A CONTRIBUTION TO THE VISCERAL ANATOMY, DEVELOPMENT, AND RELATIONSHIPS OF THE PLECTOGNATHI

C. M. BREDER, JR., AND EUGENIE CLARK

A CONTRIBUTION TO THE VISCERAL ANATOMY, DEVELOPMENT,
AND RELATIONSHIPS OF THE PLECTOGNATHI

A CONTRIBUTION TO THE VISCERAL ANATOMY, DEVELOPMENT, AND RELATIONSHIPS OF THE PLECTOGNATHI

C. M. BREDER, JR.
The American Museum of Natural History

EUGENIE CLARK
New York University

CONTENTS

INTRODUCTION

ALTHOUGH THERE IS a considerable literature on the anatomy, development, and relationships of the Plectognathi, the group still is far from being satisfactorily understood. The present contribution is an attempt to cast further light on several aspects of the group and is a combination of studies made by the two authors both separately and working together. It is in a large measure based on laboratory study of materials in the collection of the American Museum of Natural History and materials collected at the laboratory of the New York Aquarium on the west coast of Florida incidental to other work at that place.

In addition to this we had the great privilege of examining two specimens of the rare *Triodon bursarius* Cuvier from the collections of Stanford University. This was arranged through the kindness of Dr. Albert Herre, who in addition gave us permission to do a limited amount of dissection on one of these. The examination of the visceral anatomy of this species was of great value to our studies, and we take this opportunity to express our grateful appreciation to Dr. Herre and the Stanford Natural History Museum. Dr. W. K. Gregory kindly read the manuscript and rendered a number of useful criticisms.

THE DIGESTIVE TRACT of some of the plecto-gnath fishes presents what is probably the most remarkable modification to be found in the digestive tract of any animal. It is within this group that there is developed an elabo-rate mechanism for inflating the stomach to an enormous size, from which the "puffers" derive their popular name. The puffers repre-sent the group of fishes belonging to the fami-lies Diodontidae and Tetraodontidae, all the species of which exhibit the ability to inflate themselves to a noticeable extent. Also in other families of the Plectognathi there exists another mechanism for enlarging the body and distorting the fish's outline, that of ex-panding a ventral flap supported by a large, movable pelvic bone. This mechanism is char-acteristic of the families Balistidae and Monacanthidae, and reaches the zenith of development in the Triodontidae.

The fact that both of these phenomena ex-teriorly affect the belly region of the fish has given rise to a confused idea of some interrela-tionships. Early investigators (e.g., Jordan and Snyder, 1901; Goodrich, 1909; Herre, 1925) concluded that the huge, expansible skin flap of *Triodon* indicated powers of infla-tion. However, from the dissections described in this paper it can be concluded that infla-tion is not possible in this fish.

These two mechanisms appear to be inde-pendent of each other, the origin and devel-opment of each showing no evident interrela-tion. However, those fishes which exhibit the most advanced development of one mecha-nism show an absence of the other. The tetrao-donts, which have the most fully developed mechanism of inflation, show no evidence of a movable pelvic bone such as possessed by the Triodontidae and Balistidae, whereas *Trio-don*, which has the largest skin flap and most highly erectile pelvic bone of any, has a nor-mal stomach without the slightest signs of a power to inflate. Both mechanisms effect spe-cialized but different changes in the muscula-ture of the fish and the skin of the belly re-gion. They differ basically in that the inflating mechanism is essentially a modifica-tion of the digestive tract, while the pelvic bone mechanism is fundamentally a skeletal specialization.

It is interesting to note that within the Plectognathi, where there exist the change-able outlines of the puffer and trigger fishes, there are also the box fishes of the family Ostraciidae which are almost completely enclosed in a rigid carapace composed of heavy coalesced scales.

Another family group, the deep sea tria-canthids, externally shows its resemblance to the balistids and to *Triodon*, but the mam-moth, tailless molids superficially appear so vastly different from the rest of the plecto-gnaths that, aside from the fused teeth, an external examination of the Molidae shows little evident relationship to the order.

These externally multivarious types of fishes nevertheless have basic taxonomic characteristics in common which unify them into a neat and compact order.

THE DIGESTIVE TRACT OF THE GENERALIZED TELEOST

The digestive tract is poorly differentiated as to gross morphology in many teleost fishes, in some cases being an almost straight tube of nearly even diameter and texture throughout, as, for example, in the Synentognathi. It is often impossible to distinguish clearly be-tween the various regions of the digestive tract even after making microscopic exami-nations of sections. In a well-differentiated teleost gut, however, the following regions are generally distinguishable and for present pur-poses may be defined as follows:

ORAL CAVITY: The entire mouth; extending from the lips to the pharynx

PHARYNX: The gill region, perforated on each side by gill clefts, provided with a sphincter of con-siderable size, sometimes having pharyngeal teeth; extending from the oral cavity to the oesophagus

OESOPHAGUS: A short tube of striated muscles lined with squamous epithelium, possessing an oesophageal sphincter which separates it from the stomach; extending from the pharynx to the stomach

STOMACH: The region composed mostly of smooth

muscle, lined with columnar epithelium and gastric glands, frequently wider than the oesophagus; it ends in a large sphincter, the pylorus, the base of which is often provided with pyloric caeca; extending from the oesophagus to the intestine

INTESTINE: The largest portion of the gut. The lining is often of a more irregular pattern than the mostly longitudinal folds of the stomach, though in some cases there appears to be no discernible difference. In the absence of a distinct pylorus the entrance of the hepatic duct is sometimes the only indication of the beginning of the intestine. The duct is usually easily found a short distance after the pylorus. This anterior section of the intestine, the duodenum, is often larger and slightly different in lining from the main part which continues, sometimes long and variably coiled, to the anus

THE DIGESTIVE TRACT OF THE PLECTOGNATHI

ACANTHURUS, A PRE-PLECTOGNATH

Phylogenetically, the acanthurids are considered the forerunners of the Plectognathi. As early as 1850 this basic relationship was recognized by Dareste, and the acanthurids were even placed in the same order with the Plectognathi by Goodrich (1909) and Gregory (1933), although in the recent classifications of Berg (1940) and Fraser-Brunner (1935–1943) they are excluded from the order. A comparison of the gut of *Acanthurus caeruleus* Bloch and Schneider was made with the plectognath gut in order to detect any possible early evidences of a forerunner of an inflating mechanism. It was found, however, to be distincti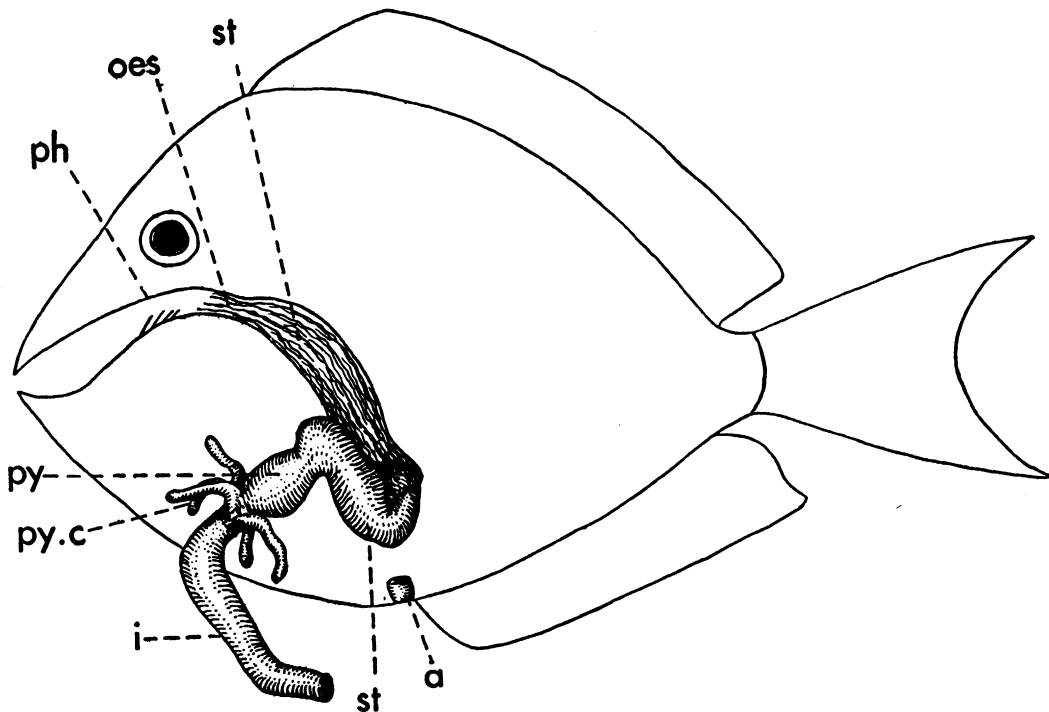vely different from even the most primitive plectognaths. *Acanthurus* has a rather long stomach, the lining of which is differentiated into two parts. The anterior part has deep longitudinal folds, and the posterior, a smoother, less folded lining. This is followed by a very large pylorus, the base of which is

FIG. 1. *Acanthurus caeruleus* Bloch and Schneider.

surrounded by prominent pyloric caeca (fig. 1). No pyloric caeca are found in any of the Plectognathi. The gut is of a fairly uniform width throughout and is about four times the standard length of the fish.

PLECTOGNATHI

Dissections were made on at least one species of each of the seven families excluding the Molidae. The visceral anatomy of the molids

has been adequately dissected and illustrated by Gregory and Raven (1934) and Raven (1939a, 1939b).

TRIACANTHIDAE

The alimentary tract of *Triacanthus biaculeatus* Bloch showed, in agreement with Thilo (1899), no evidences of an expansible portion. The gut is virtually the same width throughout, the duodenum being slightly larger than
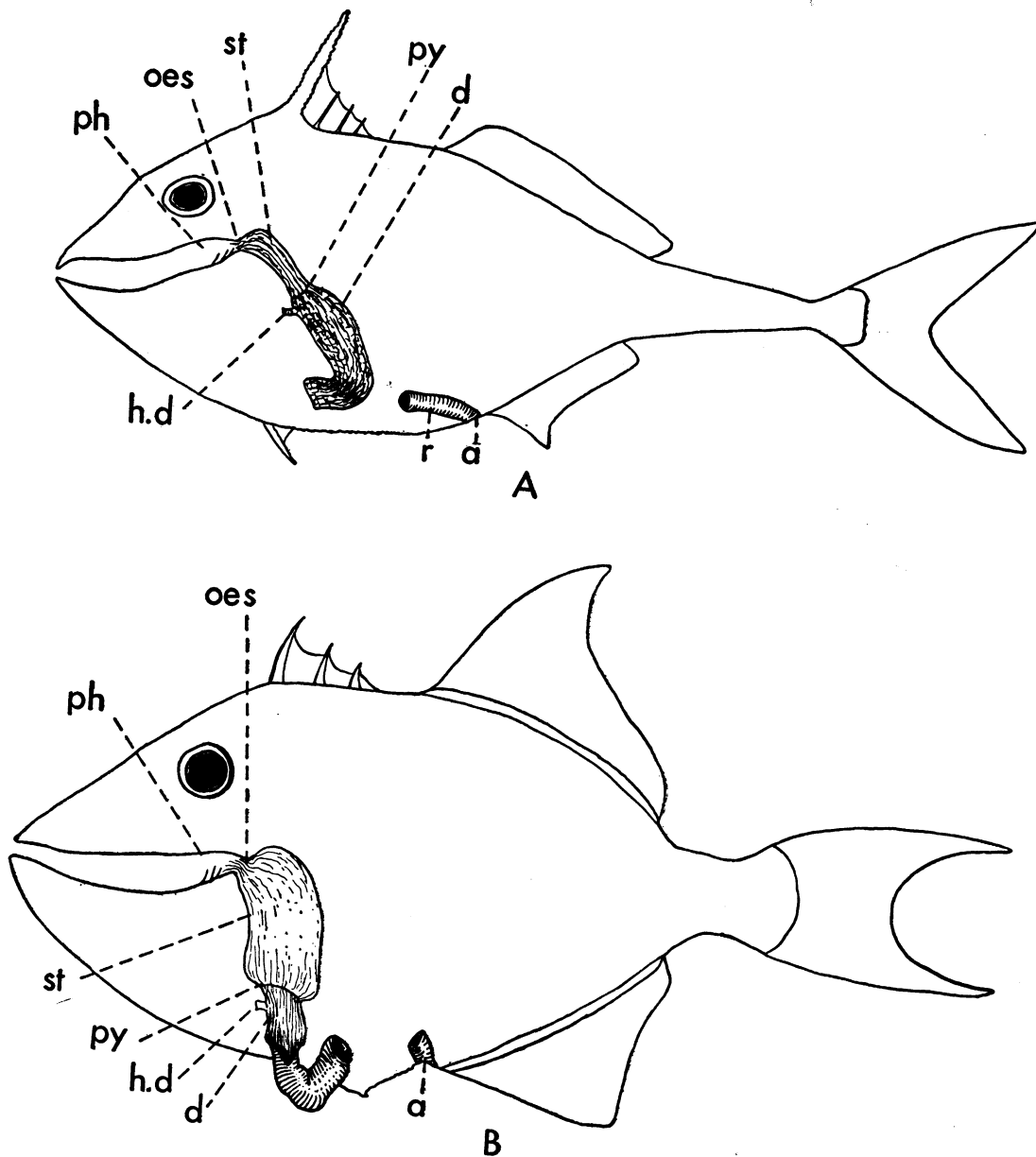

FIG. 2. A. *Triacanthus biaculeatus* Bloch. B. *Balistes carolinensis* Gmelin.

