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OF  
THE BINGHAM OCEANOGRAPHIC COLLECTION

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THE EGGS OF *BATHYGOBIUS SOPORATOR*  
(CUVIER AND VALENCIENNES) WITH A DISCUS-  
SION OF OTHER NON-SPHERICAL  
TELEOST EGGS

BY C. M. BREDER, JR.  
*New York Zoological Society*

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DANIEL MERRIMAN  
*Director and Editor*

A. E. PARR  
*Research Associate*

M. D. BURKENROAD  
*Assistant Curator*

C. M. BREDER  
*Research Associate*

G. A. RILEY  
*Research Assistant*

G. E. PICKFORD  
*Research Assistant*

Y. H. OLSEN  
*Assistant*

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ABSTRACT

The eggs of *Bathygobius soporator* are deposited in shallow water and attached to the under-side of shells, where they receive protective care from the male parent. They are elongate, somewhat cigar-shaped, with a rounded bulbous end distally and average about 2.36 mm. in length. The basal end is roundly pointed and attached to the support by a mass of adhesive threads. As the embryo develops, the head grows into the bulbous end, fitting it snugly and in such a fashion as to hold the larva immobilized except for the tail's tip. Just before hatching, the embryo fills the entire shell, which is in effect a slightly simplified outline of the contained larva.

Teleosts producing non-spherical eggs have been found in the following orders: Isospondyli, Ostariophysi, Percoidei, Scorpaenoidei, Gobioidi, Ammodytoidei, Xenopterygii and Blennioidei. The gobies show the most numerous and widest departures from the typical spherical eggs, although no others go as far as does *Bathygobius*.

Considered from a geometrical standpoint, a special form of the equation used to describe equipotential surfaces in magnetic fields could be employed to approximate the outlines of such fish eggs most closely. Physiological considerations suggest that the form of the egg is based on the detailed structure of the membrane as developed in the ovary rather than on simple chemico-physical effects at the time of

laying. Environment, habits and relationships indicate no clear reasons for the development of non-spherical eggs in teleosts.

Erythrocytes resemble marine pelagic teleost eggs in their passivity and in the nature of the fluids which bathe them. It is suggested that the two types of metazoan cells be examined with mutual reference to one another in connection with the dynamics of their osmotic features.

## INTRODUCTION

Although *Bathygobius soporator* (Cuvier and Valenciennes) is a well-known shore species widely distributed in tropical and subtropical seas, nothing seems to have been recorded concerning its reproductive habits or life history. This species is not especially common in the vicinity of the New York Aquarium field laboratory at Palmetto Key on the Florida West Coast; therefore, when the opportunity presented itself, the study of its eggs and nesting was undertaken, other matters of the moment being dropped when it developed that these eggs were clearly of unusual interest.

Without the cooperative assistance of a local commercial fisherman, Mr. Robert Spearing, and that of Mrs. E. L. Breder, it would have been impossible to develop the field studies involved. The other parts of this study were carried on in the Department of Animal Behavior of the American Museum of Natural History. Mr. J. T. Nichols and Miss Francesca La Monte of the Department of Ichthyology were helpful in connection with numerous pertinent items. Mr. L. R. Aronson of the Department of Animal Behavior kindly supplied the cichlid eggs studied. Also Mr. S. F. Hildebrand and Mr. Isaac Ginsburg of the U. S. Fish and Wildlife Service gave much assistance with the incidental taxonomic problems, and the advice of Dr. Richard Cox of New York University was most valuable in connection with the geometrical matters.

## *BATHYGOBIUS SOPORATOR*

### HABITAT

Since *Bathygobius soporator* appears to be a fish chiefly common to tide pools, it is not surprising that it is not an abundant form in and about Pine Island Sound where these studies were made. See, for example, Beebe (1931) who discusses the habitat of the species in Bermuda. His description agrees well with personal observations made there and in various of the islands making up the Bahamas. Unlike many gobies it shows no inclination to enter fresh water, and

in Panama where various species of this family may be found far up stream, it is apparently limited to tide pools, as indicated by Breder (1925). Pine Island Sound, while not exactly brackish, is definitely of lower salinity than the outside Gulf. This may have something to do with the comparative rarity of *B. soporator* hereabouts, but probably more important is the dearth of bottom approximating the type in which it is customarily found. The outside beaches are long smooth sand reaches that do not usually form tide pools and the inside shores are lined with dense stands of mangrove. Here the bottom is apt to be of smooth flocculent mud, general organic detritus with an admixture of broken shell for the most part well buried. Although these places are clearly well suited to the tastes of *Gobiosoma robustum* Ginsburg, as discussed by Breder (1942a), the much larger *Bathygobius* evidently finds them undesirable. On the island occupied by the New York Aquarium field laboratory there is a stretch of beach which was made by stripping the mangroves from that length of water front. Here occasional adult *Bathygobius* may be taken from time to time, generally in the shelter of some stray shell. Although a considerable amount of collecting has been undertaken here for the last five years, half grown or very small specimens have not been found.

At the north end of this beach a tiny dock of two planks has been used for a similar length of time for shucking scallops and the very large clams found locally. As a consequence a considerable pile of such shells has accumulated, resulting in an "island" of shells in an otherwise smooth sandy beach. At spring tides this beach is exposed sufficiently to bare this shell pile to the air. At all other times it is covered with at least several inches of water. Generally a few *Bathygobius* are to be found in residence here. This site is shown in Plate III, A, in the exposed condition which clearly indicates that it is too small to harbor many specimens, since this species appears to prefer to be solitary or nearly so. It seems that the appearance of gregariousness is due merely to the individuals fitting themselves into as many rock pools or other places as are available, dependent on population pressure. In an aquarium they customarily take up far corners, two seldom being found in the same retreat.

#### SEXUAL DIFFERENCES

There is a small but recognizable sexual dimorphism in this species. It is evidenced principally in the higher and longer posterior dorsal

and anal rays of the male. As indicated by Longley and Hildebrand (1941) for *B. curacao* (Metzelaar) the rays of the male when depressed reach to the beginning of the caudal rays, while in the female they fall short of that point. The males tend to be of a more contrasting pattern, but there is such an amount of pattern and color change in these fishes, usually taking place so rapidly, that it is difficult to describe it briefly in detail as is indicated by Beebe (1931). The condition is similar to that in *Gobiosoma robustum* as indicated by Fowler (1941) and Breder (1942a). The fishes used in this study are shown in Plate I, and represent the entire population of the shell pile mentioned. For purposes of this illustration they were photographed against a plain white background. Plate I, A, represents the male and Plate I, B, the two females. Incident to handling they changed the form and intensity of their pattern remarkably. On the natural bottom the male generally showed a more intense pattern than the smaller female shows in the photograph. Under identical conditions it will be noted that the larger female put on a plain black coloration and the smaller one a most contrasting pattern, while the male took on a light phase in which the pattern was still fairly bold. It is difficult to understand the significance of these variations in response to identical stimuli. Beebe (1931) obtained fairly definite responses with his material. The behavior of these fish in an aquarium was equally erratic.

In this material the urogenital papilla of the male was scarcely evident, while that of the larger female appeared puffy and bifid. The male may have finished spawning, but the females both had their ovaries filled with well advanced ova that certainly would have been shed the same season.

#### THE NESTING SITE

The studies on which this paper is based concern a single nest. This nest is typical of other goby species, and is therefore probably representative of the sites chosen by this species. An overturned half clam shell near the middle of the shell pile shown in Plate III, A, was selected. This had a considerable growth of oysters on one end and the top side was lightly incrustated with barnacles. The nest, before it had been disturbed in any way, together with the guarding male, is shown in Plate II. The fish was very inconspicuous, and in the plate the area of the nest and the fish has been circled. It is pointing to approximately "11 o'clock" in the circle, resting with one pectoral on an up-turned clam shell. The tail is hidden under the shell bearing

the barnacles which forms the nest proper. It will be noted that the dark band behind the pectoral insertion is especially bold. This was the livery in which this fish was always seen prior to removal. Kodachromes were also taken of the view shown in Plate II, and even in these the fish was no more evident than in monochrome. Actually one would continually "lose" the fish and usually only find it again when it moved, that is until one became so intimately familiar with the scene that one knew just where to look for the fish by sighting various "landmarks." The fish would retreat under the shell, presumably to aerate the eggs or attend to whatever activities it undertook about every three minutes, with surprising regularity.

The shell with the adherent eggs in an inverted position is shown in Plate III, B. Like most gobies the eggs were attached pendant-wise to the "ceiling" of the nest. In this view the light area indicates the

TABLE I—TEMPERATURES OF WATER AND AIR DURING DEVELOPMENT OF *BATHYGOBIUS* EGGS

Date	Hour	Temperature in Degrees Centigrade		
		Water		Air
		Laboratory	End of Dock	
July 3	2:45 p. m.	29.8	33.0	32.2
	8:15	27.8	32.0	28.0
	11:15	28.0	31.0	27.5
4	9:30 a. m.	26.7	30.0	28.0
	1:00 p. m.	29.0	30.7	32.0
	5:00	30.0	33.0	33.0
5	9:45	30.0	32.5	30.5
	10:45 a. m.	27.0	30.2	29.2
	2:15 p. m.	29.0	32.0	30.6
	4:30	29.0	32.0	30.0
	9:00	28.0	31.3	28.0
6	10:00 a. m.	26.5	30.0	29.5
	5:00 p. m.	29.5	32.5	31.0
	11:00	29.0	31.0	29.5
7	10:00 a. m.	27.0	29.3	29.0
	1:30 p. m.	28.3	32.4	31.2
	8:15	29.0	31.8	30.0
8	10:00 a. m.	27.0	30.2	29.0
	3:15 p. m.	28.0	33.7	32.0
	10:30	26.5	31.6	28.2
	Maximum	30.0	33.7	33.0
	Mean	28.8—	31.5	29.9+
	Minimum	26.5	29.3	27.5



place cleaned by the fish, which includes part of one of the smaller oyster shells. This area was nearly completely covered with the adherent eggs, which gave it the appearance of being covered with a yellowish fur. At this reduction the actual details of the small eggs are naturally not evident, presenting merely the surface of a coarse "velvet."

Since this site was laid bare by a spring tide two days after the nest was removed it is to be supposed that either the eggs would have perished or that they are able to withstand the excessively high temperatures that a summer sun gives to the fringing waters and sand at this season. Water at the shore line an inch or so in depth reached 39.0° C. Water of two or more feet in depth on the other hand seldom reached as high as 33.7° C., nor did it go below 27.7° C. during June or early July. Table I gives details of temperatures as actually encountered in the laboratory containers, at the end of the dock, and in the air while these studies were under way.

#### THE EGGS AND THEIR DEVELOPMENT

The eggs are far from the spherical condition which is common to the vast majority of teleosts. Most goby eggs are described as elliptical or approximating that form. The present eggs, while showing a basic relationship to that geometrical figure are impossible to describe by mentioning any geometrically regular outline. They are unlike any other naked teleost egg and most remarkable in that they may be likened somewhat to the outline of an Indian club or a ten-pin. More or less of the proportion of a long cigar, each possesses a rounded swelling at its distal end (see Plates IV-VI). They are attached in typical gobioid fashion, by means of strongly adhesive thread-like processes at their proximal end. When a group of them is placed on a dish they spread out radially as shown in Plate IV, A. When attached to the clam shell they are seen to be closely but evenly spaced, each egg dangling from its attachment so as to hang straight down except when waved about by water currents. Plate IV shows the eggs as they were first found in the nest. No data on the earlier stages are available, but judging from general appearance and behavior they would presumably be similar to those of any other goby egg so far as the development of the embryo is concerned. As in most goby eggs the embryos usually head away from their basal end, and in this particular species this feature has a special significance.

The yolk is a brilliant golden yellow. At this stage the embryo is nearly opaque, greyish in hue. Plate IV, B, which shows two eggs at a higher magnification, gives the maximum of optical transparency at this stage. The shell is of glass-like transparency, but under high power the surface of the egg membrane presents a finely granular appearance. Measured from tip to tip, the eggs ranged from 2.25–2.42 mm. and averaged 2.36 mm. in a series of seven eggs which included the largest and smallest seen. The embryos at this stage showed some slight movement of the tail at irregular intervals. This represents their condition on July 3, 1942 at 12:15 p. m. The photomicrographs were made at 10:00 p. m.

At 9:00 p. m. on July 4 the embryos had developed to the stage shown in Plate V, A. The larvae had become slightly more transparent and the yolk was clearly reducing in size. All the eggs that went on to hatching were now orientated with the head away from the base. It will be noted that the yolk remained substantially in the same place but that the head was being thrust into the bulbous end. The embryo was more active at this time and melanophores were beginning to appear. These do not show well in the photograph because of the slight transparency of the embryo. They may be seen as indications of a row along the ventral outline and on each side behind the yolk. There were also a few scattered on the surface of the yolk. None appeared about the optic capsule at this stage, this region remaining opaque the longest. This was the condition at 10:00 a. m. By 3:45 p. m. the iris was beginning to show some pigmentation and some "brassy" reflections typical of many larval fish eyes. Xanthophores began to appear, following the course of the melanophores. At 8:00 a. m. the hearts were beating 102.6 per minute at 26° C. At 3:45 p. m. they were beating 161.4 per minute at 29.8° C.

