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REPRODUCTIVE BIOLOGY AND DEVELOPMENTAL OSTEOLOGY OF THE FLORIDA BLENNY, *Chasmodes saburrae* (PERCIFORMES: BLENNIIDAE)

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ABSTRACT: Reproductive biology and larval development of the Florida blenny, *Chasmodes saburrae,* are described and figured; notes on life history are given. Adults spawn in the field from early March until early November with peak spawning in April/May and September. Nests, most often found in oyster shells, contain about 120 eggs/cm^2. Eggs average 0.82 mm diameter and hatch in six days at 27° C. Larvae are planktonic and 3.2-3.7 mm SL at hatching. Laboratory-reared larvae settle to the bottom in 21 days. The skeleton develops throughout larval and early juvenile stages. Adult lateral ethmoids are probably the result of fusion between two ossifications. The maxillae and premaxillae are partially resorbed during development. Some larval teeth are resorbed, while others transform into adult-type teeth. The ural centrum fuses with the dorsal and ventral hypural plates as they ossify. While hypurals 1-4 are difficult to distinguish during development, hypural 5 is nearly separate as cartilage before it fuses with the hypural plate.

The Florida blenny, *Chasmodes saburrae* (Jordan and Gilbert, 1883), is a small, benthic fish inhabiting shallow coastal waters of Florida. Previous studies of *C. saburrae* were systematic or ecological in nature and contributed little information on their reproductive biology (Reid, 1954; Springer, 1959; Springer and Woodburn, 1960; Carr and Adams, 1973; Williams, 1979).

The genus *Chasmodes* Valenciennes contains two species, *C. bosquianus* (Lacépède) and *C. saburrae.* Hildebrand and Cable (1938) reported on the embryology and newly-hatched larvae of *C. bosquianus,* which lay adhesive eggs in a single layer within oyster shells that are guarded by the male parent until hatching. Larvae are planktonic before settling to a benthic existence.

Although the osteology of the family Blenniidae has been examined, little is known of their developmental osteology. Springer (1968) studied blenniid osteology and presented a detailed analysis of the generalized blenniid *Entomacrodus nigricans* Gill. Forty-one other blenniid genera, including *C. bosquianus* from the genus *Chasmodes,* where examined and discussed when notably different from *E. nigricans* or when establishing evolutionary trends within the Blenniidae. Fishelson (1963) used stain to examine ossification in larval *Blennius pavo* Risso, but the developmental osteology of the larvae was not detailed.

This study was designed to gather quantitative information on the reproductive biology of *C. saburrae* and to obtain a larval series for subsequent description of morphological development.

METHODS

Larval and adult *C. saburrae* were collected monthly from rocks and jetties in Tampa Bay, Florida, and included at least 10 adult fish of each sex. A complete developmental series of larvae was obtained by supplementing field collections with larvae hatched from eggs collected in the field and reared in the laboratory. Larvae were reared in 30 liter aquaria at water temperatures of 21.4-27.7° C; salinities were 26 or 35 ‰ depending on the egg collection site (upper bay, 26 ‰; lower bay, 35 ‰). Larvae were fed live rotifers (*Branchionus plicatilis* Müller) until old enough to take *Artemia salina* L. nauplii. Samples were taken at half day intervals for 15 days. Six remaining larvae were preserved (two/day) on days 16, 17, and 21. All larvae were preserved in 5% buffered Formalin.

Gonads of 240 adult fish were weighed to the nearest 0.001 gram on a Mettler balance and graphed as a percent of stripped wet body weight. Stripped body weight was used because whole body weights varied considerably with the amount of undigested food in the gut. All ovaries (N = 120) were sectioned, stained, and ova classified according to their maturity stage following Moe (1969). In four separate ovaries, maturing ova (Stages 3-5) were counted and diameters measured to determine the pattern of female spawning. Peaks in size-frequency graphs for ova were separated using probability paper (Harding, 1949).

Seventy-four larvae, twenty-one juveniles, and seven adults were differentially cleared and stained for study of bone and cartilage using a method modified from Dingerkus and Uhler (1977). Drawings of bones and external features were made using a Zeiss camera lucida on a Zeiss dissecting microscope.

Measurements of eggs and larvae were made using an ocular micrometer on a Zeiss dissecting microscope. Eggs were measured to the nearest 0.01 mm across their greatest axis (from above) while alive and attached in the nest. Larval measurements were made to the nearest 0.1 mm.

For morphometric comparisons, larvae were divided into three groups depending on their state of notochord flexion following Moser, Ahlstrom, and Sandknop (1977). In addition, larvae collected in the field (all postflexion) were separated from reared larvae. Bone terminology follows that of Springer (1968) for the Blenniidae. Other definitions follow Hubbs and Lagler (1949) except as noted below:

Standard length (SL) in larvae with unflexed notochord: distance from tip of snout to tip of notochord.

Preanal length: distance along midline of body from tip of snout to a vertical line from posterior of anus (= origin of anal fin in juveniles and adults).

Prepelvic length: distance along midline of body from tip of snout to a vertical line from anterior base of pelvic fin.

Orbit length in larvae: maximum horizontal distance across pigmented portion of eye.

Pectoral length in larvae: horizontal distance from the dorsal margin of pectoral base to a vertical line from posterior margin of fin.

Interorbital space to isthmus: oblique distance from most narrow interorbital space to isthmus.

Body depth: vertical depth of fish measured from just anterior to dorsal fin base.

REPRODUCTIVE BIOLOGY

Oyster shells were the most frequently used nest site of *Chasmodes saburrae* in the study area, although holes in rocks, sponges, and discarded cans were also used. Nesting sites were always a defendable size for each individual male fish. The total number of *C. saburrae* eggs (120 eggs/cm^2) in each nest was highly variable and depended on surface area; oyster shells held 1,000-2,000 eggs, whereas a single can held about 11,000.

After examining the development of eggs collected in the field, Hildebrand and Cable (1938) hypothesized that *C. bosquianus* spawned early in the morning and that the nest was the product of multiple spawnings by one female. During this study of *C. saburrae*, spawning was observed at all times of day and several females were seen spawning with one male in rapid succession, or at the same time. Tavolga (1958) described the spawning behavior of a blenny he called *C. bosquianus* [actually *C. saburrae* (Springer, 1959)] in the laboratory. Observations of spawning behavior in the field showed no differences from those described by Tavolga (1958).

Although nests of *C. saburrae* were not found in the field until April 5, the relative size of juveniles indicated that spawning begins in early March. Many *C. saburrae* nests were found in April and May; few were found in June and July, but nests were again numerous from early August until early November. This indicated spring and fall spawning peaks and was supported by the stages of oocytes and weights of gonads during the year.

Gonad sections for all females had Stage 4 oocytes (Moe, 1969) present in all months except December. The few late Stage 4 or early Stage 5 oocytes found were in April, May, August, September, and October. During March, April, May, August, and September, the majority (> 50%) of females sampled had Stage 4 or Stage 5 oocytes.

Average monthly gonad weights for 1978 showed similar peaks for both males and females (Figure 1). Ovary weights peaked during April/May and September with monthly averages ranging from 0.9-8.7% body weight. Testes weights peaked during April/May and August with monthly averages ranging from 0.1-0.7% body weight.

Chasmodes saburrae is a multiple spawning species. Females held in the laboratory during the spring deposited eggs every one to two weeks and averaged 2,600 eggs/fish during that time. When maturing oocytes from four *C. saburrae* were measured, counted, and treated statistically (Harding, 1949), distinct size classes were evident and each contained 150-250 oocytes.

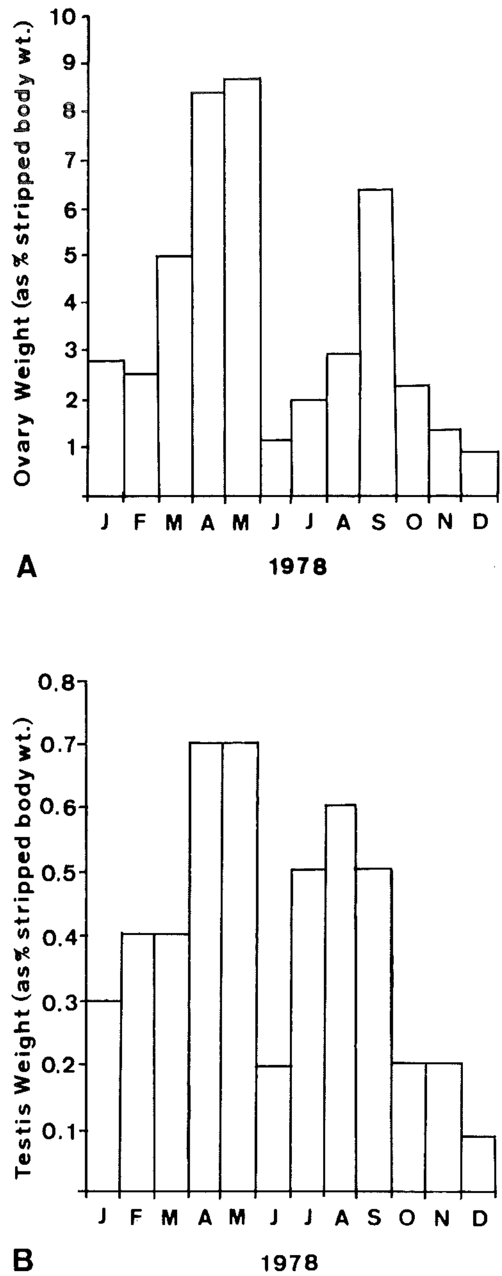

Figure 1. Average monthly gonad weights for *Chasmodes saburrae* during 1978 graphed as a percent of stripped body weight for A) females and B) males.

