caudal-fin rays 0–10; dorsal procurrent caudal-fin rays 4–5; ventral procurrent caudal-fin rays 3–5; dorsal-fin origin dorsal to posterior edge of preopercle; anal-fin origin ventral to anteriormost segmented dorsal-fin ray; dorsal-fin spines slightly shorter than segmented dorsal-fin rays; caudal fin rounded; segmented dorsal-fin rays usually unbranched, although larger individuals may have up to three branched rays; segmented anal-fin rays unbranched; first anal-fin spine of females reduced; mature males with rugosities on anal-fin spines and fleshy tips on segmented dorsal-fin and segmented anal-fin rays; membranous connections present between posteriormost rays of dorsal and anal fins and base of caudal fin; head length 25.8–37.4% SL; gill membranes broadly united to isthmus; gill rakers 10–14; mouth oblique; upper lip attached to anteriormost portion of snout; upper jaw extending posteriorly at least to vertical through anterior margin of orbit, 28.0–60.6% of head length; teeth uniserial and evenly spaced (except in rare instances where one or two teeth are found immediately posterior to main series of teeth on anteromedial portion of dentary); anterior three-fourths of premaxilla toothed; anterior one-half of dentary toothed; symphyses of premaxillae and dentaries ligamentous; each dorsal pharyngeal-tooth plate with 5–7 large teeth and 0–5 small teeth; each ventral pharyngeal-tooth plate with 4–6 large teeth and 4–6 small teeth; branchiostegal rays 6; mandibular pores

(counted following Williams 1983) 4–8; epineurals 11–13; body unscaled and elongate; body depth greatest at vertical through base of pectoral fin, tapering to its least depth at caudal peduncle; urogenital papilla smooth and without lateral lobes; precaudal vertebrae 10; caudal vertebrae 24–26; dorsal and ventral profiles of caudal peduncle straight; ventral hypural plate (hypurals 1 and 2) fused to urostylar centrum.

Pigmentation. *Chasmodes* exhibits no discernible variation in color among species. Males and females are variously mottled in brown, tan, or olivaceous hues. The lateral and dorsal surfaces of the head, as well as the posterior portions of the unpaired fins, often bear small irregular spots. The pelvic fins often have dark bands. Small individuals, females, and males without territories have irregular brown vertical bars (approximately the width of the orbit) on whitish mottled background. Light longitudinal lines may be present on large territorial males, which also have an iridescent blue spot centered on the membrane between the first and second dorsal-fin spines. A smaller noniridescent spot may be present posterior to the first, between the second and third dorsal-fin spines. A pale longitudinal streak follows these spots and ends near the posteriormost dorsal-fin spine. The chest and branchiostegal membranes of these males are orange. The spots in the dorsal fin are dark brown in preservative.

Distribution. Species of *Chasmodes* are restricted to the northwestern Atlantic Ocean and the Gulf of Mexico, where they are found in bays and estuaries from New York to Veracruz, Mexico. Like most blenniids, *Chasmodes* species are relatively reclusive and seek shelter among shells, rocks, or vegetation. Most specimens have been captured at depths less than 30 meters.

Ecology and life history. *Chasmodes* mostly consume small crustaceans, such as amphipods (Hildebrand & Schroeder 1928; Reid 1954; Carr & Adams 1973). Mating typically occurs during spring and summer. Larger territorial males perform a courtship ritual that has been described by Tavolga (1958; below, see "Ecology and Life History" section on *C. saburrae* for notes on Tavolga's identification of specimens) and Phillips (1977). Females attach eggs to protected spaces, such as the inner surfaces of empty shells. Males fertilize and protect the eggs from predators until hatching, but apparently provide no posthatching care.