At 11:00 a. m., July 5, the larvae had become very transparent and had grown to nearly fill the egg capsule, the eyes had become thoroughly pigmented, and the general pigmentation was much stronger. Their appearance is shown in Plate V, B. The fin membrane was practically in contact and parallel with the egg outline. Each fish showed little movement as it was nearly immobilized by the close fit it made with the containing membrane. With comparatively much effort an embryo sometimes managed to twitch its tail so that the tip lay just behind the yolk. This was seldom done and the position not held for long. By this time the yolk had shrunk appreciably.

From here on there was little growth in size although differentiation, of course, continued. By 9:30 a. m. on July 6 the body of each larva had become notably thick, being practically circular in cross-section. At this stage the eyes became very active, the embryo evidently following drifting particles in the water. Probably any fish retained within the confines of a transparent egg long enough for the eyes to become fully pigmented do this, but it is clearly noticeable in these immobilized fish, who, in effect, receive a preview of the world into which they are going to hatch, while being suspended immovably by their tails. By this time each larva completely filled its egg as is shown in Plate VI, A. It was now evident that actually each egg capsule presented the somewhat simplified outline of a very ordinary type of fish larvae—an outline which these embryos had grown to fit like a finger in a glove before hatching. The tip of the larval tail membrane reached to the very end of the basal part of the egg.

By 9:30 p. m. these eggs began hatching. Plate VI, B, shows some of the empty shells. As may be seen, the top of the bulbous portion has ruptured, presumably being digested away, permitting the fish to simply wriggle out head foremost. To the right in this figure is an egg of another cluster just beginning to hatch. The break in the end of the membrane may be seen plainly. In the lower right-hand corner is a dead egg; the embryo is inverted, a fact which may have been responsible for its failure to develop. At the left-hand side is a newly hatched larva, which it will be noted is very dark. Almost immediately after hatching the larvae characteristically entered a phase in which the chromatophores were widely expanded. There was considerable variation in the size of the yolk at hatching, it being smaller in some unhatched eggs than in some larvae already out of the egg. The pectoral fin was large and functional. The temperatures in the bowls in which these eggs were hatched is given in Table I.

#### THE LARVAL FISH

On hatching these fish floated in a perfectly normal position, not inverted as do so many young fish with a relatively large yolk. This is probably due to the high position of the large swim bladder, which may be seen in Plate VI, C. They were active, alert, and moved by quick darts. Between darts they held themselves rigid and floated in mid-water, near the surface. They were evidently mildly phototropic. The large transparent pectorals were apparently not usually brought

into play. These fish were retained until 11:00 a. m., July 9, when the station was closed. The photograph Plate VI, C, was taken at 9:30 p. m., July 8. No substantial change was noted thereafter. The yolk was gone and the larvae were feeding freely. At no time did they show any disposition to seek the bottom, behaving much as when first hatched. When narcotized they floated in their ordinary position, thus suggesting that they were in about a stable equilibrium. It was exceedingly difficult to take photomicrographs of them in lateral view with the equipment at hand on account of this tendency and because they were nearly circular in cross-section; this accounts for the quartering view shown in Plate VI, C. Also because of their extreme delicacy, it was not practicable to fix them as whole mounts without considerable distortion.

#### NON-SPHERICAL TELEOST EGGS

In connection with the description of the unusual egg of *Bathygobius* the literature was searched for other eggs which did not subscribe to the usual spherical shape of most teleost ova. In this connection it must be borne in mind that teleost eggs are naked, lacking a shell, the outer membrane being the zona radiata or chorion; they do not possess shells that may be variously shaped, although even in such cases contours other than "oval" or rounded are unusual. So far as is known, in vertebrates at least, the basically spherical egg is slightly distorted to fit the shell. For example, the ovarian egg of *Raja* is spherical except as pressed upon by its fellows and bears no structural resemblance to the squarish shell into which it is fitted. In all, eleven families (distributed among eight orders—see below) were found to contain at least some members which produce eggs other than strictly spherical.

**Class: PISCES**

**Subclass: ACTINOPTERI**

**Superorder: TELEOSTEI**

**Order: ISOSPONDYLI**

**Suborder: CLUPEOIDEA**

**Family: ENGRAULIDAE**

**Order: OSTARIOPHYSI**

**Suborder: EVENTOGNATHI**

**Family: CYPRINIDAE**

*Order: PERCOIDEI**Family: CICHLIDAE**Family: POMACENTRIDAE**Order: SCORPAENOIDEI**Family: SCORPAENIDAE**Family: DACTYLOPTERIDAE**Order: GOBIOIDEI**Family: GOBIIDAE**Order: AMMODYTOIDEI**Family: AMMODYTIDAE**Order: XENOPTERYGII**Family: GOBIESOCIDAE**Order: BLENNIOIDEI**Family: BLENNIIDAE**Family: CARAPIDAE*

Detailed data on the groups producing non-spherical eggs, together with the sources of the information, the size and proportions of the eggs are given in Table II. Since there is considerable taxonomic confusion in the Engraulidae and Gobiidae, the original names as used by the describers of the eggs are given. The genera to which these fish would presumably belong in modern usage is indicated above each group. Certain groups present a highly unsatisfactory condition, especially the genus *Gobius*, which certainly represents a mixed assemblage. The source of the data and the figure of the egg if used herein is indicated. The dimensions as shown in this table are variable as to accuracy, since they have been drawn from many sources. What is believed to be the mean of the available data is given. Some are based on measurements of figures and numerical data in the various papers consulted, and some are partly original. In various instances considerable data not found in the authority listed have been included in the calculations. These are referred to in the body of the text. The minor diameter is given with the major reduced to unity so that the proportionality of the eggs of one species to another may be checked.

TABLE II—DIMENSIONS AND PROPORTIONS OF EGGS WITH SOURCES AND CLASSIFICATION OF DATA

See text for full explanation

<i>Name as Used by Authority</i>	<i>Chief Source of Data</i>	<i>Basis of Figure</i>	<i>Average Major Axis in Mm.</i>	<i>Minor Axis with Major Axis = Unity</i>
<b>FAMILY ENGRAULIDAE</b>				
<b>ENGRAULIS</b>				
<i>Engraulis encrasicolus</i> (Linn.)	Raffaele (1888), McIntosh & Masterman (1897), Ehrenbaum (1909)	Same	1.37	0.594
<i>Engraulis mordax</i> Gir.	Bolin (1936)	Same	1.39	0.470
<i>Engraulis australis</i> (White)	Blackburn (1941)	Same	1.125	0.485
<i>Engraulis capensis</i> Gilchr.	Gilchrist & Hunter (1919)	Same	1.55	0.658
<i>Engraulis japonicus</i> (Temm. & Schl.)	Nishikawa (1901)	Same	1.4	0.446
<b>ANCHOVIELLA</b>				
<i>Anchovia mitchilli</i> (C. & V.)	Kuntz (1914)	Same & original	0.7	0.880
<i>Anchovia epsetus</i> (Bonn.)	Hildebrand & Cable (1930)	Same & original	1.5	0.460
<i>Anchoviella argyrophana</i> (C. & V.)	Kuntz & Radcliffe (1918)	Same	1.2	0.564
<b>STOLEPHORUS</b>				
<i>Stolephorus zolkingeri</i> (Bleek.)	Delsman (1931)	Same	1.132	0.490
<i>Stolephorus heterolobus</i> (Rupp.)	Delsman (1931)	Same	1.231	0.485
<i>Stolephorus insularis</i> Hard.	Delsman (1931)	Same	2.19	0.350
<i>Stolephorus indicus</i> (van Hass.) or <i>S. commersonii</i> Lac.	Delsman (1931)	Same	1.422	0.570
<i>Stolephorus compressus</i> (Gir.)	Eigenmann (1893)	—	0.76	1.000
<b>THRASSINA</b>				
<i>Stolephorus tri</i> (Bleek.)	Delsman (1931)	Same	1.25	0.540
<i>Stolephorus baganensis</i> Hard.	Delsman (1931)	Same	1.241	0.580
<b>SCUTENGRAULIS</b>				
<i>Engraulis grayi</i> Bleek.	Delsman (1931)	—	0.6	1.000
<i>Engraulis mystax</i> (Bl. & Schn.)	Delsman (1931)	—	1.075	1.000
<b>FAMILY CYPRINIDAE</b>				
<b>RHODEUS</b>				
<i>Rhodeus amarus</i> (Bl.)	Sorge (1932 & original)	Sorge (1932)	2.5	0.506
<b>FAMILY CICHLIDAE</b>				
<b>TILAPIA</b>				
<i>Tilapia macrocephala</i> (Bleek.)	Original	Original	2.9	0.800
<b>FAMILY POMACENTRIDAE</b>				
<b>CHROMIS</b>				
<i>Helicastes chromis</i> (Linn.)	DeGaetani (1932)	Same	0.72	0.700
<b>POMACENTRUS</b>				
<i>Pomacentrus leucurus</i> Gilb.	Breder & Coates (1933)	Same	0.85	0.529
<i>Pomacentrus leucostictus</i> Müll. & Tros.	Brinley (1939)	Same	0.8	0.500

TABLE II—(Continued)

Name as Used by Authority	Chief Source of Data	Basis of Figure	Average Major Axis in Mm.	Minor Axis with Major Axis = Unity
<b>AMPHIPRION</b>				
<i>Amphiprion percula</i> (Lac.)	Delsman (1930)	Same	2.2	0.415
<b>FAMILY SCORPAENIDAE</b>				
<b>SCORPAENA</b>				
<i>Scorpaena guttata</i> Gir.	David (1939)	Same	1.255	0.810
<i>Scorpaena porcus</i> Linn.	Raffaele (1888)	—	1.0	0.750
<i>Scorpaena scrofa</i> Linn.	Raffaele (1888)	—	1.8	0.475
<b>SEBASTODES</b>				
<i>Sebastodes ovalis</i> Ayres	Eigenmann (1893)	—	—	—
<i>Sebastodes rubrovinctus</i> Jord. & Gilb.	Eigenmann (1893)	—	—	—
<i>Sebastodes auriculatus</i> (Gir.)	Eigenmann (1893)	—	—	—
<i>Sebastodes ruber</i> (Ayres)	Eigenmann (1893)	—	—	—
<b>HELICOLENUS</b>				
<i>Helicolenus percoides</i> Rich.	Thompson & Anderton (1921)	—	—	—
<b>FAMILY DACTYLOPTERIDAE</b>				
<b>DACTYLOPTERUS</b>				
<i>Dactylopterus volitans</i> (Linn.)	Sanzo (1934)	Same	0.8	0.900
<b>FAMILY GOBIIDAE</b>				
<b>GOBIUS</b>				
<i>Gobius niger</i> Linn.	Holt (1890), Petersen (1917)	Same	1.17	0.240
<i>Gobius minutus</i> Pall.	Holt (1890), Petersen (1917), LeBour (1920)	Same	1.0	0.550
<i>Gobius paganellus</i> Linn.	Sparta (1934)	Same	2.24	0.355
<i>Gobius flavescens</i> Fabr.	Petersen (1917), LeBour (1919)	Same	0.7	0.810
<i>Gobius joso</i> Linn.	Sparta (1934)	Same	2.8	0.220
<i>Gobius capito</i> C. & V.	Holt (1890), LoBianco (1899)	—	3.6	—
<i>Gobius ferrugineus</i> Kalomb.	Sparta (1936)	Same	1.0	0.720
<i>Gobius pictus</i> Malm	LeBour (1920)	Same	0.8	0.780
<i>Gobius microps</i> Krüger.	LeBour (1920), Petersen (1917)	Same	0.9	0.760
<i>Gobius ophiocephalus</i> Pall.	Ninni (1938)	Same	—	0.460
<i>Gobius xanthozona</i> (Bleek.)	Anonymous (1934), Roloff (1936)	—	—	—
<i>Gobius nudiceps</i> C. & V.	Gilchrist (1916)	Same	1.8	0.540
<i>Gobius scorpioides</i> Coll.	Holt & Byrne (1897)	—	—	—
<i>Gobius fluviatilis</i> Bonelli	Riedel (1914)	—	—	—
<i>Gobius</i> sp.	Gilchrist & Hunter (1919)	—	0.96	0.760
<i>Gobius</i> sp.	Kowalewski (1886)	—	—	—
<b>STIGMATOGOBIUS</b>				
<i>Stigmatogobius hoevenii</i> (Bleek.)	Szabados (1937b), Vetter (1937)	Same	2.83	0.440
<i>Gobius marmoratus</i>	Szabados (1937a)			

TABLE II—(Continued)

