

SPECIATION IN THE FISHES OF THE GENUS *MENIDIA*

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The genus *Menidia*, which includes the common silversides of the Atlantic and Gulf coasts of the United States, presents several aspects of interest for an evolutionary study. Members of this genus have repeatedly entered fresh water from the sea:—two full species, *M. audens* and *M. extensa*, have evolved from such invasions, and there are rather numerous examples of less-marked fresh-water differentiation within *M. beryllina*. Two species, *M. beryllina* and *M. menidia*, occur together along the Atlantic coast from Massachusetts to Florida, thus permitting a comparative analysis of geographic gradients. Furthermore, these same two species hybridize in Florida. Thus, all gradations from incipient speciation to full specific differentiation, with and without hybridization, are found.

According to the most recent treatment (Schultz, 1948), there are only four species in *Menidia*; it is these four that are dealt with here. *M. menidia* is a salt-water form ranging from Nova Scotia to Florida. *M. beryllina* occurs in salt, brackish, and coastwise fresh water from Massachusetts to Vera Cruz, Mexico. *M. audens* is found in fresh water in the lower Mississippi Valley, and *M. extensa* is confined to Lake Waccamaw, a faunistically isolated lake in North Carolina (Hubbs and Raney, 1946). The data to be presented here are focused on *M. beryllina*, for the stock of this species seems to have given rise to *M. audens* and *M. extensa* in one direction and hybridizes with *M. menidia* in another.

The chief characters which have been used in differentiating the forms of the

genus are the numbers of anal rays² and of vertebrae, the number and degree of development of the scales, the shape of the mouth and snout, the position of the first dorsal fin, the depth of the body, and the location of the posterior extremity of the air bladder.

For a study of geographic variation in *M. beryllina*, various of the characters mentioned above may be used. Those which lend themselves most readily to statistical analysis, however, are the numbers of second dorsal and of anal rays (table 1 and figure 1). Within each of the populations examined (with one exception), these two counts are positively correlated (table 1). However, between populations there is no correlation between these characters (a correlation coefficient calculated between six representative populations gave + 0.04). Apparently some factor associated with geography affects one but not the other of these counts between localities, without disturbing the inherent correlation between these characters at any one locality. If, for marine populations, the average second dorsal counts are plotted against latitude (fig. 2), an increase in dorsal ray count is found

² The methods of making the counts and measurements used in this paper are as follows. The first full-length ray is considered the first ray in the anal and second dorsal, and the last, more or less double, ray is counted as a single ray. The predorsal scale count includes as extremities the first scale behind the dark area of the head and the last normally shaped predorsal scale. The preventral count includes all scales in the midline from the isthmus to the posterior-most scale between the ventral fins. The total scale count is taken along that series which runs just above the pectoral base. The depth of body is measured at the level of the anus. Vertebral counts include the urostyle; the first caudal vertebra is that with the first closed haemal arch.

