

Functional morphology of the head of Hawaiian and Mid-Pacific butterflyfishes (Perciformes, Chaetodontidae)

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Synopsis

The functional morphology of the jaws of six species of butterflyfishes was investigated and related to their feeding behaviors. Utilizing observations and measurements of fresh-killed specimens as well as scanning electron microscopy of their dentitions, interspecific differences in the size, shape, orientation of the mouth, dentition, degree and function of jaw protrusion were related to their different feeding behaviors. The jaws of the six species showed a variety of adaptations for feeding on or over the reef as well as a repertoire of modulated jaw movements hitherto unnoticed in many studies. This radiation in morphologies was believed to be due to relatively simple changes of a few structural elements, changes that could occur relatively rapidly in the evolutionary time scale. The benefit of naturalistic observations in such functional morphological studies was emphasized.

Introduction

The butterflyfishes, Chaetodontidae, are perciform acanthopterygian fishes. The family is represented worldwide by ten genera and approximately 114 species (Burgess 1978). Among the major Hawaiian Islands there are twenty species of butterflyfishes listed by Gosline & Brock (1960) that would be included in the classification of Burgess (1978) and similarly thirty species in the Marshall and Marianas Islands (Schultz et al. 1953).

The only studies on chaetodontid anatomy and functional morphology include osteological works by Starks (1926), Gregory (1933), Burgess (1978), a functional morphological study on the head of the inertial suction feeding *Chaetodon miliaris* (Motta 1982) and its dentition (Motta 1984b).

Feeding behaviors which are better studied primarily include coral grazing and browsing, suction

planktonic feeding and benthic omnivory. Other Chaetodon species are omnivores that take corals, crustaceans, fish eggs, gorgonians, polychaetes and zoanths (Hiatt & Strasburg 1960, Talbot 1965, Hobson 1974, Ralston 1975, 1981, Reese 1975, 1977, Neudecker 1977, 1979, Anderson et al. 1981, Birke-land & Neudecker 1981, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Motta 1982, Neudecker & Lobel 1982).

Studies on the anatomy, functional morphology and the feeding mechanisms in fishes have progressed radically from purely descriptive works of cranial anatomy (Gregory 1933), to those that tried to incorporate observations by others in a presumed functional explanation (Ebeling 1957) or simply tried to infer function or biological role from structure (Pietsch 1978) to most state-of-the-art studies that utilize extremely sophisticated electromyographic and photographic instrumentation

to study structure and function under artificial laboratory conditions (Liem 1978, 1979, 1980, Lauder 1981). In the latter technique the biological role of the feeding apparatus in the field is quite often unknown. This paper is one in a series that investigates the structure and function of the jaws of a diverse group of fishes, the butterflyfishes, incorporates naturalistic observations of the feeding behaviors and synthesizes structure, function and biological role in an attempt to elucidate the adaptations for feeding in these fishes. This synthetic method for studying adaptations is judged to be the only valid one by Bock (1980).

Materials and methods

Species studied

Choice of the species was governed by the fact that they represent a wide range of feeding guilds, they are abundant and available, and knowledge of their basic feeding and social behaviors exists.

Six species of butterflyfishes were utilized in this study: *Chaetodon miliaris* Quoy and Gaimard 1824 is one of the most common inshore fish around the Hawaiian Islands (Gosline & Brock 1960). It is a diurnal opportunistic zooplanktivore that forms aggregations about the reef most of the day, feeding primarily on calanoid copepods (Hobson 1974, Ralston 1981, Motta & Reese in preparation). This species is not found at Enewetak atoll. *Chaetodon (Megaprotodon) trifascialis* Quoy and Gaimard 1825 is rare in the major Hawaiian Islands but common at Enewetak atoll. It is an obligate hard coral browser that is exclusively associated with *Acropora* corals (Hiatt & Strasburg 1960, Reese 1973, 1975, 1977, Neudecker 1977, Anderson et al. 1981, Harmelin-Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1983, Motta 1980, Motta & Reese in preparation). The four remaining species are found at both study sites. *Chaetodon auriga* Forskål 1775, is a benthic omnivore feeding on non-coralline and coralline invertebrates with preference for alcyonarians, polychaete worms, scleractinians and algae (Hiatt & Strasburg 1960, Hobson 1974, Anderson et al. 1981, Harmelin-

Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Motta 1980, Motta & Reese in preparation). *Chaetodon trifasciatus* M. Park 1797 is an obligate hard coral browser (Talbot 1965, Reese 1975, 1977, Neudecker 1977, Harmelin-Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Anderson et al. 1981, Motta 1980, Motta & Reese in preparation) as is *C. ornatissimus* Cuvier 1831 (Hobson 1974, Reese 1977, Harmelin-Vivien & Bouchon-Navaro 1983, Motta 1980, Motta & Reese in preparation). *Chaetodon unimaculatus* Bloch 1787, is a facultative soft and hard coral grazer (Hobson 1974, Reese 1975, 1977, Boucher 1979, Harmelin-Vivien 1979, Anderson et al. 1981, Harmelin-Vivien & Bouchon-Navaro 1983, Motta 1980, Motta & Reese in preparation).

C. trifascialis specimens were speared at Chinimi reef, Enewetak Atoll, Marshall Islands. *C. miliaris* specimens were taken by spear from the Waikiki shoreline, the southshore and the Waianae coast of Oahu, Hawaiian Islands. All remaining species were caught by trap in Kaneohe Bay, Oahu, and sacrificed with MS 222 (tricaine methanesulfonate) overdoses. Specimens were preserved and stored in 70% ethanol.

Behavioral observations

Behavioral observations outlined in Motta (1980) and Motta & Reese (in preparation) were carried out with the aid of SCUBA. Basically they involve 300+ hours of underwater observation on these fishes with the unaided eye, recording prey choice, prey handling and effect of feeding on the substrate. The latter involved use of a powerful hand held magnifying lens and a sharp probe to examine the corals in the majority of cases.

Standard measurements

Standard measurements, including the angle of jaw depression, the increase in head and body length following jaw opening, the internal width and height of the orifice formed by the protruded mouth, and the length of the premaxilla and dentary, were taken on 10 fresh-killed individuals of each species. The increase in head length following

jaw opening involves depression of the lower jaw and either slight or pronounced protrusion of the upper jaw.

Angle of jaw depression was measured by means of a protractor to the nearest degree with an estimated error of $\pm 1^\circ$ based on repeated measurements of individual fish. This was measured from the posterior edge of the gill cover on a line that transects the center of the retracted relaxed mouth to the center of the caudal peduncle. The angle of jaw depression is, therefore, the angle made to the center of the maximally open/protruded mouth. In all cases the angle is below the horizontal axis due to the pivoting of the mandible on the suspensorium even though the gape in *C. ornatissimus* and *C. trifasciatus* is directed anterodorsally.

Increase in head length following maximum opening of the mouth was calculated as a percentage of the head length and total body length of the fish, with measurements made to the anterior midline of the retracted and protruded mouth.

The premaxilla and dentary were measured from the most anterior extremities of the teeth to the most posterior part of the bones and calculated as a percent of the total body length.

Interorbital width was measured on the narrowest region of the frontal bone contributing to the orbit, and eye diameter was measured on the widest portions of the bony orbit.

Maximal jaw opening was effected by manually pressing the interopercular-mandible joint dorsally.

Dentitions

Jaw teeth were prepared by surgically removing the premaxilla and dentary and removing as much tissue as possible by dissection. The jaws were then placed in 2% sodium hypochlorite solution in an ultrasonic cleaner for approximately 30 seconds until all the soft tissue was removed or just as teeth were separating from the jaw. Cleaned teeth and jaws were placed in 95% ethanol, then isoamyl alcohol and then critically point dried. The jaws and teeth were mounted on aluminum plugs, plated with gold palladium and examined under a Cambridge S4-10 Stereo Scanning Electron Micro-

scope. Specimens were examined at 5 to 10 KV and pictures made with Polaroid 4 × 5 inch P/N film. At least ten adult individuals of each species were examined under a dissection microscope to see if intraspecific differences occur in tooth shape and position, arrangement or number of rows. Only the latter yielded differences. Tooth rows were counted in the symphyseal region of the jaws on ten adults of each species. The juvenile dentition of each species was examined under the dissecting microscope and found not to differ from the adult condition. Pharyngeal tooth counts and illustrations of the first gill raker were prepared from a single adult individual of each species and confirmed on other individuals of each species.

Statistical analysis

Data on the increase in the length of the fish during maximal jaw opening, and the inside width of the open mouth, premaxilla, and dentary length, were calculated as a percent of total body length for ten individuals of each species. The increase in length of the head during maximal jaw opening was also calculated as a percent of head length. The arcsine transformation was performed on the data as advised by Sokal & Rohlf (1969). It was then checked and variances found to be homoscedastic by means of the Fmax test. Determining that the means were significantly different by a single classification analysis of variance ($\alpha = 0.05$) a student Newman-Keuls a posteriori parametric test was used to determine which means were significantly different ($\alpha = 0.05$). The back transformed mean and \pm one asymmetrical back transformed standard deviation are presented for these data (Sokal & Rohlf 1981). These and the following tests (unless otherwise indicated) were performed as outlined by Sokal & Rohlf (1969).

The data on inside height of the protruded mouth as a percent of total body length was transformed by the arcsine method and found to be heteroscedastic by means of the Fmax test. The original data on this and the angle of jaw protrusion data was then analyzed by the Kruskal-Wallis non-parametric multiple comparisons test and found to differ in 'location' indicating that the samples came

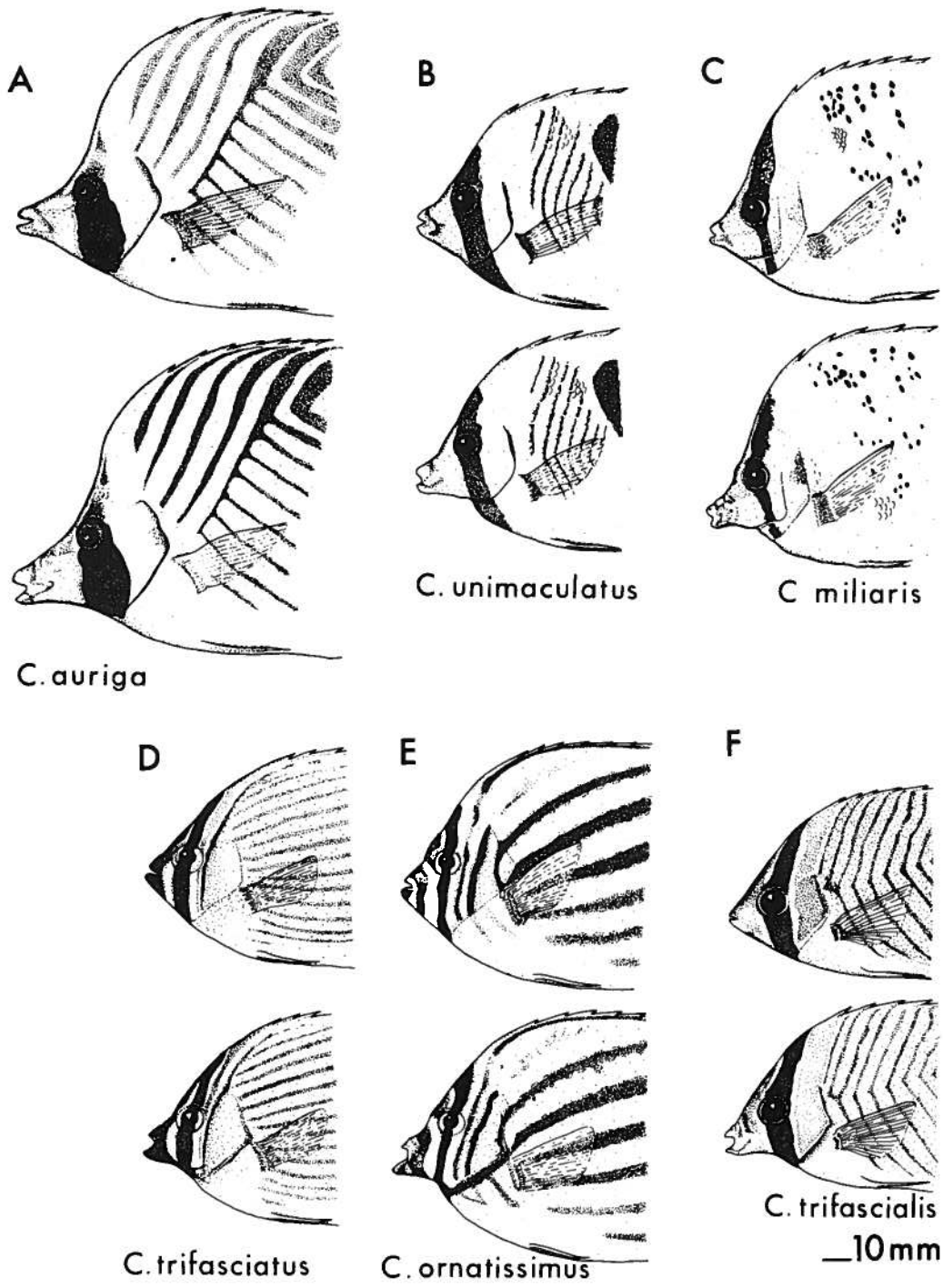


Fig. 1. Fresh-killed specimens with jaw in relaxed retracted position and jaw in maximally open and protruded position. Jaw protrusion effected by pushing manually on angular-interopercular joint.

from different populations. A non-parametric multiple comparisons test based on the Wilcoxon-Mann-Whitney statistic was then employed to indicate significant differences among the species. Internal width versus height for each species was compared by a Mann-Whitney two-tailed U-test. The original data is presented as means \pm one standard deviation around the mean.

