
*On the Anatomy and Evolution of the Locomotor Apparatus of the
Nipple-tailed Ocean Sunfish (*Masturus lanceolatus*)*

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Article IV.—ON THE ANATOMY AND EVOLUTION OF THE LOCOMOTOR APPARATUS OF THE NIPPLE-TAILED OCEAN SUNFISH (*MASTURUS LANCEOLATUS*)

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PLATE II; TEXT FIGURE 1

INTRODUCTION

Since the acquisition in 1932 by The American Museum of Natural History of a specimen of *Mola mola*, certain aspects of the anatomy of which were reported upon by Dr. William K. Gregory and myself (1934), our interest in the ocean sunfishes has continued. This interest was further stimulated by the securing, through the efforts of Dr. E. W. Gudger of the Department of Ichthyology, of a specimen of the nipple-tailed ocean sunfish (*Masturus lanceolatus*) from Florida. This fine specimen came packed in ice as a gift from Mr. Albert Pflueger, naturalist and taxidermist, of Miami, Florida. A plaster mold of the fish was made and from this were taken casts of the left and right sides. The former hangs in the Hall of Fishes of the American Museum, while the latter is in the British Museum (Natural History). The specimen was then turned over to me for dissection and study.

In his work on "Fish Skulls: A Study of the Evolution of Natural Mechanisms," Doctor Gregory (1933) summarized the probable evolution of the plectognaths as follows:

... when the advanced stage of specialization that is seen in *Xesurus* is reached one might well doubt the ability of Nature to produce viable creatures of any greater degree of specialization. But Nature's limits are not so easily determined. Not satisfied, as it were, with *Xesurus*, she next evolved the triggerfish (*Balistes*), going on to *Aleutera*, which is a libel even on *Balistes*, and culminating in *Anacanthus*, which is almost a tube-fish in appearance. Returning to the pre-balistid model, she made some minor changes and brought out the trunk-fish. Rising then to more daring improvisations, she invented the unique mechanisms of the puffers. But each new "invention" implies also a further sacrifice of the capital stock of well-tried, normal fish arrangements of the earlier types, so that when *Mola* at last issues from Nature's experimental laboratory its grotesque body might appear to the inexperienced to be

fearfully handicapped by intensive specialization. *Ranzania* is then brought forward, an elongated *Mola*, the latest but perhaps not the last word in the evolution of the plectognaths.

In seeking clues to the high specializations seen in a dissection of *Mola* and *Masturus*, a morphologic series of related but less specialized fishes was selected. It was assumed that if the series suggested by Doctor Gregory on the basis of the osteology of the skull were anything like a phylogenetic series, other parts of the anatomy of the animals in the series should reflect and corroborate his contentions.

Roccus lineatus, the striped bass, a normal-bodied percomorph fish was taken as the starting point of the series. The second stage is represented by the acanthurid genus *Hepatus*, the third by the triggerfish *Balistes* and the fourth by the porcupine fish *Diodon*. The fifth stage is a hypothetical intermediate based partly on *Diodon*, partly on the larval and partly on the adult *Masturus*. The sixth or final stage in the series is the nipple-tailed ocean sunfish *Masturus*.

Dissections of various layers of muscles in each member of the chosen series of fishes were made and recorded by photographs and by drawings made under the author's direction by Mrs. Helen Ziska and lettered by Miss D. F. L. Bradley. They are arranged so that the whole series can be compared at the same time.

BODY FORM AND FINS

I will now describe the body forms in the series, beginning with *Roccus* (Pl. II, fig. 1, A-F), which has a rounded body and a head without evident specializations. Taking next *Hepatus*, its body is more compressed, that is, deeper, with a more elongated head. *Balistes* exaggerates still further the specializations in

Hepatus. *Diodon* seems to have evolved in a different direction, so that there is a secondary widening of the body, resulting in a body comparatively round in section. *Masturus*, beginning from a form which possessed a head somewhat like that of *Diodon*, has again become compressed into a deep-bodied form.