<i>Name as Used by Authority</i>	<i>Chief Source of Data</i>	<i>Basis of Figure</i>	<i>Average Major Axis in Mm.</i>	<i>Minor Axis with Major Axis = Unity</i>
<b>ACENTROGOBIUS</b>				
<i>Acentrogobius neilli</i> (Day)	Aiyar (1935)	Same	0.4	0.345
<b>GOBIONELLUS</b>				
<i>Gobionellus boleosoma</i> (Jord & Gilb.)	Kuntz (1916), Hildebrand & Cable (1938)	—	0.3	1.000
<b>GOBIOSOMA</b>				
<i>Gobiosoma bosci</i> (Lac.)	Kuntz (1916), Hildebrand & Cable (1938)	Same	1.26	0.352
<i>Gobiosoma robustum</i> Gins.	Breder (1942a)	Same	1.5	0.350
<b>TYPHLOGOBIUS</b>				
<i>Typhlogobius californiensis</i> Stein.	Eigenmann (1893)	Same	0.67	0.265
<b>MISTICHTHYS</b>				
<i>Misticthys luzonensis</i> Smith	Smith (1901), TeWinkel (1935)	—	0.5	0.180
<b>CHASMICHTHYS</b>				
<i>Chasmichthys gulosus</i> (Guich.)	Nakamura (1936)	—	4.65	0.263
<i>Chasmichthys dolichognathus</i> (Hilg.)	Nakamura (1936)	Same	4.150	0.325
<b>GLOSSOGOBIUS</b>				
<i>Glossogobius brunneus</i> (Temm. & Schl.)	Ishikawa & Nakamura (1940)	Same	3.5	0.300
<b>RHINOGOBIUS</b>				
<i>Rhinogobius formosanus</i> Oshima	Kobayashi (1923)	—	—	—
<b>GYMNOGOBIUS</b>				
<i>Gymnogobius macrognathus</i> (Bleek.)	Moiseev (1936)	—	—	—
<b>BATHYGOBIUS</b>				
<i>Bathygobius soporator</i> (Cuv. & Val.)	Original	Original	2.385	0.173
<b>APHIA</b>				
<i>Aphia minuta</i> (Risso)	Holt & Byrne (1897), Ehrenbaum (1904)	—	1.0	0.8
<b>CRYSTALLOGOBIUS</b>				
<i>Crystallogobius nilssoni</i> (Düb. & Kor.)	Raffaele (1895)	—	1.78	0.321
<b>PSEUDAPOCRYPTES</b>				
<i>Pseudapocryptes lanceolatus</i> (Bl. & Schn.)	Hora (1936)	—	—	—
<b>PERIOPHTHALMUS</b>				
<i>Periophthalmus koelreuteri</i> (Pall.)	Mayer (1929)	—	—	—
<i>Periophthalmus cantonensis</i> (Osborne)	Suehiro (1935)	—	—	—
<b>BOLEOPHTHALMUS</b>				
<i>Boleophthalmus pectinirostris</i> (Gmel.)	Suehiro (1935)	—	—	—
<b>FAMILY AMMODYTIDAE</b>				
<b>AMMODYTES</b>				
<i>Ammodytes tobianus</i> Linn.	Ehrenbaum & Strodman (1904)	—	0.8	0.375



TABLE II—(Continued)

Name as Used by Authority	Chief Source of Data	Basis of Figure	Average Major Axis in Mm.	Minor Axis with Major Axis = Unity
<i>Ammodytes laneolatus</i> Lesauv.	Ehrenbaum & Strodman (1904)	Same	0.8	0.375
FAMILY GOBIESOCIDAE				
<b>LEPADOGASTER</b>				
<i>Lepadogaster bimaculatus</i> (Bonn.)	Guitel (1888), McIntosh & Masterman (1897)	Same	1.37	0.787
<i>Lepadogaster gouani</i> Stein.	Guitel (1888)	Same	1.8	0.834
<i>Lepadogaster candollii</i> Risso	Guitel (1888)	Same	1.24	0.860
<b>CHORISOCHISMUS</b>				
<i>Chorisoichismus dentex</i> Pall.	Gilchrist (1916)	—	1.47	0.625
FAMILY BLENNIIDAE				
<b>BLENNIUS</b>				
<i>Blennius pholis</i> Linn.	McIntosh (1903), Hefford (1910), LeBour (1927)	Hefford (1910)	1.19	—
<i>Blennius gattorugine</i> Brünn.	LeBour (1927)	—	1.6	1.000
<i>Blennius ocellaris</i> Linn.	Pieron (1914), LeBour (1927)	—	1.12	1.000
<i>Blennius inaequalis</i> C. & V.	Cipria (1936)	Same	0.78	0.800
<i>Blennius palmicornis</i> Lowe.	Cipria (1936)	Same	1.25	0.865
<i>Blennius galerita</i> Linn.			2.0	
<i>Blennius pavo</i> Risso	Cipria (1936)	Same	1.2	0.870
<i>Blennius cornutus</i> Linn.	Gilchrist (1916)	—	—	1.000
<b>HYPSOBLENNIUS</b>				
<i>Hypsoblennius hentz</i> (LeS.)	Hildebrand & Cable (1938)	—	1.4	1.000
<b>SALARIAS</b>				
<i>Salarias flavo-umbrinus</i> Rupp.	Eggert (1929)	—	—	1.000
<i>Salarias andersonii</i> Day	Eggert (1929)	—	—	1.000
<b>CHASMODES</b>				
<i>Chasmodes bosquianus</i> (Lac.)	Hildebrand & Schroeder (1928)	—	0.75	1.000
<b>HYPLEUROCHILUS</b>				
<i>Hypleurochilus geminatus</i> (Wood)	Hildebrand & Schroeder (1928)	—	0.7	1.000
<b>ANDAMIA</b>				
<i>Andamia heteroptera</i> (Bleek.)	Rao & Hora (1938)	—	—	—
FAMILY CARAPIDAE				
<b>CARAPUS</b>				
<i>Carapus dentatus</i> (Cuv.)	Sparta (1926)	—	1.32	0.795
<i>Carapus acus</i> (Brünn.)	Holt (1899)	—	0.9	0.834
<i>Fierasfer</i> sp.	Sumner (1903)	Same	—	0.350

The following conditions obtain in each of the respective families listed above.

FAMILY ENGRAULIDAE—Most of the fishes known in this family produce eggs which are a very close approximation of a true ellipse. Three species produce spherical eggs, *Scutengraulis mystax* (Bloch and Schneider) and *S. grayi* (Bleeker), and *Stolephorus compressus* (Girard), whereas all others known produce elliptical eggs. Delsman (1931) writes that all Indian *Engraulis* eggs are spherical and intimates that perhaps it should be considered as generic with elongate ones confined to *Anchovia* (*Stolephorus*). This is not in accordance with our present understanding of Anchovy genera, which is in great need of clarification. Two species, *Stolephorus insularis* Hardenberg and *Stolephorus indicus* (van Hasselt) (or *commersonii* Lacépède), depart from this general condition in that they are nearly ellipses but possess a "tip" on one end. Outlines of these several forms of anchovy eggs are shown in Figures 1, 2 and 3 separated according to genera as here understood. The eggs which Eigenmann (1893) gives as *Stolephorus ringens* (Jenyns) or *Stolephorus delicatissimus* (Girard) are apparently those of *Engraulis mordax*. Agassiz and Whitman (1885) ascribe an oval egg to *Osmerus mordax* which is almost certainly that of *Anchoviella mitchilli*. All anchovy eggs are pelagic and it is difficult to see why they have in many cases abandoned the conventional spherical egg, common to most pelagic fishes.

FAMILY CYPRINIDAE—A single species, so far as known, in this large group produces eggs other than spherical. This species, *Rhodeus amarus* (Bloch), has the unique habit of depositing its eggs within the gill chambers of fresh-water mussels. See, for example, Bade (1926), Wunder (1931), Sorge (1932) and Breder (1933). Whether this fact has any bearing on the shape of the eggs is not clear, but since there is a long slim ovipositor which is necessary for insertion into the mussel it may be that for a given volume of egg substance an elongate shape is essential. The outline of a typical egg shown in Figure 4 has been taken from Sorge (1932) from a photograph of an egg passing along the ovipositor; it has also been checked against unpublished data in notes which were used in part by Breder (1933). The average dimensions are given in Table II. Presumably other members of the Rhodininae have similar habits, but their eggs have not been studied.

FAMILY CICHLIDAE—Some, if not all the cichlids, produce eggs which are not strictly spherical. Most seen by the author are nearly elliptical. Others are distinctly irregular in shape, and, even in a single

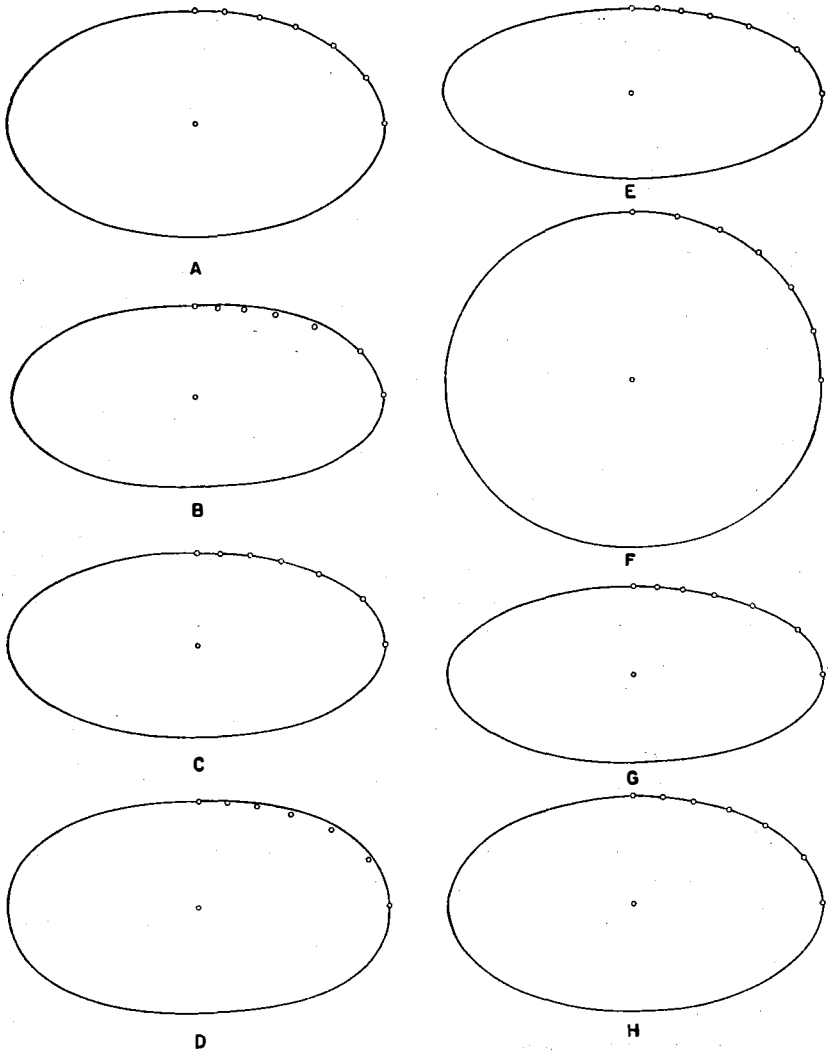


FIGURE 1. NON-SPHERICAL EGGS OF THE FAMILY ENGRAULIDAE.

A. *Engraulis encrasicolus*. B. *Engraulis mordax*. C. *Engraulis australis*. D. *Engraulis capensis*. E. *Engraulis japonicus*. F. *Anchoviella mitchilli*. G. *Anchoviella epsetus*. H. *Anchoviella argyrophana*. All eggs are arranged with the micropolar end to the left in this and the following figures.

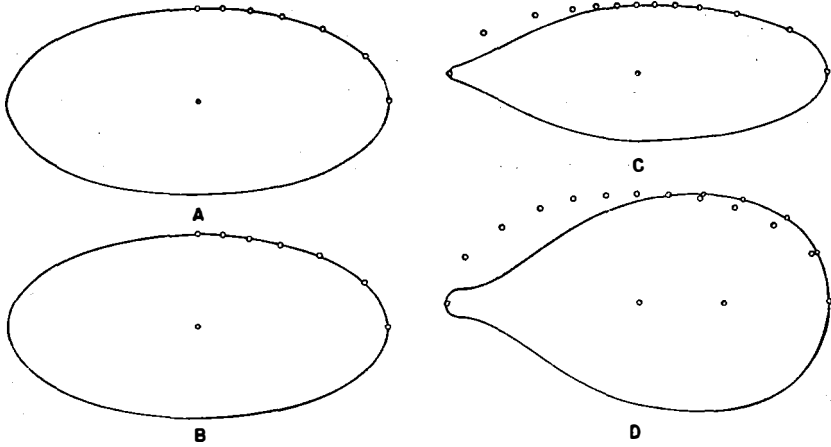


FIGURE 2. NON-SPHERICAL EGGS OF THE FAMILY ENGRAULIDAE.

A. *Stolephorus zollingeri*. B. *Stolephorus heterolobus*. C. *Stolephorus insularis*. D. *Stolephorus indicus* or *commersonii*.

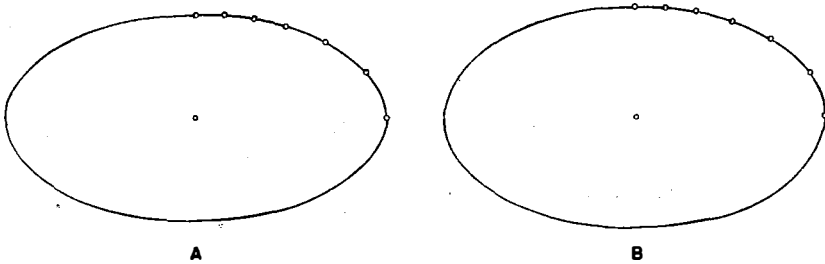


FIGURE 3. NON-SPHERICAL EGGS OF THE FAMILY ENGRAULIDAE.

