

## Tooth attachment, replacement, and growth in the butterflyfish, *Chaetodon miliaris* (Chaetodontidae, Perciformes)

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Despite much work on tooth development and attachment in fishes there has been little published on this subject in advanced actinopterygians. This paper describes tooth structure, arrangement, attachment, growth, and replacement in the butterflyfish, *Chaetodon miliaris*. Each tooth is composed of a cap, shaft, and pulp cavity, and is articulated to attachment bone pedestals by an annular ligament. Tooth growth occurs initially by cap formation followed by elongation of the tooth shaft. These growing replacement teeth remain unattached to the bone, forming in troughs in the premaxilla and dentaries. Jaw tooth replacement appears to occur either laterally or lingually to functional teeth; addition of teeth lateral to functional rows may provide increase in tooth numbers during growth. The dentition and jaw morphology of this species appears to represent a compromise between planktivory and benthic feeding and may indicate a recent entry into the planktivorous guild.

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En dépit des nombreux travaux sur le développement et l'attachement des dents chez les poissons, il existe peu de publications à ce sujet chez les actinoptérygiens évolués. On trouvera ici la description de la structure, de l'arrangement, de l'attachement, de la croissance et du remplacement des dents chez le papillon de mer, *Chaetodon miliaris*. Chaque dent se compose de la couronne, de la tige et de la cavité pulpaire et s'articule sur les attachements basaux osseux par un ligament annulaire. La croissance de la dent se fait au départ par formation de la couronne, puis par élongation de la tige. Ces dents de remplacement en développement ne sont pas attachées à l'os et elles se forment dans des sillons du prémaxille et des dentaires. Le remplacement des dents de la mâchoire semble se faire de part et d'autre de la rangée de dents fonctionnelles (du côté lingual et du côté externe); l'addition de dents latérales aux rangées fonctionnelles peut entraîner des augmentations du nombre de dents au cours de la croissance. La dentition et la morphologie de la mâchoire chez cette espèce semblent refléter un compromis entre un mode d'alimentation planctonophage et un mode d'alimentation benthique; peut-être faut-il donc inclure l'espèce dans la guildes des planctonophages.

[Traduit par le journal]

### Introduction

The butterflyfishes<sup>2</sup> (Chaetodontidae) are perciform actinopterygian fishes that derive their name from their dentition (chaitê = bristle, odôn = teeth). The family is represented worldwide by 10 genera and approximately 114 species (Burgess 1978). The millet-seed butterflyfish, *Chaetodon miliaris*, is the most abundant of the 20 species of butterflyfishes in the major Hawaiian Islands (Gosline and Brock 1960). In Hawaii this species is a facultative zooplanktivore that primarily takes calanoid copepods by inertial suction feeding but also nips at benthic organisms (Motta 1980, 1982; Ralston 1981).

In a review of tooth attachment in actinopterygian fishes, Fink (1981) concludes that although there has been some discussion of tooth development and attachment modes in primitive teleostomes, surprisingly little concerning actinopterygians has been published on these topics. No such studies have been conducted on any chaetodontid, although previous works on butterflyfish teeth include descriptions of the jaw teeth of *C. nigricans* (André 1784) and of *C. praetextatus* (Willem 1944), and generalized descriptions of the vascular supply (Tomes 1899), shape and flexibility (Ridewood 1896), vomerine teeth (Starks 1926), and jaw and pharyngeal dentitions (Gregory 1933) of butterflyfish teeth. Recently Burgess (1978) described tooth shape and arrangement in the family.

This paper describes jaw tooth structure, arrangement, attachment, growth and replacement in an advanced actinopterygian, *Chaetodon miliaris*. Jaw tooth attachment and replacement in this species is believed to be representative of the family based on comparisons with the jaw teeth of *C. trifasciatus*, *C. trifascialis*, *C. ornatissimus*, *C. unimaculatus*, *C. kleinii*, and *C. auriga*.

