BULLETIN OF MARINE SCIENCE, 29(4): 509–521, 1979

MORPHOLOGICAL DEVELOPMENT OF THE EEL *MYROPHIS PUNCTATUS* (OPHICHTHIDAE) FROM HATCHING TO METAMORPHOSIS, WITH EMPHASIS ON THE DEVELOPING HEAD SKELETON

Mark M. Leiby

ABSTRACT

Sequential development of the head skeleton is described. The chondrocranium of *Myrophis punctatus* differs from *Anguilla vulgaris* and *Leptocephalus lanceolatus* in having an epiphysial tectum. It differs from *Ariosoma balearicum* in lacking a median bar from the anterior symphysis of the supraorbital bars to the synotic tectum. Premaxillaries are not present in any stage of development and are thus not part of the premaxillo-ethmo-vomerine complex of adults as previously assumed. A symplectic process, metapterygoid and fifth ceratobranchial are present in the leptocephali. They fuse to adjacent bones during late stages of development. The opercular cartilage ossifies perichondrally, fuses with the blade of the opercle and becomes the articular facet of the opercle. There is no cartilaginous strap connecting the first epibranchial and second infrapharyngobranchial contrary to previous definitions of the family Ophichthidae. The larval teeth are not jaw dentition sensu stricto but are odontodes which form in the mesenchyme just below the epidermis.

Eldred (1966) correctly identified a series of leptocephalus larvae (48.0–79.0 mm TL) as *Myrophis punctatus*. Fahay and Obenchain (1978) examined 198 specimens (22.5–78.2 mm TL) but did not expand Eldred's description.

The large collection of ophichthid leptocephali at the Florida Department of Natural Resources, Marine Research Laboratory (MRL) makes possible the description of *M. punctatus* from recently hatched specimens (4.6 mm TL) to juveniles.

MATERIALS AND METHODS

The 281 specimens described in this study are from the MRL Pelagic Fish (PF) Collection (Presley, 1971) and the MRL Atlantic Sailfish (ASF) Collection (Jolley and Richardson, 1973).

Most specimens were preserved in 3.5–5.0% buffered Formalin. A few were preserved in 70% ethanol which proved inferior to Formalin as it resulted in wrinkled specimens which could not be accurately measured.

Measurements were made to the nearest 0.1 mm using an optical micrometer in a binocular dissecting microscope. In a few cases the condition of the specimen precluded making certain measurements. All counts and measurements are as defined in Leiby (1979).

Growth stages are as defined in Leiby (1979) except the euryodontic stage which is now defined as: Stage from engyodontic to metamorphosis. Commences with shedding of needle-like teeth in anterior end of lower jaw, shedding proceeds posteriorly on lower jaw then anteriorly on upper jaw; engyodontic teeth replaced concurrently by three series of shorter, broad-based teeth in both upper and lower jaws; lower jaw becoming shorter than upper; head length as percent of total length decreasing; opercular cartilage forming; nasal capsule developing; hypural formation and fin differentiation. All changes start or take place between time first replacement tooth is seen in lower jaw and time last replacement tooth is in place in upper jaw.

Proportional measurements given in reverse order (e.g. Preanal Length 86.0–70.4% TL) indicate that the relative size of the structure decreases during development.

Two hundred fifty engyodontic to juvenile specimens were stained differentially for bone and cartilage. Thirty-eight specimens covering all growth series were dissected for osteological study. Fifty more were partially dissected to clarify or confirm observations. Two adult specimens were cleared and stained following Taylor (1967).

Bone terminology generally follows McCosker (1977) except as noted in the text.

Drawings were made using a camera lucida on a Wild dissecting microscope.

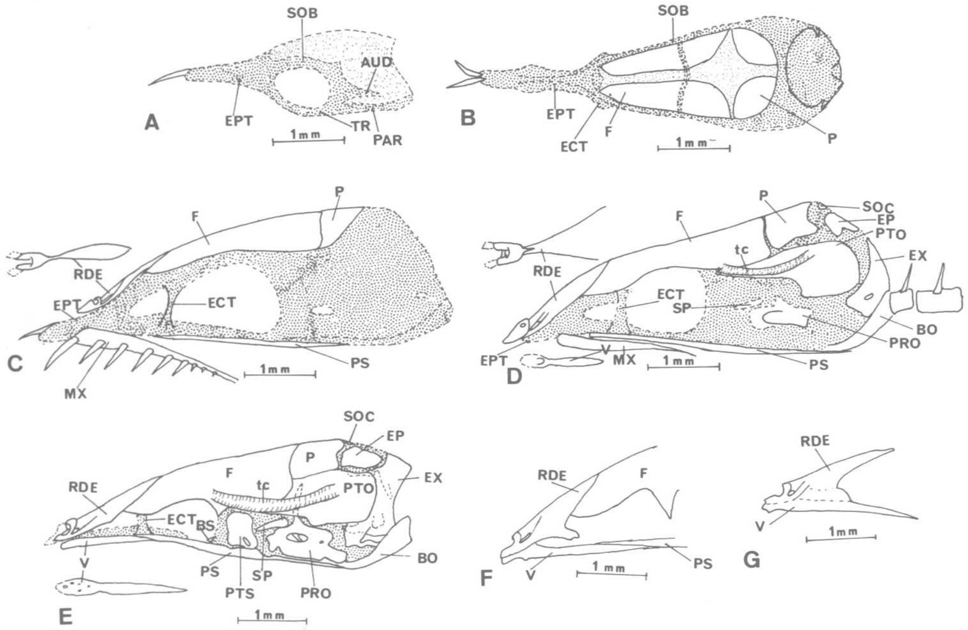

Figure 1. Developing neurocranium of *Myrophis punctatus*. A, Engyodontic Stage: 13.9 mm TL; B, Euryodontic Stage: 48.3 mm TL; C, Euryodontic Stage: 64.6 mm TL; D, Metamorphic Stage: 36.9 mm TL; E, Glass Eel Stage: 42.4 mm TL; F, Glass Eel Stage: 43.0 mm TL; G, Glass Eel Stage: 42.8 mm TL. Abbreviations: AUD, auditory capsule; BO, basioccipital; BS, basisphenoid; ECT, ectethmoid cartilage; EPT, ethmoid plate; EX, exoccipital; F, frontal; MX, maxillary; P, parietal; PAR, parachordal; PS, parasphenoid; PRO, prootic; PTO, pterotic; PTS, pterosphenoid; RDE, rostrodermethmoid; SOB, supraorbital bar; SOC, supraoccipital; SP, sphenotic; tc, temporal canal; TR, trabecula; V, vomer.

