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Eggs, Larvae and Osteological Development of the Northern Searobin, *Prionotus carolinus* (Pisces, Triglidae)[1]

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Abstract

Egg, larval and osteological development of the northern searobin, *Prionotus carolinus*, is described, principally from laboratory-reared specimens. Egg diameter ranges from 0.87 to 0.97 mm, and the eggs contain 11 to 37 oil globules, which migrate to various locations within the egg during development. Gastrulation occurs at 27 hr, embryo is halfway around the yolk at 52 hr, and hatching occurs between 120 and 155 hr at 15°C. Prominent pigmentation of the embryo consists of a dark cluster of chromatophores just posterior to the developing eye and the beginning of a transverse band halfway between the vent and notochord tip just prior to hatching. Newly-hatched larvae range from 2.8 to 3.1 mm. The transverse band of pigment is fully developed and is an important characteristic in identifying early *P. carolinus* larvae. The pectoral fins are present at hatching and remain a characteristic feature. Adult meristics are complete by 7.0 mm. Larval head length increases during development becoming 37.5% of the body length during flexion. After flexion, head size decreases to that of an adult (32%). All bones are differentiated and the majority fully ossified at 24.0 mm. Cranial spines are present at 4.0 mm and additional spines on the opercle complex at 7.0 mm. Subsequent development results in degeneration of spines to the adult number and configuration. Spine number and pattern may be useful in separating *P. carolinus* from *P. evolans* and other members of the triglid family.

Introduction

The northern searobin, *P. carolinus*, is a common triglid found in coastal waters of eastern North America from the Gulf of Maine to South Carolina, occasionally straying into the Bay of Fundy. They appear inshore in spring when the water temperature rises above 6°C and move offshore during late autumn and early winter when the temperature falls below 15°C. Spawning occurs from May to September (peak in May-June) on sandy bottom in southern New England waters. Temperatures during spawning range from 13° to 25°C. Fertilized eggs are buoyant and contain numerous oil globules. Further information on the biology and ecology of *P. carolinus* may be found in papers by Hildebrand and Schroeder (1927), Nichols and Breeder (1927), Marshall (1946), Bigelow and Schroeder (1953), Wheatland (1956), Herman (1963), Leim and Scott (1966), Mann (MS 1974), Roberts (1978), and Richards *et al.* (1979).

Reviews of the triglid fishes by Ginsburg (1950) and Teague (1951) do not include information on early development. Kuntz and Radcliff (1917) briefly described the development of *P. carolinus* from fertilization of the egg to juveniles 30 mm in length. No osteological data have been reported. In this paper, development of eggs and larvae of *P. carolinus* is described and compared with the descriptions of Kuntz and Radcliffe (1917).

Materials and Methods

Adult northern searobins were collected by trawling in Fishers Island and Long Island Sound during May-July and maintained alive in tanks of continuous-flowing seawater at ambient temperature. Fertilization was accomplished by stripping eggs and sperm from females and males respectively into 21 cm specimen dishes containing filtered seawater. Eggs were subsequently transferred to 4-liter beakers which were placed in a water bath where the temperature was maintained at 15° ± 1°C. The eggs were kept suspended by using a modified version of the circular air rings described by Houde and Ramsay (1971). Multiple fertilizations insured adequate samples at all stage of development (Table 1).

Prolarvae were stocked in beakers of various sizes and aeration was continued until the onset of feeding. Larvae were fed on cultured *Artemia* nauplii and also

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on wild zooplankton (predominantly copepod nauplii and copepodites) which was collected daily as required with plankton nets. One-quarter to one-half of the water in the beakers was replaced on alternate days throughout the study.

A complete developmental series of larvae was obtained by suplementing the samples reared by the authors with larvae reared by Carolyn Griswold at the National Marine Fisheries Service Laboratory, Narragansett, Rhode Island. Specimens were preserved in 3% buffered formalin. Pigmentation of live larvae consists of both melanophores and xanthophores, but the latter fade upon preservation. Both types of pigment are described in the text but only melanophores are represented in the illustrations.

Forty-five larvae and 12 juveniles were differentially stained and cleared according to the method described by Dingerkus and Uhler (1977) for study of osteological development. All drawings of external features and bone development were produced with the aid of a camera lucida. Where applicable in drawings, stippling denotes cartilage in order to distinguish it from ossified bone.

Measurements with an ocular micrometer were as follows: (a) notochord length (NL) — tip of snout to tip of notochord; (b) standard length (SL) — tip of snout to posterior margin of hypural elements after flexion; (c) head length (HL) — tip of snout to opercular margin; (d) body depth at pectoral fin base (BD) — vertical distance from dorsal to ventral body margins, excluding finfold or fins; (e) snout to anus length (SA) — distance along body midline from tip of snout to a vertical through the posterior margin of the anus; and (f) eye diameter (ED) — horizontal diameter of left orbit.

Egg Development

The pelagic eggs of *P. carolinus* are buoyant and highly transparent with faint yellow coloration. The chorion is unpigmented and lightly sculptured. Fertilized eggs ranged in diameter from 0.86 to 0.97 mm (mean, $\bar{x}$ = 0.92; standard deviation, SD = 0.165; number, n = 181) and contained numerous oil globules of various sizes aggregated in one hemisphere. The number of oil globules ranged from 11 to 37 ($\bar{x}$ = 19, SD = 7.8) in a sample of 239 eggs. Kuntz and Radcliff (1917) reported eggs ranging from 1.0 to 1.5 mm in diameter with 10 to 20 oil globules.

Oil globule movement

Prior to fertilization, the oil globules are scattered within one hemisphere of the egg (Fig. 1A). After fertilization and during early cell division, the globules migrate to the area of newly developed cells (Fig. 1C). At the eight cell stage (Fig. 1D), the oil globules scatter throughout the yolk periphery and generally remain scattered until the gastrula stage (Fig. 1H and 1I) when they are arranged in a band at the egg equator. With the appearance of the embryo, the oil globules move toward the site of blastophore closure (Fig. 1J, 1K and 1L), following which they disperse throughout the yolk periphery and remain scattered.

Kuntz and Radcliffe (1917) reported only slight change in the distribution of oil globules, but in the majority of eggs the globules remained distributed uniformly under the yolk surface. Wheatland (1956) used this characteristic of uniform distribution during egg development to separate eggs of *P. carolinus* and *P. evolans* collected in Long Island Sound, because oil globules in eggs of the latter species were reported to remain aggregated at one pole. Richards (1959) discontinued use of this characteristic when she discovered that it was not reliable.

Morphology

Early embryonic development is rapid, with gastrulation occurring at 27 hr (Fig. 1H and 1I) and the embryonic shield being visible as a thickening on the dorsal surface at 30 hr (Fig. 1J). The developing embryo continues to increase in length, and the optic vesicles appear, together with Kupffer's vesicle, just prior to blastopore closure. At the stage shown in Fig. 1K, two pairs of somites are visible. When the embryo extends about halfway around the yolk (Fig.1L), invagination of the optic vesicles begins, forming the lens cup, and the pericardal sac is present. By the time the embryo extends five-eighths around the yolk (Fig. 1M), the lens cups are complete and the lenses are visible, although they do not extrude beyond the optic margins. The brain begins to differentiate, and the auditory vesicles are first seen on either side of the brain. The heart appears as a curved tube-like structure. A finfold is evident in the caudal region, accompanied by a lifting of the tail off the yolk surface. At this stage of development, 16 somites are visible.

When the embryo extends three-fourths around the yolk (Fig. 1N), the lens of the eye extrudes from the optic cup, the brain is well differentiated, and the heart is two-chambered and beating. Pectoral fin buds are visible and the finfold increases in width. The tail deflects away from the embryonic axis and 19 somites are visible. First movement of the embryo is noticed at this stage. Just before hatching occurs, the tail slightly overlaps the head, 21-23 somites are visible, and the pectoral fin buds are raised off the yolk surface. At this stage, the embryo is morphologically similar to a newly-hatched larvae.

