

Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach

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Synopsis

The functional morphology of the feeding apparatus and the feeding ecology of an assemblage of ten species of butterflyfishes was investigated using a comparative ecomorphological approach. Behavioral observations in situ and in vivo, morphological measurements of fresh-killed specimens, scanning electron microscopy, and kinematic modeling were utilized. The fishes show varying degrees of morphological and behavioral specialization and generalization. The more specialized species group according to how they feed, rather than what they feed on. The feeding guild concept is therefore not very instructive in understanding the functional significance of the feeding apparatus. Many of the morphologically specialized butterflyfishes demonstrate evolutionary convergence in feeding morphology. Whereas the more morphologically specialized species do generally have more ecologically specialized diets, these data do not particularly support the ecomorphological hypothesis in that similar diets do not correspond to similar morphologies.

Introduction

In the past there have been numerous studies on the feeding habits of tropical reef fishes (Hiatt & Strasburg 1960, Jones 1968, Hobson 1975). Because the feeding structures are believed to dominate the functional morphology of the head (Liem & Osse 1975) there has been a more recent interest in this area (Liem 1980a, Liem & Osse 1975, Lauder 1983). With this upsurge has come a rekindling of the notion that to properly understand feeding mechanisms an eco-morphological approach is necessary (Bock & von Wahlert 1965, Bock 1977, 1980, Yamaoka 1983, Barel 1983, Lauder & Feder 1986, Motta 1985). This approach has been utilized to some extent in studies by Keast & Webb (1966),

Chao & Musick (1977) and most recently by Barel (1983) and his coworkers. I have attempted such an approach using six species of tropical butterflyfishes (Perciformes, Chaetodontidae) (Motta 1985).

The Chaetodontidae are a diverse, specialized group of acanthopterygian fishes that include approximately 114 species distributed circumtropically (Burgess 1978). In fact, Gosline (1985) believes that in many ways they are the most specialized family of percoid fishes. Among the major Hawaiian Islands where the bulk of this study has been conducted, there are approximately twenty species of butterflyfishes (Gosline & Brock 1960).

Although some is known on their anatomy and functional morphology (Starks 1926, Gregory 1933, Burgess 1978, Motta 1982, 1984b, 1985,

1987), more information exists on their social systems and worldwide feeding habits which include coral grazing and browsing, suction planktonic feeding and benthic omnivory (Hiatt & Strasburg 1960, Talbot 1965, Hobson 1974, Ralston 1975, 1981, Reese 1973, 1975, 1977, Ehrlich et al. 1977, Neudecker 1977, 1979, Bouchon-Navaro 1979, 1986, Anderson et al. 1981, Birkeland & Neudecker 1981, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Neudecker & Lobel 1982, Tursch & Tursch 1982, Motta 1984c, Sano et al. 1984, Lasker 1985, Tricas 1985, Hourigan unpublished).

Expanding my eco-morphological research to encompass ten of the twenty species of Hawaiian butterflyfishes, I attempt to incorporate both comparative inductive and deductive approaches (Dullemeijer & Barel 1977) that combine functional studies in the laboratory and behavioral observations in the field.

The study poses the following questions: What are the feeding adaptations of the species? What is the extent of morphological generalization and specialization of the feeding apparatus and how is this related to prey choice? Do their feeding structures demonstrate convergence or divergence in form? Are common morphotypes correlated with what the fishes feed on or with how they feed? What morphological feeding structures are probably the most evolutionarily labile? And does the study contribute to our understanding of the eco-morphological hypothesis that states that feeding morphology and ecology are intimately related?

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.

Ten species of butterflyfishes were utilized: *Chaetodon miliaris* Quoy & Gaimard, 1824, is one of the most common inshore fish around the Hawaiian Islands (Gosline & Brock 1960). It is a diurnal opportunistic zooplanktivore that feeds pri-

marily on calanoid copepods (Hobson 1974, Ralston 1981, Motta 1980). *Chaetodon (Megaprotodon) trifascialis* Quoy & Gaimard, 1825, is rare in the major Hawaiian Islands. 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, Sano et al. 1984). *Chaetodon auriga* Forskål, 1775, is a benthic omnivore that tears off pieces of noncoralline and coralline invertebrates; particularly alcyonarians, polychaete worms, sea anemones, scleractinians and algae (Hiatt & Strasburg 1960, Hobson 1974, Anderson et al. 1981, Harmelin-Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Motta 1980, Sano et al. 1984). *Chaetodon trifasciatus* M. Park, 1797, browses on hard corals (Talbot 1965, Reese 1975, 1977, Neudecker 1977, Harmelin-Vivien 1979, Harmelin-Vivien & Bouchon-Navaro 1981, 1983, Anderson et al. 1981, Motta 1980, Sano et al. 1984) as does *C. ornatissimus* Cuvier, 1831, (Hobson 1974, Reese 1977, Harmelin-Vivien & Bouchon-Navaro 1983, Motta 1980, Sano et al. 1984) and *C. multicinctus* Garrett, 1863, (Hobson 1974, Reese 1975, 1977, Tricas 1985, Motta unpublished, Hourigan unpublished). *Chaetodon unimaculatus* Bloch, 1787, is a facultative soft and hard coral grazer (Hobson 1974, Reese 1975, 1977, Boucher unpublished, Harmelin-Vivien 1979, Anderson et al. 1981, Tursch & Tursch 1982, Harmelin-Vivien & Bouchon-Navaro 1983, Motta 1980, Cox 1983, Sano et al. 1984). *Chaetodon quadrimaculatus* Gray, 1831, is an omnivore that browses on algae, anthozoans, polychaetes and hydroids (Hobson 1974, Reese 1975, 1977, Harmelin-Vivien & Bouchon-Navaro 1983, Motta unpublished, Hourigan unpublished). *Forcipiger longirostris* Broussonet, 1782, is an inertial suction feeder on small invertebrates, mostly shrimps, feeding in crevices and between coral branches (Hobson 1974, Anderson et al. 1981, Harmelin-Vivien & Bouchon-Navaro 1983, Motta unpublished) and *F. flavissimus* Jordan & McGregor, 1898, grabs and tears pieces of larger, benthic noncoralline invertebrates (Hobson 1974, Anderson et al. 1981, Harmelin-Vivien & Bouchon-Navaro 1983, Motta unpublished).

Chaetodon trifascialis specimens were speared at Chinimi Reef, Enewetak Atoll, Marshall Islands, *Chaetodon miliaris* specimens were taken by spear from the Waikiki shoreline, the southshore and the Waianae coast of Oahu, and Puako Reef, Hawaii, Hawaiian Islands. Specimens of *C. multicinctus*, *C. quadrimaculatus*, *F. longirostris*, *C. ornatissimus*, *C. trifasciatus* and *F. flavissimus* were speared at Puako Reef, Hawaii. All remaining species including further specimens of *C. ornatissimus* and *C. trifasciatus* were caught by trap in Kaneohe Bay, Oahu, and sacrificed with MS 222 (tricaine methanesulfonate) overdoses. Only adults of each species were utilized although juveniles of some species have been previously investigated (Motta 1985).

Behavioral observations

Behavioral observations are outlined in Motta (1985). Basically they involve 500+ hours of underwater observations to a depth of 33 m at Ānānā Bay, Oahu and Puako Reef, Hawaii, Hawaiian Islands. By means of the unaided eye and a magnifying lens, data on prey choice, prey handling and the effect of feeding on the substrate were taken. Data on *C. trifascialis* were taken at Enewetak Atoll, Marshall Islands.

Underwater high speed photography

To complement the behavioral observations with the unaided eye a Bell and Howell 70 sr 16 mm high speed (128 fps) movie camera with a 12.5 mm wide-angle lens was adapted to an Ewa-Marine U-BRS flexible plastic underwater housing. Using Kodak 4-X reversal film 7277 at 400 ASA and natural light at depths of 3–12 m, all species except *C. miliaris* and *C. trifascialis* were filmed during feeding at Puako Reef, Hawaii and Hanauma Bay, Oahu. Individuals of *C. miliaris* were previously filmed in the laboratory (Motta 1982). In addition specimens of the former species and *C. trifascialis* were filmed in the field with a Canon XLS-814 8 mm movie camera at 32 fps housed in an Ikelite case. Furthermore, *F. longirostris* and *F. flavissimus* were filmed

by means of a Bolex 16 mm camera at 64 fps feeding on dead brine shrimp in aquaria. Approximately 300 m of 16 mm film was analysed frame by frame with a LW motion analysis projector and data on the use of the jaws taken.

Standard measurements

Standard measurements including the angle of the maximally open jaw, the increase in standard length measured from the upper and lower jaw during jaw opening, the internal width and height of the open mouth, the length of the premaxilla and dentary, and head length as a measure of the protuberosity of the skull were taken on 10 fresh-killed individuals of each species. Gut length was measured on eight fresh-killed individuals of each species except for 8 specimens of *C. trifascialis*, which were preserved in 10% formalin and stored in 70% ethanol. Mandible length was measured on ten fresh and preserved specimens. The mean tooth bearing width of the upper and lower jaw was measured midway between the tips and the base of the teeth on the body of the premaxilla and dentary of eight specimens of each species and expressed as a percent of standard length. Techniques for measuring the angle of jaw depression, premaxilla and dentary length, and the internal width and height of the open mouth are outlined in Motta (1985). The anterior increase in standard length during jaw opening is measured from the orbit to the anterior end of the upper and lower jaws with the mouth in the closed position, and then in the maximally open position. This is then expressed as a percent of standard length. Protuberosity of the skull is expressed by head length as a percent of standard length, with the mouth in the closed, relaxed position. Mandible length is measured from the posterior end of the angular (Motta 1982) to the anterior end of the lower jaw. As with the other measurements, this includes the anterior contribution of the teeth to reflect the contribution of the jaw to feeding. Maximal jaw opening was effected by manually pressing the interopercular-mandible joint dorsally.