DEVELOPMENTAL OSTEOLOGY

Head Skeleton

The sequence of development of the head skeleton is shown in Table 1.

Engyodontic Stage
(Figures 1A, 2A)

The chondrocranium of engyodontic *M. punctatus* (Fig. 1A) resembles the chondrocrania described by Norman (1926) for *Anguilla vulgaris* and by Bauchot (1959) for *Leptocephalus lanceolatus*. In the splanchnocranium (Fig. 2A) however, there are differences. There is no line of demarcation separating the quadrate and the hyomandibula; there is a definate symplectic process (contrary to Greenwood et al., 1966) with a clear articular fissure between it and the quadrate; the first basibranchial is present, but I find no other gill arch elements.

There are three pairs of ossifications even in the 4.6 mm TL specimen. The maxillary, a thin sheet of dermal bone, is positioned along the inner surface of the lip. It lies in a broad, loosely organized sheet of tissue which connects weakly with the outer face of the quadrate and Meckel's cartilage. The posterior margin of the bone is weakly ossified and grades imperceptibly into soft connective tissue. The dentary, also a thin sheet of dermal bone, is positioned along the outer face of Meckel's cartilage (Figs. 2A, B) and lacks a clearly defined posterior

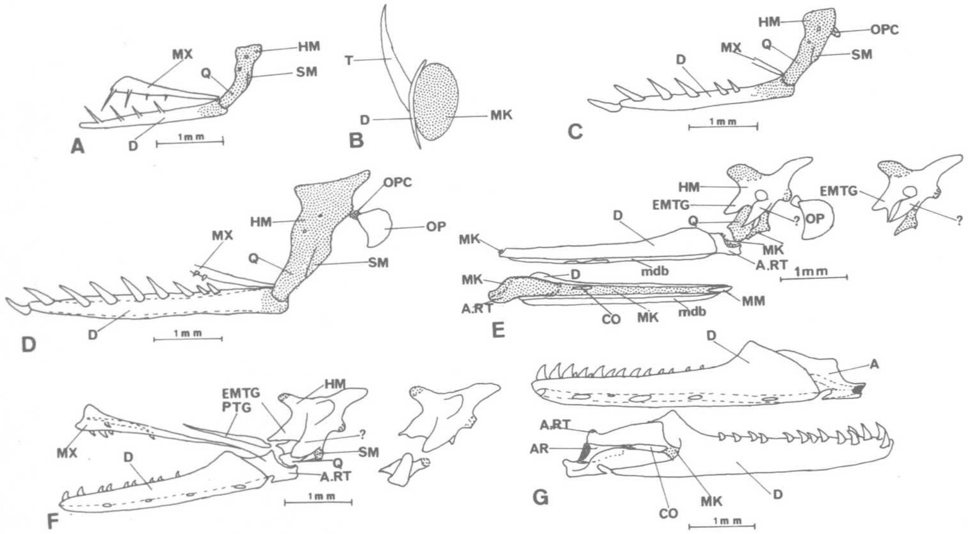

Figure 2. Development of suspensorium and jaws in *Myrophis punctatus*. A. Engyodontic Stage: 13.9 mm TL; B, Stylized drawing of sagittal section through lower jaw. C, Euryodontic Stage: 22.4 mm TL; D, Euryodontic Stage: 60.9 mm TL; E, Metamorphic Stage: 53.5 mm TL; F, Glass Eel Stage: 42.8 mm TL; G, Glass Eel Stage: 75.6 mm TL. Abbreviations: AR, articular; A.RT, anguloretroarticular; CO, Coronomeckelian; D, dentary; EMTG, endometapterygoid; HM, hyomandibula; MK, Meckel's cartilage; MM, mentomeckelian; MX, maxillary; OP, opercle; OPC, opercular cartilage; PTG, ectopterygoid; Q, quadrate; SM, symplectic process; T, tooth.

margin until midway through the euryodontic stage. Both bones have a few, forward pointing, spike-like teeth. At the tip of the rostrum are two spike-like teeth. Each is attached to a small, teardrop-shaped bone which adheres closely to the ethmoid cartilage. These are probably not premaxillae (Berry, 1964; Leiby, 1979).

I am uncertain of the function of the larval teeth, but the weak splanchnocranium morphology precludes their use as a feeding mechanism.

Euryodontic Stage
(Figures 1B, C, 2C, D, 3A, 4A)

The onset of the euryodontic stage is marked by a change in jaw dentition (Leiby, 1979). The few, narrow, spike-like teeth of the engyodontic stage are lost, possibly through a sequence of rapid partial resorption and shedding. The euryodontic teeth are formed in the mesenchyme just below the epidermis, and overlay, but do not touch, the maxillary and dentary. During development, each tooth lies parallel to the jaw (Fig. 5B). When fully formed, the tooth rotates until it is perpendicular to the jaw. The broad base of the tooth then migrates inward, becoming ankylosed to the outer surface of the jaw bone, and adjacent engyodontic teeth are lost.