A. *Thrissina tri*. B. *Thrissina baganensis*.

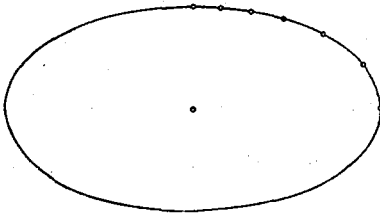


FIGURE 4. NON-SPHERICAL EGG OF THE FAMILY CYPRINIDAE, *Rhodeus amarus*.

laying, vary in such a way as to defy description in a single word. These tend to be pyriform, but are usually flattened or bulging asymmetrically in one or more places as though deformed in the ovary by pressure. Four outlines of eggs of one laying of *Tilapia macrocephala* (Bleeker) are given in Figure 5. This particular species is an oral incubator and it is hard to ascribe a reason for this condition. Oral

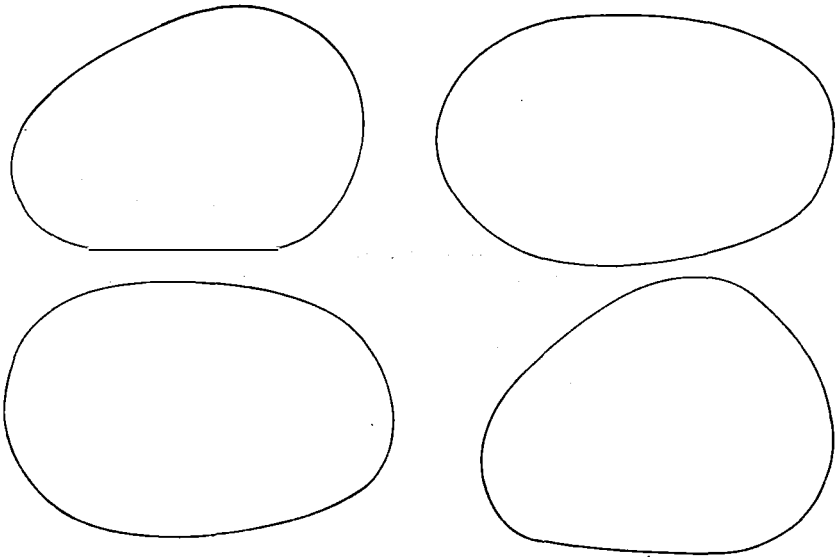


FIGURE 5. NON-SPHERICAL EGGS OF THE FAMILY CICHLIDAE.  
Four eggs from a single laying of *Tilapia macrocephala*.

incubators in other groups do not show a non-spherical condition of the eggs; for example, in the Labyrinthidae, *Betta brederi* Myers, and in the Ariinae, *Bagre marinus* (Mitchill), both produce spherical eggs.

Ripe ovarian eggs, water hardened but unfertilized, were also examined and showed the same condition. Even the flaccid ovarian eggs, when placed on a dry slide and pushed about, assumed the pyriform shape on coming to rest. The eggs illustrated were those which had been fertilized.

Although there is a large literature on the reproductive habits of this family, based mostly on aquarium observations, no data or figures that could be used in present connections have been located

in these documents, which concern themselves mostly with the behavior of the parent fish.

FAMILY POMACENTRIDAE—All known eggs of this family are other than spherical. Two species, *Chromis chromis* (Linnaeus), De Gaetani (1932), and *Pomacentrus leucurus* (Gilbert), Breder and Coates (1933), produce elliptical eggs, and two others, *Pomacentrus*

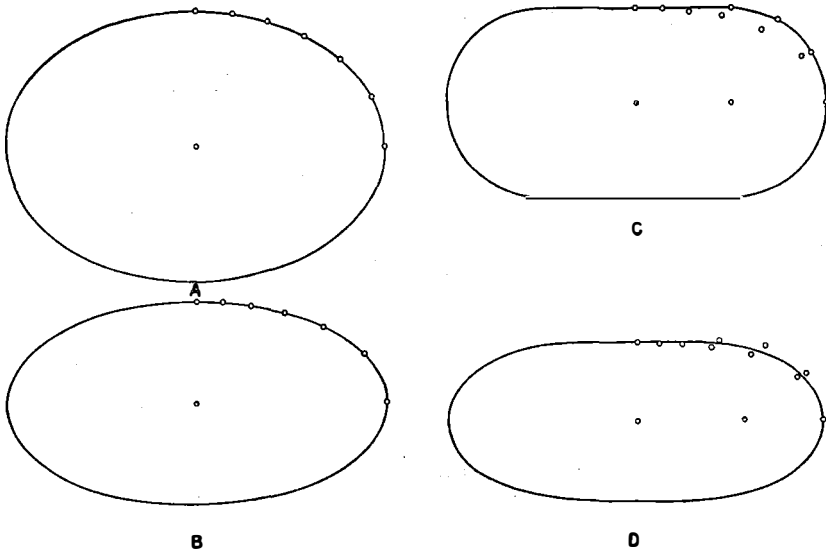


FIGURE 6. NON-SPHERICAL EGGS OF THE FAMILY POMACENTRIDAE.

A. *Chromis chromis*. B. *Pomacentrus leucurus*. C. *Pomacentrus leucostictus*. D. *Amphiprion percula*.

*leucostictus* Müller and Troschel, Brinley (1939), and *Amphiprion percula* (Lacépède), Delsman (1930), produce eggs which are actually cylinders with rounded ends. The first of these have ends which are hemispherical in outline, while the second is about midway between that condition and a true ellipse. These are illustrated in Figure 6 and have been taken from the above-mentioned papers. All are attached at one end much after the fashion common to the gobies. The parents exercise a not dissimilar type of parental care. Here again it is not clear as to why these should be other than spherical since many species in other groups produce spherical eggs which are attached in essentially similar fashion, whether they receive parental care or not.

Verwey (1930) gives extensive detail on the parental care given the eggs by *Amphiprion percula*. Delsman (1930) indicates that the eggs of *Amphiprion ephippium* (Bloch) and *Premnas biaculeatus* (Bloch) are similar to those of *A. percula* and that those of *P. biaculeatus* are slightly smaller. The photographs of Coonfield (1940) indicate that there is considerable irregularity in the form of the eggs of *Pomacentrus leucostictus*, although they appear to approximate a mean outline like that shown by Brinley (1939).

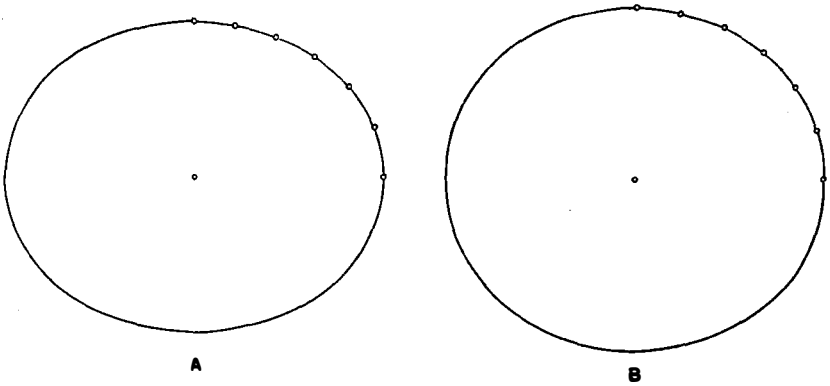


FIGURE 7. NON-SPHERICAL EGGS OF THE ORDER SCORPAENOIDEI.

A. Scorpaenidae, *Scorpaena guttata*. B. Dactylopteridae, *Dactylopterus volitans*.

FAMILY SCORPAENIDAE—Several of the few understood species of this family produce elliptical eggs in which the major axis is not greatly longer than the minor axis. The egg of *Scorpaena guttata* (Girard) is shown in Figure 7, taken from David (1939). Dimensions of other species are given in Table II from the following: Raffaele (1888), *S. porcus* Linnaeus and *S. scrofa* Linnaeus. The viviparous *Helicolenus percooides* Richardson [*H. papillosus* (Bloch and Schneider)] has nearly ripe ovarian eggs measuring 1.19 x 0.83 mm. according to Thompson and Anderton (1921). The eggs of the species illustrated are passed in a mass of mucus from which the young free themselves to become planktonic. This feature of reproduction is apparently widespread throughout the group in which internal fertilization is apparently general, the release from the female's body being nearly simultaneous with the hatching of the eggs, *Sebastes marinus* Linnaeus apparently always being ovoviviparous.

The ovarian eggs of *Sebastodes ovalis* Ayres, *S. rubrovinctus* Jordan and Gilbert, *S. auriculatus* (Girard) and *S. ruber* (Ayres) according to Eigenmann (1893) are all more or less oval, changing somewhat as incubation proceeds and hatching finally within the body of the female.

Since these eggs may or may not become elements of the oceanic plankton it is difficult to infer a value to these slightly elliptical forms, or find any correlation between habits and form of eggs.

FAMILY DACTYLOPTERIDAE—*Dactylopterus volitans* (Linnaeus) produces broadly elliptical eggs, as shown in Figure 7. The data is taken from Sanzo (1934). Evidently it is not as closely related to the triglids as generally supposed, according to Gregory (1932). The latter have spherical eggs in all cases known. *Dactylopterus* apparently goes relatively well back to the more generalized Scorpaenids where eggs which are elliptical to about the same degree are found. As with them, there is no evident connection between egg form and habit.

FAMILY GOBIIDAE—This is the family that has departed most widely from the production of spherical eggs. Not only do they exhibit the most extreme departures but they have a larger variety of different forms than any other group. They range from the spherical, through the truly elliptical to tear-drop shaped, pear shaped, pyriform, and finally to the "glove-finger" form of *Bathygobius soporator*. The various details may be found in Table II. Outline drawings of all the important forms with sufficient regularity are given in Figures 8 and 10. As in the other groups producing non-spherical eggs the functional significance of these variations are certainly not evident. Those which vary so much as to defy an attempt at regularization are given in Figure 9.

The paper describing the egg of *Rhinogobius* by Kobayashi (1923) has not been seen by this author, but apparently the eggs are somewhat like those of *Chasmichthys* or *Glossogobius*. Also Suehiro's (1935) paper could not be located in America. The inclusion of these authors in Table II is based on Nakamura (1936) who gives the following partial references: "Kobayashi, H. 1923 Journ. Fish. Japan Vol. 18 No. 4 P. 107-110" "Suehiro, Y. 1935 Nihon Suisan Gakkai-hô Vol. 6 No. 3."

In addition to the references given in Table II concerning *Gobius minutus* the following contributed to the data: Guitel (1892), Skowron (1926), and Lo Bianco (1899). McIntosh and Masterman (1897)



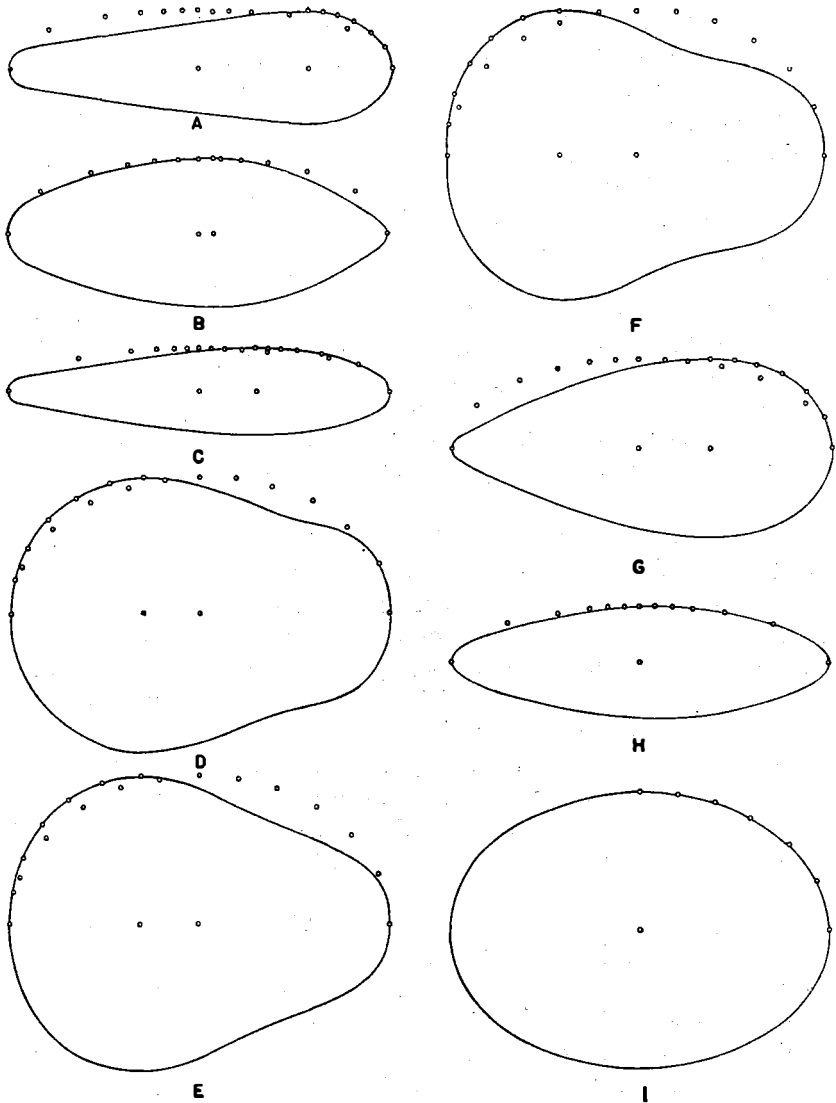


FIGURE 8. NON-SPHERICAL EGGS OF THE FAMILY GOBIIDAE.