EGGS AND LARVAE

Thirty *C. saburrae* eggs were measured

while alive and still in the nest. These eggs were found to be 0.71 to 0.92 mm in diameter ($\bar{x} = 0.82$, $s = 0.06$). The perivitelline space was 0.06 mm. Usually the embryo developed on the side of the egg opposite attachment, with a large black spot present on each side. Numerous red pigment spots (0.04-0.08 mm diameter) were scattered over bright yellow yolk in two day old embryos. In four day old embryos, the yolk mass was yellow-orange and filled approximately 50% of the egg. Red spots were few, but small black chromatophores were numerous on the yolk. The eyes of the embryo were black with pigment. In six day old embryos, the yolk mass was pale, filled less than 25% of the egg, and had fewer black markings than four day old eggs. The eyes of these embryos were well developed. Body pigment was evident as detailed later for newly-hatched larvae. Eggs incubated in the laboratory hatched in six days at 27° C.

Twenty-five live, newly-hatched *C. saburrae* larvae ranged from 3.2 mm to 3.7 mm SL ($\bar{x} = 3.4$, $s = 0.1$) and 3.5 to 3.9 mm TL ($\bar{x} = 3.7$, $s = 0.1$); each had a well-developed median finfold, small pectoral fins, pigmented eyes, and 24-25 postanal myomeres. The yolk sac, when present, was small. Dark chromatophores occured as follows: one spot on the snout, one spot below each auditory vesicle, one spot per myomere along the ventral margin of the caudal musculature (numbering from 20-27), two to seven on the yolk sac, three pair of spots dorsally along the gut, one spot centrally located over the hindgut, four to six spots on the fleshy pectoral base, and seven to eight smaller spots on the central portion of the fin membrane near the fleshy base. When viewed with top lighting against a white background, yellow pigment was visible, scattered over the snout, dorsal gut and hindbrain.

Examination of the smallest preserved larva (1/2 day, 2.5 mm SL; Figure 2A), revealed the presence of a small yolk sac. Pectoral and gut pigment was diffuse, which prohibited the analysis of individual chromatophores. Yellow pigment was not visible in the preserved specimens. At 2½ days (3.0 mm SL, Figure 2B), two lines of two to three dark chromatophores were present across the snout and above the auditory vesicles. Pigmentation was more extensive on the dorsal and posteroventral surfaces of the gut than in younger specimens. Spots along the ventral caudal musculature were more numerous and extended around the partially formed hypural plate. By 6½ days (3.9 mm SL, Figure 2C), notochord flexion, preopercular spine formation, and caudal fin ray ossification had begun. There was a large, dark chromatophore over each orbit. At 10½ days (4.7 mm SL, Figure 2D), the notochord was flexed and incipient median fin rays were present. The amount of pigment over the orbits had increased and dark chromatophores were scattered over the snout, preopercle, and beneath the opercle. By 13½ days (6.6 mm SL, Figure 2E), pelvics had formed and preopercular spines were well developed. Dark pigment covered much of the head and the entire ventral half of the pectoral fins. At settling (21 days, 6.4 mm SL; Figure 2F), all fins were well developed and pigment on the pectorals had decreased. Pigment on the head and anterior body was mottled. Spots of bronze pigment were present anteriorly on the dorsal fin. A 10.8 mm SL, wild-caught specimen (Figure 2G) had light brown pigment spots over most of its body and anterior half of the dorsal fin. In juveniles, these spots coalesced and formed mottled bars and spots similar to the adult female pigmentation.

MORPHOMETRIC CHANGES

The greatest morphometric changes in proportion took place during flexion and metamorphosis. The following measurements increased in proportion to SL from preflexion to adult stage: total, head, preanal, prepelvic, pectoral, and snout lengths; interorbital space to isthmus; and body depth. The large increase in proportion of total length to SL was due both to flexion of the notochord and a true increase in caudal fin length as rays ossified. Increases in other morphometrics were due to changes in overall head morphometry and increased gut and pectoral fin lengths. A decrease in the proportional length of the pectoral fin and depth of the caudal peduncle between late larval and adult stages reflected the adult's decreased dependence on swimming. In planktonic larvae, pectoral and caudal fins are used to maintain position near the water's surface. Adults are benthic (Jordan and Gilbert, 1883) and are rarely found hovering in the water column (personal observation).

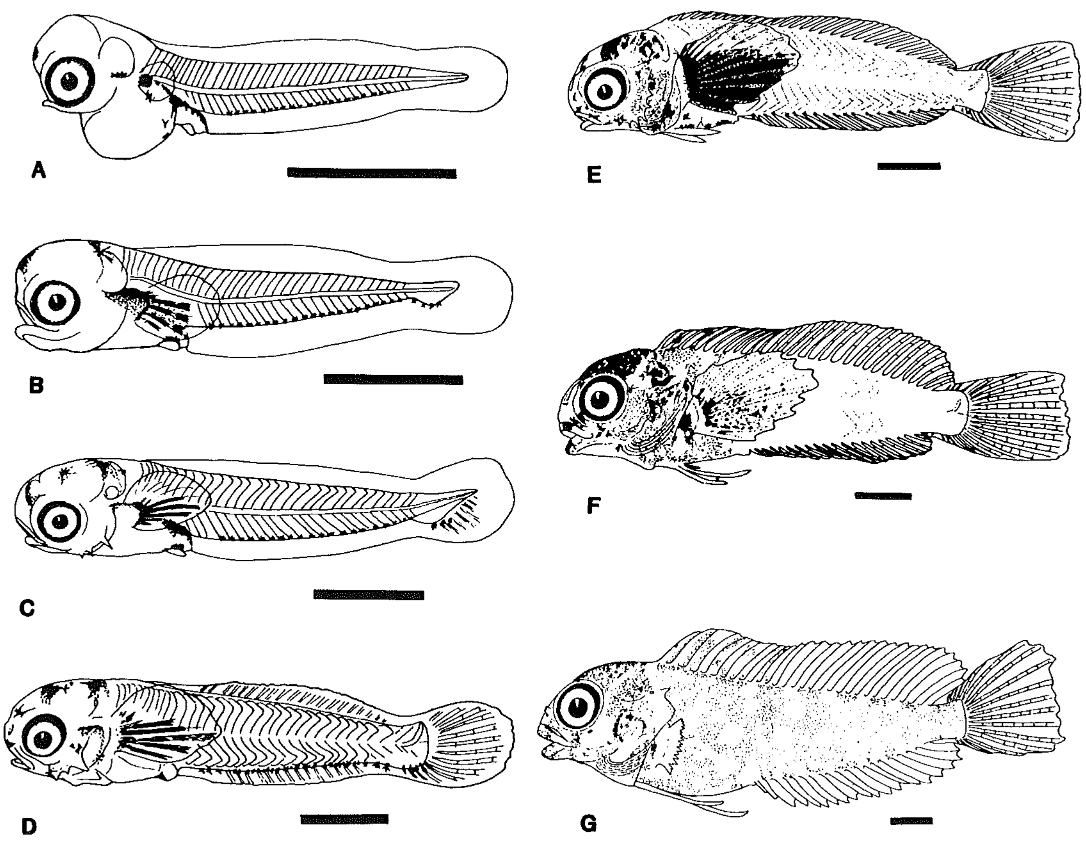

Figure 2. Development of *Chasmodes saburrae*. A) 0.5 days, 2.5 mm SL; B) 2.5 days, 3.0 mm SL; C) 6.5 days, 3.8 mm SL; D) 10.5 days, 4.7 mm SL; E) 13.5 days, 6.6 mm SL; F) 21.0 days, 6.4 mm SL; G) wild-caught juvenile, 10.8 mm SL. Horizontal bar represents 1 mm.

DEVELOPMENTAL OSTEOLOGY

Figures are representative stages and complement the text.

Neurocranium (Figure 3)

Chondrocranium (Figure 3A-D)

Most of the chondrocranium of *C.*

saburrae is formed during the first few days after hatching. In the smallest larva (1/2 day, 2.5 mm SL), the trabeculae were fused and the anterior basiscapular commissure was complete. The occipital arch, auditory capsule, and orbital cartilage were partially formed in a 1/2 day old (2.8 mm SL) larva. By day one (3.1 mm SL), the orbital cartilage and cranial tectum were complete. The synotic tectum formed by 5½ days (3.7 mm SL) and the lamina orbitonasalis formed by 6½ days (4.2 mm SL).

Parasphenoid (Figure 3A-D). The first skull element to ossify was the parasphenoid (1/2 day, 2.8 mm SL). By 5½ days (3.7 mm SL), the parasphenoid reached its proportional adult length and the lateral ascending arms were partially formed. The posterolateral corners formed by the base and ascending arms formed half of the carotid foramen in larvae, but completely surrounded the foramen in adults. The anterior end of the adult parasphenoid extended in a wide, thin plate dorsally over the posterior vomer as far as the ethmoids. Thin ossifications also extended along the sides of the vomer's ventral keel, and for a short distance ventral to the keel, enveloping the vomer's posterior end.