### Methods

Specimens of *C. miliaris* were obtained by spear from the Waikiki shoreline and from the south shore of Waianae Coast of Oahu, Hawaiian Islands, and were preserved and stored in 70% ethanol. Live specimens were caught by trap in Kaneohe Bay, Oahu, and killed with MS222 (tricaine methanesulfonate) overdoses. Jaw teeth were prepared by surgically removing the premaxilla and dentary and removing as much tissue as possible by dissection. For the observations on tooth counts in the symphyseal region of the premaxillae, fresh-killed specimens ( $N = 7$ ) were examined under the dissecting microscope. Data on medial tooth row counts of the right premaxilla were taken after specimens ( $N = 9$ ) were ultrasonically cleaned in a 2% sodium hypochlorite solution until the teeth were removed. Electron micrographs (Figs. 1A–1D) were prepared from select jaws that were placed in 2% sodium hypochlorite solution in an ultrasonic cleaner for approximately 30 s until the preparation was freed of tissue or just as teeth were separating from the jaw. Cleaned teeth and jaws were placed on 95% ethanol, then isoamyl alcohol, and then critical-point dried. The jaws and teeth were plated with gold palladium and examined under a Cambridge S4-10 Stereo Scan electron microscope. Specimens were examined at 5 to 10 kV. Other micrographs were prepared by mechanically cleaning the jaws and teeth, sonicating in a 2% sodium hypochlorite solution for 30 s, desiccating in an ethyl alcohol series, and air drying (Fig. 1E) or mechanically cleaning the

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<sup>2</sup>The Chaetodontidae and Pomacanthidae are separated into two families (sensu Burgess 1978).