A. *Gobius niger*. B. *Gobius paganellus*. C. *Gobius jazo*. D. *Gobius ferrugineus*. E. *Gobius pictus*. F. *Gobius microps*. G. *Gobius ophiocephalus*. H. *Gobius nudiceps*. I. *Gobius* sp. of Gilchrist and Hunter (1919).

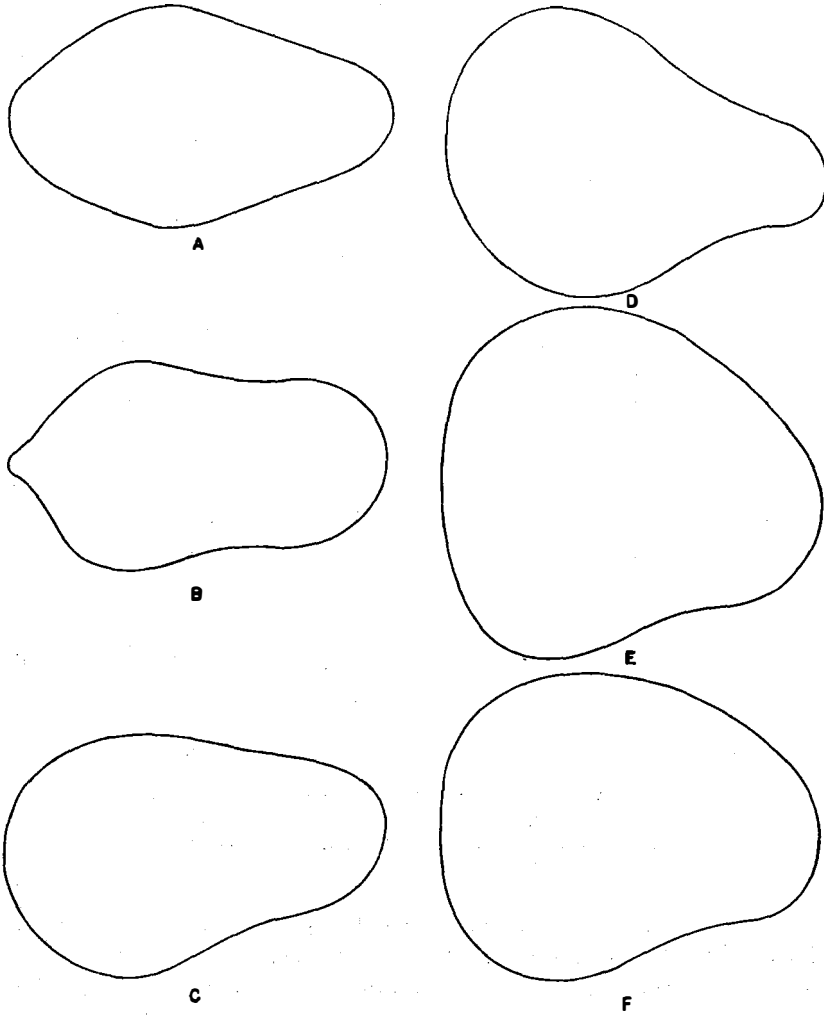


FIGURE 9. NON-SPHERICAL EGGS OF THE FAMILY GOBIIDAE.

A, B and C. *Gobius minutus* after Petersen (1917), Holt (1890) and LeBour (1920) respectively. D, E and F. *Gobius flavescens*. 'D' after Petersen (1917). 'E' and 'F' after LeBour (1920).

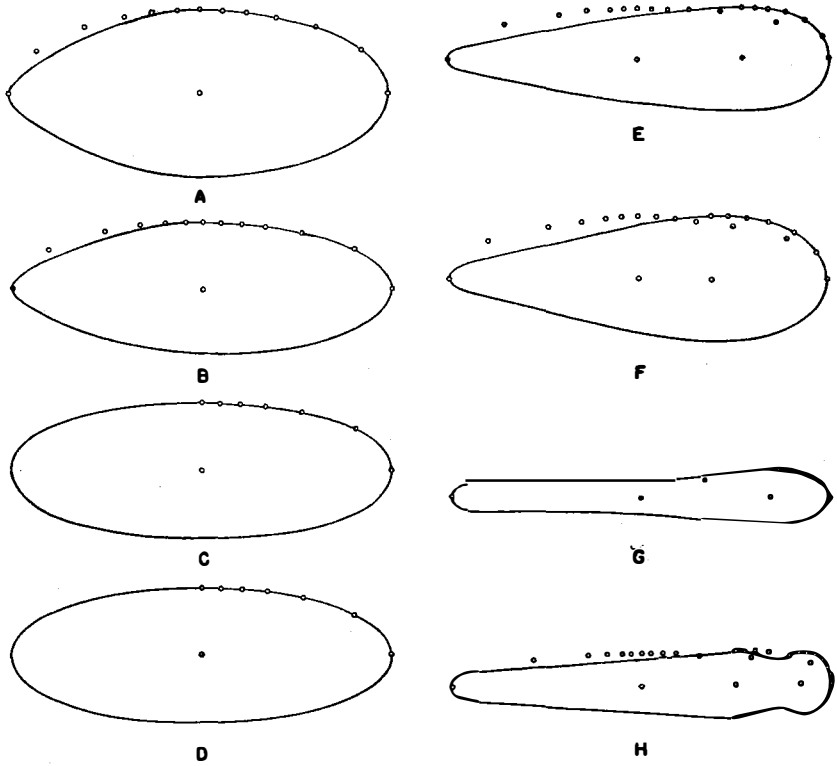


FIGURE 10. NON-SPHERICAL EGGS OF THE FAMILY GOBIIDAE.

A. *Stigmatogobius hoevenii*. B. *Acentrogobius nelli*. C. *Gobiosoma bosci*. D. *Gobiosoma robustum*. E. *Typhlogobius californiensis*. F. *Chasmichthys dolichognathus*. G. *Glossogobius brunneus*. H. *Bathygobius soporator*.

wrote, "The eggs . . . are somewhat pyriform, though as in the black goby, the outline alters with the developing embryo . . ." This may account for the considerable variation in the descriptions from one author to another. These same writers describe the egg of *G. paganellus* as differing from that of *G. niger* in that the latter is bluntly rounded at the apical end while the latter is more or less acutely pointed.

*Gobius flavescens* (= *G. ruthensparri*) has had its eggs discussed by De Buen (1923), Shann (1910), Holt (1890), Guitel (1892), and McIntosh and Masterman (1897), in addition to the authors listed in Table II.

Of *G. scorpioides*, McIntosh and Masterman (*loc. cit.*) wrote "oval or ovoid in shape but some show an approach to the shouldered condition common to other small species of this genus." They suspected that they had eggs of *G. jefferysii* Günther, which they stated were more pointed than those of *G. pictus* and ranged from 0.72–0.78 mm. by 0.55–0.58 mm.

The related Eleotridae probably produce spherical eggs but the data is very fragmentary, and there appears to be none on the Viterolidae.

FAMILY AMMODYTIDAE—The eggs of this group, as far as known, are adhesive and deposited in sandy places. The eggs themselves are elliptical as indicated in Figure 11 taken from Ehrenbaum

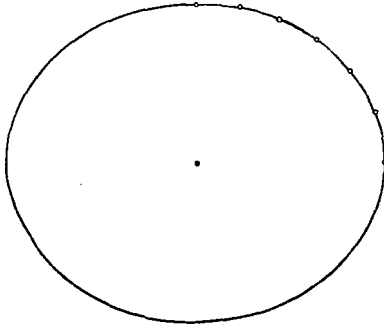


FIGURE 11. NON-SPHERICAL EGG OF THE FAMILY AMMODYTIDAE, *Ammodytes lanceolatus*.

and Strodman (1904). They figure the eggs of both *Ammodytes tobianus* Linnaeus and *A. lanceolatus* Lesauvage, the dimensions of which are apparently identical. For present purposes, consequently, a single outline is sufficient, if indeed these two forms are actually distinct. Many others give figures on the sizes of these eggs which do not differ significantly. No association with habits is evident.

FAMILY GOBIESOCIDAE—The adhesive eggs of all species known are broadly elliptical. Three are illustrated in Figure 12. These have been taken from Guitel (1888): *Lepadogaster bimaculatus* (Bonnaterre), *L. gouani* Günther and *L. candollii* Risso. The slightly elliptical and adhesive nature of these eggs place them in general terms with those of the blennies, cichlids and some gobies, without any evident correlation as to habit. From the figure of McIntosh and Masterman (1897) it is difficult to decide whether these eggs are

merely flattened by adhesion or are in truth oblate ellipsoids. Their outline is given in Figure 12 comparatively with that of Guitel (1888) for *L. bimaculatus*.

*Chorisochismus dentex* Pallas, according to Gilchrist (1916), produces eggs somewhat oval in shape. It is not clear whether these eggs are

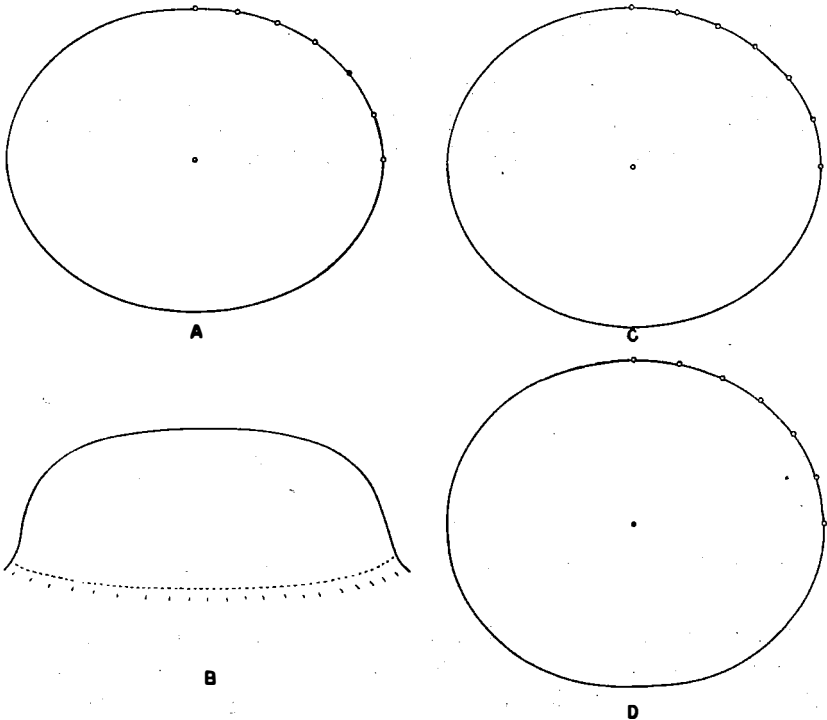


FIGURE 12. NON-SPHERICAL EGGS OF THE FAMILY GOBIESSOCIDAE.

A. *Lepadogaster bimaculatus*. B. Same species in lateral view adherent to a shell according to McIntosh and Masterman (1897). C. *Lepadogaster gouani*. D. *Lepadogaster candollei*.

oblate ellipsoids or not. It may be that they actually are such figures or that they merely deform from a primary sphere or prolate ellipsoid in adhering to their support.

FAMILY BLENNIIDAE—Several species of the genus *Blennius* produce slightly elliptical eggs although the majority of them adhere to the spherical formula. Figure 13 shows three species, from Cipria (1934 and 1936) which produce broad ellipsoids, *Blennius inaequalis*

Cuvier and Valenciennes, *B. palmicornis* Lowe, and *B. pavo* Risso. There is also shown in this figure an outline of *Blennius pholis* Linnaeus from Hefford (1910). The egg is attached and gives the appearance of flattening down to approach an oblate ellipsoid. Judging from Hefford's comments this is actually structural, but the remarks of

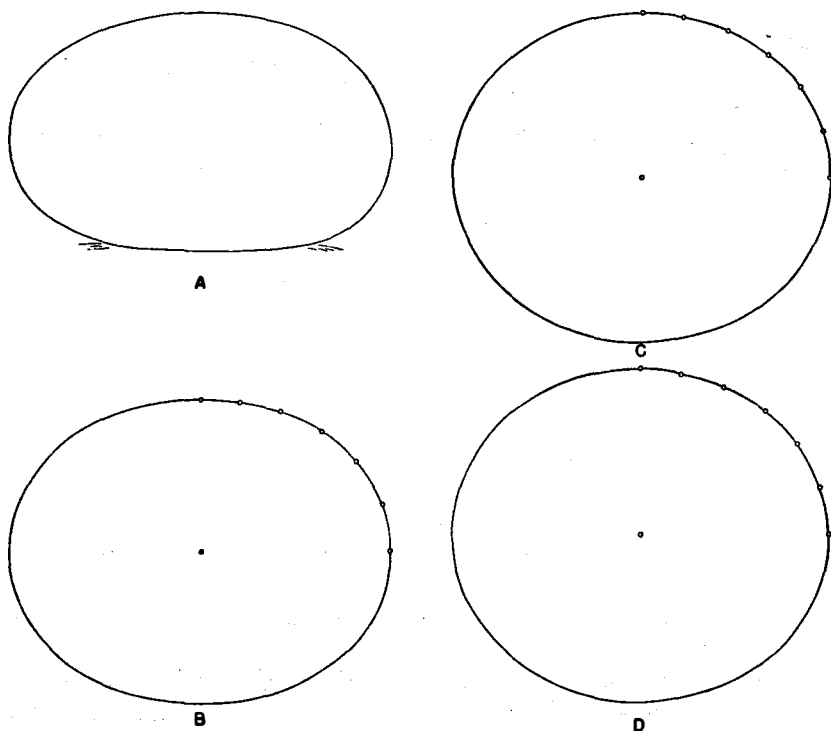


FIGURE 13. NON-SPHERICAL EGGS OF THE FAMILY BLENNIIDAE.