Chasmodes bosquianus Striped Blenny

Blennius bosquianus Lacepède 1800: 459, 493, Pl. 13 (fig. 1). Type locality: Carolinas. No types known.
Pholis novemlineatus Wood 1825: 280. Type locality: Charleston Harbor, South Carolina. Holotype: ANSP 10410.
Pholis quadrifasciatus Wood 1825: 282, Pl. 17 (fig. 1). Type locality: unknown, probably South Carolina (according to Eschmeyer 1998). No types known.
Chasmodes bosquianus bosquianus Williams 1983

Material examined. Type material is listed with a relatively precise locality, but nontype material is listed only according to state. The number of specimens examined from a particular lot is indicated in parentheses. Seventy-six specimens examined, 9.0–76.9 mm SL. ANSP 23045, 1, New Jersey. ANSP 98578, 1, Port Norris, Cumberland County, New Jersey. ANSP 121274, 2 (62.8–63.9 mm SL), Barnegat Bay, Seaside Park, New Jersey. UMMZ 109932, 1 (26.4 mm SL), Kettle Bay, Silverton, New Jersey. USNM 201352, 5 (47.3–66.7 mm SL), Patuxent River at Solomons Island, Calvert County, Maryland. USNM 291726, 5 (40.2–47.2 mm SL), Crisfield, Maryland. ANSP 112348, 1 (72.4 mm SL), east side of Potomac River, approximately 3.2 km north of span of U.S. Highway 301 bridge and just south of Popes Creek, Charles County, Maryland. ANSP 116260, 4 (31.2–40.2 mm SL), western shore of Chesapeake Bay, just northwest of Camp Conoy, Calvert County, Maryland. TU 44326, 4 (57.4–76.9 mm SL), Solomons Island, Calvert County, Maryland. USNM 091146, 4 (54.6–67.9 mm SL), James Fishery, Norfolk, Virginia. USNM 091147, 3 (48.5–58.1 mm SL), Lewisetta, Virginia. USNM 091154, 1 (48.3 mm SL), Cape Charles, Virginia. ANSP 76132, 1 (46.2 mm SL), just below U.S. Highway Bridge No. 17, York River, Virginia. ANSP 140146, 1, Ocracoke, North Carolina. AMNH 4293, 4 (21.8–29.3 mm SL), Cape Lookout, Carteret County, North Carolina. UMMZ 211944, 1 (48.8 mm SL), Tidal lagoon behind Oak Island strand, Long Beach, 16 km west of Southport, Brunswick County, North Carolina. GMBL 00-64, 1, probably South Carolina. GMBL 80-12, 1 (63.0 mm SL), North Santee Bay, South Carolina. GMBL 70-157, 1 (63.6 mm SL), Georgetown, South Carolina.

GMBL 71-110, 3 (53.8–66.7 mm SL), Georgetown, South Carolina. AMNH 73831, 1 (65.2 mm SL), Crabhaul Creek, North Inlet, Georgetown County, South Carolina. AMNH 229943, 1 (54.9 mm SL), Cat Island impoundment or Chainey Creek, Georgetown County, South Carolina. GMBL 867008, 1 (59.4 mm SL), probably South Carolina. ANSP 10410, 1 (holotype of *Pholis novemlineatus* Wood), Charleston Harbor, Charleston, South Carolina. ANSP 134228, 9 (19.2–68.3 mm SL), East Beach tide pool, Saint Simons Island, Georgia. UF 85687, 1 (51.6 mm SL), Orange Park, Clay County, Florida. USNM 188254, 3 (9.0–10.1 mm SL), Matanzas River, near Vilano Bridge, Saint Augustine, Florida. ANSP 106142, 12 (34.6–45.9 mm SL), Marineland, Flagler County, Florida. MCZ 32936, 1 (52.8 mm SL), New Smyrna Beach, Volusia County, Florida. MCZ 50793, 1, "Mouth of Saint John's River, Port Orange," Florida (see Remarks below).

Diagnosis. Characters, in combination, which serve to distinguish *Chasmodes bosquianus*: dentary teeth sharply pointed and recurved (see Williams 1983: fig. 2); mandibular pores 4–6 (usually 4; Table 2); ventral lip flaps not prominent; upper jaw length 35.8–54.4% of head length; gill rakers 11–13 (usually 12).

Description. Characters presented in generic and species diagnoses and generic description form a part of the species description and are not repeated. Snout somewhat pointed in lateral profile; dorsal and ventral profiles slightly convex; body widest in abdominal region. Body proportions are given in Table 3.