Hulet (1977) has shown that the teeth consist of dentine with no enamaloid coat or cap in leptocephali of *Ariosoma balearicum*. Although I was unable to do a histological study, my observations indicate that they fit Ørvig's (1977) criteria for odontodes and odontocomplexes. By way of contrast, teeth from glass eel through adult are attached to the medial face of the jaws (Figs. 2F, G). These

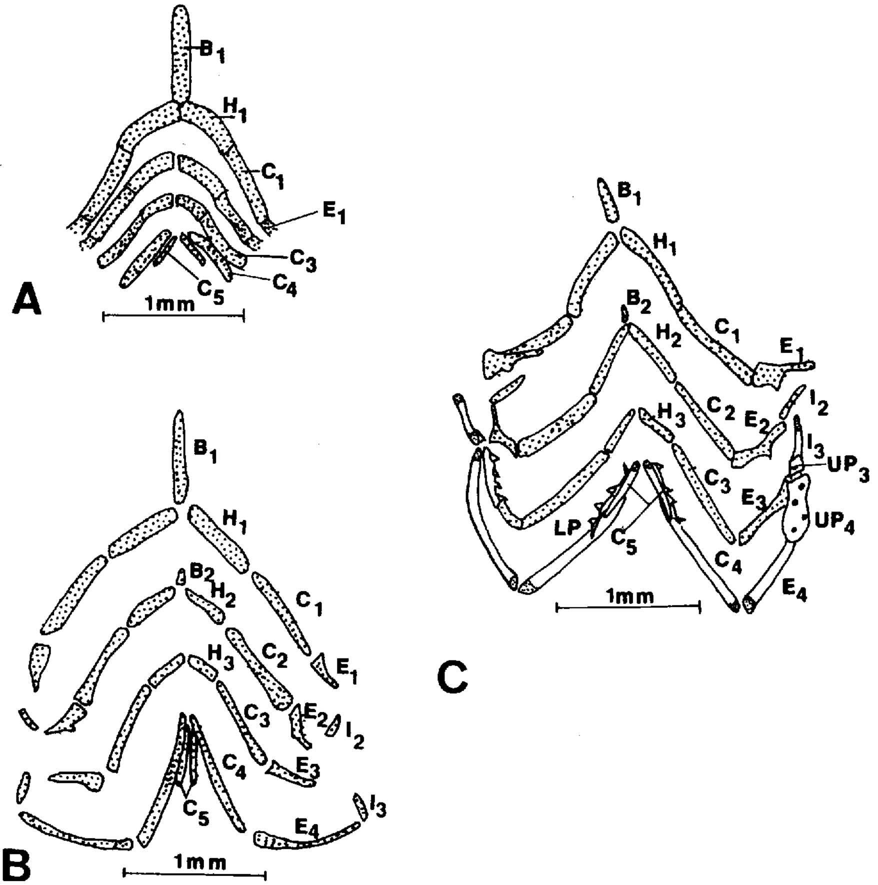

Figure 3. Development of branchial arch in *Myrophis punctatus*. A, Euryodontic Stage: 63.3 mm TL; B, Metamorphic Stage: 49.2 mm TL; C, Glass Eel Stage: 42.3 mm TL. Abbreviations: B 1–2, basibranchial 1–2; C 1–5, ceratobranchial 1–5; E 1–4, epibranchial 1–4; H 1–3, hypobranchial 1–3; LP, lower pharyngeal tooth plate; I 2–3, infrapharyngobranchial 2–3; UP 3–4, upper pharyngeal tooth plate 3–4.

teeth are clearly part of the dentition, sensu stricto (Ørvig, 1977). Based on light microscopy observations, their development qualifies them as jaw-teeth proper, sensu Ørvig (1977) and Schaeffer (1977). Since the larval teeth are not homologous, or analogous, to the teeth in later developmental stages, their ontogenetic and phylogenetic significance remains in question.

Early in the euryodontic stage an opercular cartilage (Fig. 2C) develops independently of the hyomandibula. As Norman (1926) indicated, it arises from a loosely organized mass of cells at the posteroventral border of the hyomandibula and chondrifies to become the opercular cartilage. No late engyodontic or early euryodontic specimens examined had a hyomandibular process which could pinch off to form this structure contrary to Daget and d'Aubenton's (1957) findings in *Heterotis*.

The blade of the opercle develops midway through the euryodontic stage; its anterior portion overlies the opercular cartilage. When it first appears, it is fully formed, clearly defined and thicker than in later stages of development, but it does not take up alizarin red stain. This preformed opercle is not a decalcified structure, but a collagenous matrix within which the osteoblasts ultimately lay down calcium. The frontals, parietals and parasphenoid of specimens in which this occurs do stain with alizarin red.

The branchial arches are weakly developed until metamorphosis. A 63.3 mm TL euryodontic specimen was the earliest in which I could see all the branchial arches developing. In this specimen (Fig. 3A), the articular fissures between the elements are distinct but the elements are still closely joined. The epibranchials and infrapharyngobranchials do not seem to be formed, although they may have been lost during dissection. Nelson (1966) and McCosker (1977) state that the fifth ceratobranchial (C_5) is missing in *M. punctatus*. Figure 3 clearly shows that a reduced C_5 is present.

Development of the chondrocrania described for Stage III of *A. vulgaris* (Norman, 1926), *L. lanceolatus* (Bauchot, 1959), and *A. balearicum* (Hulet, 1977) generally corresponds to that seen in early euryodontic ophichthid leptocephali. There are, however, some differences. Prior to formation of frontals and parietals, the dorsal surface of the brain in *M. punctatus* is protected by a synotic tectum, supraorbital bars and a weak epiphysial tectum. Norman and Bauchot found only supraorbital bars and the synotic tectum. Hulet shows supraorbital bars, synotic tectum, strong epiphysial tectum and a median bar extending from the anterior symphysis of the supraorbital bars to the synotic tectum.

The frontals and parietals, like the blade of the opercle, are completely preformed prior to alizarin red stain uptake. They grow posteromedially and anteromedially from the four corners of the orbito-temporal fenestra. When they meet at midline, each bone develops a separate center of ossification.