A. *Blennius pholis* as attached to a shell according to Hefford (1910). B. *Blennius inaequalis*. C. *Blennius palmicornis*. D. *Blennius pavo*.

McIntosh (1906) and LeBour (1927) apparently indicate that these eggs are primarily spherical and that such distortions are mechanical. Rao and Hora (1938) figure very irregular eggs for *Andamia heteroptera* (Bleeker). From their illustration one gathers that they approximate ellipsoids, but whether they have flattened out like Hefford's eggs of *B. pholis* is not clear.

Species with spherical eggs have been mentioned or figured by the

following students: *Salarias flavo-umbrinus* Ruppel and *S. andersonii* Day by Eggert (1929); *Blennius ocellaris* Linnaeus by Pieron (1914); evidently Guitel (1893 a and b) intended to indicate basically circular eggs for *B. montagui* Pietschmann = *B. galerita* Linnaeus and *B. sphynx* Cuvier and Valenciennes; *Chasmodes bosquianus* (Lacépède) by Hildebrand and Schroeder (1928) and Hildebrand and Cable (1938); *Hypsoblennius hentz* (LeSueur) and *Hypleurochilus geminatus* (Wood) by Hildebrand and Cable (1938); and *Cebidichthys violaceus* (Girard) by Schultz and DeLacy (1932).

Regarding the egg of *Blennius ocellaris*, Peiron (1914) gives 75 mm. as the diameter, but LeBour (1927) gives 1.12, which is listed in

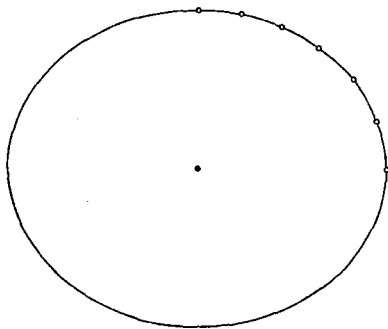


FIGURE 14. NON-SPHERICAL EGG OF THE FAMILY CARAPIDAE, *Carapus* sp.

Table II, suggesting either a very large variation in size or some confusion in identity.

The pholids apparently all have spherical eggs as discussed by the following students: *Pholis gunnellus* (Linnaeus) by Ehrenbaum (1904), Gudger (1927) and many others, *Anoplarchus purpurescens* Gill by Schultz and DeLacy (1932), and *Xerepes fucorum* (Jordan and Gilbert) by Metz (1912).

The related clinids all appear to produce spherical eggs. See Breder (1929 and 1941), for *Paraclinus marmoratus* (Steindachner) and Barnhart (1932) for *Heterostichus rostratus* Girard. On the families, Lumpenidae, Stichaeidae, and Cryptacanthodidae there is apparently no accurate data. The Anarhichadidae and Zoarcidae, when the latter are not ovoviviparous, produce large spherical eggs.

FAMILY CARAPIDAE—Pelagic eggs are produced by this group and so far as known all are broadly elliptical. Figure 14 shows an out-

line of *Carapus* sp. taken from Sumner (1903). Table II gives measurements of other forms drawn from the following sources: *Carapus dentatus* (Cuvier), from Sparta (1926), *Carapus acus* (Brunnich), from Raffaele (1888) and Holt (1899). Emery (1880), however, describes the egg of the latter species as spherical.

The reproductive conditions in the remaining families of the order Blennioidei follow: Ophidiidae produce spherical eggs, see Sparta (1929); Brotulidae are ovoviviparous so far as known. No correlation with habits is known.

In addition to these identified non-spherical eggs an elongate type of pelagic ovum has been figured by Breder (1929) and Delsman (1929). These eggs are evidently very similar and undoubtedly closely related, one from the western Atlantic and the other from the western Pacific. Their identity and relationships are not clear at this writing. The outlines of both are given in Figure 15.

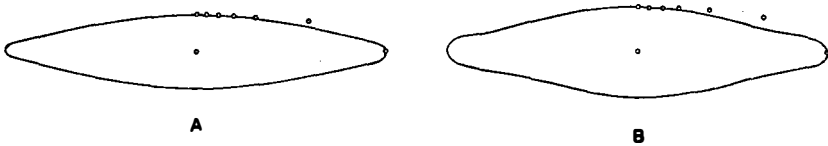


FIGURE 15. NON-SPHERICAL PELAGIC TELEOST EGGS OF UNKNOWN IDENTITY.  
A. From Florida after Breder (1929). B. From Batavia after Delsman (1929).

### GEOMETRICAL CONSIDERATIONS

As it is evident from the foregoing that most teleost eggs closely approximate a true sphere and that the majority of those which do not, approximate a prolate ellipsoid, an examination of the geometry of these two figures may be used as a basis for general analytical purposes. Any rectilinear projection of a sphere produces a circle of equal diameter since the radii are all equal. Similar projections of a prolate ellipsoid vary between a circle equal in diameter to the short axis and an ellipse with axes identical to that of the originating ellipsoid. The axial relationships are, of course, reversed in the case of an oblate ellipsoid. Consequently the text figures representing various eggs as projections on a plane parallel to both the minor and major axes show all necessary geometrical data.

A true ellipse (or a circle which can be considered a special case of the ellipse in which the axes are equal) is expressible by the Cartesian formula,



$$\frac{X^2}{M^2} + \frac{Y^2}{m^2} = 1$$

in which  $M = \frac{1}{2}$  the major axis and  $m = \frac{1}{2}$  the minor axis. For purposes of plotting on coordinate paper this is reducible to the following expressions:

$$Y = \frac{m}{M} \sqrt{M^2 - X^2}$$

$$X = \frac{M}{m} \sqrt{m^2 - Y^2}$$

It was by these calculations that the points shown on the curves in Figures 1 to 15 were located; they were checked by the graphic trammel method of drawing an ellipse. By considering only the proportions, in which the major axis may be expressed as unity, it is possible to still further simplify the formulae as follows,

$$Y = m \sqrt{1 - X^2}$$

$$X = \frac{1}{m} \sqrt{m^2 - Y^2}$$

From outlines reduced to a common size it is thus easy to determine just how far these depart from a true ellipse or circle. The outlines which subscribe to these formulae are all conic sections and the solids which they represent may be considered as figures of generation based on these plane figures. In all except the circle two figures of rotation are possible, depending on whether the major or minor axis is used as the axis of rotation. In the case of the former a prolate ellipsoid results and in the latter an oblate ellipsoid. In all the elliptical teleost eggs known, except possibly the two shown in Figure 12 B and 13 A, prolate ellipsoids are represented. Even these seeming exceptions may be artifacts as discussed in the text under the headings Family Gobiesocidae and Family Blenniidae.

The points represented by small circles in most of the text figures of teleost eggs indicate an ellipse with axes equal to those of the egg figured. In each case these points are  $15^\circ$  apart and are carried through  $90^\circ$  in most cases. In all the common center of egg and ellipse is indicated by another small circle. This gives a measure of the departure of the egg outline from a true ellipse when such is present. In

some of the more complicated figures the points have been carried through two quadrants and in some, two or more centers are indicated where such are required. These are explained where discussed. The figures themselves are based on the data given in Table II. Only obvious distortions have been corrected, or mean values used where considerable variations appeared.

The eggs which do not subscribe to the above cannot be represented as figures of generation based on conic sections. All may be considered as based on ellipses that have been distorted in various ways, the resultant solid being produced as is a prolate ellipsoid.

Since formulae for these would require the introduction of one or more additional terms, it is possible, by mathematical transformations, to arrive at formulae that would express each one of these divergent egg forms. These additional terms may be thought of as expressing distortions of the basic formula given. That, as mathematical expressions, they would be more or less remote from the simple ellipse and circle formula is evident, and in some cases, such as the extreme *Bathygobius* egg, would be extremely complicated and difficult of calculation. Indeed it should be possible to devise a lineal series of formulae showing a similar transition to that which may be arranged by placing the egg outlines in appropriate series. Since at this stage of the study it would certainly yield no further analysis, but would merely translate these facts into mathematical language, this has not been undertaken. This in no way denies the fact that the simply expressible formula of most teleost eggs, as here given, sets those that do not subscribe to it clearly apart from, but related to, the general condition.

Another way to examine these items is to distort the coordinates after the manner of the device used by Thompson (1942). These constructions are not figured, for they are sufficiently evident on simple description. If a circle is used as a starting outline, drawn on squared paper, a transformation by this method to an ellipse introduces no curving of the ordinates. Those cutting the minor axis at right angles are merely compressed together while those along the major axis are unchanged. This is also true of the oblong eggs not following the exact outline of an ellipse, differing from it only in the spacing of these compressed ordinates. All other forms may be treated in two manners. They may retain the original rectilinear quality of the ordinates crossing the major axis, but in each case those

crossing the minor become transformed into curves of various orders, or both sets of ordinates may be changed as to spacing while remaining straight lines. In the pyriform eggs this has largely to do with the fact that their sections are not symmetrical with respect to the minor axis, but remain so with respect to the major. In the case of the egg of *Bathygobius* this line becomes more than a simple smooth curve and wanders around because of the reëntrant curving at the "neck" of this egg. Such ordinates, referred to the distinctly asymmetrical eggs, all become distorted in a similar fashion. The distortion of ordinates in this situation shows nothing that cannot be inferred from the variations displayed by the eggs themselves. Obviously curvature of ordinates enters at the same place as does the introduction of additional terms in algebraic treatment and with equivalent significance.

A different approach is that of Malloch (1925) who compared the shells of birds' eggs. He erected verticals at right angles to tangents of the outline of the egg. These produced across the long axis are tangent to another curve—the evolute of the generating curve. These curves show greater differences among themselves than do the generating curves on which they are based. Like the method of Thompson (1942), their construction is sufficiently evident from the above description and they have not been reproduced. Like that method, for our present purposes, they do not seem to further elucidate the nature of the relationships of these curves, but show similar resemblances in a somewhat exaggerated form. It is of interest, however, that in this connection Malloch (1925) indicates that a capsule with walls of uniform thickness, that is with the outside diameter concentric with the inside diameter, becomes spherical when inflated; but if the walls are not of even thickness because the inner diameter is excentric to the outer, inflation produces an ovoid, much like various birds' eggs, depending on the degree of eccentricity.

It has been suggested by Hartridge (1920) and shown by Ponder (1925 a and b) that the equation for the equipotential curves of Cayley, which were developed to describe surfaces of equal potential in magnetic fields, can be used to approximate the outline of the typical bi-concave mammalian erythrocytes. This is based on the following formula for one magnetic pole,

$$\frac{m}{r} = V$$

where  $m$  = strength of pole,  $r$  = distance from pole and  $V$  = potential to which may be assigned various values. Such calculations obviously give points on a spherical surface [see Hadley (1906)].

The surfaces of equipotential value about two neighboring poles is based on the fact that the potential at any given point is equal to the algebraic sum of the potentials at that point. It is on this basis that Ponder (*loc. cit.*) arrived at his conclusions according to the following,

$$\frac{m_1}{r_1} + \frac{m_2}{r_2} = V$$

The general relationship of these equations to those concerning the ellipse is evident. As the values for  $V$  are decreased, the figure produced approaches a figure which is very nearly an equiaxial ellipse.

There is a geometrical difference in the equipotential surfaces of such magnetic fields and the surface of a mammalian erythrocyte, however, which makes the direct application of the formula to present purposes not suitable, and in fact questions its applicability to red blood cells. This becomes apparent when the solids involved are considered rather than the graphic representations of a section thereof. The erythrocyte may be thought of as a spheroid dimpled from either side, whereas the figure of the equipotential surface about two similar magnetic fields is the fusion of two spheres. Any plane passed through both poles of the latter gives a somewhat dumbbell-shaped outline, whereas in the former any plane passed through the short axis of the figure produces such an outline. Thus, the generations of the surface of the erythrocyte requires a rotation of the outline about its short axis, whereas the generation of the equipotential surface of the magnetic field requires a rotation about the long axis. Actually the plane figure cutting through the center of the erythrocyte form as shown by Ponder (*loc. cit.*) represents in its two fields, not two polar fields, but rather the section of the field of an annular band or circle, in which the distance between the two places cut represents the diameter of the annulus of influence. Thus the erythrocyte form may be considered an oblate figure of revolution based on an interpolar section of a figure of equipotential surface. It is therefore apparent that the two forms are geometrically different. Whether or not this permits of the interpretation given it by Ponder need not concern us here, but it is evident that the equation cannot be used in just that form to describe the non-spherical eggs under consideration, although all these forms and

their mathematical treatments are evidently closely connected and interrelated.