Size. Individuals of this species reach nearly 80 mm SL. The largest specimen examined was 76.9 mm SL (TU 44326).

Distribution. *Chasmodes bosquianus* occurs along the east coast of the United States from New York, New York, to New Smyrna Beach, Florida, but is rare north of Chesapeake Bay.

Ecology and life history. This species typically inhabits shallow seagrass flats, rocky bottoms, and oyster reefs in bays and estuaries. *C. bosquianus* is usually found in areas of moderate salinity (15–25 ‰) but has been collected in coastal rivers and in waters of less than 10 ‰. Hildebrand and Schroeder (1928) found that insect larvae, small crustaceans, and mollusks are common prey items for this species. Phillips (1971a, 1971b, 1977) and Phillips and Swears (1979) reported on various aspects of the behavior of the Striped Blenny, including its avoidance of a predator, *Opsanus tau* (Linnaeus; Batrachoididae). The spawning season is thought to commence in mid-March and end in August (Williams 1983). Embryonic development was described by Hildebrand and Cable (1938).

Remarks. The collection locality of one specimen (MCZ 32936) is south of the previously reported southern limit of this species (Marineland, Flagler County, Florida). The species range is therefore extended southwards by about 85 km to New Smyrna Beach, Florida. The stated collection locality of another specimen (MCZ 50793) is confusing, as it is listed as "Mouth of Saint John's River, Port Orange." The city of Port Orange, Florida, and the mouth of St. John's River, near Jacksonville, are not in close proximity. If the specimen was collected near Jacksonville, then it falls well within the previously reported range of *C. bosquianus*. If, however, the specimen was collected near Port Orange (15 km north of New Smyrna Beach), then its collection there further supports a southerly extension of the species' range.

Chasmodes longimaxilla Stretchjaw Blenny

Chasmodes bosquianus longimaxilla Williams 1983: 72, 85, fig. 6. Type locality: East end seawalls, rock jetties on northeast side of island, Fort Gaines, Dauphin Island, Alabama. Holotype: USNM 219830.
Chasmodes longimaxilla Williams 2003: 1770, 1772.

Material examined. Fifty-five specimens examined, 21.2–86.8 mm SL. Florida: FMNH 57043 (paratypes), 2 (50.2–76.7 mm SL), Pensacola, Escambia County, Florida. CAS-SU 00435, 5 (48.5–64.7 mm SL), Pensacola, Escambia County, Florida. UMMZ 139186, 1 (23.9 mm SL), Santa Rosa Sound, approximately 8 km from bridge over Pensacola Bay on U.S. Highway 98, Florida. USNM 005721 (paratype), 1 (55.9 mm SL), Fort Morgan Point, Baldwin County, Alabama. USNM 342666, 2 (55.8–65.5 mm SL) Fort Morgan Point, Baldwin County, Alabama. UF 31478 (paratype), 1 (58.8 mm SL), Dauphin Island, Mobile County, Alabama. UF 31479 (paratype), 1 (71.6 mm SL), Dauphin Island, Mobile County, Alabama. FMNH 62465 (paratype), 1 (64.6 mm SL), Gulf Coast Research Laboratory, Ocean Springs, Jackson County, Mississippi. GCRL 2061

