A New Toadfish (Batrachoididae) Considered to be a Glacial Relict in the West Indies

By Vladimir Walters[1] and C. Richard Robins[2]

INTRODUCTION AND ACKNOWLEDGMENTS

Many fishes that are abundant in the Bahamas are scarce or absent from the Florida Keys, and the reverse is also true. In other instances the two regions are represented by different subspecies or allopatric species pairs. The inshore fish fauna of Cuba is less well known than that of the Keys or that of the Bahamas. The toadfish genus *Opsanus* affords an example of the faunal difference between Cuba and the Bahamas on one hand and Florida on the other. Three species [*O. tau* (Linnaeus), *O. pardus* (Goode and Bean), and *O. beta* (Goode and Bean)] known from Florida are absent from the Bahamas and Cuba. The form of *Opsanus* that occurs in Cuba and the Bahamas represents an undescribed species, named in the present paper.

No member of the Batrachoididae has previously been reported from the Bahamas. Moreover, James E. Böhlke notes (*in litt.*) that none has been taken in his extensive collections from the eastern Bahamas. Most of the Bahamian specimens of the new species were collected in the course of field work at the Lerner Marine Laboratory of the American

Museum of Natural History at Bimini by Walters and other laboratory personnel.

Dr. Marie Poland Fish of the Narragansett Marine Laboratory recorded the sounds produced by Bimini toadfishes in aquaria at the Lerner Marine Laboratory and has kindly lent three of her specimens for this study. Dr. Ernest A. Lachner, of the United States National Museum, examined material and, with Dr. Leonard P. Schultz, Mr. Robert H. Kanazawa, and Dr. Giles W. Mead, aided the authors in many ways during their visits to that institution. Dr. James E. Böhlke of the Academy of Natural Sciences of Philadelphia made available specimens and information. The authors are especially indebted to Drs. Charles M. Breder, Jr., Max K. Hecht, Norman D. Newell, and Donald F. Squires of the American Museum of Natural History, to Drs. Cesare Emiliani and Gilbert L. Voss of the Marine Laboratory, University of Miami, and to Dr. Reeve M. Bailey of the Museum of Zoology, University of Michigan, for advice and criticisms. Mr. Walter R. Courtenay photographed the specimens.

The following abbreviations are employed:

A.M.N.H., the American Museum of Natural History
A.N.S.P., the Academy of Natural Sciences of Philadelphia
B.M., specimens auditioned by Marie Poland Fish
U.M.M.L., the University of Miami Marine Laboratory
U.S.N.M., the United States National Museum

The numbers in parentheses that follow the museum catalogue numbers indicate the numbers of specimens and their ranges in standard lengths. Counts and measurements were performed according to the methods suggested by Hubbs and Lagler (1947, pp. 8–15), unless otherwise indicated.

Opsanus phobetron, new species

Figures 1A, 2A

DIAGNOSIS: An *Opsanus* with roof and floor of mouth, tongue, gill arches, gill rakers, and inner surface of gill cover black. Inner lining of swim bladder with a black reticulum. Posterior vomerine teeth often canine-like. Dark markings on body and fins approximating cross bands, not vermiculations or rounded discrete spots. Some light-colored spots on sides of body; pectoral fin with vertical rows of light-colored spots, imparting a banded appearance to the fin. Dorsal and anal fins with irregular dark markings.

MATERIAL EXAMINED: Holotype: A.M.N.H. No. 20336 (1, 168); from an old conch shell (*Strombus gigas*) in about 2 feet of water at low tide,

TABLE 1

NUMBERS OF FIN RAYS AND MERISTIC INDICES FOR SEVERAL FORMS OF *Opsanus*[a]

| | phobetron | Unidentified | | beta | tau | pardus |
		Little Bahama	Campeche Gulf			
Dorsal rays						
23	—	—	—	2	—	—
24	15	1	3	10	1	—
25	2	—	2	47	18	1
26	1	—	—	3	13	8
27	—	—	—	—	1	—
Anal rays						
19	—	—	—	2	—	—
20	7	1	2	2	5	1
21	9	—	2	29	16	4
22	2	—	1	26	12	5
23	—	—	—	2	—	—
Pectoral rays						
17	9	2	1	2	—	—
18	21	—	3	70	1	1?
19	5	—	5	45	36	2
20	—	—	1	5	27	7
21	—	—	—	—	1	7
22	—	—	—	—	—	3
Meristic Index						
37	1	—	—	1	—	—
38	4	1	—	1	—	—
39	4	—	2	1	—	—
40	6	—	—	2	—	—
41	2	—	1	1	—	—
42	—	—	1	5	1	1
43	—	—	1	2	—	—
44	—	—	—	1	2	—
45	—	—	—	—	1	1

[a] Compiled from Schultz and Reid (1937) and specimens that are listed in the text.

on the northern edge of the *Thalassia* bed just north of Tokas Key, Bimini, Bahamas, on December 18, 1956, by Vladimir Walters; female, ovaries 75–80 per cent of the body cavity length. Paratypes: A.M.N.H. No. 16638 (1, 124); Bimini, Bahamas, 1945; male. A.M.N.H. No. 20337 (1, 104); taken from another conch shell at the same locality and date as the holotype; female, ovaries small. A.M.NH. No. 20338 (1, 116); in a conch shell at Tokas Key, Bimini, Bahamas, December 28, 1957; male. A.N.S.P. No. 79480 (1, 115); near dock at South Bimini, Bahamas, Feb-

Fig. 1. Lateral views of toadfishes. A. *Opsanus phobetron*, new species, U.M.M.I.L. No. 498, 114 mm. in standard length, from Tokas Key, Bimini, Bahamas. B. *O. beta*, U.M.M.I.L. No. 1492, 158 mm. in standard length, from Bear Cut, Virginia Key, Dade County, Florida.

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ruary 28, 1952; kept in aquarium until April 13, 1952; male. A.N.S.P. No. 79481 (1, 114); Bimini, Bahamas, no other data; male (fig. 2A). U.S.N.M. No. 170961 (1, 128); in a conch shell at low tide 500 feet north of the Lerner Marine Laboratory dock, North Bimini, Bahamas, July 19, 1947; male. U.S.N.M. No. 170962 (1, 86); in a conch shell at low tide on the flats near Tokas Key, Bimini, Bahamas, April 13, 1957; male. Additional specimens, not designated as paratypes, are as follows: U.M.M.L. No. 498 (1, 114); in a conch shell at low tide on the flats near Tokas Key, Bimini, Bahamas, late December, 1950; female, ovaries about 80 per cent of the length of the body cavity (fig. 1A). B.M. No. 01.054 (1, 129); Tokas Key, Bimini, Bahamas, November 15, 1952. B.M. No. 02.015 (1,101); in a conch shell at low tide on the flats near Tokas Key, Bimini, Bahamas, December 20, 1956. B.M. No. 02.021 (1, 75); flats near Tokas Key, January 2, 1957; female, ovaries small. A.M.N.H. No. 11412A (1, 136); Havana, Cuba, July, 1924. U.S.N.M. Nos. 4788 (1, 170) and 37546 (1, 46); Cuba (Poey, 1868, as *Batrachus tau*). U.S.N.M. No. 107433 (2, 46–80); Cuba, latitude 22° 05′ 47″ N., longitude 82° 28′ 16″ W. U.S.N.M. No. 107435 (2, 72); Isle of Pines, Siguanea Bay.