the other parts. The oesophagus is a short, muscular tube leading into the stomach, the walls of which are lined with longitudinal folds. The end of the stomach is marked by a slight pyloric constriction, after which the gut lining shows a slight change, the individual folds being less marked. The hepatic duct enters shortly after the weak sphincter and indi-cates the region of the duodenum, which is marked off posteriorly from the main part of the intestine by another slight constriction where the gut makes a turn anteriorly. These different regions, barely discernible by view-ing the external surface of the gut, are more clearly seen when the gut has been laid open longitudinally (fig. 2A).
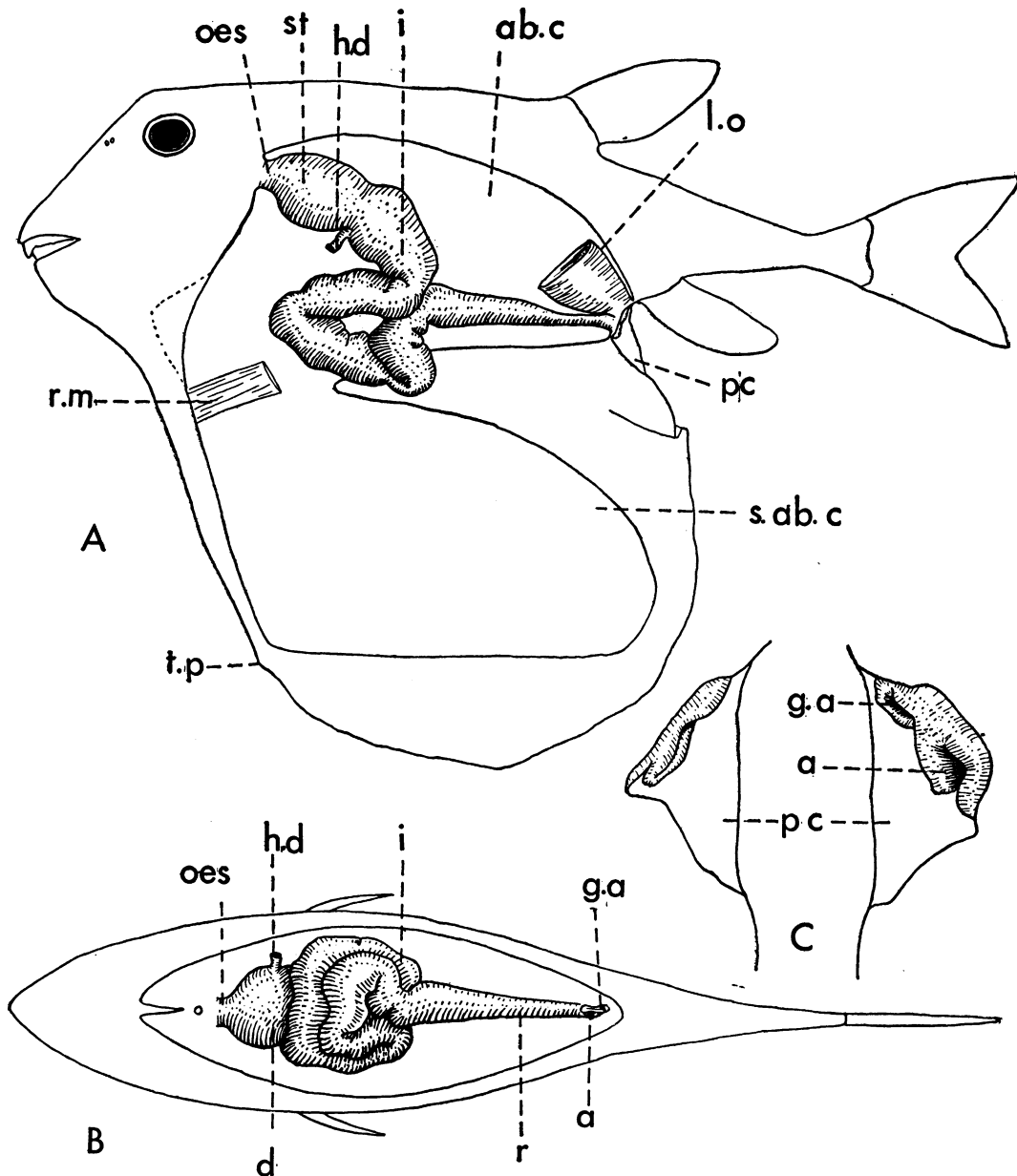

FIG. 3. *Triodon bursarius* Cuvier. A. Lateral view. B. Ventral view. C. Detail of "pseudocloaca"; view from left and right sides, respectively.

TRIODONTIDAE

Triodon bursarius Cuvier is the only species in this family. Although the literature contains various short descriptions of the large sac which gave *Triodon* its specific name (*bursarius*, purse like), the exact nature of its relationship to the gut has not been described. External drawings are found in the literature (Lesson, 1826, pl. 4; Cuvier, 1836, p. 340, pl. 112, figs. 1 and 1a; Bleeker, 1865, pl. 214, fig. 1) but none of the internal anatomy. Günther (1870) describes the condition as " . . . abdomen dilatable into a very large, compressed pendant sac, the lower part of which is merely a flap of skin, into which the air does not penetrate. The sac is kept expanded by the very long pelvic bone." Rosen (1912) suggests, although not having dissected any specimens, " . . . perhaps this form is provided with a dilated stomach as in *Monacanthus setifer* and *M. trossulus*, but it is not unlikely that the condition is the same as in *Monacanthus occidentalis* which has no air sac, but the ventral body-wall behind the pelvic bone is highly dilatable. This movable skin flap is quite solid, the body cavity not entering into it." Goodrich (1909) describes *Triodon* as having a dilatable oesophageal sac but, as is shown later, he probably did not base this statement on a dissection of the fish.

A dissection of one of the specimens secured through Dr. Herre showed that the lower part of the sac is solid, while the upper part contains a hollow ventral pocket of the abdominal cavity. This pocket is empty of any viscera but is lined with peritoneum and it is clearly a continuation of the peritoneal cavity (fig. 3). There is no trace of expansion in the oesophagus or the stomach, the entire gut being of nearly uniform width and thickness. Since the gut is a closed system running through the peritoneal cavity, the coelomic space in the ventral skin flap has no way of inflating by means of the digestive tract as in the case of the puffers. The nature of this skin sac and long pelvic bone is similar to, but shows a greater development than, that in the Balistidae or Monacanthidae. It is, as Rosen conjectured, much like the condition in *Monacanthus occidentalis* Günther [=*M. ciliatus* (Mitchill)] except that the body cavity extends into the flap, which is not the case in any of the balistids examined.

The posterior part of the intestine shows several interesting peculiarities that seem worth mentioning although not directly concerned with the problem on hand. There is a long, straight, muscular portion of the intestine just before the anus. Unlike the rectum of most fishes it does not appear able to hold any intestinal contents but is rather like a much elongated rectal sphincter. This, however, may be just an individual peculiarity or condition of the specimen studied. The anus is at one side of an odd muscular appendage which surrounds the aperture of the genital organs (fig. 3C). This appendage, which appears capable of swelling, may have some connection with reproductive behavior. The specimen examined was a female. Together with the anal opening the appendage is contained in a sizable vestibule which appears to be an invagination of the large skin flap. This vestibule may be called a "pseudo-cloaca" since it forms a common opening to the exterior for both the intestinal and genital tracts. It is certainly of secondary origin. A much slighter development of a similar sort has been found in species of *Balistes* and *Monacanthus* by Kaschkaroff (1914). Such a condition, developed at least to this extent, appears to be absent in all other orders of teleost fishes.

BALISTIDAE AND MONACANTHIDAE

In these two closely related groups two noticeable modifications are found. As in *Triodon*, most of the species have a skin flap which, although not so well developed, is expanded by a large pelvic bone. Several species show enlargements of the stomach region of the gut which Rosen (1912) thought indicated the beginnings of an inflatable sac.

The expansible skin flap should not be confused with the inflatable sac, which is a portion of the gut. In no case does the abdominal cavity enter the skin flap as it does in the Triodontidae. In all the species of the Balistidae examined, the laterally compressed skin flap is quite solid, some species with the most well-developed skin flaps showing no trace of an expansible gut region.

In order to study the possible origin of the air sac in this group dissections were made of *Monacanthus ciliatus* (Mitchill), *Stephanolepis hispidus* (Linnaeus), *Alutera schoepfii*

(Walbaum), *Balistes vetula* Linnaeus, and *B. carolinensis* Gmelin. All these species showed slight development in the stomach except in the case of *M. ciliatus* where an enlargement was found in the region of the duodenum. These widened parts were slightly more thin walled than the rest of the alimentary canal and puffed to a small degree when air was blown into the gut, which may have been, however, only a mechanical circumstance. Unfortunately these dissections did not reveal any good evidences for the beginnings of the dilatable sac such as Rosen believes is present in *M. setifer* Bennett and *M. trossulus* (Richardson). In no case is the slightly expansible part of the gut localized in the ventral wall of the stomach as is true in puffing fishes. Two species of the Monacanthidae are

shown in plate 11, indicating differences in the size of the expansible flap, and a dissection of the gut of *Balistes carolinensis* is shown in figure 2B.

OSTRACIIDAE

The gut of *Lactophrys tricornis* (Linnaeus) naturally shows no inflating powers. The short stomach, ending in a weak pylorus, is followed by a very long and coiled intestine nearly three times the standard body length of the fish. The duodenum is the widest part of the fairly uniform alimentary canal (fig. 4).

DIODONTIDAE

In this family the first well-developed inflatable sac is found. Since the digestive tracts of the two species studied, *Diodon hystrix*
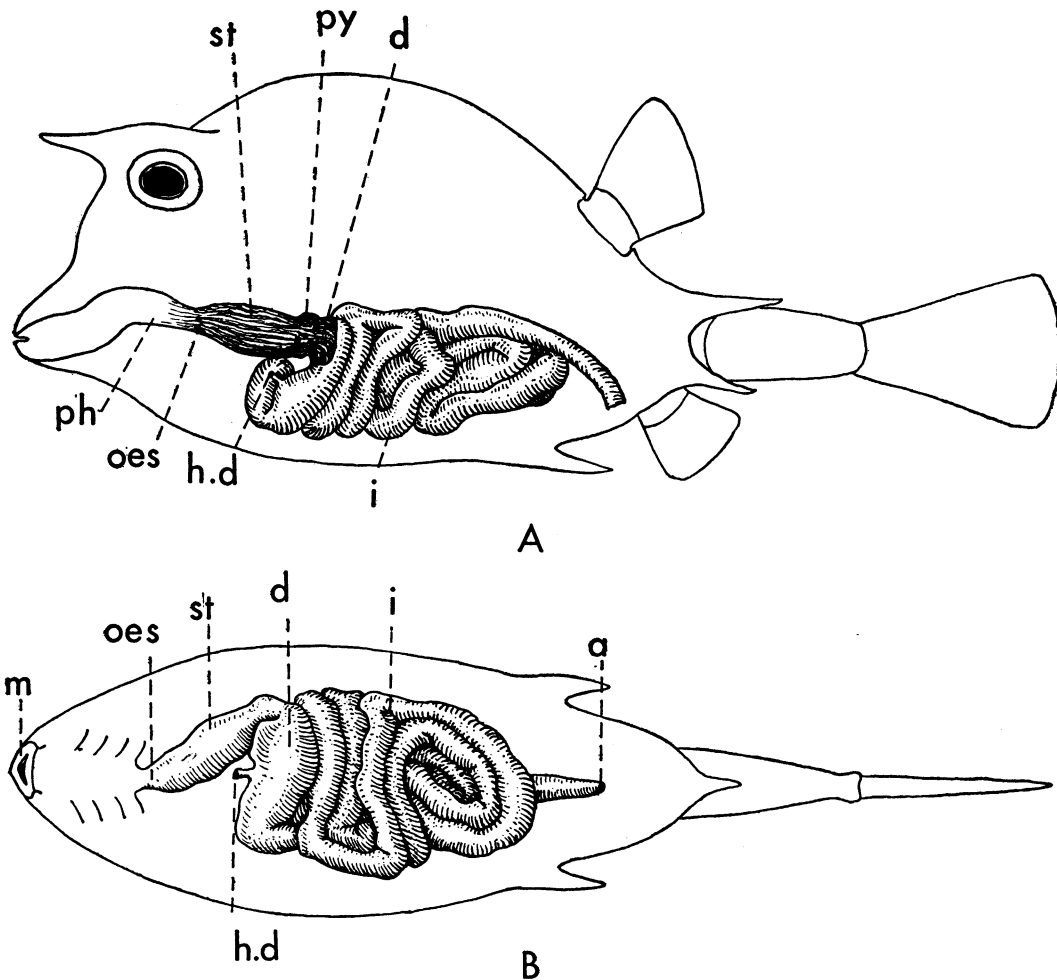

FIG. 4. *Acanthostracion quadricornis* (Linnaeus). A. Lateral view. B. Ventral view.

Linnaeus and *Chilomycterus schoepfii* (Walbaum), are so similar, the following description may be applied to both.

There is a large dilatable sac which is a ventral expansion of the stomach and not separated from the main part of the stomach by any constriction or sphincter. The sac has a thin elastic wall as compared to the rest of the tract. It opens into the oesophagus anteriorly, this opening being controlled by an oesophageal sphincter. Posteriorly it enters the intestine on the right side of the fish (eight specimens examined), this entrance being regulated by a strong pyloric sphincter. The
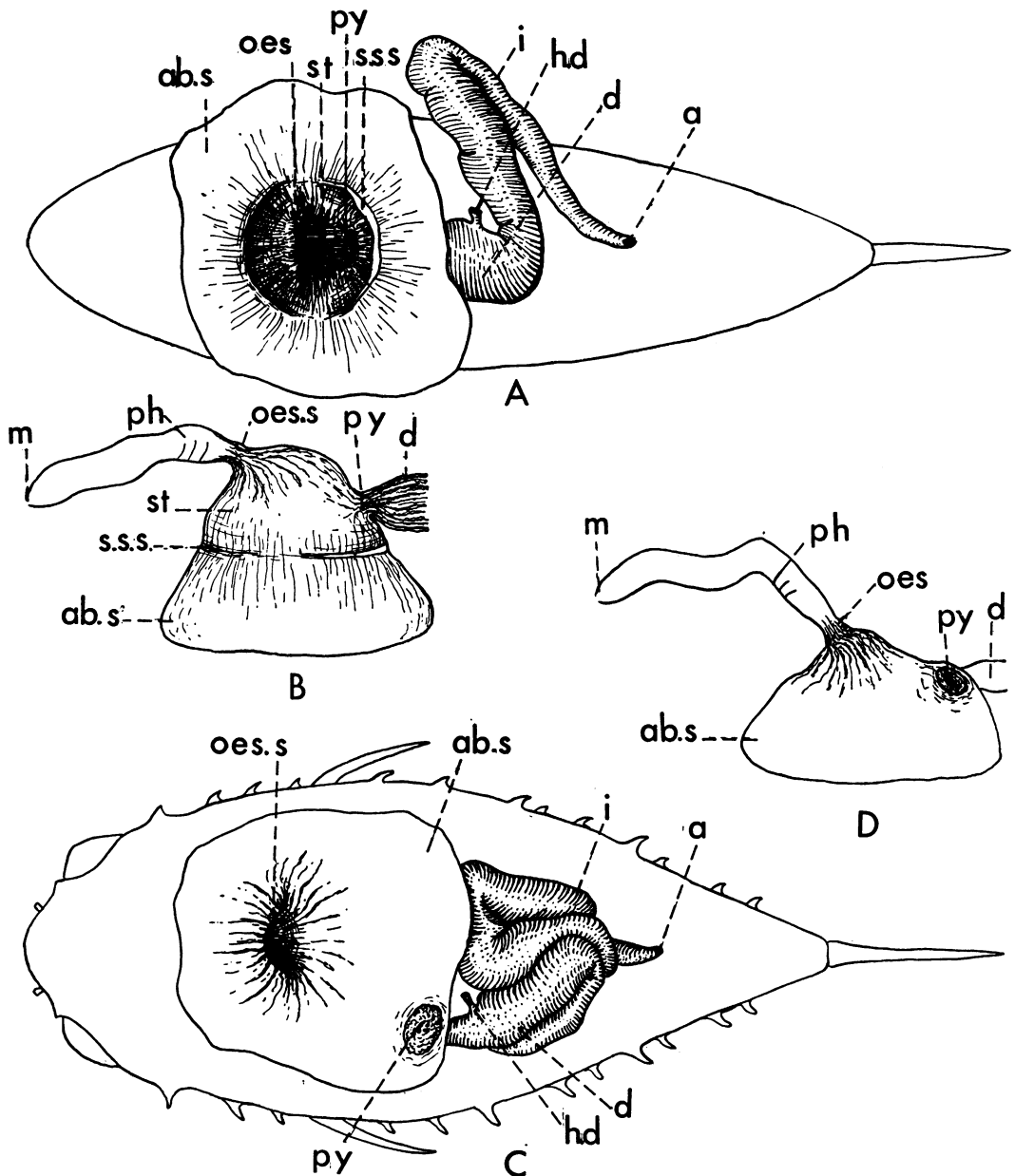