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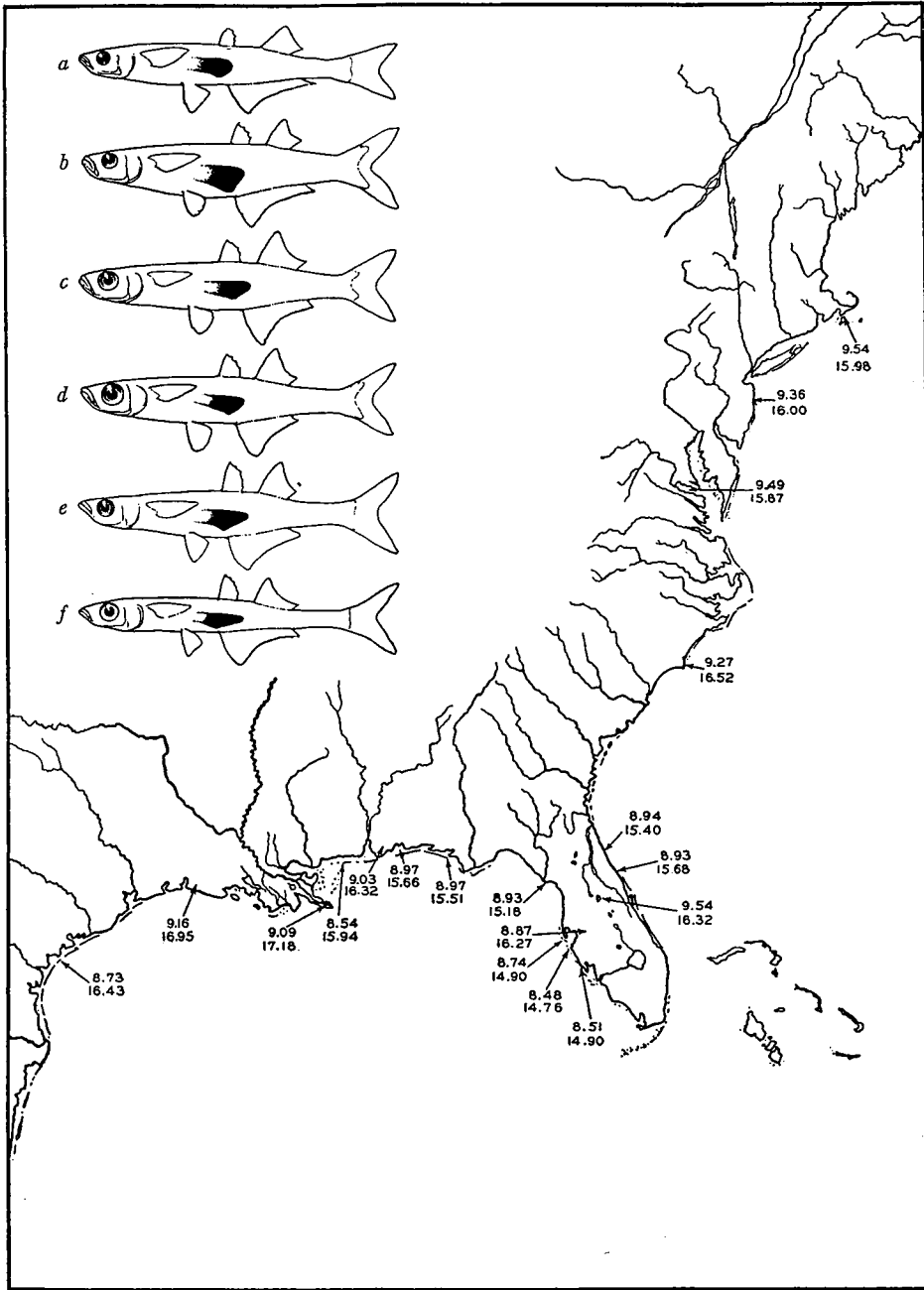


FIG. 1. Average second dorsal and anal ray counts in various samples of *Menidia beryllina*. Dorsal rays are given above, anal rays below for each sample. Insets: a, Massachusetts specimen of *Menidia menidia*; b, Florida specimen of *M. menidia*; c, Massachusetts specimen of *M. beryllina*; d, Florida specimen of *M. beryllina*; e, *M. audens*; f, *M. extensa*. In the insets the position of the posterior extremity of the air bladder is indicated in black. Inset figures a-d redrawn from Kendall (1902).

