Reprinted from “Copeia” Volume 1987, number 4, 1987, pp.1041-1046, Govoni: The ontogeny of dentition in Leiostomus xanthurus. With permission from the American Society of Ichthyologists and Herpetologists.

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THE ONTOGENY OF DENTITION IN *LEIOSTOMUS XANTHURUS*.—The dentition of teleostean fishes is characterized as polyphyodont (Peyer, 1968), meaning that teeth are replaced continually throughout their lives. While this is true as a general categorization (Fink, 1981), when tooth replacement begins and ends and in what pattern tooth replacement proceeds in different fishes, is less clear (see conflicting observations in Osborn [1973], Lawson and Manly [1973], Wakita et al. [1977], and Motta [1984]). Tooth replacement affects both the form and arrangement of teeth. Accounts of the form and arrangement of teeth are typical of taxonomic descriptions of adult fishes, and the emergence of teeth is often reported along with descriptions of the osteological development of larvae. Considerable change in dentition is evident from this literature, yet few have examined the dentition of fishes throughout their ontogeny (Dunn, 1983); Stoner and Livingston (1984) are a notable exception. This dearth of information is troublesome in view of the well documented ontogenic changes in the diets of fishes along with the functional linkage, to one extent or another, of their dentition with their diets.

The Sciaenidae is a speciose family of percoid fishes that displays considerable adaptive variation in dentition and jaw structure among its species. Teeth are borne on the premaxillaries and dentaries of the jaws and on the pharyngobranchials, epibranchials, and ceratobranchials of the branchial baskets of the sciaenid fishes (Chao, 1978) and are functionally related to diets (Chao and Musick, 1977). Here I present the observation that for a single, common, and previously much studied sciaenid, *Leiostomus xanthurus*, changes in dentition are not completed during transformation, tooth replacement ceases on one tooth bearing element during juvenile development, and diet changes markedly in apparent association with changes in dentition.

Leiostomus xanthurus ranges from Cape Cod to the Bay of Campeche in the western North Atlantic and spawns over the continental shelf where its planktonic larvae feed and grow (Govoni et al., 1983). Transformation of larvae begins at about 7 mm notochord length (NL) and is complete by about 18 mm standard length (SL) (Powell and Gordy, 1980). Juveniles move into estuarine nursery areas where they may remain until fish reach sexual maturity (Chao and Musick, 1977). Sexual maturity is reached at lengths of 125–214 mm SL; south of Cape Hatteras, fish mature at the lower end of this range (Hata, 1985).

Materials and methods.—Larvae were obtained from laboratory reared populations (Hettler and Powell, 1981). Juveniles and adults were collected from the York River, Virginia, and Back and Core Sounds, North Carolina. Specimens were prepared for examination by a modification of the Taylor technique (Potthoff, 1984). Dry skeletal preparations were also examined. All teeth on the left premaxillary and dentary of larvae were counted. Because of the number of teeth in juveniles and adults, teeth were counted only on the first three labial tooth rows of the left elements, although additional rows of teeth were apparent above the gum.

Histological preparations followed the procedures outlined in Govoni (1984); specimens were not decalcified. Specimens for examination with the scanning electron microscope were prepared by the methods of Fink (1981). The digested, dehydrated epithelium surrounding the base of teeth was laid aside with a jet of air (Ebeling, 1957) before preparations were air dried.

Results and discussion.—The teeth of *L. xanthurus* develop in the typical manner of fishes (Peyer, 1968). An enameloid bud first develops in the epithelial connective tissue overlying the anlagen of the tooth bearing bones (Fig. 1a). Collagenous predentine (Shellis, 1978) then develops beneath the tooth bud (Fig. 1a). Next, mineralization of predentine to dentine proceeds (Fig. 1b). Finally, the mature tooth develops a bone of attachment as a pedestal (Fig. 2a and b). The mode of attachment of the mature jaw and pharyngeal teeth is Type 2 (sensu Fink, 1981) with a collagenous ring separating the predentine of the tooth shaft from the bone of attachment (Fig. 2a and b).