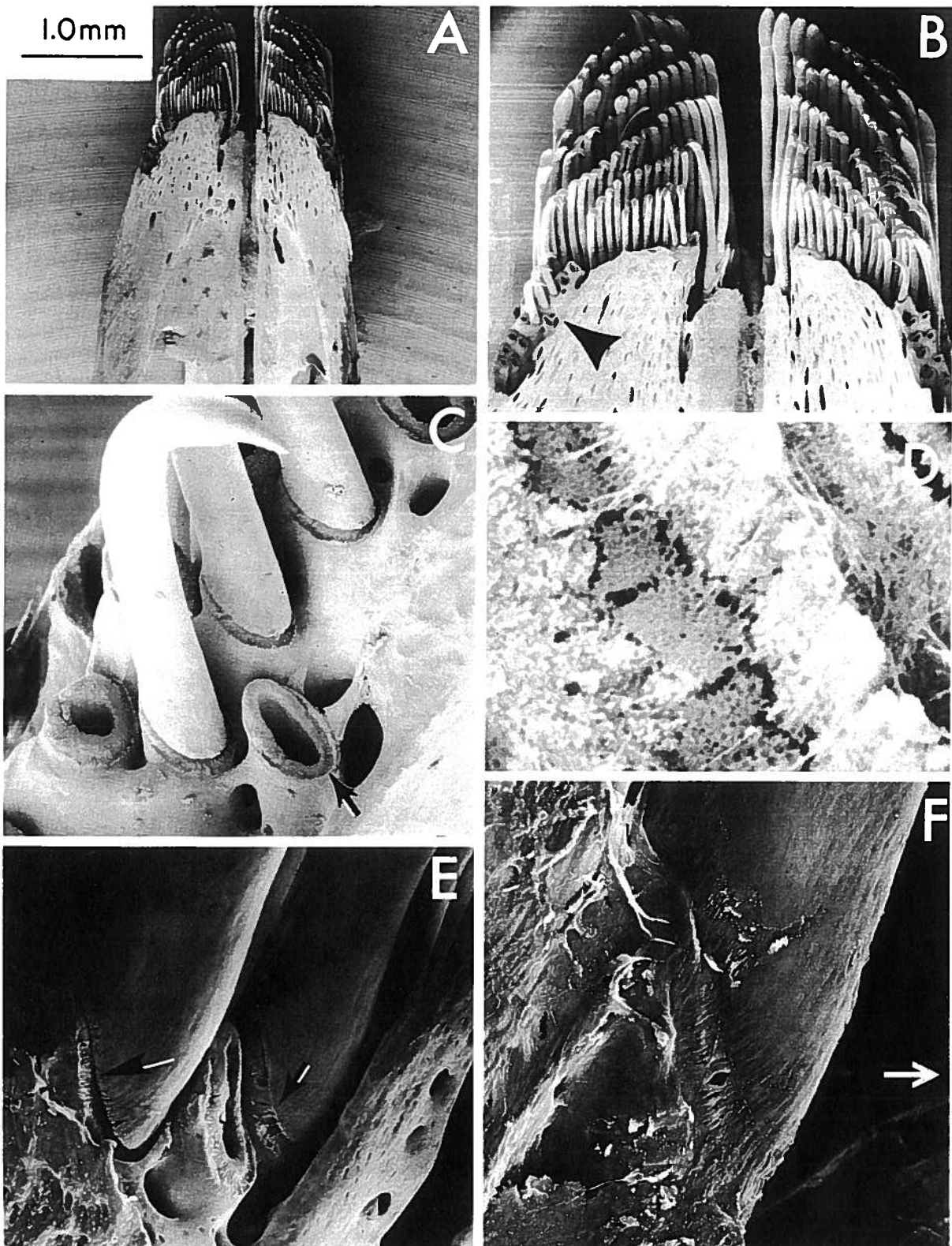


FIG. 1. (A–D) Dorsal view of juvenile *C. miliaris* (SL = 4.4 cm) dentary cleaned with sodium hypochlorite. (A)  $\times 23$ . (B) Arrow indicates region further enlarged in C;  $\times 52$ . (C) Bony pedestals and three attached teeth with region of further enlargement indicated;  $\times 475$ . (D) Fibers of attachment in the bony pedestal;  $\times 9500$ . (E) Anterolateral view of adult *C. miliaris* sodium hypochlorite cleaned right dentary with two partially removed collagenous annular ligaments (arrows) and an attachment bone pedestal after tooth loss (center);  $\times 325$ . (F) Lateral view of adult *C. miliaris* mechanically cleaned left premaxilla showing intact collagenous annular ligament joining tooth base to attachment bone pedestal. Labial side indicated by arrow;  $\times 600$ .

jaws and teeth, desiccating in an ethyl alcohol series and air drying (Fig. 1F), plating with gold palladium, and examining under a Zeiss Novascan electron microscope at 15 kV. All photographs were made

with Polaroid 4  $\times$  5 in. P/N film. To differentiate the enameloid tooth cap from the shaft, jaws and attached teeth were stained with alizarin red and examined under the dissecting microscope. For the study on