DESCRIPTION: In the following meristic values, the first figure given is for the holotype; the figures in parentheses indicate the range in variation for all specimens examined (see table 1 for frequency distributions). The last two dorsal and anal rays are counted as one when they arise from common interspinals. First dorsal spines III (III); second dorsal rays 24 (24–26); anal rays 20 (20–22); pectoral rays (both fins) 18, 18 (17–20); meristic index (second dorsal rays plus total pectoral rays minus anal rays) 40 (37–41).

No appreciable differences could be detected in the proportions of the body parts over a range in standard length of 75 to 168 mm. The head length enters the standard length 2.6 (2.5–2.7) and the preanal length (snout to anus) enters 1.8 (1.7–2.0) times. Measurements of the holotype and other specimens are given in table 2.

Teeth are present on the premaxillae, dentaries, vomer, palatines, and upper and lower pharyngo-branchials. The vomerine teeth number six or seven (three or four on each side), arranged in an arc; the posteriormost tooth on each side is enlarged and canine-like in the holotype and most other specimens.

In life the dark blotches on the body and fins are ordinarily suppressed, and as a result the fish appears pale, with dirty gray markings. This coloration is also maintained in an aquarium against a background of "coral" sand with a conch shell or piece of rose coral provided for concealment purposes. When the fish is preserved, its melanophores disperse

TABLE 2

PROPORTIONAL MEASUREMENTS OF *Opsanus phobetron* EXPRESSED AS
HUNDREDTHS OF STANDARD LENGTH

Specimens	Standard Length (in Millimeters)	Head Length	Tip of Snout to Anus
Holotype			
A.M.N.H. No. 20336	168	39	53
Paratypes			
A.M.N.H. No. 16638	98	37	52
A.M.N.H. No. 20337	104	37	50
A.M.N.H. No. 20338	116	39	54
A.N.S.P. No. 79480	115	41	54
A.N.S.P. No. 79481	114	39	52
U.S.N.M. No. 170961	128	39	54
U.S.N.M. No. 170962	86	37	53
Non-types			
A.M.N.H. No. 11412A	136	38	54
U.M.M.L. No. 498	114	37	54
B.M. No. 01.054	129	40	57
B.M. No. 02.015	101	38	55
B.M. No. 02.021	75	38	59
U.S.N.M. No. 4788	170	36	55
U.S.N.M. No. 107433	80	39	52
U.S.N.M. No. 107435	72	36	49
U.S.N.M. No. 107435	72	37	52

to bring out the following color pattern. The sides of the body have four broad, vertical, dark blotches of irregular shape, often suggesting the letter H; they vary from gray through brown to black in different individuals. They are neither paler nor reduced dorsolaterally, so that there is no longitudinal pale stripe underlying a dark dorsal stripe, a pattern often seen in *Opsanus beta*. The first blotch lies above and immediately behind the pectoral fin from the level of the spinous dorsal fin to the first rays of the second dorsal fin; the second lies above the anus; the third is above the middle rays of the anal fin; the fourth is centered on the base of the caudal peduncle. The four blotches are edged with black or dark brown dorsally, and, as the first three blotches are split dorsally, there appear to be seven equally spaced, large, dark spots near the mid-dorsal line on each side. These are arranged as follows: the first is at the bases of dorsal spines 2 and 3, the second is at the origin of the soft dorsal, and the last is at the caudal peduncle base.

The throat, chest, and venter are spotted with dark, mottled with gray, or whitish; smaller individuals have lesser amounts of pigment on the ventral surface.

The second dorsal fin has seven or eight triangular, dark bands the apexes of which are directed ventrad and caudad. Five to seven dark, vertical bands cross the caudal fin, but they are frequently ill defined. The pattern on the anal fin is similar to that on the second dorsal fin. The pelvic fins are unmarked in smaller individuals and variously marked with dark pigment in adults. As in specimens of *Opsanus beta* the pectoral fins have numerous cream-colored spots arranged in vertical rows which impart a banded appearance; the spots are placed close together and often merge vertically. In one specimen vertical fusion is complete, a condition more typical of *Opsanus tau*.

The oral and branchial chambers and all associated structures are black (see fig. 2A), with the exception of the white dentigerous areas. In smaller specimens the oral valves are pale, while in larger individuals they are black. Some variation in oral pigmentation has been noted, especially in small individuals. During ontogeny the pharyngeal area darkens first, next the tongue and the floor of the mouth darken, and the last area in the lower half of the oral chamber to darken lies between the tongue and the oral valve. The roof of the mouth darkens as a curtain of black pigment migrates forward from the throat towards the oral valve. This sequence is best seen in the Cuban material listed above. The lining of the swim bladder is finely reticulated with black.

The name *phobetron* is taken from the Greek word for "scarecrow" and refers to the menacing attitude assumed by the fish when its lair is approached.

DISCUSSION

DISTRIBUTION, HABITAT, AND HABITS

Opsanus phobetron is known from the Great Bahama Bank at Bimini, the northern coast of Cuba at Havana, the southern coast of Cuba in Batabano Gulf, and the Isle of Pines. As noted below, it may exist in Campeche Gulf off the Yucatan Peninsula. It is seemingly absent from Florida and the Florida Keys, even though it occurs within 45 miles of shallow Florida water, at Bimini.

Most specimens of *O. phobetron* have been found within old conch shells lying in shallow water. Seven were found under such conditions at Bimini; habitat data are unknown for five others. The toadfish is seemingly uncommon at Bimini; the four taken by Walters were the only individuals found by him in six months spent on the islands during

the period 1950–1957, in which time numerous collecting forays were made. Robins, in six brief visits to Bimini and Cat Cay, did not encounter the species. Three specimens were taken on December 18 and 20, 1956, near Tokas Key in Bimini harbor. Despite many trips to the Tokas Key area during ensuing months in search of *Opsanus,* only two additional specimens were found, one on January 2 and another on April 13. During this period thousands of conch shells were examined,
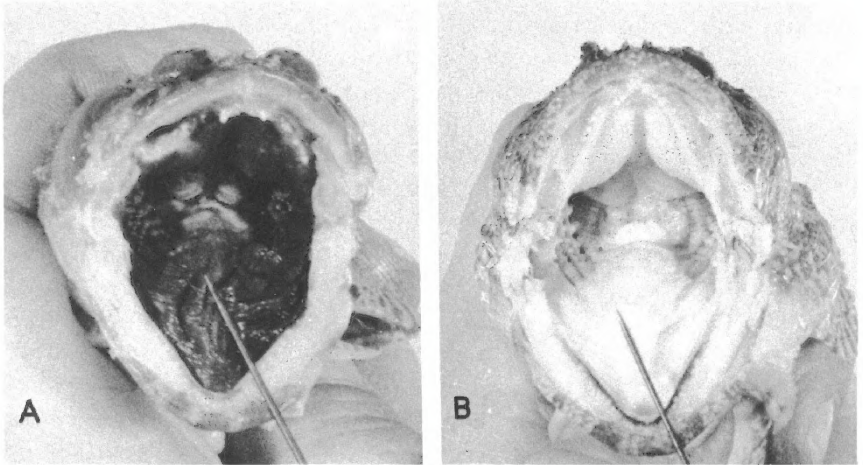