Kinematic coefficients

The techniques for measuring the kinematic coefficients is outlined by Anker (1974), Barel et al. (1975, 1977), and Liem (1980b). From three to five individuals of each species were utilized.

Head profiles and anatomical illustrations

The head profiles with the jaws in the relaxed, retracted positions and in the maximally open position were photographed and drawn. Gill rakers from the first arch were removed and illustrated by means of a camera lucida. To make sure that the rakers were representative, gill rakers from all the arches of approximately five specimens of each species were checked. Skulls of each species were prepared with dermestid beetles and cleaned in 5% sodium hypochlorite, then drawn with a camera lucida.

Dentitions and scanning electron microscopy

These techniques are outlined in Motta (1985).

Statistical analyses

Data on the head length as percent of standard length, premaxilla and dentary length as percent of standard length, and the anterior increase in the upper and lower jaws during maximal jaw opening as percent of standard length were all arcsine transformed as advised by Sokal & Rohlf (1981). The variances were found to be homoscedastic at the $\alpha = 0.05$ level 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 the asymmetrical back-transformed 95% confidence intervals were graphically presented as advised by Sokal & Rohlf (1981).

The data on the mean tooth bearing width of the upper and lower jaws as percent of standard length, mandible length as percent of standard length, and width and height of the mouth as percent of standard length were also arcsine transformed. Using the Fmax test their variances were found to be significantly different at the $\alpha = 0.05$ level, i.e. they were heteroscedastic. The untransformed data on the angle of jaw depression and gut length as percent of standard length were also found to be heteroscedastic. These data were then analysed by the Kruskal-Wallis non-parametric multiple comparisons test and found to differ in 'location', indicating that the samples came 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 ($\alpha = 0.05$, Sokal & Rohlf 1981). Internal width versus height of the mouth of each species was compared by a Mann-Whitney two-tailed U test as well as the mean tooth bearing width of the premaxilla and maxilla of each species ($\alpha = 0.05$). Because these are multiple comparisons tests the error rate is conservative. The back-transformed means and the asymmetrical 95% confidence intervals were presented for the originally transformed data; mean and standard errors were presented for the gut length and the angle of jaw opening data.

The technique of drawing lines under the graph connecting values that are not significantly different as outlined by Sokal & Rohlf (1981) was employed.

Results

Head morphology

The head profiles with the mouth in the relaxed and maximally open position vary among the species (Fig. 1). *C. auriga* and *F. flavissimus*, which both grasp and tear their prey, have prognathous mouths (Fig. 2) with large lateral gaps in the open mouth. Whereas that of *C. auriga* is relatively large, *F. flavissimus* has one of the smallest mouths (Fig. 3). In both species, the upper and lower jaws

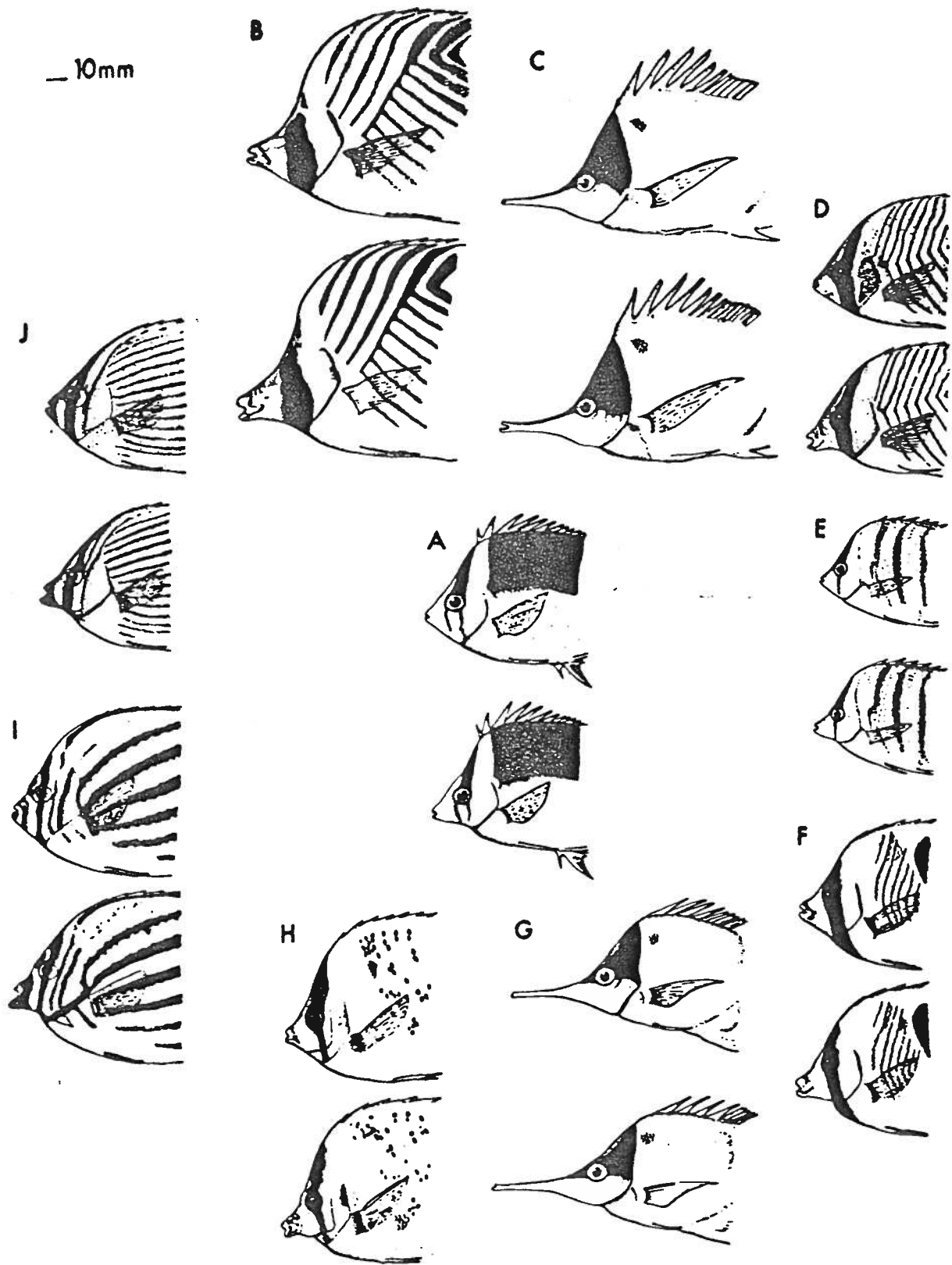


Fig. 1. Fresh-killed specimens with jaw in relaxed retracted position and jaw in maximally open and protruded position: A - *C. quadrimaculatus*; B - *C. auriga*; C - *F. flavissimus*; D - *C. trifascialis*; E - *C. multicoloratus*; F - *C. unimaculatus*; G - *F. longirostris*; H - *C. miliaris*; I - *C. ornatissimus*; J - *C. trifasciatus*.

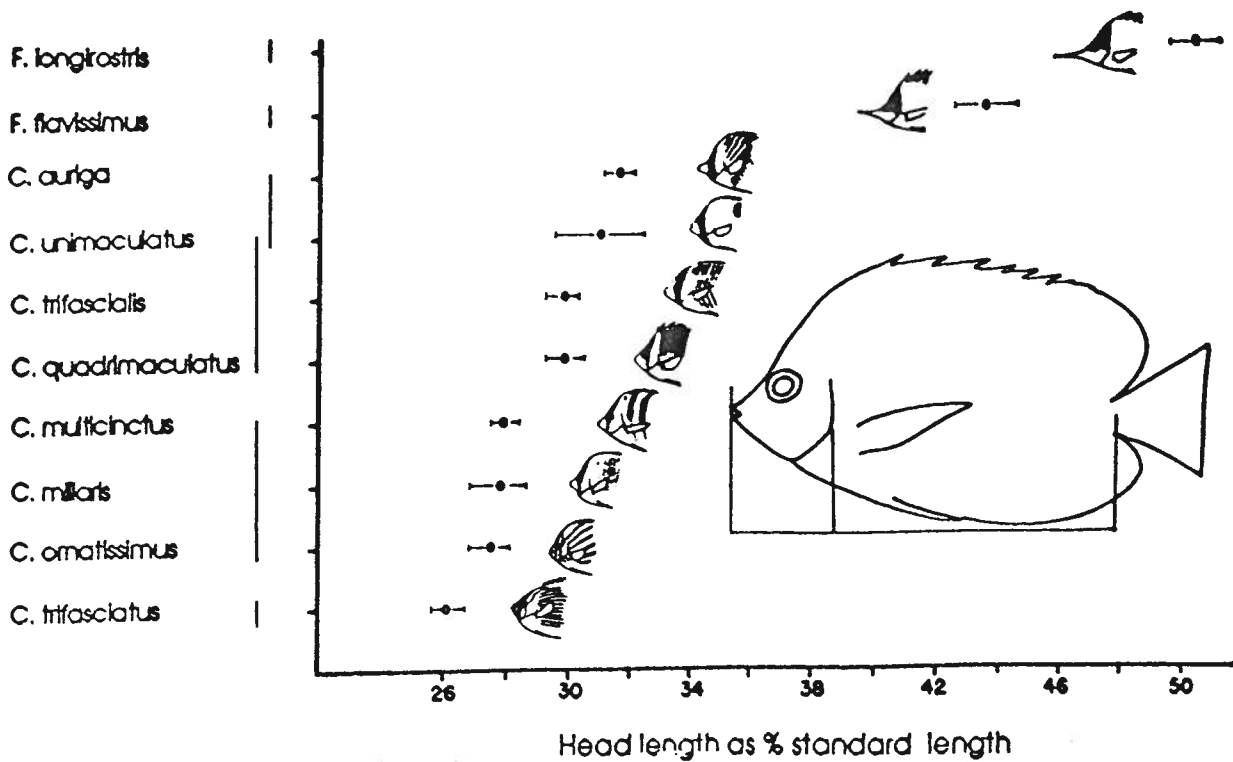


Fig. 2. Degree of head protuberosity expressed as head length as percent of standard length. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

