

Leis' Conundrum: Homology of the Clavus of the Ocean Sunfishes. 2. Ontogeny of the Median Fins and Axial Skeleton of *Ranzania laevis* (Teleostei, Tetraodontiformes, Molidae)

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ABSTRACT One of the most conspicuous characters of the ocean sunfishes, family Molidae, is the punctuation of the body by a deep, abbreviated, caudal fin-like structure extending vertically between the posterior ends of the dorsal and anal fins, termed the clavus by Fraser-Brunner. Homology of the clavus has been a matter of debate since the first studies on molid anatomy in the early 1800s. Two hypotheses have been proposed: 1) It is a highly modified caudal fin; 2) It is formed by highly modified elements of the dorsal and anal fins. To resolve this homology issue, we studied the ontogeny of the molid vertebral column and median fins and compared it to that of a less morphologically derived gymnodont (see Part 1 of this study), a member of the family Tetraodontidae. We show that in molids the chorda never flexes during development, that the claval rays form from the posterior ends of the dorsal and anal fins toward the middle, thus closing the gap inward, and that elements of the molid clavus have an identical development and composition as the proximal-middle and distal radials of the regular dorsal and anal fins. We thus conclude that the molid clavus is unequivocally formed by modified elements of the dorsal and anal fin and that the caudal fin is lost in molids. *J. Morphol.* 266:11–21, 2005. © 2004 Wiley-Liss, Inc.

KEY WORDS: axial skeleton; median fins; pterygiophores; clavus; ontogeny; homology; Molidae

The ocean sunfishes (Tetraodontiformes: Molidae) include the most massive and some of the most bizarre of the teleost fishes. They comprise three (Nelson, 1994), to five pelagic species (Fraser-Brunner, 1951; Heemstra, 1986), with an almost cosmopolitan distribution. Due to their highly unusual form they have been illustrated in the earliest published books dealing with fishes (Fig. 1; Rondelet, 1554; Gesner, 1558; see historical account in Steenstrup and Lütken, 1898).

Among numerous peculiar autapomorphic features (see Winterbottom, 1974a; Tyler, 1980; Santini and Tyler, 2002), molids are distinctively characterized by a deep, abruptly abbreviated "tail" (Fig. 2), termed the clavus by Fraser-Brunner (1951). The clavus comprises a series of rod-like bones and fin

rays that extend vertically between the posterior-most rays of the dorsal and anal fins (Fig. 2C), the homology of which has remained controversial since the earliest studies of molid anatomy at the beginning of the 19th century (Meckel, 1828; Goodsir, 1841). Two hypotheses about the identity of the clavus have been proposed: 1) it is a highly modified caudal fin (Goodsir, 1841; Cleland, 1862; Schmidt, 1921; Gudger, 1937a,b; Winterbottom, 1974a); 2) it comprises highly modified components of the dorsal and anal fins that have replaced the caudal fin (Ryder, 1886; Boulenger, 1904; Regan, 1903; Raven, 1939a; Fraser-Brunner, 1951; Tyler, 1970a, 1980; Santini and Tyler, 2002). Many previous authors have favored one of these hypotheses (usually the latter) over the other, but have offered little or no explanation for this. Others (Meckel, 1828; Rosén, 1913; Grenholm, 1923; Gregory and Raven, 1934; Leis, 1977) have remained undecided based on the available evidence. The goal of this article is to review the problem of homology of the clavus of molids from an ontogenetic perspective. In Part 1 (Britz and Johnson, 2004) we described the ontogeny of the axial skeleton and the dorsal, anal, and caudal fins and supporting structures in *Monotretes leirus*, a member of the less modified family Tetraodontidae, belonging to the putative sister group of the Molidae. In this second part we provide an account of the ontogeny of the axial skeleton and median fins and their supports in the molid *Ranzania laevis* and compare it with that of the tetraodontid *M. leirus*

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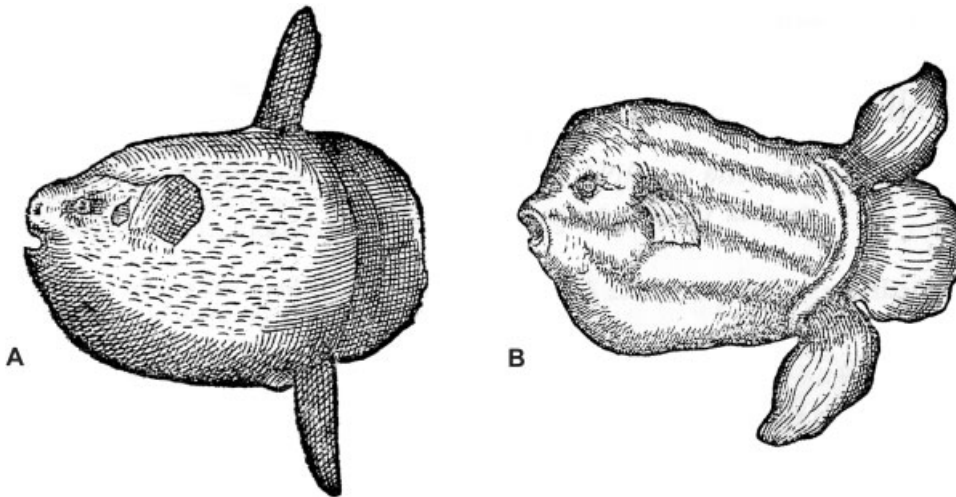


Fig. 1. Reproductions of two of the earliest illustrations of ocean sunfishes. **A:** From Rondelet (1554). **B:** From Gesner (1558).

to elucidate relative modification of various elements.

MATERIALS AND METHODS

We use the following abbreviations in the text: NL, notochord length; PU, preural centrum; SL, standard length. The term “membrane bone” used throughout was adopted from Patterson (1977). Our descriptions and illustrations are based on three developmental stages of cleared and double-stained *Ranzania laevis* following the protocol of Taylor and Van Dyke (1985): 2.1 mm standard length (SL) (MCZ 87036), 4.2 mm SL (MCZ 87035), and 7.2 mm SL (MCZ 87035). Additional material studied comprises: *R. laevis*, 36 alizarin-stained specimens (USNM, uncataloged), 1.7 mm NL–26.6 mm SL; *Masturus lanceolatus*: 5.8 mm SL (USNM uncataloged), 11.5 mm SL (MCZ 157343).