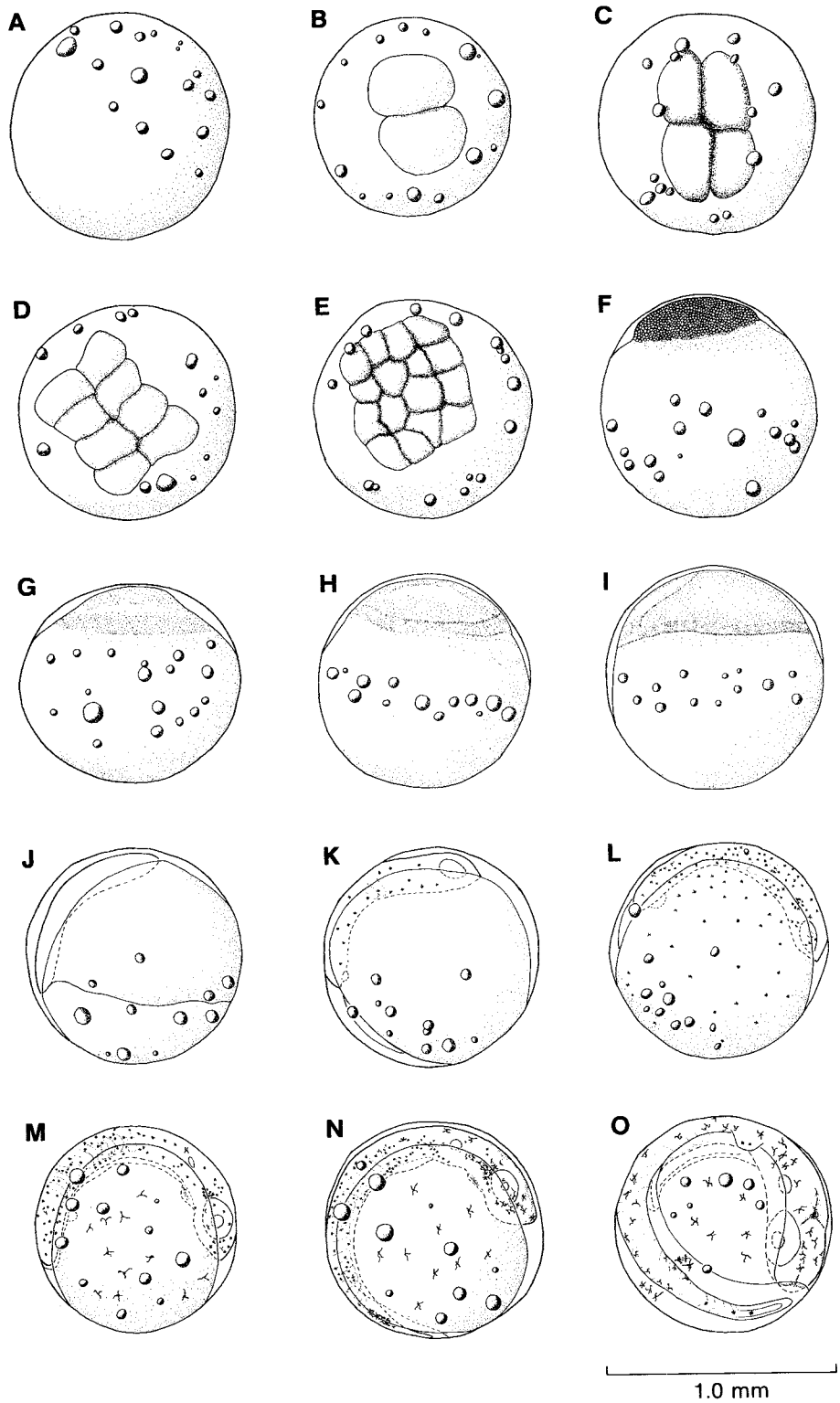

Fig. 1. Development stages of *P. carolinus* eggs: **A**, fertilized eggs; **B**, two-cell (2.0 hr); **C**, four-cell (3.5 hr); **D**, eight-cell (4.0 hr); **E**, 16-cell (5.0 hr); **F**, multicell (6.0 hr); **G**, blastula (17 hr); **H**, gastrula (27 hr); **I**, gastrula (30 hr); **J**, early embryo (37 hr); **K**, embryo 1/3 around yolk (42 hr); **L**, embryo 1/2 around yolk (52 hr); **M**, embryo 5/8 around yolk (69 hr); **N**, embryo 3/4 around yolk (89 hr); **O**, embryo fully around yolk (115 hr).

Pigmentation

Pigment is first observed when the embryo extends one-third around the yolk (Fig. 1K), with contracted melanophores and xanthophores scattered lightly over the body. When the embryo extends one-half around the yolk, both types of pigment are present on the yolk surface, and pigmentation of the embryo continues to increase (Fig. 1L). When the embryo extends five-eighths around the yolk, a characteristic dense cluster of melanophores and xanthophores are visible just posterior to the developing eyes, along with light pigmentation anterior to the eyes (Fig. 1M). This characteristic was not described for eggs reared by Kuntz and Radcliffe (1917). Also, at this stage, melanophores and xanthophores on the dorsal surface of the head and on the yolk surface are stellate. When the embryo encircles three-fourths of the yolk, melanophores and xanthophores are present along the ventral and dorsal margins near the notochord tip (Fig. 1N). Just prior to hatching, body pigment and the cluster posterior to the eyes are reduced in density. Two to three isolated melanophores are evident on the dorsal surface of the pectoral fin bud and on the tail just anterior to the notochord tip. Also, melanophores and xanthophores on the tail about halfway between the vent and notochord tip have spread onto the finfolds (Fig. 1O). Kuntz and Radcliff (1917) did not mention this pigment pattern until after hatching had occurred. This characteristic transverse band of pigment halfway between the vent and notochord tip may be useful for distinguishing late stage embryos of *P. carolinus* from those of *P. evolans*.

Larval Development

The incubation period ranged from 112 to 155 hr (Table 1). Newly-hatched larvae (Fig. 2A) ranged in size (NL) from 2.8 to 3.1 mm NL ($\bar{x}$ = 3.0 mm, SD = 0.09). The finfold is continuous from the head posteriorly around the notochord tip and anteriorly to the vent, the eyes are unpigmented, and the mouth is undeveloped. Twenty-three myomeres are present, and 12–19 oil globules ($\bar{x}$ = 14, SD = 2.0) are located in the posterior half of the yolk sac. At 3.4 mm NL (Fig. 2B), the yolk sac is fully absorbed, the eyes are pigmented, the mouth is functional, and a single loop is present in the digestive track. Larvae of this size commence feeding, 3.5 to 5 days after hatching. At 4.0 mm NL (Fig. 2C), a single row of teeth is present on the upper jaw. At 5.4 mm NL (Fig. 2D), teeth are present on the lower jaw and the anterodorsal part of the head is slightly flattened. Flattening of the head continues through development until the characteristic head shape of the adult is attained. At 7.0 mm SL (Fig. 2F), the young searobin exhibits the adult complement of fin rays and spines.

TABLE 1. Hatching times after fertilization of *P. carolinus* eggs in five series of experiments at 15° C.

Series	Number of parents	Hours to hatching after fertilization
1	5	120–140
2	4	135–155
3	2	119–134
4	3	125–145
5	3	112–140

Pigmentation

Pigment of the newly-hatched larvae (Fig. 2A) consists of stellate melanophores and xanthophores scattered sparsely on the head and trunk. A transverse band of pigment extends onto the finfold about halfway between the vent and notochord tip. A row of melanophores and xanthophores is present along the ventral margin from the vent posteriorly to just beyond the transverse band. A few large melanophores are present on the finfold above the pectoral bud, along the vent, and on the ventral margn near the notochord tip. Although pigment is present on the finfold above the pectoral buds, the transverse band, described by Kuntz and Radcliffe (1917), was not observed. Both contracted melanophores and xanthophores are present on the surface of the yolk sac.

At 3.4 mm NL (Fig. 2B), pigment consists of melanophores only, as xanthophores are absent at this and larger sizes. Pigmentation of the trunk is similar to that of newly-hatched larvae except that the transverse band on the finfold is reduced in intensity. Stellate melanophores occur on the dorsal, ventral and anterior surfaces of the gut and inside the auditory capsule. Single large melanophores are located on the dorsal surface of the mid-brain and hind-brain, and deep in the musculature under the hind-brain. A row of melanophores is visible along the margin of the lower jaw and individual melanophores are present on the opercle and jaw-complex.

At 4.0 mm NL (Fig. 2C), the gut and trunk are more heavily pigmented than in smaller larvae, and melanophores are scattered on the opercle complex, on the upper and lower jaws and at their junction. Melanophores along the ventral margin of the trunk extend to the developing hypural plates, with individual melanophores on the developing caudal rays and near the notochord tip. A few melanophores remain in the vicinity of the vent, but the transverse band, located midway between the vent and notochord tip in smaller larvae, is absent.