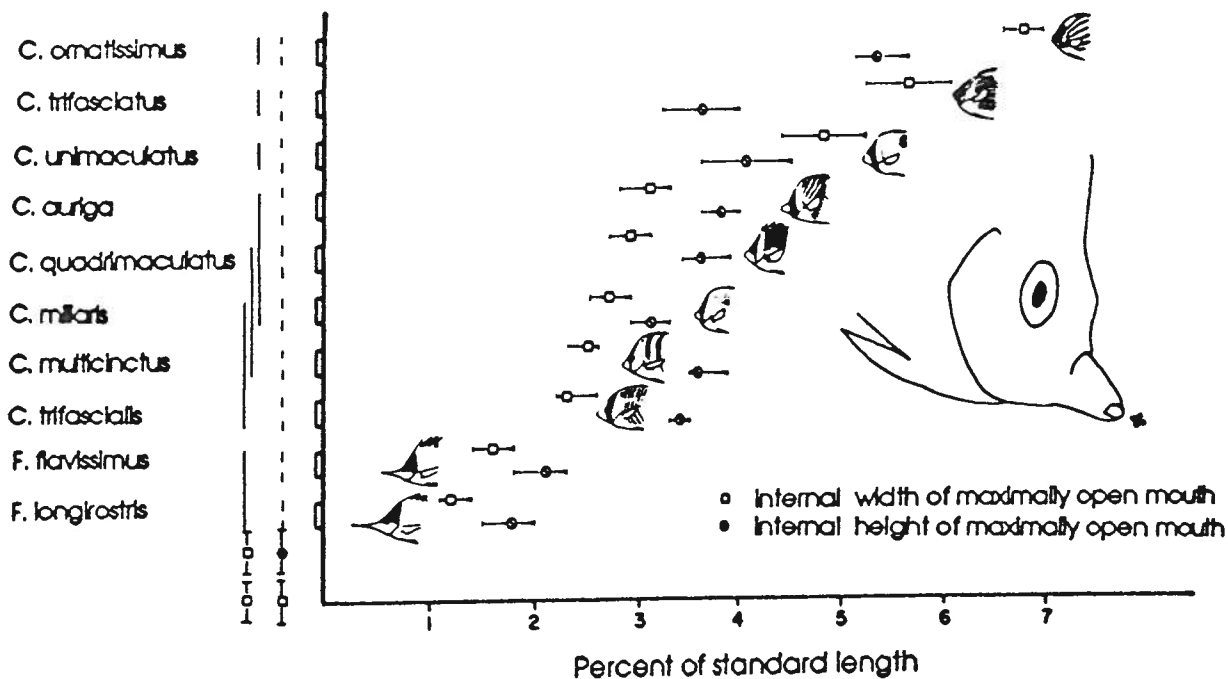


Fig. 3. Internal width and height of the maximally open mouth as percent of standard length. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

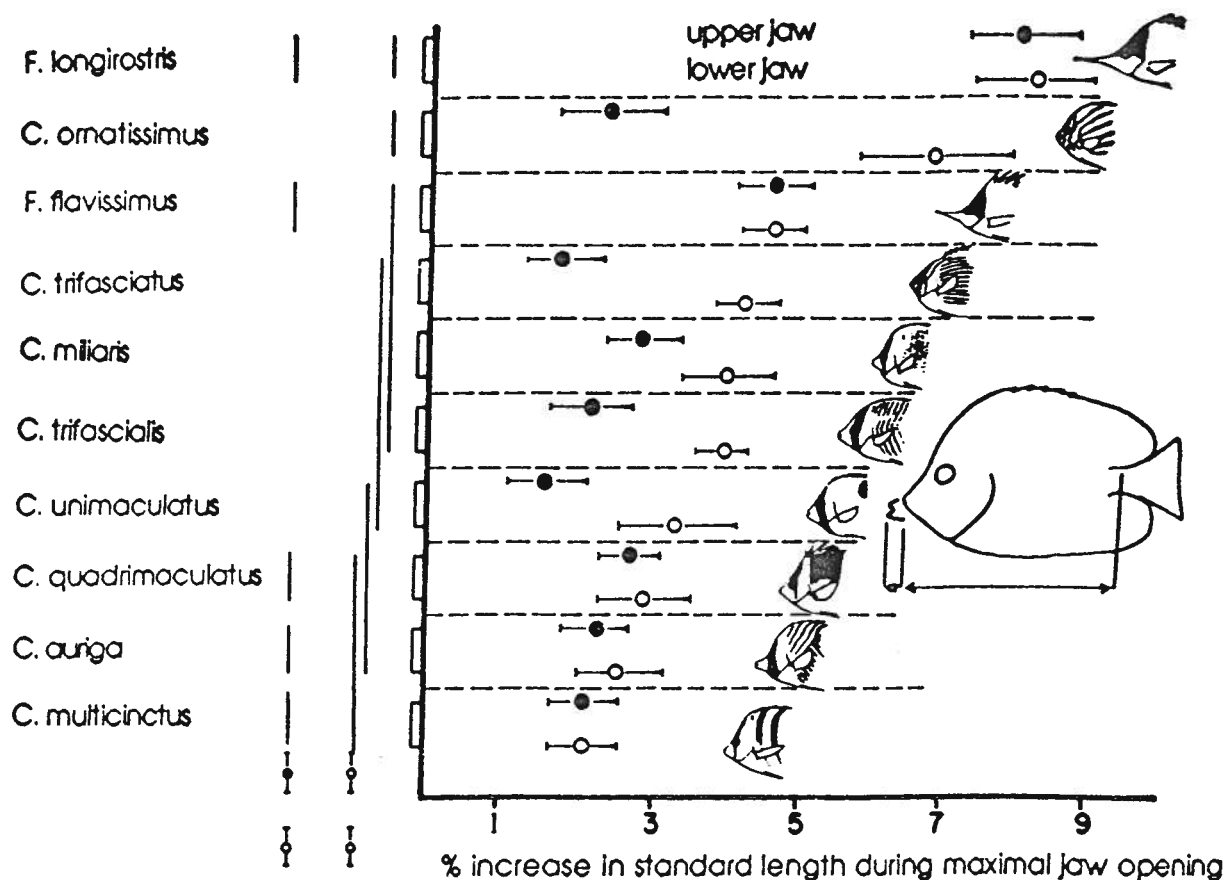


Fig. 4. Anterior increase in length of the upper and lower jaw as percent of the standard length during maximal jaw opening. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

move anteriorly to the same degree (Fig. 4) but the jaws of *F. flavissimus* are more protractile (Fig. 4). The prognathousness of their jaws is due, in part, to significantly longer premaxillae, dentaries and mandibles (Fig. 5, 6).

The coral nipping *C. trifascialis* and *C. multincinctus* have small (Fig. 3), moderately prognathous (Fig. 2), forceps-like mouths (Fig. 1). The jaw of *C. trifascialis* is more protractile than the other browser *C. multincinctus* (Fig. 4), but the upper jaw and mandible are not different in relative length (Fig. 5, 6). *C. unimaculatus* has a large, robust jaw (Fig. 1, 3) that is somewhat prognathous (Fig. 2) due to relatively long jaw bones (Fig. 5, 6). During maximal jaw opening the jaws slightly protrude in this coral grazer (Fig. 4).

The coral scraping *C. ornatissimus* and *C. tri-*

fasciatus have very wide, large, asymmetrical shovel-shaped mouths (Fig. 1, 3). In only *C. unimaculatus* and these two species is the mouth significantly wider than tall (Fig. 3). The heads of *C. ornatissimus* and *C. trifasciatus* are less prognathous (Fig. 2), particularly the latter. The jaw bones are relatively short in *C. trifasciatus*, and less so in *C. ornatissimus* (Fig. 5, 6). The degree of the asymmetry of the mouth during jaw opening is shown in Figure 4, where in both cases the upper jaw only protrudes slightly, whereas the lower jaw markedly increases the length of the head when it pivots open.

The facultative plankton feeder *C. miliaris* has a moderately protrusible, laterally enclosed mouth (Fig. 1, 2, 4) that is not significantly different in width from the small-mouthed coral nippers *C.*