Shortly after the frontals and parietals have started to ossify, a noncartilaginous structure is preformed in the connective tissue above the ethmoid plate (Fig. 1C). It first appears as two unconnected tubular prongs. The two prongs join posteriorly forming a tubular "U," and a thin, basal plate develops from its posteroventral edge. About the time this expanding plate reaches the frontals, a median septum develops joining the posterior edge of the "U" with the upward curving basal plate. I was unable to detect sutures at any stage of development, but the posterior end of the plate, where it overlies the frontals, is occasionally divided along the midline. This structure is the dermal ethmoid of McDowell (1973) and the fused rostrodermethmoid/supraethmoid of Patterson (1977). The "U" shaped prongs, erroneously called premaxillae in *A. vulgaris* (Norman, 1926; Trewavas, 1932), carry a remnant of Allis's loop (McDowell, 1973). McCosker (1977) labeled the cartilaginous portion of this loop, which curves downward from the rostrodermethmoid (RDE), the ethmoid section of supraorbital pores. His "ethmoidal pore" is a suitable name for the pore at the end of the disjunct loop, but, it is part of the infraorbital rather than the supraorbital canal. The anteriormost pore of the supraorbital canal occurs where the supraorbital canal anastamoses with the infraorbital canal at the RDE.

Prior to metamorphosis the ethmoidal pore is situated at the anterior end of the RDE in a direct line with the supraorbital series. This gives euryodontic *M. punctatus* the appearance of having five, rather than four, supraorbital pores.

I could not find a connection between the anterior end of the main infraorbital canal and the remnant Allis's loop in any ophichthid leptocephali or adults. However, unlike McDowell (1973) I have seen a connection, probably the adnasal canal, which curves anterodorsally in front of the eye in *A. rostrata* leptocephali and adults. Asano (1962) and Smith (1971) have indicated such a connection in many congrids.

Metamorphic Stage
(Figures 1D, 2E, 3B, 4B)

Resorption of the cartilaginous ethmoid plate begins in the metamorphic stage but is not completed until the glass eel stage (Figs. 1D, E). As resorption takes place, rostral teeth and the teardrop shaped bones on which they articulate are lost. Hulet (1977) and others, have called these bones the premaxillae. However, Berry (1964) indicated that these bones are in *Albula* leptocephali which also develop true premaxillae.

When the ethmoid plate has receded past the tip of the RDE, the ethmoidal pore migrates downward to its final position at the ventral tip of the snout.

The vomer develops late in metamorphosis, after the ethmoidal plate has receded past the "U" of the RDE (Fig. 1D). From the time it can first be seen, the vomer is expanded anteriorly. This expanded anterior portion has long been considered the ontogenetic fusion of the premaxillas and vomer. However, it seems more likely that the premaxilla, closely associated with the anterior portion of Allis's loop in other extant primitive fish (McDowell, 1973), has been lost. The expanded portion of the vomer is probably homologous with the expanded portion of the vomer in other fish which retain the premaxillae (i.e. *Elops*).

During metamorphosis the suspensorium and jaws undergo marked change. Larval teeth on the maxillary and dentary are lost, apparently by partial resorption and shedding. The anterior end of the dentary and terminal fang, at the symphysis of Meckel's cartilage, is lost (Fig. 2E). An ossification along the lateral face of Meckel's cartilage posterior to the dentary [the phylogenetic fusion of the angular and retroarticular (Nelson, 1973)], takes shape. It extends posterior to the articulation of the quadrate and Meckel's cartilage, but does not become part of the articulation (Fig. 2E). A mentomeckelian develops in the anterior end of Meckel's cartilage and fuses ontogenetically with the dentary. A coronomeckelian develops on the medial surface of Meckel's cartilage; it remains independent.

The maxillary is attenuated and changes position. Anteriorly, it leaves its location just under the epidermis of the lip and moves posteromedially until it is in position near the developing vomer. Posteriorly, it tapers to a fine thread, loses its weak attachment to the quadrate/Meckel's cartilage juncture and becomes firmly attached by strong ligament to the dorsal process of the angulo-retroarticular (Figs. 1D, 2F).

Early in metamorphosis, before there is any ossification in the hyomandibula, a small dermal bone forms at the anteromedial edge of the hyomandibula (Fig. 2E). This bone, probably a phylogenetic fusion of the endopterygoid and metapterygoid, ultimately fuses with the ossifying hyomandibula. Soon after the endometapterygoid develops, a narrow, apparently dermal, bone forms over the lateral face of the hyomandibula (Fig. 2E). I can find nothing in the literature which identifies this bone or its homolog. When the hyomandibula ossifies, this bones fuses with it to become the ridge seen on the face of the hyomandibula in adults which provides lateral support for the quadrate.

The quadrate separates from the hyomandibula and, late in metamorphosis, starts to ossify. The symplectic starts to ossify soon after the quadrate, but remains attached to the hyomandibula until metamorphosis is complete.

Patterson (1977) questions whether the opercular cartilage is ever ossified. He

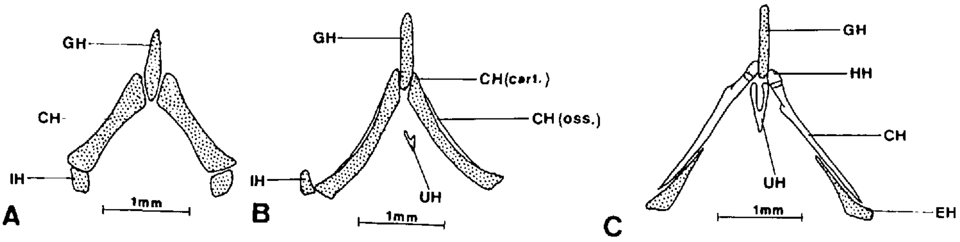

Figure 4. Development of hyoid arch in *Myrophis punctatus*. A, Euryodontic Stage: 63.3 mm TL; B, Metamorphic Stage: 53.5 mm TL; C, Glass Eel Stage: 42.8 mm TL. Abbreviations: CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyal; IH, interhyal; UH, urohyal.

indicates that a layer of cartilage lines the articular facet of the opercular bone in *Elops* and that it lacks a perichondrium where it contacts the bone. He also cites Daget and d'Aubenton (1957) as finding the same thing in *Heterotis*. In metamorphic *M. punctatus* the opercular cartilage ossifies perichondrally, fuses with the blade of the opercle and is itself the articular facet of the opercle.