Fig. 2. Oral chambers of toadfishes; the angles of the jaws were cut to permit reflection of the floor of the mouth. A. *Opsanus phobetron,* new species, A.N.S.P. No. 79481 (paratype), 114 mm. in standard length, from Bimini, Bahamas. B. *O. beta,* U.M.M.L. No. 1492, 158 mm. in standard length, from Bear Cut, Virginia Key, Dade County, Florida.

slabs of coral turned over, and sponges torn apart in this and other portions of Bimini harbor and the Great Bahama Bank within a 10-mile radius of the laboratory, without success. It is unlikely that *O. phobetron* is as rare at Bimini as the records imply. If empty shells are preferred, there is an abundance of available habitat. Apparently the Tokas Key fishes represent strays from the main population. As all the specimens from Tokas Key, North Bimini, and South Bimini were taken rather close to the channel that leads from Bimini lagoon to the harbor mouth on the western edge of the Great Bahama Bank, the main population may be located somewhere in the channel. The most likely situation would be in the vicinity of rocky ledges, such as those near the harbor mouth. This habitat was not investigated owing to its depth and strong currents.

On the senior author's first trip to Bimini in late December, 1950, one

of the laboratory aquaria contained a medium-sized adult toadfish which was attending a brood of eggs in a conch shell. The young emerged from the nest before the end of the year. None of the young was saved, and the sex of the parent was not determined. Breder (1941) found no great differences between the life history of *O. beta* on the west coast of Florida and that of *O. tau* of the northern Atlantic Coast. *Opsanus phobetron* presumably resembles the others in its life history.

The new species is fully as pugnacious as its relatives. Individuals gape their mouths when the investigator's hand is placed several inches away. If no further encroachment is made, no further action is taken. If the investigator's hand is moved to within an inch or so of the fish it pounces forward and inflicts a vigorous bite.

On first consideration the presence of a black mouth in *O. phobetron* is puzzling; all other species of *Opsanus* that were examined have a pale mouth. However *Opsanus* from coastal waters of the United States live in more turbid water against dull-colored or dark surroundings. At Bimini the new species is found on white "coral" sand, or at least the vegetation is covered with a whitish silt. The water at Bimini is extremely clear, much more so than that along the Florida Keys where *Opsanus* occurs. Such clarity allows higher light intensities on the bottom and permits lower albedo values through minimal reduction of reflected light by suspended particles (Breder and Rasquin, 1955, p. 88). The mouth-gaping habit of *Opsanus* finds a famous reptilian parallel in the cottonmouth moccasin (*Agkistrodon piscivorus*) of the southeastern United States. Plainly, mouth-gaping is a device to warn away intruders. The effectiveness of a warning device depends upon how well it contrasts with the background. The white mouth of the venomous, dark-colored cottonmouth is conspicuous against the somber background of a stream bank or swamp. The white mouths of toadfish on the Gulf or Atlantic coasts of the United States similarly are readily noted by trespassers. In Bimini, with a white or gray toadfish on a white background, in clear water and under intense sunlight, a black warning would be more conspicuous than a white warning, hence the black mouth of *O. phobetron* may be of social significance. The black pigmentation of the mouth appears to be a stable character. Rasquin (1958) observed a gradual graying of the mouth only some time after the body had turned white in response to an injection of adrenalin. The black mouth was never observed by Walters to pale in normal aquarium fishes, regardless of background.

COMPARISON AND RELATIONSHIPS

No appreciable differences were detected among any of the species of

Opsanus studied in the complicated lateralis system, cirri on the head, relative sizes of body parts and fins, or in internal morphology. For this reason only a few basic measurements are given for the series of *O. phobetron* in table 2. Diagnostic characters for toadfishes are not wholly morphological. Tavolga (1958) found differences between the "boat-whistle" call of *O. tau* and that of *O. beta,* and the voice of *O. phobetron* differs from that of other toadfish (Fish and Mowbray, 1959).

Two lots of specimens in the United States National Museum deserve consideration. One lot (U.S.N.M. No. 38668; 2, 152–202) was collected by the "Albatross" and is listed in the catalogue as from the "West Indies"; these are typical *O. beta.* It is possible they were actually collected at Key West, Florida, where *O. beta* is common, because the "Albatross" material which follows in the catalogue is listed from "Key West." In any event the locality is uncertain, and it is unwise to list *O. beta* from the West Indies on this record. Another "Albatross" collection (U.S.N.M. No. 39274; 5, 176–221) bears the locality data "Mexico: Gulf of Campeche"; the specimens are in poor shape but may have had dark mouths. Their meristic index is higher than that for Cuban and Bahamian material of *O. phobetron.* Additional material is needed to determine whether *O. phobetron* occurs on Campeche Bank. Specimens typical of *O. beta* are known from the region, and some overlap in ranges may thus occur at Campeche.

An *Opsanus* from Little Bahama Bank, collected by Luis R. Rivas and examined by Robins, may belong to an undescribed form related to *O. phobetron.* The fish was collected 20 miles north-northwest of Mangrove Cay, at a depth of 3 fathoms, on a white sand and grass bottom. Counts and measurements are: standard length, 126 mm.; dorsal rays, III–24; anal rays, 20; pectoral rays, 17, 17. The anterior portion of the mouth is white; the posterior portion, including the gill arches, is dusky; the gill chamber is partially dusky; the inner epithelium of the swim bladder is pale; the pectoral fin bears a broad vertical dusky band; the caudal fin is dusky, with a light bar at its base and a pale band at its free edge; the dorsal fin is uniform, except for five equidistant pale spots along its base and a pale bar through the first two rays; and the sides of the body are pale, with dusky markings but not blotches. The mouth coloration is not unlike that described above for small individuals of *O. phobetron,* but the fin and body coloration is so unlike that of *O. phobetron* or any other recognized form that the authors believe this individual possibly represents an undescribed species.