At 5.4 mm NL (Fig. 2D), the pectoral fin is densely pigmented and melanophores intensify on the trunk and viscera, but pigmentation of the head and finfold is

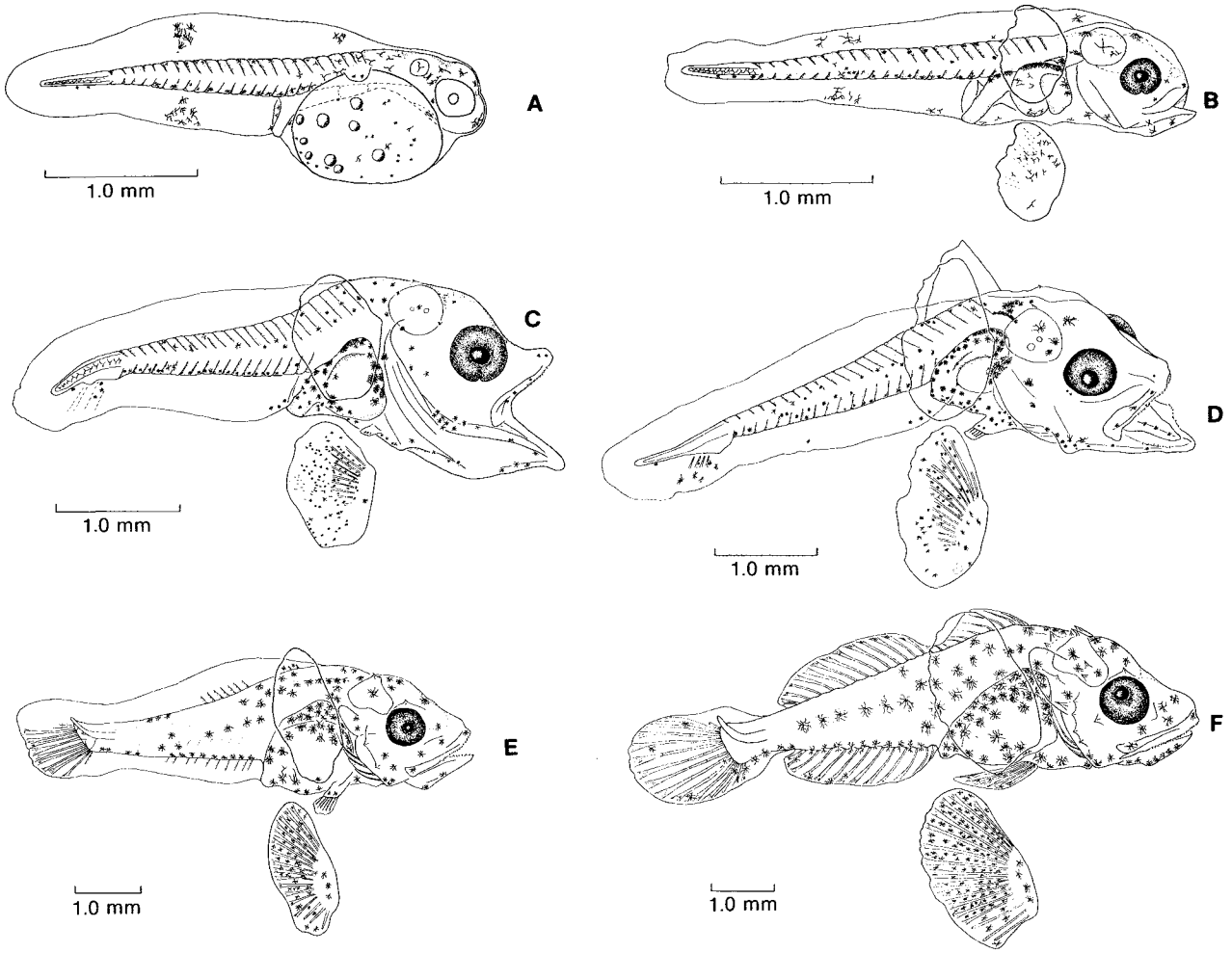

Fig. 2. Developmental stages of *P. carolinus* larvae: **A**, hatched at 3.0 mm NL (120 hr); **B**, 3.4 mm NL; **C**, 4.0 mm NL; **D**, 5.4 mm NL; **E**, 6.0 mm SL; **F**, 7.0 mm SL.

similar to that of 4.0 mm larvae. At 6.0 mm SL (Fig. 2E), all trunk and gut pigment increases in density and pigment on the dorsal and lateral surfaces of the head increases slightly. Stellate melanophores are visible at the site of formation of the first dorsal fin.

At 7.0 mm SL (Fig. 2F), increased pigmentation is evident on the lower jaw and on the head in the vicinity of the auditory vesicles. The dorsal surface of the gut is heavily pigmented, but no substantial change in trunk pigment is evident. Melanophores are present on the body dorsal to the gut and as a row along the lateral midline. Melanophores along the ventral margin of the trunk expand onto the anal and caudal fins, and few individual melanophores are present on the distal portions of these fins. The pectoral fins are heavily pigmented, the pelvic fins are lightly pigmented, and the dorsal fins are unpigmented.

Fin development

The finfold, which is predominant in all larvae smaller than 6.0 mm SL, diminishes as the median fins develop and is completely absent at 7.0 mm SL. The sequence of fin development is pectoral, pelvic, caudal, first dorsal, second dorsal, and anal (Table 2).

The pectoral fin is evident at hatching as a fleshy bud (Fig. 2A). The first eight rays are visible at 4.0 mm NL (Fig. 2C) and the full complement is attained by 5.7 mm NL. However, the three feeler rays, which are separate in the adult, are still contained in the fin membrane, even at 7.0 mm SL. The feeler rays are separate at 24 mm SL, but the lack of specimens between 7 and 24 mm SL precluded observation on the exact size at which they separate.

The pelvic fin bud is evident at 4.0 mm NL (Fig. 2C), a spine and three rays are present at 5.4 mm NL, and the fin is complete at 6.3 mm SL. When larvae attain 5.0 mm NL, four caudal rays are visible, and the full adult complement of 13 principal rays are present at 7.0 mm SL. Two dorsal spines, 7 dorsal rays and 10 anal rays are visible at 6.0 mm SL and the full complement of spines and rays are present at 7.0 mm SL (Table 2).

TABLE 2. Development of fins in reared larvae of *P. carolinus*.

Fins	Buds first appear	Spines and rays: First appear	Spines and rays: Full complement	Spines and rays: Number in fully developed fins
Pectoral	<3.0 NL	4.0 NL	5.7 NL	13–14 (rarely 15) and 3 feeler rays
Pelvic	4.0 NL	5.4 NL	6.3 SL	I,5
Caudal (principal)	—	5.4 NL	7.0 SL	13
Anal	—	6.0 SL	7.0 SL	12 (rarely 11,13)
First dorsal	—	6.0 SL	7.0 SL	X (rarely IX)
Second dorsal	—	6.0 SL	7.0 SL	13 (rarely 12,14)

Further descriptions of fins and supporting structures are presented in the section on osteology.

Head spine development

Spine development in *P. carolinus* occurs in two stages: an increase in number during larval development until metamorphosis, followed by a decrease in number to that present in the adult. Only the first stage will be described here.

At 4.0 mm NL (Fig. 2C), a parietal spine appears dorsal to the otic capsule and increases in height throughout larval development. At 6.0 mm SL, three preopercle spines and one sphenotic spine are present (Fig. 2E and 2F). Visible at 6.2 mm SL is an opercle spine, which expands into a ridge bearing two spines by 7.0 mm SL (Fig. 5D). Also, at 7.0 mm SL, one circumorbital and two pterotic spines are present, the number of preopercle spines has increased to eight, and three posttemporal spines are visible posterior to the large pterotic spine (Fig. 2F).

Teague (1951), in a description of head spines of *P. carolinus*, noted that most are present until approximately 100 mm SL, after which they disappear before adulthood is attained. His description was based on fish of 82–204 mm SL, at which sizes the number of spines would have been less than the number found in 4–7 mm NL larvae of this study. The rostral, preorbital and nuchal spines described by Teague (1951) were not observed in larvae up to 7.0 mm SL and are presumed not to have yet developed. Additional descriptions of spines associated with the opercle and pectoral complexes are presented in the section on osteology.

Morphometrics

Various morphological measurements of reared *P. carolinus* larvae and captured adults are given in Table 3. The proportion of head length to body length increases from 24.1% at hatching to 33.0–37.5% during flexion and decreases to 32.3% at postflexion, which is only slightly higher than the value of 32.0% (range 30.4–35.4%) for adults. The proportion of body depth to body length increases from 20.6% at hatching to 29.7–32.8% during flexion and to 33.8% at postflexion, in contrast to 22.4% (range 19.8–25.6%) for adults. The proportion of eye diameter to body length is relatively constant during preflexion (9.6–10.7%), flexion (9.8–11.2%) and postflexion (11.1%), in contrast to

TABLE 3. Morphometric data for reared larvae by size group and for adult *P. carolinus*. (BL = body length, HL = head length, ED = eye diameter, SA = snout to anus length. Data in **bold** refer to specimens undergoing notochord flexion.)