To describe the association between dorsal and anal pterygophores and neural and hemal spines, we have chosen a formula in which neural spines are symbolized by / and hemal spines by \. The number of pterygophores between two successive neural or hemal spines is then indicated with the numerals 1 or 2, so that, e.g., /1/ describes a dorsal-fin pterygophore interdigitating with two subsequent neural spines, and \2\ describes two anal-fin pterygophores interdigitating between two successive hemal spines.

RESULTS

Ranzania laevis 2.1 mm (Fig. 3A,C)

The vertebral column curves ventrally along the first few vertebrae, so that it is oriented at an angle of about 120° to the occipital basicranium. Twelve neural arches, of which the anterior nine belong to abdominal vertebrae, are ossified, decreasing in size posteriorly. The distal tips of the anterior four arches are widely separated in the dorsal midline, those of arches 5–9 succeedingly approach each other more and more closely, and those of arches 10–12 are again widely separated. Centra are developed on the anterior nine vertebrae. Vertebrae 10–12 bear short hemal arches. Eleven cartilaginous dorsal proximal-middle radials are present, the first one short and wide and inserted between neural arches six and seven. The remaining 10 are elongate

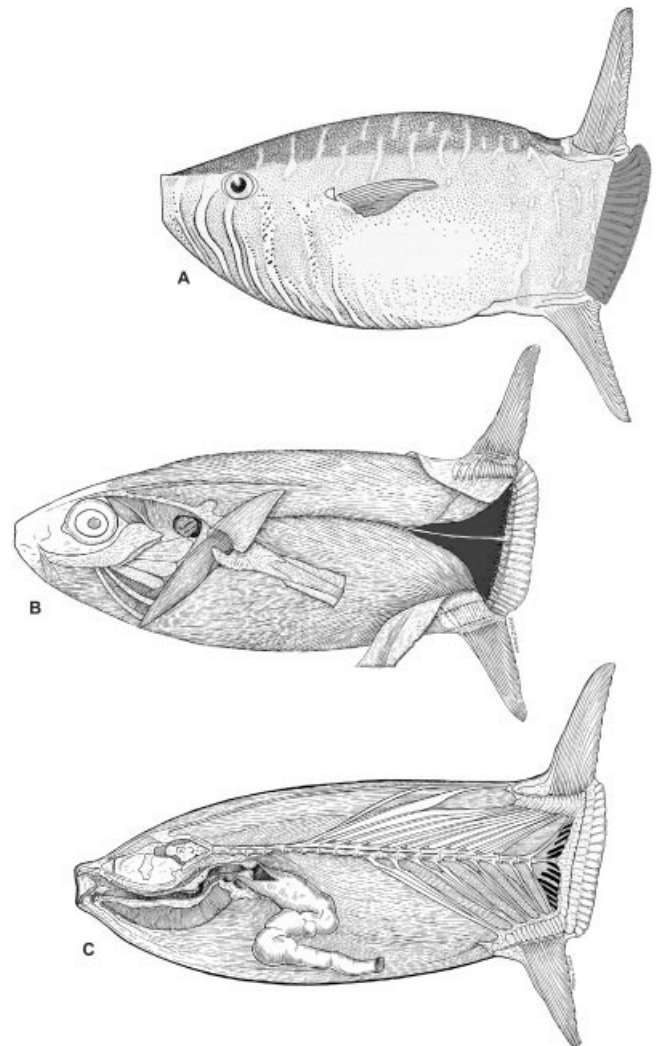


Fig. 2. Lateral view of adult *Ranzania laevis*. **A:** Habitus with clavus in gray, modified from Fraser-Brunner (1951). **B:** Body musculature with claval muscles in dark gray, modified from Raven (1939b). **C:** Skeleton with claval supports in black, modified from Raven (1939b).