FIG. 5. A. *Spheroides maculatus* (Bloch and Schneider). B. Lateral view of inflatable sac. C. *Chilomycterus schoepfii* (Walbaum). D. Lateral view of inflatable sac.
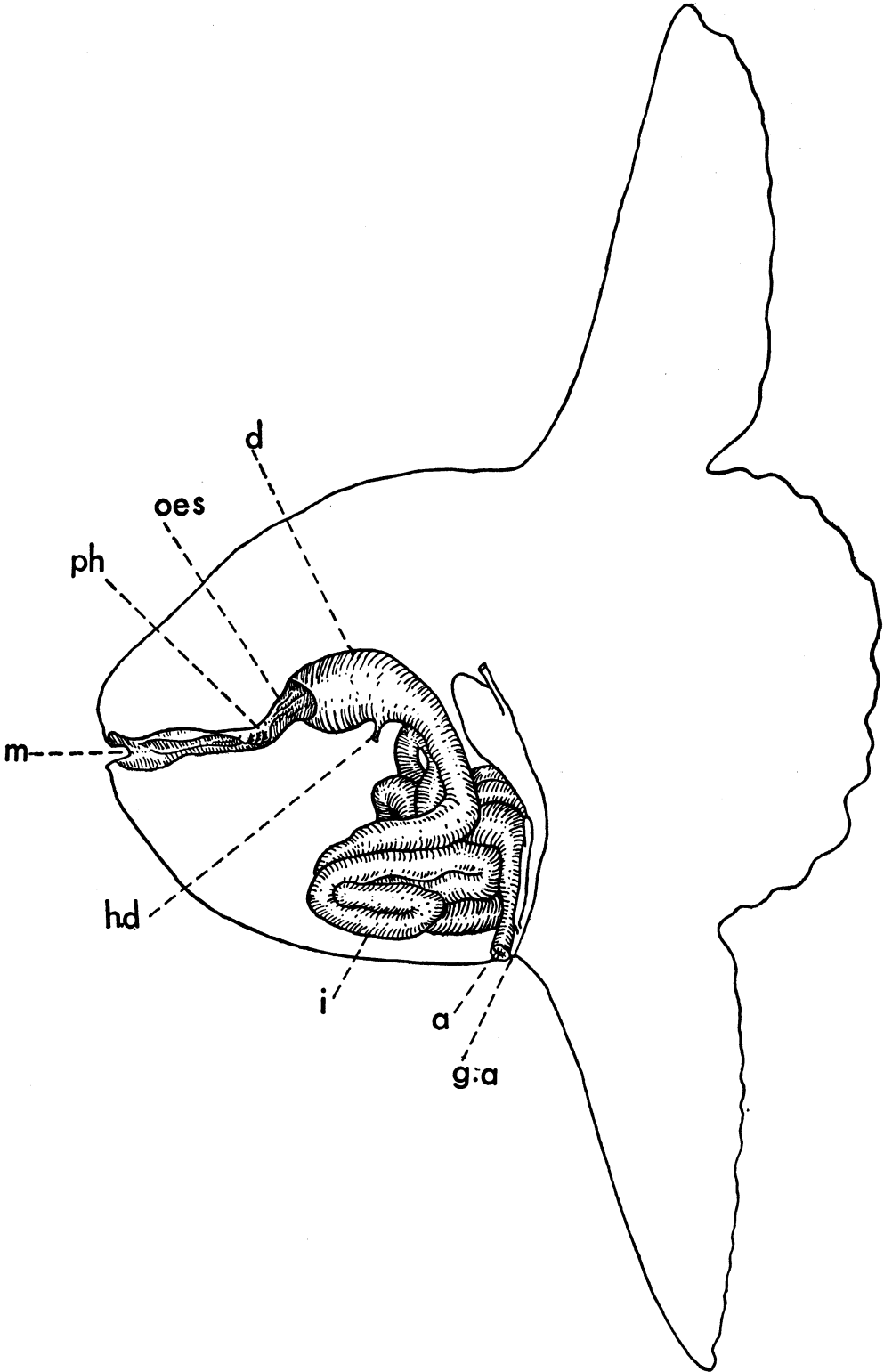
FIG. 6. *Mola mola* (Linnaeus), based on Gregory and Raven (1934).

wall of the air sac is quite smooth except for a few small folds anterio-dorsad arising from the oesophagus. The condition in *Chilomycterus* is shown in figure 5C and D. It is partly attached to the ventral body wall anteriorly and ventrally. Rosen (1912) describes this condition as follows, " . . . a highly enlarged stomach from the anterior and ventral wall of which narrow chords arise uniting it with the abdominal wall. These chords consist of connective tissue, without any muscular or elastic fibres. Their origin from the stomach is generally very broad, and the base of several chords are often united, forming large flaps. Their attachment to the ventral body wall is slightly enlarged." The length of the digestive tract is about two times the standard body length of the fish.

TETRAODONTIDAE

Dissections of *Spheroides maculatus* (Bloch and Schneider), *S. harperi* Nichols, and *Lagocephalus laevigatus* (Linnaeus) showed an even more highly specialized inflating mechanism. The inflatable sac, a ventral diverticulum of the stomach, is separated from the main part of the stomach by a weak, circular ridge more clearly defined posteriorly as a small shelf. Although this sphincter-like ridge may have some small control over the opening between the dorsal portion of the stomach and the ventral inflatable portion, it is not very contractile. About this Gabriel (1940) makes the following statement, "This 'sphincter' is not very contractile and remains open throughout the act of puffing. It does not serve to retain air in the sac, and inflation takes place perfectly well after its excision." The wall of the sac is quite smooth, elastic, and thinner than the rest of the gut. The wall of the stomach proper is thicker, less elastic, and dorsally lined with folds, somewhat deeper around the oesophageal and pyloric openings. Ventrally the sac is firmly attached to the ventral body wall. It is bifid anteriorly when blown up owing to the longitudinal muscles and lateral vein arising directly in

front of the uninflated sac, a feature absent in the Diodontidae. The gut is about one and one-half times the standard length of the fish. The conditions in *Spheroides maculatus* are shown in figure 5A and B.

MOLIDAE

The digestive tracts of *Mola*, *Ranzania*, and *Masturus*, the only three genera of Molidae, are shown in figures by Gregory and Raven. From these drawings it can be noted that the digestive tract is quite long, and it is clear that there are no evidences of a puffing apparatus in this group. Gregory and Raven (1934) state, however, that " . . . in view of the presence of a vestigial muscle connecting the post cleithrum with the skin it may be assumed that *Mola* has lost the power of inflation. . . . " The reference is again made (Raven, 1939b) to the presumed former presence of a puffing apparatus " . . . by retention of the m. retractor post clavicularis." Parr (1927) recognized the retractor post clavicularis as part of the musculature of the postclavicular apparatus which he observed in *Spheroides maculatus* to function, contrary to the beliefs of Thilo and Gregory and Raven, not in the pumping activity producing inflation but in locomotor operations in the form of burying and for support when the fish is resting on the bottom, replacing the ribs as a protection for the body cavity.

The experiments on *S. maculatus* by Gabriel (1940), who observed the inflation in this fish through a celluloid window sewed into the ventral body wall, confirm the conclusions of Parr that the post-clavicular apparatus and hence the m. protractor post clavicularis is not connected with inflation in the puffers and therefore cannot be indicative of a former puffing apparatus in the Molidae. Gabriel observed that "The post-clavicles are quite motionless during the inflation, and fishes with both post clavicles and the associated muscles removed showed no impairment of the inflating power." The digestive tract of *Mola* is shown in figure 6.

THE MECHANISM OF INFLATION

The power of inflating the body as a means of defense appears to be limited to the lower vertebrates. Lizards (Noble, 1931) and many

Salienta (Hinsche, 1928) when annoyed will inflate their lungs, increasing the size of their bodies. Several species of fish, including some

sharks, will also inflate to some extent. How-
ever, it is only in the Plectognathi that we
find a highly developed and elaborate mech-
anism directed towards this end.

By the middle of the nineteenth century a
number of zoologists had reported the re-
markable ability of *Diodon* and other blowfish
to fill with air an enormous dilatation of their
gut. Brisout de Barnville (1846) describes the
inflatable sac in *Diodon* as being an expansion
of the oesophagus which occupies the length
of the abdomen and adheres to the perito-
neum and to the muscles under the spinous
skin which is also greatly expansible. From
dissections of *Spheroides maculatus*, Jackson
(1848) first noted that the inflatable sac is
really a part of the stomach and not the
oesophagus as was commonly believed.

As far as we know, inflation is employed
only as a defense mechanism. In some species
of the Diodontidae it is accompanied by the
erection of skin spines. Fishes in this swollen
state are both difficult to seize and difficult to
swallow.

Frightened or annoyed blowfish will readily
gulp down the fluid medium of their sur-
roundings. Blowfish were first observed to in-
flate with air only. The early literature
(Brisout de Barnville, 1846; Jordan and Sny-
der, 1901; Herre, 1924; etc.) contains many
statements of how these fish swallow air when
disturbed or frightened, float at the water
surface belly up, in order to escape their ene-
mies, and later return into the sea by releasing
the air. As late as 1912 Rosen stated that no
observations had been made to support a
"theory" of Oken's that it is possible for blow-
fish to inflate with water. It is, of course, well
known that in their natural environment wa-
ter is normally swallowed in the process, and
there is no evidence that these fish, when in
water, will come to the surface in order to in-
flate with air. The early stories of blowfish
floating on the water's surface were probably
conjectured from the observation that, on
being caught and pulled out of the water,
these fish inflate with air and, if thrown back
into the water, float for a short time in this
condition, then release the air and swim
down.

The inflating mechanism itself has been
carefully studied by Gabriel (1940) who
worked with *Spheroides maculatus*. The essen-

tial part of the apparatus consists of the pow-
erful muscles of the first branchiostegal ray,
which depress a pad covering the ceratohyals,
thus expanding the mouth cavity and draw-
ing in water or air. The elevation of the cera-
tohyals forces the fluid into the sac, which is
a ventral diverticulum of the stomach, par-
tially separated from it by a sphincter-like
ring. Fluid is retained in the diverticulum by
the strong oesophageal sphincter and by the
pylorus. The flap-like breathing valve in the
mouth does little or nothing in this connec-
tion. The opercular valves prevent leakage
during the compression stroke, but the dis-
tended state of the sac can be maintained even
when they are held open or removed. The
fluid in the sac is released by the relaxation of
the oesophageal sphincter which allows the
fluid to escape from the fish through the oral
and opercular openings.

It is interesting to note how the inflatable
sac manages to function effectively without
interfering with the digestive processes of the
stomach. The stomachs of blowfishes do not
exhibit well-developed digestive glands, from
which one may infer that the greater part of
digestion takes place in the intestine. How-
ever, it is a fact that some of the food does
remain for a time in the stomach, and dissec-
tions usually revealed partially digested food
in this region of the gut. Blowfish deflate rap-
idly and when expelling water do not regurgi-
tate stomach contents. How they manage to
retain the food is still a problem. Further in-
vestigations, such as Gabriel has undertaken
with celluloid windows, might throw some
light on this subject.

By means of the structures and methods
discussed, the various species of the Gymno-
dontes are capable of inflating their bodies to
relatively tremendous proportions. *Spheroides
maculatus* Schneider in the inflated state
is shown in plate 12 and *Diodon hystrix* Lin-
naeus in plate 13. In order to obtain some
estimate of the amounts of water engulfed, a
series of *Spheroides* of various sizes were caused
to inflate while held under water and then
allowed to discharge the water into a gradu-
ate. The data so obtained, including length
and weight of fish, the volume of the water
and the weight of it in percentage of the
weight of the fish, are given in table 1. A
medium large specimen of little over 20 cm.

was found to hold about a liter when fully inflated which weighed nearly 300 per cent of the fish's body weight. The relationship of the contents in cubic centimeters to the standard length of the fish is shown graph-

ically in figure 7. On this graph is also given the relation of the diameter of a sphere in millimeters to its volume in cubic centimeters according to the formula given as footnote b to table 1. This curve, displaced ap-

TABLE 1

THE INFLATION CAPACITY OF *Spheroides maculatus*

(All values read to the nearest unit of the quantities mentioned.
Data obtained from specimens in lower New York harbor, May and June, 1926.)