Early in metamorphosis the lateral edge of the ceratohyals start to ossify and a urohyal appears. By the end of metamorphosis, the epihyals have separated from the ceratohyal, but have not started to ossify, and the glossohyal begins ossifying.

Except for pharyngeal tooth plates, all elements of the branchial arches are developed but none are ossifying.

Glass Eel Stage
(Figures 1E–G, 2F, G, 3C, 4C)

During the glass eel stage, the rest of the ethmoid plate is resorbed; the vomer becomes ankylosed to the parasphenoid and RDE; and vomerine teeth develop. The ethmoid (sensu Harrington, 1955) develops as an outgrowth of the RDE which extends downward to fuse with the vomer (Figs. 1E–G).

The dentary encases most of the receding Meckel's cartilage, fuses with the mentomeckelian and develops teeth. I did not find a separate coronoid series in any developmental stage. The angulo-retroarticular extends around the ventral and medial surface of Meckel's cartilage, but is not included in the joint surface of the quadrate. The articular develops as an endochondral ossification at the posterior end of Meckel's cartilage. This bone supports the entire joint surface with the quadrate (Fig. 2G). Later in development, the angulo-retroarticular and articular fuse with no visible sutures.

The maxillary develops a dorsomedial process which is apposed to, but not articulated with, the ethmoid. It is firmly attached to the neurocranium by a ligament between the dorsomedial process and the ethmoid.

The hyomandibula becomes completely ossified except for a cartilaginous cap on the articular surfaces. The symplectic separates from the hyomandibula and fuses with the quadrate (Fig. 2F). The only sign of its independent existence is the cartilaginous joint between it and the hyomandibula.

Early in the glass eel stage, the interhyals are lost, the epihyals and the glossohyal ossify and the anterior end of the ceratohyal cartilages ossify, pinch off and form the hypohyals (Fig. 4C).

The branchial arches ossify from the fourth arch forward (Fig. 3C). All elements except basibranchial two, when present, and hypobranchial three ossify. The

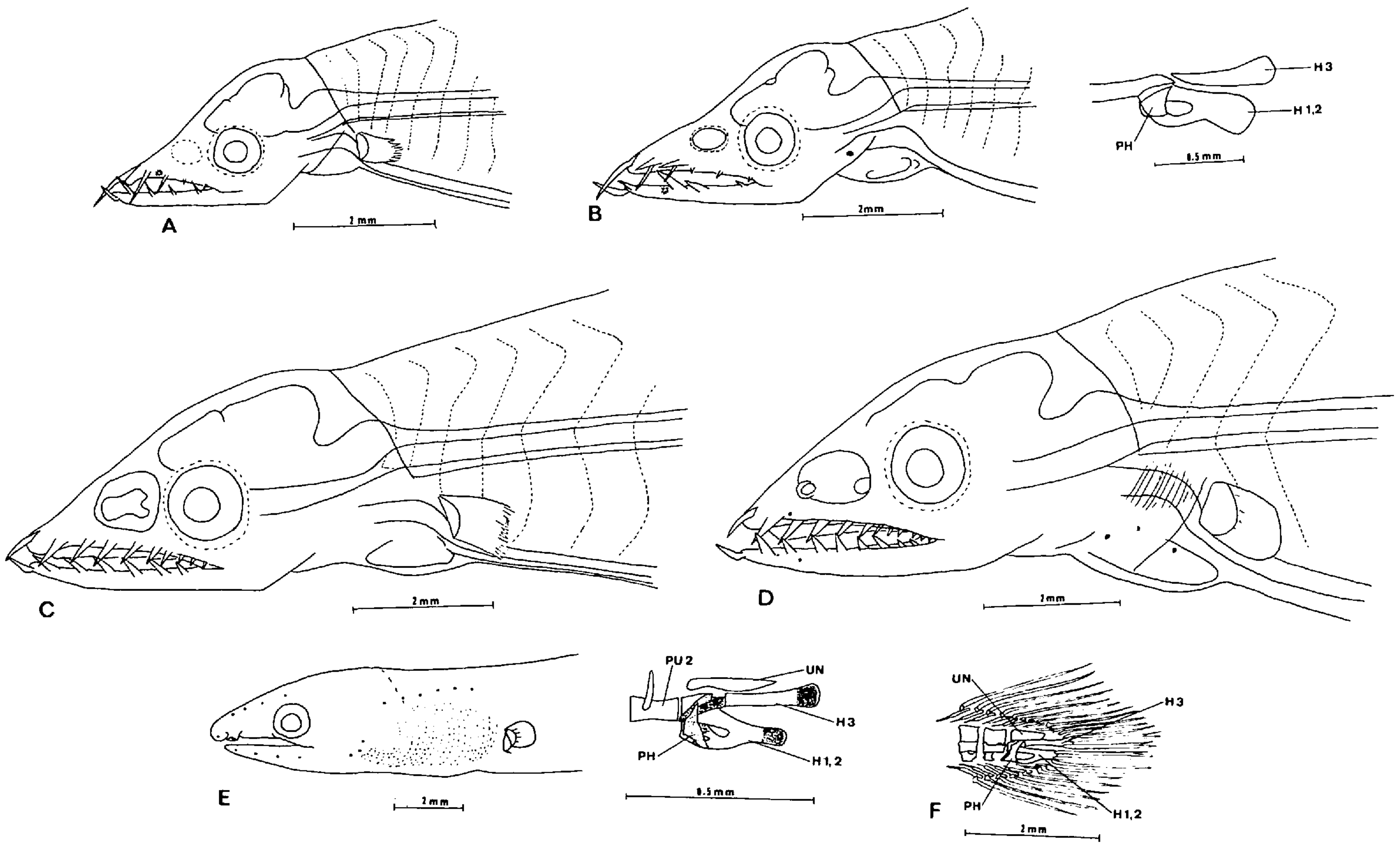

Figure 5. Head and caudal region of larval *Myrophis punctatus*. A, Engyodontic Stage: 13.9 mm TL; B, Euryodontic Stage: 18.1 mm TL; C, Euryodontic Stage: 49.0 mm TL; D, Metamorphic Stage: 65.3 mm TL; E, Metamorphic Stage: 43.6 mm TL; F, Glass Eel Stage, Caudal complex only: 75.6 mm TL. Abbreviations: H 1–3, hypurals 1–3; PH, parhypural; PU 2, preural centrum 2.

pharyngeal tooth plates develop. The fifth ceratobranchial fuses with, and becomes indistinguishable from, the lower pharyngeal tooth plate.