Mineralization proceeds from the distal cap toward the proximal base of teeth. When they first erupt, the teeth of larval *L. xanthurus* do not stain with either alizarin red or alcian blue, a condition evident in other larval fishes (Nakajima, 1979; Mochizuki and Fukui, 1983). This is apparently the result of the lack of mineralization in the enameloid matrix. As tooth de-

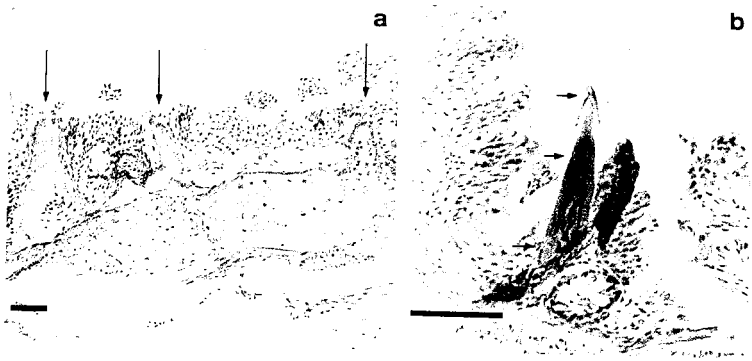

Fig. 1. Photomicrographs of tooth development: a) three teeth in different stages of development on the ceratobranchial of a 13 mm SL larval *Leiostomus xanthurus* showing a tooth with an enameloid cap in the epithelium (left arrow), a tooth with an enameloid cap and unmineralized dentine (center arrow), and a tooth near eruption with an enameloid cap, mineralized dentine in its distal shaft, and unmineralized dentine in its proximal shaft (right arrow) (scale bar, 70 μm); and b) an erupted tooth on the ceratobranchial of a 14 mm SL larva (scale bar, 110 μm).

velopment proceeds, the enameloid cap stains with alizarin indicating mineralization, the distal shaft does not stain, and the collagen of the predentine in the proximal shaft stains with alcian blue. When they erupt, replacement teeth of juveniles and adults exhibit unstained caps, alizarin stained distal shafts, and alcian-blue stained proximal shafts, a condition evident in other juvenile and adult fishes (Motta, 1984). Mature teeth of juveniles and adults have an unstained cap, a shaft stained with alizarin along its entire length, and a clear band above the bone of attachment. SEM reveals this band as collagenous material (Fig 2a). The unstained cap of mature teeth indicates alizarin-impermeability possibly owing to the presence of a cuticle (Shellis and Berkovitz, 1976) or a highly crystalline form of enameloid (Suga et al., 1981).

The form of the teeth of larvae of *L. xanthurus* differs from that of juveniles and adults. When they erupt, jaw teeth of larvae are simple, retrorse, and conical. I found no evidence of tooth replacement in larvae, but recurved, villiform teeth are added in tooth rows on the labial aspect of the jaw elements of transforming larvae and replace larval teeth; replacement is complete in fish 17 mm SL. A clear pattern of tooth replacement is difficult to discern in *L. xanthurus*, owing to the number of teeth and tooth rows. Single replacement teeth appear on the symphyseal side of the mature teeth of the jaws and on the mesial side of the pharyngeal elements. Mature teeth of juveniles and adults are recurved and villiform and have a distinct cap that is separated from the shaft by a ring of collagen (Fig. 2c and d). Tooth caps are composed of dense enameloid, while shafts are collared with a sheath of enameloid overlying predentine and dentine (Fig. 1b), a structure common to teeth of prehensile action in other fishes (Shellis, 1978). Pharyngeal teeth are recurved and villiform when they erupt in larvae, as they are in juveniles and adults. Molariform teeth are added, however, to the first three mesial rows of the ceratobranchial of arch 5 and the pharyngobranchial of arch 3 of juveniles beginning at about 20 mm SL. Molariform pharyngeal teeth are simple with no distinct cap. The addition of molariform teeth is complete in fish 50 mm SL, wherein mesial molariform teeth grade laterad to bulbous, conical, then villiform (Fig. 2e). Molariform teeth number about 34 on the pharyngobranchials and 28 on the ceratobranchials of adults.