	Size group (mm)	Sample size	Mean body length (mm)	Ratios of mean measurments, as percentages: HL/BL	BD/BL	ED/BL	SA/BL
Larvae	2.5–2.9	9	2.9	—	—	10.3	46.6
	3.0–3.4	30	3.2	24.1[a]	20.6[a]	9.7	45.3
	3.5–3.9	21	3.7	24.9	21.9[a]	10.0	45.3
	4.0–4.4	7	4.3	27.0	23.3	10.0	45.3[b]
	4.5–4.9	2	4.8	27.5	24.8	9.6	50.8
	5.0–5.4	3	5.2	28.8	26.2	9.8	49.0
	5.5–5.9	5	5.7	30.5	27.7	10.7	49.8
	6.0–6.4	**3**	**6.1**	**33.0**	**29.7**	**9.8**	**50.8**
	6.5–6.9	**3**	**6.5**	**37.5**	**32.8**	**11.2**	**57.8**
	7.0–7.4	1	7.1	32.3	33.8	11.1	54.5
Adults	152–198	24	175.3	32.0	22.4	6.3	55.7

[a] Based on 19 specimens.
[b] Based on 6 specimens.

6.3% (range 5.7-7.2%) for adults. The proportion of snout anus length to body length increases from about 45-46% at hatching to 49-50% during late preflexion, to 50.8-57.8% during flexion and averages 54.5% at postflexion, which is similar to the value of 55.7% (range 52.7-61.0%) for adults.

Osteology

Osteological terminology follows that of Gosline (1961), Potthoff (1974, 1975), Houde and Potthoff (1976), Leiby (1979) and Peters (1981). Details of ossification of the various bones are incomplete due to the lack of specimens between 7 and 24 mm SL.

Jaws (Fig. 3)

The hyomandibular, quadrate and Meckel's cartilages are present as separate parts in the smallest larvae examined (2.9 mm NL). At 3.2 mm NL, the extended hyomandibular lies in close proximity to the pterotic region of the skull and extends ventrally to join the quadrate cartilage (Fig. 3A). The major dorsal and opercle condyles are visible at 4.4 mm NL (Fig. 3B). A prominent posterior ridge is evident at 7.0 mm SL for articulation with the preopercle (Fig. 3D). Ossification of the hyomandibular is complete in a 24 mm SL specimen (Fig. 3E).

The quadrate contacts the anteroventral margin of the hyomandibular and the condicular process of the dentary-articular cartilage at approximately 3.1 mm NL (Fig. 3A). Dorsal and ventral expansions begin at 5.2 mm NL and the quadrate joins the ethmoid region of the skull at 7.0 mm SL, forming the palato-quadrate complex (Fig. 3D). This complex then differentiates into the various components of the jaw suspensorium. At 24 mm SL, the quadrate envelopes the symplectic

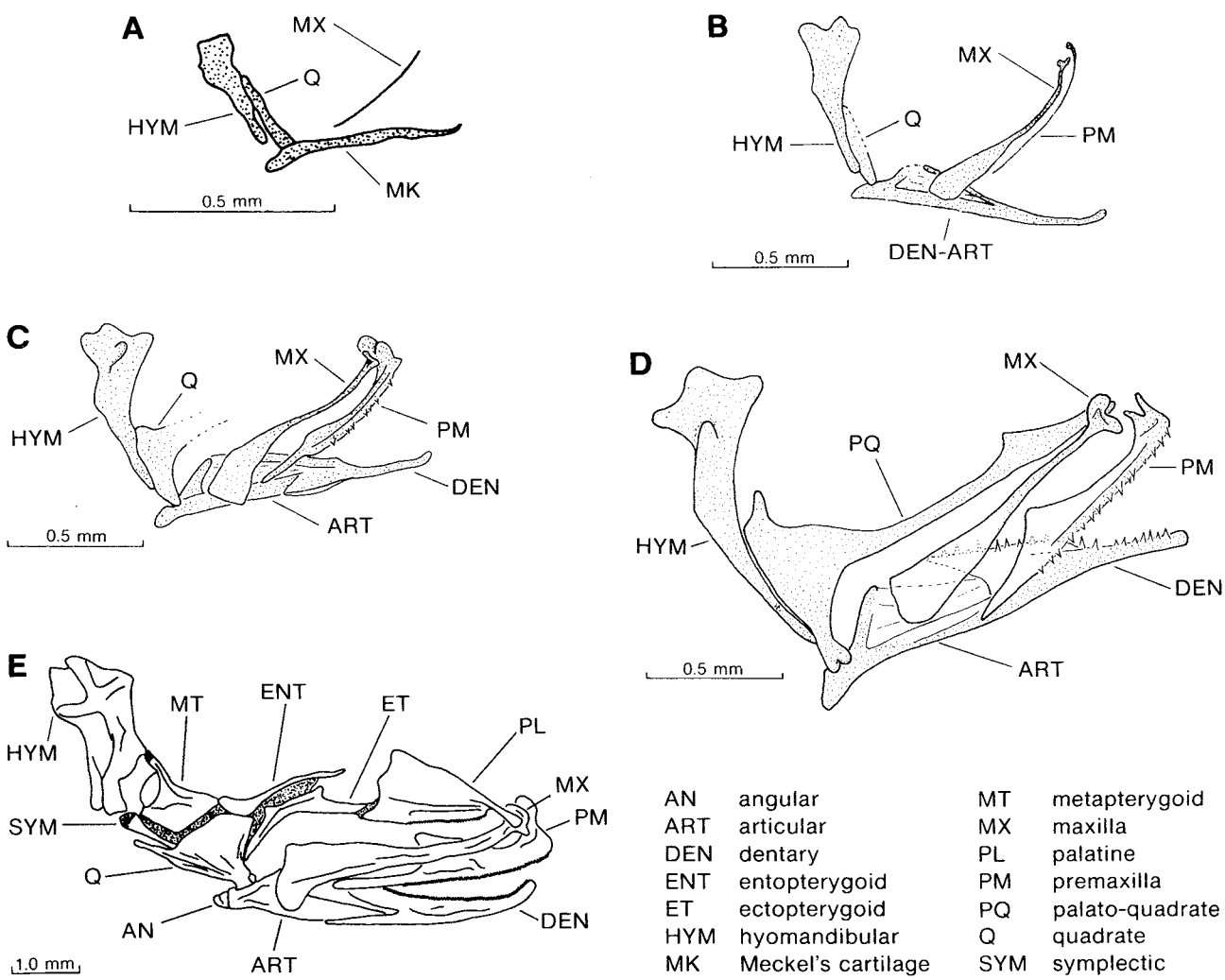

Fig. 3. Right lateral view of jaw and suspensorium development in *P. carolinus*: **A**, 3.2 mm NL; **B**, 4.4 mm NL; **C**, 5.2 mm NL; **D**, 7.0 mm SL; **E**, 24.0 mm SL.

which articulates with the ventral tip of the hyomandibular (Fig. 3E). The metapterygoid forms dorsal to the quadrate and joins the hyomandibular at a mid-anterior condyle. The entopterygoid and ectopterygoid complete the complex linking the quadrate to the palatine. The palatine articulates with the olfactory region of the skull and saddles the premaxillary (Fig. 3E).

The articular and dentary cartilages begin to differentiate at 4.4 mm NL (Fig. 3B). At 7.0 mm SL, the dentary is expanded dorsally to receive the articular (Fig. 3D). The articular expands dorsally just anterior to the quadrate articulation and continues anteriorly as a thin sheet of bone supported by a thicker cartilage rod. Ossification of both structures begins at 7.0 mm SL along their dorsal margins and is complete in the 24 mm SL specimens.

The maxilla is first evident as a thin bar of cartilage in the upper lip at 3.2 mm NL (Fig. 3A). The premaxilla develops from a thin bar of cartilage anterior to the maxilla at 4.4 mm NL (Fig. 3B). Expansion of the dorsal tip of the premaxilla results in a saddle-shaped process which joins the maxilla at 5.2 mm NL (Fig. 3C). Ossification of both maxilla and premaxilla is first noted in the posterior region at 7.0 mm SL and proceeds anteriorly (Fig. 3D). Short conical teeth are first evident on the premaxilla at 5.2 mm NL and on the dentary at 6.0 mm SL (Fig. 3C and 3D), developing initially as a single row and subsequently as numerous rows of sharp teeth, some being recurved in larger larvae. They all become reduced to bands of cardiform teeth in adults. Initial formation of teeth on the vomer and patatine was not observed in larvae at 7.0 mm SL but they were present in 24 mm specimens (Fig. 3E).

Pectoral fins (Fig. 4)

The cleithrum, first visible at 3.2 mm NL as a thin cartiloginous structure (Fig. 4A), continues to expand dorsally and ventrally (Fig. 4B and 4C). By 6.6 mm SL, an attachment for the supracleithrum is formed at the dorsal tip of the cliethrum (Fig. 4D). The large characteristic cleithral spine of the adult is first seen embedded in the musculature at 7.0 mm SL. Ossification is complete at 7.0 mm SL. This spine becomes a prominent external feature at approximately 60 mm SL.

The coricoid-scapula is present at 3.2 mm (Fig. 4A) and begins to ossify at 6.6 mm (Fig. 4D). The coricoid, positioned at the concave ventral end of the cleithrum, is fully ossified at 24 mm SL. The scapula is partially ossified at 24 mm SL and remains fused to the coracoid (Fig. 4E).