To follow through this same series (Pl. II, fig. 1, A-F) again with reference to the mouth, that of *Roccus* is comparatively large and, as in a normal predaceous fish, provided with a great number of small teeth. In *Hepatus* the mouth is much reduced in size but the head is elongate as well as deep. It has numerous small teeth. *Balistes* has a head even longer than that of *Hepatus*, a mouth as small or smaller, with a reduction in the number of teeth. *Diodon* has a less compressed head and mouth, with the teeth fused to form a specialized beak. *Masturus* has the same type of head as in *Diodon*, somewhat deepened and with the teeth likewise fused, forming a beak.

The gill-opening (Pl. II, fig. 1, A-F) in *Roccus* is very large, extending from the dorsal to the ventral surface of the head. In *Hepatus* it is still large but occupies only about two-thirds of the distance from the ventral to the dorsal surface of the head. In *Balistes* it is reduced much further, so that the opening is not more than one-fourth that seen in *Roccus*, while in *Diodon* and *Masturus* it is reduced to a mere spiracle.

As to body covering (Pl. II, fig. 1, A-F), the scales of *Roccus* are those typical of normal percomorphs. In *Hepatus* they are somewhat reduced though of the same character. In *Balistes* their character has changed and resembles somewhat the ganoid type, whereas in *Diodon* the body is covered with strong imbricated spines and in *Masturus* a further specialization has produced pebble-like scales, each with a minute spine beneath which is enormously thickened collagenous skin.

The pectoral fins (Pl. II, fig. 1, A-F) in *Roccus* are well developed, as in typical percomorphs. In *Hepatus* they are more strongly developed, and of primary importance in swimming. In *Balistes* the

external portion of the fin is short and rounded and somewhat higher on the side of the body. In *Diodon* it is still higher, though of the *Balistes* type. The reduction has been carried further in *Masturus*, so that the pectoral fin is probably used only as a balancer.

The pelvic fins (Pl. II, figs. 1, A-F, and v, A-F) in *Roccus* have spines and soft rays typical of percomorphs. In *Hepatus* the pelvics are more slender, while in *Balistes* they have been lost entirely as fins though the bases of the fins and their joints with the pelvic bones remain. In both *Diodon* and *Masturus* all traces of the pelvis have been lost.

The spiny dorsal (Pl. II, figs. 1, A-F, and v, A-F), well developed in *Roccus*, is separated from the soft dorsal. In *Hepatus*, although the spiny dorsal is well developed, it is continuous with the soft dorsal. In *Balistes* the spiny dorsal is very much reduced in the number of its spines, those which remain being specialized as in a trigger mechanism. In *Diodon* and in *Masturus* all trace externally of the spiny dorsal has been lost.

The soft dorsal (Pl. II, fig. 1, A-F) in *Roccus* is more or less paired with the anal and moderately developed. In *Hepatus* the soft dorsal is better developed than it is in *Roccus* and is paired with the enlarged anal. In *Balistes* the soft dorsal is still more specialized and differentiated in that the anterior rays are elongate. The same is true of the anal. In *Diodon* the soft dorsal is shorter antero-posteriorly than in *Balistes* and of the same size, though not exactly paired with the anal. In *Masturus* the soft dorsal and anal are very high, short antero-posteriorly and paired.

In *Roccus* the caudal fin (Pl. II, fig. 1, A-F; v, A-F) is of the normal homocercal type. The same is true of *Hepatus* and *Balistes*. In *Diodon* it is proportionately smaller and weaker. In *Masturus*, what appears to be the tail is a greatly expanded skin-covered mass with no free dermal rays.