The arrangement of teeth changes as *L. xanthurus* grow. Teeth first erupt on the premaxillary near the medial symphysis of larvae when they reach about 4 mm NL and on a like region of the dentary by 5 mm SL (Fig. 3). Teeth are added posterolaterally as larvae grow. Additional rows of teeth erupt linguad on the premaxillaries and dentaries beginning in transforming larvae of about 17 mm SL. The complete complement of teeth on the premaxillaries is seen in adults larger than 125 mm SL (Fig. 3); the teeth in the three rows of the labial aspect are longer than those in the additional four rows on the lingual aspect (Fig. 2f). The

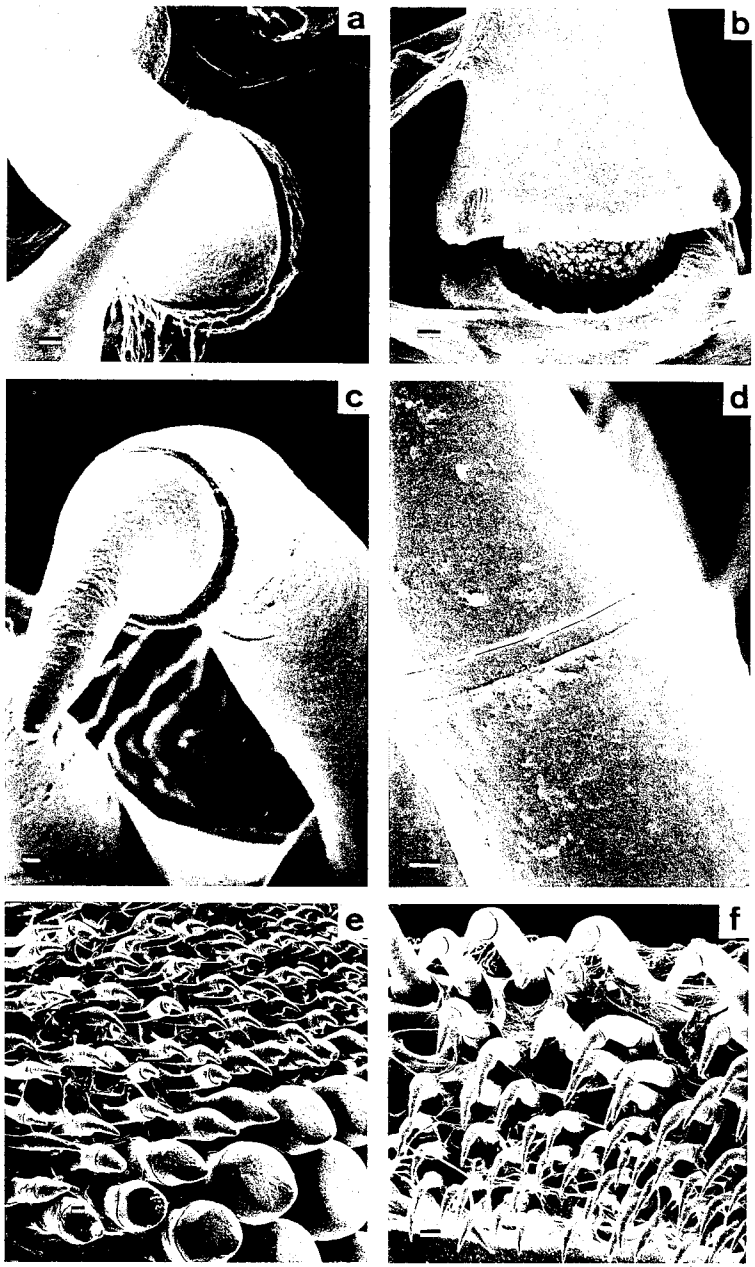

Fig. 2 Scanning electron micrographs of tooth attachment, form, and arrangement: a) recurved villiform tooth with Type 2 attachment on the premaxillary of a 200 mm SL adult *Leiostomus xanthurus* (scale bar 10 μm); b) bone of attachment at the base of a tooth that has been depressed linguad (scale bar 10 μm); c) tooth cap and shaft in a 190 mm SL adult (scale bar 10 μm); d) collagenous ring separating the tooth cap and shaft (scale bar 10 μm); e) recurved villiform, conical, and molariform teeth on pharyngobranchial 3 of a 200 mm SL adult, mesial aspect at the bottom (scale bar 100 μm); and f) recurved villiform teeth on the premaxillary of a 190 mm SL adult, labial aspect at the top (scale bar 100 μm).