The technique of drawing lines under the graph connecting values that are not significantly different as outlined in Sokal & Rohlf (1969) was employed.

Results

The osteology, myology and functional morphology of a representative chaetodontid has been described for the inertial suction feeding *Chaetodon miliaris* (Motta 1982). In brief, the tooth bearing bone of the upper jaw is the premaxilla and that of the lower jaw, the dentary. In many perciform acanthopterygians the upper jaw protrudes anteriorly, anteroventrally or anterodorsally as the lower jaw is depressed (Motta 1984a). Figure 1 illustrates the position of the resting mouth and the fully opened mouth for the six species studied.

Standard measurements

C. ornatissimus increases its head and body length following jaw opening significantly more than all of the other species; *C. unimaculatus*, *C. trifasciatus*, *C. auriga*, and *C. miliaris* form a second homogeneous group in terms of their values not being significantly different; and *C. auriga*, *C. miliaris*, and *C. trifascialis* form a third homogeneous group (Fig. 2).

C. trifascialis and *C. ornatissimus* have a significantly greater angle of jaw depression than the

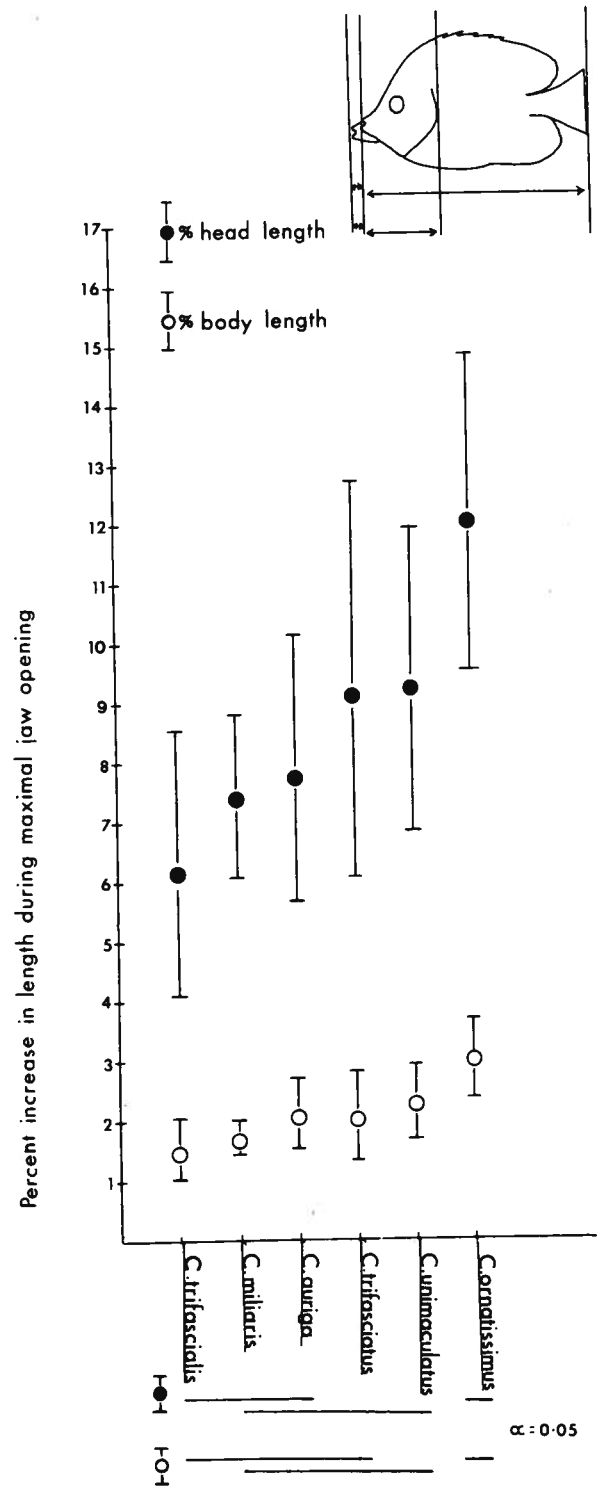


Fig. 2. Anterior increase in length during maximal jaw opening as a percent of head length and total body length. Mean \pm 1 standard deviation indicated. Lower lines connect means that are not significantly heterogeneous at $\alpha = 0.05$; any means not connected by a line are considered significantly different. Student-Newman-Keuls test, N = 10.

remaining species (Fig. 3). The measurement is influenced by a lower jaw that pivots greatly about its axis. This angle of jaw depression is not necessarily equivalent to an angle of jaw protrusion as for example, in *C. ornatissimus* and *C. trifasciatus*, protrusion of the upper jaw per se is minimal.

C. auriga has a significantly longer premaxilla (in terms of its body length) than all of the other species; followed by *C. unimaculatus*; then *C. ornatissimus* and *C. miliaris* which form a homogeneous group; *C. miliaris* and *C. trifascialis* which

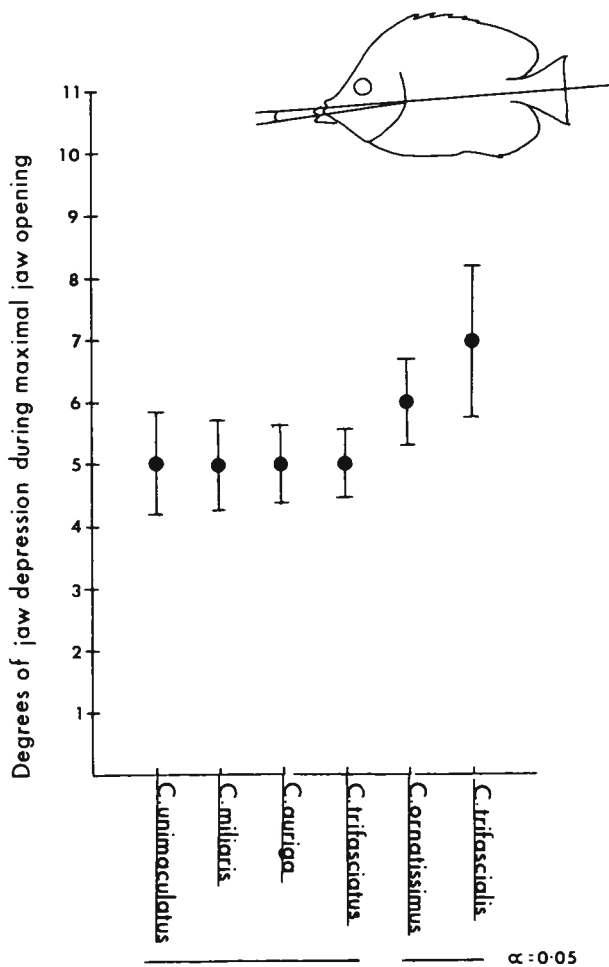


Fig. 3. The angle of jaw depression below the longitudinal axis of the fish during maximal jaw opening. Mean \pm 1 standard deviation indicated. Lower lines connect species that are not significantly different at $\alpha = 0.05$. Nonparametric multiple comparisons by simultaneous test procedure, $N = 10$.

form a second homogenous group; and finally by *C. trifasciatus*, which has the shortest premaxilla (Fig. 4). Dentary length as a percent of total body length presents essentially a similar picture (Fig. 5).

C. ornatissimus has the significantly widest mouth, followed by *C. trifasciatus* and *C. unimaculatus*. *C. auriga* and *C. miliaris* are not significantly different as are *C. miliaris* and *C. trifascialis* (Fig. 6).

The internal heights of the protruded mouths are not as clearly distinguishable as the widths, probably in part owing to measuring error (Fig. 6).

When the widths and heights are compared intraspecifically *C. ornatissimus* and *C. unimaculatus* have essentially round mouths, the widths not

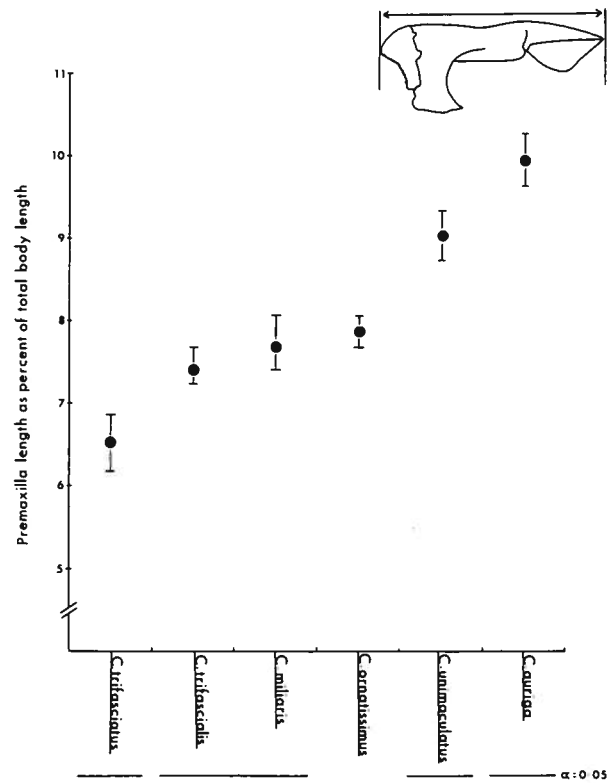


Fig. 4. Premaxilla length expressed as a percent of total body length. Mean \pm 1 standard deviation indicated. Lower lines connect values that are not significantly heterogeneous at $\alpha = 0.05$, any means not connected by a line are considered significantly different. Student-Newman-Keuls test, $N = 10$.

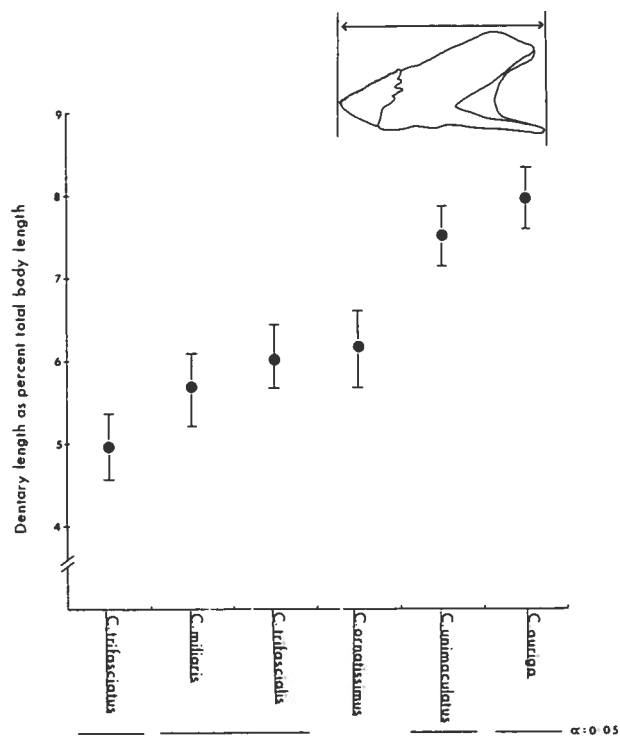


Fig. 5. Dentary length expressed as a percent of total body length. Mean ± 1 standard deviation indicated. Lower lines connect means that are not significantly heterogeneous at $\alpha = 0.05$, any means not connected are considered significantly different. Student-Newman-Keuls test, $N = 10$.

being significantly different from the heights. *C. trifasciatus* has a protruded mouth with a width significantly greater than its height. *C. auriga*, *C. miliaris* and *C. trifascialis* all have protruded mouths with heights significantly greater than their widths.