MUSCULATURE

In primitive forms of recent fishes the myosepta form V's with their apices di-

rected caudally; dorsal to the lateral line are two such V's, and two more are ventral to the lateral line. The most dorsal and most ventral V's, or parts of this metameric musculature, soon become specialized in bony fishes into longitudinal muscles, which lose their metameric character. Thus if we examine the musculature of an ordinary bony fish such as the salmon, it is at once evident that it is the parts of the metameric musculature just dorsal, epaxial, and just ventral, hypaxial, to the lateral line, which have become dominant. These parts of the metameric musculature seem no sooner to have reached this advanced stage, where they extend from the lateral line dorsally nearly to the dorsal midline and ventrally nearly to the mid-ventral line, than they begin to divide into superficial and deep parts. The first of these superficial longitudinal muscles to be formed is one called by Greene and Greene (1915) *Musculus lateralis superficialis*, which is thin and parallel with the lateral line. It is thickest at the lateral line and both its epaxial and its hypaxial divisions become thinner as they extend dorsally and ventrally from the lateral line.

When a generalized grade of plectognath organization is reached, such as that seen in *Balistes*, it is much more specialized than that seen, for instance, in *Perca fluviatilis* (Owen, 1866). In *Balistes* the *Musculus lateralis superficialis* is better developed than in either the salmon or the perch and has lost some of its metameric character. In *Balistes*, furthermore, the deep layer of metameric musculature in the region of the body cavity is more specialized than in the perch, in that the fibers of the lower section of that muscle which extend dorso-caudally, instead of stopping at the angles formed by the myocommata, overlap them and reach nearly to the lateral line, thus obscuring the V's (Pl. II, fig. III, c).

With the specialization of *Balistes* away from the more normal percoid form of body, which resulted in a deeper, shorter fish, and with the changes mentioned above in the musculature, there has also been a decided reduction in the thickness of the

muscles of the body wall and a shortening of the ribs. These latter characters are doubtless related to the habit of inflating the body cavity slightly when the pelvic and dorsal and anal spines are erected as a means of defense.

Upon removal of the skin (Pl. II, fig. II, A-F) there may be seen at the base of the dorsal and anal fins extremely thin, small muscles arising from a fascia just beneath the skin and inserting on the postero-lateral aspect of the base of each dermal ray. These muscles are known as the *Musculus inclinator dorsalis* of the dorsal fin and *M. inclinator analis* of the anal fin. In *Roccus* these muscles are quite uniform. The same is true of *Hepatus*. In *Balistes* the *inclinator dorsalis* is much more pronounced than it is in *Roccus* and *Hepatus* but still uniform. The *inclinator analis* in *Balistes* has its anterior segments much enlarged. In *Diodon* the *inclinator dorsalis* forms a thin muscular sheath arising far forward on the lateral aspect of the body and, extending postero-dorsally, separates into segments only at its insertion. In this form, too, the *inclinator analis* covers the whole ventral aspect of the body, merging with the *inclinator dorsalis* on the side and extending backward, inserting by separate digitations on the rays of the anal fin. In *Masturus* the *inclinator dorsalis* and *analis* have been lost, for in *Masturus* there are no muscles having the same extent that the *inclinator*s have in *Diodon*.

In *Roccus* the metameric musculature (Pl. II, fig. III, A-F), as in most normal-bodied fishes, comprises more than ninety per cent of the total musculature, and the characteristic metameric arrangement is not interrupted. In *Hepatus* the total metameric musculature is slightly less than in *Roccus* and is interrupted in the abdominal region by the extremely long postcleithrum. In *Balistes* the proportion of fin musculature to metameric musculature has increased. Furthermore, the metameric musculature in the region of the body cavity is not only interrupted by the postcleithrum but the fibers of the *lateralis* mass overlap the myosepta so that the V-pattern is lost, and the air-

bladder, close to the shoulder-girdle, has herniated through the metameric musculature so that it comes in contact with the skin, forming the well-known tympanum. There is a greater gap between *Balistes* and *Diodon* than between *Balistes* and *Hepatus*. Nevertheless, *Diodon* clearly indicates the evolutionary degeneration of the metameric musculature, for in *Diodon* no metameric musculature is lateral to, or ventral to, the body cavity. This goes with the reduction of its tail and its more or less ostraciiform structure, which permits much less wriggling motion. In figure E (Pl. II), the hypothetical intermediate, this metameric musculature is presumed to be still more reduced, so that it does not reach the anterior vertebrae; and in *Masturus* this metameric musculature has been entirely lost.