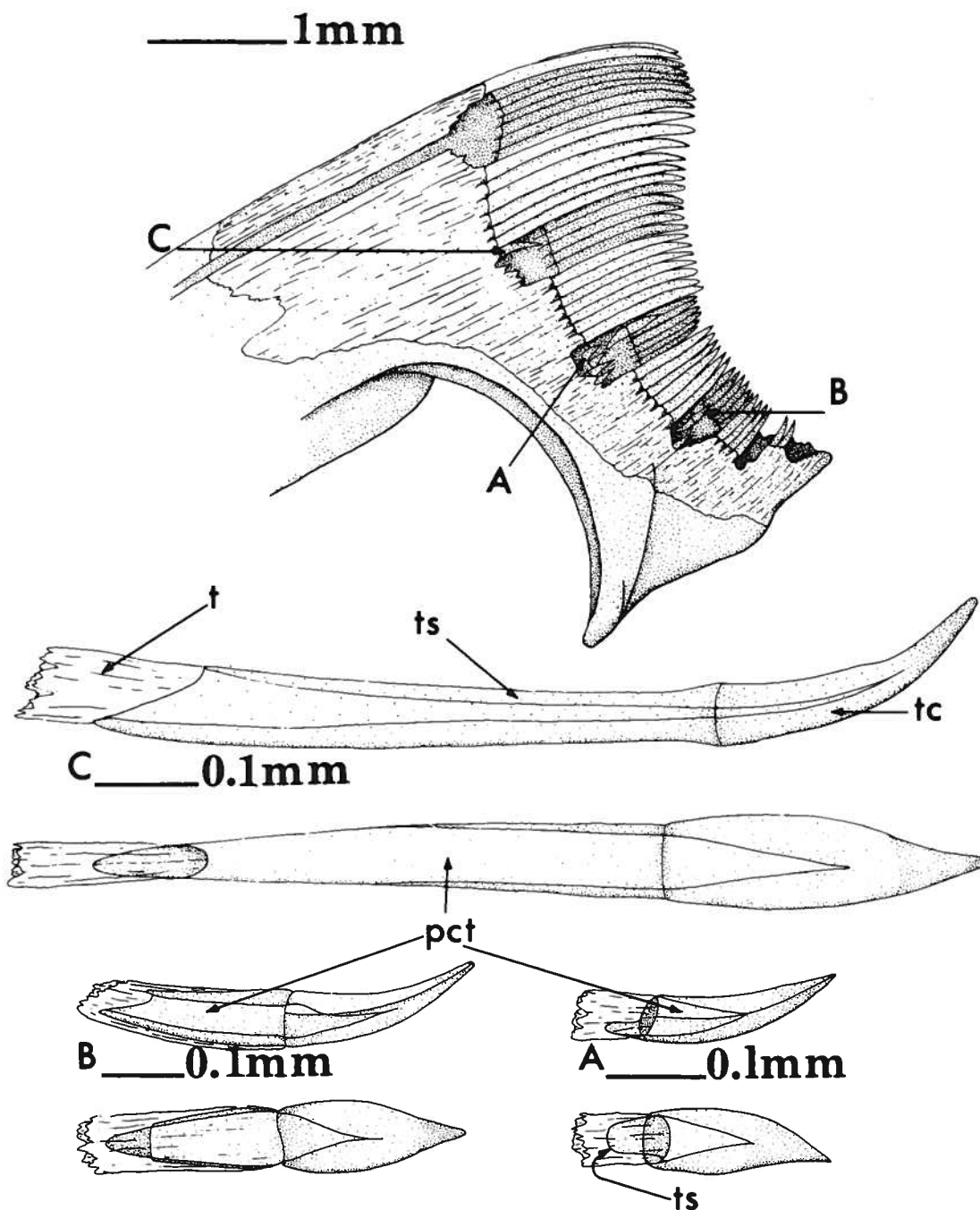


FIG. 2. Dorsolateral view of the anterior section of the premaxilla of *C. miliaris* indicating replacement teeth visible from this view. A, B, C, are progressively more developed teeth. See text for explanation. *pct*, pulp cavity of tooth; *t*, soft tissue; *ts*, tooth shaft; *tc*, tooth cap.

tooth replacement, over 40 adult fresh-killed and preserved specimens were examined under the dissecting microscope and illustrations of the jaws and replacement teeth prepared by means of a camera lucida and freehand illustration. Following this, the jaws were removed and ultrasonically cleaned in a 2% sodium hypochlorite solution until the majority of the functional teeth were removed. With some of the replacement teeth remaining, a composite illustration of the position of the replacement teeth could be prepared.

### Results

#### *Jaw tooth arrangement, structure, size, and shape*

The jaw teeth lie in discrete rows on the premaxilla and dentary (Figs. 1, 2, 3). Soft tissue lies around and between the

teeth so that only their tips are exposed. The teeth extend onto the lower extremities of the descending process of the premaxilla (Fig. 3) and part way along the ascending process of the dentary (Fig. 3) and part way along the ascending process of the dentary (Fig. 1B arrow). The teeth are composed of a cap, shaft, and a pulp cavity that extends into the cap (Fig. 2). A line of demarcation is revealed between the alizarin red stained tooth shaft and the cap which does not stain. Inner teeth are villiform while peripheral teeth are larger and spatulate at their tips (Fig. 1). There is no discernible difference in tooth shape, arrangement, or attachment between juvenile and adult specimens.