Mouth shape and position

The retracted mouths of *C. auriga*, *C. unimaculatus*, and *C. miliaris* are prognathous to differing degrees when compared to the other species. Their protruded mouths are even more prognathous (Fig. 1). The head profiles of *C. trifasciatus*, *C. ornatissimus*, and *C. trifascialis*, with the jaws retracted, are similar and less prognathous than the former. The premaxillae of *C. trifasciatus* and *C. ornatissimus* protrude only slightly when the lower

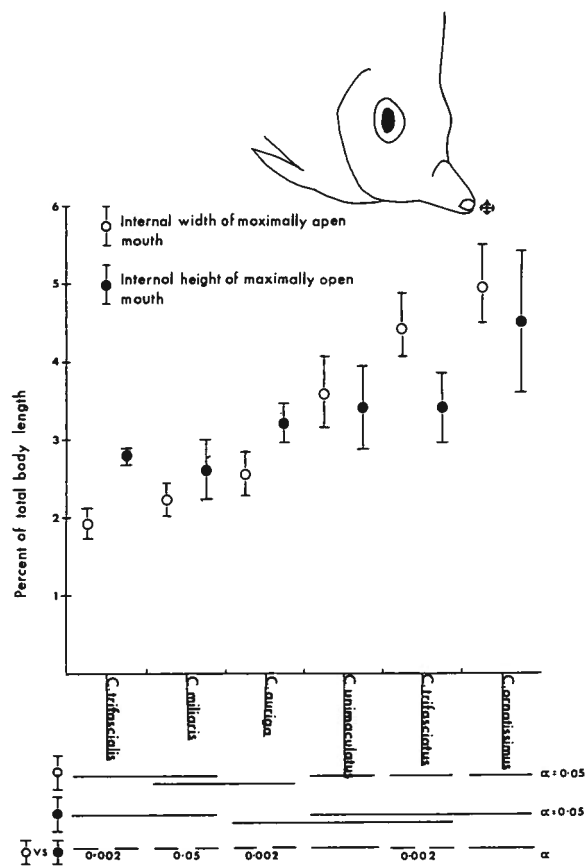


Fig. 6. The internal width and height of the maximally opened mouth as a percent of total body length. Mean ± 1 standard deviation indicated. Lower lines connect species that are not significantly different at $\alpha = 0.5$. Internal width calculations based on Student-Newman-Keuls test, internal height on non-parametric multiple comparisons by simultaneous test procedure, $N = 10$.

jaw is depressed, forming a shovel-like mouth profile. The protruded mouth of *C. trifascialis* is prognathous and forceps-like. The gape of the protruded mouths is directed anteroventrally in *C. miliaris*, *C. auriga*, *C. unimaculatus*, and *C. trifascialis*; in *C. trifasciatus* and *C. ornatissimus* it is directed anterodorsally.

Dentition

The upper jaw teeth of *C. auriga* are arranged in 9–11 distinct rows ($N = 10$). The teeth are long and hooked at the tips. The peripheral teeth are both

hooked and spatulate at their tips, the inner ones shorter and simply hooked. The teeth are located almost completely down the labial side of the descending process of the premaxilla and up the ascending process of the dentary, therefore ringing the mouth with teeth (Fig. 7, 8). The 9–12 rows (N = 10) of teeth on the dentary are similar to those on the premaxilla (Fig. 9). In *C. auriga* just the tips of the teeth protrude through the tissue.

C. miliaris has six distinct rows of teeth on the premaxilla and six to seven rows on the dentary (N = 8 specimens). The teeth, which are few in number, extend on to the lower extremities of the descending process of the premaxilla and part way along the ascending process of the dentary (Fig. 7, 8, 9). Inner teeth are villiform and peripheral teeth are spatulate at their tips. All teeth are hooked at the tips.

There are five to eight distinct rows of teeth on both upper and lower jaws (N = 10) of *C. unimaculatus*. The teeth are massed toward the anterior part of the jaw with few teeth on the descending process of the premaxilla. The inner teeth are hooked and villiform, the outer ones are broad and spatulate. The peripheral teeth which contact the biting surface are very stout throughout their length (Fig. 7, 8, 9). The tips of the large peripheral teeth, and occasionally the tips of the smaller teeth, protrude through the tissue that surrounds them.

C. trifascialis has five to six rows of teeth on the upper and lower jaws (N = 7) (Fig. 7, 9). The teeth are massed toward the anterior ends of the jaws to form a pad. The teeth are essentially of the same length, except the innermost rows which grade in length to match outer rows. The teeth are villiform and hooked at their ends (Fig. 8). Inner teeth are pointed and round; peripheral biting teeth are spatulate at their tips. The tooth pad is not as large or as thick as that of *C. ornatissimus* or *C. trifasciatus*.

The teeth of *C. trifasciatus* are essentially all of the same length and massed toward the anterior to form a pad. All teeth are villiform, hooked and slightly spatulate at the tips. Teeth do not extend on to the descending process of the premaxilla nor the ascending process of the dentary (Fig. 7, 8, 9). Removal of the teeth reveals seven rows on the premaxilla and eight to ten rows on the dentary

(N = 10). In this species two bands or pads of tooth tips are exposed on the outer margins of the upper and lower jaws. All the remaining portions of the teeth are embedded in soft tissue.

The teeth of *C. ornatissimus* are all of approximately the same length, numerous and massed toward the anterior as a large pad of teeth. All of the teeth are villiform, long, slightly hooked, and slightly spatulate at their tips (Fig. 7, 8, 9). The teeth do not lie on the descending process of the premaxilla nor the ascending process of the dentary. There are seven to eight rows of teeth on the premaxilla and 11–13 rows on the dentary (N = 10). The tips of the teeth in the upper and lower jaws protrude through the tissue that surrounds them.

The dentitions of juvenile individuals of all of the above species are compared regarding tooth shape and distribution and found not to differ from the adults. These teeth are not illustrated.

The pharyngeal teeth from all of the species are villiform, slightly hooked at their tips, mounted on bony pedestals, have a pulp cavity, and are arranged transversely in the bucco-pharyngeal cavity. Upper pharyngeal teeth are borne on pharyngobranchials II, III and IV. Pharyngobranchial II is small in all cases and bears few teeth. The lower pharyngeal teeth are distributed in a (hook)? shaped pattern on ceratobranchial V (Fig. 10 in Motta 1982). Replacement teeth are often visible beside functional pharyngeal teeth (Motta 1982). The upper teeth are longer than the lower teeth in all species.

One specimen of each of the species had the following numbers of upper and lower pharyngeal teeth: *C. miliaris* (TL = 13.1 cm), 80/100; *C. auriga* (TL = 17 cm), 60/80; *C. trifascialis* (TL = 12.3 cm), 60–80/20; *C. unimaculatus* (TL = 13.5 cm), 60/50; *C. trifasciatus* (TL = 12.8 cm), 46/22; and *C. ornatissimus* (TL = 12.5 cm), 40/30.

Vomerine teeth are found in *C. miliaris* and *C. auriga* and not in *C. trifasciatus*, *C. ornatissimus*, *C. trifascialis*, or *C. unimaculatus*.

In the former two there is a V shaped pad of teeth on the ventral side of the vomer. The teeth are numerous and all villiform, being slightly hooked at their tips. The teeth lie in a pad of tissue with only their tips protruding.

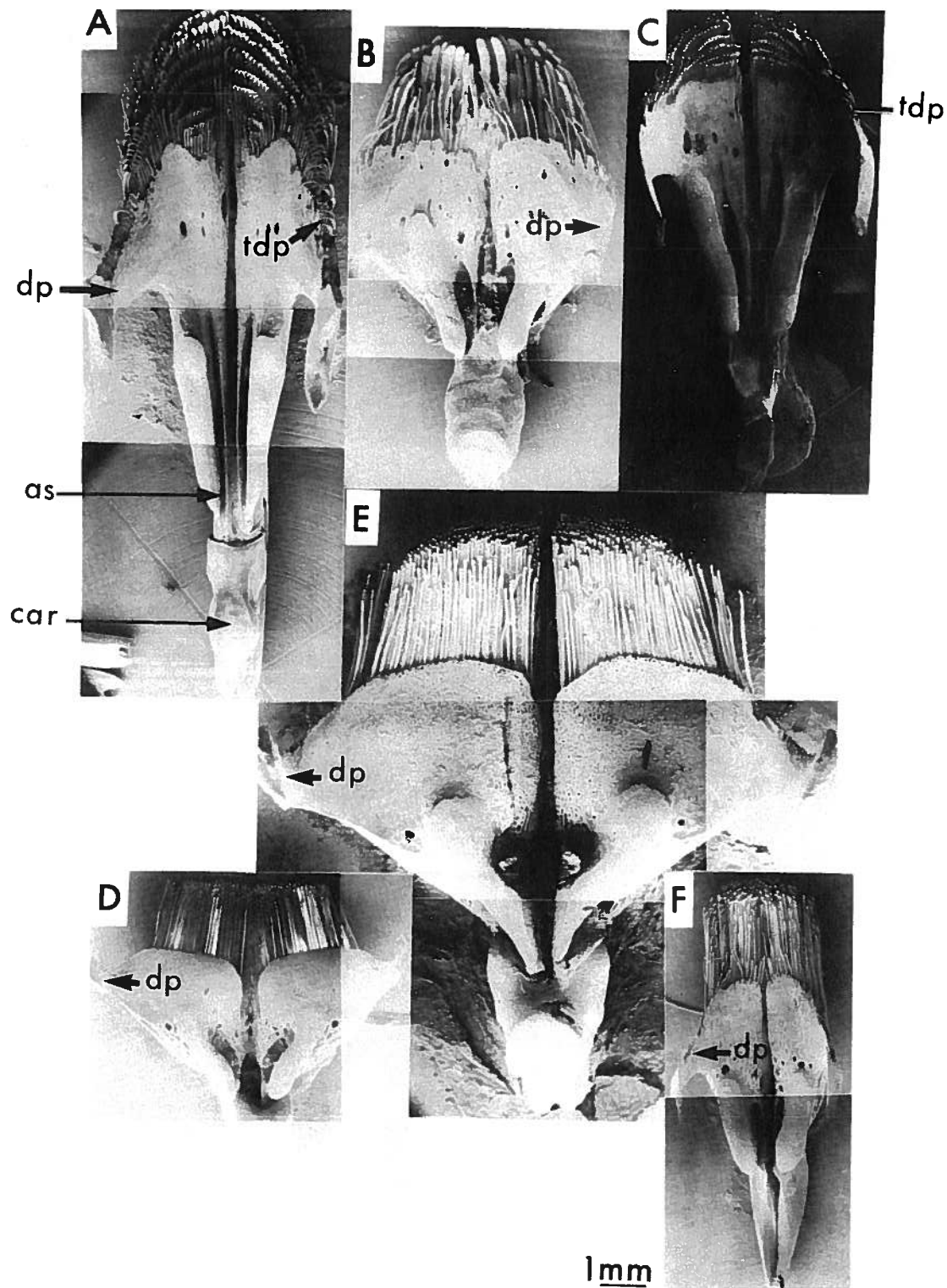
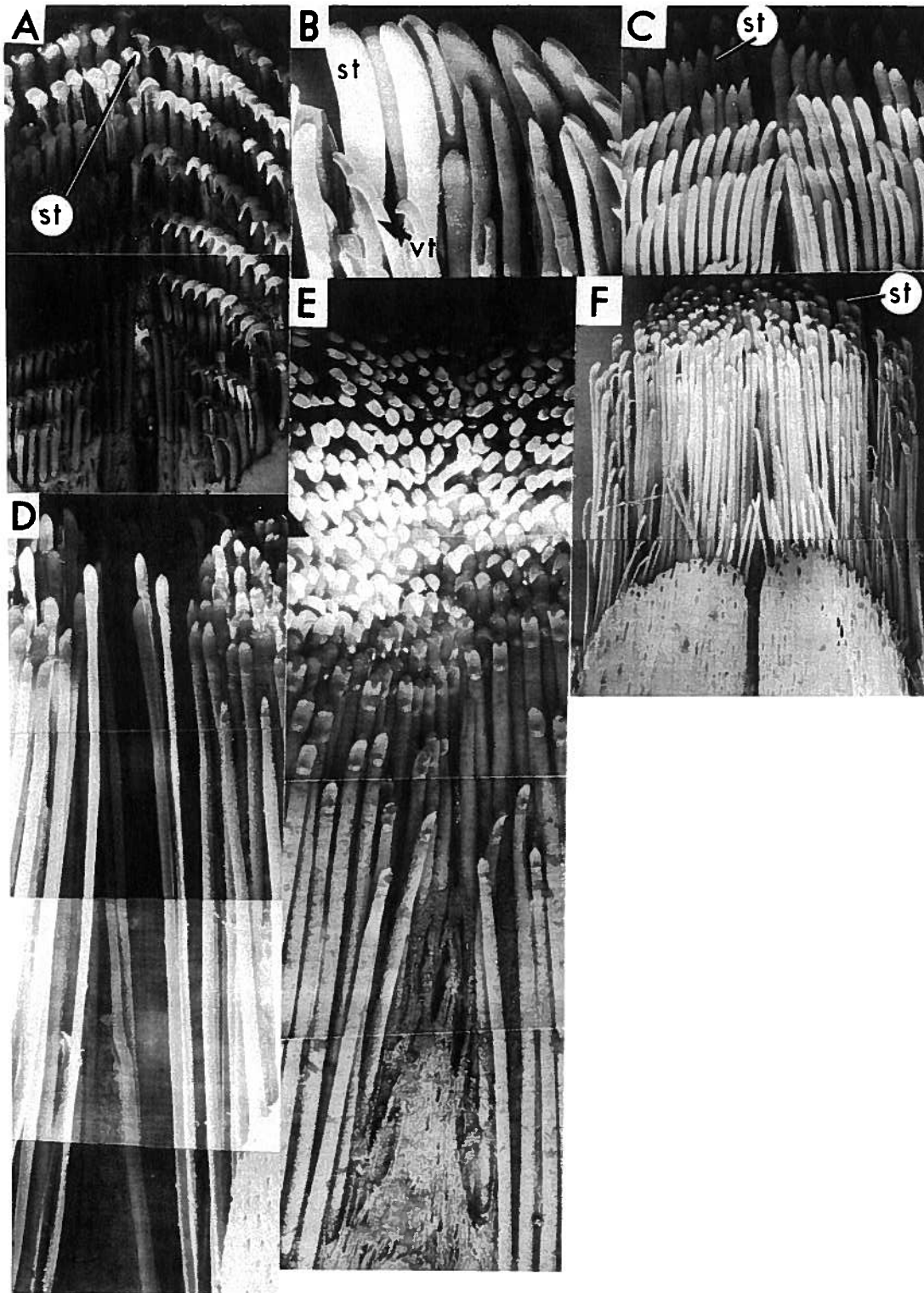