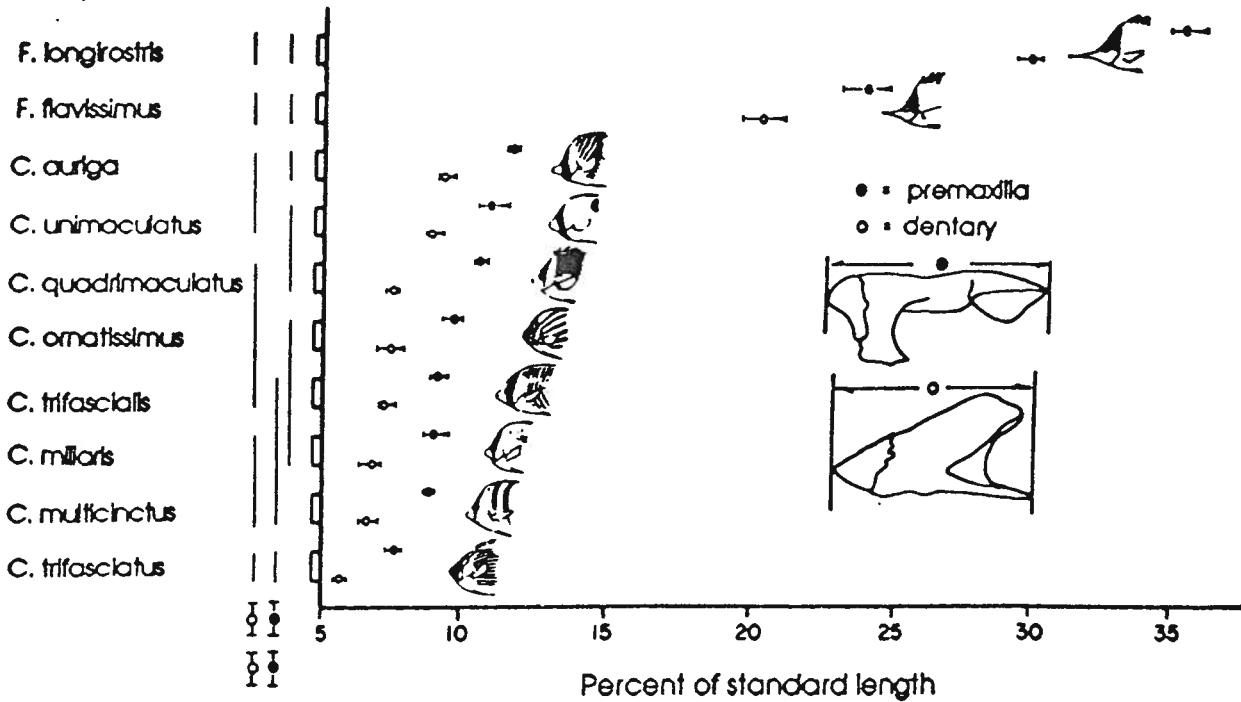


Fig. 5. Premaxilla and dentary length as percent of standard length. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

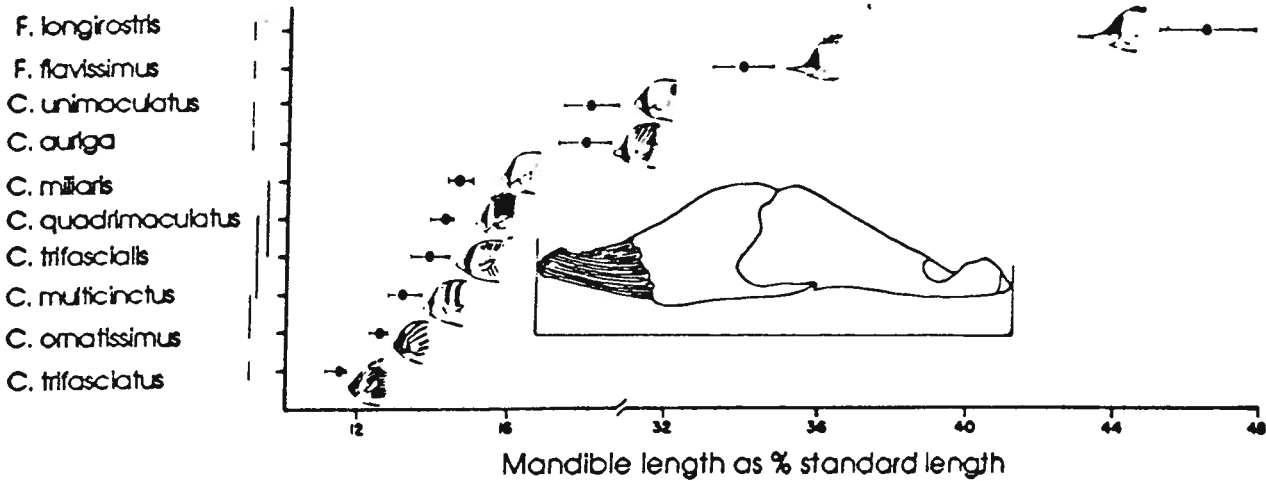


Fig. 6. Mandible length as percent of standard length. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

multinctus and *C. trifascialis* (Fig. 3). The premaxilla and dentary are comparable in length to these species as well (Fig. 5). The pipette, suction-feeding *F. longirostris* has the most prognathous head (Fig. 1, 2), with the longest jaw bones (Fig. 5, 6), and one of the smallest mouths (Fig. 3) that

lacks a lateral gap. Its mouth protrudes anteriorly more than any other species studied (Fig. 4). Finally, the omnivorous *C. quadrimaculatus* has about the most average jaw of the species, with a moderately sized mouth (Fig. 3) that is about average in head length (Fig. 2) and protrudes slightly (Fig. 1,

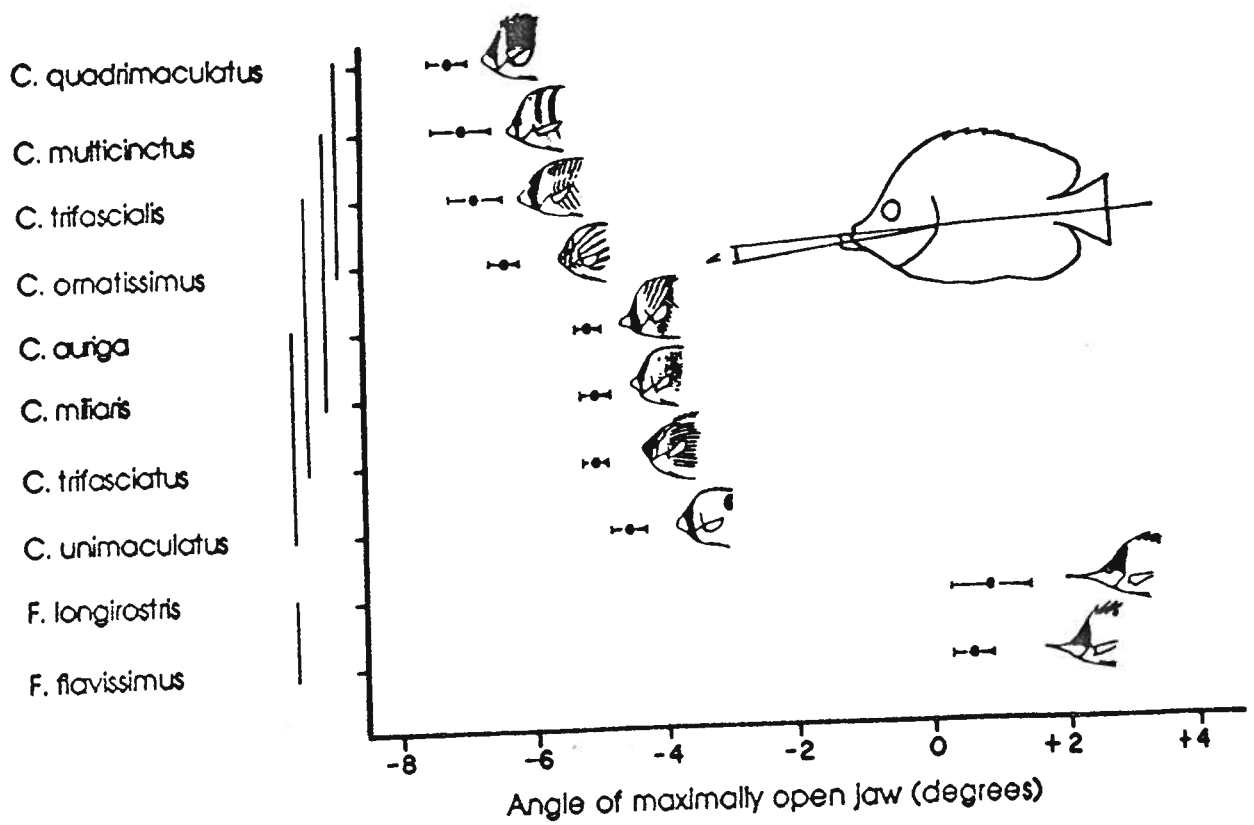


Fig. 7. The angle of the maximally open jaw to the retracted-relaxed position. The majority of the species direct the gape below the longitudinal axis of the fish. Mean \pm 1 standard error shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

4). The lengths of the jaw bones is again mostly intermediate (Fig. 5, 6). During jaw opening the mouth is directed anteroventrally in eight of the species, except in *F. longirostris* and *F. flavissimus* where it is directed anteriorly (Fig. 7).

Skulls

The extent of the contribution to the jaw by the tooth bearing premaxillae and dentaries is demonstrated in Figure 8. The robust jaws of *C. unimaculatus*, and the asymmetrical jaws of *C. ornatissimus* and *C. trifasciatus* are shown, as are the more delicate bones of *C. multinctus* and *C. trifascialis*.