Standard Lengths (in mm.)	Weight of Fish (in grams)	Capacity (in cc.)	Weight[a] of Water (as % of fish)	Spherical Values[b]		
				Diameter (in mm.)	Volume (in cc.)	39% Greater than 'D'[c]
99	57	141	248	10	0.5	16
106	57	177	314	50	64	82
106	57	192	340	75	221	123
116	71	207	292	100	524	164
118	71	207	292	120	901	197
128	85	244	288	130	1150	213
131	99	266	268	150	1768	246
133	85	200	236	200	4189	328
140	—	301	—	250	8181	410
143	99	370	373			
144	133	355	314			
145	127	422	330			
149	219	406	185			
150	127	437	346			
162	141	414	284			
169	198	630	318			
172	226	732	323			
174	226	694	307			
174	254	819	322			
175	227	561	248			
180	219	677	308			
184	283	769	272			
195	290	755	260			
195	283	800	283			
195	255	814	319			
198	283	875	309			
202	340	979	288			
215	397	1185	298			
Means *157*	*181*	*522*	*295*			

[a] The figures in this column represent the weight of the contained water as "x" % of the weight of the fish.
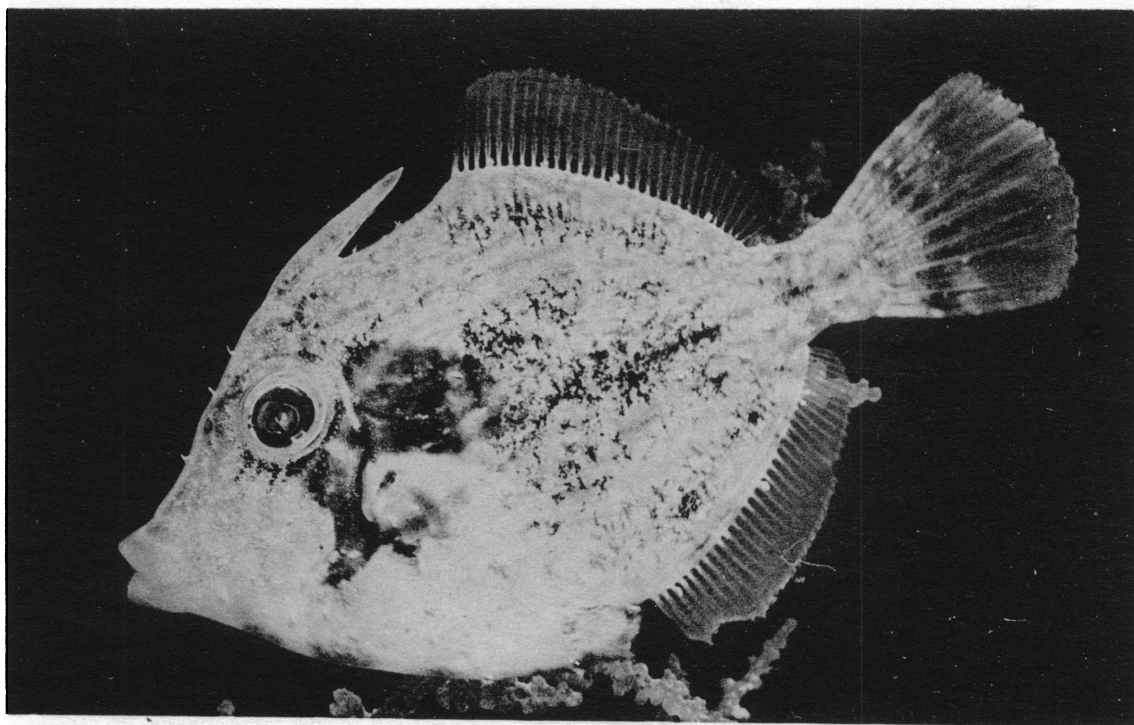
[b] The values for the volume of a sphere calculated according to the formula:

$$D^3 \cdot 0.0005236$$

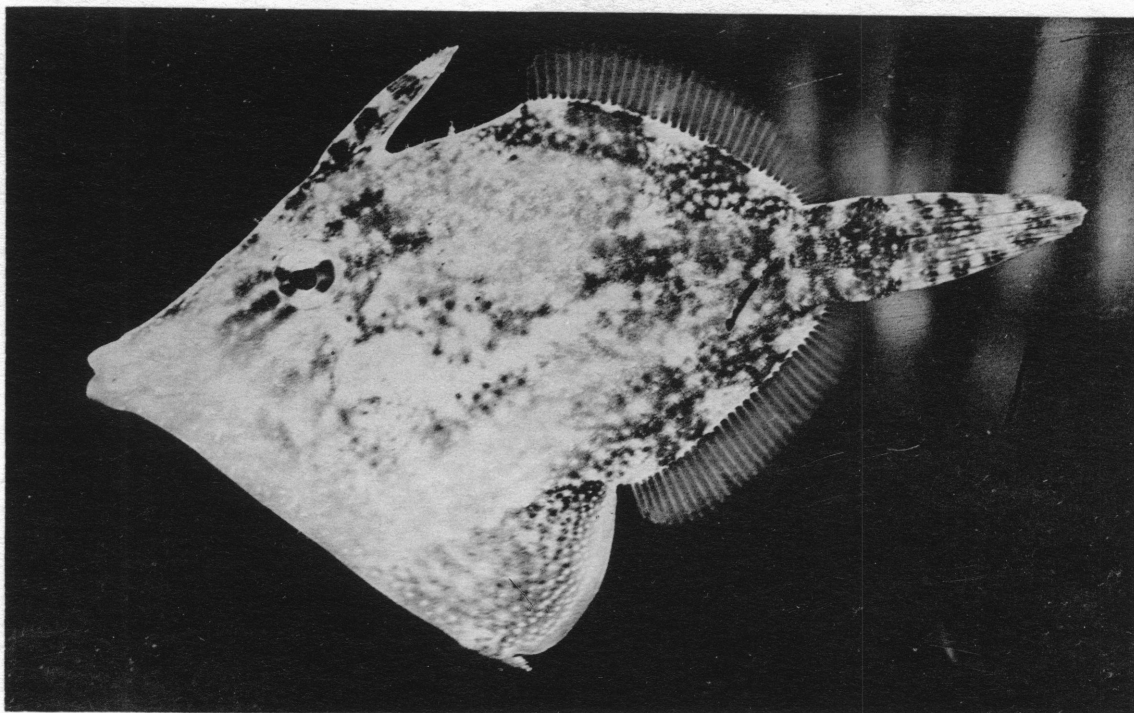in which D = diameter and 0.0005236 = a constant which is equal to $1/6\pi$ moved to the appropriate decimal place to accommodate mm. of diameter and cc. of volume since

$$V = \pi D^2 \, 1/6D \text{ or } 1/6\pi D^3$$

[c] These values represent the diameter of the sphere increased by 39%. See figure 7.