I was unable to find any indication of a cartilaginous strap between the second infrapharyngobranchial and the first epibranchial in any *M. punctatus* leptocephali, glass eels or adults. In a number of cases, the second infrapharyngobranchial was reduced and almost lost. McCosker's (1977) osteological definition of the family Ophichthidae should be amended accordingly.

Fins and Axial Skeleton
(Figures 5B, E, F)

A median fin-fold persists until the euryodontic stage. Pterygiophores are first apparent as translucent blocks at the base of the dorsal and anal fin-folds. The first noticeable fin rays occur adjacently in dorsal, anal and caudal fins. Development is from posterior to anterior. The full complement of fin rays is developed and countable in unstained specimens as small as 41.7 mm TL. However, the rays do not take up alizarin red stain until late in the euryodontic stage. Median fin pterygiophores do not ossify until the glass eel stage.

The pectoral fin is a large fleshy tab with no apparent skeletal structure until actinotrichia develop late in metamorphosis. Pectoral fin rays first start staining with alizarin red in the glass eel stage. Unlike *Ophichthus gomesi* larvae (Leiby, 1979), no cartilaginous pectoral fin support is visible in any of the specimens examined. The cleithrum appears shortly before the supracleithrum; neither appear until metamorphosis is well underway. The cleithrum appears to be preformed, taking up alcian blue in a few early specimens. Leiby (1979) misinterpreted this preformed structure as cartilage. The supracleithrum takes up alizarin red throughout development. Scapula, coracoid and actinosts were not visible in any leptocephali or glass eel examined. They apparently do not form until late in juvenile development.

Formation of the caudal skeleton starts in the euryodontic stage (approx. 34 mm TL). The first structures to appear are three hypurals directly followed by the parhypural. Hypurals 1, 2 and 3 are fused at the base (Fig. 2B, E, F) and arise, along with the parhypural, from the terminal half centrum. The uroneural, preformed in cartilage, appears much later in development (approx. 64 mm TL). Ossification of the caudal skeleton starts after metamorphosis is underway.

Soon after the hypurals appear, the notochord starts constricting. Centrum formation is from posterior to anterior, and ossification of the centra appears to mark the onset of metamorphosis. Neural arch formation commences immediately after centrum ossification begins. Initial arch development is posterior to anterior for 15–20 centra, but then starts on the anterior-most centra also, and proceeds from both ends. Haemal arch formation apparently occurs during the transition from metamorphosing leptocephalus to glass eel. There are no haemal arches in a specimen which has almost completed metamorphosis (36.9 mm TL), but all haemal arches, parapophyses, ribs and intermuscular bones are present in a glass eel 42.3 mm TL.

LARVAL DESCRIPTION

Neither Eldred's (1966) or Fahay and Obenchain's (1978) description of *M. punctatus* leptocephali included engyodontic stage larvae; and neither accounted for the changes in external morphology which take place from stage to stage. Consequently, I here redescribe the leptocephali from engyodontic to glass eel and include morphometric data not provided by either one.

Table 1

Development of the Neurocranium, Suspensorium and Jaws in 35 *Myrophis punctatus* Larvae.
(-, absent; +, present but not ossifying; o, present and ossifying)

	Specimens TL (mm)																																		
Bones	Engyodontic		Euryodontic														Metamorphic												Glass Eel						
	4.6	13.9	22.4	34.4	43.2	49.0	53.9	54.2	63.3	64.6	65.4	65.6	67.2	67.8	69.2	60.0	53.0	53.1	55.4	58.6	57.8	53.6	65.3	54.0	53.3	48.2	43.6	36.9	42.4	42.3	42.4	42.8	51.0	54.0	75.6
Maxillary	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Dentary	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Mentomeckelian	-	-	-	-	-	o	?	o	o	?	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Coronomeckelian	-	-	-	-	-	-	-	-	-	-	-	?	-	?	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Anguloretroarticular	-	-	-	-	-	?	?	-	?	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Articular	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	?	?	o	o
Hyomandibular	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Quadrate	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o
Symplectic	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o
Endometapterygoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Unnamed Bone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Ectopterygoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Interhyal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-
Ceratohyal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Glossohyal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o
Urohyal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Epihyal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	o	o	o	o	o	o
Hypohyal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o
Branchiostegal Rays	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Opercular Cartilage	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Opercle	-	-	-	-	-	-	-	-	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Subopercle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Preopercle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	?	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Interopercle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Parasphenoid	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Frontal	-	-	-	-	+	+	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Parietal	-	-	-	-	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Rostrodermethmoid	-	-	-	-	-	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Basioccipital	-	?	?	?	?	?	?	?	+	+	+	+	+	+	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Exoccipital	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Epiotic	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Pterotic	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Prootic	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Nasal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Supraoccioital	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Sphenotic	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o
Pterosphenoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	-	o	o	o	o	o	o	o	o
Vomer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o
Ethmoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	-	o	o	o	o	o
Basisphenoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o
Cleithrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Supracleithrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Scapula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?
Coracoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?