Frontals (Figure 3A-D). The frontals, the next skull elements to ossify, were first visible at 2½ days (3.0 mm SL) as oval ossifications above the orbits. By 7 days (3.9 mm SL), the frontals met dorsomedially and extended from the sphenethmoid commissure to the parietals. The interorbital space was relatively wide compared to adults (3/4 vs. 2/5 length of orbit wide). The supraorbital shelves were well developed and each was pierced by four or five foramina along its medial edge near the skull. In adults, a frontal ridge forms posteromedially.

Basioccipital, exoccipitals (Figure 3A-D). The basioccipital and exoccipitals began to ossify at 5½ days (3.7 mm SL). The basioccipital was first ossified around the notochord and by 8 days (4.3 mm SL) was ossified laterally and anteriorly along the sides of the parasphenoid. In adults, the posterior surface of the basioccipital formed the floor of the foramen magnum. The exoccipital ossified first along the ventrolateral margins of the foramen magnum. By 12 days (4.8 mm SL), the internal laminar projections were partially formed and ossification was nearly complete from the basioccipital to the supraoccipital. In adults, the exoccipitals meet at the midline dorsally, forming the roof of the foramen magnum.

Parietals, pterotics, sphenotics, lateral ethmoids (Figures 3B-D, 4). The parietals, pterotics, sphenotics, and lateral ethmoids began to ossify at 7½ days (4.2 mm SL). The parietals formed as thin, oval ossifications lateral to the anterior semicircular canals. By juvenile stages, the parietals met dorsally at the midline. In adults, parietal crests are present along the supratemporal sensory canals. The pterotics formed lateral to the horizontal semicircular canals. At 13½ days (6.6 mm SL), the pterotics' blade-like anterior processes were developed and overlapped the sphenotics. By 21 days (6.4 mm SL), they met with the ventralmost tip of the frontals at the posterior margin of the orbit. The sphenotics formed anteroventral to the parietals, near the orbit.

At 7½ days (4.2 mm SL), the lateral ethmoids were present as thin, intramembranous ossifications along the lateral edges of the lamina orbitonasalis (Figure 4A). At 11 days (4.8 mm SL), a second ossification center was present around the medial edge of the lamina orbitonasalis (Figure 4B). By 13½ days (6.6 mm SL), this second ossification extended to the lateral edge of the cartilaginous ethmoid plate and fused with the intramembranous ossification (Figure 4C). According to Patterson (1977:97), the first ossification, if dermal, must be an antorbital (or homologue) not a prefrontal as suggested by DeBeer (1937: 498). If this ossification was the lateral ethmoid, then the question arises as to the source of the second ossification. It does not appear to be the endochondral ossification of the lateral ethmoid.

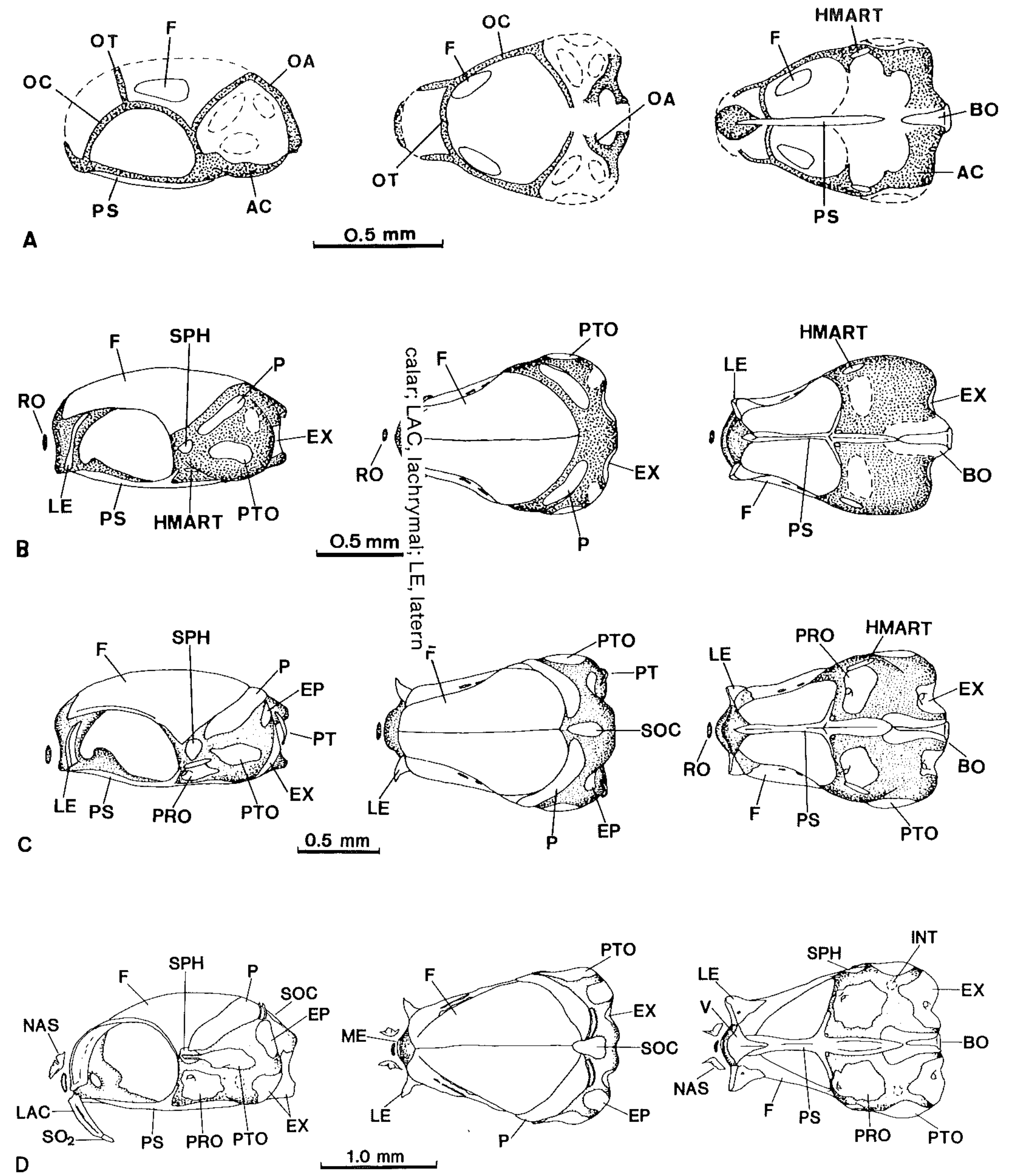

Figure 3. Development of *Chasmodes saburrae* neurocranium. A) 5.0 days, 4.0 mm SL; B) 10.0 days, 4.4 mm SL; C) 13.5 days, 6.6 mm SL; D) 21.0 days, 6.4 mm SL. Stippled, cartilage; AC, auditory capsule; BO, basioccipital; EP, epiotic; EX, exoccipital; F, frontal; HMART, hyomandibular articulation site; INT, intercalar; LAC, lachrymal; LE, lateral ethmoid; NAS, nasal; OA, occipital arch; OC, orbital cartilage, OT, orbital tectum; P, parietal; PRO, prootic; PS, parasphenoid; PT, posttemporal; PTO, pterotic; RO, rostral cartilage; SO_2, suborbital 2; SOC, supraoccipital; SPH, sphenotic; V, vomer.

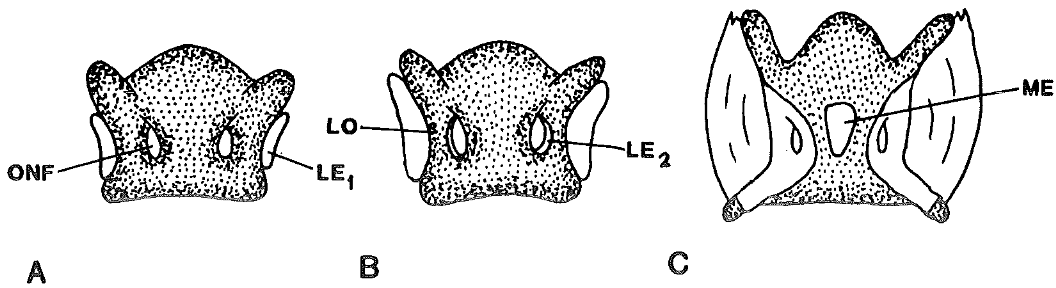

Figure 4. Diagrammatic ossification sequence in ethmoid region of *Chasmodes saburrae*. Anterior view A) 7.5 days, 4.2 mm SL; B) 11.0 days, 4.8 mm SL; C) 13.5 days, 6.6 mm SL. Stippled, cartilage; $LE_{1,2}$, lateral ethmoid original and secondary ossification centers; LO, lamina orbitonasalis; ME, median ethmoid; ONF, olfactory nerve foramen.

Epiotics, prootics (Figure 3C-D). The epiotics and prootics began ossifying at 8 days (4.3 mm SL). The epiotics ossified lateral to the posterior semicircular canals and anchored the dorsal arms of the posttemporals. The prootics ossified posterolateral to the ascending arms of the parasphenoid, surrounded the small foramen of the trigemino-facial nerve complex by 11 days (5.1 mm SL) and formed the posteroventral two thirds of the large foramen in juveniles and adults.