1. *Stephanolepis hispidus* (Linnaeus). 2. *Monacanthus ciliatus* (Mitchill).   Courtesy of Dr. Myron Gordon
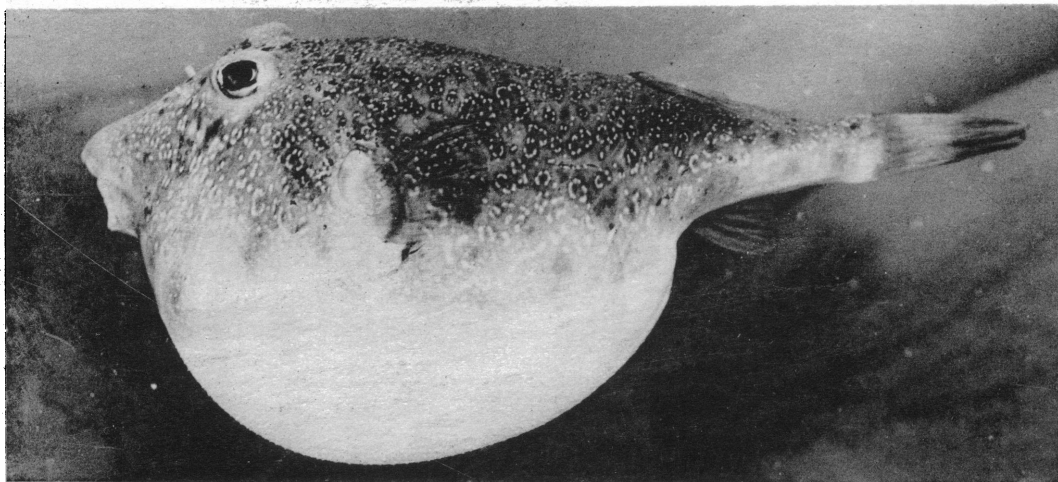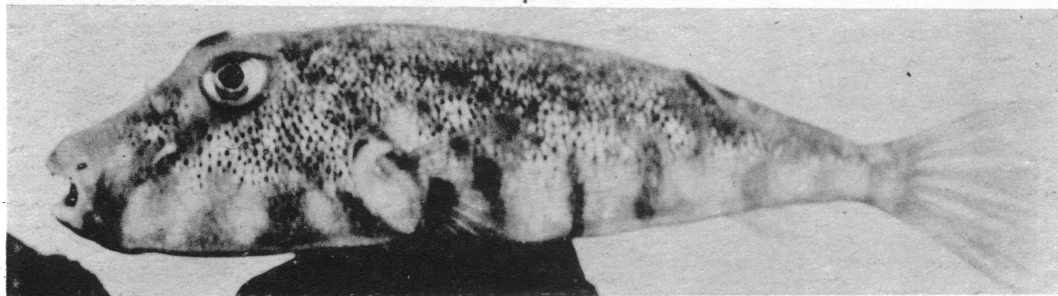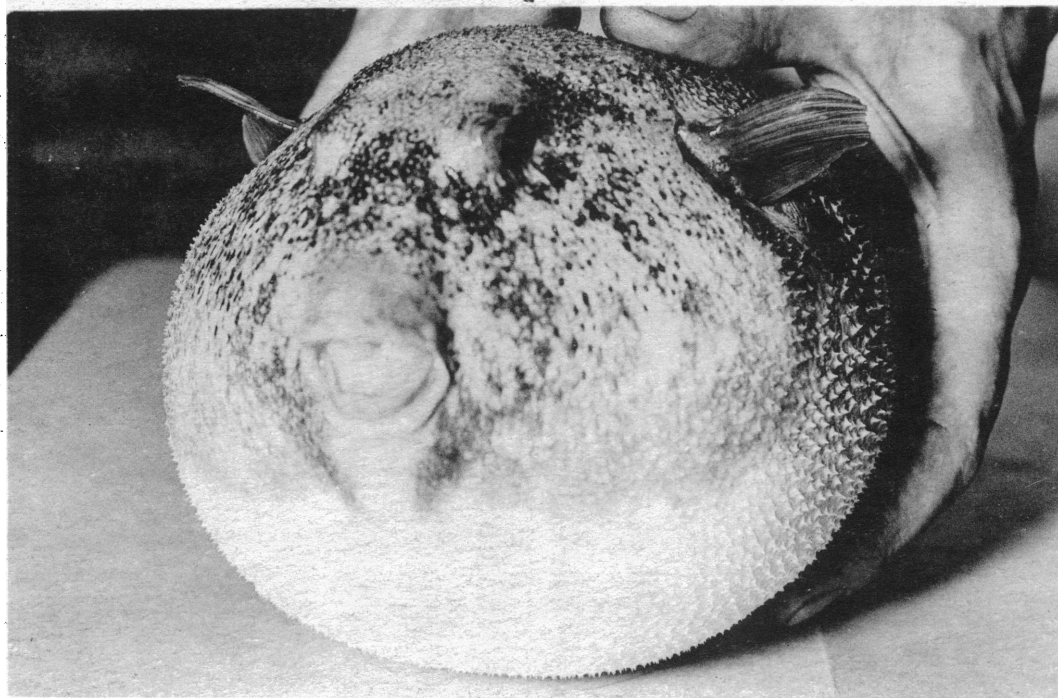
1. *Spheroides harperi* Nichols in the inflated state. 2. *Spheroides maculatus* (Bloch and Schneider) in the uninflated state. 3. *S. maculatus* in the inflated state. Courtesy of the New York Aquarium
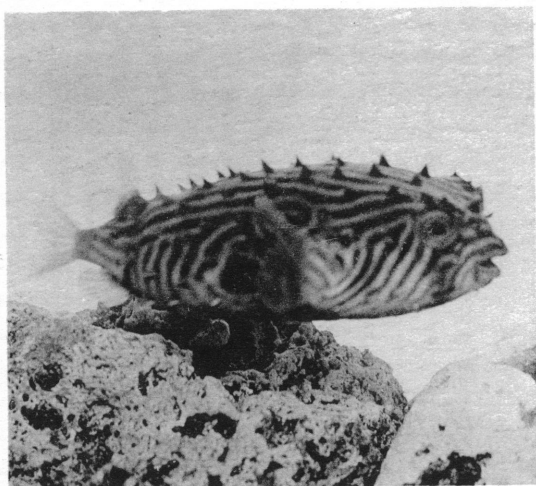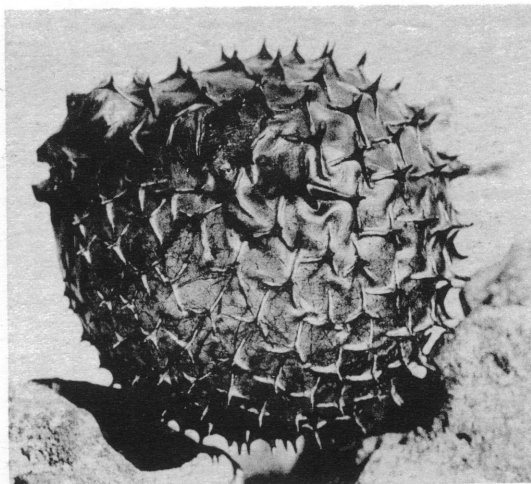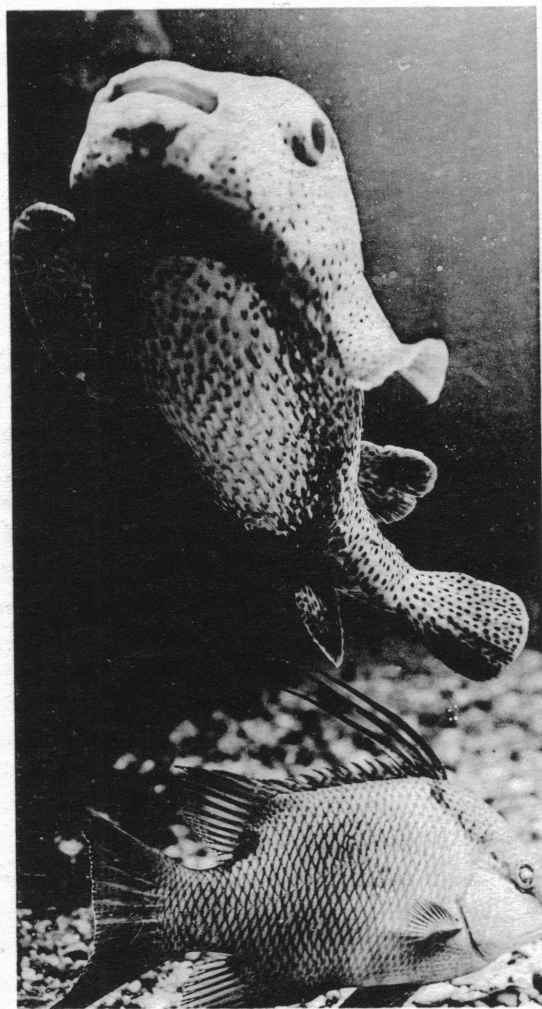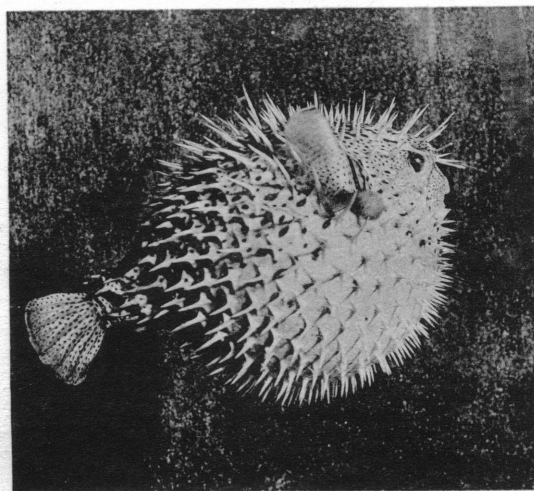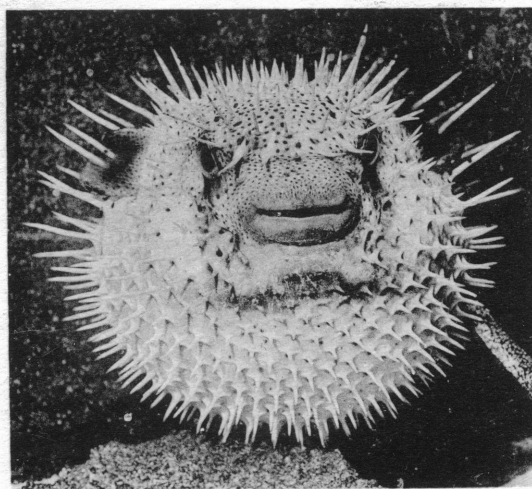
1. *Chilomycterus schoepfi* (Walbaum) in the uninflated state. 2. *C. schoepfi* in the inflated state. 3. *Diodon hystrix* Linnaeus in the uninflated state. 4, 5. *D. hystrix* in the inflated state. Courtesy of the New York Aquarium
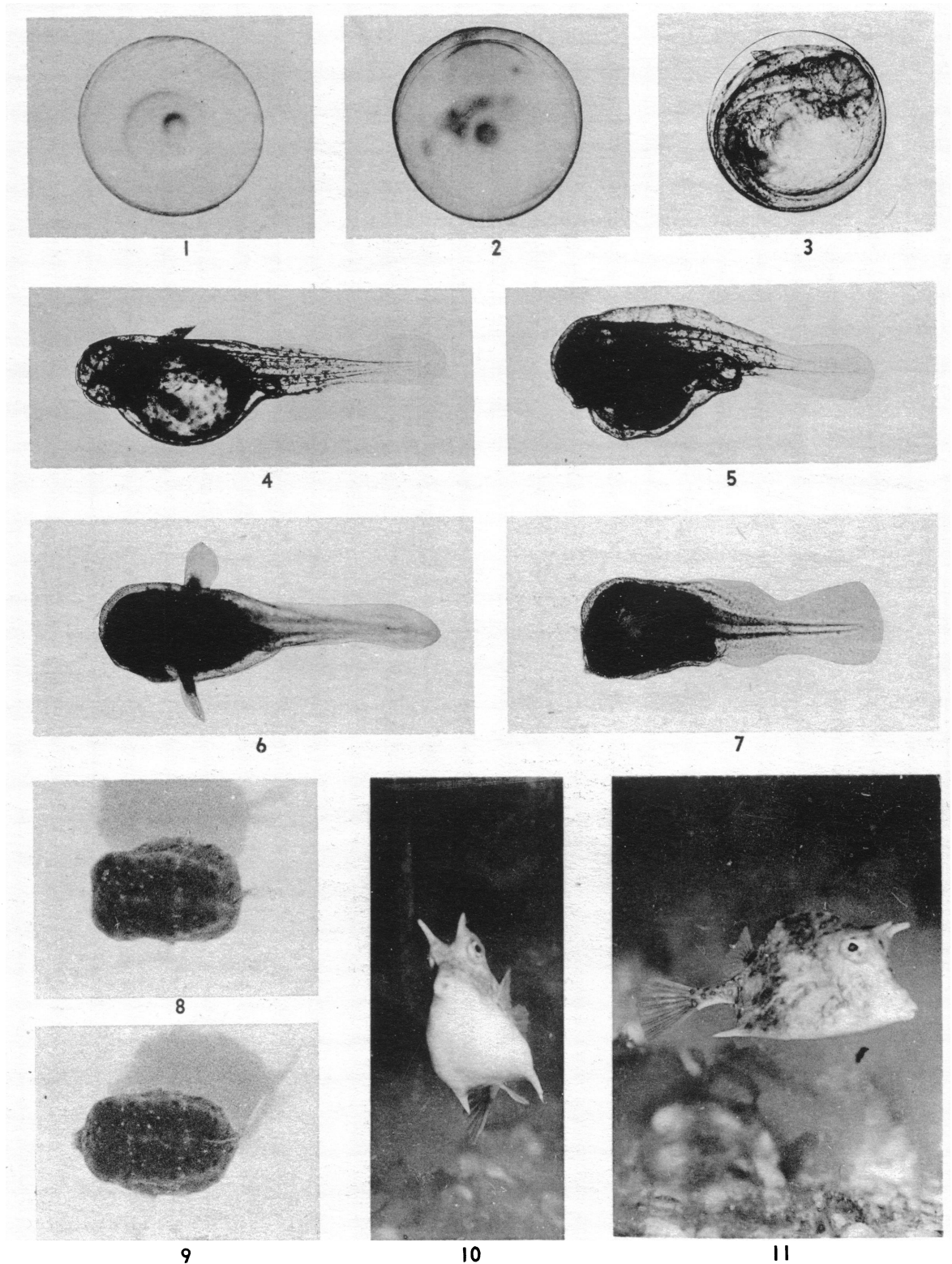
Development of *Acanthostracion quadricornis* (Linnaeus). 1. Egg four hours after fertilization with polar cap opposite viewer. × 10. 2. Egg somewhat older with polar cap in profile. × 10. 3. Egg of 40 hours from fertilization, nearly ready to hatch. × 10. 4. Larva at hatching in dorsal view as normally floating. × 10. 5. Larvae 48 hours from hatching, in profile. × 10. 6. Larva 72 hours from hatching, in dorsal view. × 10. 7. Larva 114 hours from hatching, in lateral view. × 10. 8. Post-larval fish in dorsal view slightly tipped downward. × 3. 9. Post-larval fish in dorsal view showing mouth. × 3. 10. Young fish in front view. × ½. 11. Young fish in side view. × ½
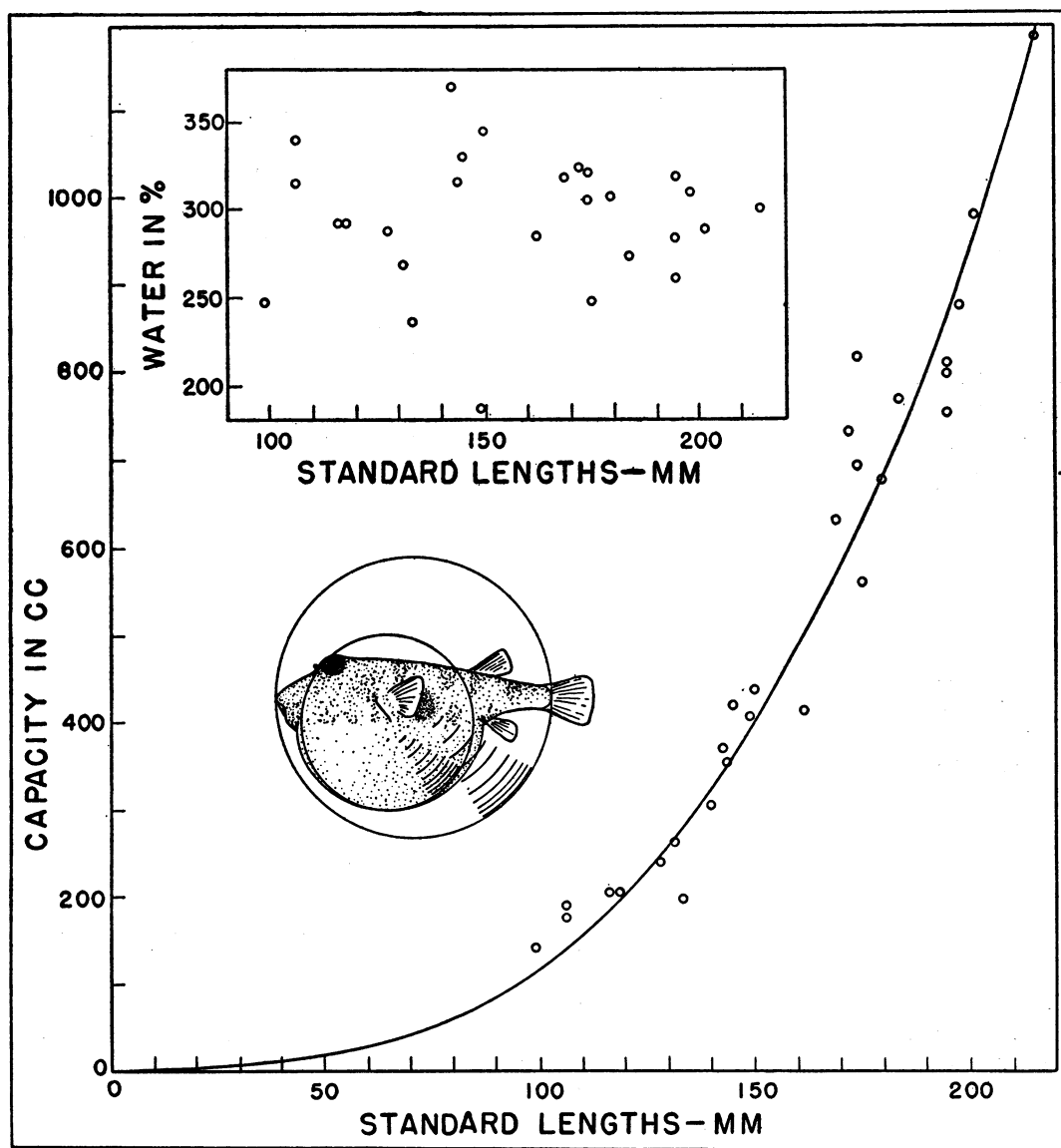
FIG. 7. Inflation in *Spheroides maculatus* Schneider. In the main graph showing the relationship between standard length of fish and capacity in cubic centimeters the small circles indicate measurements of fish from table 1. The smooth curved line is *not* based on the distribution of values from the fish but is an expression of the relationship between the diameter of a sphere and its volume: $V = \frac{1}{6}\pi D^3$. It is plotted with the volume against values 39 per cent greater than the corresponding diameters. The upper inserted scatter diagram represents the standard lengths plotted against the weight of the engulfed water expressed as percentage of the weight of the fish. The diagram of an inflated fish is shown with a sphere circumscribed about its standard length and another 61 per cent less than the standard length (the standard length being 39 per cent greater). This is placed with its center on a line perpendicular to a tangent to the inflated sac parallel to the longitudinal axis of the fish to which the inscribed sphere is likewise tangent.

propriately, is obviously close to that established by measurements of the fishes. Thus it is clear, within the limits of our series of specimens, that the inflation capacity bears a direct relationship to the length of the fish, which is in close agreement with that between the diameter of a sphere and its volume. The curve of the latter relationship was displaced by plotting the spherical volumes against values 39 per cent greater than their corresponding diameters. Thus it follows that the relationship between the length of the fish and its inflated volume is such that a given volume corresponds to the standard length 39 per cent greater than the diameter of a sphere corresponding to that volume. The sketch in figure 7 indicates this relationship, in which the standard length of the fish and its inflated outline is compared with a sphere with a diameter equal to the standard length and to one equal to 61 per cent less than that. The relationship of that sphere to the inflated outline of the fish is evident. The volume occupied in that sphere by the part of the head and body included is offset in part by the oblate nature of the inflated portion which may be seen to extend both ahead of and behind the spherical surface. The greatest compensation, however, is due to the larger size of the transverse diameter of the expanded region as may be noted from the frontal view of plate 12.

It is evident from table 1 that the weight of the engulfed water varies from a little less than twice to nearly four times the weight of the fish. This relationship, in which the weight of the water is expressed as percentage of the weight of the fish, is shown in the insert of figure 7. That there is no clear trend in this scatter diagram is evident and is another way of indicating that, in the size range considered at least, the relation of length of fish to volume contained is actually less than might have been anticipated. These fish, on being handled, puff themselves up to what appears to be their limit of turgidity, but there is no advance guarantee that they always, on each inflation, reach exactly the same volume. In fact, it is not unusual for one to stop inflating when about half full, regurgitate the water, and attempt escape movements. Despite this slight uncertainty as to whether or not the final and complete state of inflation has been reached, the obtained values showed only slight departures from a line based on the relationship of the diameter of a sphere to its volume. The comparatively larger variation of the relationship of weight of water to weight of fish is conditioned by the natural variations of weight of fish such as those due to sex, condition, and amount of food present in the digestive tract, combined with those already present, as noted for the length to volume relationship.

Because of the relationships discussed above and indicated in table 1 and figure 7, it is possible to express the relationship of the inflating ability to the length of *Spheroides maculatus* by the following expression:

$$(s.l. \cdot 0.61)^3 \cdot 0.0005236 = cc.$$

in which s.l. equals standard length in millimeters and cc. equals capacity in cubic centimeters. Since V equals $\frac{1}{6} \pi$ D^3 or V equals 0.5236 D^3 and there are 1000 cubic millimeters in 1 cc., a sphere the diameter of which is 61 per cent of the standard length has an equivalent volume.

THE ONTOGENY AND HABITS OF THE PLECTOGNATHI

ONTOGENY

ALTHOUGH THERE IS STILL MUCH to be learned about the development of the Plectognathi in terms of ontogeny, there is sufficient known to make a brief review of it of some significance in present conditions. In addition to what has already appeared in the literature we are able to present new data on development of one group, the Ostracodermi, which otherwise has apparently escaped such study. Considering the aggregation, group by group, the following data present what is known concerning their development as well as indicating desiderata.

PRE-PLECTOGNATHS

The acanthurids, which are generally considered close to the ancestral line giving rise to the Plectognathi proper, are virtually unknown from a developmental standpoint. Various small translucent acanthurids with very deep folds or scales have been more or less questionably referred to well-known species.