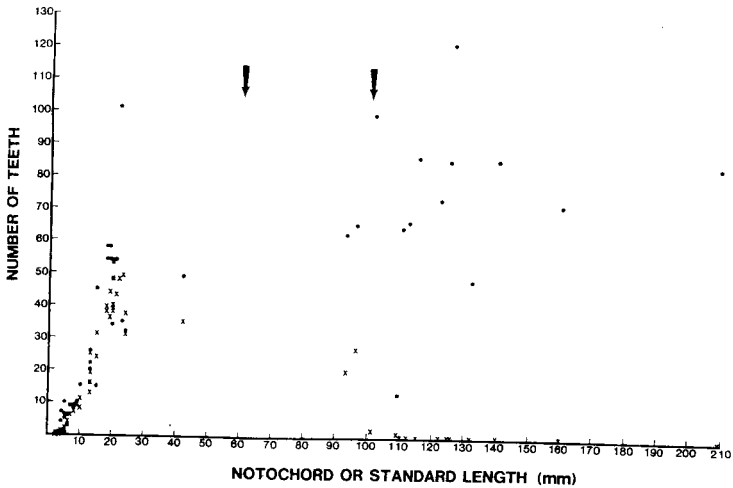

Fig. 3. Counts of teeth on the first three labial rows of the left premaxillaries (dots) and dentaries (x's) and the length of *Leiostomus xanthurus*. Arrows indicate breaks in diet composition.

variation in the number of premaxillary teeth in adults (Fig. 3) probably reflects abrasive loss and replacement. Juveniles about 40 mm SL have the greatest number of teeth on the dentaries (Fig. 3), where they are arranged in three rows that oppose the labial three rows of the premaxillaries. Pharyngeal teeth begin to erupt on tooth plates on the ceratobranchials of arch 5 and on the pharyngobranchials of arches 2, 3, and 4 in larvae as small as 6 mm NL. Pharyngeal teeth in tooth rows increase in number throughout larval development, and the complete complement is seen in juveniles 40 mm SL. Chao and Musick (1977) reported upper pharyngeal teeth mainly on the epibranchials of six sciaenids including *L. xanthurus*, yet I found no teeth on the epibranchials; the tooth plates depicted in Chao and Musick are located on the pharyngobranchials. A similar, but not exact, condition is evident in *Sciaenops ocellatus*, which has a few teeth scattered on the epibranchials, but most of its pharyngeal teeth lie on the pharyngobranchials and ceratobranchials (Topp and Cole, 1968). (There is no evidence of bilateral symmetry or sexual dimorphism in either the form or arrangement of the teeth.)

Changes in the dentition of *L. xanthurus* are not completed at transformation; *L. xanthurus* loses dentary teeth as juveniles. Many larval fishes have teeth on both the premaxillaries and dentaries, only to lose them during the transformation of larvae to juveniles; the clupeids are a prominent example (June and Carlson, 1971). *Leiostomus xanthurus* is unusual inasmuch as teeth are added to the dentary of juveniles until they reach 40 or 50 mm SL and are thereafter lost (Fig 3). Loss of dentary teeth is complete in fish 110 mm SL or so (Fig. 3). Dentary teeth are probably shed for I did not observe resorption of teeth, although I did observe resorption of the bone of attachment as indicated by alcian-blue stained areas at the base of the tooth shaft and in the underlying bone matrix. The longevity of mature teeth is not known, but continuous abrasion as the result of the scooping action of the dentary does not account for the absence of dentary teeth in adults inasmuch as fish held in cylindrical tanks with hard bottoms that prohibited scooping showed no replacement teeth on the lower jaw. Tooth replacement on the dentary ceases.