Upon removal of the metameric musculature in *Roccus* (Pl. II, fig. iv, A-F), the erectors and depressors of the dorsal and anal fins are exposed. The erectors and depressors of the dorsal fin take their origin from the pterygiophores, or radials. The erectors insert on the anterior aspect of the base of each fin ray, the depressors on the posterior part of the base of each fin ray. They are uniform in size throughout. In the anal fin, however, the anterior erectors and depressors are somewhat enlarged, corresponding to the enlargement of the anterior spines of the anal fin. Nevertheless, in *Roccus* these muscles are comparatively small. In *Hepatus* the anterior ones are clearly larger, and in *Balistes* still larger and the individual segments very much longer. However, the skeleton shows that the pterygiophores do not reach nearly to the centra between the neural and haemal spines. In *Diodon* the erectors and depressors have enlarged to such an extent that they do reach the column, that is, the dorsal series of muscles meets the anal series on either side. In the hypothetical intermediate stage (Pl. II, fig. E), the erectors and depressors of the dorsal and anal fins have usurped much of the territory of the metameric musculature. In *Masturus*, with the complete elimination of the metameric muscu-

lature, they have become the sole locomotor equipment.

LOCOMOTION

It appears that the erectors and depressors of the dorsal and anal fins have in the plectognaths undergone a change of function. In typical percomorphs like *Roccus* the right and left erectors of each fin ray work together to erect it, and, likewise, a pair of depressors are their antagonists. In the plectognaths, that swim principally by waving the dorsal and anal fins from side to side, the action is accomplished by all the erectors, depressors and inclinators (where the latter exist) of one side working together serially to warp the fin toward that side and being opposed by all those muscles of the opposite side. In *Roccus* the inclination of the dorsal and anal fins is slight and is accomplished by the action of the inclinators alone. Ryder (1866) clearly described the fin movements in a large *Mola*, as follows:

One does not need to watch this fish long in its native element to discover that the great dorsal and anal fins are almost its sole organs of propulsion. In the figure, both are shown with their tips thrown over to the right side. This movement is synchronous in these great fins; that is, both strike in the same direction at the same time. But the most remarkable feature about them is, that they are twisted into the form of the blade of a propeller-wheel at the commencement of each stroke, as shown (not very clearly) in the figure, where the foreshortened dorsal is indicated in the condition which it presents at the moment when the stroke to the left is about to begin. The direction of the peculiar twist of these fins is also reversed at each successive stroke, in opposite directions, so that a most effective propelling apparatus exists, which it would be somewhat difficult to imitate by a mechanical device. This contrivance is rendered all the more effective in consequence also of the great width of the fish, by which great stability is secured.

A very peculiar soft oval ring of dermal tissue around the bases of the dorsal and anal, renders them readily movable by means of the tendinous terminations of the muscles which are inserted into the strong bases of their rays. A similar band of soft dermal tissue is found on both sides of the base of the broad, crenulated, rigid tail, which is moved on its base just as the rigid rudder-blade of a vessel is moved by means of the rudder-chains. In the case of *Mola*, however, the single pair of rudder-chains as found

in a vessel is replaced by a single series of tendons on either side of the median line, running parallel, and passing through round canals in the soft elastic base of the caudal, and inserted into the bases of the caudal rays.

The office of the curiously modified caudal of *Mola* seems to be solely that of a rudder, no vibration whatever of the tail being apparent when the animal is swimming in a straight line. Only when the creature wishes to turn is it deflected from the median line at its tip; and even then its apex sweeps through an arc of not more than twenty-five degrees at most, usually much less.