Dentition, tooth-bearing bones, and gill rakers

The dentition of *C. miliaris*, *C. trifasciatus*, *C. ornatissimus*, *C. auriga*, *C. unimaculatus*, and *C. trifascialis* is reported in Motta (1984b, 1985, 1987). In brief, *C. ornatissimus* and *C. trifasciatus* have large pads of teeth of approximately the same length. They do not lie on the ascending process of the dentary or on the descending process of the premaxilla, otherwise they do not encircle the mouth. The teeth of *C. unimaculatus* likewise do not encircle the mouth, but the peripheral teeth are massive and spatulate. That of *C. multinctus* is similar to *C. trifascialis* in that the teeth are massed towards the anterior and do not lie on the descending process of the premaxilla or the ascending process of the dentary (Fig. 9). *C. quadrimaculatus* has teeth encircling the jaw lying on both the descending and ascending processes, as well as distinct rows of teeth. Similar to *C. multinctus*, the more lin-

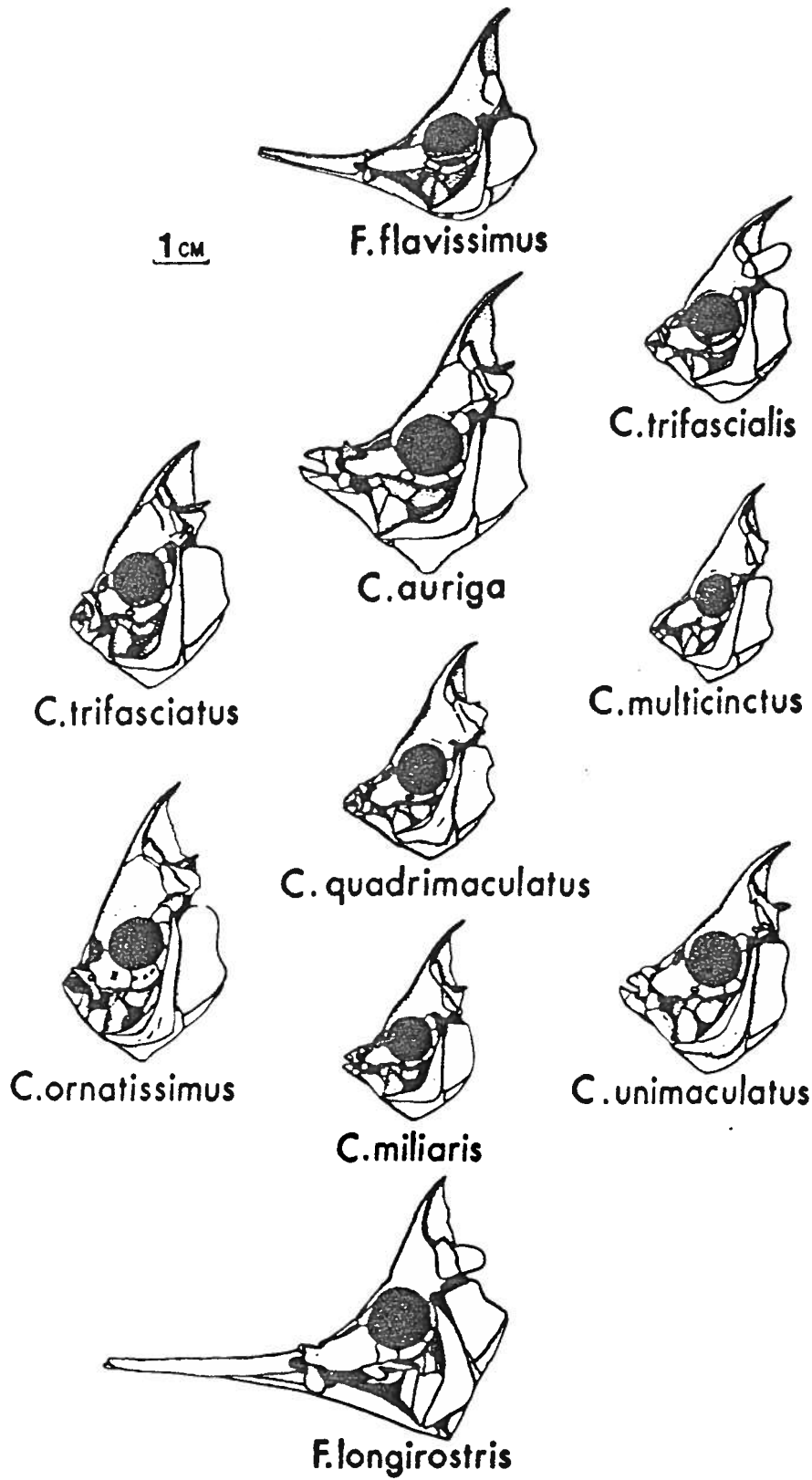


Fig. 8. Skulls of butterflyfishes under study. Details of neurocrania are omitted. See Motta (1982) for skull osteology.

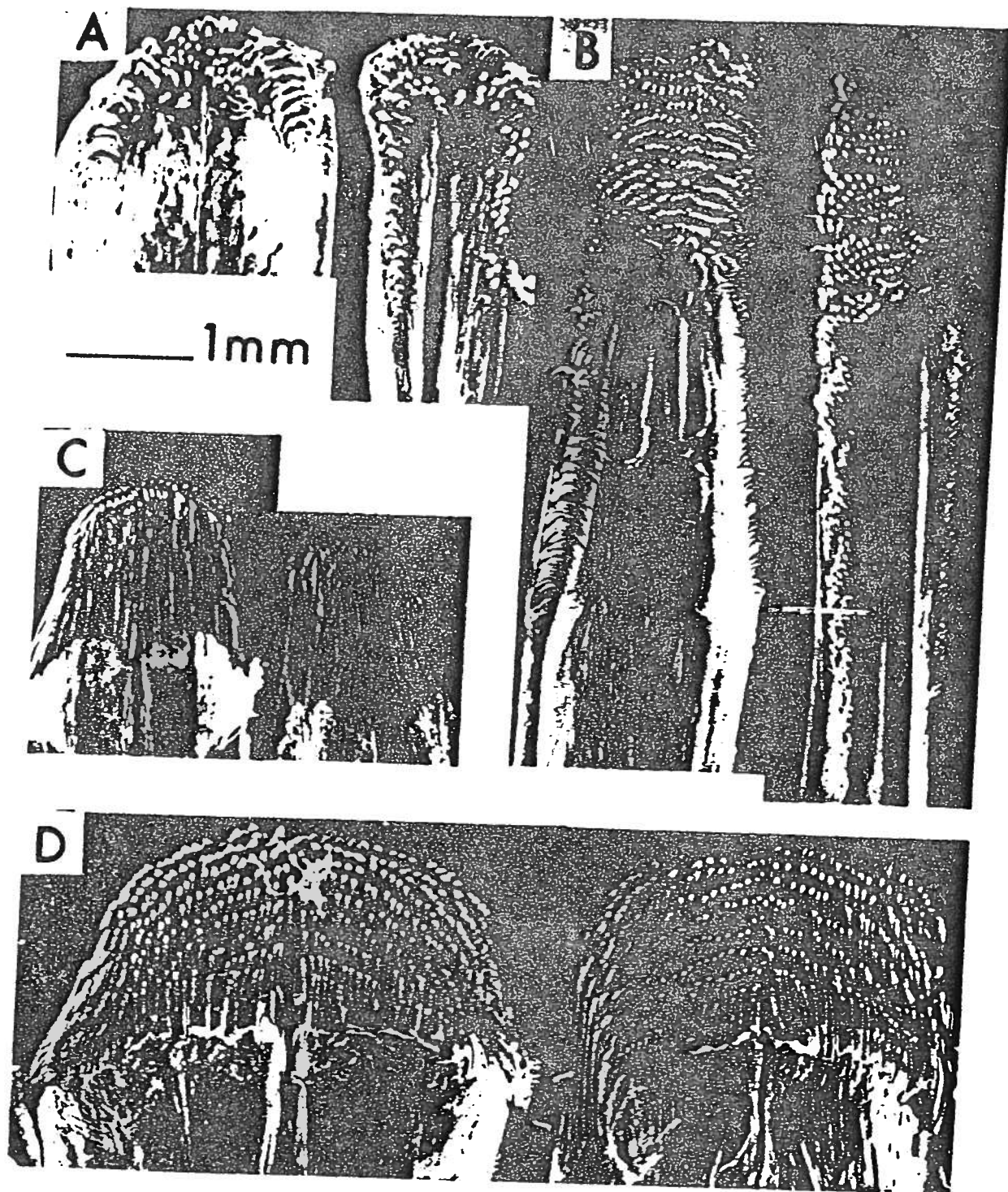


Fig. 9. Ventral view of teeth and tooth bearing area of the premaxilla (left) and dorsal view of the dentary (right) of: A - *F. longirostris* TL 15.7 cm, SL 13.3 cm; B - *F. flavissimus* TL 15.1 cm, SL 12.2 cm; C - *C. multinctus* TL 9.3 cm, SL 7.8 cm (premaxilla) TL 9.1 cm, SL 7.5 cm (dentary); D - *C. quadrimaculatus* TL 12.8 cm, SL 10.7 cm.

gual teeth are villiform and the more labial ones are more spatulate. *F. flavissimus* has numerous rows of short, villiform-like teeth that completely encircle the mouth including the large lateral gap, a dentition somewhat similar to *C. auriga*. However, *F. longirostris* has a greatly reduced dentition which on the upper jaw is confined to the anterior margin and consists of only a few tooth rows. The lower jaw also has few teeth that lie only anteriorly and partially along the lateral margin of the jaw (Fig. 9). These teeth are also short and villiform. *C. miliaris* has a somewhat reduced dentition of a few rows of relatively short teeth that encircle the mouth.

Comparing the average tooth bearing width of the jaws in the ten species, the two scraping species *C. ornatissimus* and *C. trifasciatus* have the widest tooth pads, followed by the coral grazing *C. unimaculatus* (Fig. 10). The omnivorous *C. quadrimaculatus* lies below these, as does the biting and tearing *C. auriga*. Below the facultative planktivore *C. miliaris*, the two coral-picking species, *C. trifascialis* and *C. multicinctus* form a group. Lastly, the two long-nosed butterflyfish have the narrowest tooth pads. Comparing the upper and lower jaws against each other, the obligate coral scraping *C. ornatissimus* is the only species to have a mandibular tooth pad significantly wider than the premaxilla pad. Figures 11 and 12 illustrate the upper and lower jaws with the tooth arrangement (see discussion). Gill rakers from the first arch vary somewhat with only three species, *C. trifasciatus*, *C. ornatissimus* and *C. unimaculatus* lacking spines (Fig. 13).

Gut length

The two coral-scraping species *C. ornatissimus* and *C. trifasciatus* have the longest guts (Fig. 14). These are followed by a group comprised of *C. multicinctus*, *C. auriga*, *C. trifascialis*, *C. unimaculatus*, and *C. quadrimaculatus*. The facultative planktivore *C. miliaris* has a gut that is shorter than some of these species, whereas the non-coraline sessile invertebrate feeding *F. flavissimus* has a shorter gut, and *F. longirostris* that feeds on suspended non-coraline invertebrates has the shortest gut.