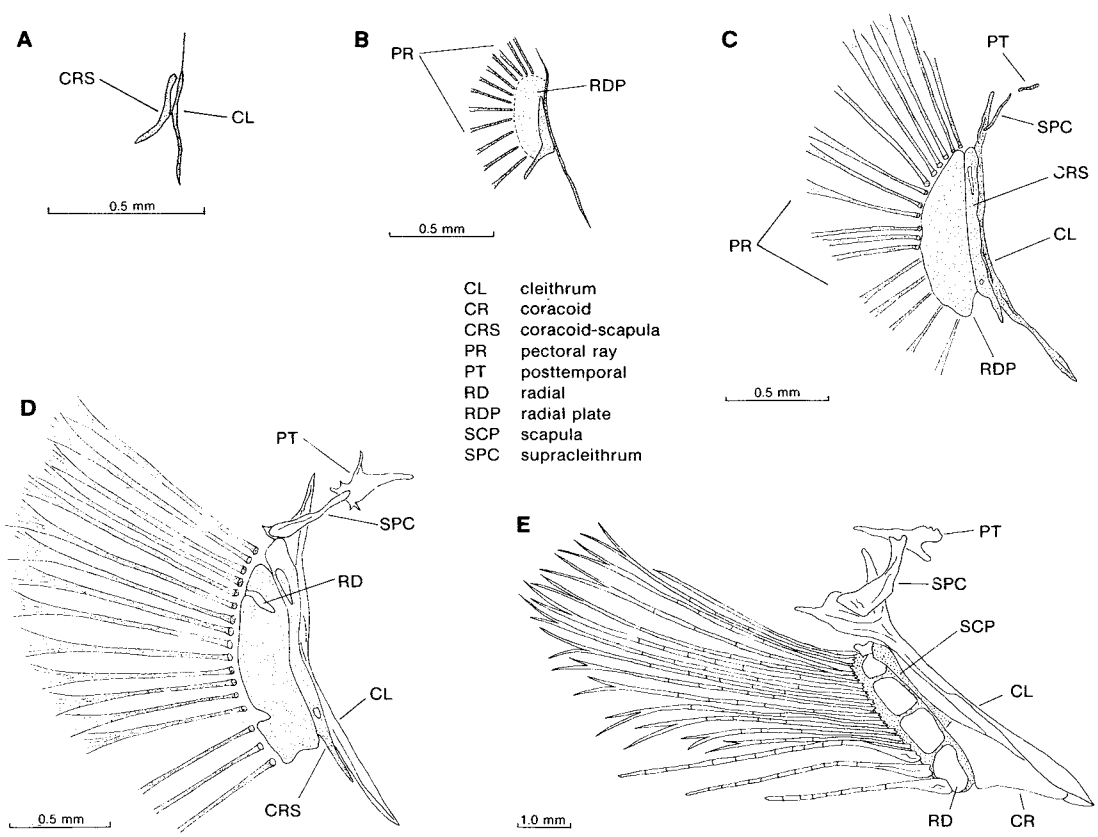

Fig. 4. Right lateral view of pectoral girdle development in *P. carolinus*: **A**, 3.2 mm NL; **B**, 4.3 mm NL; **C**, 5.7 mm NL; **D**, 6.6 mm SL; **E**, 24.0 mm SL.

The radials are represented as a broad catilaginous plate at 4.3 mm NL (Fig. 4B). Ossification of individual radials begins dorsally at 6.6 mm SL (Fig. 4D), and the four radials are complete at 24 mm SL (Fig. 4E).

The supracleithrum, first visible as a slender cartilage overlapping the cleithrum, expands dorsally to meet the posttemporal at 5.7 mm NL (Fig. 4C), and ossification is complete at 6.6 mm SL. The posttemporal develops from an isolated cartilage lying between the supracleithrum and the occipital region of the skull at 5.7 mm SL (Fig. 4C). Development of three spines and contact with the skull and supracleithrum is complete at 6.6 mm SL (Fig. 4D). The spines are reduced in size at 24 mm SL (Fig. 4E).

Pectoral fin rays are first evident at 4.0 mm NL, and the full adult complement are present at 5.7 mm NL (Fig. 4C). The adult characteristic pattern of 14 bifuricated rays and three separate feeler rays is present at 24 mm SL (Fig. 4E).

Opercle series (Fig. 5)

The opercle complex consists of opercle, preopercle, subopercle and interopercle. The opercle appears

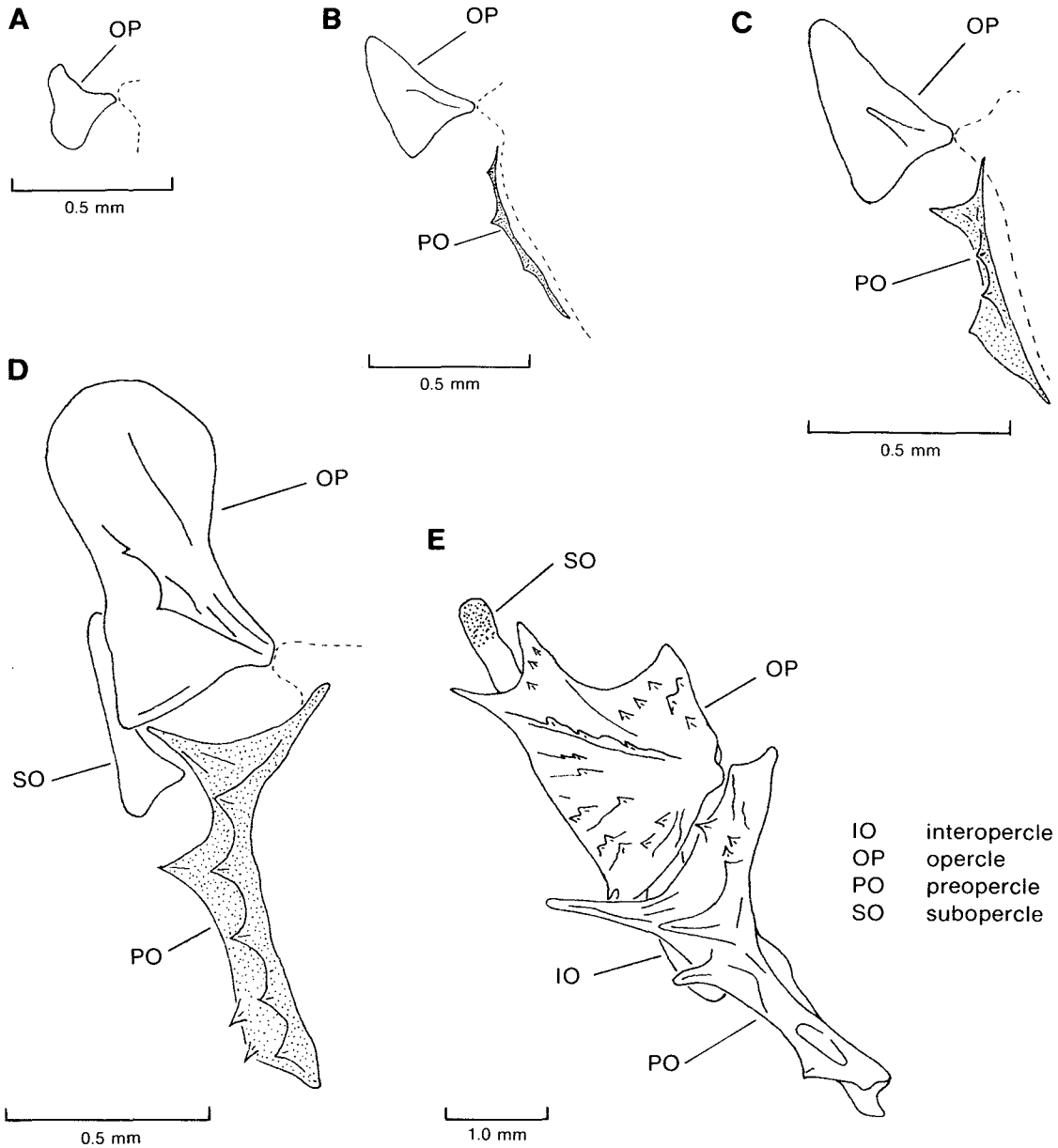

Fig. 5. Right lateral view of opercle complex development in *P. carolinus*: **A**, 5.2 mm NL; **B**, 6.0 mm SL; **C**, 6.2 mm SL; **D**, 7.0 mm SL; **E**, 24.0 mm SL.

as a thin sheet of bone articulating with the hyomandibular at 5.2 mm NL (Fig. 5A). The expanded opercle has two spines at 7.0 mm SL (Fig. 5D) and is fully ossified at 24 mm SL (Fig. 5E).