(paratype), 1 (68.8 mm SL), off Round Island, Mississippi Sound, Mississippi. GCRL 2903 (paratype), 1 (54.3 mm SL), Mississippi Sound, Mississippi. USNM 072333 (paratype), 1 (66.1 mm SL), Three Mile Bayou, Mississippi. USNM 121994 (paratypes), 2 (46.6–67.2 mm SL), southeast end of Deer Island, Mississippi. USNM 162591 (paratype), 1 (76.6 mm SL), near Chauvin, Terrebonne Parish, Louisiana. TU 5564, 1 (76.1 mm SL), Terrebonne Parish, Louisiana. TU 164153, 1, Plaquemines Parish, Louisiana. TU 164504, 1 (65.7 mm SL), Jefferson Parish, Louisiana. CAS-SU 21377, 1 (86.8 mm SL), Cameron, Cameron Parish, Louisiana. CAS-SU 21380, 5 (45.8–56.9 mm SL), Cameron, Cameron Parish, Louisiana. UMMZ 114470 (paratypes), 5 (56.9–70.3 mm SL), Lavaca Bay, Calhoun County, Texas. USNM 069338 (paratypes), 3 (59.5–69.0 mm SL), Matagorda Bay, Texas. UMMZ 111743 (paratypes), 3 (49.6–62.0 mm SL), vicinity of Rockport, Aransas County, Texas. UF 4233 (paratype), 1 (21.2 mm SL), Ransom Island, Redfish Bay, San Patricio County, Texas. ANSP 129692 (paratype), 1 (34.6 mm SL), La Quinta Channel, approximately 3.2 km south-southwest of Ingleside, Ingleside, San Patricio County, Texas. FMNH 40311 (paratypes), 2 (42.6–59.9 mm SL), within 80 km of Corpus Christi, Texas. USNM 156556 (paratypes), 5 (36.6–53.6 mm SL), Hog Island, Corpus Christi, Texas. ANSP 71181-2 (paratypes), 2 (47.6–69.1 mm SL), Flower Bluff, Laguna Madre, Texas. TU 21596, 1 (42.9 mm SL), West Bay, 3.2 km east of San Luis Pass on Galveston Island, Galveston County, Texas. TU 21665, 2 (35.2–40.4 mm SL), bay side of Harbor Island, Aransas Bay, Nueces County, Texas. ANSP 145208, 1 (51.8 mm SL), Flower Bluff, Laguna Madre, Texas.

Diagnosis. Characters, in combination, which serve to distinguish *Chasmodes longimaxilla*: dentary teeth sharply pointed and recurved; mandibular pores 4–6 (usually 4; Table 2); ventral lip flaps not prominent; upper jaw length 40.0–60.6% of head length; gill rakers 9–12 (usually 11).

Description. Characters presented in generic and species diagnoses and generic description form a part of the species description and are not repeated. Snout somewhat pointed in lateral profile; other salient features similar to those of *C. bosquianus*. Body proportions are given in Table 3.

Size. Maximum size about 87 mm SL.

Distribution. *Chasmodes longimaxilla* occurs in coastal waters from Pensacola, Florida, to Veracruz, Veracruz State, Mexico (Bath 1977). This species is sympatric with *C. saburrae* from Pensacola to the Chandeleur Islands, Louisiana, but seems to be allotopically distributed with respect to the latter. In the area of sympatry, Williams (1983) characterized this segregation as "almost exclusive" such that *C. saburrae* prefers seagrass beds and *C. longimaxilla* associates more with rocks and shells.

Ecology and life history. The Stretchjaw Blenny typically inhabits seagrass flats, rocky bottoms, and oyster reefs in bays and estuaries. *C. longimaxilla* has not been reported in rivers or other waters with salinities less than about 10 ‰ (Williams 1983). The spawning season begins in March and ends in October or early November (Williams 1983).

Remarks. The name *longimaxilla* was described as a noun in apposition (Williams 1983). Williams (1983) mentioned that the original identification and locality data for FMNH 80505 (*C. saburrae* from Key Largo, Florida) are probably erroneous. The shape of the teeth, number of mandibular pores, and morphometric characters suggest that the specimen is probably *Chasmodes longimaxilla*, and therefore unlikely to have been collected at Key Largo. The meristic and morphometric data that we report are consistent with Williams' (2003) classification. The common name "Stretchjaw Blenny" is used by Nelson *et al.* (2004), owing to the relative length of the upper jaw.

Chasmodes saburrae Florida Blenny

Chasmodes saburrae Jordan and Gilbert 1882: 298. Type locality: Pensacola, Florida. Lectotype: USNM 30824, designated by Jordan and Evermann (1898: 2393).

Blennius fabbri Nichols 1910: 161. Type locality: Miami, Florida. Holotype: AMNH 2537.