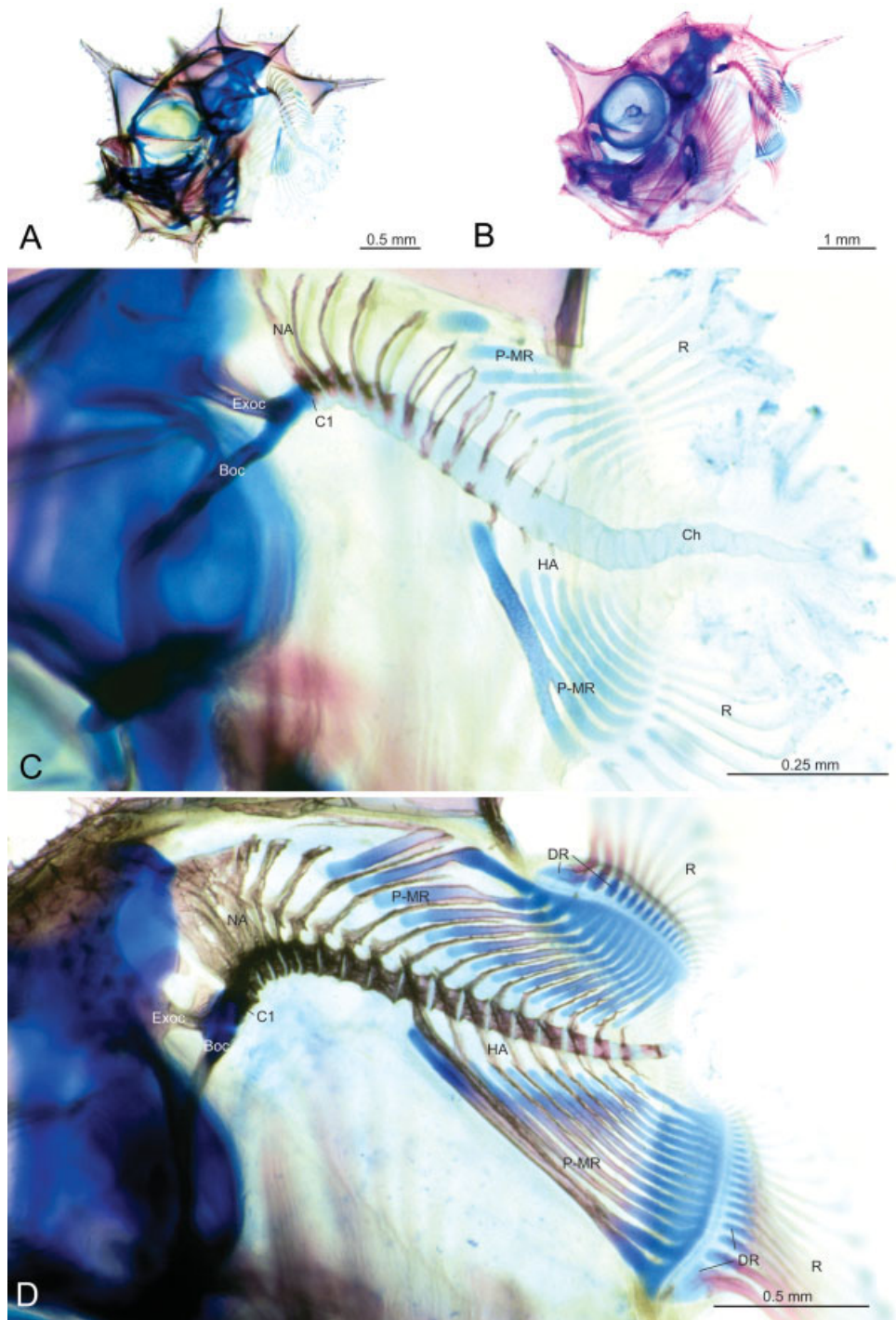


Fig. 3. Lateral view of dissected cleared and stained specimens of *Ranzania laevis*. **A:** 2.1 mm specimen. **B:** 4.2 mm specimen. **C:** Close-up of 2.1 mm specimen. **D:** Close-up of 4.2 mm specimen; Boc, basioccipital; C1, first vertebra. Ch, chorda; DR, distal radial; Exoc, exoccipital; HA, hemal arch; NA, neural arch; P-MR, proximal-middle radial; R, fin ray.

cylindrical cartilages, of which the anterior six (2–7) insert between the neural arches of vertebrae 6–12. The posterior four proximal-middle radials are situated posterior to the last developed neural arch, that of vertebra 12. Seven dorsal-fin rays are developed, of which only the anterior three embrace cartilaginous distal radials. Distal radials are absent posteriorly. The first dorsal-fin ray is serially associated with the second proximal-middle radial, thus leav-

ing the anteriormost proximal-middle with neither a supernumerary nor serially associated ray, and the second without a supernumerary. There are nine anal proximal-middle radials, all cartilaginous, decreasing greatly in size posteriorly, with the last one being barely chondrified (cannot be seen in Fig. 3C). The anteriormost element is the longest and best-developed and bifurcates distally into two elongate arms. Its proximal end inserts anterior to the first

hemal arches on vertebra 10 and bears two lateral expansions that articulate with their distal tips. The whole arrangement thus strongly resembles that of the first anal-fin pterygiophore of *Monotrete leiurus* (see Part 1, Britz and Johnson, 2004: fig. 1). There are eight anal-fin rays, of which the anterior four articulate with small cartilaginous distal radials, which are lacking from more posterior fin rays. The anterior two fin rays are serially associated with the two distal bifurcations of the first proximal-middle radial. The chorda projects straight into the caudal larval fin fold. No fin rays or supporting bones are developed in this area.

***Ranzania laevis* 4.2 mm (Figs. 3B,D, 5A)**

Although only twice the size of the previous stage, this stage is much further developed. The angle between the vertebral column and the occipital basiocranium is about 100°, with the inclination now starting at the third centrum. The full complement of 19 vertebrae is present. The first vertebra is very closely associated with the occipital area of the neurocranium. Its broad centrum is separated from the basioccipital by a narrow band of cartilage. Each half of its neural arch is broadly expanded, especially at its distal tip, the very thin lamellae of which are tightly bound to the dorsolateral face of the tectum synoticum of the skull, and do not meet in the dorsal midline. The second vertebra has a much shorter centrum, but also a laterally expanded neural arch. Its halves parallel the course of those of the first arch and extend also to the dorsolateral area of the tectum synoticum, where their distal tips are tightly bound to the dorsal surface of those of the first arch. The third neural arch roughly parallels the course of that of the second, but at about half of its length turns posteriorly. A spine-like anterodorsal projection is developed at this angle and reaches anteriorly to the second neural arch. As with the anterior two neural arches, the left and right halves of the third arch do not meet in the dorsal midline. The centrum of the third vertebra is as narrow as that of the second. The fourth neural arch parallels the course and shape of the third, but its distal tips approach each other more closely in the dorsal midline. Its centrum is subequal in breadth to that of the second and third. The course of the fifth neural arch again parallels that of the fourth; however, its dorsal half is inclined further posteriorly so that its distal tips, which are fused in the dorsal midline, are further removed from those of the fourth. The breadth of its centrum equals those of vertebrae 2–4. All subsequent centra increase in breadth to the ninth and then decrease again, so that 18 is as narrow as 2. The neural arches of vertebrae 6–17 resemble each other in appearance and course, but decrease in size posteriorly, as do their long, well-developed neural spines. The neural arch subsequent to 17 is still relatively small and short and