Rostral cartilage (Figure 3B-D). The small distinct rostral cartilage was present at day 10, but did not ossify as in some blennies (Springer, 1968:42). In adults, the cartilage was still present, although reduced in proportional size.

Supraoccipital (Figure 3C-D). The supraoccipital formed at 11 days (5.1 mm SL) as a small, pear-shaped ossification, with the narrow end variable in length and usually separating the parietals at the midline. In adults, a V-shaped crest forms anteriorly on the supraoccipital, joining the parietal and frontal crests.

Median ethmoid, vomer (Figures 3D, 4). The median ethmoid and vomer both began to ossify at 12½ days (5.3 mm SL). The median ethmoid formed on the mid-anterior face of the ethmoid plate and was not fully ossified in any of the reared larvae. The vomer ossified as a thin plate anterior and ventral to the parasphenoid. The toothless vomer joined the lateral ethmoids at an interdigitating joint. Posteriorly, a ventral keel formed at the midline and was partially enveloped by the parasphenoid.

Nasals (Figure 3D). The nasals were first visible at 13½ days (6.6 mm SL). Ossification began medially and fanned out around the sensory canal. In adults, the nasals consist of the sensory canal ossicles with no lateral projections except a slightly expanded ventral end.

Intercalars (Figure 3D). The intercalars first began to form at 15½ days (6.5 mm SL) just below the posteroventral edge of the pterotics. In juveniles, the intercalars were triangular in shape and each corner inserted into a shallow pocket in its respective prootic, pterotic, and exoccipital.

Basisphenoid, pterosphenoids (Not figured). The basisphenoid and pterosphenoids formed early in juvenile stages. The basisphenoid's lateral arms formed before the medial shaft and at first attached to the posterodorsal ends of the parasphenoid's ascending arms. In adults, the lateral arms of the basisphenoid joined on the inner surface of the skull where the prootics and pterosphenoids meet the parasphenoid. The pterosphenoids were disc-shaped and attached to the anteroventral edge of the sphenotics. The posterior margin of the pterosphenoids formed one third of the large foramen for the trigemino-facial nerve complex.

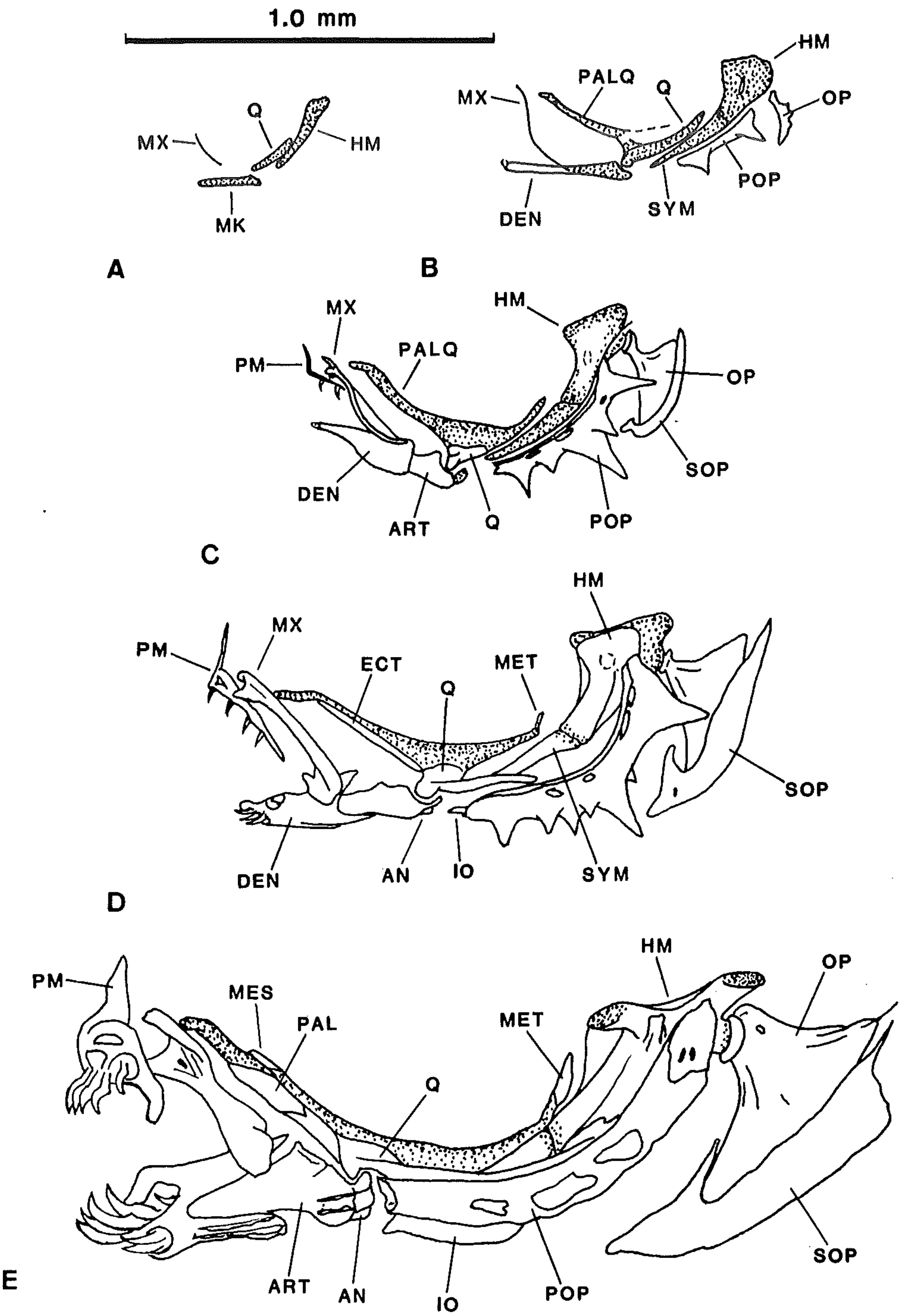

Figure 5. Development of jaws and suspensorium of *Chasmodes saburrae*. A) 0.5 days, 2.5 mm SL; B) 5.0 days, 4.0 mm SL; C) 7.5 days, 4.2 mm SL; D) 11.0 days, 5.1 mm SL; E) 21.0 days, 6.4 mm SL. Stippled, cartilage; AN, angular; ART, articular; DEN, dentary; ECT, ectopterygoid; HM, hyomandibula; IO, interopercle; MES, mesopterygoid; MET, metapterygoid; MK, Meckel's cartilage; MX, maxilla; OP, opercle; PAL, palatine; PALQ, palatoquadrate; PM, premaxilla; POP, preopercle; Q, quadrate; SOP, subopercle; SYM, symplectic.

Jaws and Suspensorium (Figures 5-7)

Maxillae, quadrates, hyomandibulae (Figure 5). The maxillae, quadrates, and hyomandibulae were partially formed in the smallest larva (1/2 day, 2.5 mm SL). The maxillae were first visible as thin streaks of ossification in the dorsal lip. By 6½ days (4.2 mm SL), the forked anterodorsal tips of the maxillae curved towards the ethmoid plate. The forked tips contained concave ossifications that saddled the premaxillae in adults. Medially, a thin intramembranous ossification extended along the length of the maxilla, detached along the central portion. This medial ossification strengthened and expanded ventroposteriorly. By 10½ days (4.7 mm SL), the original thin ossification was resorbed, leaving the strong second ossification to become the shaft of the adult maxilla.

The cartilaginous quadrate had a small pterygoid process at 1½ days (3.0 mm SL). By 5½ days (3.7 mm SL), the process had fanned out dorsally with its anterior tip fused to the pterygoid process of the palatine. At 6½ days (4.2 mm SL), the quadrate began to ossify on the anterodorsal face of its original base. At 10 days (4.4 mm SL), an intramembranous ossification had developed posteriorly from the anteroventral end of the base and encased the symplectic from below on three sides. By 13½ days (6.6 mm SL), ossification of the dorsal fan portion and the articular condyle was nearly complete. In adults, a thin intramembranous ossification extends ventrolaterally from the quadrate and covers the anterolateral end of the preopercle.

The cartilaginous hyomandibula's facial nerve foramen was visible at day one (3.2 mm SL). By 2½ days (3.0 mm SL), the opercular condyle was forming and at 5 days (4.0 mm SL), the suture between the hyomandibula and symplectic was visible. Ossification began ventral to the facial nerve foramen at 5½ days (3.7 mm SL). By 10 days (4.4 mm SL), a thin intramembranous ossification extended anteriorly from the curved anterior margin of the hyomandibula. At 13½ days (6.6 mm SL), the two major dorsal condyles were forming at the antero- and posterodorsal corners and the facial nerve canal was forming along the posterior margin. In adults, a dorsal process, continuous with the ridge of the facial nerve canal, is attached by ligaments to the skull.