Material examined. One hundred fifty-two specimens examined, 12.8–71.5 mm SL. Florida: CAS-SU 440 (paralectotypes, 12, 39.6–72.6 mm SL, Pensacola, Florida), UF 118293 (1, 35.3 mm SL), UF 118300 (5, 26.3–47.4 mm SL), UF 23686 (5, 33.0–45.1 mm SL), UMMZ 139366 (5, 16.3–55.6 mm SL), UF 23688 (21, 12.8–

30.1 mm SL), AMNH 17245 (1, 23.4 mm SL), UF 208183 (1, 52.7 mm SL), UF 203132 (3, 23.9–33.8 mm SL), UF 210739 (1, 30.0 mm SL), UF 65583 (1, 40.0 mm SL), ANSP 78555 (1, 41.0 mm SL), ANSP 131944 (1), UF 32656 (1, 15.3 mm SL), TU 21035 (1, 40.2 mm SL), UF 54108 (10, 20.4–36.9 mm SL), ANSP 74119 (1, 69.7 mm SL), UMMZ 113268 (1, 44.4 mm SL), USNM 084040 (1, 50.6 mm SL), ANSP 86332 (13), UF 2576 (1, 26.2 mm SL), UF 1084 (1, 51.0 mm SL), TU 21869 (5, 29.8–65.4 mm SL), UF 54179 (1, 57.9 mm SL), TU 16713 (1, 56.2 mm SL), UF 75127 (1, 53.9 mm SL), UF 51529 (1, 49.9 mm SL), UF 64651 (9, 18.6–40.8 mm SL). Mississippi: GCRL 5777 (3, 28.4–39.1 mm SL), GCRL 5781 (4, 10.4–23.2 mm SL), FMNH 46657 (1, 38.6 mm SL), USNM 188248 (18, 28.6–71.5 mm SL). Louisiana: TU 76601 (10, 35.6–50.3 mm SL), TU 78298 (3, 38.3–42.6 mm SL), TU 188444 (2, 41.7–62.3 mm SL), CAS-SU 21380 (5, 45.8–56.9 mm SL).

Diagnosis. Characters, in combination, which serve to distinguish *C. saburrae*: dentary teeth bluntly pointed (see Williams 1983: fig. 2); mandibular pores 5–8 (usually 6); ventral lip flaps prominent; upper jaw length 28.0–43.3% of head length; gill rakers 12–14 (usually 13).

Description. Characters presented in generic and species diagnoses and generic description form a part of the species description and are not repeated. Snout somewhat steep in lateral profile. Body proportions are given in Table 3.

Size. The maximum standard length of *C. saburrae* is about 80 mm SL (Williams 1983).

Distribution. This species is distributed along the coast from Edgewater, east coast of Florida, westward to the Chandeleur Islands, Louisiana. Between Pensacola, Florida, and the Chandeleur Islands, *C. saburrae* is sympatric with *C. longimaxilla*, but the former occupies seagrass beds "almost exclusively" rather than shells that it sometimes inhabits and that the latter prefers (Williams 1983). In other parts of Florida, this species has been collected from lagoon reefs (Gilmore 1974), seagrass beds, and in oyster or conch shells.

Ecology and life history. Reid (1954) gave a qualitative account of the stomach contents of 30 specimens. Carr and Adams (1973) verified these findings and showed that juveniles eat mostly amphipods and later become omnivorous. The reproductive biology and developmental osteology of this species have been characterized by Peters (1981). Tavolga (1958) described courtship sounds made by male *C. bosquianus* taken from Gasparilla Sound (west coast of Florida). The identification of those individuals may have been in error, because there is no other documentation of *C. bosquianus* from that part of Florida. It is therefore more likely that those specimens were *C. saburrae*.