bears only a tiny neural spine. The long neural spine of vertebra 6 extends between the first two proximal-middle radials of the dorsal fin and almost reaches their distal tips. The pattern of association of neural spines and dorsal proximal-middle radials is then as follows: /1/1/1/1/1/1/1/2/1/2/1/. Hemal arches and spines are developed on vertebrae 10–18. As with the neural arches and spines, the hemal arches and spines decrease in size posteriorly. The first is stout and long and extends along the posterior face of the first anal proximal-middle radial to the level of its distal bifurcation. The second hemal spine, that of vertebra 11, extends along the posterior edge of the first. Thus, two hemal spines are inserted between the first two anal proximal-middle radials. The pattern of association of all subsequent hemal spines and proximal-middle radials is then as follows: 1\0\2\1\2\1\2\2\1\1. The last centrum, 19, bears neither neural or hemal arches or spines and is just a short cylinder of bone covering the posteriormost tip of the chorda. Fifteen dorsal proximal-middle radials are developed. The first, which is not serially associated with a fin ray or distal radial, is an elongate cartilaginous rod, whose distal three-fourths is perichondrally ossified. Its anterodorsal tip bears a long, thin, almost needle-like process of membrane bone that projects anteriorly in the dorsal midline to the level of the fourth neural arch. Its posterior edge bears a short and narrow flange of membrane bone. The second proximal-middle radial is also a long cartilaginous rod, but its distal half is directed posteriorly, thus forming an angle of about 135° with the lower half. Its proximal end and the entire posteriorly directed distal portion are still cartilaginous, but its middle length is perichondrally ossified to the beginning of the latter, the tip of which is fused to the anterodorsal corner of the third proximal-middle radial. All subsequent proximal-middle radials are more similar in appearance, being elongate, cartilaginous rods, ossified in the middle and with their distal fourths bent first posteriorly and then dorsally. The degree of ossification and inclination decrease posteriorly, so that the last few elements are fully cartilaginous, almost straight rods. The distal tips of all proximal-middle radials except that of the first are fused with each other, resulting in a continuous rostrocaudal strip of cartilage. Sixteen cartilaginous distal radials are developed and embraced by the open bases of their respective fin rays. The first distal radial differs from the remainder in being comparatively large and almost triangular with only its posterodorsal corner extending between the proximal halves of the first fin ray. All subsequent distal radials are similar in appearance. They are unusually elongate and extend dorsally far between the left and right halves of the respective fin rays. The last few distal radials are less elongate, but these are also the more recently developed ones and thus not yet fully formed. There are 16 dorsal-fin rays articulating with the 16

distal radial cartilages. Thus, there are two more fin rays and distal radials than proximal-middle radials with which they can serially associate. However, the last proximal-middle radial has a comparatively broad dorsal tip, with some signs of vertical fissures in the cartilage, but without additional developmental stages we are unable to say if more than one proximal-middle radial forms this last element.

The 12 proximal-middle radials of the anal fin approximately mirror those of the dorsal fin, except they are all elongate, relatively straight, unmodified rods. Their proximal and distal tips are cartilaginous and their middle parts are perichondrally ossified, successively less so posteriorly, so that the last is completely cartilaginous. As in the dorsal fin, the distal tips of all proximal-middle radials of the anal fin are fused to each other, forming a cartilaginous strip from the first to the last pterygiophore. There are 16 anal-fin rays and cartilaginous distal radials. They resemble those in the dorsal fin closely in shape and arrangement, with the first one being much larger than the subsequent ones and triangular rather than elongate. The first two distal radials are serially associated with the distal tips of the bifurcate first proximal-middle radial. The serial association of all subsequent distal radials and pterygiophores becomes less and less obvious posteriorly, and there are four more distal radials and fin rays (16) than proximal-middle radials (12, one bifurcated). However, as in the dorsal fin, the last proximal-middle radial has a comparatively broad dorsal tip with signs of vertical fissures in the cartilage, and again, this may mean that more than one proximal-middle radial forms this last element.

In addition to the proximal-middle radials directly associated with the dorsal and anal fins, the first elements of the supporting skeleton of the clavus and its fin rays are developed. Identification of these as claval supports and fin rays and rejection as proximal-middle radials and fin rays of dorsal or anal fins is somewhat arbitrary, as the latter lead continuously into the former. About eight short cartilaginous rods occupy the space between the last proximal-middle radial of the dorsal fin and the terminal centrum. About seven fin rays are ossified in the dorsal lobe of the clavus, of which the dorsalmost articulates with the posterodorsal edge of the last dorsal proximal-middle radial. All other fin rays are gradually oriented more parallel to the horizontal axis. The ventral lobe of the clavus mirrors that of the dorsal lobe. About eight elongate cartilaginous rods occupy the space between the last anal proximal-middle radial and the terminal centrum. The distal tip of the first (anteriormost) of them is fused to that of the last anal proximal-middle radial. There are about 10 claval fin rays in this lower lobe, of which the first two articulate with the ventrocaudal edge of the fused cartilage of the last anal proximal-middle radial and the first claval cartilage.

***Ranzania laevis* 7.2 mm (Figs. 4A-C, 5B,C)**

This stage differs significantly in external appearance from that of the previous two stages. Most of its long larval body spines are resorbed, and numerous small dermal ossifications have developed extensively in the skin. The vertebral column and the fins also show striking differences from the previous stages. The angle between the axial skeleton and the occipital basicranium remains about 100°, with the inclination now starting at the fourth centrum. The centrum of the first vertebra is fused with the basioccipital (not shown in Fig. 4). The anterior four neural arches have expanded further along the anteroposterior axis, so that they overlap each other dorsally and are difficult to separate. The anterodorsal projection of the fourth arch has developed into a strong prezygapophysis that fits tightly into a groove on the third neural arch. The first four neural arches thus form the lateral wall and roof of the neural canal anteriorly, although their distal tips do not contact each other in the dorsal midline. The fifth neural arch is also expanded anteroposteriorly and bears a strong prezygapophysis, which projects into a groove on the fourth neural arch. The subsequent six neural arches also bear such prezygapophyses, but a tight association with the more anterior neural arch only to the ninth. The sixth neural arch is the first with a long neural spine. This and all subsequent neural arches do not show the strong anteroposterior expansion of the first five. The pattern of association of the neural spines of vertebrae five to 18 and the respective pterygiophores is identical to that in the previous stage: /1/1/1/1/1/1/1/2/1/2/1/.

The hemal arches are longer and their spines relatively thinner and needle-like when compared to the previous stage. The pattern of association between them and the proximal-middle radials of the anal fin is identical to that of the previous stage: 1\0\2\1\2\1\2\2\1. All centra are well developed and the differences in width are similar to that of the previous stage, with centra 2 to 5 being just about half the breadth of that of subsequent vertebrae. The terminal vertebra consists of the centrum only, a short cylinder surrounding the chorda. Its posterior tip extends as a conical cartilage.