SCLERODERMI

The Triacanthidae, a relatively deep-water group, is without data as to ontogeny, and there are none for the Triodontidae, known only from rather large specimens, and the Balistidae proper. A single species of monacanthid, *Monacanthus hispidus*, has been studied by Hildebrand and Cable (1930) who had specimens as small as 1.7 mm. in length. The eggs, which are almost surely pelagic, are still unknown. Even at this smallest size the single dorsal spine is already developed and prominent. At this stage two fin folds are present, evidently representing pelvic fins which fail to develop. The body is already deep for a larval fish, and there is no difficulty in recognizing the evident affinities. By the time a length of 2 mm. is reached these two fin folds are replaced by a single median fold which the enlarging pelvis is growing to support. Before 3 mm. is reached this structure is already well developed, and at 8 mm. the fish is clearly recognizable. By the time 15 mm. is reached the fish is virtually a miniature adult except for minor proportional differences.

OSTRACODERMI

The only known developmental study in this group is given below for the West Indian species *Acanthostracion quadricornis* (Linnaeus). This form produces spherical, nonadhesive, pelagic eggs. These may be obtained by tow-net operations or stripped from females during the summer months on the west coast of Florida. The material here described was so obtained at the field station of the New York Aquarium in the summer of 1942.

The eggs averaged 1.46+ mm. in diameter and ranged from 1.40 to 1.60 in a measured sample of 19. They just barely float in the inshore waters of this place but float well in the slightly denser offshore water. On artificial fertilization the eggs sink slightly until thoroughly water hardened. They possess a single, light amber, oil globule which averages about 0.15 mm. in diameter. Hatching occurs in about 48 hours at a temperature of 27.5° C. Developmental stages are shown in plate 14 in which the age of the various stages is indicated. The resulting larvae are short and chunky and of a character unlike that of the Sclerodermi but resembling the Gymnodontes, as may be noted by a reference to the figures of Welsh and Breder (1922).

At the stage shown in plate 14, figure 4, the larvae spend most of their time lying on the bottom or floating inverted as shown, interrupting this with occasional short darts. This passes soon into a more active stage in which the pectoral fins play an active locomotor role. This and a rapid vibration of the tail's tip accomplish locomotion. They tend to sink when such activity ceases. Feeding, in laboratory dishes, consisted of a series of bumping of noses along the bottom; at each "bump" a small organism was engulfed. As development proceeded they rapidly darkened in the body portions, so that transmitted light did not serve to expose interior organization, as may be noted in plate 14. By the time 114 hours from hatching had passed the fish were already beginning to take on a postlarval appearance and behavior (pl. 14, fig. 7). At this stage there is evidently no

flexibility of the body anterior to the clear caudal portion. It seems that the heavy body pigmentation occupies approximately the same region as that of the solidified test of the adult. The general swimming behavior and general "stance" are very like those of the adults. Owing to the limitations of time this is as far as we were able to carry the fry, although it would seem that they could be cultured much further in a laboratory dish.

While this study was in progress there could be found in the nearby waters small specimens of about 8 to 10 mm. in standard length as shown in plate 14, figures 8 and 9. These were evidently of an early spawning and perhaps a month or so from their date of hatching. Immature specimens of about 80 to 90 mm. were also present. Evidently these were from a much earlier spawning or of the year previous. Such are shown in plate 14, figures 10 and 11. At this size the characteristic frontal "horns" have developed.

GYMNODONTES

The only full description of the developmental stages of a species in this group is that of Welsh and Breder (1922) for *Spheroides maculatus* (Schneider). This species produces strongly adhesive demersal eggs, spherical in form, and provided with a gelatinous covering which cements the eggs to the substrate and to one another. Spawning occurs during the summer months on the New Jersey coast. The eggs proper average 0.87+ mm. in diameter and range from 0.85 to 0.91 mm. They are provided with a cluster of virtually colorless oil globules in a froth-like mass which averages about 0.34 mm. in diameter. Hatching occurs at about 112 hours after fertilization at about 18.5° C. The resulting larvae are chunky and bear a marked resemblance to those of *Acanthostracion*.

In January, 1936, a pair of *Spheroides maculatus* in the old New York Aquarium spawned. The time was presumably advanced because the fish had been kept in water held at 72° F. The actual spawning was not observed, but the eggs were disposed in a ring about equal in diameter to the length of the fish. They were partly buried in the sand on the floor of the tank in an agglutinated mass. There was no evident parental care. The eggs were first discovered on January 28

and hatched on January 31. The hatchlings were evidently strongly phototropic and immediately rose to the surface where they hung for some time. There were only four fish in a rather large aquarium.

At other times in generally crowded tanks puffers brought in after the middle of June often shed their spawn broadcast. Whether this ring formation is typical of the way these fishes spawn should be checked.

Munro (1945) figured and briefly described the eggs, larvae, and postlarvae of *Spheroides hamiltoni* (Richardson) and the larvae and postlarvae of *S. pleurogramma* (Regan). These are rather similar to those of *S. maculatus* in all essential details.

Reproduction of *Tetraodon cutcutia* (Hamilton-Buchanan) and *T. fluviatilis* (Hamilton-Buchanan) has been observed and discussed by Cohn (1912) and Randow (1934). These brackish to fresh-water forms place their adhesive eggs on a rock or similar support and guard them and circulate water over them. Schreitmuller (1929, 1930a, 1930b) discusses in considerable detail the spawning of *T. cutcutia*. He found the eggs to number from 200 to 300 adherent to rocks, and states that the young lie on the bottom and that the male makes a hole in the sand in which the young fish are sheltered.

Nothing is known of the reproductive behavior or development of the Diodontidae. Eggs stripped from a ripe female of *Chilomycterus schoepfii* in July on the New Jersey coast (Nichols and Breder, 1926) were non-adhesive, highly transparent and demersal, and averaged about 1.8 mm. in diameter. Whether the fact that the eggs sank is to be considered normal cannot be decided at this time, but their lack of an adhesive covering suggests that they may be normally pelagic.

MOLOIDEA

This group, often not separated from the Gymnodontes, evidently produces pelagic eggs. The larvae, a variety of which have been studied, resemble to some extent those of the Gymnodontes, but are further specialized in the production of a variety of spines and other outgrowths. Various young stages of these fishes have been given by Putnam (1871), McCulloch (1912), Schmidt (1921a, 1921b, 1926, 1932), and Gudger (1935, 1936, 1937a, 1937b, 1939).

SEXUAL DIMORPHISM

Sexual dimorphism is not especially marked in this group, but in certain cases very definite differences have been found. Tanaka (1931) showed marked sexual dimorphism in *Xanthichthys lineopunctatus* (Hollard), as did Ebina (1932) in *Monacanthus modestus* Günther. Fraser-Brunner (1940a) describes it in *Ostracion cyanurus* Rüppell and *O. lentiginosus* Bloch and Schneider and suggests that numerous other species in this family may show it. In all the above there is considerable modification of form, and the sexes in each

case have passed as different species. In the case of *Acanthostracion quadricornis* the males are smaller, narrower across the carapace, and more brightly colored. There is much incidental variation in pattern, but those of each sex average about a slightly different norm. Welsh and Breder (1922) showed that the males of *Spheroides maculatus* (Bloch and Schneider) averaged less in size than did the females, a condition common to many fishes and very likely carrying through this group.

HABITS

In addition to the evident peculiarities shown by these fishes, there is also a variety of special habits to be found in the different groups that have not been considered in connection with the phylogeny of the order.

The production of sound, for example, is a well-marked feature of the plectognaths and most, on being handled, make some sort of sounds that are produced either by grinding the jaw teeth, the pharyngeal teeth, or by means of vibrating the swim bladder. The Balistidae are perhaps most specialized in this direction, having the swim bladder connected with a specialized area of the skin above the pectoral fin which has been appropriately called the "tympanum" by Gregory (1933). Sometimes when handled these fishes give out a grunting sound which may be stopped by pressing a finger on the tympanum on either side. At such times it may be felt to vibrate, the sound returning when the fingers are released. This feature is missing in the monacanthids, which nevertheless give vent to faint grunting sounds. Burkenroad (1931) wrote, "*Monacanthus hispidus*[1] was observed to produce a sharp whining, scraping noise by sliding the biting edges of the lower incisors upward over the sloping posterior surfaces of the upper incisors during the rapidly repeated closing of the mouth. The posterior surfaces of the two

median pairs of upper incisors of the inner series are striated with a number of fine transverse ridges, which are not present on any of the other tooth surfaces. These are certainly to be considered stridulatory ridges. The possession of such specially modified stridulatory surfaces on the teeth does not appear to have been previously noted in fishes." *Acanthostracion* makes similar faint sounds under such handling. Both the tetraodontids and the diodontids make a considerable noise during inflation by grinding their heavy jaw teeth. Tower (1908) and Burkenroad (1931) discuss various species. In an aquarium, similar sounds may be heard by means of the aquatic stethoscope described by Breder and Rasquin (1943). In the ordinary process of feeding of *Spheroides* such sounds are notable and evidently, as based on the behavior of other specimens remote from the feeder, serve as an attractant to others. There is as yet no reason to presume that these sounds are associated with reproductive behavior.

There are evidently no data on the possible sound production of either the triacanthids or the molids.

The peculiar development of the pelvis and the clavicles calls for special comment. In the Balistidae, Monacanthidae, and Triodontidae the pelvis, elongate and erectile, serves the purpose of dilating the ventral outline which in *Triodon* assumes amazing proportions (see fig. 3). In these the clavicles are not excessively developed. Apparently with the substitution of the ingestion of water to inflate the ventral outline rather than the employ-

[1] Fishes of this genus have been previously described as producing sound by means of the swimbladder, and by dorsal spine stridulation, neither of which methods was used by this species." See, for example, Boulenger (1904).

ment of an erectile pelvis to dilate it, the post clavicles, in some cases, have been enlarged into long processes which are employed directly, by virtue of the loose baggy skin, for the purpose of digging and burying the fish in sandy places. Parr (1927) has described in detail this digging behavior in *Spheroides* and has shown that in the diodontid *Chilomycterus* the post clavicles cannot function in this fashion. He also indicates, as do Rosen (1913) and Gabriel (1940), that the post-clavicular apparatus is in no way connected with the puffing mechanism.

A peculiar feature involving locomotor disorganization in the young of several plectognaths on the incidence of a strong light was described by Breder and Harris (1935) which could not be repeated in other similar environments (Breder, 1942). It is thought that a further understanding of this matter might throw light on other items in the behavior of plectognaths, both juvenile and adult.

Protective coloration in the plectognaths has been reported in a number of cases, as well as associated postural behavior which is evidently somewhat related to the above detail and is reviewed by Breder (1946).

The locomotor behavior of the Plectognathi shows a progressive decrease in the use of the tail as a propelling organ. This is foreshadowed in the pre-plectognaths. In the Chaetodonidae and more especially in the acanthurids, the pectorals largely take over the propulsive efforts, the tail acting chiefly as a passive rudder except at times of great stress. We know nothing directly of the locomotor methods of the Triacanthidae, but their structure would indicate that they may be quite similar to that of the acanthurids.

In the balistids the pectorals function in a similar fashion but are relieved of a considerable load by the increasing mobility of the dorsal and anal fin rays which become the chief locomotor organs, the tail remaining mostly as a rudder.

In the Ostraciidae both pectorals and dorsal and anal are employed with evidently not dissimilar effect. The same is true in the Diodontidae and Tetraodontidae and presumably in the Triodontidae. In addition, especially in the Diodontidae, the exhaled water is of marked locomotor aid, remarkably so in *Chilomycterus* at least, as has been shown by Breder (1926). This is evidently associated with the restricted gill openings of the Plectognathi and emphasized in those forms which have a powerful oral pumping mechanism associated with the power of inflation.

In the Molidae, the rudder-like tail is completely gone, and the major locomotor thrust is furnished by the enlarged and powerful dorsal and anal. The pectorals are evidently too small to be of great locomotor significance, and nothing is known of the possible magnitude of thrust from exhalant water.

THE PHYLOGENY OF THE PLECTOGNATHI

VARIOUS ATTEMPTS have been made in the past to arrange the plectognaths in a phylogenetic sequence, and in broad terms there has been general agreement among various authors, but the actual details of relationship between the various subgroups are far from clear. Because of the new data herewith presented, various aspects of these interrelationships may be further considered, even if it must be admitted that some of these new data raise new questions rather than settling old ones.

Long ago Dareste (1850) indicated the basic derivation of the plectognaths from a line close to the acanthurids, which no one has seen fit to contest (see, for example, Regan, 1902, and Gregory, 1933). In fact certain authors (Goodrich, 1909), have included them in the Plectognathi, and Gregory (1933) includes both plectognaths and acanthurids in his Balistoidei. Berg (1940) and Fraser-Brunner (1935a, 1935b, 1940a, 1940b, 1941a, 1941b, 1941c, 1943) exclude them. Although certain skull characters are notably similar, we can see no valid reasons at this time for enlarging the essentially compact Plectognathi to cover the acanthurids and their relatives. If anything, such added data as we have on this group show another difference which has not been previously noticed in such work. All the plectognaths so far studied have no pyloric caeca, which in the acanthurids are well developed (see fig. 1).

Although the triacanthids may be considered an essentially deep-water modification, they are certainly close to the base of the plectognath stem, as all authors agree. The other Sclerodermi present a distinct problem owing to the curious mixture of characters in some of the members. The balistids, monacanthids, and triodontids are not so easy to place. The first two, with evident affinities to the triacanthids, by themselves would not be particularly hard to place in a reasonable scheme, but *Triodon*, which is so clearly balistid in certain features and so definitely gymnodont in others, is somewhat of a problem. The new data on the character of the digestive tract and its evidently more primitive condition than that shown by the other two do not help to disentangle the problem.

The Ostracodermi have been placed in the Sclerodermi by Regan (1902), a course which has been followed by Boulenger (1904) and Gregory (1933). This has not been done by Goodrich (1909) or Berg (1940). In view of the marked differences shown in the digestive tract of this group and the differences in the ontogeny from that of *Monacanthus* and its resemblance to that of *Spheroides*, we cannot feel justified in holding these fishes within the Sclerodermi almost solely on the basis of cranial characters.

The Gymnodonti, while seemingly a rather unified group, have so many of various characters also displayed by the Sclerodermi (*Triodon*), by the Ostracodermi, and by the Moloidea that for phylogenetic alinement they present a very puzzling situation.

The Moloidea of Berg (1940) or Moliformes of Fraser-Brunner (1943) we accept as a worthwhile separation. Although these fishes represent an offshore modification of the gymnodontid type, they are so much further modified as, in our judgment, to warrant such a separation. The fact that they have lost their tail fin and its associated musculature, as established by Gregory and Raven (1934) and Raven (1939a, 1939b), indicates a fundamental change in the whole plan of organization. The resemblance of the larvae to Gymnodontes we take to indicate phyletic relationship but of insufficient weight to keep the groups in an unseparated whole.