The pectorals are comparatively small, and, in swimming in a straight line, are extended horizontally and kept rigid and motionless by the animal, as if merely for the purpose of keeping the body vertical. When swimming with the sides of the body at an angle with the plane of the horizon, one or the other of the pectorals is folded closely against the side.

It thus becomes evident that *Mola* uses almost exclusively the dorsal and anal fins as locomotive appendages, and that the tail and pectorals act, respectively, as the rudder and as balancers, and take no active, but only a very subordinate, share in effecting the creature's movements. Even the rudder-like tail may be said to be defective; for it was noticed that the fish, when first placed in the pool, was unable to turn quickly enough to avoid bumping its snout against the stone walls at the angles of the enclosure.

Ryder described almost the end stage in plectognath locomotion, the gradual evolution of which becomes evident when one observes locomotion in less specialized plectognaths; for instance, in the young and smaller *Balistes* the dorsal and anal fins are relatively long rostro-caudally, with their very numerous dermal rays separated, one from the other by integument, which allows some freedom of movement. Thus in watching *Balistes* swim I observed the first part of the dorsal and anal fins to sweep toward the same side, synchronously initiating undulations which passed backward in rapid succession as the fore-parts of the fins were inclined from side to side. Thus there were several (four or more) undulations in progress along the fin at once.

In *Canthidermis*, the ocean turbot, a much larger balistid, the anterior or rostral part of both dorsal and anal fins is provided with longer and stronger dermal rays with relatively less integument between the rays; consequently when the

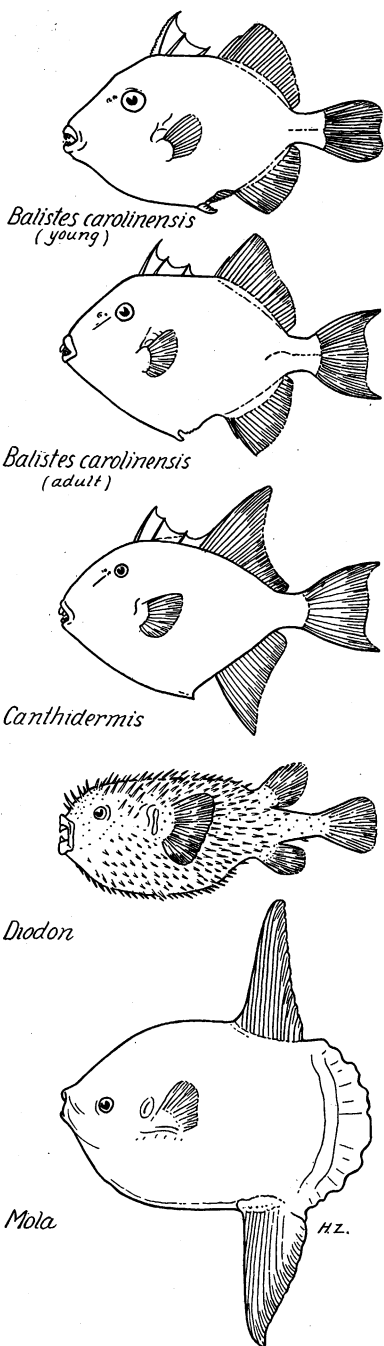


Fig. 1. A series showing change in proportions of anal and dorsal fins in the development of the molid type of locomotion.

fore-part of the fins is inclined from side to side, fewer undulations are produced, not because of any difference in muscular action but purely for mechanical reasons due to the greater length of the anterior fin rays, their proximity to each other, and the smaller number of rays in the fins.

The order of progress toward the molid type would then be from *Balistes*, with 27-29 dorsal and 24-27 anal rays; thence through *Canthidermis*, with 20-27 dorsal and 17-25 anal rays, to the molids, with from 16-19 dorsal and 16-19 anal rays. Figure 1 shows in this same series change in proportions due to the increase in height and decrease in rostro-caudal length of the dorsal and anal fins in the development of the molid type of locomotion.