The first proximal-middle radial of the dorsal fin is ossified, with the exception of its proximal third. The anterior needle-like process of membrane bone at its distal tip extends much farther anteriorly above the tectum synoticum, almost reaching the supraoccipital. Along the posterior edge of the first proximal-middle radial there are two posterolaterally directed flanges that embrace the distal half of the anterior face of the neural spine of the sixth vertebra. The distal tip of this radial bears a short posteriorly directed projection that contacts the anterodistal corner of the second proximal-middle radial, the shape of which is further modified relative

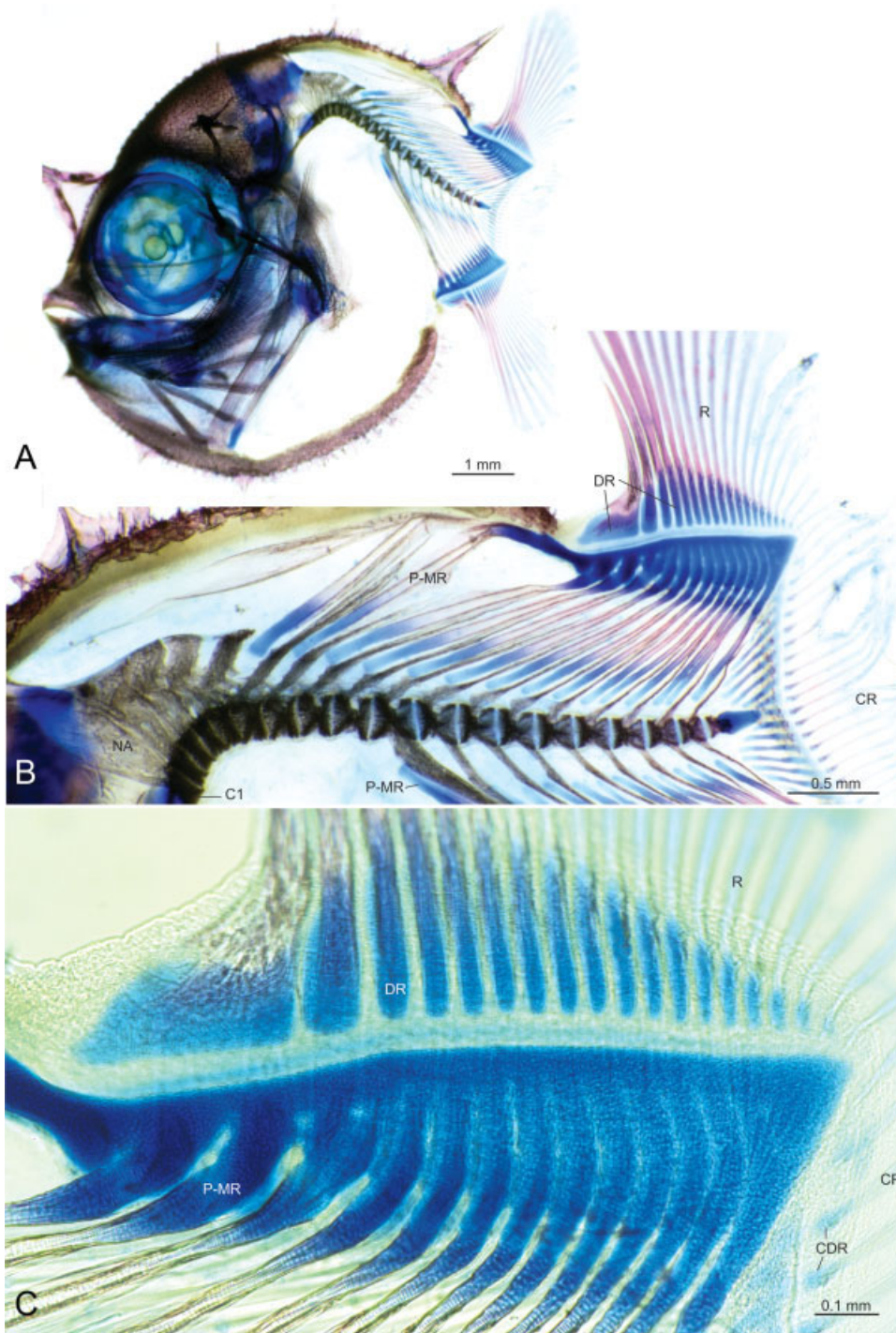


Fig. 4. Lateral view of dissected cleared and stained 7.2 mm specimen of *Ranzania laevis*. **A:** Whole specimen. **B:** Close-up of axial skeleton and dorsal-fin pterygiophores and rays. **C:** Close-up of distal tips of proximal-middle radials, distal radials and proximal parts of fin rays of dorsal fin. C1, first vertebra; CDR, claval distal radials; CR, claval rays; DR, distal radial; NA, neural arch; P-MR, proximal-middle radial; R, fin ray.

to the previous stage. It is straight along the proximal two-thirds of its length, at which point it bends almost 90°, and the remaining entirely cartilaginous third extends posteriorly along the dorsal margin of the body, where its tip is fused with the tip of the third and all remaining proximal-middle radials. This results in a large triangular gap between the second and third proximal-middle radials. All subsequent proximal-middle radials are oriented ob-

liquely to the body axis, although the angle increases posteriorly from 25° at the third to 45° at the 15th radial. The fusion of the distal tips of all dorsal proximal-middle radials, except the first, is more extensive than in the previous stage, so that the band of coalesced cartilage is much deeper. There are 18 distal radial cartilages associated with the proximal-middle radials, all more elongate relative to the previous stage and thus embraced more