Schultz and Reid (1937) removed *Opsanus pardus* (Goode and Bean) and *Opsanus beta* (Goode and Bean) from the synonymy of *Opsanus tau*
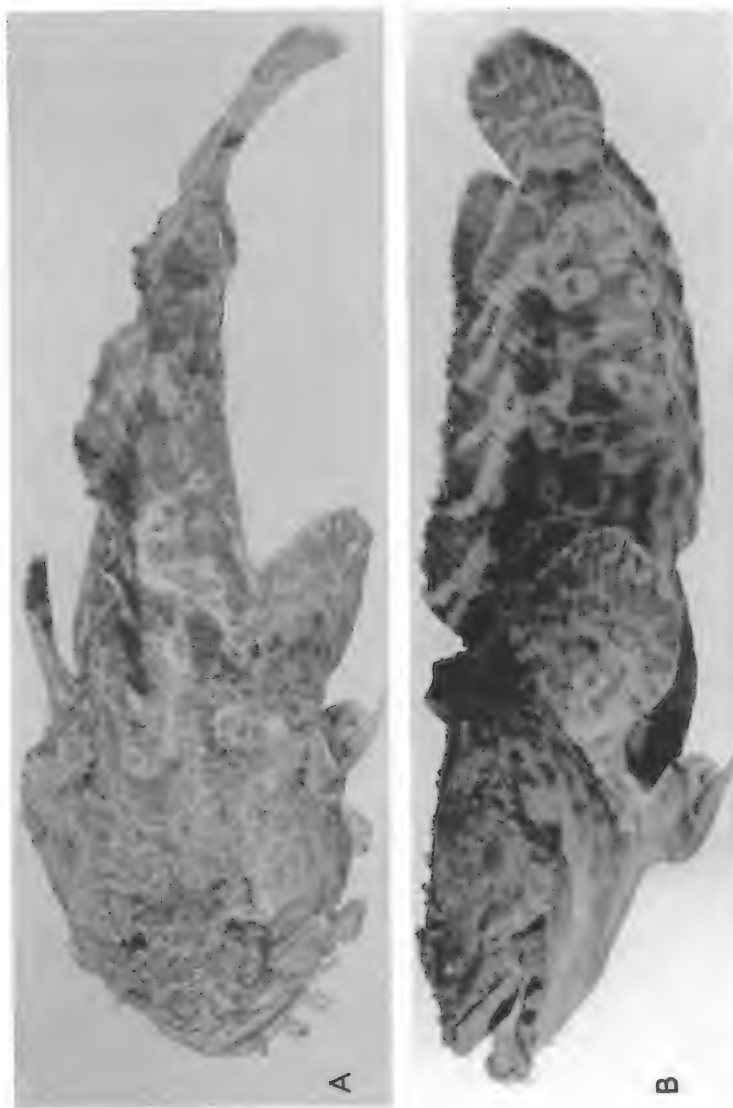
FIG. 3. *Opsanus pardus*, U.M.M.L. No. 189, 181 mm. in standard length, from the Dry Tortugas shrimp grounds, Florida. A. Dorsal view. B. Lateral view.

(Linnaeus). *Opsanus pardus,* known from moderate depths on the fishing banks and shrimp grounds in the Gulf of Mexico, is distinctive in having a pale background coloration, with rounded dark spots (figs. 3A, 3B). It also has more dorsal rays than the others (25 in one specimen, 26 in eight specimens) and a more variable but modally higher number of pectoral rays. [See table 1 for frequency distribution of fin-ray counts; these data were taken from Schultz and Reid (1937), with the addition of counts for adults from the Tortugas shrimp grounds (U.M.M.L. No. 189; 1, 181) and from Appalachicola, Florida (U.M.M.L. No. 1409; 1, 310).]

Opsanus tau ranges along the Atlantic coast from Miami, Florida, north to Cape Cod, with a few individuals straying into the Gulf of Maine. It is uncommon in southeastern Florida; the Miami record is based on a specimen (U.M.M.L. No. 1410) taken at Virginia Key in Biscayne Bay on January 14 or 15, 1957. *Opsanus tau* is identified by its barred pectoral fins (no spots except in large adults), the presence of dark vermiform markings scattered over the head and body, the absence of white spots and H-shaped markings, and its higher meristic index (41–45). [See table 1 for frequency distributions of meristic characters. In addition to figures and specimens given by Schultz and Reid (1937), counts on the following specimens are included: New Jersey: A.N.S.P. No. 18595 (1, 116), and uncatalogued (1, 150); North Carolina: A.N.S.P. uncatalogued (1, 190); Florida: U.M.M.L. No. 1410 (1, 251).]

Opsanus beta ranges along the periphery of the Gulf of Mexico from Campeche Bank through the Florida Keys (present in Key West but apparently absent from the Dry Tortugas) and thence northward along the Atlantic coast of Florida at least to Palm Beach. This species closely resembles *O. phobetron* in general appearance but lacks the black mouth, gill chamber, and inner lining of the swim bladder of that species (fig. 2B). Many specimens of *O. beta* possess a longitudinal dark band running just beneath the bases of the dorsal rays, with a pale band immediately below (fig. 1B). In *O. phobetron* these bands are absent. Both *O. beta* and *O. phobetron* are small species. Most of the adults of *O. phobetron* listed above measure 101–129 mm. in standard length, and Breder (1941, p. 230) noted that adults of *O. beta* average about 130 mm. In contrast *O. tau* and *O. pardus* average larger in size. At New York, breeding *O. tau* average 280 mm. (Nichols and Breder, 1926, p. 158). Judging by material the authors have seen, *O. pardus* may average slightly larger in size than *O. tau.* Frequency distributions of meristic characters for *O. beta* (table 1) include data from Schultz and Reid (1937) in addition to counts made on the following material: Florida: U.M.M.L. Nos. 133 (5, 44–67), 215 (1, 58), 1362 (1, 101), 1408 (1, 133), 1542 (1, 158), A.N.S.P. Nos. 31727

(1, 144), 49800 (1, 112), 68269 (1, 177; holotype of *O. vandeuseni*, see below), uncatalogued (1, 52; Key West), uncatalogued (1, 75; Key West); Louisiana: A.N.S.P. Nos. 55855, 55856 (2, 86–133). The meristic index employed by Schultz and Reid (1937) to separate *O. beta* from *O. tau* and *O. pardus* is useful, but, as seen in table 1, the differences are not so sharply defined as those authors indicated.

Three other described species of *Opsanus* remain to be considered: *barbatus, vandeuseni,* and *hildebrandi.* Only the type of *Opsanus barbatus* Meek and Hildebrand (1928) from Colon Reef, Panama, is known (U.S.N.M. No. 81009). It differs trenchantly from the other species in being uniformly colored and in having 32 dorsal rays and 27 anal rays. Moreover the large size of the holotype (390 mm. in standard length) makes it easily the largest known species of *Opsanus.*

Fowler (1939) described *Opsanus vandeuseni* from a single specimen taken at Sand Key, Florida. Presumably this refers to the Sand Key lying south-southwest of Key West. Fin-ray counts for the holotype (A.N.S.P. No. 68629) are as follows: dorsal, III–25; anal, 19; pectoral, 18, 18; and the meristic index is 42. These figures are lower than those listed by Fowler (1939), who may have counted the branched tips rather than exposing the bases of the rays. The new counts are in agreement with counts for *Opsanus beta.* Moreover the darkened belly and fins (the spots and bands are reduced) and pigmented pelvic fins apparently characterize large or old individuals of *O. beta.* As the specimen was kept alive in a public aquarium for several years, it may have attained an extreme in some of its pigmentary features. All the features have been noted in adults of *O. beta* though not all in one specimen. In the absence of any other differences, *O. vandeuseni* is synonymized with *O. beta.*