The preopercle, bearing three small spines, is present at 6.0 mm SL posterior to the hyomandibular (Fig. 5B). At 7.0 mm SL, there are five small lateral spines, two larger posterior spines and two postero-ventral spines (Fig. 5D). These decrease in number by 24 mm SL, but the large preopercle spine characteristic of the adult remains. Ossification begins at 6.3 mm SL and is complete at 24 mm SL (Fig. 5E).

The subopercle is visible at 7.0 mm SL as a separate cartilage posterior to the preopercle and partially underlying the postero-ventral tip of the opercle (Fig. 5D). Ossification is partially complete at 24 mm SL (Fig. 5E). The interopercle is first seen at 24 mm SL as a flat oval bone underlying the preopercle.

Hyoid arch (Fig. 6)

The hyoid arch, evident as a bar of cartilage at hatching (Fig. 6A), is ossified and separated into its epihyal and ceratophyal components at 24 mm SL (Fig. 6E). Four branchiostegal rays are present at 4.4 mm NL (Fig. 6B), and the adult complement of seven rays is attained at 6.3 mm SL (Fig. 6D). Ossification of rays proceeds anteriorly. The interhyal and basihyal structures appear first as cartilage at 4.4 and 5.2 mm NL respectively (Fig. 6B and 6C). The basihyal is fully ossified at 24 mm SL, but the dorsal and ventral tips of the interhyal are still cartilage. The urohyal is present as a thin sheet of bone at 6.3 mm SL (Fig. 6D). The partially ossified glossohyal is present in 24 mm SL larvae (Fig. 6E).

Pelvic fins (Fig. 7)

The basipterygia are first seen at 5.2 mm NL (Fig. 7A) as separate oblong cartilaginous structures

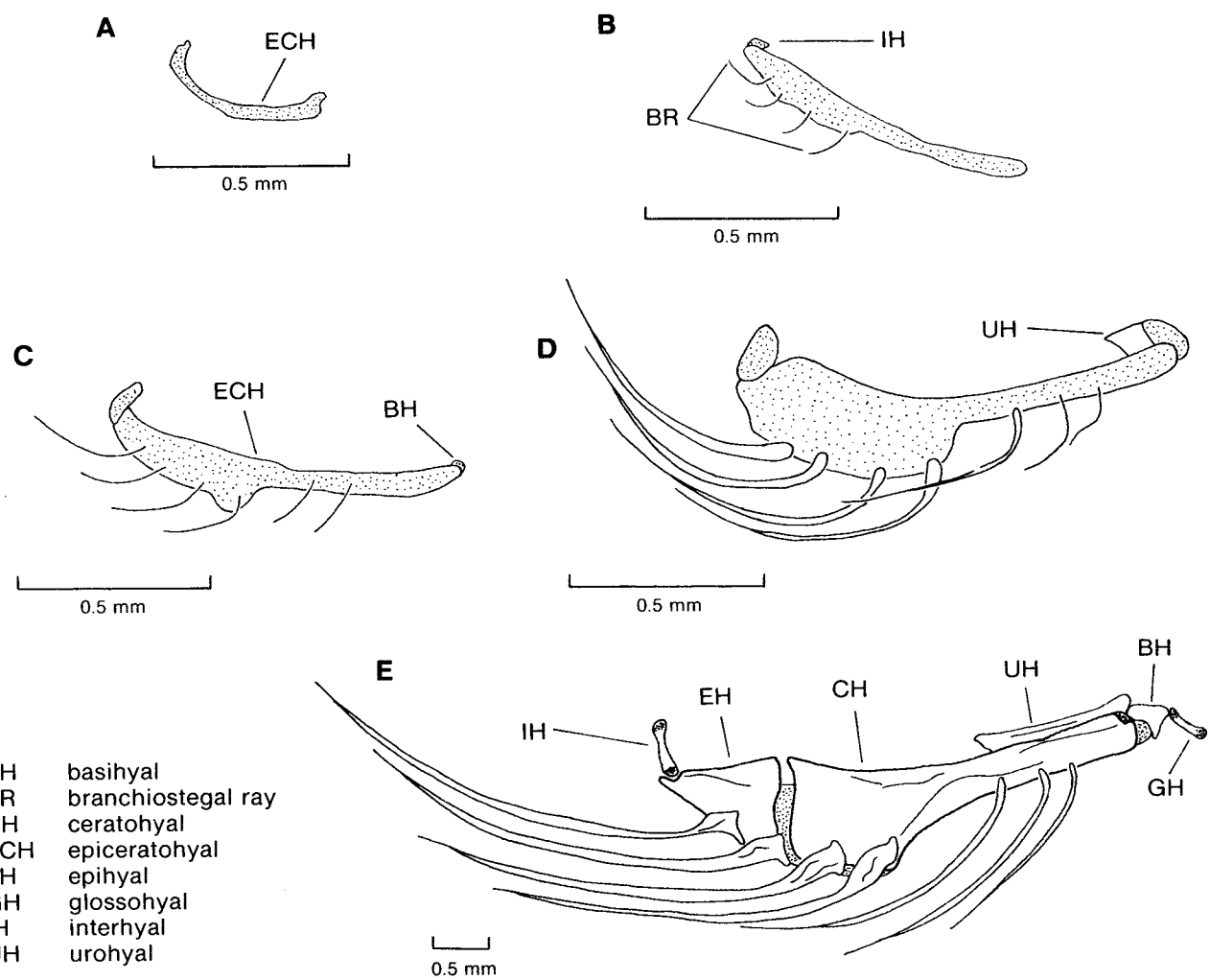

Fig. 6. Right lateral view of hyoid arch development in *P. carolinus*: **A**, 3.2 mm NL; **B**, 4.4 mm NL; **C**, 5.2 mm NL; **D**, 6.3 mm SL; **E**, 24.0 mm SL.

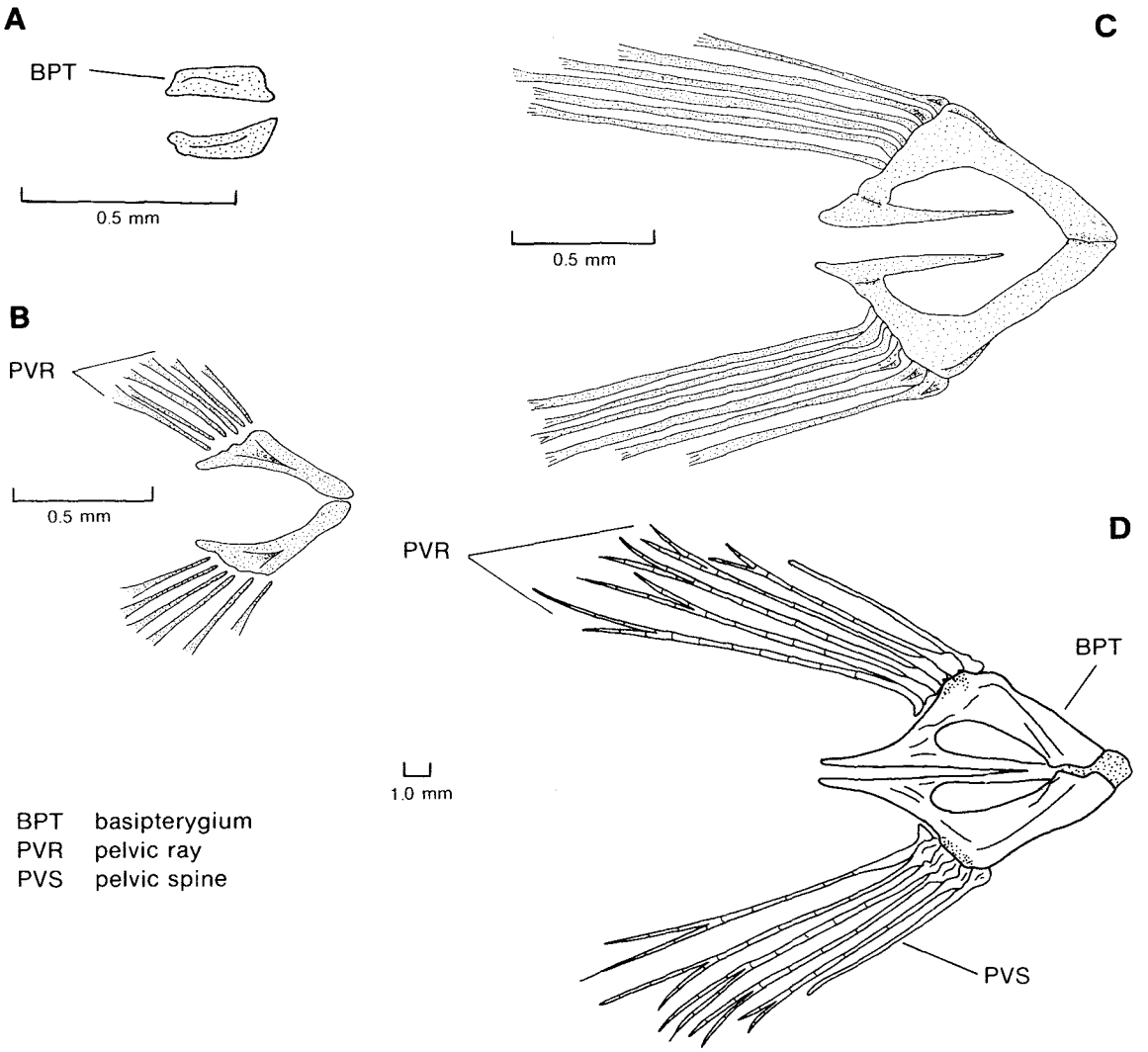

Fig. 7. Ventral view of pelvic girdle development in *P. carolinus*: **A**, 5.2 mm NL; **B**, 6.3 mm SL; **C**, 7.0 mm SL; **D**, 60.0 mm SL.