Kinematic coefficient

This coefficient k gives a measure of the efficiency of the jaw opening movement and, therefore, the velocity of mandibular depression. It transforms the levator operculi coupling into a four-bar-linkage system (Anker 1974, Barel et al. 1975, 1977, Liem 1980b). Measuring k on *C. miliaris* is explained in Motta (1982). *C. unimaculatus* has a mean k value of 4.4 ($N = 3$), *C. auriga* 5.1 ($N = 3$), *C. quadrimaculatus* 5.2 ($N = 3$), *C. miliaris* 6.2 ($N = 5$), *C. trifascialis* 6.3 ($N = 3$), *C. trifasciatus* 7.2 ($N = 3$), *C. multicinctus* 7.6 ($N = 3$), and *C. ornatissimus* 9.1, ($N = 4$). The unusual jaw mechanism of the two long-nosed species in which the entire suspensorium pivots during protrusion, precludes comparison to the others.

Prey capture

Chaetodon ornatissimus primarily uses its lower jaw to scrape the coral surfaces, removing 16–50 polyps per bite without damaging the coral skeleton (Motta 1985). In most cases one to three bites are made on a single location, and there is slight lunging at the surface during the bite. The coral polyps are seen to be scraped off to a depth of 1–2 mm inside the calices, the bite forming a circular whitish area of approximately one square cm. The cine analysis reveals that there is some upper jaw protrusion. The approximate average duration of a bite from the initiation of mouth opening to mouth retraction and closure is 0.1 second (12.7 frames at 128 fps, $N = 18$ bites).

Similar to the former species, *C. trifasciatus* primarily uses its lower jaw to comb the coral surface browsing on 3–10 polyps per bite, taking 1–3 bites per location (Motta 1985). It too lunges slightly at the corals. The approximate average duration of a bite is 0.06 seconds ($N = 5$ bites) and there is some upper jaw protrusion.

The omnivorous *C. quadrimaculatus* may lunge or use lateral jerks of its head when browsing. The upper jaw is protruded during most bites taking an approximate average duration of 0.06 seconds ($N = 6$ bites). Maximum jaw protrusion occurs

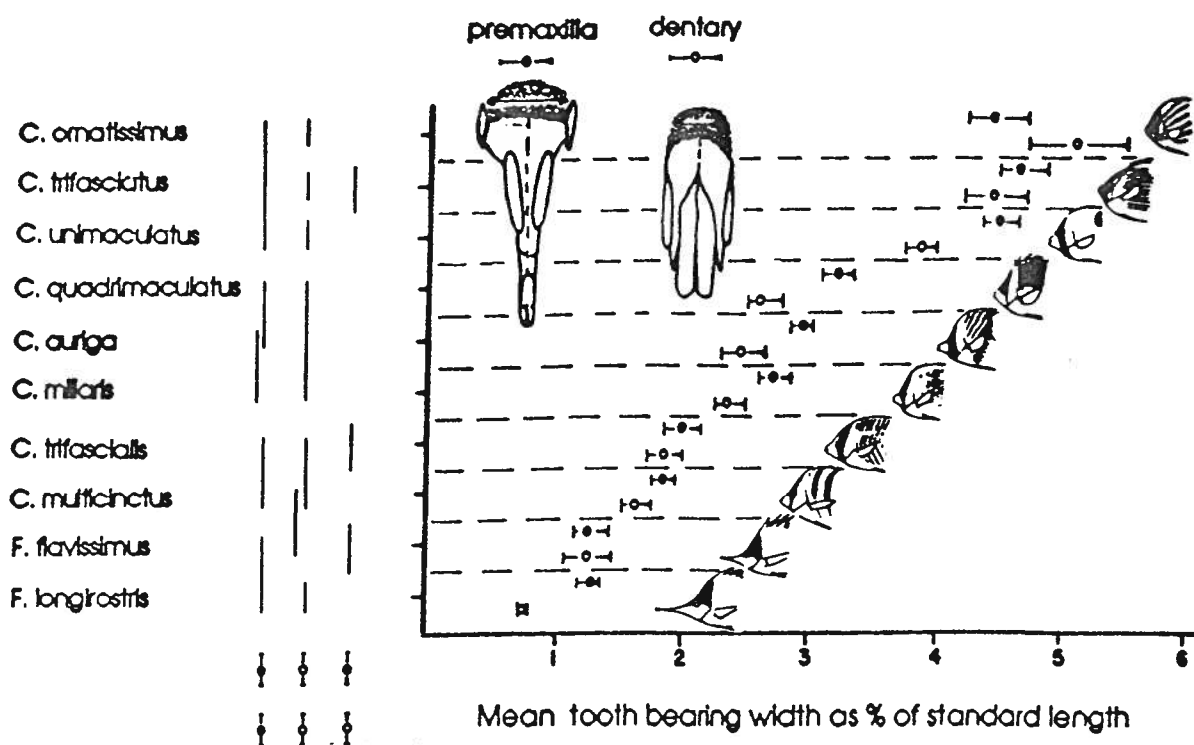


Fig. 10. Average tooth bearing width of the premaxilla and dentary. Back-transformed mean and asymmetrical back-transformed 95% confidence intervals shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

approximately 0.02 seconds after the initiation of mouth opening. It often feeds in coral crevices.

Chaetodon multinctus uses jaw protrusion when browsing on individual coral polyps accompanied by slight body lunges. In some unidentified bites it did not use jaw protrusion, and when it did feed on algae it sometimes used lateral jerks of the head with or without protrusion. One polyp per bite is removed from inside the corallite. The jaw reaches maximum protrusion in 0.02 seconds, and the approximate average duration of a bite is 0.04 seconds ($N = 6$ bites).

Chaetodon trifascialis also uses jaw protrusion when browsing on individual coral polyps which may be accompanied by slight body lunges. It also may use lateral jerks of the head. The speed of jaw protrusion is not available, but like most of the species studied it can vary considerably.

The grazing *C. unimaculatus* uses vigorous anterior lunges at the corals, biting off pieces of the skeleton along with the polyps. At Enewetak Atoll, Marshall Islands, I have observed it remove

large pieces of soft coral tissue in this manner. Its gut is most often filled with calcareous material. Jaw protrusion and retraction take place in approximately 0.05 seconds ($N = 7$ bites), with maximum protrusion occurring approximately 0.02 seconds after the initiation of mouth opening.

Chaetodon auriga mostly searches coral rubble and crevices for sessile invertebrates such as polychaete worms, using vigorous or gentle forward lunges and some times lateral jerks of the head. It uses jaw protrusion for such bites, but apparently does not when it occasionally feeds on algae (algae bites not filmed). Jaw opening, protrusion and retraction occur in approximately 0.06 seconds, with maximum protrusion occurring in 0.02 seconds, although the data are very limited in this regard ($N = 2$ bites filmed).

Chaetodon miliaris used jaw protrusion in most of its midwater suction bites on plankton. In the majority of such bites it temporarily stops swimming and protrudes the jaw, in other cases it protrudes the jaw when swimming, or does not use

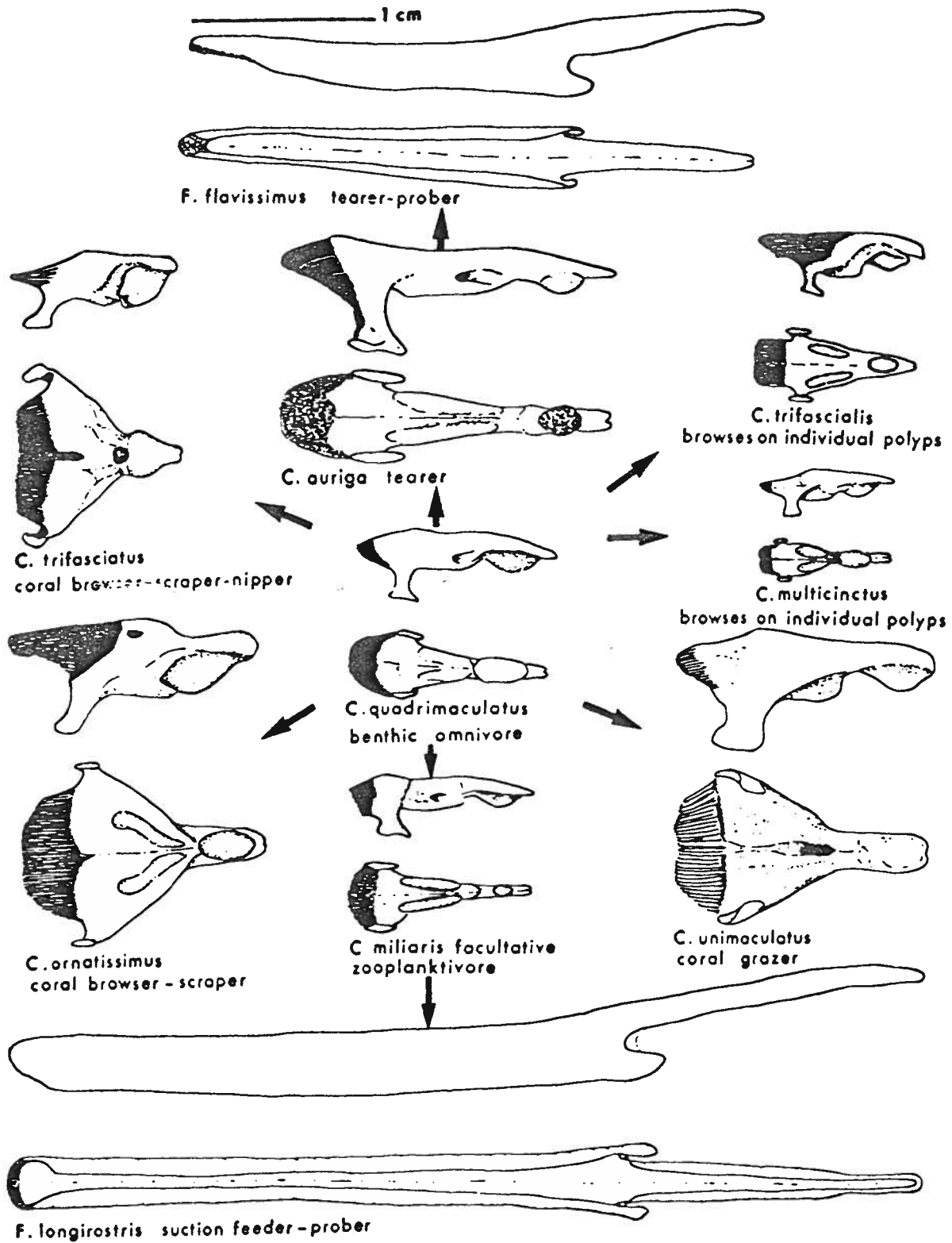


Fig. 11. Left lateral and ventral views of the premaxillae and teeth with the summarized feeding behavior. One of the most morphologically generalized species, *C. quadrimaculatus* is shown centrally, with other feeding types surrounding it. No phylogenetic significance is implied by the arrangement.