TABLE 1. Numbers of second dorsal and anal rays, and correlations between them, in various samples of *Menidia beryllina*

Starred samples are those not included in figure 1

Locality	Number of specimens	Second dorsal rays		Anal rays		Coefficient of correlation
		Mean	Standard deviation	Mean	Standard deviation	
Mass.: Barnstable Co.	66	9.54	±.65	15.98	±.89	+.30
N. J.: Ocean Co.	36	9.36	±.67	16.00	±.97	+.55
Md.: Charles Co.	61	9.49	±.69	15.87	±.97	+.66
N. C.: New Hanover Co.	71	9.27	±.58	16.56	±1.02	+.32
Fla.: St. Johns Co.	35	8.94	±.54	15.40	±.59	-.03
Fla.: Volusia Co.	75	8.93	±.61	15.68	±.85	+.61
Fla.: Lake Co.	37	9.54	±.60	16.32	±.64	+.39
Fla.: Charlotte Co.	70	8.51	±.65	14.90	±1.00	+.50
Fla.: Manatee Co.	50	8.48	±.57	14.76	±.73	+.57
Fla.: Pinellas Co.	113	8.74	±.54	14.90	±.91	+.50
Fla.: Hillsborough Co.	55	8.87	±.66	16.27	±.88	+.37
Fla.: Levy Co.	28	8.93	±.65	15.18	±1.04	+.71
Fla.: Bay Co.	66	8.97	±.58	15.51	±.89	+.38
Fla.: Santa Rosa Co.	67	8.97	±.46	15.66	±.80	+.66
Ala.: Baldwin Co.	31	9.03	±.60	16.32	±.96	+.38
Miss.: Jackson Co.	52	8.54	±.77	15.94	±1.01	+.48
Miss.: Jackson Co.*	65	8.80	±.56	16.15	±1.10	+.33
Miss.: Jackson Co.*	50	9.00	±.66	16.60	±.98	+.52
La.: Orleans Parish*	80	9.09	±.57	17.11	±1.20	+.40
La.: Plaquemines Parish	54	9.09	±.62	17.18	±.94	+.38
La.: Cameron Parish	44	9.16	±.56	16.95	±1.00	+.38
Texas: Aransas Co.	60	8.73	±.66	16.43	±.96	+.37

from south to north. However, the number of anal rays shows at best an erratic increase with latitude. For example, the average anal counts in many Gulf Coast samples (table 1 and fig. 1) is higher than that from Massachusetts. It is apparently this geographic fluctuation in anal count, as opposed to a rather level gradient in dorsal count, which causes the lack of cor-

relation between these two characters between populations.

In neither the dorsal nor the anal counts do the marine populations of *M. beryllina* show a continuous gradient from Texas to Massachusetts (table 1 and fig. 1). Rather, fish from both coasts of the Florida peninsula are set off by their minimal fin counts from the populations both to the northeast and to the west.

If only the marine populations of *M. beryllina* are considered, it might be possible on the basis of fin counts to divide the species into two or more, relatively homogeneous races. However, the situation is greatly complicated by the populations of this species which occur in fresh water. Such populations have been taken on Long Island, in the Potomac River, in North Carolina (Kendall, 1902, pp. 259 and 260), and from various localities in Florida and near the Gulf Coast. The fresh-water populations seem to differ from the salt-water fish in having a

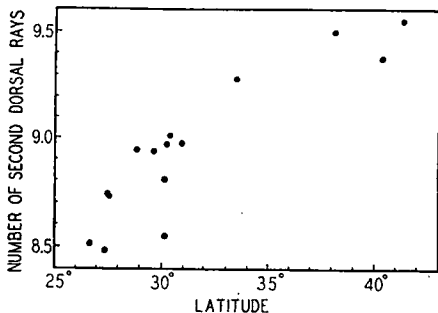


FIG. 2. Correlation between number of second dorsal rays and latitude in marine samples of *Menidia beryllina*.

greater number of soft fin rays and scales, and, with some exceptions, in having a more elongate body. The relationship of these characters to decreasing salinity may be traced in series of adjacent populations (table 2). The two Florida series shown in this table consist of two populations each, one from fresh water and one marine. But the same gradient seems to apply in the three more or less marine populations from near Biloxi. Also, from the point of view of geographic proximity those samples beginning with that from the outer shore of Horn Island to the one

TABLE 2. *Change in morphological characters from salt to fresh water in Menidia beryllina and related fresh-water species*

Means are given above, and number of specimens and standard error of the mean below in parentheses. Data for the starred item from Hubbs and Raney (1946).