Breder (1925) described *Opsanus hildebrandi* from a single specimen obtained in the market at Colon, Panama. The locality at which the fish was taken is unknown, although a Caribbean source is indicated, owing to the position of Colon. Schultz and Reid (1937) transferred the species to *Amphichthys,* stating that the absence of an axillary pore necessitated generic reassignment; it is not clear from their article whether they had looked at the holotype. The holotype (A.M.N.H. No. 8443) was examined by Walters. In place of an axillary pore near the middle of the pectoral fin, as occurs in *Opsanus,* there is a peculiar structure in the upper half of the axil. This is vertically ovate and almost as large as the eye; it consists of about 18 lengthwise ridges resembling the slats on a venetian blind which anastomose with one another. There are no interradial glandular pores on the medial surface of the pectoral fin; such pores are characteristic of *Opsanus.* The glandular structure on the dor-

sal medial wall of the gill chamber is present. The dorsal spines are solid. Breder's species therefore does not belong in *Opsanus*. James E. Böhlke examined the batrachoidid material in the Academy of Natural Sciences of Philadelphia, and the only catalogued material resembling *O. hildebrandi* in the features listed above is identified as *Amphichthys* (*Marcgravia*) *cryptocentrus*. *Opsanus hildebrandi* Breder certainly fits the diagnosis of *Marcgravia* Jordan (1887, p. 546) but does not appear to be identical with *M. cryptocentra* (Cuvier and Valenciennes) as described by Jordan. It is beyond the scope of this paper to comment on the relationship of *Marcgravia* to *Amphichthys* or the numerous genera that have been split off from *Marcgravia* in recent years.

Schultz and Reid (1937) noted a variation in dorsal and anal rays of 18–32 and 15–27, respectively, in *Opsanus*. This variation is not explained by their table nor have the present authors noted such low finray counts in any of the species examined. Dr. Schultz kindly let the authors utilize his files, and the opportunity is taken here to clarify the situation. The low counts of 18 (= 19) dorsal and 15 anal rays are based on three species placed by Ogilby (1908) in *Batrachoemus* (*B. minor* Ogilby, *B. coecus* de Vis, and *B. broadbenti* Ogilby), a genus considered by Schultz (*in litt.*) to be synonymous with *Opsanus*. We do not comment on the status of *Batrachoemus* but note that it is included in the generic definition of *Opsanus* by Schultz and Reid (1937).

GLACIAL RELICTS

It has been suggested many times that tropical regions were markedly cooler during the Pleistocene glacial periods than they are at the present time. For example, Daly (1915, pp. 166–171) discussed the probable extinction of coral reefs from many regions during glacial periods and suggested that tropical sea temperatures were 5° to 10° C. cooler than they are at present. Von Ihering (1927, p. 59) believed that the Greater Antilles formerly were 7° C. cooler, and Deevey (1950) postulated a depression of at least 5° C. at Key West. Büdel (1957) reviewed the subject as it pertains to terrestrial areas. Emiliani (1958) showed that surface temperatures of the tropical Atlantic and Caribbean rose 6° C. beginning 18,500 years ago and culminating in the hypsithermal interval of about 5000 years ago. These determinations, correlated with radiocarbon datings, were based on isotopic oxygen analyses of epipelagic Foraminifera from bottom cores (for a discussion of the theory, techniques, and limitations of the method, see Emiliani, 1957). The significance of such a temperature change is considerable for aquatic poikilotherms. In general, terrestrial poikilotherms seek out suitable microclimates, and an arctic

species has essentially the same metabolic response to temperature as does a tropical species, but with aquatic poikilotherms there is a considerable metabolic adaption to the water temperature (Scholander and others, 1953).

Widespread and gradual changes in temperature, such as those that took place during the Pleistocene glacial and interglacial periods, did not induce any marked changes in temperature response of aquatic poikilotherms. Instead, many species were eliminated from a region when temperature changed sufficiently that they could no longer compete successfully with species invading from neighboring regions. Such slight climatic fluctuations as occur today are sufficient to alter the distribution patterns of marine fishes; only two papers need be cited here—the study by Jensen (1939) and the recent contribution by Taylor and his co-authors (1957). Faunal displacements accompanying Pleistocene climatic changes were marked for aquatic poikilotherms. When figures 15 and 45 of Hedgpeth's paper (1953) are compared, it is seen that a lowering of 6° C. would extend the trans-Florida (= transatlantic of Hedgpeth) faunal province southward along both coasts of Florida to include all the Keys; the now disjunct trans-Florida distributions would become continuous. With the exception of deep-sea bottom cores the Pleistocene marine fossil record from the West Indian and Gulf of Mexico regions shows little or no evidence for the glacial replacement of the former warm-water fauna by one characteristic of cold waters, for the reason that, unless considerable postglacial uplift has occurred, cold-water fossils, if extant, lie in deep water. Sea level during the last glacial period was at least 450 feet lower than it is today. It began to rise about 18,000 years ago and reached its present height about 5000 years ago (Russell, 1957, p. 424; Godwin and others, 1958). Pleistocene marine fossils lying near present-day sea level were preserved under climates similar to or warmer than that of the present, if no uplift or subsidence has occurred.

During the last glacial period it is likely that there was a substantial reduction in the coral reef habitat of the West Indies, because a temperature 6° lower implies that most or all of the Caribbean was below an annual mean of 22° C., which is the minimal thermal tolerance of many reef corals, according to Smith (1954). West Indian coral reefs are shallow structures, based on terrace platforms which are much higher than the minimal sea level of the last glacial period (cf. Vaughan, 1919, pp. 319–329), which suggests that postglacial sea temperatures did not reach a mean of 22° C. or above until the sea level had risen to near its present height. As Ekman (1953, p. 4) limited the boundaries of the

tropical zone to the northern and southern limits of coral reefs (where coral reefs can develop) by definition, the West Indies were not tropical during the last glacial period. During the last glacial period the West Indian shore fauna was predominantly temperate in character in the north and predominantly subtropical in character in the south. The tropical marine elements may have been restricted to the southernmost of the Lesser Antilles and along the northern coast of South America. North Atlantic coastal species, now with disjunct populations in the northern Gulf of Mexico (the trans-Florida fauna), probably had extensive distributions in the Gulf of Mexico and West Indies in the past. Exemplary species are the sturgeon (*Acipenser oxyrhynchus*), gizzard shad (*Dorosoma cepedianum*), and striped bass (*Roccus saxatilis*).

Rivas (1954, p. 504) suggested that these species entered the Gulf of Mexico by way of northern Florida during interglacial periods when the neck of the Florida peninsula was submerged. Briggs (1958, pp. 241–246) subscribed to this viewpoint. Neill's interpretation of Florida biogeography (1957, pp. 187 ff.) utilized an early interglacial marine submergence of 270 feet with succeeding interglacial submergences to lesser depths. Neill followed other authors in calling the resultant marine channel across the peninsula neck the Suwannee Straits. Hedgpeth (1953, pp. 127–130) favored the concept of Pleistocene submergence of the Florida peninsula to account for disjunct trans-Florida distributions, and, though citing data in support of formerly much cooler climates in the Gulf of Mexico, suggested that the cooling was local. The present authors do not agree with these views.