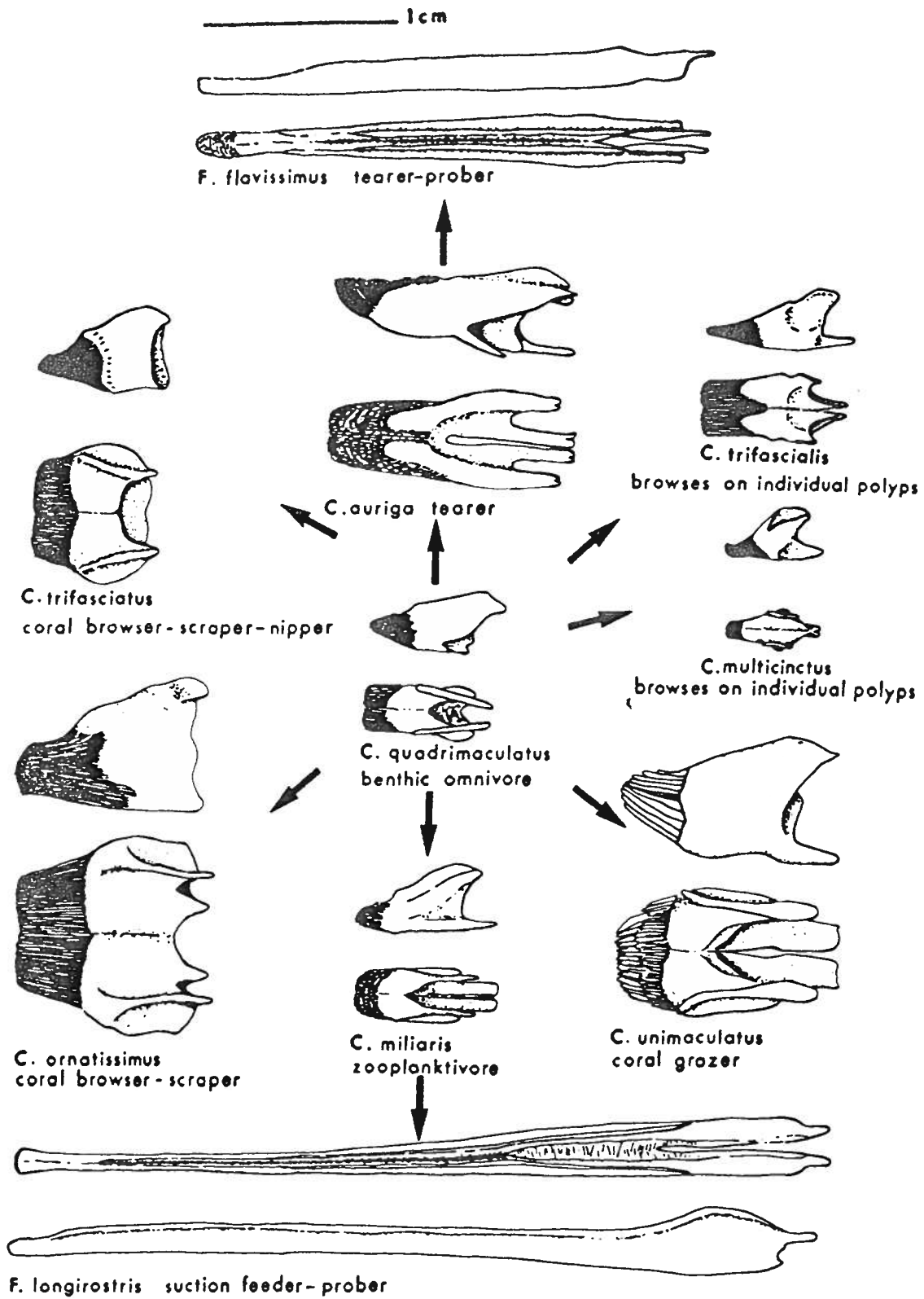


Fig. 12. Left lateral and dorsal views of the dentaries and teeth with the summarized feeding behavior. One of the most morphologically generalized species, *C. quadrimaculatus* is shown centrally, with other feeding types surrounding it. No phylogenetic significance is implied by the arrangement.

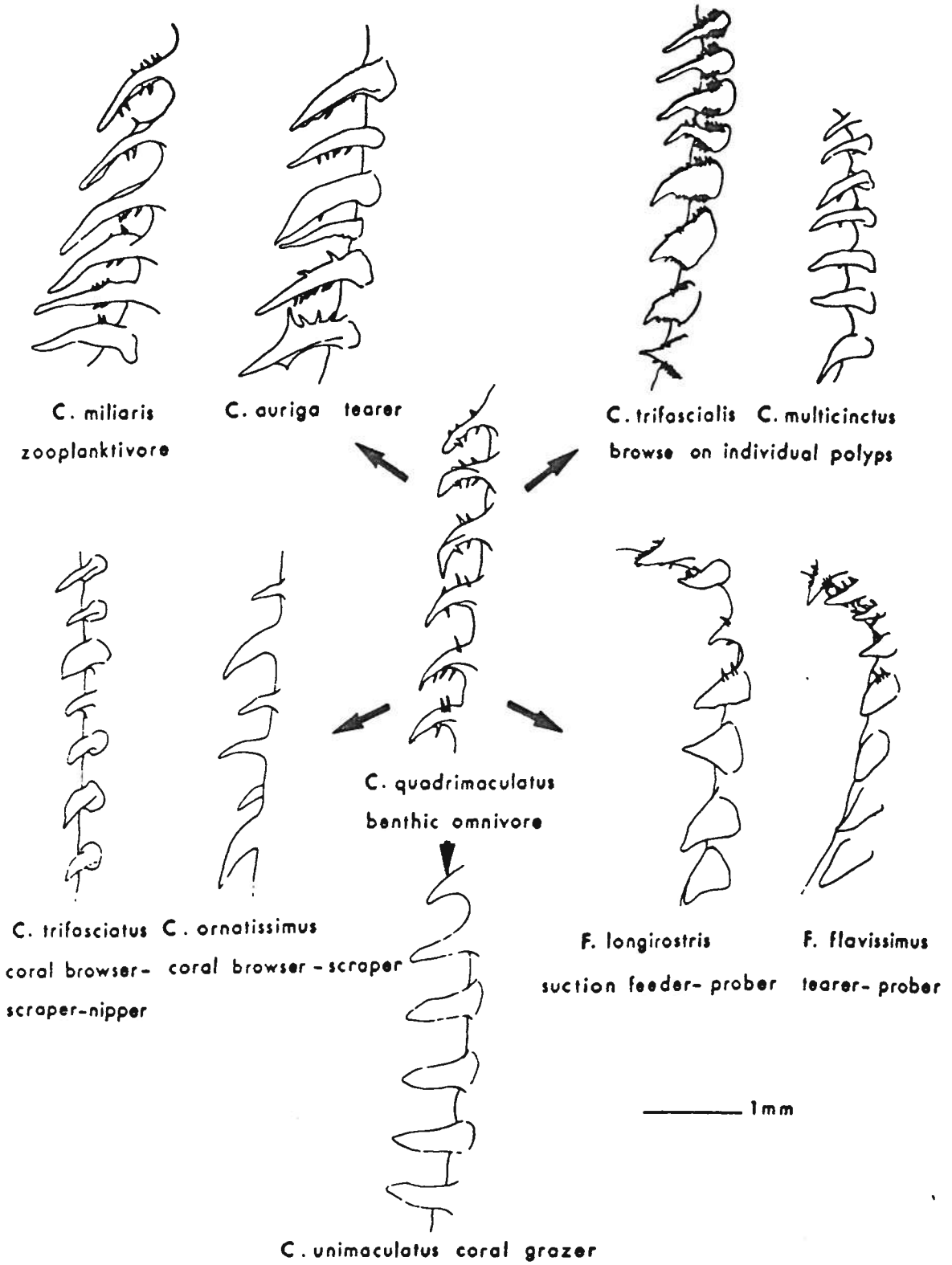


Fig. 13. Representative gill rakers from the mid region of the left first arch with the summarized feeding behavior. One of the most generalized species, *C. quadrimaculatus* is shown centrally. No phylogenetic significance is implied by the arrangement.