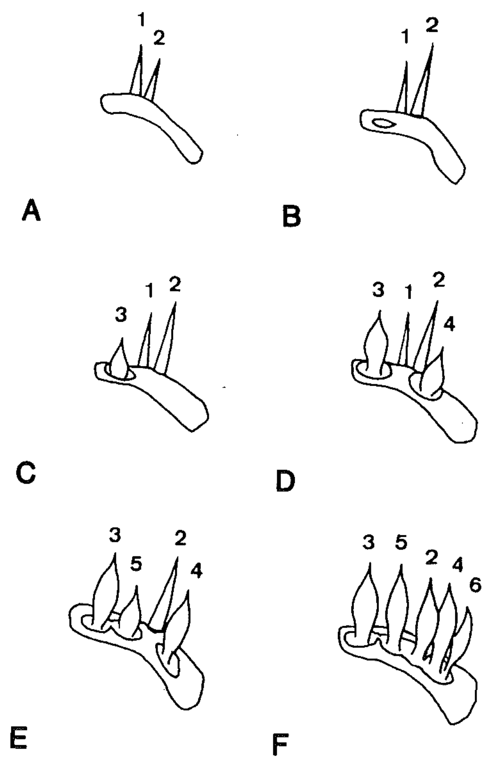

Figure 6. Diagrammatic sequence of dentary tooth formation in *Chasmodes saburrae*. Anteroventral view of left dentary. Teeth numbered in order of appearance. A) 7.0 days, 3.9 mm SL; B) 10.5 days, 4.7 mm SL; C) 11.0 days, 5.1 mm SL; D) 11.5 days, 4.2 mm SL; E) 14.5 days, 6.6 mm SL; F) 17.5 days, 7.3 mm SL.

Dentary (Figures 5, 6). The dentary first appeared at 2 days (3.0 mm SL) as a thin ossification along the anterolateral edge of Meckel's Cartilage. By 2½ days (3.0 mm SL), the dentary reached most of its adult proportional length and curved slightly around Meckel's Cartilage. At

5½ days (3.7 mm SL), the posterior end of the dentary was enlarged to receive the articular. Anterolaterally, there were several large foramina for tooth formation. Teeth, numbered in order of appearance (Figure 6), formed in the following sequence. At 6 days (3.8 mm SL), a single, spike-like, larval tooth (#1) projected anteriorly from the corner of each dentary. By 7 days (3.9 mm SL, Figure 6A), a second larval tooth formed lateral to #1 and by 10½ days (4.7 mm SL, Figure 6B), tooth #2 was larger than #1. By 11 days (5.1 mm SL, Figure 6C), a third tooth, robust and adult-like, formed medial to #1. A fourth tooth, also robust, formed lateral to #2 by 11½ days (4.8 mm SL, Figure 6D). By 14½ days (6.6 mm SL, Figure 6E), tooth #1 was partially resorbed and an adult tooth (#5) was forming in its place. By 17½ days (7.3 mm SL, Figure 6F), a sixth tooth formed lateral to #4, while #2 became robust and adult-like.

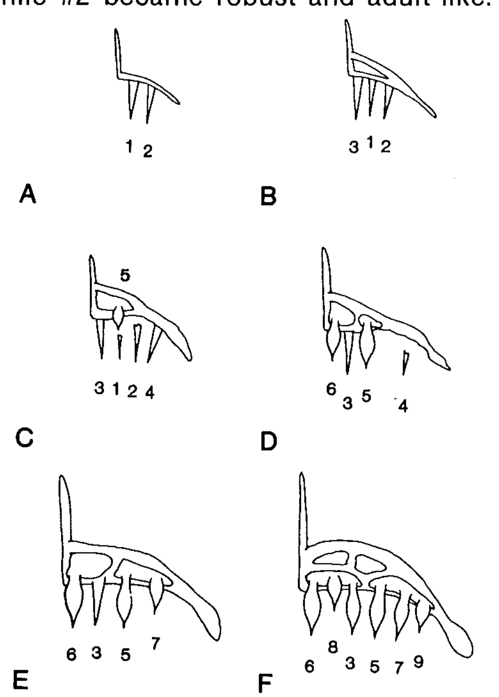

Figure 7. Diagrammatic sequence of premaxillary tooth formation in *Chasmodes saburrae.* Anterior view of left premaxilla. Teeth numbered in order of appearance. A) 6.5 days, 4.2 mm SL; B) 10.5 days, 4.7 mm SL; C) 10.5 days, 4.6 mm SL; D) 13.5 days, 6.6 mm SL; E) 15.5 days, 6.5 mm SL; F) 21.0 days, 6.4 mm SL.

The oldest larva (21 days, 6.4 mm SL), had five permanent teeth in each dentary.

Palatine (Figure 5). By 3 days (3.7 mm SL), the pterygoid process of the palatine was chondrifying in a preformed matrix from near the ethmoid plate towards the quadrate. By 5 days (4.0 mm SL), the cartilaginous palatine and quadrate had fused. At 11½ days (4.6 mm SL), the palatine was ossified on the ventrolaterally curved surface between the original chondrification and the maxillary process. Ossification was complete by 13 ½ days (6.6 mm SL).

Symplectic (Figure 5). The symplectic separated by 5 days (4.0 mm SL), and first ossified at 8 days (4.3 mm SL). In specimens greater than 10 days (4.4 mm SL), the anteroventral end was enveloped by the quadrate. None of the adult intramembranous ossifications were present in reared larvae.

Articular (Figure 5). The articular first appeared as a thin ossification along the posterolateral side of Meckel's Cartilage at 5½ days (3.7 mm SL). By 11 days (5.1 mm SL), ossification was present around most of Meckel's Cartilage and by 13½ days (6.6 mm SL), had attained the adult shape.

Angular (Figure 5). At 6½ days (4.2 mm SL), the angular was ossified as a cap at the posteroventral tip of Meckel's Cartilage and served as a point of ligament attachment for the interopercle and epihyal.

Premaxilla (Figures 5, 7). Ossification in the premaxilla was preceded by development of two teeth anteriorly in the lip. Ossification began in the thin ascending process and in the medial portion of the base by 7 days (3.9 mm SL). From the base, ossification extended laterally past the second tooth. By 11 days (5.1 mm SL), ossification spread laterally well beyond the second tooth and large foramina were developing between the base and ascending process for adult tooth formation. During tooth formation, upward growth of the premaxilla took place along the dorsal margin while the ventral margin was resorbed. Teeth, numbered in order of their appearance (Figure 7), formed in the following sequence. By 5½ days (3.7 mm SL), a single, spike-like, larval tooth (#1) formed medially in the dorsal lip. A second larval tooth formed lateral to #1 by 6½ days (4.2 mm SL, Figure 7A), and by 10½ days (4.7 mm SL, Figure 7B), a third larval tooth formed medial to #1. A fourth larval tooth had formed lateral to #2 at 10½ days (4.6 mm SL, Figure 7C). Tooth #1 with its ossified base was partially resorbed; a fifth tooth, robust and adult-like, formed in its place. By 13½ days (6.6 mm SL, Figure 7D), #1, #2, and the base of #4 were resorbed and a robust tooth (#6) formed medial to #3. By 15½ days (6.5 mm SL, Figure 7E), adult tooth #7 had formed lateral to #5. By 21 days (6.4 mm SL, Figure 7F), an eighth tooth formed between #3 and #6, and a ninth formed lateral to #7. Tooth #3 became robust and adult-like. The oldest reared larva (21 days, 6.4 mm SL) had six adult teeth in each premaxilla.

Ectopterygoid (Figure 5). The ectopterygoid ossified by 10½ days (4.7 mm SL) along the ventral edge of the cartilaginous pterygoid process. By 13½ days (6.6 mm SL), the ectopterygoid reached full adult proportional length with its ends covered by the palatine and quadrate.

Mesopterygoid (Figure 5). The mesopterygoid ossified by 11 days (4.8 mm SL) along the dorsal margin of the pterygoid process. In later stages, it ossified posteriorly and ventrally, medial to the fanned portion of the quadrate.

Metapterygoid (Figure 5). The metapterygoid, first visible at 11 days (4.8 mm SL), began as a tiny, intramembranous ossification extending dorsally from the posterodorsal process of the quadrate cartilage. In later stages, this ossification expanded dorsally along the anterior margin of the hyomandibula, and anteroventrally into the quadrate cartilage.

Opercular Series (Figure 5, B-E)

The opercle was first visible as a condyle and a small portion of the blade at 1/2 day (2.8 mm SL). By 6½ days (4.2 mm SL), the opercle was nearly complete. The preopercle, also present at 1/2 day (2.8 mm SL), formed posterolateral to the hyomandibula. By 5½ days (3.7 mm SL), two spines were present; by 6½ days (4.2 mm SL), five spines had formed. Laboratory-reared larvae usually had five spines, while wild-caught larvae usually had six. Preopercular spines were resorbed in late larval stages. The subopercle ossified by 7 days (3.9 mm SL) with adult shape present from its beginning. By 11 days (5.1 mm SL), ossification of the subopercle was nearly complete. The interopercle was first ossified at 10½ days (4.6 mm SL) in the ligament connecting the angular and the epihyal. Its adult shape was not present in any reared larvae.