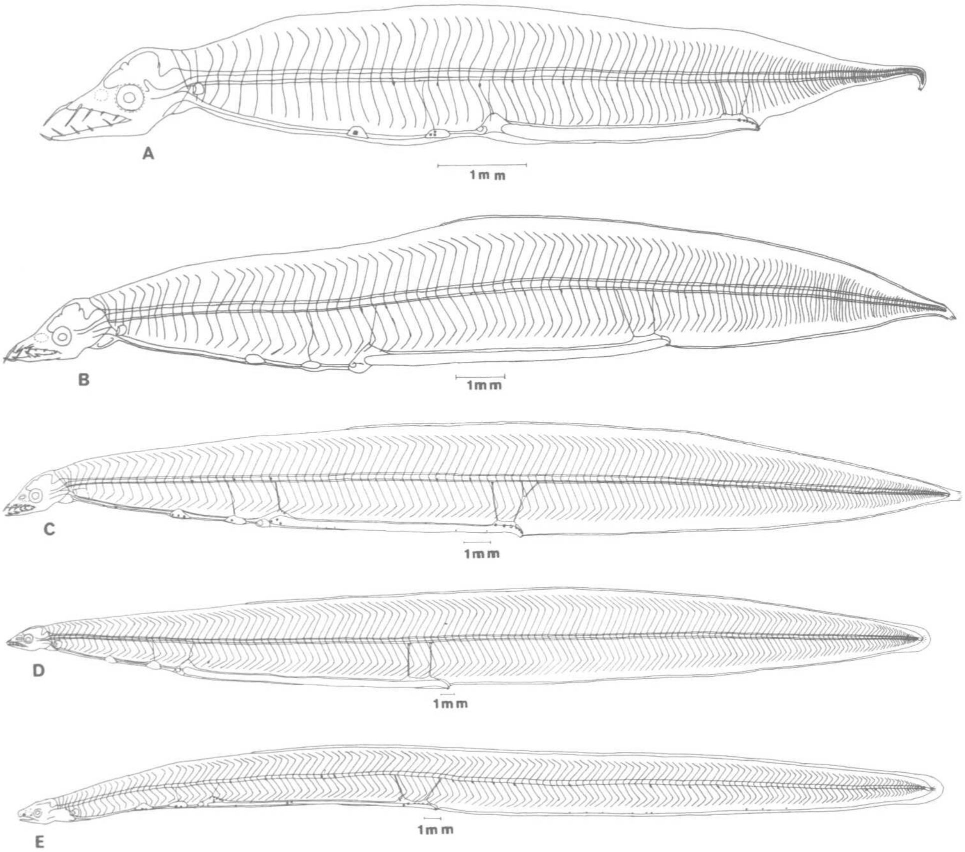

Figure 6. Developmental stages of *Myrophis punctatus*. A, Engyodontic Stage: 13.9 mm TL; B, Euryodontic Stage: 18.1 mm TL; C, Euryodontic Stage: 49.0 mm TL; D, Euryodontic Stage: 65.4 mm TL; E, Metamorphic Stage: 53.0 mm TL.

General Morphology

Body relatively elongate, much compressed, clear. Total myomeres 137–150 (x̄ = 144.0; n = 186); nephric myomeres 53–60 (x̄ = 56.5; n = 261); preanal myomeres 54–62 (x̄ = 58.1; n = 244) prior to late metamorphosis; predorsal myomeres 30–38 (x̄ = 34.1; n = 195). Five to six attached branchiostegal rays; 35–40 free branchiostegal rays. Anal fin rays 226–297 (x̄ = 253.8; n = 18); dorsal fin rays 261–351 (x̄ = 313.4; n = 14); caudal fin rays generally 7 (4 + 3). Caudal fin continuous with dorsal and anal fin throughout life. Pectoral fin rays 9–11. Pectoral fin base at myomeres 2–4 before metamorphosis. Three low gut loops along esophagus; first two, indicated by lobes of liver, under myomeres 12–19 (most commonly 15–16) and myomeres 17–24 (most commonly 20–22); the third, indicated by lobe of liver, gall bladder and expansion of esophagus into gut, under myomeres 22–30 (most commonly 25–28) (Fig. 6). Opisthonephros swollen at juncture of renal portal artery and renal portal vein under myomeres 52–60 (Fig. 6).

Pigmentation in Formalin preserved specimens as described by Eldred (1966) and Fahay and Obenchain (1978). Chromatophore patches on anterior portion of upper and lower lips; on body wall below pectoral fin; on esophagus and liver lobes; along kidney; sporadically on myosepta along midline; at base of anal fin rays.

Engyodontic Stage
(Figures 5A, 6A)

Total length 4.6–16.9 mm. Greatest body depth midway between head and anus. Preanal length 86.0–70.4% TL. Head length 18.3–11.0% TL. Eye diameter 36.8–22.2% HL. Snout length 3.7–6.7% TL; 26.3–41.0% HL. Reduction in relative preanal length and head length due to differential growth in tail region. Preanal myomere number remains stable.

Euryodontic Stage
(Figures 5B–D, 6B, C)

Includes Eldred's (1966) early larvae stage. Total length 18.0–87.1 mm. Greatest body depth shifts posteriorly to anus. Preanal length 71.7–44.2% TL; midway through euryodontic stage preanal length 44.2–56.5% TL. Predorsal length 44.2–25.0% TL; 25.0–30.5% TL by end of euryodontic stage; 54.0–70.3% preanal length. Predorsal and preanal myomere numbers remain constant. Head length 11.3–4.5% TL; 4.5–5.5% TL by end of euryodontic stage; 9.9–15.7% preanal length. Reduction in relative preanal, predorsal and head length due to differential growth in tail region. Eye diameter 17.1–25.0% HL. Snout length 4.4–1.2% TL; 40.0–27.0% HL. Decrease in relative snout length due to loss of rostral teeth and resorption of median ethmoid cartilage.