located between and posterior to the ventral tips of the cleithra. They expand anteriorly and posteriorly, forming a symphysis at the anterior tip at 6.3 mm SL (Fig. 7B). Ossification is not complete until 60 mm SL (Fig. 7D). The pelvic fin spine and three rays are evident at 5.4 mm NL, and the adult complement of one spine and five rays (I, 5) is present at 6.3 mm SL (Fig. 7B). The five rays are segmented and bifurcated at 60 mm SL (Fig. 7D).

Branchial arch (Fig. 8)

The branchial arch in 3.2 mm NL larvae consists of fused basibranchials 1-3, ceratobranchials 1-3, and hypobranchials 1-3. The hypobranchials are joined to the ceratobranchials but not to the fused basibranchials at this stage (Fig. 8A). Connection of the hypobranchials and basibranchials begins at 5.2 mm NL (Fig. 8B). The fourth ceratobranchial is present at this size, along with the upper and lower pharyngeals which are visible as separate cartilages. The posterior tips of the ceratobranchials begin to curve dorsally to join the four cartilaginous epibranchials, which also extend dorsally and attach to the upper pharyngeals at 6.2 mm SL (Fig. 8C). At this stage, 5-10 sharp conical teeth are present on both upper and lower pharyngeals. Subsequently, these teeth degenerate to cardiform teeth which completely cover the pharyngeals. Ossification is nearly complete at 24 mm SL (Fig. 8D).

Caudal complex (Fig. 9)

The caudal complex consists of five hypurals, three epurals, two neural spines, three haemal spines, urostyle and parhypural. Development of the caudal fin supports begins at 4.0 mm NL, with the presence of four hypurals and two haemal spines ventrally near the tip of the notochord (Fig. 9A). Neural spines and two

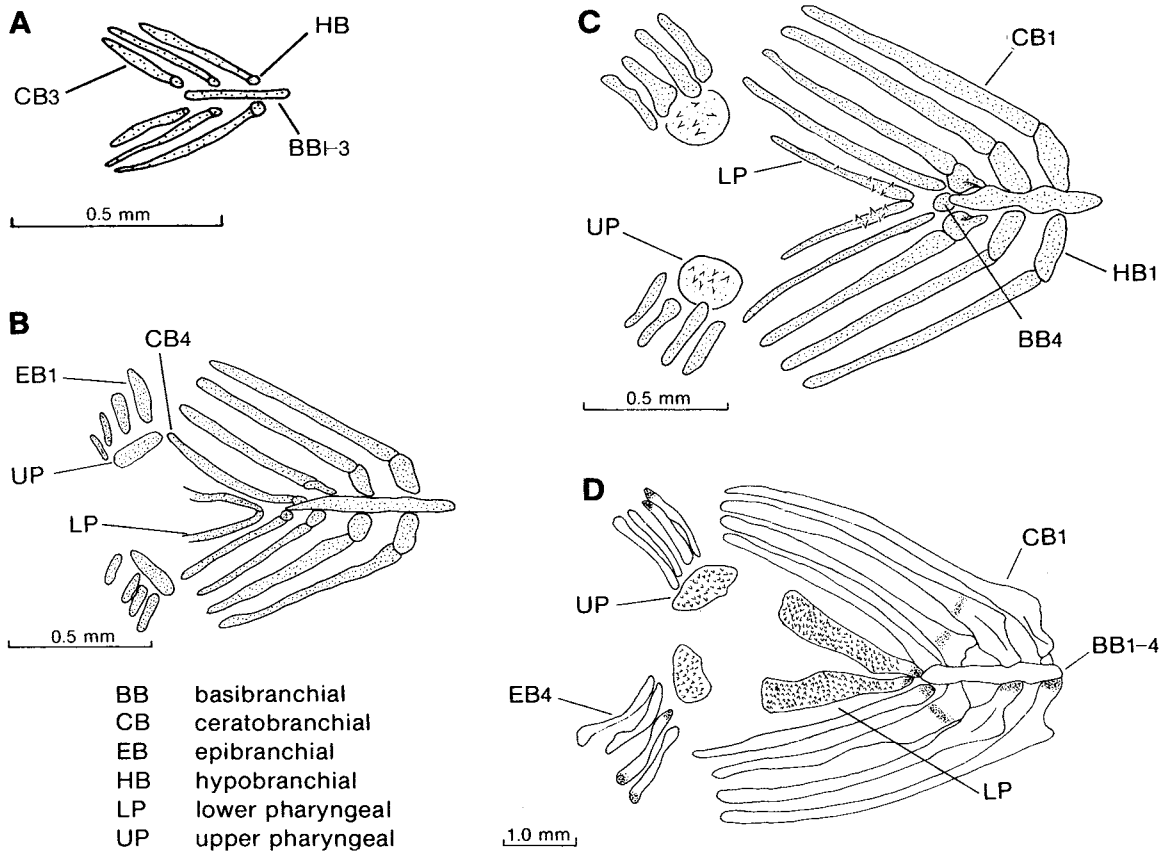

Fig. 8. Ventral view of branchial arch development in *P. carolinus*: **A**, 3.2 mm NL; **B**, 5.2 mm NL; **C**, 6.2 mm SL; **D**, 24.0 mm SL.

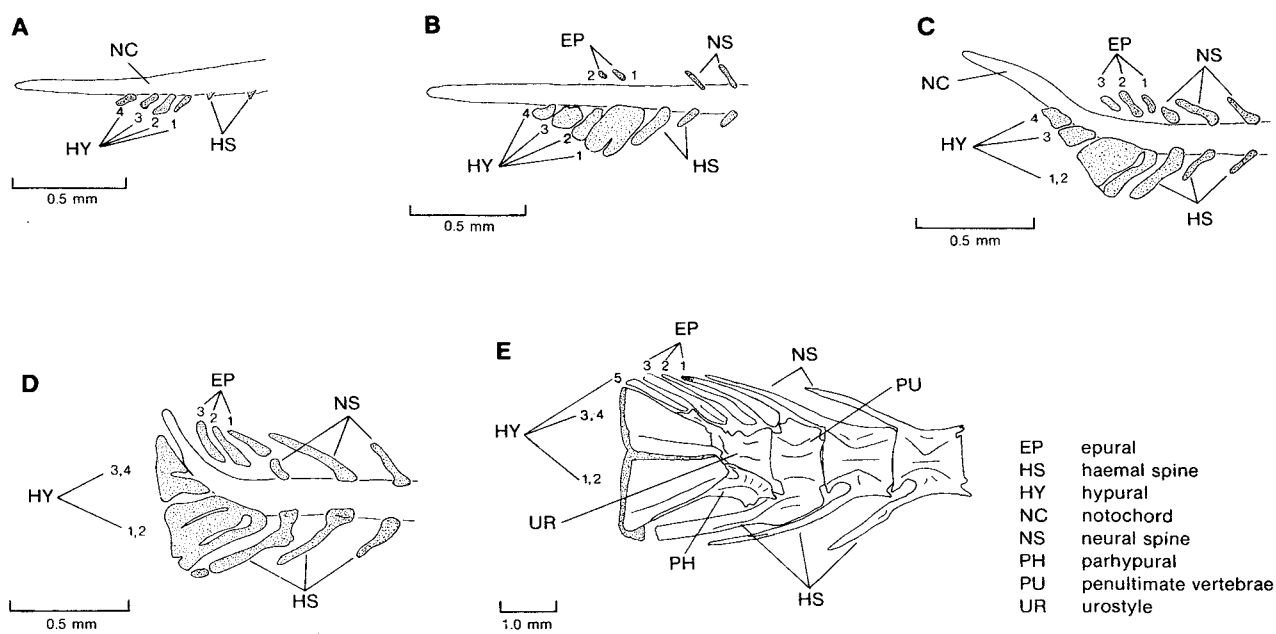

Fig. 9. Left lateral view of caudal complex development in *P. carolinus*: **A**, 5.2 mm NL; **B**, 6.0 mm NL; **C**, 6.3 mm SL; **D**,, 7.0 mm SL; **E**, 24.0 mm SL.

epurals are visible at 6.0 mm SL (Fig. 9B), with the third forming at 6.3 mm SL (Fig. 9C). Notochord flexion begins at this size, and hypurals 1 and 2 are now fused. A neural spine has formed anterior to the first epural. Hypurals 3 and 4 are fused at 7.0 mm SL (Fig. 9D), and, together with the fused hypurals 1 and 2, form the dorsal and ventral hypural plates.