Fig. 7. Ventral view of premaxillae from six species of butterflyfishes: A – *C. auriga* TL 14.2, SL 12.2 cm; B – *C. unimaculatus* TL 12.0, SL 10.2 cm; C – *C. miliaris* TL 14.5, SL 12.3 cm; D – *C. trifasciatus* TL 10.8, SL 9.4 cm; E – *C. ornatissimus* TL 17, SL 14.4 cm; F – *C. trifascialis* TL 12.3, SL 10.2 cm. *C. miliaris* teeth with glue among them and rostral cartilage missing on *C. trifascialis* (as – ascending process of premaxilla, dp – descending process of premaxilla, car – rostral cartilage, tdp – teeth on descending process).



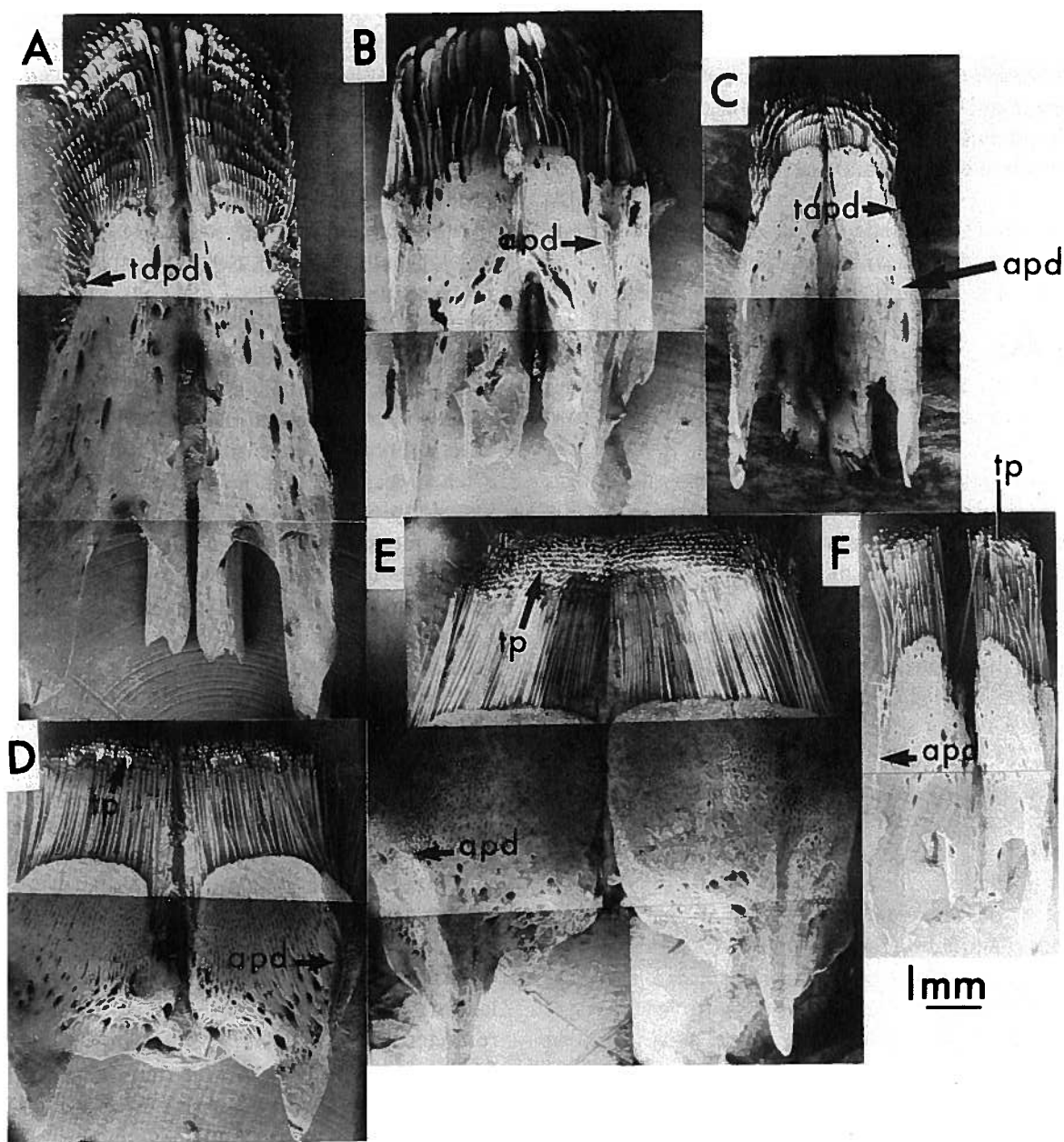


Fig. 9. Dorsal view of dentaries from six species of butterflyfishes: A – *C. auriga*, TL 14.2, SL 12.2 cm; B – *C. unimaculatus* TL 12.0, SL 10.2 cm; C – *C. miliaris* TL 14.5, SL 12.3 cm; D – *C. trifasciatus* TL 12.1, SL 10.7 cm; E – *C. ornatissimus* TL 17.0, SL 14.4 cm; F – *C. trifascialis* TL 12.3, SL 10.2 cm. Symphysis of latter partly disarticulated (apd – ascending process of dentary, taped – teeth on descending process of dentary, tp – tooth pad).



Fig. 8. Enlarged view of symphyseal teeth from six species of butterflyfishes: A – *C. auriga* premaxilla; B – *C. unimaculatus* premaxilla; C – *C. miliaris* dentary; D – *C. trifasciatus* dentary; E – *C. ornatissimus* dentary; F – *C. trifascialis* premaxilla (st – spatulate teeth, vt – representative villiform teeth).

The gill rakers of the various species are illustrated in Figure 10. Those of *C. auriga*, *C. miliaris*, *C. trifascialis* and *C. unimaculatus* are relatively longer and the first three bear spines on the rakers. The gill rakers of *C. trifasciatus* and *C. ornatissimus* are relatively short and lack spines.

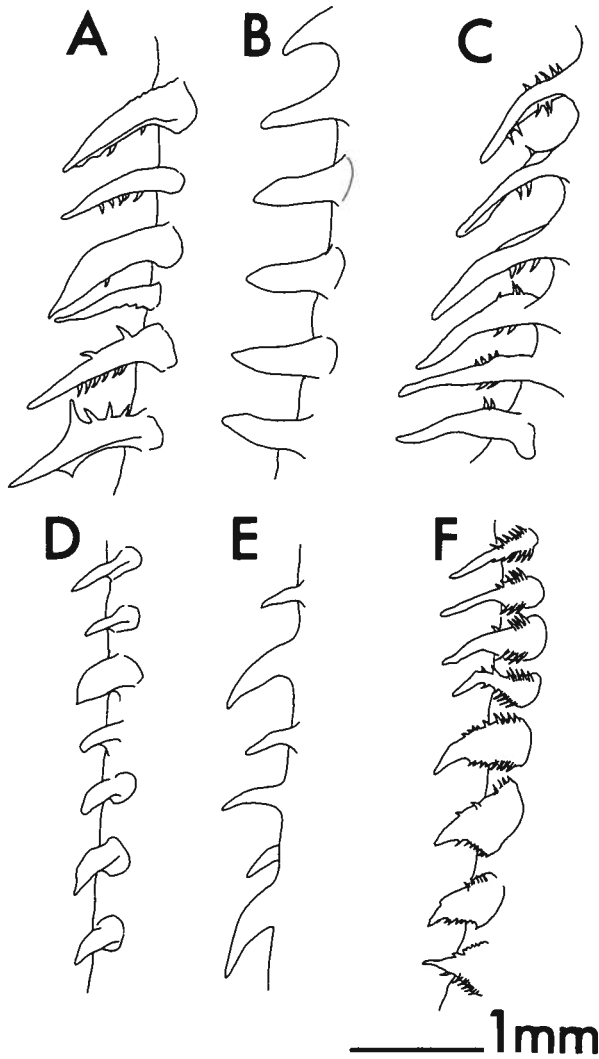


Fig. 10. Gill rakers from the first gill arch, approximately midway along first ceretobranchial of left side: A - *C. auriga* SL 13.0 cm; B - *C. unimaculatus* SL 11.4 cm; C - *C. miliaris* SL 11.1 cm; D - *C. trifasciatus* SL 10.8 cm; E - *C. ornatissimus* SL 10.0 cm; F - *C. trifascialis* SL 9.3 cm.

Discussion

Mouth shape, degree of jaw protrusion and protuberance

The mechanics of jaw opening, protrusion, closure of the protruded mouth, and retraction of the jaws for a model butterflyfish, *Chaetodon miliaris*, have been described (Motta 1982) as well as a thorough review of the mechanics and functions of jaw protrusion in teleost fishes (Motta 1984a). Jaw protrusion involves an anterior, anteroventral or anterodorsal movement of the upper jaw and a pivoting of the lower jaw so that the entire mouth is moved anteriorly or anteroventrally (Motta 1982).