Hyoid Arch (Figure 8)

The posteriormost branchiostegal ray ossified by 1½ days (3.0 mm SL). Other rays ossified in an anterior direction with all six present by 7 days (3.9 mm SL). The urohyal was first apparent at 7 days (3.9 mm SL) as a wedge-shaped ossification with no cartilaginous precursor. The ceratohyal, hypohyal and interhyal were present as separate cartilages in the smallest larva (1/2 day, 2.5 mm SL). The basihyal was first visible at day one (3.1 mm SL). There were two centers of ossification in the ceratohyal cartilage; the first in the region of the adult ceratohyal by 10½ days (4.4 mm SL), the second in the region of the adult epihyal by 10½ days (4.7 mm SL). Both were nearly complete by 21 days (6.4 mm SL). Two centers of ossification also occurred in the hypohyal cartilage. The ventral hypohyal ossified by 11 days (5.1 mm SL); the dorsal hypohyal ossified by 12 days (4.2 mm SL). Ossification of the hypohyals was not complete in any reared larvae. Ossification of the interhyal was first present by 13½ days (6.6 mm SL) and ossification of the basihyal was first present at 21 days (6.4 mm SL).

Gills Arches (Figure 8)

Basibranchials 1-3, hypobranchials 1-3, ceratobranchials 1-4, and epibranchials 1-3 were all present in the smallest larva (½ day, 2.5 mm SL). Basibranchials 1-3 first formed as a single cartilage extending from the hypohyals to half way between hypobranchials 1 and 2. By 8 days (4.3 mm SL), three separate basibranchials were apparent. At 1/2 day (2.8 mm SL), a cartilaginous infrapharyngobranchial 2 was present and by 5½ days (3.7 mm SL), both infrapharyngobranchials were visible. By 1½ days (3.0 mm SL), basibranchial 4, ceratobranchial 5, and epibranchial 4 were present.

One upper pharyngeal tooth was present by 1/2 day (2.8 mm SL). By 5½ days (3.7 mm SL), three teeth were present with dermal ossification around their bases. By 13½ days (6.6 mm SL), all of the dermal tooth plate was ossified. Infrapharyngobranchials 1 and 2 remained as cartilaginous caps on the tooth plate at articulation points. One lower pharyngeal tooth was present at 5½ days (3.7 mm SL). By 7 days (3.9 mm SL), two teeth were ossified along with the tooth plate.

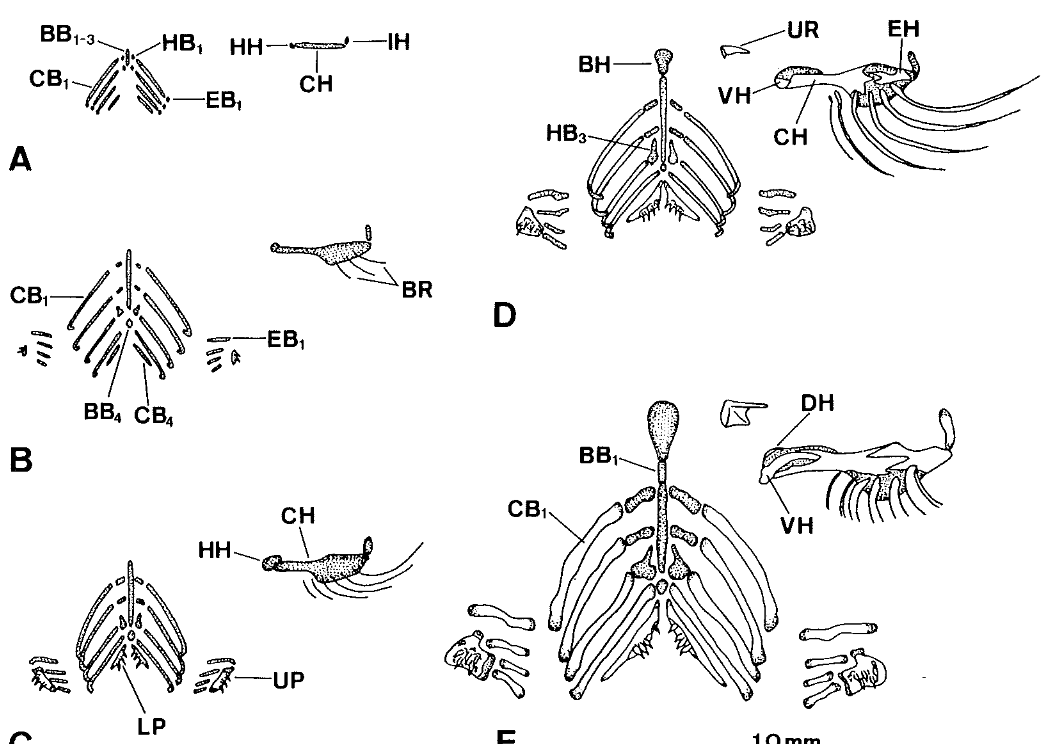

Figure 8. Development of gill arches (dorsal view) and hyoid arch (left side) of *Chasmodes saburrae*. A) 0.5 days, 2.5 mm SL; B) 5.0 days, 4.0 mm SL; C) 7.5 days, 4.2 mm SL; D) 11.0 days, 5.1 mm SL; E) 21.0 days, 6.4 mm SL. Stippled, cartilage; BB $_{1-4}$, basibranchials 1-4; BH, basihyal; BR, branchiostegals; CB, ceratobranchial; CH, ceratohyal; DH, dorsal hypohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HH, hypohyal; IH, interhyal; LP, lower pharyngeal; UP, upper pharyngeal; UR, urohyal; VH, ventral hypohyal.

The tooth plate, fused with ceratobranchial 5, was completely ossified except for cartilaginous caps at each end by 13½ days (6.6 mm SL). Ceratobranchials 1 and 2 were ossified by 11 days (5.1 mm SL) and all five had ossified by 13½ days (6.6 mm SL). Hypobranchials 1-3, epibranchials 1-4, and basibranchials 1-3 also ossified by 13½ days (6.6 mm SL). Basibranchial 4 remained cartilaginous.

Laterosensory Canal System

The bony ossicles of the laterosensory canal system began to ossify by 13½ days (6.6 mm SL). The first to form were the circumorbitals, the preopercular ossicles, and the nasals. The lachrymal was the first circumorbital to ossify and all five were ossified in a 7.8 mm SL wild-caught larva. The preopercular canal ossicles ossifed at between 13½ days (6.6 mm SL) and the end of the larval stage. The juveniles and adults examined typically contained five pores (occasionally four) in the preopercular canal. Bath's (1977) figure of a *C. saburrae* paratype showed six pores in the preopercular canal.

At 15½ days (6.5 mm SL), the partially ossified supraorbital laterosensory ossicles formed as lateral extensions from the braincase of the frontals and met dorsal extensions from the supraorbital shelf. Juveniles and adults had four pores associated with the supraorbital canal; two pores in the supraorbital canal posterodorsal to the orbit, one pore at the midline between the orbits (where opposite canals meet), and one pore anterodorsal to the orbits. Neither of the anterodorsal pores (one per side) were shown in the figure of the paratype (Bath, 1977). The supratemporal canal ossicles began to ossify by 17½ days (7.3 mm SL). The remaining laterosensory canal ossicles (articular, dentary, pterotic, lateral extrascapular, posttemporal, and supracleithral) and the lateral line ossicles were ossified in late larval or early juvenile stages.

Axial Skeleton (Figures 9-11)

Caudal Fin (Figures 9-10). The first incipient caudal rays were present at 3 days (3.7 mm SL). The ossification of rays proceeded both dorsally and ventrally from the middle rays. At 9 days (4.8 mm SL), the adult complement of 6+5 principal rays was ossified along with two dorsal and three ventral procurrent caudal rays. The adult complement of procurrent rays, which may vary, was reached by 13½ days (6.5 mm SL).

The ventral hypural plate, visible by 2½ days (3.0 mm SL), began as a small spot of cartilage about four myomeres distance from the tip of the notochord. By 3 days (3.5 mm SL), the dorsal hypural plate was present. As the ventral plate expanded, two anterior processes formed; one along the notochord and the other

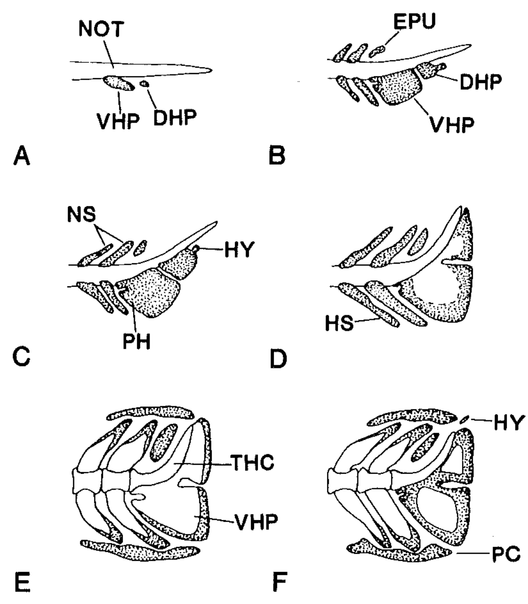

Figure 9. Development of caudal skeleton of *Chasmodes saburrae.* Diagrammatic. A) 3.7 mm SL; B) and C) 4.2 mm SL; D) 4.3 mm SL; E) and F) 6.5 mm SL. Stippled, cartilage; DHP, dorsal hypural plate; EPU, epural; HS, haemal spine; HY, hypural 5; NOT, notochord; NS, neural spine; PC, procurrent cartilage; PH, parhypural; THC, terminal half centrum; VHP, ventral hypural plate.

below the caudal blood vessels. By 7 days (3.9 mm SL), the cartilage joined laterally around the blood vessel bifurcation to form the parhypural. As the dorsal hypural plate expanded, a small, nearly separate cartilage was seen at the posterodorsal tip. This, apparently, is the fifth hypural or "minimal hypural" which Springer (1968:56) hypothesized was lost in *Chasmodes*. This fifth hypural usually remained fused with the dorsal hypural plate, but was probably lost when separated. The single epural cartilage was present by 6½ days (4.2 mm SL).