Only Kaschkaroff (1914) in recent times departs at all radically from the general terms of the above arrangement. His classification calls for a separate suborder for *Triodon* on a basis of its combination of characters, and is that of Hollard (1853, 1860). It is given below, compared with the present usage.

Sclerodermi   {Sclerodermi
             {Ostracodermi
Loganiosomes Sclerodermi   (*Triodon*)
Spherosomes   Gymnodontes
Ellipsomes   Moloidea

We are satisfied with Regan's (1902) placing

TABLE 2

COMPARISON OF CHARACTERS WITHIN THE ORDER PLECTOGNATHI

(Question marks indicate that there seems to be probability that the condition will be found as noted. In some cases it amounts to almost certainty.)

	Triacanthidae	Balistidae	Monacanthidae	Triodontidae	Ostraciidae	Tetraodontidae	Diodontidae	Molidae
Teeth								
Not fused	x	x	x	—	x	—	—	—
Fused								
4	—	—	—	—	—	x	—	—
3	—	—	—	x	—	—	—	—
2	—	—	—	—	—	—	x	x
Pelvis								
Movable	—	x	x	x	—	—	—	—
Fixed	x	—	—	—	—	—	—	—
Absent	—	—	—	—	x	x	x	x
Fourth pharyngeal								
Toothed	x	—	—	—	—	x	x	x
Rudimentary	—	x	x	x	x	—	—	—
Inflation								
Absent	x	—	—	x	x	—	—	x
Rudimentary	—	x	x	—	—	—	—	—
Developed	—	—	—	—	—	x	x	—
Cover								
Carapace	—	—	—	—	x	—	—	—
Scales or spines	x	x	x	x	—	x	x	x
Dorsal								
With spines	x[a]	x[b]	x[c]	—	—	—	—	—
No spines	—	—	—	x	x	x	x	x
Ventral								
Present	x[d]	x[e]	x[e]	—	—	—	—	—
Absent	—	x	x	x	x	x	x	x
Caudal								
Present	x	x	x	x	x	x	x	—
Absent	—	—	—	—	—	—	—	x
Swim bladder								
Present	x	x	x	x	x	x	x	—
Absent	—	—	—	—	—	—	—	x
Epipleurals								
Present	x	x	x	x	—	—	—	—
Absent	—	—	—	—	x	x	x	x
Palatine								
Movable	—	x	x	?	?	—	—	—
Immovable	x	—	—	—	—	x	x	x
Premaxillary								
Protractile	x	—	—	—	—	—	—	—
Fixed	—	x	x	x	x	x	x	x

[a] Two to six dorsal spines.
[b] Three spines.
[c] One or two spines, the second very small.
[d] One spine and 0 to 2 rays.
[e] One rudimentary spine or none at end of long pelvis.

TABLE 2—(*continued*)

	Triacan-thidae	Balis-tidae	Mona-can-thidae	Triodon-tidae	Ostra-ciidae	Tetrao-dontidae	Diodon-tidae	Molidae
Fourth gill								
Present	x	x	x	?	x	—	—	x
Absent	—	—	—	—	—	x	x	—
First branchiostegal								
Normal	x	x	x	x	x	—	—	x
Expanded	—	—	—	—	—	x^f	x^f	—^{f}
Eggs								
Pelagic	?	?	x	?	x	—	?	?
Adhesive	—	—	—	—	—	x	—	—
Parental care								
Present	—	—	—	—	—	x	—	—
Absent	?	?	x	?	x	—	?	?
Larvae								
Compressed	?	?	x	?	—	—	—	—
Rotund	—	—	—	—	x	x	?	x
Voice								
Swim bladder	—	x	—	—	—	—	—	—
Jaw teeth	—	—	x	?	—	x	x	?
Pharyngeal teeth	?	?	—	—	?	—	—	—
Absent	—	—	—	—	—	—	—	?
Postclavicles								
Digs with	—	—	—	—	—	x	—	—
Do not dig	x	x	x	x	x	—	x	x
Food								
Sessile	—	x	x	?	x	x	x	—
Pelagic	x	—	—	—	—	—	—	x

f Six branchiostegals.

Triodon within the Sclerodermi which the present findings on specimens tend to strengthen.

A phylogenetic tree given by Kaschkaroff (1914) appears superficially to be more different from the present interpretations than it actually is in fact. It is reproduced below. Examination will show that in deriving the Plectognathi from an unknown "Vorfahr" the transformations seen must for the most part have to follow. It is so well established that this group stems from the acanthurid-like fishes that it seems no longer necessary to call in a hypothetical ancestor. The relationships of these fishes to *Triacanthus* are reasonably clear. By dropping *Triacanthus* to a point somewhat below "der Vorfahr," the tree of Kaschkaroff immediately becomes
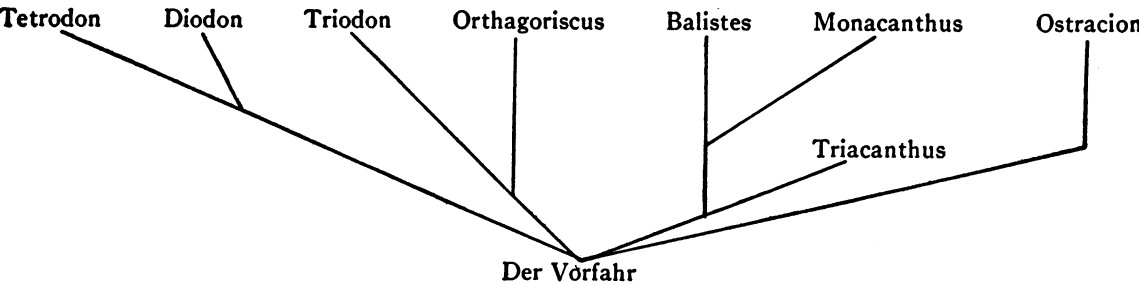
rather similar to the present concepts. By placing *Triodon* in a separate suborder and relating it to *Mola* (*Orthagoriscus*), it is, in our opinion, much too far removed from its evident affinities within the Sclerodermi. Other differences are essentially trivial.

Among many other interesting structural items discussed by Kaschkaroff is the confluence of the digestive tract and the urogenital tract which he figures for *Balistes* and *Monacanthus*. Unfortunately he did not have a specimen of *Triodon* available. In this form the development of this condition is much more marked, as has been indicated previously. Kaschkaroff uses the term "Kloake" for the connection with the common exterior opening. (In a functional sense this is of necessity a cloaca and to that extent sets these fishes apart from all other teleosts.) This structure is evidently based on the backward extension of the ventral flap which the movable pelvis serves to expand. In *Triodon*, as previously shown, this is a very large, flattened, triangular pit with the "cloacal" opening a long slit in the edge of the flap at a point where it merges into the body posteriorly.

Taking the available data on the Plectognathi, it is possible to construct a table, such as table 2, which shows at once resemblances and differences between the various groups as well as indicating the unknown items that would help to a better understanding of the problems of the relationships of these highly specialized fishes. It shows at once the essential similarities and differences, and on it as well as on other considerations not so readily expressed by tabular arrangement the phylogenetic tree of figure 8 has been constructed. In many ways this resembles the tree of Kaschkaroff (1914) but has been modified and extended by data not available to him.

For present purposes none of the current classifications of the Order Plectognathi is followed exactly. The divisions here used are more finely split than those of Berg (1940) but not so finely drawn as those of Fraser-Brunner (1935a, 1935b, 1940a, 1940b, 1941a, 1941b, 1941c, 1943) and to this extent may be considered as more or less of a compromise between them. Reasons for minor divergencies from them have been already indicated. As here used, the divisions accepted are listed

below, for which no especial plea is made at this time other than to point out that this arrangement makes for considerable convenience in connection with the present discussion and we hope serves to clarify our interpretations.

Order Plectognathi
  Suborder Sclerodermi
    Spinacanthidae[1]
    Triacanthidae
      Triacanthodinae
      Triacanthinae
    Balistidae
    Monacanthidae
      Monacanthinae
      Aluterinae
    Triodontidae
  Suborder Ostracodermi
    Ostraciidae
      Aracaninae
      Ostraciinae
  Suborder Gymnodontes
    Tetraodontidae
      Canthigasterinae
      Lagocephalinae
      Colomesinae
      Tetraodontinae
      Chonerhininae
    Diodontidae
  Suborder Moloidei
    Molidae

It will be noted from this list that no hope of aid can be had by appealing to the fossil evidence, for aside from a few evident triacanthid-like remains (Spinacanthidae) and some fused teeth, evidently plectognath and not scarid (Trigonodontidae), there is nothing. Thus the evidence in living forms is all that can be used as a basis of inference.

Figure 8 indicates pictorially our present concepts of the family relationships within the Order Plectognathi, superimposed on which are the indicated limits of various "taxonomic" characters in which each suborder is separated from the others in the four groups recognized, while the only character that cuts across these groups is indicated by a dashed line.

That the Triacanthidae should be placed at the base of the plectognath stem seems to call for no comment, as all authors agree that

[1] Fossil only. Incertae sedis: Trigonodontidae; upper Cretaceous to Pliocene. Formerly referred to the Scaridae.

they are related to the acanthurids and through them to the chaetodontids. Indeed, as already noted, certain authorities (Goodrich, 1909, and Gregory, 1933) group them all together.

The Balistidae and the Monacanthidae stem naturally from some triacanthid-like form. Evidently most authors consider the Monacanthidae as having been derived from the Balistidae, which would presuppose that they passed through a stage bearing the trigger mechanism. Whether they did or not is apparently indeterminate, which is the reason for placing the branch leading to the Mona-
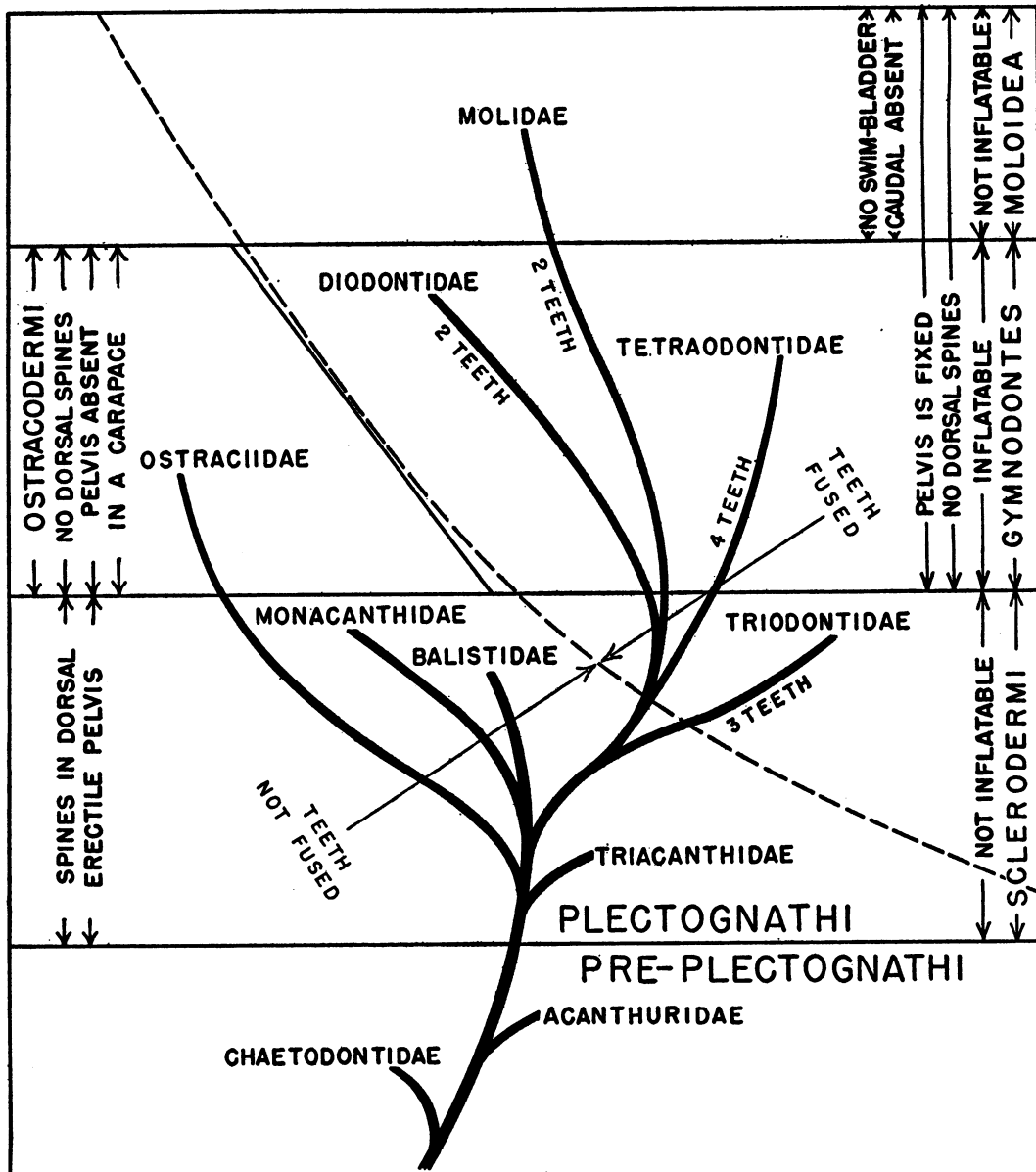
FIG. 8. Phylogenetic tree of the Plectognathi. Suborders enclosed in straight solid lines. Overlapping character indicated by dashed line. Limits of certain characters indicated by arrows. See text for full explanation.

canthidae as springing from some point below the Balistidae rather than passing through it. Fraser-Brunner (1941b), calling attention to the difficulties in generic separation of the former, shows a phylogenetic tree of the genera of this complicated family.

The Ostraciidae, superficially very different looking fishes, have been generally considered as actually close to the Balistidae on a basis of skull characters. For example, Gregory (1933) wrote, "But when the armor is stripped off, the skull . . . is seen to be fundamentally identical with that of *Balistes* with but few minor changes." Despite this, the many other changes, including the development of a carapace, the loss of the pelvis, the excerted eyes, the apparent loss of the palatine, the extensive opercular changes, the differences in the digestive tract, and the resemblance of the ontogeny to that of the Gymnodontes rather than to the Sclerodermi, suggest that these fishes are considerably removed from the balistids and arose at some point along the line leading from the triacanthids to the balistids at a point before the peculiarities of the balistids were introduced.