The species studied here can extend their jaws anteriorly 6 to 12% of the head length (Fig. 2). These measurements lie within the lower half of the range for acanthopterygian fishes which can extend their head lengths by 7–33% (Lauder & Liem 1981). Head extension, as measured here, can arise by at least two mechanisms: (1) by pivoting of the lower jaw and pronounced protrusion of the upper jaw, e.g., *C. miliaris*. The closer to the longitudinal axis of the fish the protruded mouth lies the greatest anterior increase it will effect; (2) by simply pivoting the lower jaw even with little or no upper jaw protrusion e.g., *C. ornatissimus*. Again, the closer to the longitudinal axis it lies when depressed the greatest increase in head length effected. The head profiles of *C. trifasciatus*, *C. ornatissimus* and *C. trifascialis* are somewhat similar when the mouth is closed and the upper jaws retracted (Fig. 1). The open mouths of *C. trifasciatus* and *C. ornatissimus* are shovel-shaped and anterodorsally directed (Fig. 1). Both the field observations and the manipulation experiments reveal that the two species accomplish similar mouth profiles by a reduction of upper jaw protrusion. Both species have premaxillae that protrude only slightly, yet *C. ornatissimus* which has a premaxilla of moderate length (Fig. 4), anteriorly extends its jaw slightly more than any other species (Fig. 2). Extension is brought about by a relatively long dentary (Fig. 5) that pivots through a slightly greater angle (Fig. 3) to lie on the longitudinal axis of the fish. *C. trifasciatus* has a shorter premaxilla

(Fig. 4) which protrudes even less than that of *C. ornatissimus* (Fig. 1), the shortest dentary (Fig. 5) and a mouth that pivots through a slightly smaller angle than *C. ornatissimus* (Fig. 3) such that an asymmetrical mouth is formed when the lower jaw is depressed.

C. trifascialis has an anteroventrally directed, prognathous, forceps-like mouth when protruded (Fig. 1). It has a greater angle of jaw depression than most of the other species (Fig. 3) and its premaxilla and dentary length is among the shortest examined (Fig. 4, 5). However, the increase in head length is among the shortest. The short premaxilla and dentary, slightly greater angle of jaw protrusion and the fact that the protruded jaw lies below the longitudinal axis of the fish and not on it (Fig. 1) result in the little apparent increase in head length (Fig. 2).

Even though the premaxillae (Fig. 4) and dentaries (Fig. 5) of *C. auriga*, *C. miliaris* and *C. unimaculatus* are significantly different in length they have a relatively protrusible premaxillae (Fig. 1) along with jaws that pivot through the same angle (Fig. 3) to equally extend the head length (Fig. 2) that results in an anteroventrally directed protruded jaw in each case. *C. auriga* has the longest premaxilla and dentary resulting in its extremely prognathous unprotruded mouth.

Therefore in all of these species the degree of jaw protrusion and anterior increase in head length are not simply related. Other workers have found a positive correlation between the length of the ascending process of the premaxilla and the degree of jaw protrusion (Delsman 1925, Gregory 1933, Eaton 1935, Schaeffer & Rosen 1961, Dutta 1968, 1979, Dutta & Chen 1983, Emery 1973), or the latter with the length of the ligamentous attachments and the rotational freedom of the premaxilla (Liem 1967) or the length of the mandible (Liem 1970). In the butterflyfishes studied the anterior increase in head length is complexly related to the length of the upper and lower jaw and the angle through which they pivot during jaw opening, and jaw protrusion per se, which is greatly reduced in *C. ornatissimus* and *C. trifasciatus*, does not show clear relationships with premaxilla or dentary length or angle of jaw depression.

Mouth size, shape and jaw kinetics

C. ornatissimus, *C. trifasciatus* and *C. unimaculatus* have the widest open mouths respectively and also the greatest internal heights. *C. auriga*, *C. miliaris* and *C. trifascialis* have the smallest open mouths (Fig. 6).

C. ornatissimus, an obligate hard coral browser, uses its lower jaw almost exclusively to scrape coral surfaces, removing from 16 to 50 polyps of *Porites* coral per bite. Its bites are relatively slow, taking approximately 2–3 bites per second on one area of the coral before moving to another (Motta 1980, Motta & Reese in preparation). The wide lower jaw, steeper head profile, reduced premaxillary protrusion, and greater angle of jaw depression allow the lower jaw to be closely applied to relatively large areas on the coral surface. Reduction in the upper jaw protrusion in this species and *C. trifasciatus* prevents the upper jaw from interfering with the scraping lower jaw.

C. trifasciatus is also an obligate hard coral browser. Using faster bites than the former species, it both scrapes coral surfaces with its lower jaw and nips at individual polyps with its upper and lower jaws. When the effects of feeding are visible, from 1 to 10 polyps on *Acropora* and *Porites* corals are seen to be removed per bite (Motta 1980, Motta & Reese in preparation). Its jaw is not as kinetic or as wide as *C. ornatissimus* but the relatively wide mouth presents a large scraping and nipping surface. Observations show that its asymmetrical, anterodorsally directed mouth and reduced upper jaw protrusion also permit it to scrape coral surfaces.

C. unimaculatus is a facultative soft and hard coral grazer that utilizes rapid jaw protrusion to remove entire polyps with their calices or pieces of soft coral of 1 cm in diameter per bite (Motta 1980, Motta & Reese in preparation). Its large robust mouth (Burgess 1978) of relatively large internal diameter allows it to withstand the very vigorous lunges it makes on the corals and get a purchase on the coral surfaces.

C. auriga, a benthic omnivore that tears its prey uses rapid jaw protrusion when feeding on its preferred polychaete worms, yet does not use protrusion

sion when nipping at algae (Motta 1980, Motta & Reese in preparation). Small mouths are suited for taking small food items (Gregory 1933, Hiatt & Strasburg 1960, Lagler et al. 1962) and are often associated with fishes that feed on plankton, plant food, or small benthos (Aleev 1969). *C. auriga* has the most prognathous mouth which is relatively small in internal width. This permits probing with the coral rubble for its small benthic prey items. Projecting tubular mouths are often associated with probing in small crevices (Lagler et al. 1962).

The small, prognathous, forceps-like protruded mouth of *C. trifascialis* is suited for its habit of picking individual or few coral polyps at a time from within the branches of *Acropora* corals. Visual observations (PJM) reveal that this obligate hard coral browser utilizes jaw protrusion of variable speed (Motta 1980, Motta & Reese in preparation).

C. miliaris is an inertial suction planktonic feeder that uses very rapid jaw protrusion in the majority of its bites (Motta 1980, 1982, Motta & Reese in preparation). The protruded mouth is tubular, laterally enclosed and relatively small in diameter. Such a mouth has been shown to be favorable for suction feeding (Alexander 1974, Osse 1969, Pietsch 1978, Lauder 1979).

Jaw, vomerine and pharyngeal dentitions

Burgess (1978) described all butterflyfishes teeth as being similar, slender, long, flattened and slightly curved at their tips. This is not entirely correct. The teeth examined in this study vary considerably interspecifically. Two of Burgess' three basic patterns of tooth arrangement are confirmed; series of discrete rows were found in *C. miliaris*, *C. auriga*, and *C. unimaculatus* and a single anterior band or pad of teeth in *C. trifasciatus*, *C. trifascialis*, and *C. ornatissimus*. The tooth row counts for *C. miliaris*, *C. auriga*, and *C. ornatissimus* given by Burgess are not confirmed.

Jaw tooth attachment, replacement and growth has been described for *C. miliaris* (Motta 1984b). The teeth of the butterflyfishes reported on here are similar to that of *C. miliaris* in being composed of a cap, shaft and pulp cavity, and being articula-

ted to attachment bone pedestals by a collagenous annular ligament. The teeth of *C. miliaris* and *C. kleinii* (Motta 1980) both zooplanktivores, are similar and could be classified as the 'typical butterflyfish tooth types', according to Burgess (1978) (Fig. 7, 8, 9).

Plankton feeding fishes often have few or no jaw teeth (Suyehiro 1942, Lagler et al. 1962, Davis & Birdsong 1973, Alexander 1974) as teeth are thought to interfere with suction and ingestion of prey (Alexander 1974), however small and numerous teeth when present, are believed to help prevent planktonic prey from escaping (Alexander 1967). *C. miliaris* and *C. kleinii* (Motta 1980) have dentitions somewhat reduced in number (6 upper rows, 6–7 lower rows) correlating with their planktivorous feeding behavior. The relatively few jaw teeth also permits foraging on the benthos. They also have mouths encircled with teeth that lie on the descending processes of the premaxillae, and on the ascending processes of the dentaries as well as on the bodies of these bones. This may reduce the chance of prey escape from the mouth.

Foraging in the water column is generally associated with fishes that have their mouths directed straight ahead or even upward when protruded (Jones 1968, Aleev 1969, Hobson 1975, Chao & Musick 1977), have a more lunate form of caudal fin, more falciform type of pectoral fin, tendency towards a more terrate body outline, narrow and more streamlined, including a sharper profile of the nose and head, a relatively large eye in proportion to the head, finer dentition on the jaws and pharyngeal plates, longer and more numerous gill rakers, reduced ossification of the jaw and head bones and longer premaxillary ascending processes (Davis & Birdsong 1973). Within the acanthurids studied by Jones (1968) the midwater dwellers are among the most elongate species of their respective genera. These trends are not realized in *C. miliaris* although there do appear to be some modifications such as the small tubular mouth, rapid jaw protrusion (Motta 1982), modified dentition and relatively long gill rakers. This may be due to at least three non-mutually exclusive reasons. Deep bodied, spinous forms such as found in chaetodontids, may be an anti-predator adaptation (Hobson

& Chess 1978), planktivory may be a recent advent in the species as is described for *Acanthurus thompsoni* (Jones 1968), and/or the species maintains a morphology between that suited for planktivory and benthic feeding. At least the latter two appear to be true for this species (Ralson 1981, Motta 1984b).

The numerous tooth rows of *C. auriga* (8–11 upper, 9–12 lower) that encircle the mouth more than in any other species (Fig. 5, 7, 9) and the large lateral gap in the mouth permits the gripping of its prey with almost any part of the mouth. These teeth are more hooked at their tips than those of *C. miliaris*, allowing a better grip on the food items. The rapid backwards or sideways jerk that often accompanies its feeding on sessile organisms helps to tear the animal tissue (Motta 1980, Motta & Reese in preparation). The inwardly curved teeth of the common sole, *Solea solea*, are similarly suited for seizing the polychaete worms that they feed on (Yazdani 1969).

C. miliaris and *C. auriga* both have vomerine teeth, a greater number of pharyngeal teeth than any of the other species, and gill rakers that are long and branched (Fig. 10). Long, closely spaced gill rakers with better developed spines (lateral processes) are found in fishes that strain or filter food from the water (Lagler et al. 1962, Chao & Musick 1977) and are used to retain prey and to act as a sieve, separating food from other material (Alexander 1974, Lagler et al. 1962). Such physical limitations as gill raker size, dentition, mouth shape and size are known to affect patterns of food selection in fishes (Werner 1974, Werner & Hall 1976, Werner et al. 1977, Eggers 1977, Stoner 1980, Laur & Ebeling 1983). In *C. miliaris* these structures most likely help prevent the escape of plankton from the mouth or gills. In *C. auriga* they may be important in trapping and retaining the soft-bodied prey and preventing the organisms that are picked from the sand and rubble from being lost through the gills.

Pharyngeal teeth are used for pharyngeal manipulation and transport of food (Lauder 1983). Both of these species ingest relatively intact prey (plankters and pieces of polychaete worms) compared to the masticated portions of coral polyps in the other

species, so perhaps manipulation of the prey is more necessary in these species.

C. unimaculatus is a grazing chaetodontid, removing portions of the calcareous skeleton along with the soft tissue. Lunging vigorously at the corals it utilizes its stout peripheral teeth (Fig. 8) to break off the corallite. Examination of its gut reveals large quantities of calcareous coral material. Its relatively large and robust gill rakers may prevent coralline material from passing into the delicate gill filaments.

The teeth of *C. trifascialis* are few in number, relatively long, and massed towards the anterior part of the jaw bone as a single pad (Fig. 7, 8, 9). Hiatt & Strasburg (1960) correctly described these teeth and said they were especially suited for feeding exclusively on coral polyps. More correctly, the teeth, along with the jaws, are apparently suited for individually picking small items in a forceps-like manner, items such as coral polyps. The spinous gill rakers may prevent loss of the small polyp fragments through the gills (Fig. 10).