Since it is evident that the erythrocyte has an annular band of influence, in the mathematical sense at least, and is an oblate figure, it is also evident that a similar construction in the prolate eggs would call not for a bipolar or multipolar field, but instead for the field of a linear distribution of pole strength, which would be in the long axis of such figures. This is tantamount to saying that if a single pole gives a spherical surface about itself as a central point, then the drawing out of such into a line segment could produce an ellipse, capsule, or other figure if the polar density along it were varied appropriately. Such a condition would be approached in the previous treatment by increasing the number of poles infinitely and similarly reducing their distances. That the formula given could be extended to cover such a case is evident; but it is of no significance at this time to carry out the calculations. Assuming the infinitely close and numerous poles to be ranged along a curve instead of a straight line, the tendency for the longer, narrower eggs to distort slightly could also be taken into account.

Whatever mechanical significance one wishes to attach to the forms taken by these eggs, it is apparent that most of them subscribe to very simple geometrical configurations. Even in those that have departed furthest from the most simple types, there are still evidences of such a tendency exhibited in the details of parts of these eggs. Reference to the figures will show that in the pyriform type the large end is generally in the form of an ellipse whose minor axis is equal to the widest part of the egg or in a semicircle centered the same way. Note also the spherical tip in *Bathygobius*. In the text figures of these atypical eggs, the small circles, marking portions of true ellipses, clearly indicate the tendency toward the recurrence of this type of geometrical regularity.

#### PHYSIOLOGICAL CONSIDERATIONS

Since the zona radiata of a teleost egg is a semi-permeable membrane and is ordinarily exposed to the water of the parents' habitat in all cases here under consideration, it follows that the nature of the physiological needs of the contained developing embryo must be satisfied by its osmotic characteristics. Unfortunately the data bearing on the passage of gases and fluids through this membrane is not sufficiently

detailed to enable one to employ it for any closely reasoned argument. Krogh (1939) gives a good summary of the present data on the subject.

Before the embryo develops a functional kidney and other means of regulating the nature of the internal milieu, the contained materials are exposed to whatever environment the permeability of the membrane permits, modified only by the nature of the cellular activity of the early stages. Since teleost eggs are exceedingly delicate and generally do not survive any puncturing of the membrane, it may be inferred that the zona radiata provides a very important protection to the embryo.

Most teleost eggs are spherical, and it may be thought that they assume this shape on a purely physical basis, as a droplet, or that there is a physiological demand tending to produce a maximum of substance with a minimum of surface. However, in view of the fact that there are eggs which depart from the spherical form, it follows that the tendency is neither a fully mechanical nor a physiological obligate.

As it has been shown in the preceding section that these egg forms approximate the formula that applies to certain types of magnetic fields, it would appear that they are following some physical regularity for either mechanical or physiological reasons. That a related formula approximates that of erythrocytes, which are oblate figures and are physiologically active in the sense that they carry on a rapid exchange of gases, also suggests this regularity. The eggs under consideration are prolate figures and may have the tendency to retard diffusing processes. The study that this suggests is outside the province of the present contribution and requires the accumulation of much more data on the physiological activity of teleost eggs than is at present available, especially on those of non-spherical outline.

Much of the data on the permeability of fish eggs is inconclusive or contradictory. Very probably part of the difficulty is in the nature of the material, involving as it does wide variations in the osmotic qualities of the membranes of various types of fish eggs. On the basis of the large differences in other features of fish physiology, behavior, and morphology, similar differences are to be expected in such a structure as the chorion of the eggs. For example Loeb and Wasteneys (1915) concluded that the eggs of *Fundulus* were impermeable to salts and almost so to water, while Manery, Warbritton and Irving (1933) noted an increase of over 80 per cent in water content during the period

of incubation. Since all known teleost eggs "water harden," that is are shed in a fairly flaccid state and become hard and turgid in a short time, it is difficult to imagine that any do not admit water osmotically. This is true of both fresh water and marine species. The permeability of the vitelline membrane is another matter, a discussion of which need not be undertaken here. Suffice it to say that the eggs of *Salmo*

TABLE III  
COMPARISON OF NON-SPHERICAL EGGS

<i>Group</i>	<i>Type of egg</i>	<i>Environment</i>	<i>Parental Care</i>	<i>Species with Spherical Eggs</i>
ORDER ISOSPONDYLI				
Suborder Clupeoidea				
Family Engraulidae	Pelagic, non-adhesive	Marine	None	Present
ORDER OSTARIOPHYSI				
Suborder Eventognathi				
Family Cyprinidae	Demersal, non-adhesive	Fresh water	Deposited in gill-chamber of mussel	Present
ORDER PERCOIDEI				
Family Cichlidae	Demersal, adhesive or non-adhesive	Fresh water	Guarded by parents or orally incubated	Present (?)
Family Pomacentridae	Demersal, attached at one end	Marine	Guarded by parents	Absent
ORDER SCORPAENOIDEI				
Family Scorpaenidae	Pelagic, non-adhesive or viviparous	Marine	None	Absent
Family Dactylopteridae	Pelagic, non-adhesive	Marine	None	Absent
ORDER GOBIOIDEI				
Family Gobiidae	Demersal, attached at one end	Marine, brackish and fresh water	Guarded by male or sometimes both parents	Present
ORDER AMMODYTOIDEI				
Family Ammodytidae	Demersal, adhesive	Marine	Probably none	Absent
ORDER XENOPTERYGII				
Family Gobiesocidae	Demersal, adhesive	Marine	Guarded by both parents	Absent
ORDER BLENNIOIDEI				
Family Blenniidae	Demersal, adhesive or attached at one end	Marine	Guarded by male	Present
Family Carapidae	Pelagic, non-adhesive	Marine	None	Absent

apparently change in this respect during development (see Krogh (1939), who also gives an extended bibliography of the subject).

The erythrocyte is about the only other metazoan cell type that is normally freely supported in a fluid medium, is not pressed upon by adjacent neighbors as in tissues, and is not modified by cilia, pseudopodia or other structures as in the protozoa. In a physiological sense pelagic fish eggs and erythrocytes have their existence in not dissimilar environments. The basic chemical similarity between sea water and blood has often been noted, see for example Macallum (1926), Beutner (1938), and Breder (1942 b). Plasma is considerably more dilute than the water of the open ocean, but any gradation down to fresh water may be found, and, as has been indicated, non-spherical eggs appear in a wide variety of environments. If there is a close correlation between the chemical environment and form it is not evident from the data indicated in Table III. Considering these items, as well as the fact that plasma contains far more dissolved protein than sea water, it is suggested that pelagic fish eggs, both spherical and non-spherical, be examined from the standpoint of the blood physiologist. As a practical matter such fish eggs are large enough to permit techniques of study that are prohibited by the much smaller erythrocytes.

### DISCUSSION

It has been shown that a variety of fishes produce other than spherical eggs, and some of the characteristics of these eggs have been discussed; therefore, an attempt to interpret the significance of these features may now be undertaken. The non-spherical eggs are arranged by groups in Table III, with reference to the type of egg involved, the environment, and the details of their developmental care. From this table it is at once evident that both free pelagic eggs and demersal adherent eggs are found in the sea, while only demersal, adhesive and non-adhesive are found in fresh water. This could have been anticipated for there are exceedingly few fresh water pelagic eggs. There are many fewer groups showing non-spherical eggs in fresh water than in the sea. Fishes which guard their eggs, and those which do not, are represented in about equal numbers. The number of groups containing other members which produce spherical eggs and the number among which such a habit is unknown is about equal. It is evident from this that there is no very marked tendency for these departures from spherical eggs to be closely associated with environment, or





FIGURE 16. Phylogenetic tree of teleosts, showing occurrence of species producing non-spherical eggs and indicating their distribution in the group. Based on the phylogeny of Dr. W. K. Gregory as used at the American Museum of Natural History, with some modifications pertinent to the present purposes. See text for full explanation.

parental care. Obviously the data is insufficient to treat the matter in a quantitative sense.

If these groups are spotted on a phylogenetic tree of teleosts certain features appear that are suggestive. Except for the Engraulidae and the Cyprinidae all find their places in one general area of the Acanthopterygian branches. The development of non-spherical eggs by the Engraulidae, which is close to the spherical-egg-producing Clupeidae, is clearly an independent specialization common to most of the known species of the family. The lone member of the Cyprinidae is likewise a special case within that group and is associated with a unique type of breeding habit.

All the remainder are Acanthopterygians on three closely related main lines. The usage on Dr. Gregory's chart, Figure 16, is somewhat different from the text usage, but this in no way invalidates the relative placement of the fishes involved. While all through these groups there are fishes which produce the conventional spherical eggs, it seems that this major association of fish groups is 'charged' with a potentiality to produce non-spherical eggs, which are in no way related to the two non-acanthopterygian developments of this sort. Looked at this way, there are evidently three completely independent origins of the development of non-spherical eggs. In the Acanthopterygians there may have been several such independent developments, or the presence of non-spherical eggs could conceivably indicate the retention of a primitive condition within that group. If such were assumed it might even be possible to tie in the non-Acanthopterygians as well, but such a view would be difficult to support because of the widespread distribution of spherical eggs.

It is thus clear that while there are evidently some fairly definite phylogenetic tendencies, the distribution of these fishes which produce other than spherical eggs, with respect to phylogeny, environments, and breeding habits, is well scattered and that no very clear evolutionary significance is apparent. If, however, a purely physico-chemical approach is made, certain features appear which warrant discussion.

As in most, if not all, cases of specialization involving a departure from a common structure or activity, the question is raised as to what biological value the new element might have. When the particular use to which a given structure is suited becomes evident, such developments are customarily referred to as an 'adaptation.' When such a

use is not evident it usually passes as a 'specialization.' In the situation under discussion there is no obvious value to the form of the egg in a clear mechanical sense. Most fishes get on very well by having their embryos jammed into a spherical membrane that certainly has no structural reference to the shape of the developing creature; this is generally true of oviparous and ovoviviparous animals. Obviously a basic requirement is that there be room enough for the developmental activity to go on adequately, but it would appear that the *shape* of the space is of very minor importance. The only instance which has been found even remotely comparable to that of *Bathygobius* is that of the shells of Chimaeroids. Dean (1904 and 1912) has discussed this at length, and he refers to it as 'determinative evolution.' Be that as it may, all other oviparous elasmobranchs produce eggs whose shape has no more reference to that of the developing embryo than do those of most other animals. This is in keeping with the oft-noted condition that forms showing 'adaptations' or 'specializations' are living side by side with others lacking these features, and that the latter are commonly the most abundant.

In the present case it may be that the non-spherical teleost eggs are so shaped in response to differences in the osmotic and other qualities of those eggs as compared with the spherical ones. This would give adequate reason for the form of all, thus changing the emphasis of the problem to finding the reason why fish produce different types of zona radiata. It would refer the entire matter to the structure of the membrane. Since the form of the membrane is evident in the flaccid ovarian eggs, which only take on their full form when they have been extruded and become turgid, such would seem to be a reasonable hypothesis. However, in *Bathygobius* the peculiar fit of the egg membrane to the embryo just before it is ready to hatch is still without any satisfactory interpretation. If it can be shown that the reëntrant curve forming the 'neck' of the egg is a necessary concomitant to the nature of the chorion, which on the face of it would seem not unlikely, the rest would have to follow on a simple mechanical basis, the embryo, as it grows, simply fitting itself into the available space, as indeed all embryos do as soon as they become motile. This would refer the locking of the head into the 'knob' end as a simple mechanical result of the demands of the egg membrane, and would leave it without direct biological value to the embryo in reference to form.

This view leaves one with the question as to whether many of the so-called 'adaptative' structures may not be of a similar nature. Such a discussion is without the province of this paper, but it may be noted in passing, that if the above question could be answered in the affirmative, it would leave many of the specialized divergencies so common to living forms, that are hard to explain by conventional methods, with a pure physico-chemical basis. At the same time, these divergencies would be without any particular evolutionary significance except as by chances of circumstance and environment they opened up a new environmental niche or some other similar feature. However, it would be hard to imagine such a feature involved in the case of the various shapes of goby or anchovy eggs, since none have moved into obviously different environments or placed their eggs in special places, although in the Cyprinidae *Rhodeus* is an exception to this generalization.

In any event the entire problem calls for a study of the nature of the egg-envelope in physico-chemical terms and with reference to the details of its ovarian development; it also calls for a consideration of such eggs from the approaches used for the study of erythrocytes. The latter should be helpful to students in both fields.

### SUMMARY

1. *Bathygobius soporator* deposits its eggs in shallow water and attaches them to the under-side of shells, where they receive protective care from the male parent.

2. The eggs are elongate, somewhat cigar-shaped, with a rounded bulbous end distally and average about 2.36 mm. in length. The basal end is roundly pointed and attached to the support by a mass of adhesive threads.

3. As development of the embryo takes place the head grows into the bulbous end, fitting it snugly and in such a fashion as to hold the larva immobilized except for the tail's tip. Just before hatching the embryo fills the entire shell which is in effect a slightly simplified outline of the contained larva.