Changes in the dentition of *L. xanthurus* cooccur with changes in its habitat, feeding mode, and diet. Larvae are raptorial planktivores with terminal mouths. Their feeding mode is comparable to that of scombroid larvae (Hunter, 1981) in that it approximates ram feeding of adult fishes (sensu Liem, 1980a). The diet of larvae less than 18 mm SL consists of zooplankton: pteropods, pelecypods, and naupliar, copepodid and adult copepods (Govoni et al., 1983). The retrorse conical teeth of larvae seem well suited for seizing and retaining single zooplankters. As larvae grow, the width of food con-

sumed increases (Govoni et al., 1986) along with the number of premaxillary and dentary teeth. The feeding behavior of juveniles and adults is plastic, but changes in their dentition are again reflected in changes in their diet. After entering estuaries, juveniles, with their inferior jaws, become opportunistic benthic feeders. Their feeding behavior varies among filter feeding, prey seizure, and sediment winnowing (Yetman, 1979), but my observations indicate their feeding mode is inertial suction, the predominant mechanical mode of teleosts (Liem, 1980a). The diet of small juveniles (17–24 mm SL) consists largely of epibenthic harpacticoid copepods (Kjelson et al., 1975). Larger juveniles add other benthic epifauna to their diets (see review in Chao and Musick, 1977). The recurved, villiform teeth of the premaxillaries and dentaries serve in prey seizure, while the villiform and molariform pharyngeal teeth serve in filter feeding and sediment winnowing. Food, along with benthic substrate, is sucked into the buccopharynx and is winnowed from the accompanying debris by the action of the villiform pharyngeal teeth and gill rakers (Yetman, 1979). Molariform pharyngeal teeth effect mastication. As fish grow beyond 60–100 mm SL, their diets become increasingly diverse (Sheridan and Livingston, 1979). Sheridan and Livingston's (1979) gut content data conform well with most other published accounts of diet and indicate two marked breaks in diet composition that correspond with changes in the dentition of *L. xanthurus.* When partitioned according to 10 mm SL classes of fish and grouped according to similarity, their data indicate that the diet of *L. xanthurus* changes when fish reach about 60 mm SL and again when fish reach 100 mm SL (Fig. 3). At 60 mm SL, fish begin to eat more detritus and less plankton as their dentary teeth are being shed. At 100 mm SL when dentary teeth are absent, fish begin to eat more infauna. This may reflect a structural adjustment that accommodates scooping with the dentary in addition to suction.

There is ongoing discussion over the extent to which jaw structure and dentition constrain the diets of fishes given the flexibility in feeding behaviors within single species (see discussion in Stoner and Livingston, 1984). The examination of the dentition of a single species, albeit over its entire ontogeny, is not likely to resolve this debate. Ontogenetic changes in dentition and diet, as observed in *L. xanthurus,* do nonetheless underscore the need for the consideration of the complexity of teleost dental ontogeny when attempting to infer adaptive functionality (Liem, 1980b) and polymorphism (Roberts, 1974; Sage and Selander, 1975).

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KINEMATICS AND POWER OUTPUT OF JET PROPULSION BY THE FROGFISH GENUS *ANTENNARIUS* (LOPHIIFORMES: ANTENNARIIDAE).—Jet propulsion is used as a means of aquatic locomotion by some soft-bodied invertebrates (Trueman, 1980), as well as fish (Breder, 1926; Wolf, 1963; Gradwell, 1971). Jet propulsion requires a body form which can: 1) allow a large mass of water to be forcibly expelled; and 2) expand after contraction to take in more water for additional thrust (Trueman, 1975). Pulsed water jets generate large thrust forces for a given mass of water expelled (Weihs, 1977).

Breder (1924, 1926) argued that the force of water exhaled from the gill openings in fish could be utilized for jet propulsion. Gradwell (1971) reported that banjo catfish (Aspredinidae) are able to locomote by jet propulsion using opercular exhalations. In the Antennariidae, *Histrio histrio* has been observed previously locomoting by jet propulsion (Wolf, 1963), and