The numerous teeth on the lower jaws of *C. ornatissimus* (7–8 upper, 11–13 lower) and *C. trifasciatus* (7 upper, 8–10 lower) are primarily used to scrape coral surfaces. The former uses the lower jaw almost exclusively and has more teeth on the lower jaw and a wider jaw (unpublished data) in terms of its body length than the latter.

The teeth of these two species are arranged as large pads on the upper and lower jaws. These very long, flexible teeth (Fig. 7, 8, 9) conform to the irregularities of the coral surface, effectively scraping off coral tissue in a way such as that described for *Plecostomus* (Alexander 1974) and for *Girella*, *Microspathodon*, and *Ophioblennius* (Norris & Prescott 1959). This dentition is so effective it can remove coral tissue down to a depth of approximately 1 mm within the corallites of *Porites lobata*, and in *C. ornatissimus* 16–50 polyps per bite are removed in such a manner (Motta 1980, Motta & Reese in preparation).

The pharyngeal teeth are fewest in number and the gill rakers the shortest on *C. ornatissimus* and *C. trifasciatus*. The coral tissue (and mucus) that is removed is so masticated and therefore apparently rapidly digested, that gut content analysis alone on

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C. ornatissimus (Hobson 1974, Reese 1977) has repeatedly failed to identify anything but coral mucus. In these two scrapers the masticated mass of coral tissue and mucus that results from the scraping behavior, might not require as much manipulation by the pharyngeal teeth for swallowing. However, the relationship between pharyngeal tooth numbers and prey is not clear in these fishes.

The feeding mechanisms of the latter two species may not require long, spinous gill rakers. Scraping the coral surfaces may produce a bolus of tissue and mucus that is relatively large and unlikely to pass between the gill rakers. Greenwood (1974) postulated a similar hypothesis for cichlid phytoplankton feeders that entangle their prey in mucus boli.

A preliminary analysis of the inorganic chemical composition of these teeth revealed concentrations of iron compounds on the tooth tips. A general trend indicates that those species feeding on hard surfaces have more iron on the tooth tips, compared to such species as *C. miliaris* and *C. auriga* that feed on soft-bodied prey (Motta 1980). Shellis & Berkovitz (1976) and Preuschoft et al. (1974) believe that the iron inhibits the initiation of cracks in the underlying layers thereby hardening the teeth. These data add weight to the morphological adaptations for feeding observed in these dentitions and further research in this area is underway.

Harmelin-Vivien & Bouchon-Navaro (1983) correlated a global repletion index based on gut weight and weight of the entire fish with diet for five of the six species investigated here (*C. miliaris* excluded). They found that coral feeders have among the proportionally heaviest guts due to the fact that physiologically coral represents more of a vegetable food than an animal food owing to the large amount of symbiotic algae. *C. auriga* with its mixed diet had a proportionally lighter gut and *Hemitaurichthys polylepis* a planktivore with a diet similar to *C. miliaris* had among the lightest guts.

Adaptations of the jaws

The study of adaptations involves the study of form and function in the laboratory and the synerg in the field. The latter is the link between the biological role and the selection force (Bock 1980). One

method of determining the relation between form and function is the inductive method which is based on a comparison of closely related recent organisms (Dullemeijer & Barel 1977). A combination of form and function constitutes a faculty. A faculty may have one or more biological roles which can only be ascertained by observation of the organism living freely in its natural environment (Bock 1980). Utilizing this synthetic approach, which Bock (1980) considers to be the only valid method for studying adaptations, and assuming that the primary selection force governing the evolution of the jaws is one that increases the energy acquired compared to the energy required, then the examination of these six species of butterflyfishes reveals a variety of feeding adaptations (Table 1).

The dentitions of *C. miliaris* and *C. auriga* allow feeding on a great variety of food items. However, the jaws are adapted for their preferred feeding modes. The small, laterally enclosed tubular mouth, rapid protrusion, reduced jaw dentition, long and spinous gill rakers and numerous pharyngeal and vomerine teeth make *C. miliaris* an efficient planktivore. The prognathous mouth encircled with numerous hooked teeth, the spinous gill rakers and numerous pharyngeal and vomerine teeth suit *C. auriga* for tearing pieces off sessile organisms, picking small prey items of the benthos, and probing in crevices, more so than for biting very small items such as coral polyps from within callices.

The prognathous robust mouth and stout, hardened peripheral teeth of *C. unimaculatus* make it an efficient grazer. These plus its habit of lunging at its prey permit it to feed on a variety of soft and hard corals.

The relatively wide jaws, reduced premaxillary protrusion, modified tooth pads, flat head profile and anterodorsally directed gape of *C. ornatissimus* are adapted for scraping coral surfaces or in the case of *C. trifasciatus* for both scraping and nipping at coral surfaces. These species not only have similar morphologies, but diets as well (Motta 1980, Motta & Reese in preparation).

C. trifascialis with its small, prognathous, forceps-like protruded mouth, relatively long gill

Table 1. Summary of feeding habits and adaptations in six species of butterflyfishes. See text for thorough description.

	<i>C. miliaris</i>	<i>C. auriga</i>	<i>C. unimaculatus</i>	<i>C. trifascialis</i>	<i>C. ornaticus</i>	<i>C. trifasciatus</i>
Feeding behavior (Motta & Reese, in preparation)	Opportunistic zooplanktivore that uses high speed inertial suction feeding.	Benthic omnivore feeding on noncoralline and coralline invertebrates. Probes in rubble for prey. Grasps prey with front or sides of jaw.	Facultative soft and hard coral grazer that lunges at the coral surface.	Obligate hard coral browser that nips at individual polyps.	Obligate hard coral browser that almost exclusively scrapes corals with its lower jaws.	Obligate hard coral browser that both scrapes corals with its lower jaw and nips with both jaws.
Effect on substrate (Motta & Reese, in preparation)		Tears noncoralline prey loose.	Removes coral skeleton along with polyps.	Removes 1 polyp per bite.	Removes 16–50 polyps per bite.	Removes 3–10 polyps per bite.
Mouth direction, shape and size when maximally open	Anteroventrally directed, prognathous, tubular, laterally enclosed and small.	Anteroventrally directed, prognathous, lateral gap, relatively small.	Anteroventrally directed, somewhat prognathous, laterally enclosed, very robust, relatively large.	Anteroventrally directed, forceps-like, lateral gap, prognathous, small.	Anterodorsally directed gape, shovel-like, large.	Anterodorsally directed, shovel-like, large.
Upper jaw protrusion.	Pronounced, variable speed and extent.	Pronounced, protrudes jaw when lunging at polychaete worms, no lunges or protrusion on algae.	Some protrusion.	Pronounced, of variable speed and extent.	Reduced protrusion results in shovel-like mouth.	Reduced protrusion results in shovel-like mouth.
Premaxilla.	'Typical' in form, relatively long ascending and descending process.	Long ascending process.	Large and robust.	Relatively small with relatively long ascending and descending processes.	Relatively large and broad with short ascending process.	Relatively small and broad with short ascending process.
Jaw dentition (# rows in pmx/ # rows in dentary)	Reduced in number, recurved teeth encircle mouth (6/6–7)	Numerous rows of very recurved teeth that encircle mouth (9–11/9–12)	Massive spatulate shaped peripheral teeth, do not encircle mouth (5–8/5–8)	Teeth massed toward anterior to form a pad (5–6/5–6)	Jaw teeth form pads, lower pad larger than upper, do not encircle mouth (7–8/11–13)	Jaw teeth form a pad, lower pad larger than upper, do not encircle mouth (7/8–10)
Pharyngeal teeth (upper/lower)	80/100	60/80	60/50	60–80/20	40/30	46/22
Gill rakers	Relatively long, has spines	Relatively long, has spines	Moderate length, no spines	Moderate length, has spines	Relatively short, no spines	Relatively short, no spines
Global repletion index of gut $R = I/W \times 100$ I = mean weight of gut; W = mean weight of specimens (Harmelin-Vivien & Bouchon-Navaro 1983)	5.2	5.8	8.5	5.5	10.2	8.0

rakers, numerous pharyngeal teeth, and anteriorly massed jaw teeth make it adapted for probing within crevices and nipping at individual polyps.

Upon close examination it appears that the majority of these interspecific structural differences are relatively simple differences in the size and

shape of certain elements (elements, sensu Dullemeijer 1974). Skeletal elements can be classified as either dominant or subordinate. The former influence other elements and have little plasticity and include such things as the eye of fishes and parts of the pharyngeal jaw apparatus (Dutta 1968, Dutta &

Chen 1983, Dullemeijer 1974, Witte & Barel 1976, Dullemeijer & Barel 1977). Subordinate elements are characterized by high plasticity and a function demanded by the surroundings (Dullemeijer 1974, Dullemeijer & Barel 1977). Dullemeijer considers such things as the lower jaw, maxilla and ectopterygoid as examples of subordinate elements. Suggesting that the premaxilla be included in this category and based upon the aforementioned properties of subordinate elements perhaps one could hypothesize that such elements evolve relatively rapidly permitting a radiation in feeding adaptations. Greenwood (1974) found that generally jaw form is relatively constant throughout a flock of African cichlid fishes, what interspecific differences there are can, in most instances, be attributed to the results of allometric growth. Differences such as the length of the jaws and its processes, length of the teeth and their curvature, or simple alterations in the growth pattern of a generalized syncranial type, and proportional myological change account for a great deal of the morphological specializations. The simplicity of the mechanisms could explain the rapidity of adaptive modifications of the African cichlids (Greenwood 1974).

In a study of the pharyngeal apparatus of African cichlids Liem & Osse (1975) found that the evolution of this exceedingly efficient precision instrument was governed by fundamental functional changes such as accelerated growth rates of certain parts, shifts of muscle attachments and alterations in the shape, size and position of certain articular surfaces. All of these changes are governed by simple morphogenetic factors and can therefore, they argue, evolve very rapidly. Within the Nandidae a variety of adaptive patterns of the jaw are correlated with differences in the relative growth of the bones and in the degree of ossification of certain cartilages and connective tissue membranes. It is again believed that relatively minor genetic changes might govern these changes (Liem 1970).

Within the chaetodontids studied relatively simple morphological changes have permitted a radiation in feeding morphs.

Premaxilla length has increased in *C. miliaris* where it is primarily concerned with protrusion and

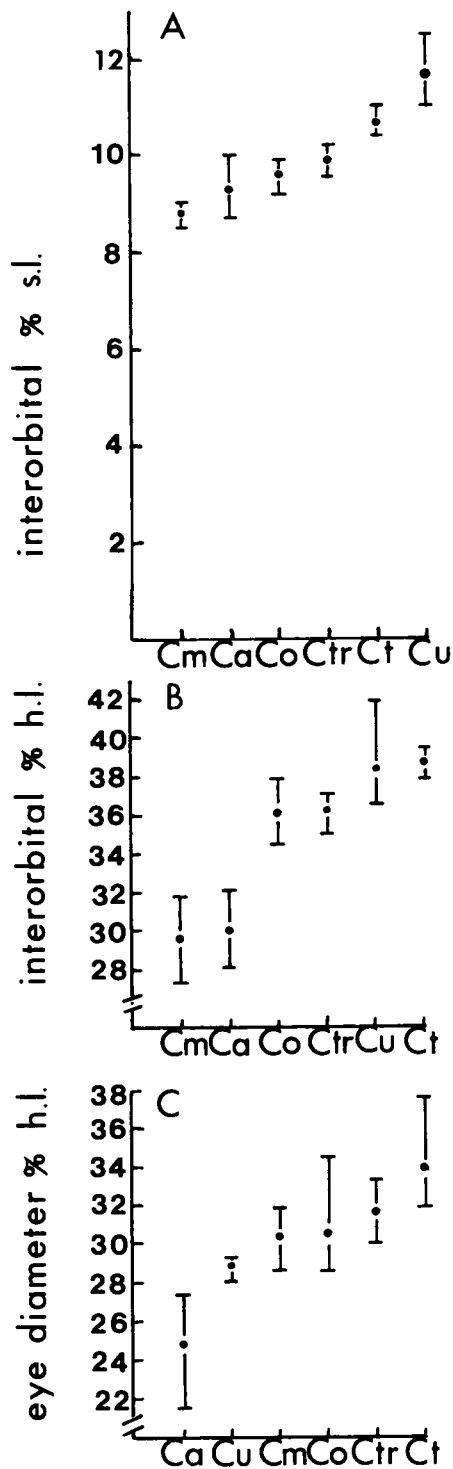
suction planktonic feeding, whereas in *C. auriga* it forms a very prognathous mouth that is utilized for probing in crevices and protrusion for sudden grasping of elusive prey (see following section).