No centra or haemal and neural arch formation is evident in the caudal region at 7.0 mm SL, but these are complete at 24 mm SL (Fig. 9E). Additional structures present at 24 mm SL include the fifth hypural, located dorsal to hypurals 3-4, and the parhypural, located ventral to the urostyle. Ossification of the caudal complex begins at 6.0 m SL in hypural 1 (Fig. 9B) and is complete at 24 mm SL (Fig. 9E).

Backbone (Fig. 10)

There are 25 centra, 25 neural spines, 17 haemal spines and 10 pleural ribs in the adult, and one pterygiophore is present in each interneural and interhaemal

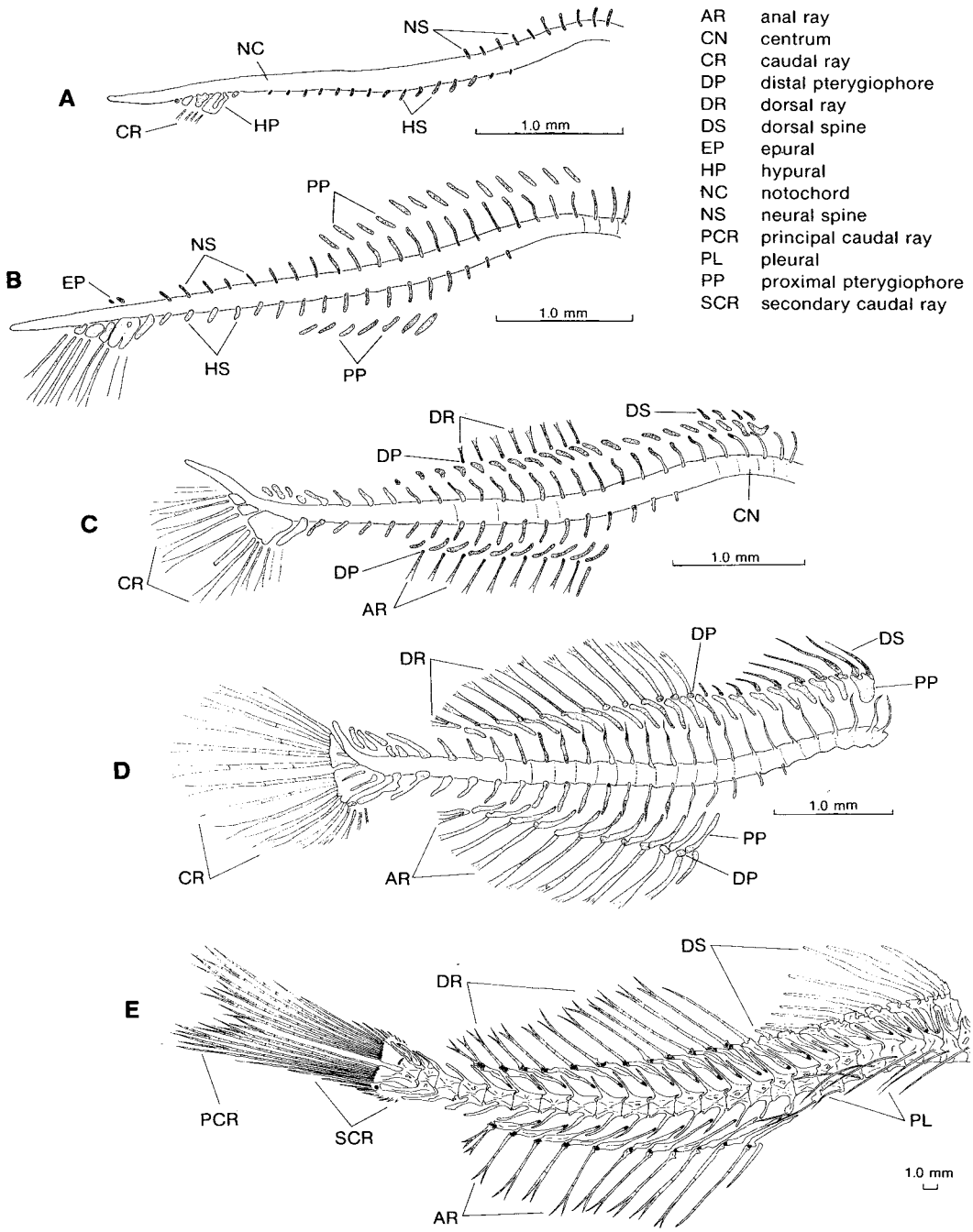

Fig. 10. Left lateral view of backbone and median fin development in *P. carolinus*: **A**, 5.4 mm NL; **B**, 6.0 mm NL; **C**, 6.3 mm SL; **D**, 7.0 mm SL; **E**, 60.0 mm SL.

space, with the exception of interneural spaces 3 and 11 where two are found. The anterior neural and haemal spines are first visible in 5.2 mm NL larvae (Fig. 10A). These spines develop posteriorly and the adult complement is attained at 6.3 mm SL (Fig. 10C). Ossification begins at the bases of the anterior neural and haemal spines at 6.0 mm SL, and the first centrum is visible near the base of the skull (Fig. 10B). Development of centra proceeds toward the caudal region, with some advance development in the mid-notochord region. Centra ossification is complete at 24 mm SL. The adult configuration of the spinal column is illustrated in Fig. 10E.

Caudal and median fins (Fig. 10)

Four caudal fin rays are visible at 5.4 mm NL (Fig. 10A). The number increases to 8 rays at 6.0 mm SL (Fig. 10B) and to 12 rays at 6.3 mm SL (Fig. 10C). The adult complement of 13 principal rays is present at 7.0 mm SL (Fig. 10D).

The first dorsal fin in adults consists of 10 spines which are supported by 9 pterygiophores. Each pterygiophore is comprised of distal and proximal parts, articulating with a single spine, except the anteriormost pterygiophore which supports two spines. The proximal pterygiophores are visible as cartilage dorsal to the neural spines in 6.0 mm SL larvae (Fig. 10B). The four anteriormost spines articulate with the distal pterygiophores at 6.3 mm SL (Fig. 10C), and the proximal pterygiophores extend ventrally between the neural spines. A single pterygiophore is present in each interneural space except space number 3 which contains pterygiophores 3 and 4 (Fig. 10D and 10E). Two spines are present at 6.0 mm SL, and 10 (adult number) are formed at 7.0 mm SL (Fig. 10D). Articulation with the proximal pterygiophores begins at spine 1 and proceeds posteriorly. Onset of ossification of the first dorsal fin was not observed in the larvae, but only the ventral tips of the pterygiophores remain as cartilage at 60 mm SL (Fig. 10E).

The second dorsal fin is comprised of 13 rays which are supported by an equal number of pterygiophores. The anteriormost four pterygiophores are visible dorsal to the neural spines at 6.0 mm SL (Fig. 10B). Eight dorsal rays are present at 6.3 mm SL (Fig. 10C), and nine more pterygiophores have developed posteriorly at 7.0 mm SL (Fig. 10D). Also, at this size, the pterygiophores have extended ventrally between the developing neural spines. A single pterygiophore is located in each interneural space, except for space 11 which contains two (Fig. 10D and 10E). Eight dorsal rays are fused to eight distal pterygiophores at 6.3 mm SL (Fig. 10C). Fusion of the proximal and distal pterygiophores occurs first within the middle ray at 7.0 mm SL (Fig. 20D) and continues both anteriorly and posteriorly. Ossification is incomplete at 60 mm SL, but serial articulation of the second dorsal rays, which become segmented and bifurcated, is complete at this size (Fig. 10D).

The anal fin of the adult is comprised of 12 rays which are supported by 11 pterygiophores. The anterior proximal pterygiophores are present at 6.0 mm SL, with development proceeding posteriorly (Fig. 10B). The adult complement is present at 7.0 mm SL, each pterygiophore occupying a separate interhaemal space (Fig. 10D). The anteriormost pterygiophore supports the first and second anal rays. The anal rays appear fused to the distal pterygiophores at 6.3 mm SL and ultimately become fused to the proximal pterygiophores in a pattern similar to that of the second dorsal fin. The adult complement of rays is complete at 7.0 mm SL (Fig. 10D). Ossification is incomplete at 60 mm SL, but serial articulation of the segmented, bifurcated rays is complete at this size (Fig. 10E).

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