Among the obstacles to a postulated drowning of the neck of the Florida peninsula are the following: (1) The highest terraces containing Pleistocene marine fossils and which lie outside areas affected by subsidence are only 25 feet above sea level (Deevey, 1950, p. 360); higher terraces are not definitely known to be of marine origin and are estimated to be Pleistocene in age. (2) It is necessary to postulate a sea level 30 meters higher than that of the present time just to submerge the neck of the peninsula, which would apparently be sufficient to establish a waterway between the Atlantic and Pacific oceans across Central America; however, the evidence points to a separation of the Atlantic from the Pacific throughout the Pleistocene. (3) The evidence is fairly conclusive that shoreline features which lie at different elevations have resulted from differential uplift of rising land masses, which "renders it difficult to determine whether Pleistocene sea levels ever attained elevations in excess of those of the present day" (Russell, 1957, pp. 427–428). (4) During the 13,000 years between the maximum of the last glacial period and the

hypsithermal interval, the sea level rose 450 feet while surface temperatures increased 6° C.; thus for every 75 feet of change in the sea level, surface temperatures changed 1° C. If earlier Pleistocene sea levels were 30 meters higher than those during the hypsithermal interval, such a difference should be detectable in the paleotemperature measurements. The data presented by Emiliani (1955, fig. 15) show surface temperatures were not measurably higher during earlier Pleistocene times, thereby supporting Russell's suggestion.

Neill (1957, pp. 197–198) regarded the presence of marine fishes in some Florida fresh waters as indicative of a former Pleistocene marine submergence, and cited Odum's (1953) work on fresh-water salinities in evidence. The latter believed the high salt content of the waters at an elevation of less than 20 feet reflects an interglacial submergence. Neill did not consider the importance of Ca^{++} in enabling marine fishes to enter fresh water. This was pointed out by Breder (1934) who had observed that the ichthyofauna of fresh-water Lake Forsyth, Andros Island, consists entirely of marine species. Breder found a high Ca^{++} content to Forsyth water (about 45 p. p. m., comparable to Florida values) and experimentally maintained a variety of stenohaline marine fishes in New York City tap water, to which an excess of calcium salts had been added. The effect is partly due to a reduction in cell permeability (Black, 1951, p. 75). Odum's data show that Florida fresh waters for the most part have chlorinities under 100 p. p. m. (higher values obtain near the coast only), which is equivalent to a dilution of one part sea water with 193 parts or more of distilled water. It is questionable whether such great dilution would affect the ichthyofauna. The present authors contend that the presence of marine fishes in Florida fresh waters can be correlated with the presence of Ca^{++} but cannot be given any historical zoogeographic significance.

Odum regarded the high fresh-water salinities in low-lying parts of Florida as dating from the last interglacial marine submergence. But it would be difficult to distinguish interglacial salt from salt that may have been left behind by a submergence during the hypsithermal interval. Odum's reasons for not considering the salts as being continually deposited by atmospheric and other phenomena are not convincing, because meteorologically deposited salts usually do not have the same ionic proportions as does sea water (cf. Hutchinson, 1957, chap. 8). One would think that, during and after the interval of low sea level since the last interglacial period, the interglacial salt deposits would have been leached out of the porous Florida land mass. In addition to the hypsithermal and cyclic salt components in Florida fresh waters, one would suspect that elevated

fresh-water salinities in low elevations are in part man-induced through drainage projects and other practices.

If it be assumed for the moment that a submersion of the Florida peninsula neck was sufficient to enable marine fishes to move across northern Florida during a Pleistocene interglacial period, in place of the cool pocket of the northern Gulf of Mexico there would have been a shallow warm-water drift of the Gulf Stream across the Suwannee Straits. According to Rivas (1954), it is the high temperature of the Gulf Stream which is maintaining the present-day isolation of the Gulf of Mexico disjunct populations. Thus the interglacial origin of the disjunct, trans-Florida, distribution patterns appears unlikely. It seems more reasonable to suggest that such fishes as *Acipenser, Dorosoma,* and *Roccus* were characteristic elements of the West Indian fauna until recently. With the postglacial rise in sea temperatures these were forced northward, with the result that the populations that entered the Gulf of Mexico were isolated instead of following the Atlantic coast. What was at first mainly a thermal barrier to the southward movements of these fishes was subsequently strengthened by the establishment of coral formations during the hypsithermal interval, so that suitable habitats no longer exist for these northern species in southern Florida. Deevey (1950) reached very nearly the same conclusions, using hydroids rather than fishes as a starting point. These events are similar to the postglacial picture that unfolded in the northern North Pacific, when a number of Arctic species were trapped in the Sea of Okhotsk as the low water temperatures retreated northward (Walters and Robins, 1956) and the Kuroshio took a more northerly course as the sea level rose. If the Gulf of Mexico resembles the Sea of Okhotsk in serving as a refuge for glacial relics, it is suspected that each Pleistocene glaciation was followed by isolation and occasional differentiation of relics; relics of the earliest glaciation would generally be more highly differentiated than relics of the most recent glaciation. Several trans-Florida species pairs of *Brevoortia* are recognized, perhaps corresponding to relict differentiation following two or more glacial periods. Vladykov (1955) named the Gulf of Mexico sturgeon *Acipenser oxyrhinchus desotoi;* here again differentiation may have begun during the last interglacial period or even earlier. A detailed analysis of the Florida fauna lies beyond the scope of this report; forms that are identified above as glacial relics constitute but a fraction of such species.

Opsanus is known from only four places in the West Indies: Cuba, Isle of Pines, Great Bahama Bank (*O. phobetron*), and Little Bahama Bank (unidentified form). The genus is widely distributed in Atlantic and Gulf coastal waters of North America; *O. tau* ranges north to Cape Cod in

abundance. Breder (1941, p. 231) pointed out that *O. tau* spawns "for the most part in water in the middle and high sixties extending where the temperature rise is rapid, into the seventies or even the low eighties." *Opsanus beta* on the west coast of Florida spawns in late winter at a temperature of 67° F. (19.5° C.) (Breder, 1941, p. 229). Such a temperature is close to that of Bimini water in late December, when *O. phobetron* was observed to be nesting. These observations suggest that *O. tau, O. beta,* and *O. phobetron* require a temperature of 19°–20° C. or slightly lower to initiate spawning. Nothing is known concerning the other members of the genus. Interestingly, adult *O. tau* can withstand periods of rather low temperatures when they hibernate in the mud (Nichols and Breder, 1926, p. 157). Although adult *O. beta* survive cold snaps in Florida, the eggs of *O. beta* are apparently killed if the temperature drops much below the spawning threshold (Breder, 1941). It is evidently the spawning threshold of 19°–20° C. that limits the distribution of *Opsanus tau* and its relatives both in the north and in the south. These fishes therefore belong to temperature zonation "type 2" as outlined by Hutchins (1947), in which the latitudinal limits of distribution are governed by the temperature required for repopulation. The thermal requirement of 19°–20° C. of *Opsanus* parallels the minimal thermal tolerance for reef corals (19° C.; Smith, 1954), which suggests that *Opsanus* may be a useful "indicator" for temperate coastal waters.