#### *Tooth attachment and placement*

The teeth are attached to bony pedestals of attachment bone

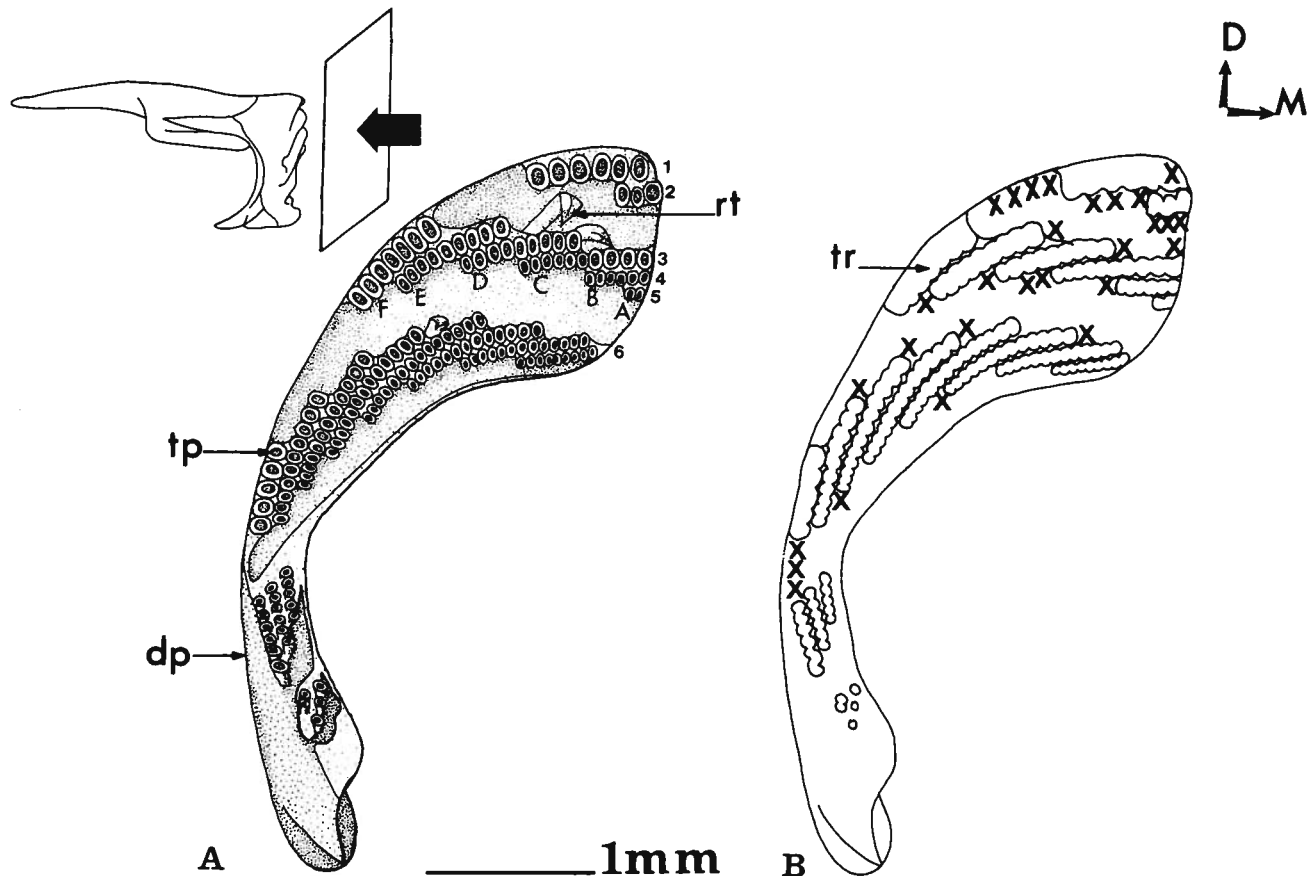


FIG. 3. (A) Anterior or transverse view of left premaxilla from an adult *C. miliaris* with teeth removed to show bony pedestals upon which teeth are attached. Three replacement teeth, slightly displaced in cleaning, remain. Inset illustrates left premaxilla, without rostral cartilage, in plane of view. See Table 1 for explanation of numbers and letters. *dp*, descending process of premaxilla; *rt*, replacement tooth; *tp*, tooth pedestal. (B) Anterior or transverse schematic view of left premaxilla of an adult *C. miliaris*.  $\times$  marks locations of replacement teeth remaining after removal of functional teeth from over 40 specimens. Dorsal (D) and medial (M) planes indicated at the top. *tr*, tooth rows.

(Tomes 1874; Ridewood 1896; Moy-Thomas 1934; Kerebel et al. 1979; Fink 1981) that is in turn ankylosed to the spongy bone of the jaws. (Figs. 1A, 1B, 1C) Mechanical manipulation of the teeth from fresh or preserved specimens results in a movable articulation between the tooth base and the bony pedestal. Examination of the tooth base-pedestal articulation in the nondissolved specimen reveals a ring of unmineralized collagen fibers (Fink 1981) that do not stain with alizarin red and are longer on the lingual side of the tooth (Fig. 1F). When the teeth are ultrasonically cleaned in sodium hypochlorite solution the majority of the organic matter which surrounds and anchors the teeth is dissolved, freeing some of the teeth and exposing the attachment bone pedestals (Fig. 1C). These are slanted, with their labial sides being longer than their lingual sides. A hollow pulp cavity (Moy-Thomas 1934; Kerebel et al. 1979; Fink 1981) is exposed in the tooth center, and increased magnification of the pedestal reveals what appear to be bundles of collagen fibers (Fig. 1D). Another specimen cleaned in sodium hypochlorite reveals some of the remaining fibers anchoring the teeth (Fig. 1E).