Metamorphic Stage
(Figures 5E, 6D, E)

Includes Eldred's (1966) transitional and metamorphic stages. Total length 81.0–36.9 mm. Preanal length 44.9–37.1% TL. Reduction in relative preanal length due to anterior relocation (5–10 myomeres) of anus and anal fin late in metamorphosis. Anus and anal fin now situated anterior to terminus of kidney at myomeres 49–53. Predorsal length 22.6–27.6% TL; 55.7–67.1% preanal length. Predorsal myomere number remains constant. Head length 5.0–10.6% TL; 11.2–25.7% preanal length. Increase in relative head length due to posterior relocation or pectoral fin; TL decreasing with onset of metamorphosis. Eye diameter 20.0–14.6% HL. Snout length 1.2–2.2% TL; 30.0–18.2% HL. Decrease in relative snout length due to posterior relocation of pectoral fin. Leiby (1979) erred in attributing relative reduction of snout length, in part, to a slight forward movement of the eye. Eye position remains constant.

Glass Eel Stage

Includes Eldred's (1966) elver stage. Upper size limit of this stage undetermined. Data below for 10 specimens only. Total length 42.3–75.6 mm. Preanal length 39.4–41.6% TL. Preanal vertebrae 50–52; no further forward movement of anus and anal fin occurs. Predorsal length 26.2–27.7% TL; 65.4–70.4% preanal length. Predorsal vertebrae number remains constant. Forward movement of dorsal fin does not occur in *M. punctatus* or any member of subfamily Myrophinae. Head length 11.3–12.3% TL; 28.6–30.2% preanal length. Eye diameter 8.1–10.6% HL. Snout length 1.8–2.4% TL; 17.7–18.9% HL.

ACKNOWLEDGMENTS

I thank J. Darovec (MRL), M. Moffler (MRL) and G. Smith (MRL) for their comments on this manuscript. I especially thank J. Graves for her encouragement and help during this study.

LITERATURE CITED

Asano, H. 1962. Studies on the congrid eels of Japan. Bull. Masaki Mar. Biol. Inst. No. 1. 143 pp.

Bauchot, M. L. 1959. Etude des larves leptocephales du groupe *Leptocephalus lanceolatus* Strömman et identification a la famille des Serrivomeridae. Dana Report No. 48. 1959. 148 pp.

Berry, F. H. 1964. Aspects of the development of the upper jaw bones in teleosts. Copeia 1964(2): 375–384.

Daget, J., and F. d'Aubenton. 1957. Development et morphologie du crane d'*Heterotis niloticus* Ehr. Bull. Inst. Fr. Afr. Noire (A) 19: 881–936.

Eldred, B. 1966. The early development of the spotted worm eel, *Myrophis punctatus* Lütken (Ophichthidae). Fla. Board Conserv. Mar. Res. Lab. Leafl. Ser. 4: 1–13.

Fahay, M. P., and C. L. Obenchain. 1978. Leptocephali of the ophichthid genera *Ahlia, Myrophis, Ophichthus, Pisodonophis, Callechelys, Letharchus* and *Apterichtus* on the Atlantic continental shelf of the United States. Bull. Mar. Sci. 28: 442–486.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131: 339–456.

Harrington, R. W. 1955. The osteocranium of the American cyprinid fish *Notropis bifrenatus*, with an annotated synonymy of teleost skull bones. Copeia 1955: 267–290.

Hulet, W. H. 1977. Structure and functional development of the eel leptocephalus *Ariosoma balearicum* (De La Roche, 1809). Philos. Trans. R. Soc. Lond. B Biol. Sci. 282: 107–138.

Jolley, J. W., and R. C. Richardson. 1973. Plankton, nightlight and additional collections (ASF series) with pertinent data (June 1970–October 1971). Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 39. 7 pp.

Leiby, M. M. 1979. Leptocephalus larvae of the eel family Ophichthidae. 1. *Ophichthus gomesi* Castelnau. Bull. Mar. Sci. 29: 329–343.

McCosker, J. E. 1977. The osteology, classification, and relationships of the eel family Ophichthidae. Proc. Calif. Acad. Sci. 4: 123 pp.

McDowell, S. B. 1973. Order Heteromi (Notacanthiformes). Pages 1–31 *in* D. M. Cohen, ed. Fishes of the western North Atlantic. Sears Found. Mar. Res. Mem. No. 1: 1–31.

Nelson, G. J. 1966. Gill arches of teleostean fishes of the order Anguilliformes. Pac. Sci. 20: 391–408.

———. 1973. Relationships of clupeomorphs, with remarks on the structure of the lower jaw in fishes. Pages 333–349 *in* P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of fishes. Academic Press, London.

Norman, J. R. 1926. The development of the chondrocranium of the eel (*Anguilla vulgaris*) with observations on the comparative morphology and development of the chondrocranium in bony fishes. Philos. Trans. R. Soc. Lond. B Biol. Sci. 214: 369–464.

Ørvig, T. 1977. A survey of odontodes ('dermal teeth') from developmental, structural, functional, and phyletic points of view. Pages 53–75 *in* S. M. Andrews, R. S. Miles, and A. D. Walker, eds. Problems in vertebrate evolution. Academic Press, London.

Patterson, C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. Pages 77–121 *in* S. M. Andrews, R. S. Miles, and A. D. Walker, eds. Problems in vertebrate evolution. Academic Press, London.

Presley, R. F. 1971. Plankton, nekton, and nightlight collections (PF series) with pertinent data. Yucatan Straits, Florida Straits and offshore Florida waters. (December 1967–October 1969). Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 27. 21 pp.

Schaeffer, B. 1977. The dermal skeleton in fishes. Pages 25–51 *in* S. M. Andrews, R. S. Miles, and A. D. Walker, eds. Problems in vertebrate evolution. Academic Press, London.

Smith, D. G. 1971. Osteology and relationships of the congrid eels of the western North Atlantic (Pisces, Anguilliformes). Ph.D. Dissertation. University of Miami, Miami, Florida. 163 pp.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122: 1–17.

Trewavas, E. 1932. A contribution to the classification of the fishes of the order Apodes, based on the osteology of some rare eels. Proc. Zool. Soc. Lond. Part 3: 639–659.

DATE ACCEPTED: December 1, 1978.

ADDRESS: *Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Ave. S.E., St. Petersburg, Florida 33701.*