Most of the West Indian region is rarely subjected to temperatures of 19°–20° C. at the present time. If midwinter surface temperatures in the Caribbean should drop 6° C., then *Opsanus* and other similarly restricted species would be able to spawn throughout most of the West Indies and could become common elements in the fauna, provided their remaining ecological requirements were met. Because paleotemperature measurements indicate surface temperatures, were this low at the maximum of the Wisconsin glaciation, *Opsanus* may have been of widespread distribution in the West Indies until recent times. Toadfish were eliminated from most of the West Indies as surface temperatures rose postglacially. There was no "adaptive migration" downward to cooler water, as figures given by Bsharah (1957) show that the 20° isotherm is located at a depth of 200 meters off Bimini, and toadfish are not known to range so deep. Temperatures of 20° C. or lower are available on the Bahama banks today only during winter cold snaps. In other words, *Opsanus* has disappeared from most of the West Indies and occurs in a few places today as a glacial relict.

Accompanying the southward expansion of the range of *Opsanus* during the last glacial period there was undoubtedly a southward withdrawal

of the northern limit of distribution, from Cape Cod to the southeastern United States and possibly as far as southern Florida. This is not inconsistent with the finds of cold-water (arctic to boreal) Foraminifera underlying the present subtropical forms in bottom cores from the Gulf of Mexico and the Caribbean (Deevey, 1950, p. 362; Phleger, 1951, pp. 78–81).

An objection to the foregoing discussion could be raised on the ground that *Opsanus* is a sluggish, bottom-dwelling fish without any pelagic life-history stage (Gudger, 1910; Breder, 1941). Such difficulty disappears when it is considered that toadfish occur in several isolated West Indian populations today, so that they must at times be transported across deep-water barriers. The minimal deep-water gap between Florida and the Bahamas, 44 miles in width, exceeds the present-day, deep-water gaps between any of the shallows in the Bahamas and the Greater Antilles. Robins observed several individuals of another batrachoidid (*Porichthys*) rafting on logs 25 miles from land in the Gulf of Panama during the summer of 1957, and possibly *Opsanus* can also be rafted in this manner. A more likely means of dispersal for *Opsanus* would involve passive transport in waterlogged coconut husks during storms. In addition, young *O. beta* often hide in sponges, which in stormy weather may be torn free of the bottom and float suspended in the water, pushed onward in advance of the storm. It would thus seem that the presently restricted West Indian toadfish populations are localized not by inability to disperse but rather by inability to reproduce elsewhere. Speciation in a group lacking pelagic life-history stages might be expected to proceed more rapidly than in a group with one or more pelagic stages, as the local gene pool would become contaminated less often with genes flowing in from outside populations. Postglacial rises in sea level and temperature would serve to isolate the toadfish populations further, while changing the values of selective pressures. The evident absence of *O. phobetron* from Florida waters may indicate that it cannot compete with the three species of *Opsanus* that already live there, as the white bottom associated with high water transparency is absent from the bays of Florida. It may also indicate that the gap from Cuba to the Keys is an effective barrier, and that the Florida Current of the Bimini-Florida gap may carry the fishes too far northward to reach the Florida coast.

SUMMARY

Opsanus phobetron is described from the western Bahamas, Cuba, and the Isle of Pines. It was observed to nest in late December at Bimini, Bahamas. The black mouth functions as a warning mechanism, and under low albedo conditions, as at Bimini, the dark coloration is indicated

to be of social significance.

Attention is called to unidentified samples of *Opsanus* from Little Bahama Bank and the Gulf of Campeche. The ranges and recognition characters of *O. pardus, O. tau, O. beta,* and *O. barbatus* are discussed. *Opsanus vandeuseni* Fowler is referred to the synonymy of *Opsanus beta* (Goode and Bean). *Opsanus hildebrandi* Breder is placed in *Marcgravia* Jordan and appears not to be identical with *M. cryptocentra* (Cuvier and Valenciennes). The low numbers of dorsal and anal rays attributed to *Opsanus* in the literature are valid if the Queensland genus *Batrachoemus* Ogilby is considered identical with *Opsanus.*

Published paleotemperature measurements indicate that the "tropical" Atlantic and Caribbean regions were not tropical during the last glacial period. The trans-Florida faunal province, now absent from southern Florida, was continuous around the southern tip of the Florida land mass; at the same time coral reefs were absent from most of the West Indies, and the shore fauna was predominantly temperate in the north and predominantly subtropical in the south. It is improbable that the Florida peninsula neck was submerged during Pleistocene interglacial periods. The presence of marine fishes in Florida fresh waters is not considered significant from the standpoint of historical zoogeography, and it is suggested that the elevated chlorinities in Florida fresh waters are maintained by current processes. Even if the neck of the Florida peninsula had been drowned, the Gulf of Mexico populations of trans-Florida fishes probably could not utilize the passage, as the temperatures would have been too high. The Gulf of Mexico disjunct trans-Florida populations are interpreted as glacial rather than interglacial relicts, and a comparison is drawn between the Gulf of Mexico and the Sea of Okhotsk.

Because the spawning threshold temperature of *Opsanus* parallels the minimal thermal tolerance of reef corals, *Opsanus* is considered to be an "indicator" of temperate coastal waters. Owing to thermal requirements and tolerances, *Opsanus* survives as a glacial relict in a few West Indian localities. During the last glacial period, the northern distributional limit for *Opsanus* may have been as far south as southern Florida. *Opsanus,* lacking pelagic life-history stages, could have dispersed through the West Indies by passive transport during storms.

LITERATURE CITED

BLACK, VIRGINIA S.
  1951. Some aspects of the physiology of fish. II. Osmotic regulation in teleost fishes. Univ. Toronto Studies Biol. Ser. no. 59, Publ. Ontario Fish. Res. Lab., no. 71, pp. 53–89.