In the scraping and nipping *C. trifasciatus* the premaxilla length is reduced to permit efficient foraging. In this species and *C. ornatissimus* the length of the ascending process of the premaxilla is greatly reduced resulting in reduced premaxillary protrusion and an asymmetrical mouth that permits efficient scraping with the lower jaw.

Of the three basic tooth arrangements, series of discreet rows is the most common within the Chaetodontidae (Burgess 1978). Assuming that this is the ancestral tooth type, a variety of arrangements have arisen. Pads of teeth form efficient scraping surfaces in *C. ornatissimus* and *C. trifasciatus*, anteriorly massed teeth in *C. trifascialis* contribute to the forceps-like mouth, and sharply recurved teeth in distinct rows form efficient gripping surfaces in *C. auriga* and *C. miliaris*.

In five of the species it is differences in length and distribution of the teeth that account for the dentition variability. The basic tooth form is long, slender, recurved and flattened at the tip. *C. unimaculatus* possesses the only extremely different morph with its spatulate peripheral teeth (finding similar dentitions in the juveniles of all of these species precludes the possibility of ontogenetic or environmentally induced change in tooth form). Greenwood (1974) had similar findings with African cichlid dentitions. Apart from differences in the jaw bones, Burgess (1978) found the skeletons of various butterflyfish species to be essentially similar. Dullemeijer & Barel (1977) argue that natural selection should affect the variability of dominant components as subordinate ones have to follow the dominant component, when this does not happen the result is an abnormal or lethal ontogeny. However, it appears to me that when the variability of the subordinate component does not affect the dominant one, then natural selection can operate on the subordinate. As an example, the premaxilla and dentary lengths of these butterflyfishes vary greatly, in part being directly related to the protuberosity of the mouth, yet these subordinate elements appear not to duly influence close

dominant components such as the eye. Interorbital width as a percentage of standard length and head length is not related to premaxilla and dentary



length, nor to the relative protuberosity of the mouth (Fig. 4, 5, 11); similarly eye diameter is unrelated (Fig. 11). However, in some cases the subordinate elements might come to influence dominant components. The very long premaxilla and dentary of the long-nosed butterflyfishes *Forcipiger longirostris* and *F. flavissimus* are associated with a jaw protrusion mechanism not 'typical' of other butterflyfishes (Motta 1982). Manipulation experiments reveal that the long-nosed butterflyfishes protrude both the upper and lower jaws by pivoting the entire suspensorium in a sagittal plane. This different mechanism demands a unique osteology and myology in the suspensorium (in preparation). Possibly correlated with the very prognathous mouth, the interorbital width is significantly lower than the other six butterflyfishes species (*F. longirostris* $\bar{x} = 6.8$, $N = 7$, *F. flavissimus* $\bar{x} = 6.0$, $N = 4$). Therefore structural elements such as the premaxilla, dentary, maxilla and teeth have undergone relatively simple changes during the evolution of the different species; these changes which would probably be relatively rapid in the evolutionary time scale, have led to multiple adaptive pathways (Bock 1959) in the feeding structures.

Repertoire of jaw movements

The earlier studies on teleost feeding mechanisms considered them as preprogrammed (stereotyped) motor activities that may not respond to peripheral sensory feedback mechanisms (Liem 1978). Only recently, mostly through electromyographic studies, have researchers shown that some fishes have a repertoire of muscle actions and jaw movements that depends on prey type and/or location (Elshoud-Oldenhavé & Osse 1976, Liem 1978, 1979, 1980, Lauder & Liem 1980, Lauder 1981, Rand & Lauder 1981, Grobecker 1983). The majority of

← Fig. 11. A - interorbital width as a percent of standard length; B - interorbital width as a percent of head length; C - eye diameter as a percent of head length. Mean and ranges of adult specimens indicated, see text for further explanation (Ct - *Chaetodon trifasciatus* $N = 3$, Cu - *C. unimaculatus* $N = 3$, Ctr - *C. trifasciatus* $N = 3$, Co - *C. ornatissimus* $N = 4$, Ca - *C. auriga* $N = 4$, Cm - *C. miliaris* $N = 3$).

these studies are confined to aquaria observations with the fish feeding on artificial prey. The naturalistic observations of butterflyfishes is sufficient to elucidate a repertoire of jaw movements in most of the species. *C. miliaris*, for example, exhibits at least four planktonic feeding behaviors, some involving protrusion and others not (Motta 1980, Motta & Reese in preparation). In addition the speed of jaw protrusion varies visibly among bites. *C. trifascialis* can likewise use fast protrusion or slow probing protrusion bites; *C. auriga* utilizes rapid protrusion bites when trying to capture polychaete worms before they retreat but simply uses bites without protrusion when feeding on algae (Motta 1980, Motta & Reese in preparation). Intuitively, the species that appears to have the least variability in jaw feeding movements is *C. ornatissimus* which feeds exclusively by scraping hard coral surfaces with its mandible. Perhaps the relative lack of variability in its feeding behavior places little demand for a modulated repertoire of feeding patterns. Therefore, protrusion is not an all or none phenomenon. In these species there exists a continuum regarding the degree and speed of jaw protrusion, and a range of foraging behaviors that are suited for the particular prey items and situations. High speed cine analysis would probably reveal an even greater repertoire of jaw movements. Based on the degree of specialization of the pharyngeal jaw apparatus Kaufman & Liem (1982) postulate that feeding versatility was a chief factor in shaping the refuging strategies (territorial behavior, schooling, etc.) in the labroids (Pomacentridae, Cichlidae, Embiotocidae, Labridae, Odacidae, Scaridae). The labroids which generally lack defensive features such as toxins, venom, spines and dermal armor limit their mobility on the reef. These fishes exhibit greater trophic mobility (more specialized and versatile pharyngeal jaws) as a consequence of limited spatial mobility. In contrast they believe the armored butterflyfishes and surgeonfishes have greater spatial mobility due to their protection from predation and consequently less trophic mobility due to functional limitations related to gape, mouth position, jaw mobility and pharyngeal jaw mechanism. They believe these seriously limit feeding versatility in comparison to

similar sized pomacentrids or labrids. As evidence they cite feeding data by Randall (1967), Hobson (1974) and Reese (1975). My data indicates that these butterflyfishes are more morphologically and trophically diverse than is believed. These six species feed on a wide variety of prey and also exhibit a range of morphological feeding adaptations with many having a repertoire of feeding behaviors that match their prey. Future studies on the feeding behavior and the functional morphology of the feeding apparatus of fishes must consider the possibility of such diversity; diversity which may become visible by detailed field and laboratory observation.

Functions of jaw protrusion

In a review of jaw protrusion in teleost fishes I outlined numerous hypothetical functions for jaw protrusion that were influential in either (1) resulting in a decrease in predation or (2) making feeding energetically more efficient than without it (Motta 1984a). The majority of studies on jaw protrusion have speculated or formed conclusions on the function based on manipulative and tank observations without actual hypothesis testing (Schaeffer & Rosen 1961, Alexander 1967) but few have actually tested these ideas (Nyberg 1971, Lauder 1979, Norton 1982). Testing the hypothesis that protrusion decreases the angle of the fish to the substrate during feeding, (a) facilitating a more rapid escape from piscivorous predators as supposedly, the feeding fish has to return to a horizontal position to flee (Alexander 1967), (b) making feeding less difficult in flowing water (Alexander 1967), (c) or that it simply decreases handling time if the fish does not have to assume such an oblique stance every time it feeds, I measured the feeding angles of *C. trifasciatus*, *C. ornatissimus*, *C. unimaculatus*, *C. auriga* and *C. trifascialis*. I found that there was so much variability in the feeding angles compared to the 5–7° closer to the horizontal effected by jaw protrusion, and that shelter and/or food in these fishes does not always lie below the fish, that this function is probably not operationable in these species (Motta 1980). Circumstantial evidence from cine observations of feeding *C. miliaris*, and

over 300 hours of underwater feeding observations on this and other species permits me to hypothesize functions of jaw protrusion in the species.

The laterally enclosed, small and tubular mouth, reduced dentition, relatively high kinematic coefficient and rapid jaw protrusion in *C. miliaris* (Motta 1982, 1984b), combined with the fact that it uses jaw protrusion in the majority of its suction feeding bites (Motta 1980, Motta & Reese in preparation) indicates that the jaw of this species is suited for high speed inertial suction feeding. Jaw protrusion probably contributes to (1) momentarily increasing the effective rate of approach of the predator, reducing the possibility of prey escape, (2) increasing the distance from the predator that prey items may be sucked into the mouth by physically moving the mouth closer to the prey and by increasing the negative pressure generated by the buccal cavity, (3) forming a hydrodynamically, more efficient mouth opening by the formation of a small, laterally enclosed orifice. That its planktonic prey can escape has been observed. On more than one occasion its prey (most likely copepods) were seen to dart away from the mouth, the fish taking numerous protrusion bites to procure the prey. This species often uses suction feeding with and without jaw protrusion when swimming (Motta 1980, Motta & Reese in preparation). Weihs (1980) has shown that this increases the efficiency of suction feeding thereby increasing the distance from which anteriorly located prey can be ingested by suction. *C. miliaris* can suck prey into the mouth from a distance of up to 20% of the head length (Motta 1982). This distance is in agreement with hypothetical calculations for an addition protrusion suction component (Alexander 1967).

Jaw protrusion in *C. auriga* and *C. trifascialis* is probably not as important for suction feeding as it is in *C. miliaris*. In the former species a relatively large lateral gap remains in the mouth after jaw protrusion (Fig. 1). Alexander (1967, 1974), Osse (1969), Osse & Muller (1980), Muller et al. (1982) and others have discussed and made calculations on flow patterns and rates through small, laterally enclosed orifices. Lauder (1979) tested flow rates through such an aperture and also concluded that the laterally enclosed aperture represents a signifi-

cant increase in water flow indicating that the round opening is far more efficient than a notched opening for suction feeding. The large lateral gap or notch in the jaw of *C. auriga* allows the fish to grasp prey with the front or side of the jaws. Indeed, the jaw is encircled with very recurved teeth and it grasps polychaete worms with either a forward lunge or lateral swipe of the head. Jaw protrusion most likely (1) momentarily increases the effective rate of approach of the predator, reducing the possibility of prey escape and (2) it may allow the fish to procure prey items from otherwise unreachable locations or make it easier to remove prey from confined locations by the formation of an anteriorly extended, prognathous mouth.

In *C. auriga* and *C. trifascialis* even though jaw protrusion might not significantly increase buccal suction pressure, the rapid buccal expansion that drives jaw protrusion will create suction forces. These may aid feeding by momentarily orienting the flexible prey in the direction of suction for more efficient harvesting.

Rapid escape of the coral polyp prey is not a factor for *C. trifascialis* so perhaps jaw protrusion in this species also aids in the formation of the anteriorly extended, prognathous mouth allowing it to probe within the coral branches nipping off individual polyps. The anteriorly massed teeth that do not encircle the mouth accentuate this prognathous jaw.

The lateral enclosure of the jaw in *C. unimaculatus* is probably a modification for strengthening and bracing the jaw for its powerful lunges at the coral. Jaw protrusion contributes to the somewhat prognathous mouth which may facilitate its lunging probes that occasionally occur within coral branches or it could momentarily increase the force of the bite, which is important in its grazing habit.

Jaw protrusion or its lack thereof, can serve a variety of functions within and between species, facilitating a variety of feeding strategies and presumably opening further feeding niches.