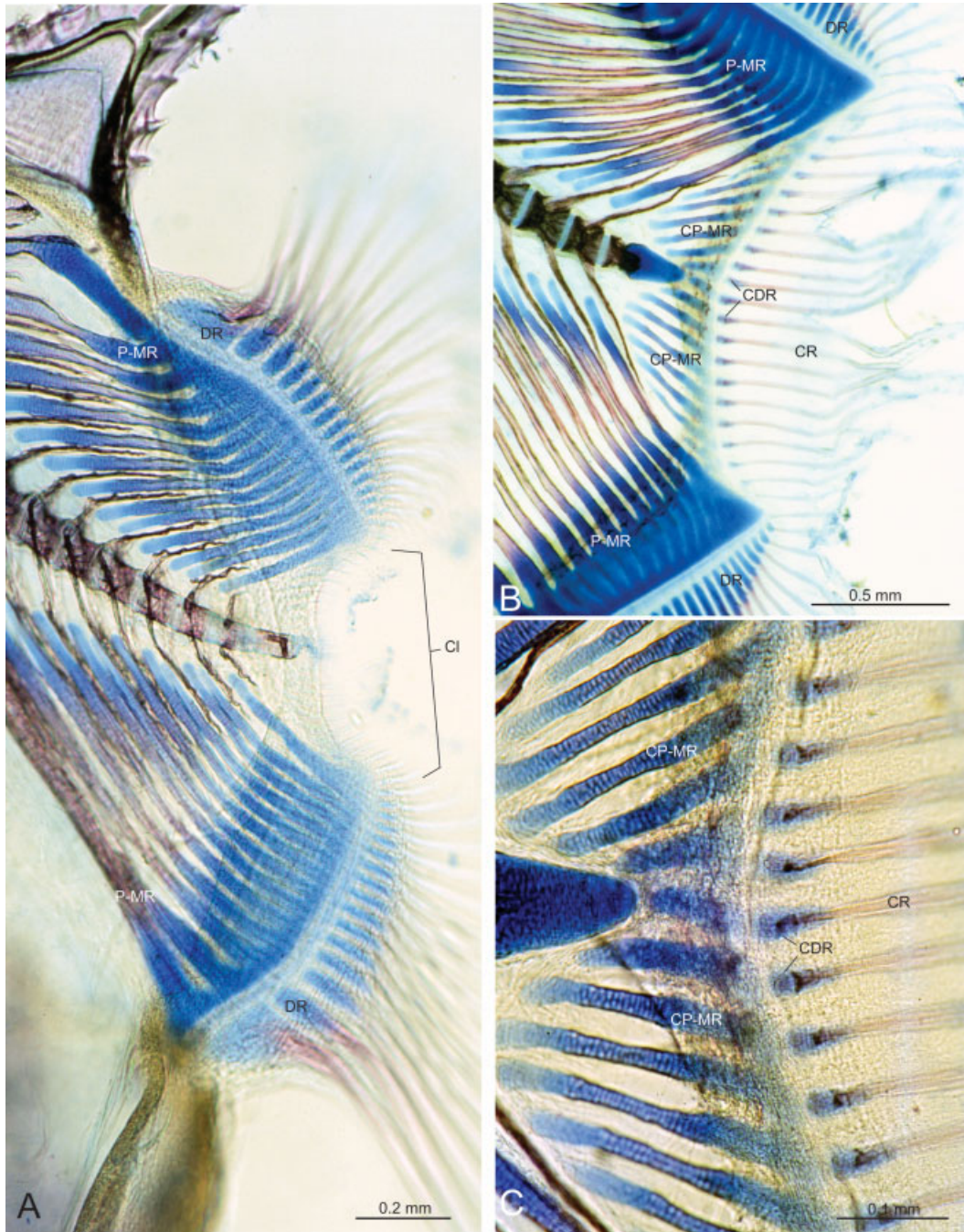


Fig. 5. Lateral view of dissected cleared and stained specimens of *Ranzania laevis*. **A:** Dorsal and anal fins and developing clavus of 4.2 mm specimen. **B:** Same of 7.2 mm specimen. **C:** Close-up of middle part of clavus. CDR, claval distal radials; Cl, clavus; CP-MR, claval proximal-middle radials; CR, claval rays; DR, distal radial; P-MR, proximal-middle radial.

deeply by the proximal halves of the serially associated soft ray. They increase in vertical length from 1–5 and then decrease posteriorly, so that the last (18) is almost spherical. The first fin ray has a wide base that embraces most of the large triangular first distal radial. The last ray associated with the dorsal fin has no distal radial yet and is situated at the

cartilaginous caudodorsal edge of the last proximal-middle radial.

All proximal-middle radials of the anal fin are ossified now along their middle, leaving only the proximal and distal tips cartilaginous. Fusion of their distal tips is more extensive, resulting in a deep band of cartilage. There are 19 elongate carti-

laminous distal radials, closely resembling those in the dorsal fin, and being embraced deeply by the proximal halves of the serially associated soft ray. The last fin ray associated with the anal fin has no distal radial yet and is situated at the cartilaginous posteroventral edge of the last proximal-middle radial.

The claval supporting elements and fin rays are located in the two areas bordered by the last centrum and its conical cartilage and the last neural and hemal arches and spines. The clavus has eight dorsal and eight ventral supports, the distal tips of which are fused with each other, like the proximal-middle radials of the dorsal and anal fins. Unlike the uppermost claval support, the lowermost is also fused to the last anal proximal-middle radial. An additional claval support, the posterior tip of which points slightly ventrally, is present posterior to the conical cartilage of the last centrum. The upper claval lobe has 10 elongate cartilages, each embraced by the bases of a claval ray, and an additional ray, the uppermost, not associated with a cartilage. The lower claval lobe has nine elongate cartilages, each also embraced by the bases of a claval ray, and an additional ray, the lowermost not associated with a cartilage. As with the claval supports, there is an additional elongate cartilage articulating with a ray that appears to be associated with the claval support posterior to the conical cartilage of the last centrum.

DISCUSSION

Ontogeny of Axial Skeleton

A striking early developmental character that distinguishes *Ranzania* from the closely related *Monotretes* (see Part 1, Britz and Johnson, 2004) is the lack of the flexion of the chorda, first pointed out by Leis (1977). Another unusual feature of *Ranzania* is the sharp angle between the occiput and the anterior vertebrae, which only straightens gradually during further development. A similar, though less pronounced, curvature is also present during the development of the axial skeleton of *Monotretes* (Britz and Johnson, 2004) and may occur in a number of other tetraodontiforms.

All neural and hemal arches and spines of the vertebral column of *Ranzania* develop in membrane bone, as described for most of these elements in the tetraodontid *Monotretes* (Britz and Johnson, 2004). It is unclear at present if the lack of cartilaginous preformed elements of the vertebral column is a more widespread condition among tetraodontiforms.

Ranzania and the other molids are highly unusual in having the ultimate centrum ending in a conical cartilage with which some of the claval supporting elements articulate (Figs. 4A,B, 5B,C). This cartilage is absent from our two small stages, but is well-developed in the 7.2 mm specimen of *Ranzania* and the 11.5 mm *Masturus*. As a comparable structure does not occur in any other tetraodontiform or

even teleost, this conical cartilage is an autapomorphy of molids, obviously correlated with the development of the clavus.