Locality	Salinity	Anal rays	Second dorsal rays	Predorsal scales	Depth of body in per cent of standard length
<i>M. beryllina</i>					
East-Central Florida Volusia Co.	Salt?	15.68 (75, \pm .10)	8.93 (75, \pm .07)	14.2 (10, \pm .25)	20.8 (10, \pm .19)
Lake Eustis, Lake Co.	Fresh	16.32 (37, \pm .10)	9.54 (37, \pm .10)	15.5 (10, \pm .37)	17.3 (10, \pm .27)
West Coast of Florida Pinellas Co.	Salt	14.90 (113, \pm .09)	8.74 (113, \pm .04)	14.4 (10, \pm .30)	20.2 (10, \pm .29)
Hillsborough Co.	Fresh?	16.27 (55, \pm .12)	8.87 (55, \pm .09)	15.4 (10, \pm .23)	18.0 (10, \pm .19)
Biloxi, Mississippi region Horn Island, seaward side	Salt	15.94 (52, \pm .14)	8.54 (52, \pm .11)	15.7 (20, \pm .18)	18.1 (10, \pm .23)
Horn Island, landward side	Salt	16.15 (65, \pm .14)	8.80 (65, \pm .17)	15.0 (20, \pm .16)	17.8 (10, \pm .16)
Biloxi Bay	Brackish?	16.60 (50, \pm .14)	9.00 (50, \pm .09)	15.8 (20, \pm .12)	18.5 (10, \pm .34)
Lower Mississippi valley Lake Pontchartrain	Fresh?	17.11 (80, \pm .14)	9.09 (80, \pm .06)	15.8 (20, \pm .20)	17.8 (10, \pm .24)
Mississippi delta	Fresh?	17.18 (54, \pm .08)	9.09 (54, \pm .04)	15.7 (20, \pm .16)	18.0 (10, \pm .23)
<i>M. audens</i>					
Ark., Chicot Co.	Fresh	18.24 (53, \pm .11)	9.37 (53, \pm .08)	19.4 (20, \pm .32)	16.0 (10, \pm .25)
Tenn., Reelfoot Lake	Fresh	17.72 (54, \pm .14)	9.24 (54, \pm .09)	21.8 (20, \pm .36)	16.2 (10, \pm .20)
<i>M. extensa</i>					
North Carolina Lake Waccamaw*	Fresh	19.05 (43, —)	9.4 (43, —)	22.0 (18, —)	13 (19, —)

from the Mississippi delta might be considered as one continuous series. Kendall (1902) found the same character gradient in the Potomac River. The conclusion that changes in these four characters are correlated with salinity seems inescapable.

Two fresh-water species of *Menidia* have been described, both of which seem distinct from one another and from *M. beryllina* (tables 2 and 3). *M. audens* is now distributed over a moderately large area of the lower Mississippi valley; it appears to be monophyletic. Structurally, though probably not phylogenetically, it is transitional between *M. beryllina* and *M. extensa* (Hubbs and Raney, 1946). *M. extensa* is the most elongate species in the genus, with an increased number of fin rays, scales, and vertebrae. In all of these characters, except perhaps vertebrae, both *M. audens* and *M. extensa* appear to represent continuations of the salt-to-fresh-water gradient indicated for *M. beryllina*.