Molecular phylogeny. DNA sequences, including two acquired from GenBank, were aligned to produce a data matrix with 24 specimens (representing ten species) and 407 characters. Of those, 79 were parsimony-informative and 328 were parsimony-uninformative and therefore excluded from further consideration. Sequences that were collected for this study have been deposited in GenBank (Table 1). A single most parsimonious tree was found to have a length of 179 steps, a consistency index (CI) of 0.65, and a retention index (RI) of 0.85 (Fig. 3). *Parablennius parvicornis* was the most basal species of the ingroup. The tree also showed *Chasmodes* as the sister group to a clade consisting of *Hypleurochilus*, *Scartella*, and *Hypsoblennius*. Within the *Chasmodes* clade, *C. bosquianus* and *C. saburrae* did not form reciprocally monophyletic groups. At least 97% of the 1000 bootstrap pseudoreplicates sampled with a heuristic search (tree bisection-reconnection algorithm of branch-swapping) supported nodes that joined pairs of congeners, but intergeneric relationships were supported by bootstrap frequences of less than 50%. Bremer support values also exhibited a wide range, with some nodes only supported by a value of one, whereas the highest Bremer support value (14) was found at the node representing the most recent common ancestor of *Chasmodes* specimens (Fig. 3).

Discussion

Mean numbers of countable features and body proportions differed significantly among the three species of *Chasmodes*. Sheared principal components analysis, a multivariate statistical method, was used to quantify such variation in shape. Combinations of raw measurement data were demonstrated to be useful for interspecific discrimination. Given their allopatric distributions and significant morphological differences,

Gulf and Atlantic *Chasmodes* should be valid as evolutionary species (in the sense of Wiley & Mayden 2000a, 2000b, 2000c). *C. bosquianus* occurs in the western north Atlantic, from New York to eastern central Florida; *C. saburrae*, from eastern central Florida to the Chandeleur Islands, Louisiana, and *C. longimaxilla*, from Pensacola, Florida, to Veracruz, Mexico.

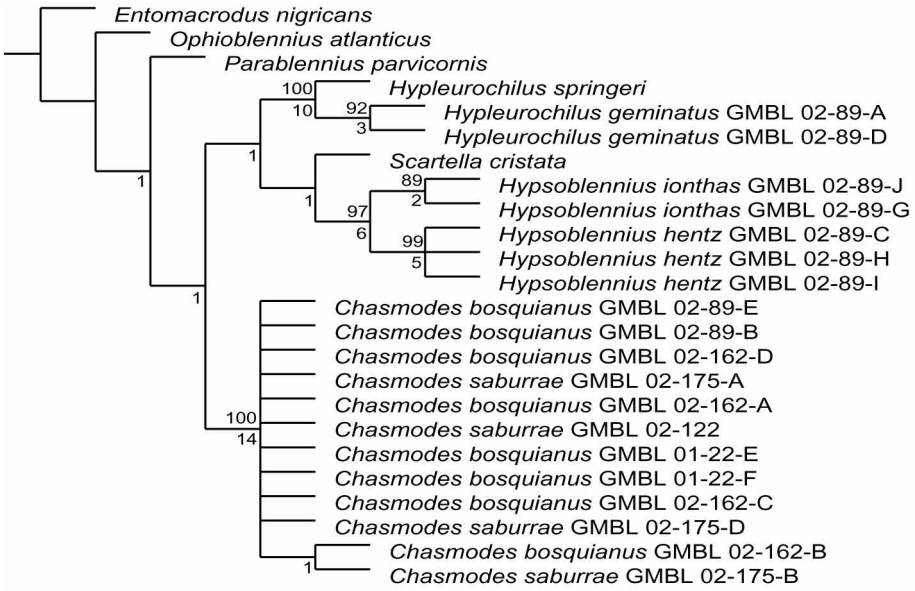

FIGURE 3. Most-parsimonious cladogram derived from 12S DNA sequences from ten blenniid species. Length = 179 steps, CI = 0.65, RI = 0.85. In cases where multiple specimens of a species are present, collection numbers are listed. Support values are to left of nodes, bootstrap values above and Bremer support values below.

Long-distance dispersal of *Chasmodes* is unlikely in light of their general life history patterns. Like other blenniids, adult *Chasmodes* usually do not swim continuously for long distances, but instead live demersally and travel between objects that provide cover (Phillips 1977). Females typically attach eggs to the inner surface of bivalve shells; males guard these at least until hatching (Hildebrand & Cable 1938; Peters 1981). Because *Chasmodes* are found in shallow waters, it is unlikely that newly hatched larvae are transported far by oceanic currents. Thus, it would appear that the present distributions of *Chasmodes* species are not the result of recent dispersal.