The movements of the dorsal and anal fins of the molids fall under the Balistiform type of Breder (1926) but are so much modified by the shortening and heightening of the fins that they merit a new descriptive term, MOLIFORM; this has been due to the change of function of the erector and depressor muscles into warping muscles or secondary inclinators. The nearest structural approach is in *Diodon*, but the nearest functional resemblance is in *Canthidermis*.

VISCERA

Plate II, figure IV, A-F, shows the condition of the air-bladder in the series. It will be seen in *Roccus* extending the entire length of the body cavity, lying against the ventral surface of the column. Here it is a thin membranous sac, well known as a functional hydrostatic organ. In *Hepatus* it appears that the air-bladder is functional as in *Roccus*, but due to the shortening of the body cavity, the posterior extremity of the air-bladder forks and extends beyond the third haemal spine. In *Balistes* the duct of the air-bladder is closed, the walls are thickened, the organ itself is shorter and appears to be losing or changing its function. In *Diodon* the duct of the air-bladder is closed, the organ is proportionately about one-half the size of that seen in *Balistes* and its walls are still thicker and more fibrous. In *Mas-*

turus and *Mola* the air-bladder has been entirely lost.

In *Roccus* the body cavity may be said to be normal for percomorph fishes. In *Hepatus*, coincident with the deepening of the body, the body cavity is deeper and shorter than in *Roccus*, doubtless due to the enlargement and forward migration of the anal fin and its related pterygiophores and haemal spines. In *Balistes* the body cavity is still deeper than in *Hepatus* and shows evidence to some extent of the puffing mechanism, which is so much better developed in *Spheroides* (Parr, 1927) and its allies. *Diodon*, which retains a functional puffing apparatus, has a secondarily enlarged body cavity. In *Masturus* the musculature for the anal fin has expanded forward to such an extent that it encroaches on the body cavity, as shown by its position far forward of the first haemal spine, reaching to the fourth post-cranial vertebra.

SKELETON

The vertebrae in *Roccus* are normal. In *Hepatus* there are five dorsals and thirteen caudals, the body cavity being about one-third the length of the entire column. The number is the same in *Balistes* but the anterior dorsals are highly specialized. In *Diodon* there is a total of nineteen vertebrae. In *Masturus* there are eight dorsals and eight caudals in our specimen, but the last caudal seems abnormally long. At first it was thought to be two vertebrae but no suture could be found.

In *Roccus* (Pl. II, fig. v, A-F) the ribs are normal. The same is true of *Hepatus*. In *Balistes* they are very much reduced and do not extend down over the sides of the body cavity. In *Diodon* and *Masturus* they are entirely lost.

In looking at the skeleton of *Roccus* it will be noticed that the pterygiophores barely reach down to the tips of the neural spines, and the pterygiophores of the anal fin likewise barely reach to the tips of the haemal spines. In *Hepatus*, with the enlargement of the erector and depressor muscles, the pterygiophores of both dorsal and anal fins have expanded flattened plates and here the pterygiophores have

more of a connection with the neural and haemal spines. In *Balistes* this tendency has been accentuated so that the pterygiophores form almost a continuous plate, interlocking with the neural and haemal spines. In *Diodon* the pterygiophores of both the dorsal and anal fins approach the centra. In *Masturus* the pterygiophores of the dorsal fin are consecutively interlocked with the neural spines. The same is true of the anal fin and the haemal spines.