In other fishes that have been studied there is usually an increase in meristic counts, not with decrease, but rather with increase in salinity. As a matter of fact, the typically marine species *M. menidia* shows such an increase in counts over *M. beryllina*, which is essentially a brackish-

salt-water form (table 3). However, the cause of these high counts in *M. menidia* lies, I believe, in geography, as I shall point out below. However, because of the relatively large number of meristic elements in *M. menidia* the possibility exists that *M. audens* and *M. extensa* are derivatives of this species rather than of *M. beryllina*. This seems unlikely for several reasons. Although *M. menidia* is found on the Carolina coast near *M. extensa*, it does not occur off the mouth of the Mississippi through which *M. audens* must have gone. *M. menidia* rarely occurs in fresh or even in brackish water. A chain of morphologic forms has been shown to link *M. extensa* with *M. beryllina*. In *M. menidia* the air bladder does not reach much beyond the anal origin whereas in *M. beryllina*, *M. audens*, and *M. extensa* respectively it extends backward beyond that point in increasing amounts (fig. 1, insets, and table 3³). Thus in the development of the air bladder *M. beryllina* is a logical intermediate between *M. extensa* and *M. menidia*.

The question remains then as to the

³ The increased length of the air bladder is reflected in the higher number of abdominal vertebrae (or vice versa) shown for *M. audens* and *M. extensa* in table 3.

TABLE 3. Comparison of morphological characters in the four species of *Menidia*

Data for the starred items from Hubbs and Raney (1946). Means are given above, and number of specimens and range below in parentheses.

Species and locality	Abdominal vertebrae	Caudal vertebrae	Total vertebrae	Number of anal rays with base under air bladder	Scales	Anal rays	Snout-dorsal distance in per cent of length
<i>Menidia menidia</i> Massachusetts	19.2 (8; 18-20)	24.8 (8; 24-26)	44.0 (8; 43-45)	0.5 (4; 0-1)	45.8 (6; 44-48)	23.3 (10; 21-25)	51.7 (10; 50.2-53.3)
Florida	16.7 (10; 15-19)	22.7 (10; 22-24)	39.4 (10; 37-42)	0.8 (4; 0-2)	39.9 (9; 37-43)	22.2 (10; 21-24)	57.3 (10; 54.0-59.7)
<i>M. beryllina</i> Massachusetts	18.4 (15; 17-19)	20.0 (15; 19-21)	38.4 (15; 37-39)	3.2 (4; 2-4)	39.2 (10; 37-41)	15.98 (66; 14-19)	51.6 (10; 48.4-53.3)
Florida	18.1 (10; 17-19)	19.7 (10; 19-21)	37.8 (10; 37-39)	3.0 (4; 3-3)	39.9 (9; 37-43)	15.40 (35; 14-16)	53.3 (10; 52.3-54.8)
<i>M. audens</i> Arkansas	19.7 (10; 18-21)	19.6 (10; 19-21)	39.3 (10; 38-42)	6.0 (10; 4-8)	40.9* (20; 39-44)	18.15* (20; 16-20)	50.2 (10; 48.1-53.2)
<i>M. extensa</i> North Carolina	22.5 (2; 22-23)	20.5 (2; 20-21)	43.4* (13; 42-45)	7.5 (2; 7-8)	46.4* (25; 44-50)	19.05* (43; 16-21)	49.8 (10; 48.4-50.7)

relationship between *M. beryllina* and *M. menidia*. The latter species, as stated, shows an increase in meristic counts over *M. beryllina* (table 3). In the area between Massachusetts and Florida where the two species occur together, the direction of the morphological gradients is the same, but the degree to which these gradients are developed is very different. *M. beryllina* shows very little south-north increase, whereas *M. menidia* has developed into two subspecies well differentiated in the number of meristic elements (Kendall, 1902). Of these two subspecies, the southern in most respects resembles *M. beryllina* far more than the northern (table 3).

Finally as mentioned in the introduction, hybrids between *M. menidia* and *M. beryllina* have been found in northern Florida (Hubbs and Raney, 1946, p. 23). In the Michigan collections, hybrids between these two species were identified by Hubbs from two salt- or nearly salt-water localities in northeast Florida: Matanzas River, about 11½ miles south of Matanzas Inlet (called Matanzas Inlet population in table 4), St. Johns County; and Mosquito Lagoon, between Daytona Beach and Mosquito Inlet. (Both parent species were taken with the hybrids.) In order to verify the hybrid nature of these fishes, I have chosen four more or less independent characters which permit separation of the parent species in the area concerned. Means, their standard errors, and sample standard deviations for these characters are given in table 4. The degree of intermediacy of the hybrids between the means of the parent populations is shown in fig. 3.