Ontogeny and Homology of the Clavus

The identity of the elements comprising the molid clavus has been the subject of considerable debate for over 150 years, beginning with Goodsir (1841). Two hypotheses about the homology of the clavus have been proposed, neither having been conclusively confirmed nor rejected to date. 1) Some (e.g., Goodsir, 1841; Cleland, 1862; Schmidt, 1921; Gudger, 1937a,b; Winterbottom, 1974a) have maintained that it represents a highly modified, vertically expanded caudal fin. 2) Others (e.g., Ryder, 1886; Boulenger, 1904; Regan, 1903; Raven, 1939a; Fraser-Brunner, 1951) have argued that it comprises highly modified components of the dorsal and anal fins that have replaced the caudal fin. Still others (Grenholm, 1923; Tyler, 1970a; Leis, 1977) have addressed the controversy, but were unwilling to embrace one or the other hypothesis based on the available evidence. Questions about the homology of the clavus have not been alluded to since Leis (1977), and all subsequent authors (Tyler, 1980; Nelson, 1984, 1994; Santini and Tyler, 2002) have simply accepted the "dorsal and anal fin" hypothesis without explicit justification.

Since the earliest descriptions and discussions of the composition of the clavus, evidence addressing the two hypotheses has emanated from two anatomical systems, the musculature and the skeleton, each entailing fundamental questions. Regarding the musculature (Fig. 2B): are the muscle bundles that insert on each ray of the clavus homologs of the erector and depressor muscles of the dorsal and anal fins, or are they highly modified epaxial and hypaxial body muscles that typically insert on caudal-fin rays?

Regarding the skeleton (Fig. 2C): are the bony supporting rods that are associated with the claval rays homologs of the proximal-middle pterygiophores of the dorsal and anal fins, or are they derived from extreme modification of the caudal skeleton, or neither?

We will first discuss the muscle evidence. Molids have a highly derived body musculature first pointed out by Meckel (1828), and subsequently confirmed by a number of authors (Goodsir, 1841; Cleland, 1862; Ryder, 1886; Rosén, 1913; Gregory and Raven, 1934; Raven, 1939a,b; Fraser-Brunner, 1951; Winterbottom, 1974a). However, the homology of the muscles serving the dorsal, anal, and claval fin rays has been controversial. Meckel (1828) and Ryder (1886) were uncertain if some or all of the muscles associated with the dorsal and anal fins represent their original fin muscles or modified axial musculature. In contrast, all remaining authors (Goodsir, 1841; Cleland, 1862; Rosén, 1913; Gregory

and Raven, 1934; Raven, 1939a,b; Fraser-Brunner, 1951; Winterbottom, 1974a) agreed that the axial musculature is lost and that the extremely hypertrophied musculature serving the dorsal and anal fins are true fin muscles. Disagreement about the homology of the claval muscles consists of their interpretation as either modified caudal-fin muscles (Goodsir, 1841; Cleland, 1862; Gregory and Raven, 1934; Winterbottom, 1974a) or modified dorsal- and anal-fin muscles (Rosén, 1913; Raven, 1939a, b; Fraser-Brunner, 1951).

We find no evidence inherent in the claval musculature that would justify choosing between the two hypotheses. Innervation is irrelevant, as both lateral body muscles as well as fin muscles are innervated by spinal nerves (see Winterbottom, 1974b). Ontogeny of the musculature is unknown, so we have no information on how the myotomes develop into the musculature of the adult. The only potentially relevant argument that may be raised is that the muscle bundles are arranged in a fashion very similar to the dorsal and anal-fin ray muscles. A further argument that will be developed below is that these muscles serve fin rays that are clearly dorsal- and anal-fin rays, and therefore the muscles must be modified dorsal- and anal-fin ray muscles.

The homology of the bony rods that are associated with the claval rays has also been controversial. A number of authors (Cleland, 1862; Ryder, 1886; Rosén, 1913; Kaschkaroff, 1914; Raven, 1939a; Fraser-Brunner, 1951; Tyler, 1970a, 1980) pointed out the close similarities in structure of the dorsal and anal pterygiophores with the supports of the claval rays. Some of them (Cleland, 1862; Rosén, 1913; Kaschkaroff, 1914; Tyler, 1970a) and others (Grenholm, 1923; Gregory and Raven, 1934), however, were still uncertain about the identity of the claval supports and did not rule out the possibility that they are highly modified elements of the caudal fin. Ryder (1886:1033) was the first to conclude that “the interneural and interhaemal pieces which support the caudal fin of *Mola* are serially homologous with the interspinous pieces which support the dorsal and anal fins...,” an idea further elaborated, and elegantly advocated by Fraser-Brunner (1951), the last author to critically address the issue. Fraser-Brunner (1951:91) reviewed evidence (myological and osteological) previously presented in support of each of the two alternative hypotheses, and, based on his additional observations, concluded that the claval rays are “in the main, supported by elements that have all the *appearance* of belonging (emphasis added) to the series of *interspinous supports of the dorsal and anal fins*, with the muscles having split off the dorsal and anal inclimators.”

Below, as a prelude to a discussion of the implications of our results and the presentation of our conclusions, we briefly review the relevant subsequent literature, which seems to have added little but uncertainty and confusion to the issue.

The only myological evidence brought to bear subsequently was that of Winterbottom (1974a), wherein (see above) he identified the muscles inserting on the rays of the clavus to be parts of the epaxial and hypaxial musculature, rather than dorsal and anal-fin muscles, and accordingly identified them as caudal-fin rays. He did not discuss the homology controversy, nor did he provide any justification for his muscle identification.

In an article on vertebral reduction in tetraodontiforms, Tyler (1970a) seemingly accepted Fraser-Brunner's conclusion (citing Gudger, 1937a,b, and Raven, 1939a). Nonetheless, he (Tyler, 1970a:27) labeled the claval supporting rods “R” for “radial,” stating that “The vague term ‘radial elements’ for the bones supporting the pseudocaudal fin indicates my lack of understanding about the true nature of these bones.”