The hypural bones in *Roccus* are expanded and bear the caudal fin. The same is true of *Hepatus*, *Balistes*, and *Diodon*. In our paper of 1934, Doctor Gregory and I at first considered that the true tail of *Mola* had been lost. Other evidence, however, made us decide that this was wrong and we concluded that the true tail of *Mola* had been greatly expanded and that the hypurals had been retained. We now feel that our first conclusion, which agrees with that of numerous other authors, was the correct one. The present series and larval specimens of *Masturus* figured by Dr. E. W. Gudger (1937) have strengthened this conclusion. In general, the hypural bones of fishes originate as disconnected haemal arches of the caudal vertebrae. In some individual cases the hypurals and caudal fin rays may be the same in number but their muscular relationships are in no case the same as that to be seen between the pterygiophores and the fin rays. In both *Mola* and *Masturus* the relationship between each dermal ray, its bony or cartilaginous support, and its musculature is exactly the same for the whole series in the dorsal, anal, and pseudocaudal fin. It therefore seems conclusive that the tail fin of *Mola* and *Masturus* is a gephyrocercal tail made secondarily by the migration and fusion of parts of the

dorsal and anal fins. The figures of the larval stages of *Masturus*, which we examined earlier, do not show this evident extension of the dorsal and anal to the true caudal. The later figures, however, in Dr. Gudger's paper, clearly indicate this extension of dorsal and anal fins and the loss during early larval life of the true tail.

ADAPTATIONS

Mola and *Masturus* are occasionally captured in shallow water or at the surface of the sea. It seems that all those taken under such conditions are sickly, for they idle at or near the surface, sometimes on their sides or at an angle, and do not attempt to escape approach by, and attack from boats. Further, many writers have reported sunfishes heavily infested with parasites of many varieties, both external and internal. This sluggishness and the presence of parasites, frequently coupled with an empty stomach, seem to indicate an unhealthy, abnormal condition seen in fishes that are about to die.

It has, however, been observed that *Mola* is capable of rapid movement, as attested by the following quotation from Bigelow and Welsh (1925): "... we have seen one 'come to life' with surprising suddenness and sound swiftly, sculling with strong fin strokes, just before we came within harpoon range."

The small mouth, provided with teeth fused in the form of a hard beak like that of other plectognaths, seems to be adapted to bottom-feeding, probably at considerable depth as they are not seen about shallow reefs.

Further indications that the normal habitat of *Mola* and *Masturus* is in fairly deep water may be their very thick collagenous skin and secondarily chondrified skeletons.

SUMMARY AND CONCLUSIONS

The purpose of this study was to discover, through a structural series from primitive percomorph to *Masturus*, the evolutionary changes which gave rise to the peculiar locomotor apparatus of the molids.

The structural series: (1) generalized

percomorph, (2) acanthurid, (3) balistid, (4) diodont, (5) molid, which was worked out by Gregory on skull structure, was adopted as a provisional basis for the present study and the present study affords additional evidence for its validity.

In general the following major changes

are involved in passing from generalized percomorph to molid:

- (1) great shortening and deepening of body;
- (2) extreme emphasis and vertical growth of dorsal and anal fins;
- (3) corresponding hypertrophy of erector and depressor muscles of dorsal and anal, involving their great extension forward and eventual atrophy and disappearance of mm. inclinatores;
- (4) corresponding reduction and eventual loss of the lateralis mass of metameric musculature;
- (5) correlated reduction and loss of undulation of the body and of the true caudal fin;
- (6) formation of new or pseudo-caudal fin by extension of dorsal and anal, meeting around the shortened caudal end of the column;
- (7) crowding of the posterior dorsal and anal

pterygiophores against the seventh neural and eighth haemal spines;

- (8) crowding of the body cavity by forward growth of the erector plus depressor muscles of the anal fin;
- (9) reduction and loss of the puffing habit (will be treated more fully in a paper on *Ranzania*);
- (10) the long ligament, from supraoccipital crest to the anterior border of the dorsal fin, probably represents a vestige of the trigger mechanism of balistoids.

The characters of the alimentary tract suggest that these fishes are bottom-living forms; the skin, skeleton, and the loss of the air-bladder suggest that they live in deep water and the form of the fins with their powerful muscles indicates an active existence.

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COMPARATIVE SERIES SHOWING EVOLUTION OF LOCOMOTOR APPARATUS IN OCEAN SUNFISH