One possibility in connection with these two populations is that such hybrids are fertile and, by backcrossing with one or both parents, contribute to the resemblance between the parent species in southern waters. The best check available on this point is a sample of pure *M. menidia* from the Matanzas River. This collection shows no significant differences from the Matanzas River Inlet population in which

hybrids occur (table 4), indicating the conclusion that backcrossing has at least not effectively modified the *M. menidia* population in the Matanzas River Inlet.

On the basis of the foregoing data, certain conjectures concerning the processes of speciation in the genus *Menidia* may be permitted. In the first place, it seems fairly clear that *M. audens* has developed through invasion by *M. beryllina* stock of the Mississippi, and by subsequent isolation and differentiation in the lower Mis-

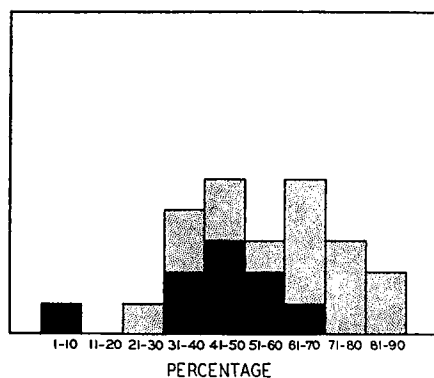


FIG. 3. Degree of intermediacy between hybrids and their parent species, *Menidia beryllina* and *M. menidia*. Percentage intermediacy calculated according to the formula

$$\frac{100(\text{hybrid value} - \text{mean of } M. \textit{beryllina})}{\text{mean of } M. \textit{menidia} - \text{mean of } M. \textit{beryllina}}$$

for each of the four characters shown in table 4 and the characters averaged. According to this method of calculation true *M. beryllina* would show a peak around 0 and true *M. menidia* a peak around 100. The nine Matanzas Inlet hybrids are shown in black and the fifteen Mosquito Lagoon hybrids in the stippled area.

Mississippi valley. *M. extensa* seems to have become isolated from the Atlantic coastal stock of *M. beryllina* when Lake Waccamaw became separated from the sea in late Pleistocene time (Hubbs and Raney, 1946).

The present relationship between *M. beryllina* and *M. menidia* appears to have had a more complex history. Both these species increase in the number of meristic counts to the northward; also, *M. menidia* has higher meristic counts than *M. beryl-*

TABLE 4. Comparison of morphological characters between *Menidia beryllina*, *M. menidia*, and hybrids between the two

"P." equals the probability that the samples of *M. menidia* from Matanzas River and that from Matanzas Inlet were taken from the same population. Means are given above, and number of specimens, standard error of the mean, and range below in parentheses.