Ten years later in his well-known osteological monograph on tetraodontiforms, Tyler (1980:375–377, 390) unconditionally accepted Fraser-Brunner's hypothesis, but, inexplicably, made no reference to Winterbottom's (1974a) conclusion, or to any aspect of the homology controversy. Furthermore, Fraser-Brunner's conclusion about the nature of the claval supports and rays seems challenged by Tyler's diagnostic characterization of the molid clavus (Tyler, 1980:368), which does not reflect his statements on pages 375–377 or his labeled figure 312 of *Mola mola*. That ambiguous characterization was paraphrased by Nelson (1984, 1994) and stated verbatim as a synapomorphy of the Molidae in Santini and Tyler's (2001:40, character 38) recent analysis of molid phylogeny: “Caudal fin aborted, either absent altogether, or represented by a few rays in the central region of the pseudocaudal caudal fin formed by posteriorly migrated soft dorsal and anal-fin rays and supported mostly by equally posteriorly migrated basal pterygiophores from the soft dorsal and anal fins.” In the first alternative, there is no indication of what elements form the pseudocaudal fin, whereas in the second, only its central region is considered to be represented by a few migrated soft dorsal and anal-fin elements, with no indication of the identity of the remaining pseudocaudal elements that lie dorsal and ventral to those few in the center, one possible implication being that they are true caudal-fin rays.

It appears, then, that our current understanding of the composition of the molid clavus has not really progressed beyond the conundrum encountered by Leis (1977). He described the developing vertebral column, dorsal and anal fins, and clavus in a selected series of cleared and alizarin-stained specimens and briefly discussed specific aspects that might shed light on the homology of the clavus. Significantly, Leis (1977:463) noted that the notochord “does not flex upward” and that the claval rays “form from the sides closing the gap inward.” As described and illustrated above, our investigation

confirms and more clearly documents those two important observations, and we fully concur with Leis' (1977:448) resultant conclusion that an "ossified caudal complex homologous to that of more typical teleosts does not form."

Leis' ultimate conundrum, however, emanated from his inability to corroborate or refute the homology hypothesis of Fraser-Brunner, and was stated as follows (1977:464): "Neither the clavus or the dorsal and anal fins are normal with regard to their supporting elements..., so it is difficult to assess the correctness of Fraser-Brunner's statement from examination of these structures." However, it is precisely in a comprehensive understanding of the structure of the pterygiophores of the dorsal and anal fins and the rods associated with the rays of the clavus that the key to resolving the homology of the molid clavus clearly lies. Therefore, our approach has been to systematically address the following questions.

I. *What bony and cartilaginous elements comprise a typical teleost soft-ray pterygiophore, and how do these pterygiophores typically develop?* The development, composition, and configuration of a typical teleost pterygiophore are described in Part 1 (Britz and Johnson, 2004: fig. 3A,B). Each proximal-middle radial is distally asymmetrical, being bent posteriorly, so that its serially associated distal radial comes to rest on the anterodistal corner of the succeeding proximal-middle radial.

II. *How do "typical" pterygiophores compare to those of tetraodontiforms?* Again, as described in Part 1 (Britz and Johnson, 2004), members of the Tetraodontiformes differ from most teleosts in having distally symmetrical proximal-middle radials, and they exhibit two discretely modified pterygiophore configurations. The more derived condition, found in tetraodontids, diodontids, molids, and ostraciids, is relevant to the homology of the molid clavus and was described and illustrated for *Monotrete leiurus* in Part 1 (Britz and Johnson, 2004: fig. 2A-C) and here (Part 2) for *Ranzania leiurus* (Figs. 3D, 4, 5). Here, the proximal-middle radials are also upright and distally symmetrical, but their cartilaginous distal tips coalesce ontogenetically, so that they are eventually connected by a deep continuous band of cartilage. The distal radials, rather than being roughly triangular, are spherical (except in molids) and lie well removed spatially from the proximal-middle radial band of cartilage. Molids are unusual in having distinctly ovoid to very elongate distal radials that are consequently much more deeply embraced by the bases of the fin rays than those of other tetraodontiforms.

III. *How do the bony supporting rods of the molid clavus compare to the uniquely modified pterygiophores of the dorsal and anal fins of molids and their close relatives?* The development and structure of the supporting rods of the molid clavus are entirely consistent with the hypothesis that they are homo-

logues of the proximal-middle radials of the dorsal and anal fins, with which they develop in continuity. Like these elements, the claval rods develop as separate, straight rods of cartilage whose distal tips coalesce ontogenetically, so that they are eventually connected by a continuous band of cartilage. Furthermore, each of these rods is associated with a smaller, separate ovoid cartilage that is in turn embraced by the open bases of each claval ray, as are the unusually ovoid to elongate distal radials of dorsal and anal-fin pterygiophores. Thus, the overall composition, configuration and arrangement of the claval supports and fin rays confirms unequivocally that they are modified dorsal and anal fin pterygiophores and their associated fin rays that have entirely replaced the caudal fin.

CONCLUSION

We have presented three lines of evidence that we believe provide unequivocal confirmation that the clavus of ocean sunfishes does not represent a modified caudal fin, but is formed by elements of the dorsal and anal fin: the chorda never flexes, the claval supports and rays form from dorsal and ventral closing the gap inwards, and the claval supports with their elongate cartilages are identical in structure to the dorsal and anal fin pterygiophores. It is surprising that the caudal fin, which has a major functional role in the swimming performance of teleosts, could be lost in pelagic oceanic fishes like the Molidae. We found no trace of the caudal fin in the ontogeny of molids, so that even the earliest stage of caudal fin development, the flexion of the chorda, does not occur.

Although we make no claim to understand the evolutionary processes leading to this phenomenon, two uncommon characteristics of tetraodontiforms could be relevant:

Tetraodontiform locomotion generally relies to a large extent on movement of the dorsal and anal fin (Breder, 1926; Lindsey, 1978). The existence in collections of a number of malformed adult tetraodontiforms without caudal fins (Tyler, 1970b) suggests that tetraodontiforms might survive the accidental loss of the caudal fin better than most other teleosts, the locomotion of which relies more heavily on the caudal fin.

Tetraodontiform larvae, especially those of ostraciids and the gymnodont subgroups, are characterized by precocious development of dorsal and anal fins well before the caudal fin begins to form (see Leis, 1984a,b), possibly facilitating the loss of even early developmental stages of the caudal fin in molids.

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