Removal of all teeth reveals the rows of pedestals (Figs. 3A, 4). In the symphyseal region of the premaxilla there are six distinct rows of pedestals corresponding to the six rows of teeth observed in intact specimens. There are similarly six to seven rows in the symphyseal region of the dentary. A count of the medial tooth rows and number of pedestals per row on the right premaxilla of varying sized specimens reveals six or seven

rows with some variation in the number of pedestals per row (Table 1, Fig. 3). Situated between and beside the rows are deep troughs in the bone in which lie the replacement teeth (Fig. 3A).

#### *Tooth growth and replacement*

At least three stages of tooth growth are apparent in the replacement teeth (Fig. 2). First to be formed is the tooth cap, which in the stages examined, has only the beginnings of a tooth shaft (Fig. 2A). The caps vary in size depending on the location of the tooth in the jaw. The cap of the developing tooth is equal in size to those of the functional teeth in that region. Soft tissue lies around the cap at this stage. The following stage involves growth of the tooth shaft (Fig. 2B). At this stage, it is still open at the proximal end, with tissue lying inside and around the shaft. Another growth stage is represented by Fig. 2C. This tooth has a long shaft which is open proximally and not yet articulated to the attachment bone.

Replacement and possibly new teeth<sup>3</sup> of adults and juveniles lie lateral to (at the ends of) the rows of functional teeth, although some appear to lie anterior or posterior to these rows (Fig. 3B). Caution must be exercised, however, as the cleaning procedure prior to these examinations could lead to substantial

<sup>3</sup>New teeth are those that form along with bony pedestals at a site other than that of preexisting teeth and therefore do not replace other teeth.

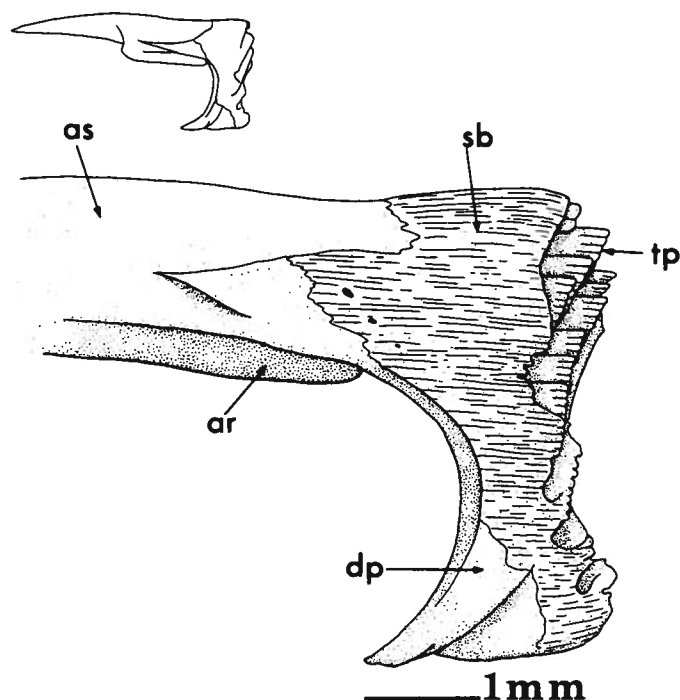


FIG. 4. Lateral view of right premaxilla of adult *C. miliaris* with all teeth removed. Bony pedestals to which teeth are attached are indicated. Inset illustrates right premaxilla with rostral cartilage removed. *ar*, articular process of premaxilla; *as*, ascending process of premaxilla; *dp*, descending process of premaxilla; *sb*, spongy (cancellous) bone; *tp*, tooth pedestal.

loss of replacement teeth, particularly smaller teeth. The techniques utilized do not reveal the mechanism of replacement tooth attachment.