Ossification was present in the hypural plates and the terminal half centrum by 11 days (4.8 mm SL). When the cartilage of the hypural plates was fused near the notochord, it ossified from one ventral center of ossification. When separate, two centers of ossification were present, with later fusion. The half centrum ossified from one center of ossification and fused with both of the hypural plates as they ossified. Springer (1968: 56-57) indicated that the ventral hypural plate in adults was not fused with the centrum. The epural ossified by 13½ days (6.6 mm SL).

Vertebral column (Figure 10). At 2½ days (3.0 mm SL), 15 cartilaginous haemal arches were partially formed below future centra 11-26. By 3 days (3.7 mm SL), 3 parapophysis, 23 haemal arches, 2 precaudal neural arches, and 18 caudal neural arches were formed. By 6 days (3.8 mm SL), the adult complement of arches was present. The first neural arch was ossified at 8 days (4.3 mm SL) and the first few parapophysis were ossified at 11 days (5.1 mm SL). The arches ossified from anterior to posterior except for the last few which ossified before those anterior to them. Spines ossified with the arches and all were nearly complete by 13½ days (6.6 mm SL). The penultimate arches were often composed of a double arch with fused spines attached to a single elongate centra. In addition, these spines were often fused to the parhypural, epural, or antepenultimate spines. Anomalies of this type were found to be common in both reared and wild-caught larvae.

The first six centra were ossified by 10½ days (4.6 mm SL) in the area of the neural arches and by 11 days (5.1 mm SL), most centra were ossifying. Ossification proceeded in an anterior to posterior direction except for the last few which ossified posterior to anterior.

Epipleural ribs, first present at 13½ days (6.6 mm SL), developed as thin ossifications attached high on the neural arches of the first two vertebrae. At 17½ days (7.3 mm SL), six more were ossifying on vertebrae 3-8. The adult complement of 12 was not present in any of the reared larvae. Four cartilaginous pleurals, present at 13½ days (6.6 mm SL), developed on vertebrae 3-6. By 21 days (6.4 mm SL), all eight were present, although none had ossified.

Dorsal and anal fins (Figure 10). Thirteen cartilaginous dorsal proximal pterygiophores were seen below the future soft rays at 6½ days (4.2 mm SL). By 9 days (4.8 mm SL), the adult complement of 28 was present. Often, two proximal pterygiophores were present below the last dorsal ray. Ossification of the proximal pterygiophores began at 13½ days (6.6 mm SL). Ossification in proximal pterygiophores of the spinous dorsal began in the ring joint of the first pterygiophore and proceeded posteriorly. Ossification in the proximal pterygiophores of the soft dorsal began anteriorly on their medial faces and proceeded posteriorly. Ossification was not complete in any of the reared larvae. At 9 days (4.8 mm SL), 13 distal pterygiophores were visible anteriorly beneath the dorsal soft rays. The adult complement of 19 was present by 11 days (4.8 mm SL), but

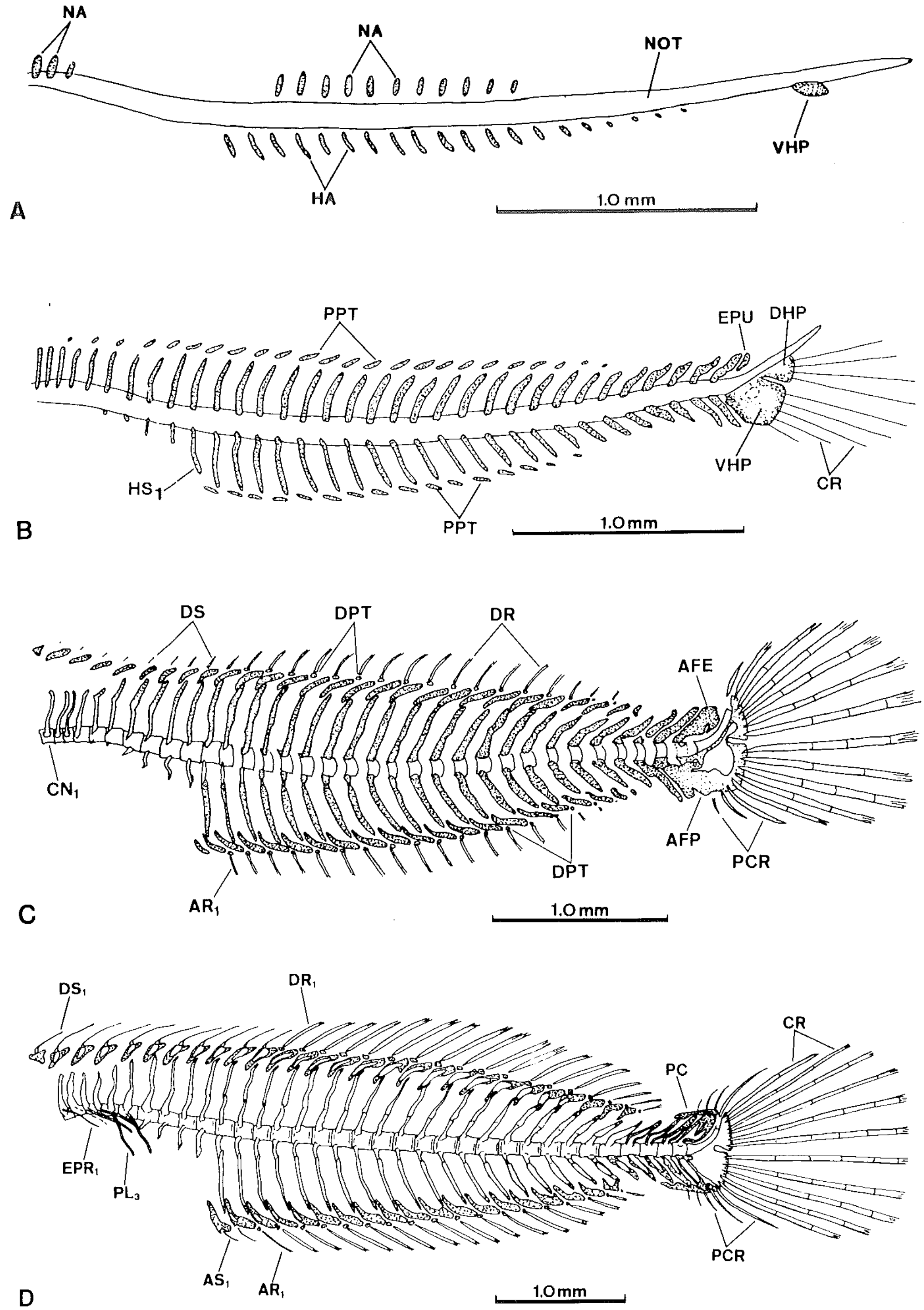

Figure 10. Development of axial skeleton and unpaired fins of *Chasmodes saburrae*. A) 5.0 days, 4.0 mm SL; B) 7.5 days, 4.2 mm SL; C) 11.0 days, 5.1 mm SL; D) 21.0 days, 6.4 mm SL. Stippled, cartilage; AFE, anomalous fused epural and neural spine; AFP, anomalous fused parhypural and haemal spine; AR, anal ray; AS, anal spine; CN, vertebral centrum; CR, caudal ray; DPT, distal pterygiophore; DR, dorsal ray; DS, dorsal spine; EPR, epipleural rib; HA, haemal arch; NA, neural arch; PCR, procurrent caudal ray; PL, pleural rib; PPT, proximal pterygiophore. For other abbrevations see Figure 9.

none was ossified in any of the reared larvae.

Incipient soft dorsal rays were seen forming at 8 days (4.3 mm SL). By 9 days (4.8 mm SL), 15 anterior soft rays were partially ossified; by 11 days (4.8 mm SL), all rays were present. The dorsal spines began to form by 9 days (4.8 mm SL). They ossified in a posterior to anterior direction, and all were present by 13½ days (6.6 mm SL).

Ten cartilaginous proximal pterygiophores were present above the anterior soft anal ray region at 6½ days (4.2 mm SL). By 9 days (4.8 mm SL), the adult complement was present. As in the dorsal fin, two proximal pterygiophores often formed in conjunction with the last soft ray. Ossification of the anal pterygiophores was similar to the dorsal pterygiophores and began above the anterior soft rays at 13½ days (6.6 mm SL), but was not complete in any reared larvae. The distal pterygiophores began to form at 9 days (4.8 mm SL). They developed in an anterior to posterior direction. By 11 days (4.8 mm SL), all were present, but none were ossified in any reared larvae.

Soft anal fin rays, first noted at 9 days (4.8 mm SL), developed in an anterior to posterior direction. By 11 days (4.8 mm SL), the adult complement was present. The anal spines ossified in a posterior to anterior direction. The first was visible at 11 days (4.8 mm SL) and both were present by 12½ days (5.3 mm SL).