Character	<i>Menidia beryllina</i>	Difference between means of hybrid and of <i>M. beryllina</i>	Hybrid	Difference between means of hybrid and of <i>M. menidia</i>	<i>M. menidia</i>	Population of pure <i>M. menidia</i> from the Matanzas River	P.
No. of specimens							
Mosquito Lagoon	78		15		8		
Matanzas Inlet	34		9		99		
Anal rays							
Mosquito Lagoon	15.68 (75, \pm .04) (13-19)	4.02	19.70 (15, \pm .24) (18-22)	3.30	23.00 (8, \pm .42) (22-25)		
Matanzas Inlet	15.40 (35, \pm .03) (14-16)	3.16	18.56 (9, \pm .36) (17-20)	3.44	22.00 (10, \pm .60) (20-24)	22.20 (10, \pm .42) (21-24)	.76
Predorsal scales							
Mosquito Lagoon	14.25 (8, \pm .25) (13-15)	2.95	17.20 (15, \pm .19) (16-18)	1.18	18.38 (8, \pm .35) (17-20)		
Matanzas Inlet	14.30 (10, \pm .23) (13-15)	1.48	15.78 (9, \pm .27) (14-17)	1.82	17.60 (10, \pm .24) (17-19)	17.30 (10, \pm .37) (16-19)	.60
Preventral Scales							
Mosquito Lagoon	14.25 (8, \pm .30) (13-15)	1.48	15.73 (15, \pm .24) (13-17)	.77	16.50 (8, \pm .50) (15-19)		
Matanzas Inlet	12.80 (10, \pm .33) (11-14)	1.31	14.11 (9, \pm .35) (13-16)	2.09	16.20 (10, \pm .44) (14-18)	16.20 (10, \pm .42) (14-19)	1.00
Snout-dorsal (in per cent of length)							
Mosquito Lagoon	51.89 (8, \pm .44) (49.7-53.5)	3.49	55.38 (15, \pm .26) (53.2-57.1)	2.61	57.99 (8, \pm .34) (56.8-59.7)		
Matanzas Inlet	53.27 (10, \pm .24) (52.3-54.8)	1.75	55.02 (9, \pm .47) (52.2-57.3)	2.24	57.26 (10, \pm .58) (54.0-59.7)	56.60 (10, \pm .25) (55.5-57.6)	.29

lina. Therefore, it seems that an original *beryllina-menidia* stock may have split into a northern form which is now *M. menidia* and a southern form, now *M. beryllina*. This suggestion is strengthened by the fact that now *M. beryllina*

ranges farther to the south (to which it has presumably become better adapted) than *M. menidia*, whereas the latter extends farther to the north.

It may be further speculated that this split in the *beryllina-menidia* stock was

caused by the rise of the Florida peninsula from the sea, leaving the ancestors of *M. beryllina* in the Gulf of Mexico and those of *M. menidia* on the Atlantic Coast. Under this hypothesis *M. beryllina* would have since spread up the Atlantic Coast. That *M. menidia* is the older form of the two along this coast is suggested by the fact that it has formed two well-differentiated subspecies there, whereas *M. beryllina* has not. However, if *M. beryllina* is postulated as the ancestor of *M. extensa*, *M. beryllina* must have been along the Carolina coast in the Pleistocene.

If the two species have lived together on the Atlantic Coast since the Pleistocene, the question arises, why do they now hybridize in Florida? This question does not reflect adversely upon the hypothesis set forth, since it would have come up in connection with any hypothesis whatever. Perhaps the best answer is that *M. menidia* is now in the process of extending its range southward, and that its southern outposts undertake spawning under conditions which they do not encounter in their normal range. These conditions in Florida might include such factors as overlap in spawning season or habitat with *M. beryllina*, the absence of sufficient numbers of *M. menidia* to undertake spawning alone, etc.

I wish to thank R. M. Bailey and E. T. Hooper of the Museum of Zoology, University of Michigan, for reading this paper and for suggestions concerning the hypothetical treatment of the processes of speciation in the genus. All specimens reported on in this paper are in the University of Michigan collections.

SUMMARY

The phylogeny of the genus *Menidia* was approached through a study of morphological characters, ecology, and geographical distribution of the four species now attributed to the genus. The two fresh-water species, *audens* (Lower Mississippi Valley) and *extensa* (Lake Waccamaw, North Carolina), appear to be recent (Pleistocene or later) derivatives of the stock of *beryllina*, a species now abundant in coastal salt and fresh water along the Atlantic Coast from Vera Cruz, Mexico to Massachusetts. The two coastal species, *beryllina* and *menidia*, seem to have evolved from a single ancestral form through geographical isolation and differentiation in a northern group of populations, now represented by *menidia*, and a Gulf of Mexico population, now represented by *beryllina*. There is some hybridization between the species *menidia* and *beryllina* in northern Florida, and a preliminary analysis indicates that this hybridization has not altered the phenotypic characters of populations of the parent species *menidia* from the same area.

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