## Discussion

### Tooth structure

The classification of lower vertebrate hard tissues has varied greatly and is not resolved, but the majority of actinopterygian teeth are composed of a form of dentine partly covered by an enameloid substance (Ørvig 1977; Poole 1971). The thickness and extent of the enameloid and relative volume of the tooth occupied by enameloid varies considerably from species to species and it can be distributed either as cap or collar enameloid, the former constituting the tooth tip and the latter a layer of variable thickness on the sides of the teeth (Shellis 1978). The jaw teeth of *C. miliaris* are composed of an alizarin red staining dentine shaft and a nonstaining enameloid cap (W. L. Fink, personal communication). The pulp cavity extends into the cap.

### Tooth attachment

The jaw and pharyngeal teeth are attached to bony pedestals by collagenous fibers that are extensions of the longitudinal fibers found embedded in the dentine (Kerr 1960; Schmidt and Keil 1971; Shellis and Berkovitz 1976; Kerebel et al. 1979) and in the pedestals (Kerebel et al. 1979).

Tooth attachment in *C. miliaris* appears to be of the type 2 described for the majority of Perciformes by Fink (1981). The type 2 attachment is characterized by the mature tooth not being fully ankylosed to the bone, there being a small area of unmineralized collagen at its base. Such an attachment has been compared with the mammalian periodontal ligament

TABLE 1. Number of sagittal tooth rows (numbered 1 to 6 on Fig. 3A) on the premaxilla and dentary, as well as number of coronal midline tooth rows, including number of bony pedestals per row, in a frontal plane of right premaxilla (lettered A to F on Fig. 3A). Standard length of specimens (SL, in centimetres) is also indicated

SL	(A) No. of sagittal tooth rows		(B) No. of coronal midline tooth rows						
	Premaxilla	Dentary	SL	A	B	C	D	E	F G*
9.7	6	6	3.4	2	7	9	7	8	7
10.3	6	6	8.0	3	7	9	9	8	7
			9.7	2	7	12	13	12	10
10.9	6	6	10.8	2	7	9	10	10	7
11.3	6	6	11.7	4	9	10	12	12	9
11.6	6	7	12.1	2	6	10	10	9	7
			12.3	2	6	9	9	9	7
11.7	6	6	12.4	2	6	11	10	10	8
12.3	6	6 or 7?	12.7	3	8	11	11	12	9 8

\*Three specimens had a seventh coronal row of pedestals, G. Not shown on Fig. 3.

(Noble 1969, cited in Kerebel et al. 1979; Soule 1969). Because of this collagenous annular ligament (Tomes 1923) some tooth movement is possible (Kerr 1960; Fink 1981). In addition, *C. miliaris* has a greater area of unmineralized collagenous fibers on the labial margin of the teeth (Figs. 1E, 1F). Such an attachment permits slight tooth movement in all directions with even greater movement towards the labial side. This would allow the teeth to depress during its benthic prey feeding, particularly in the direction of greatest stress, thereby helping to prevent breakage of these delicate teeth at the tooth-pedestal interface.

### Replacement and growth

In most teleosts (Shellis and Berkovitz 1976), as in most lower vertebrates (Miles and Poole 1967), teeth are continuously being replaced. Among other things, this may be a mechanism to permit replacement of smaller teeth by larger ones as such teeth cannot grow once they have erupted (Osborn 1973). When teleost teeth are regularly aligned, as along the jaws of conger eels, the new teeth are usually derived from the inner external dental epithelial faces of the old teeth, to give a one-for-one replacement (Kerr 1960). In general, actinopterygian replacement teeth are positioned directly lingual to the individual mature teeth (Fink 1981) so the new tooth develops up the adjacent face of the older tooth facilitating accurate replacement. Then the older tooth is shed (Kerr 1960). In *C. miliaris* the number of sagittal tooth rows (Table 1, A; Fig. 3A, 1–6) and coronal midline rows (Table 1, B, Fig. 3A, tooth rows lettered A–F) remains relatively constant over fish of varying lengths. However, there is variation in the number of attachment sites and consequently row length (Table 1, B) and many of the replacement teeth are either situated at the ends or lingual to the rows of functional teeth (Fig. 3B). I suspect that (i) one-for-one replacement may be occurring lingually and possibly laterally to the functional teeth, and (ii) new teeth, and consequently new attachment bones, are being added to the ends of the rows of functional teeth as the fish grows.<sup>4</sup> Variable positions for replacement teeth have been reported. Huysseune and Verraes (1981) found pharyngeal replacement teeth in *Haplochromis elegans* forming on the lateral