Pectoral Girdle (Figure 11). In the smallest larva (1/2 day, 2.5 mm SL), the pectoral fin was present as a small, rounded, transparent membrane. It soon became larger, strengthened by an opaque, fleshy support. At 5½ days (3.7 mm SL), the rays had started forming, and at 7½ days (4.2 mm SL), ossification was present in all 12 rays. After 5½ days (3.7 mm SL), the shape of the pectoral fin became oval, similar to the adult shape.

The cleithrum had begun to ossify in the smallest larva (1/2 day, 2.5 mm SL). Ossification began in the ventral half of a preformed matrix and extended from the coracoid anteroventrally, halfway to the midline. By 6½ days (4.2 mm SL), the dorsal half of the cleithrum had ossified. The ventral end had begun to widen out and became laterally convex. By 10 days (4.4 mm SL), the dorsal tip of the cleithrum was flattened and the midportion was beginning to widen and overlap the coracoid cartilage. The coracoid fused with the cleithrum at 13½ days (6.6 mm SL).

The supracleithrum, visible at 8 days (4.3 mm SL), developed as a thin ossification in the ligament extending between the dorsal tip of the cleithrum and the skull. By 11 days (4.8 mm SL), it had adult shape, but none of the sensory ossicles.

The posttemporal, first visible at 10½ days (4.7 mm SL), developed in the connective tissue posterior to the epiotic. It soon became more elongate, curved around the skull and by 21 days (6.4 mm SL), had its adult shape.

A cartilaginous coracoid, present in the smallest larva (1/2 day, 2.5 mm SL), had a large posteroventral process. By 10½ days (4.6 mm SL), the posteroventral process was partially resorbed and the coracoid was beginning to ossify in the corner between the posterior and ventral margins. At 13½ days (6.6 mm SL), most of the coracoid's posterior process was resorbed and the coracoid was fusing with the cleithrum.

The scapula chondrified by 1½ days (3.0 mm SL). The anterior edge of the scapula became indented as it formed the scapular foramen. At 10½ days (4.6 mm SL), the posterodorsal tip of the scapula was developing a process for ligamentous attachment to the dorsal tip of the first radial. The scapula began to ossify in the region of this process at 13½ days (6.6 mm SL), but was not completely ossified in any reared larvae.

The cartilaginous pectoral fin support

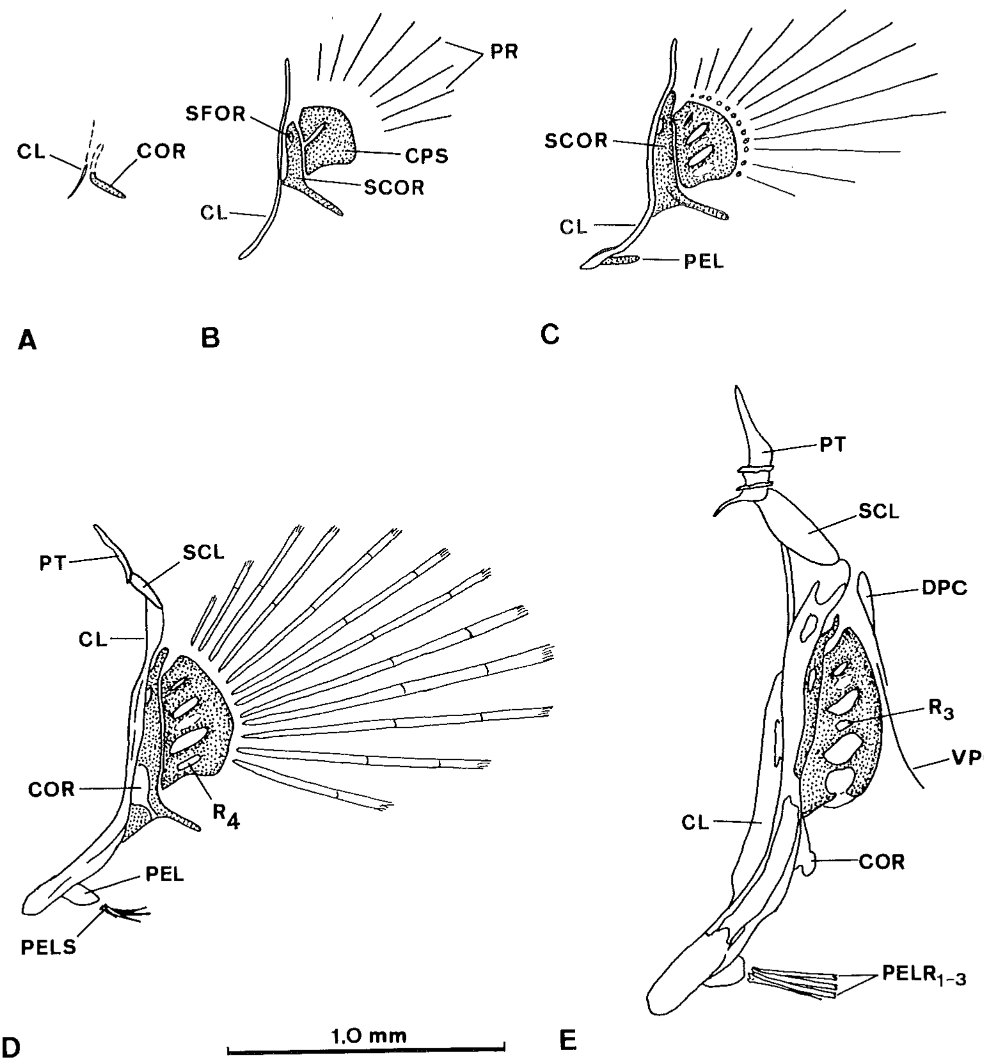

Figure 11. Development of paired fins of *Chasmodes saburrae*. A) 0.5 days, 2.5 mm SL; B) 5.0 days, 4.0 mm SL; C) 7.5 days, 4.2 mm SL; D) 11.0 days, 5.1 mm SL; E) 21.0 days, 6.4 mm SL (posttemporal and postcleithrum displaced). Stippled, cartilage; CL, cleithrum; COR, coracoid; CPS, cartilaginous pectoral fin support; DPC, dorsal postcleithrum; PEL, pelvis; PELR, pelvic ray; PELS, pelvic spine; PR, pectoral ray; PT, posttemporal; R, radial; SCL, supracleithrum; SCOR, combined scapula and coracoid; SFOR, scapular foramen; VPC, ventral postcleithrum.

was visible by 1/2 day (2.8 mm SL). Initially, a gap was observed between the future radials 2 and 3 which was open proximally until 5½ days (3.7 mm SL). At that time, the gap between future radials 3 and 4 was visible. The third opening (between radials 1 and 2) did not appear until 8 days (4.8 mm SL). Ossification was present on the medial face of radial 4 at 11 days (5.1 mm SL). By 13 days (6.0 mm SL), radials 3 and 4 were ossified, along with the medial areas of radials 1 and 2.

The ventral postcleithrum was first ossified at 11 days (5.1 mm SL). By 13½ days (6.6 mm SL), the dorsal postcleithrum had also ossified.

Pelvic Girdle (Figure 11). The first sign of the pelvics was an oblong cartilage lying between and posterior to the laterally convex ventral tips of the cleithra. This was first visible at 5½ days (3.7 mm SL). Ossification began at 11½ days (4.6 mm

SL) on the lateral faces of the pelvics and surrounded most of the cartilage. The pelvic spine was first to ossify, 11 days (5.1 mm SL), followed by three soft rays.

SUMMARY

Chasmodes saburrae in the study area generally made nests containing 1.000-2,000 eggs in a single layer in empty oyster shells. The male parent guards the eggs which are deposited by more than one female. A single female may spawn at least 2,600 eggs over her lifetime during many individual spawnings. The spawnings occur throughout the day from early March until early November, with peak spawning during the spring and fall.

Embryonic and larval development took place in 27 days. The eggs are nearly spherical, averaging 0.82 mm in their greatest diameter. They hatch in 6 days at 27° C. Newly-hatched larvae are planktonic and average 3.4 mm SL (range 3.2-3.7 mm SL). In the smallest preserved larva (1/2 day, 2.5 mm SL), a small yolk sac was present and pigment was most noticeable in the eyes and dorsal portion of the gut. In larvae 10½ days old (4.7 mm SL), the notochord was flexed, the median fins were forming, and preopercular spines were present. Dark pigment spots were scattered over the head. The ventral portion of the pectoral fin was streaked with dark bars which coalesced into a dense dark area by 13½ days (6.6 mm SL). By 21 days (6.4 mm SL), all fins were present and the larva had settled out of the water column. Body pigment was darkest in the head region and pectoral fin pigment had nearly disappeared.

Head length, gut length, caudal fin length, and depth of the body increased in proportion to SL during larval and juvenile growth. The proportional length of the pectoral fin increased during larval growth, but decreased between the larval and adult stages.

Most of the bones of *C. saburrae* ossified during the middle of the larval stage. In the earliest sample (1/2 day), the parasphenoid, maxillae, opercles, preopercles, and the cleithra were ossified. Between the 1/2 day and the 5th day samples, the frontals, dentaries, branchiostegals, and caudal fin rays had begun to ossify. The majority of the remaining bones ossified between the 5th and 15th day except for the intercalars and basihyal, which began to ossify between the 15th and 21st days and the basisphenoid, pterosphenoids, and distal pterygiophores, which did not ossify until after the 21st day.

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