4. Teleosts producing non-spherical eggs have been found in the following orders: Isospondyli, Ostariophysii, Percoidae, Scorpaenoidei, Gobioidae, Ammodytoidei, Xenopterygii and Blennioidei. The gobies produce the most numerous and widest departures from the typical

spherical eggs, although no others go as far in this respect as does *Bathygobius*.

5. Considered from a geometrical standpoint a special form of the equation used to describe equipotential surfaces in magnetic fields could be employed to most closely approximate the outlines of such fish eggs.

6. Physiological considerations suggest that the form of the egg is based on the detailed structure of the membrane as developed in the ovary rather than on simple chemico-physical effects at the time of laying.

7. Environment, habits and relationships indicate no clear reasons for the development of non-spherical eggs in teleosts.

8. Erythrocytes resemble marine pelagic teleost eggs in their passivity and in the nature of the fluids which bathe them. It is suggested that the two types of metazoan cells be examined with mutual reference to one another in connection with the dynamics of their osmotic features.

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*Breder: Eggs of Bathygobius soporator*

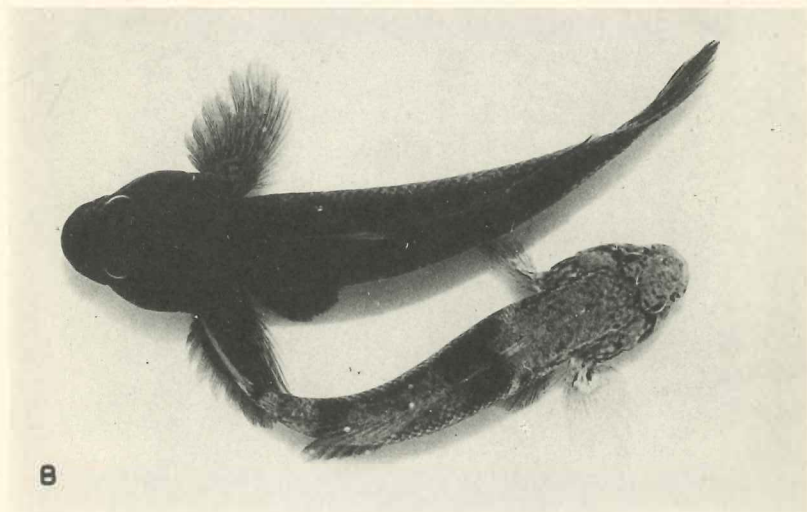
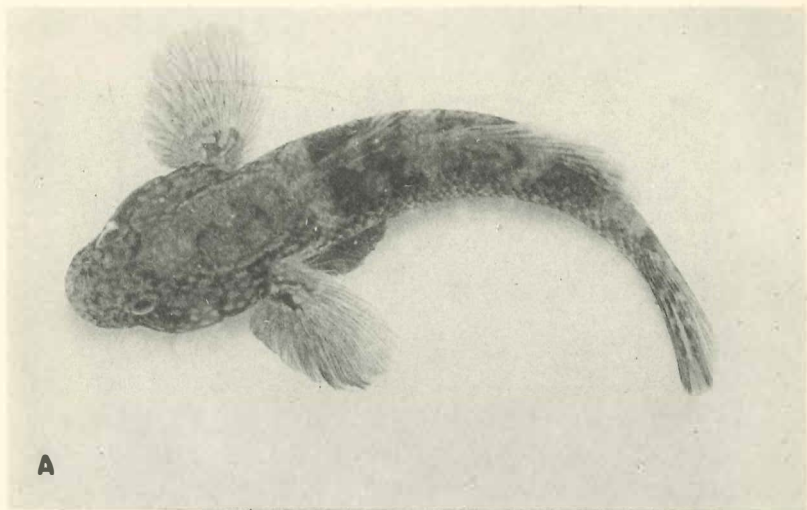


PLATE I. A. The male shown in Plate II removed to a white background. Actual standard length of fish 65 mm. B. Two females removed to a white background, showing two extreme pattern phases. Actual standard lengths of fish 73 and 55 mm.

Breder: Eggs of *Bathygobius soporator*



PLATE II. Male *Bathygobius soporator* guarding nest. The fish and nest are circled. The fish is pointing to about "11 o'clock." Its striking color and pattern phase is clearly indicated, although, for resemblance to the general color scheme of the background makes it appear obscure. The tail of the fish is still in the nest cavity which is under the large clam shell covered with barnacles.

Breder: Eggs of *Bathygobius soporator*



PLATE III. A. The nesting site at extreme low water. The entire population of *Bathygobius* consisted of the three individuals shown in Plate I. The nest occupied about the center of the pile. B. The nesting shell inverted. The light area on the clam shell and part of an oyster shell is occupied by the eggs which at this reduction present a yellowish fur-like appearance.

*Breder: Eggs of Bathygobius soporator*

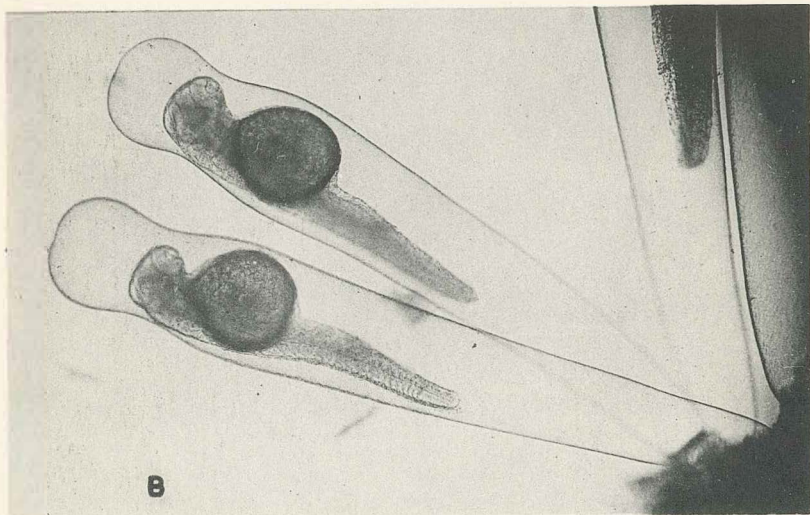
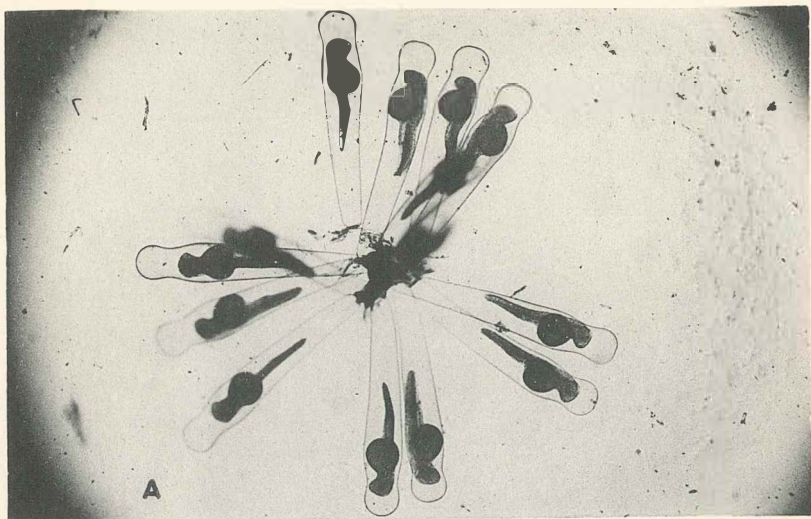


PLATE IV. A. The eggs as taken from the nest and here seen spread out in a bowl. The eggs average 2.36 mm. in length. B. Two eggs in the same stage of development as those shown above in A, but at a higher magnification.



Breder: Eggs of *Bathygobius soporator*

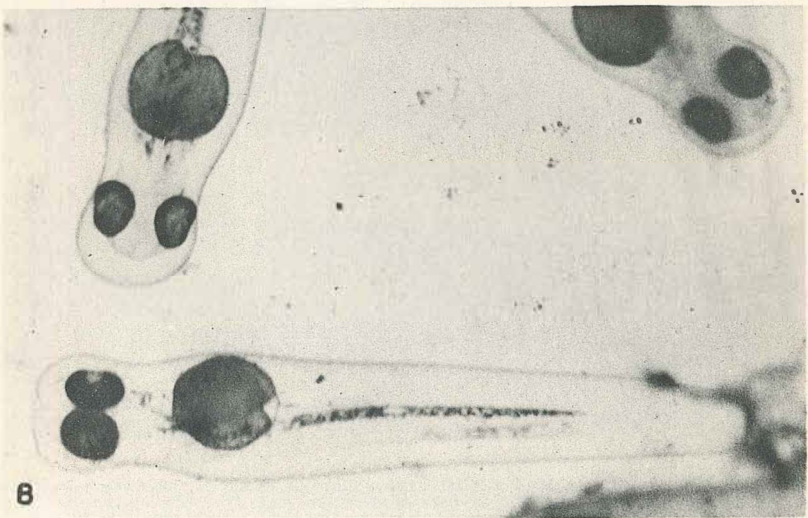
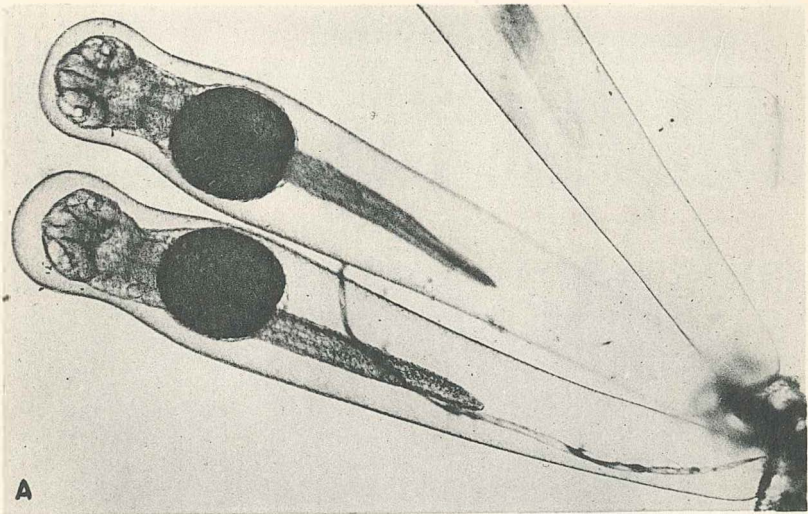


PLATE V. A. The eggs 23 hours after those shown in Plate IV. B. The eggs 37 hours after those shown in Plate IV.

*Breder: Eggs of Bathygobius soporator*

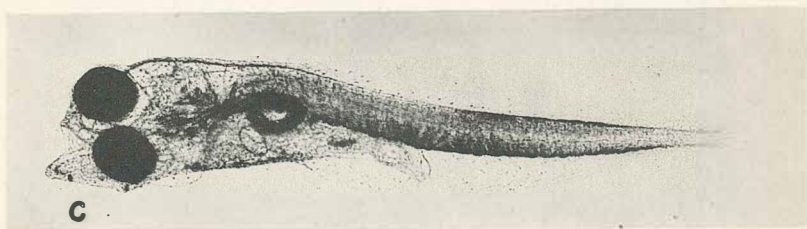
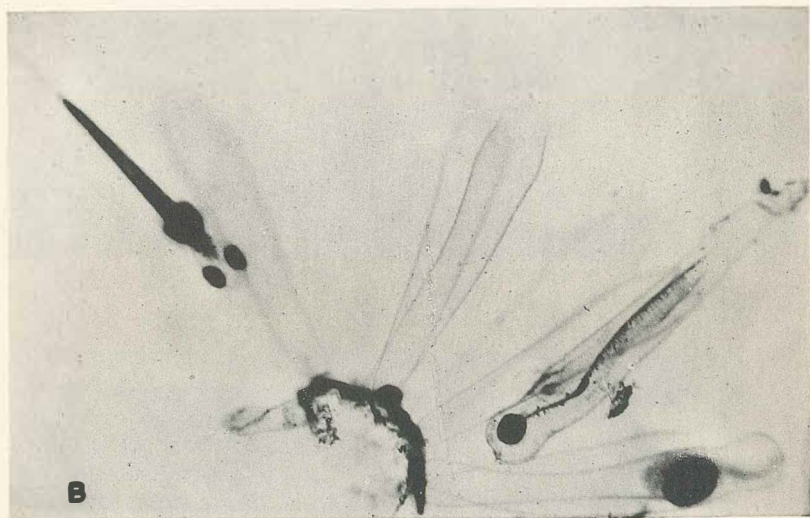
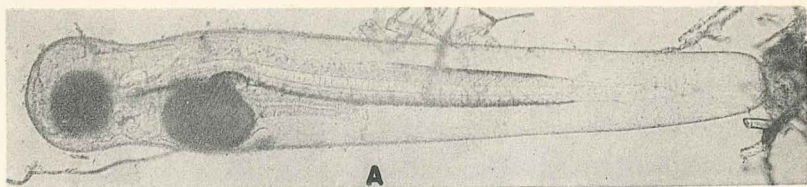


PLATE VI. A. An egg 59½ hours after those shown in Plate IV, just before hatching. B. The eggs at hatching, 71½ hours after those shown in Plate IV. The empty shells may be seen centrally, one egg just breaking at the tip to the right, a dead egg with the embryo inverted in the lower right corner, and a newly hatched fish at the left. C. A larval fish 48 hours after hatching.