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References cited

- Aleev, Y.G. 1969. Function and gross morphology in fish. Akad. Sci. USSR, Sevastopol Biol. Stn., Israel Program. for Sci. Transl., Jerusalem. 268 pp.
- Alexander, R. McN. 1967. The functions and the mechanisms of the protrusible upper jaws of some acanthopterygian fish. J. Zool. Lond. 151: 43-64.
- Alexander, R. McN. 1974. Functional design in fishes. Hutchinson University Library, London. 160 pp.
- Anderson, G.R.V., A.H. Ehrlich, P.R. Ehrlich, J.D. Rough-garden, B.C. Russel & F.H. Talbot. 1981. The community structure of coral reef fishes. Amer. Nat. 117: 476-495.
- Birkeland, C. & S. Neudecker. 1981. Foraging behavior of two Caribbean chaetodontids *Chaetodon capistratus* and *C. aculeatus*. Copeia 1981: 169-178.
- Bock, W.J. 1959. Preadaptation and multiple evolutionary pathways. Evolution 13: 194-211.
- Bock, W.J. 1980. The definition and recognition of biological adaptation. Amer. Zool. 20: 217-227.
- Boucher, L. 1979. Group structure and related social behavior of *Chaetodon unimaculatus* Bloch, 1788, family Chaetodontidae. Fourth Annual Albert Tester Memorial Symposium: 16.
- Burgess, W.E. 1978. Butterflyfishes of the world. T.F.H. Publications, Neptune City. 832 pp.
- Chao, L.N. & J.A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenic fishes in the York River estuary, Virginia. U.S. Fish. Bull. 75: 657-702.
- Davis, W.P. & R.S. Birdsong. 1973. Coral reef fishes which forage in the water column. Helgol. Wiss. Meeresunters. 24: 292-306.
- Delsman, H.C. 1925. Fishes with protrusible mouths. Treubia 6: 98-106.
- Dullemeijer, P. 1974. Concepts and approaches in animal morphology. Van Gorcum and Company, Assen. 264 pp.
- Dullemeijer, P. & C.D.N. Barel. 1977. Functional morphology and evolution. pp. 83-117. In: M.K. Hecht, P.C. Goody & B.M. Hecht (ed.) Major Patterns in Vertebrate Evolution, Plenum Publishing Corporation, New York.
- Dutta, H.M. 1968. Functional morphology of the head of *Anabas testudineus* (Block). Knips Repro N.V., Meppel. 146 pp.
- Dutta, H.M. 1979. Form ad function of jaws during feeding: *Ctenopoma acutiroster*, *Anabas testudineus* and *Macropodus opercularis*. Acta Morphol. Neerl. Scand. 17: 119-132.
- Dutta, H.M. & E.K. Chen. 1983. Structural basis of jaw protrusion in the largemouth bass, *Micropterus salmoides*: a microscopic analysis. Can. J. Zool. 61: 1251-1264.
- Eaton, T.H. 1935. Evolution of the upper jaw mechanism in teleost fishes. J. Morphol. 58: 157-172.
- Ebeling, A.E. 1957. The dentition of Eastern Pacific mullets with special reference to adaptation and taxonomy. Copeia 1957: 173-185.
- Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58: 46-59.
- Elshoud-Oldenhav, J.J.W. & J.W.M. Osse. 1976. Functional morphology of the feeding system in the ruff-*Gymnocephalus cernua* (L.1758) (Teleostei, Percidae). J. Morphol. 150: 399-422.
- Emery, A.R. 1973. Comparative ecology and functional osteology of fourteen species of damselfishes (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. Bull. Mar. Sci. 23: 649-770.
- Gosline, W.A. & V.E. Brock. 1960. Handbook of Hawaiian fishes. University of Hawaii Press, Honolulu. 372 pp.
- Greenwood, P.H. 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. Bull. Br. Mus. (Nat. Hist.) Zool. Suppl. 6: 1-34.
- Gregory, W.K. 1933. Fish skulls; a study of the evolution of the natural mechanisms. Trans. Amer. Philos. Soc. 23: 75-479.
- Grobecker, D.B. 1983. The 'lie-in-wait' feeding mode of a cryptic teleost, *Synanceia verrucosa*. Env. Biol. Fish. 8: 191-202.
- Harmelin-Vivien, M.L. 1979. Ichtyofaune des recifs corallien de Tulear (Madagascar): Ecologie et relations trophiques. Ph.D. Dissertation, Unversity Aix-Marseille, Marseille. 258 pp.
- Harmelin-Vivien, M.L. & Y. Bouchon-Navaro. 1981. Trophic relationships among chaetodontid fishes in the Gulf of Aqaba (Red Sea). Proc. 4th Intl. Coral Reef Symp. 2: 537-544.
- Harmelin-Vivien, M.L. & Y. Bouchon-Navaro. 1983. Feeding diets and significance of coral feeding among chaetodontid fishes in Moorea (French Polynesia). Coral Reefs 2: 119-127.
- Hiatt, R.W. & D. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs on the Marshall Islands. Ecol. Monogr. 30: 65-127.
- Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii, U.S. Fish. Bull. 72: 915-1031.
- Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. Amer. Sci. 63: 382-392.
- Hobson, E.S. & J.R. Chess. 1978. Trophic relationships among

- fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. U.S. Fish. Bull. 76: 133-153.
- Jones, R.S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). *Micronesica* 4: 309-361.
- Kaufman, L. & K.F. Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* 472: 1-19.
- Lagler, K.F., J.E. Bardach & R.R. Miller. 1962. *Ichthyology*. John Wiley and Sons, Inc., New York. 497 pp.
- Lauder, G.V. 1979. Feeding mechanisms in primitive teleosts and in the halecomorph fish *Amia calva*. *J. Zool. Lond.* 187: 543-578.
- Lauder, G.V. 1981. Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* 1981: 154-168.
- Lauder, G.V. 1983. Functional design and evolution of the pharyngeal jaw apparatus in the euteleostean fishes. *Zool. J. Linn. Soc.* 77: 1-38.
- Lauder, G.V. & K.F. Liem. 1980. The feeding mechanism and cephalic myology of *Salvelinus fontinalis*: form, function and evolutionary significance. pp. 365-390. In: E.K. Balon (ed.) *Charrs: Salmonid Fishes of the Genus Salvelinus*, Perspectives in Vertebrate Science 1, Dr W. Junk.
- Lauder, G.V. & K.F. Liem. 1981. Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes. *Env. Biol. Fish.* 6: 257-268.
- Laur, D.R. & A.W. Ebeling. 1983. Predator-prey relationships in surfperches. *Env. Biol. Fish.* 8: 217-229.
- Liem, K.F. 1967. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other recent teleosts. *J. Morphol.* 121: 103-134.
- Liem, K.F. 1970. Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana Zool.* 56: 7-166.
- Liem, K.F. 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. 1. Piscivores. *J. Morphol.* 158: 323-360.
- Liem, K.F. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool. Lond.* 189: 93-125.
- Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Amer. Zool.* 20: 295-314.
- Liem, K.F. & J.W.M. Osse. 1975. Biological versatility, evolution and food resource partitioning in African cichlid fishes. *Amer. Zool.* 15: 427-454.
- Motta, P.J. 1980. Functional anatomy of the jaw apparatus and related feeding behavior of the butterflyfishes (Chaetodontidae) including a review of jaw protrusion in fishes. Ph.D. Dissertation, University of Hawaii, Honolulu. 435 pp.
- Motta, P.J. 1982. Functional morphology of the head of the inertial suction feeding butterflyfish, *Chaetodon miliaris* (Perciformes, Chaetodontidae). *J. Morphol.* 174: 283-312.
- Motta, P.J. 1984a. The mechanics and functions of jaw protrusion in teleost fishes: a review. *Copeia* 1984: 1-18.
- Motta, P.J. 1984b. Tooth attachment, replacement, and growth in the butterflyfish *Chaetodon miliaris* (Chaetodontidae, Perciformes). *Can. J. Zool.* 62: 183-189.
- Muller, M., J.W.M. Osse & J.H.G. Verhagen. 1982. A quantitative hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* 95: 49-79.
- Neudecker, S. 1977. Transplant experiments to test the effect of fish grazing on coral distribution. *Proc. 3rd. Intl. Coral Reef Symp.* 1: 318-323.
- Neudecker, S. 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60: 666-672.
- Neudecker, S. & P.S. Lobel. 1982. Mating systems of chaetodontid and pomacanthid fishes at St. Croix. *Z. Tierpsychol.* 59: 299-318.
- Norris, K.S. & J.H. Prescott. 1959. Jaw structure and tooth replacement in the Opaleye, *Girella nigricans* (Ayres) with notes on other species. *Copeia* 1959: 275-283.
- Norton, S.F. 1982. A mechanical model for studying suction feeding in fishes. *Amer. Zool.* 22: 922.
- Nyberg, D.W. 1971. Prey capture in large mouth bass. *Amer. Midl. Nat.* 86: 128-144.
- Osse, J.W.M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.* 19: 289-392.
- Osse, J.W.M. & M. Muller. 1980. A model of suction feeding in teleostean fishes with some implications for ventilation. pp. 335-352. In: M.A. Ali (ed.) *Environmental Physiology of Fishes*, Plenum Publishing Corporation, New York.
- Pietsch, T.W. 1978. The feeding mechanism of *Stylophorus chordatus* (Teleostei: Lampridiformes): functional and ecological implications. *Copeia* 1978: 255-262.
- Preuschoft, H., W.E. Reif & W.H. Muller. 1974. Funktionsanpassungen in Form und Struktur an Haifischzähnen. *Z. Anat. Entw.-Fesch.* 143: 315-344. (In German).
- Ralston, S.V.D. 1975. Aspects of age and growth, reproduction and diet of the millet-seed butterflyfish *Chaetodon miliaris* (Pisces: Chaetodontidae), a Hawaiian endemic. M.S. Dissertation, University of Hawaii, Honolulu. 102 pp.
- Ralston, S.V.D. 1981. Aspects of the reproductive biology and feeding ecology of *Chaetodon miliaris*, a Hawaiian endemic butterflyfish. *Env. Biol. Fish.* 6: 167-176.
- Rand, D.M. & G.V. Lauder. 1981. Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior. *Can. J. Zool.* 59: 1072-1078.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Ocean.* 5: 655-847.
- Reese, E.S. 1973. Duration of residence by coral reef fishes on 'home' reefs. *Copeia* 1973: 145-149.
- Reese, E.S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. *Z. Tierpsychol.* 37: 37-61.
- Reese, E.S. 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. *Proc. 3rd. Int. Coral Reef Symp.* 1: 267-274.
- Schaeffer, B. & D.E. Rosen. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Amer. Zool.* 1: 187-204.

- Schultz, L.P., E.S. Herald, E.A. Lachner, A.D. Welander & L.P. Woods. 1953. Fishes of the Marshall and Marianas Islands, Vol. 1, Smithsonian Inst. Bull. 202, Washington. 685 pp.
- Shellis, R.P. & B.K.B. Berkovitz. 1976. Observations on the dental anatomy of piranhas (Characidae) with special reference to tooth structure. *J. Zool. Lond.* 180: 69–84.
- Sokal, R.R. & F.J. Rohlf. 1969. *Biometry*. W.H. Freeman and Company, San Francisco. 776 pp.
- Sokal, R.R. & F.J. Rohlf. 1981. *Biometry*. W.H. Freeman and Company, San Francisco. 859 pp.
- Starks, E.C. 1926. Bones of the ethmoid region of the fish skull. *Stanford Univ. Publ. Univ. Ser. Biol. Sci.* 4: 141–338.
- Stoner, A.W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses. *U.S. Fish. Bull.* 78: 337–352.
- Suyehiro, Y. 1942. A study on the digestive system and feeding habits of fish. *Jap. J. Zool.* 10: 1–301.
- Talbot, F.H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa), and its fish fauna. *Proc. Zool. Soc. Lond.* 145: 431–470.
- Weihls, D. 1980. Hydrodynamics of suction feeding of fish in motion. *J. Fish. Biol.* 16: 425–433.
- Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Board Can.* 31: 1531–1536.
- Werner, E.E. & D.J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science* 191: 404–406.
- Werner, E.E., D.J. Hall, D.R. Laughlin, D.J. Wagner, L.A. Wilsman & D.C. Funk. 1977. Habitat partitioning in a freshwater fish community. *J. Fish. Res. Board Can.* 34: 360–370.
- Witte, F. & C.D.N. Barel. 1976. The comparative functional morphology of the pharyngeal jaw apparatus of piscivorous and intrapharyngeal mollusc-crushing *Haplochromis* species. *Rev. Trav. Inst. Peches marit.* 40: 793–796.
- Yazdani, G.M. 1969. Adaptation in the jaws of flatfish (Pleuronectiformes). *J. Zool. Lond.* 159: 181–222.

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