All the other plectognaths have fused teeth. The Triodontidae evidently arose at some point further along than did the Ostraciidae, after a time when the erectile pelvis was developed. Aside from the loss of fin spines and the development of a more or less gymnodontid-like appearance, *Triodon* is largely balistid in nature. Examination of this form, as here reported, shows no inflatable diverticulum of the gut. Gregory (1933) wrote, "In *Triodon bursarius* of the Indian Ocean we have an important structural link between the balistid stock on the one hand and the puffers (tetraodonts) and porcupine-fish (diodonts) on the other. Regan (1929, p. 325) reported that *Triodon* has an air sac or diverticulum of the oesophagus like the puffers and the porcupine-fishes which is clearly not the case. He noted that it retains the pelvis which these others have lost and it '. . . resembles the Balistidae in having the pelvis a long movable bone that dilates the air sac. It differs, however, in having no spinous dorsal fin and in having the teeth represented by a beak.'" Aside from lacking an inflatable sac, this form

is essentially as described by Goodrich (1909) and Regan (1929). The stem leading to this form and to the other beaked plectognaths evidently branched early.

The branch leading to the Gymnodontes and the Moloidea lost the erectile pelvis and has instead an inflatable sac. A lack of intermediate forms handicaps any attempt to understand more clearly the details of this complex of mixed characters. The Diodontidae divide nicely from the more advanced Tetraodontidae and evidently lead back to some form retaining the pelvis not unlike *Triodon*. Of this Gregory (1933) wrote, "Although excessively specialized in the form of the body, the Molidae retain gills on all four branchial arches instead of on three only, as in both tetraodontids and diodontids (Tate Regan, 1929, p. 325); their beak is undivided as in the diodontids but in their osteology they are very similar to the Tetrodontidae (Regan). Their larvae also suggest close relationship with the Diodontidae. Hence we may assume that they are an offshoot of the common stock of the tetrodontids."

Fraser-Brunner (1943) made the following interpretation: "The Diodontidae also is probably derived from the same stem as the Tetraodontidae, its skull having more in common with that family and with the Chonerhinidae than with the Lagocephalidae.

"The Molidae, on the other hand, is certainly not derived from a *Diodon*-like form, as usually supposed, despite the complete fusion of the jaws. Apart from that character, the skull is almost exactly similar to that of *Lagocephalus*, even possessing the posterolateral limbs on the frontals characteristic of that genus. The Molidae must, in my view, be considered to have arisen from the same main stem as the rest of the Tetraodontoidea but probably earlier, for it lacks certain of their specialized features, such as the absence of the fourth gill, the expansion of the first branchiostegal, the air-sac and so on, while, of course, developing its own grotesque modifications."

This is taken to indicate again that the three families diverged from each other at not too remote place on a tree, perhaps just at about the point that led to the Gymnodontes and Moloidei respectively.

SUMMARY

1. THE GROSS MORPHOLOGY of digestive tracts of all the suborders of the Plectognathi are described from representatives, with especial reference to the development of the mechanism of inflation.

2. The structure and operation of the inflation mechanism are discussed in detail.

3. The capacity for inflation of *Spheroides maculatus* is shown to vary directly with the length of the fish and to be proportional to the volume of a sphere, the diameter of which is 61 per cent of the standard length.

4. The comparative ontogeny of the various groups is discussed.

5. The ontogeny of *Acanthostracion quadricornis* is described and figured and shown to resemble that of the Gymnodontes more closely than that of the Sclerodermi.

6. The phylogeny of the Plectognathi is discussed in its broader aspects.

BIBLIOGRAPHY

BERG, L. S.
1940. Classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. U.R.S.S., vol. 5, pp. 7–517.

BLEEKER, PIETER
1865. Atlas ichthyologique des Indes Orientales Néerlandaises, publié sans le auspices du gouvernement colonial néerlandais. Amsterdam, vol. 5, p. 84.

BOULENGER, E. S.
1904. Systematic account of the Teleostei. Cambridge Nat. Hist., vol. 7, pp. 541–727.

BREDER, C. M., JR.
1926. The locomotion of fishes. Zoologica, vol. 4, pp. 159–297.
1942. On the phenomenon of locomotor disorganization induced by strong light in small plectognath fishes. Copeia, no. 4, pp. 211–213.
1946. An analysis of the deceptive resemblances of fishes to plant parts, with critical remarks on protective coloration, mimicry and adaptation. Bull. Bingham Oceanogr. Lab., vol. 10, art. 2, pp. 1–49.

BREDER, C. M., JR., AND J. E. HARRIS
1935. The effect of light on the orientation and stability of young plectognath fishes. Papers Tortugas Lab., vol. 29, pp. 23–36.

BREDER, C. M., JR., AND PRISCILLA RASQUIN
1943. Chemical sensory reactions in the Mexican blind characins. Zoologica, vol. 28, pp. 169–200.

BRISOUT DE BARNVILLE, C.
1846. Note sur les diodoniens. Rev. Zool., pp. 136–143.

BURKENROAD, M. D.
1931. Notes on the sound-producing marine fishes of Louisiana. Copeia, no. 1, pp. 20–28.

COHN, FRITZ
1912. *Tetrodon* cf. *T. cutcutia*, seine Pflege und Zucht. Blätt. Aquar.- Terrarienk., vol. 23, pp. 582–585.

CUVIER, G. L. C. F. D.
1836. Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Troisieme edition. Paris, vols. 7 and 8.

DARESTE, CAMILLE
1850. Recherches sur la classification des poissons de l'ordre des Plectognathes. Ann. Sci. Nat. (Zool.), ser. 3, vol. 14, pp. 105–133.

EBINA, KEN-ICHI
1932. Sexual dimorphism in a file fish, *Cantherines modestus* (Gunther). Jour. Imp. Fish. Inst., Tokyo, vol. 27, pp. 15–18.

FRASER-BRUNNER, A.
1935a. Notes on the plectognath fishes. I. A synopsis of the genera of the family Balistidae. Ann. Mag. Nat. Hist., ser. 10, vol. 15, pp. 658–675.
1935b. Notes on the plectognath fishes. II. A synopsis of the genera of the family Ostraciontidae. *Ibid.*, ser. 10, vol. 16, pp. 313–320.
1940a. Notes on the plectognath fishes. III. On *Monacanthus setifer* and related species, with a key to the genus *Stephanolepis* and descriptions of four new species. *Ibid.*, ser. 11, vol. 5, pp. 518–536.
1940b. Notes on the plectognath fishes. IV. Sexual dimorphism in the family Ostraciontidae. *Ibid.*, ser. 11, vol. 6, pp. 390–392.
1941a. Notes on the plectognath fishes. V. The families of triacanthiform fishes, with a synopsis of the genera and description of a new species. *Ibid.*, ser. 11, vol. 7, pp. 420–430.

1941b. Notes on the plectognath fishes. VI. A synopsis of the genera of the family Aluteridae and descriptions of seven new species. *Ibid.*, ser. 11, vol. 8, pp. 176–199.

1941c. Notes on the plectognath fishes. VII. The Aracanidae, a distinct family of ostraciontoid fishes, with descriptions of two new species. *Ibid.*, ser. 11, vol. 8, pp. 306–313.

1943. Notes on the plectognath fishes. VIII. The classification of the suborder Tetraodontoidea, with a synopsis of the genera. *Ibid.*, ser. 11, vol. 10, pp. 1–18.

GABRIEL, M. L.
1940. The inflation mechanism of *Spheroides maculatus*. Biol. Bull., vol. 79, p. 372. [Abstract.]

GOODRICH, E. S.
1909. Vertebrata, craniata (cyclostomes and fishes). *In* Lankester, E. R., Treatise on zoology, vol. 9. London, xvi +518 pp.

GREGORY, W. K.
1933. Fish skulls: A study of the evolution of natural mechanisms. Trans. Amer. Phil. Soc., vol. 23, pp. 75–481.

GREGORY, W. K., AND H. C. RAVEN
1934. Notes on the anatomy and relationships of the ocean sunfish (*Mola mola*). Copeia, no. 4, pp. 145–151.

GUDGER, E. W.
1935. Some undescribed young of the pointed-tailed ocean sunfish, *Masturus lanceolatus*. Copeia, no. 1, pp. 35–38.

1936. From atom to colossus. Nat. Hist., vol. 38, pp. 26–30.

1937a. The structure and development of the pointed-tail of the ocean sunfish, *Masturus lanceolatus*. Ann. Mag. Nat. Hist., ser. 10, vol. 19, pp. 1–46.

1937b. The natural history and geographical distribution of the pointed-tailed ocean sunfish (*Masturus lanceolatus*), with notes on the shape of the tail. Proc. Zool. Soc. London, ser. A, pt. 3, pp. 353–396.

1939. Three six-inch pointed-tailed ocean sunfish, *Masturus lanceolatus*, the largest post-larva on record. Jour. Elisha Mitchell Sci. Soc., vol. 55, pp. 305–313.

GÜNTHER, ALBERT
1870. Catalogue of the fishes of the British Museum. London, vol. 8, p. 270.

HERRE, A. W. C. T.
1924. Poisonous and worthless fishes. An account of Philippine plectognaths. Philippine Jour. Sci., vol. 25, pp. 415–511.

1925. A supplement to poisonous and worthless fishes. *Ibid.*, vol. 27, pp. 167–168.

HILDEBRAND, S. F., AND L. E. CABLE
1930. Development and life history of fourteen teleostean fishes at Beaufort, N. C. Bull. U. S. Bur. Fish., vol. 46, pp. 383–488.

HINSCHE, G.
1928. Kampfreaktionen bei einheimischen Anuran. Biol. Zentralbl., vol. 48, pp. 577–616.

HOLLARD, H. L. G.
1853. Monographie de la famille des balistides. Ann. Sci. Nat. (Zool.), ser. 3, vol. 20, pp. 71–114.

1860. Mémoire sur le squelette des poissons plectognathes, étudié au point de vue des caractères qu'il peut fournir pour la classification. *Ibid.*, ser. 4, vol. 13, pp. 5–46.

JACKSON, J. B. S.
1848. Observation on the mode of inflation in *Tetraodon turgidus*. Proc. Boston Soc. Nat. Hist., vol. 2, p. 52.

JORDAN, D. S., AND J. O. SNYDER
1901. A review of the gymnodont fishes of Japan. Proc. U. S. Natl. Mus., vol. 24, pp. 229–264.

KASCHKAROFF, D. N.
1914. Materialien zur vergleichenden Morphologie der Fische. Vergleichendes Studium der Organisation von Plectognathi. Bull. Soc. Nat. Moscou, new ser., vol. 27, pp. 263–370.

LESSON, R. P.
1826. Voyage autour du monde, executé par ordre du roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822–1825, ... par M. L. I. Duperrey. Histoire naturelle, Zoologie. Paris, atlas.

McCULLOUGH, A. R.
1912. A description and figures of three specimens of *Malacanthus*. Proc. Linnean Soc. New South Wales, vol. 37, pp. 553–555.

MUNRO, I. S. R.
1945. Postlarval stages of Australian fishes—No. 1. Mem. Queensland Mus., vol. 12, pp. 135–153.

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

NOBLE, G. K.
1931. The biology of the Amphibia. New York, xiii +577 pp.

PARR, A. E.
1927. On the functions and morphology of the

post clavicular apparatus in *Spheroides* and *Chilomycterus*. Zoologica, vol. 9, pp. 245–269.

PUTNAM, F. W.
1871. On the young of *Orthagoriscus mola*. Proc. Amer. Assoc. Adv. Sci., 19th meet., pp. 255–260.

RANDOW, HEINZ
1934. *Tetrodon cutcutia* and *Tetrodon fluviatilis* Hamilton-Buchanan. Wochenschr. Aquar.- Terrarienk., vol. 31, pp. 561–563.

RAVEN, H. C.
1939a. On the anatomy and evolution of the locomotor apparatus of the nipple-tailed ocean sunfish (*Masturus lanceolatus*). Bull. Amer. Mus. Nat. Hist., vol. 76, pp. 143–150.
1939b. Notes on the anatomy of *Ranzania truncata*, a plectognath fish. Amer. Mus. Novitates, no. 1038, pp. 1–7.

REGAN, C. T.
1902. On the classification of the fishes of the suborder Plectognathi; with notes and descriptions of new species from specimens in the British Museum collection. Proc. Zool. Soc. London, pt. 2, pp. 284–303.
1929. Fishes. *In* Encyclopaedia Britannica. 14th ed. London and New York, vol. 9, pp. 305–329.

ROSEN, NILS
1912. Studies on the plectognaths. 2. The air sac, with notes on other parts of the intestines. Arkiv Zool., Uppsala, vol. 7, no. 30, pp. 1–23.
1913. Studies on the plectognaths. 4. The body muscles. *Ibid.*, vol. 8, no. 18, pp. 1–14.

SCHMIDT, JOHANNES
1921a. Contributions to the knowledge of the young of the sunfishes (*Mola* and *Ranzania*). Meddel. Komm. Havundersøg., ser. Fiskeri, vol. 6, no. 6, pp. 1–15.
1921b. New studies of sunfishes made during the "Dana" expedition, 1920. Nature, London, vol. 107, pp. 76–79.
1929. Further studies of sunfishes made during the "Dana" expedition, 1921–1922. *Ibid.*, vol. 117, pp. 80–81.
1932. Dana's Togt omkring Jorden, 1928–1930. Copenhagen, 369 pp.

SCHREITMULLER, WILHELM
1929. *Tetrodon fluviatilis* (Ham-Buch) green ballfish. Aquatic Life, vol. 13, pp. 23–24.
1930a. Vom Aufblasen der Kugel- und Igelfische und alles unter Wasser. Wochenschr. Aquar.- Terrarienk., vol. 27, pp. 472–473.
1930b. Kugelfische. Aquarium, Berlin, vol. 4, pp. 12–16, 20–26.

TANAKA, SHIGEHO
1931. On the distribution of fishes in Japanese waters. Jour. Fac. Sci. Imp. Univ. Tokyo, Zool., vol. 3, p. 5.

THILO, OTTO
1899. Die Entstehung der Luftsacke bei den Kugelfischen. Anat. Anz., vol. 16, pp. 73–87.

TOWER, R. W.
1908. Production of sound in drumfish, toadfish, and searobins. Ann. New York Acad. Sci., vol. 18, pp. 149–180.

WELSH, W. W., AND C. M. BREDER, JR.
1922. A contribution to the life history of the puffer, *Spheroides maculatus* (Schneider). Zoologica, vol. 2, pp. 261–276.

ABBREVIATIONS USED IN THE FIGURES

a., anus
ab.c., abdominal cavity
ab.s., abdominal sac
d., duodenum
g.a., genital aperture
h.d., hepatic duct
i., intestine
l.o., left ovary
m., mouth
oes., oesophagus
oes. s., oesophageal sphincter

pc., pseudocloaca
ph., pharynx
py., pylorus
py.c., pyloric caeca
r., rectum
r.m., retractor muscle of pelvic bone
s.ab.c., sac from floor of abdominal cavity
s.s.s., sac-stomach separation
st., stomach
t.p., tip of pelvic bone