<sup>4</sup>Ebeling (1957) similarly found that the number of teeth in the eastern Pacific Mullet he examined increased with growth of the fish.

or rostral side of functional teeth. Santos Filho and Santos (1982) recorded replacement teeth directly underneath functional teeth in *Rivulus santensis*. Ebeling (1957) saw such teeth labial to the functional teeth in Eastern Pacific Mulletts and Shellis and Berkovitz (1976) report replacement teeth lying lingually to functional teeth of the dentary and premaxilla of *Serrasalmus rhombeus* but labially on the ectopterygoids. In teleosts, the commonest condition in tooth attachment is for tooth growth to be followed by the formation of a cylindrical attachment bone (bony pedestal). At one end this is connected to the tooth by fibers and at the other fused to the underlying bone (Kerr 1960).

After the formation of the tooth cap in *C. miliaris*, the tooth increases in length by addition of predentine at its inner end (Kerr 1960; Fink 1981). The predentine, which is composed primarily of collagen, mineralizes to form the dentine of the developing teeth (Fink 1981). The soft tissue that is attached to and surrounds the developing tooth (Fig. 2, t) probably corresponds to the dental epithelium which is continuous with the epidermis (Kerr 1960). Usually the inner end of the tooth approaches the underlying bone before the tooth has reached its full length and movement outwards then commences before the pedestal appears and eruption is a combined growth effect of both (Kerr 1960). The mechanism for movement of the replacement teeth to their functional sites in *C. miliaris*, as in all lower vertebrates (Poole and Shellis 1976), remains as one of the most enigmatic problems.

#### Evolution of the dentition

*Chaetodon miliaris* presents an enigma regarding its jaw morphology and feeding behavior in that it appears partially suited for both planktivory and benthic feeding. Plankton-feeding fishes often have few or no jaw teeth (Suyehiro 1942; Lagler et al. 1962; Davis and Birdsong 1973; Alexander 1967a) as teeth are thought to interfere with suction and ingestion of prey (Alexander 1967a); however, small and numerous teeth, when present, are believed to help prevent planktonic prey from escaping (Alexander 1967b; Osse 1969). *Chaetodon miliaris* and another facultative planktivore, *C. kleinii*, have somewhat reduced tooth numbers (six premaxilla rows, six to seven dentary rows) and tooth length compared with five substrate-feeding Hawaiian butterflyfishes (Motta 1980). This may be correlated with reduced interference with inertial suction feeding yet at the same time hinder prey escape from the mouth and still permit benthic foraging. In the latter case, some tooth movement as permitted by the annular ligament, is beneficial in preventing breakage of the teeth. *Chaetodon miliaris* has a large enameloid tooth cap. The extent of the enameloid cap in fishes varies according to the function of the dentition. Fishes feeding on hard materials such as corals usually have teeth covered on the functional surface with a thick layer of relatively hard enameloid (Shellis 1978). Furthermore, X-ray diffraction analysis of this enameloid cap in *C. miliaris* reveals iron compounds, albeit quantitatively one of the least amounts, compared with the five other substrate-feeding butterflyfishes (Motta 1980). The iron supposedly inhibits the initiation of cracks and hardens the teeth (Shellis and Berkovitz 1976). Conversely, *C. miliaris* has a jaw shape, size, kinematic transmission efficiency and speed of jaw protrusion suiting it for high speed inertial suction feeding (Motta 1982) as well as long, branched gill rakers, vomerine teeth, and numerous pharyngeal teeth characteristic of planktivores (Motta 1980). Ralston (1981) found that although *C. miliaris* is primarily a

zooplankton picker, it is clearly an opportunistic feeder. The jaw morphology and dentition of this species appears to represent a compromise between benthic feeding and planktivory and possibly indicates a recent entry in the planktivore guild. Ralston (1981) believes that the entry of this species into the planktivore guild may have been the evolutionary result of competition among species of *Chaetodon* for benthic invertebrates, especially stony corals, rather than the reverse, as planktivory is unusual in this genus. The retention of a morphology not unlike that of other benthic feeding Hawaiian butterflyfishes, which permits it to forage opportunistically on the benthos yet at the same time effectively forage in the water column, leads me to agree with him.

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