BREDER, CHARLES M., JR.
   1925.   A new toadfish from Colon, Panama. Amer. Mus. Novitates, no. 188, pp. 1–2, 1 fig.
   1934.   Ecology of an oceanic fresh-water lake, Andros Island, Bahamas, with special reference to its fishes. Zoologica, vol. 18, pp. 57–88, figs. 26–35.
   1941.   On the reproduction of *Opsanus beta* Goode & Bean. *Ibid.*, vol. 26, pp. 229–232, 2 pls.
BREDER, CHARLES M., JR., AND PRISCILLA RASQUIN
   1955.   Further notes on the pigmentary behavior of *Chaetodipterus* in reference to background and water transparency. Zoologica, vol. 40, pp. 85–90, 2 pls.
BRIGGS, JOHN C.
   1958.   A list of Florida fishes and their distribution. Bull. Florida State Mus., vol. 2, pp. 221–318, 3 figs.
BSHARAH, LEWIS
   1957.   Plankton of the Florida current. V. Environmental conditions, standing crop, seasonal and diurnal changes at a station forty miles east of Miami. Bull. Marine Sci. Gulf and Caribbean, vol. 7, pp. 201–251, 45 figs.
BÜDEL, JULIUS K.
   1957.   The ice age in the tropics. Universitas, vol. 1, pp. 183–191, 2 figs.
DALY, REGINALD A.
   1915.   The glacial-control theory of coral reefs. Proc. Amer. Acad. Arts Sci., vol. 51, pp. 157–248, 48 figs.
DEEVEY, EDWARD S.
   1950.   Hydroids from Louisiana and Texas, with remarks on the Pleistocene biogeography of the western Gulf of Mexico. Ecology, vol. 3, pp. 334–367, 11 figs.
EKMAN, SVEN
   1953.   Zoogeography of the sea. London, Sidgwick and Jackson, Ltd., xiv + 417 pp., 121 figs.
EMILIANI, CESARE
   1955.   Pleistocene temperatures. Jour. Geol., vol. 63, pp. 538–578, 15 figs.
   1957.   Oxygen isotopes and paleotemperature determinations. Acts Fourth Internatl. Congr. Quaternary Rome, 1953, vol. 2, pp. 831–844, 5 figs.
   1958.   Paleotemperature analysis of core 280 and Pleistocene correlations. Jour. Geol., vol. 66, pp. 264–275, 5 figs.
FISH, MARIE P., AND WILLIAM H. MOWBRAY
   1959.   The production of underwater sound by *Opsanus* sp., a new toadfish from Bimini, Bahamas. Zoologica, vol. 44, pp. 71–76, 3 pls.
FOWLER, HENRY W.
   1939.   Description of the red toadfish, a new species of *Opsanus* from Florida. Notulae Nat., Philadelphia, no. 31, pp. 1–2, 1 fig.
GODWIN, H., R. P. SUGGATE, AND E. H. WILLIS
   1958.   Radiocarbon dating of the eustatic rise in ocean-level. Nature, vol. 181, no. 4622, pp. 1518–1519.
GUDGER, EUGENE W.
   1910.   Habits and life history of the toadfish (*Opsanus tau*). Bull. U. S. Bur. Fish., no. 28 (1908), pp. 1071–1109, pls. 107–113.
HEDGPETH, JOEL W.
   1953.   An introduction to the zoogeography of the northwestern Gulf of Mexico

with reference to the invertebrate fauna. Publ. Inst. Marine Sci., Univ. Texas, vol. 3, pp. 107–224, 46 figs.

HUBBS, CARL L., AND KARL F. LAGLER
1947.   Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci., no. 26, xii + 186 pp., 251 figs., 26 col. pls., map on end papers.

HUTCHINS, LOUIS W.
1947.   The bases for temperature zonation in geographical distribution. Ecol. Monogr., vol. 17, pp. 325–335, 8 figs.

HUTCHINSON, GEORGE EVELYN
1957.   A treatise on limnology. Volume 1. Geography, physics, and chemistry. New York, John Wiley and Sons, Inc., xiv + 1015 pp., 228 figs.

VON IHERING, HERMANN
1927.   Die Geschichte des Atlantischen Ozeans. Jena, Gustav Fischer, x + 237 pp., 8 maps.

JENSEN, ADOLF S.
1939.   Concerning a change of climate during recent decades in the arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. Biol. Meddel., vol. 14, no. 8, pp. 1–75, 2 charts.

JORDAN, DAVID STARR
1887.   Notes on typical specimens of fishes described by Cuvier and Valenciennes and preserved in the Musée d'Histoire Naturelle in Paris. Proc. U. S. Natl. Mus., vol. 9 (1886), pp. 525–546.

MEEK, SETH E., AND SAMUEL F. HILDEBRAND
1928.   The marine fishes of Panama. Part III. Publ. Field Mus. Nat. Hist., zool. ser., vol. 15, pp. xxv–xxxi, 709–1045, pls. 72–102.

NEILL, WILFRED T.
1957.   Historical biogeography of present-day Florida. Bull. Florida State Mus., vol. 2, pp. 175–220.

NICHOLS, JOHN T., AND CHARLES M. BREDER, JR.
1926.   The marine fishes of New York and southern New England. Zoologica, vol. 9, pp. 1–192, 263 figs.

ODUM, HOWARD T.
1953.   Factors controlling marine invasion into Florida fresh waters. Bull. Marine Sci. Gulf and Caribbean, vol. 3, pp. 134–156, 4 figs.

OGILBY, J. DOUGLAS
1908.   Revision of the Batrachoididae of Queensland. Ann. Queensland Mus., vol. 9, pp. 43–57.

PHLEGER, FRED B.
1951.   Ecology of Foraminifera, northwest Gulf of Mexico. Part 1. Foraminifera distribution. Mem. Geol. Soc. Amer., no. 46, pp. i–ix, 1–88, 37 figs., 2 pls.

POEY, FELIPE
1868.   Synopsis piscium cubensium. In Repertorio fisico-natural de la isla de Cuba. Havana, vol. 2, pp. 279–484, 4 pls.

RASQUIN, PRISCILLA
1958.   Studies in the control of pigment cells and light reactions in recent teleosts. Part 1. Morphology of the pineal region. Part 2. Reactions of the pigmentary system to hormonal stimulation. Bull. Amer. Mus. Nat. Hist., vol. 115, pp. 1–68, pls. 1–10.

Rivas, Luis R.
    1954.   The origin, relationships and geographical distribution of the marine
             fishes of the Gulf of Mexico. Fish. Bull. U. S. Fish Wildlife Serv., vol. 55,
             no. 89, pp. 503–505.
Russell, Richard S.
    1957.   Instability of sea level. Amer. Sci., vol. 45, pp. 414–430, 3 figs.
Scholander, Per F., Walter Flagg, Vladimir Walters, and Laurence
        Irving
    1953.   Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zoöl.,
             vol. 26, pp. 67–92, 12 figs.
Schultz, Leonard P., and Earl D. Reid
    1937.   The American Atlantic toadfishes of the genus *Opsanus*. Copeia, no. 4, pp.
             211–212.
Smith, F. G. Walton
    1954.   Gulf of Mexico Madreporaria. Fish. Bull. U. S. Fish Wildlife Serv., vol.
             55, no. 89, pp. 291–295, 1 fig.
Tavolga, William N.
    1958.   Underwater sounds produced by two species of toadfish, *Opsanus tau* and
             Opsanus beta. Bull. Marine Sci. Gulf and Caribbean, vol. 8, pp. 278–284,
             2 figs.
Taylor, Clyde C., Henry B. Bigelow, and Herbert W. Graham
    1957.   Climatic trends and the distribution of marine animals in New Eng-
             land. Fish. Bull. U. S. Fish Wildlife Serv., vol. 57, no. 115, pp. i–iv, 293–
             345, 29 figs.
Vaughan, Thomas W.
    1919.   Fossil corals from Central America, Cuba, and Porto Rico, with an ac-
             count of the American Tertiary, Pleistocene, and Recent coral reefs. Bull.
             U. S. Natl. Mus., no. 103, pp. i–vi, 189–524, i–xiv, 25 figs., pls. 68–152.
Vladykov, Vadim D.
    1955.   A comparison of Atlantic sea sturgeon with a new subspecies from the
             Gulf of Mexico (*Acipenser oxyrhynchus de sotoi*). Jour. Fish. Res. Board
             Canada, vol. 12, pp. 754–761, 8 pls.
Walters, Vladimir, and C. Richard Robins
    1956.   *Review of* Ryby Okhotskogo Moria, by P. IU. Shmidt. Copeia, no. 1,
             pp. 67–68.