The fluctuating level of the sea around the Florida Platform during the Miocene, Pliocene, and Pleistocene (Scott 1997) prompted both Springer (1959) and Williams (1983) to postulate about its connection to allopatric speciation in *Chasmodes*. Springer (1959), on one hand, felt that an ancestral species of *Chasmodes* inhabited most or all of the Atlantic and Gulf coasts during the Pliocene. Inundation of Florida, except for the highlands, resulted in the establishment of continental and island populations that were separated by perhaps 200 km. During the Pleistocene, these allopatric populations diverged genetically to the point of species-level distinctness. Through its tolerance for warmer waters, the island endemic, *C. saburrae*, partly displaced the mainland species, *C. bosquianus*, as the sea fell near the close of the Pleistocene and resulted in the establishment of divergent allopatric Gulf and Atlantic coast populations of the latter. Williams (1983), on the other hand, agreed with Springer as to the vicariant mechanism of evolution, but hypothesized that Gulf and Atlantic subspecies of *C. bosquianus* have been isolated since the sea level minimum of the last glaciation (ca. 18,000 YBP). In addition, he suggested that *C. saburrae* excluded other species of *Chasmodes* from peninsular Florida through their tolerance for higher water temperatures (Williams 1983).

The origins of other genera that contain Gulf-Atlantic species pairs are also probably related to post-Miocene sea-level fluctuations. The distributions of *Chasmodes* species, rather than populations, are largely congruent with other western Atlantic species and may be explained by vicariance. Atlantic and Gulf species are sister taxa, excluded from southern Florida by a third species that evolved in, and is therefore more tolerant of those warmer waters. The similarity between *C. bosquianus* and *C. longimaxilla* is likely due to their relatively recent divergence. Based on biogeographical inferences as opposed to a molecular clock, *C.*

saburrae, the most outwardly distinctive species of *Chasmodes*, has been genetically isolated from its congeners for longer (since ca. 125,000 YBP) than *C. bosquianus* and *C. longimaxilla* have been from one another (since ca. 18,000 YBP).

The results reported above, based on mitochondrial sequence data, form a hypothesis of relationship among *Chasmodes* and other blenniid genera present in the northwest Atlantic. The results reported here agree with those of Pázmándi (2000: fig. 1.23), who also inferred that *Chasmodes* is more closely related to *Hypsoblennius* than either is to *Parablennius*. As far as is known, however, our analysis is the first to include molecular data from *Chasmodes*, *Hypleurochilus*, *Parablennius*, and *Hypsoblennius*. These analyses were not critical tests of monophyly for the genera included. Rather, exemplar species were sampled from each genus. Future work may test our phylogenetic hypothesis through the inclusion of data from other taxa and characters. For example, morphological diversity was not taken into account. Perhaps it is noteworthy that some morphological characters are congruent with an alternative hypothesis of a sister-group relationship between *Chasmodes* and *Hypsoblennius*. These taxa share the absence of both enlarged canine teeth and hypural five (Williams 2003).

Benthic species that constitute critical habitat for species of *Chasmodes*, namely seagrasses and oysters, experienced marked decline in abundance during the last century. Declines in abundances of seagrasses are partly attributed to increased shading by algae (Hall *et al.* 1999). Oysters in Chesapeake Bay and the Gulf of Mexico have been particularly susceptible to disease, over-harvesting, and siltation (MacKenzie 1996). Small demersal fishes serve as important trophic links between primary producers and higher-level consumers, including birds and larger fishes. Species of *Opsanus* (toadfishes) occur sympatrically with *Chasmodes* species and prey upon them (Phillips & Swears 1979). Reduction of suitable habitat for *Opsanus* and *Chasmodes* species may affect the predator-prey relationships between species of these genera and therefore alter the sizes of *Chasmodes* populations. Matheson *et al.* (1999) showed that while many more *Opsanus beta* were caught in Florida Bay during the 1990s than in the 1980s, catches of small fishes such as *Chasmodes saburrae* and *Paraclinus marmoratus* (Marbled Blenny) dropped greatly. Future studies of *Chasmodes* species might examine in greater detail their population structure and roles in marine food webs.

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