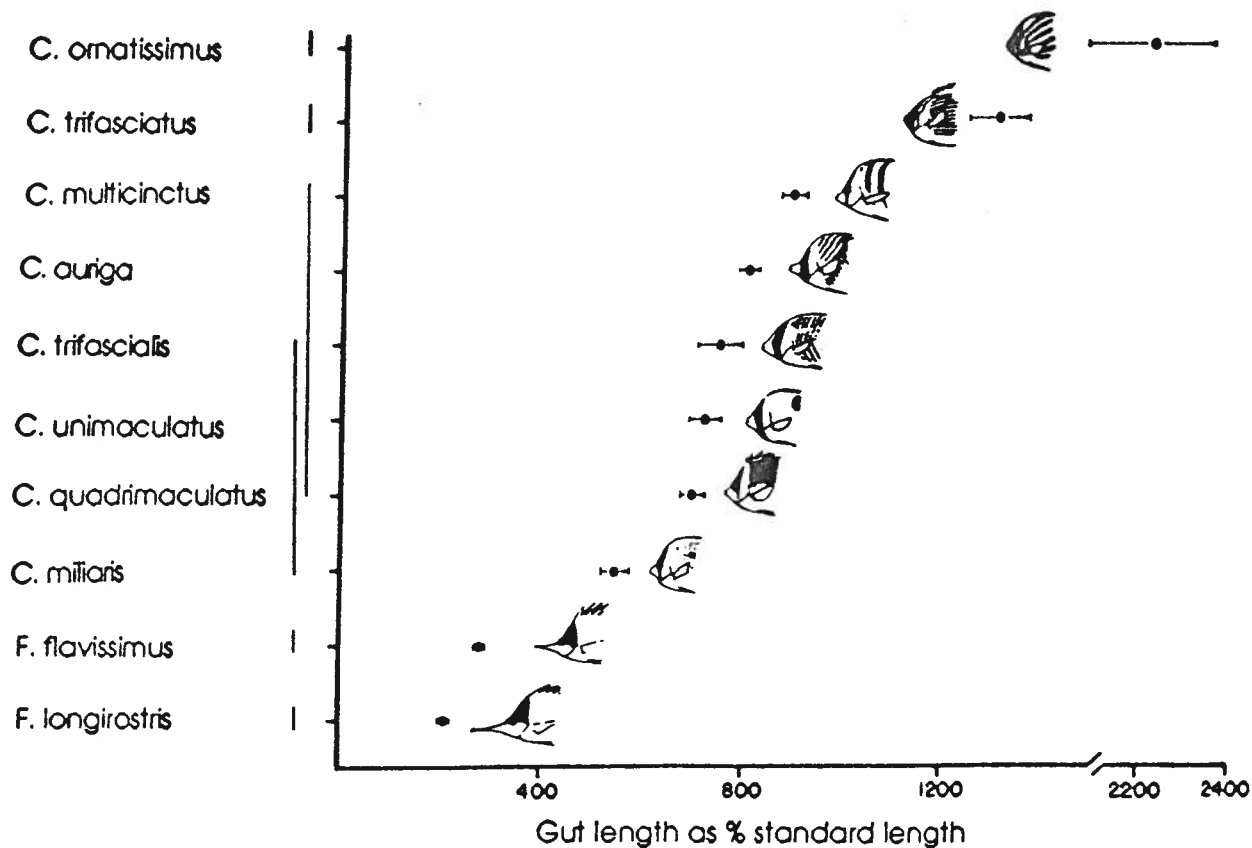


Fig. 14. Gut length as percent of the standard length. Mean \pm one standard error shown. Lines connect values that are not significantly different ($\alpha = 0.05$).

protrusion, simply opens the mouth and engulfs the prey while swimming. The approximate average duration of such a protrusion bite is 0.08 seconds, with the mouth reaching maximum protrusion in approximately 0.04 seconds ($N = 38$ bites, from Motta 1982).

Forcipiger longirostris captures small free-swimming, non-coralline invertebrates on and around coral, frequently probing within crevices. It swims slowly while searching, and then momentarily either stops just before it rapidly protrudes both its upper and lower jaws at the prey or it may lunge at the prey simultaneously. The approximate average time for protrusion and retraction is 0.04 seconds ($N = 9$ bites), with maximum protrusion occurring in approximately 0.01 seconds.

Forcipiger flavissimus grasps and tears small non-coralline sessile invertebrates such as polychaete and vermetid worms in Hawaii, in addition

it picks at the soft parts of larger invertebrates such as sea urchins. Most of the bites involve rapid lunges and jaw protrusion. It may use rapid lateral swipes of the head in order to catch prey before the worms withdraw into their tube. The prey is grasped with either the anterior or lateral part of the jaw. Like many of the other species it will feed on plankton if it is very abundant, and in aquaria such bites have an approximate average duration of 0.08 seconds with maximum protrusion occurring in 0.03 seconds.

Discussion

Functional morphology of the jaws

These butterflyfishes exhibit a remarkable range of specializations and generalizations for feeding.

Morphological specialization is defined here in a manner similar to that of Reif (1983), it implies the morphological distance of a character from the mean morphology of the same character in representatives of a taxon. In this regard, *C. quadrimaculatus* is one of the most generalized species studied (Table 1). In terms of the morphological attributes of the jaw, this species is intermediate in many. It has a mouth of moderate size (Fig. 3), jaw bones of intermediate size (Fig. 5, 6), and a head of approximately average length (Fig. 2). The dentition consists of numerous, distinct rows of teeth that encircle the jaws, grading from small villiform ones to more spatulate teeth at the periphery (Fig. 9). This dentition pattern appears to be the most common type in the butterflyfishes (Burgess 1978). Its om-

nivorous diet is also one of the most generalized of all the species studied. Therefore, relatively placing this species as one of the most morphologically generalized species (Fig. 1, 11, 12), some patterns begin to emerge. The facultative inertial planktonic suction feeder, *C. miliaris*, has a somewhat similar jaw morphology, but one that is more suited for inertial suction feeding. High speed suction feeders typically have protrusible, small, round mouths that are laterally enclosed, very rapid protrusion, and either lack a dentition or have a reduced one (see Motta 1984a for a review). *C. miliaris* has a relatively small tubular mouth, about average degree of jaw protrusion, and a laterally enclosed mouth with a reduced dentition (Table 1, Motta 1985). This species protrudes, closes and

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

	<i>C. ornatissimus</i>	<i>C. trifasciatus</i>	<i>C. unimaculatus</i>	<i>C. quadrimaculatus</i>	<i>C. auriga</i>
Feeding behavior	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.	Facultative soft and hard coral grazer that lunges at the coral surface	Browsing omnivore	Benthic omnivore feeding on noncoralline and coralline invertebrates. Probes in rubble for prey. Grasps prey with front or sides of jaw.
Effect on substrate	Removes 16-50 polyps per bite.	Removes 3-10 polyps per bite.	Removes coral skeleton along with polyps.	Removes prey without damage to substrate	Tears noncoralline prey loose.
Mouth direction, shape and size when maximally open	Anterodorsally directed gape, less prognathous, large	Anterodorsally directed, shovellike, not prognathous, large	Anteroventrally directed, somewhat prognathous, laterally enclosed, very robust, relatively large	Anteroventrally directed, lateral gap, moderate in size and prognathousness	Anteroventrally directed prognathous, lateral gap, moderate size.
Upper jaw protrusion	Reduced protrusion results in shovellike mouth.	Reduced protrusion results in shovellike mouth.	Slight protrusion.	Protrusion during feeding.	Protrudes jaw when lunging at polychaete worms, no hinges or protrusion on algae.
Average mean time for protrusion and retraction/msec	100	60	50	60	60
Premaxilla	Relatively short with short ascending process.	Very short with short ascending process.	Moderate in length with moderate ascending process.	Long with long ascending process.	Very long with long ascending process.
Dentary	Moderate length	Very short	Long	Moderate length	Long
Jaw dentition	Jaw teeth form pads, lower pad larger than upper, do not encircle mouth	Jaw teeth form a pad, lower pad larger than upper, do not encircle mouth	Massive spatulate shaped peripheral teeth, do not encircle mouth	Many rows of evenly spaced teeth that encircle mouth	Numerous rows of very recurved teeth that encircle mouth
Mean tooth bearing width	Very wide, dentary wider than maxilla	Wide	Wide	Moderate	Moderate
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) /gut length	10.2/long	8.0/long	8.0/moderate	4.5/moderate	5.8/moderate
Kinematic coefficient	9.1	7.2	4.4	5.2	5.1

retracts its jaw in 60–110 msec (Motta 1982), with a mean time of 80 msec. This is comparable to other velocity suction feeding fishes: *Gymnocephalus cernuus* (250 msec, Elshoud-Oldenhave & Osse 1976) and *Luciocephalus pulcher* (75 msec Lauder & Liem 1981), but slower than the ultrafast suction feeder *Antennarius hispidus* (4 msec for oral expansion and prey engulfment, Grobecker & Pietsch 1979) and *Pterois russeli* (10 msec for protrusion of the mouth, Osse & Muller 1980).

However, the morphologically specialized *F. longirostris* more nearly approaches the optimal pipette suction feeder. It has a very small, laterally enclosed mouth, the most protrusible jaw that is one of the fastest of the species examined (10 msec to maximum protrusion, and 40 msec for protru-

sion, closure and retraction), and a greatly reduced dentition (Table 1).

Fishes such as *C. miliaris* and *F. longirostris* that use rapid protrusion without extensive swimming are characterized by Muller & Osse (1984) as those that enlarge the velocity of the prey relative to the mouth aperture by using protrusion. Therefore, feeding can be shortened and the total impulse added to the fish's body and the water volume containing the prey kept small (van Leeuwen 1984). This type of feeding mechanism is useful for non-streamlined fish when feeding anywhere from open water to restricted spaces and from the bottom (Muller & Osse 1984). Therefore, in this feeding type, suction of a small volume of water with a very high velocity is possible. During the feeding

<i>F. flavissimus</i>	<i>C. trifascialis</i>	<i>C. multincinctus</i>	<i>C. miliaris</i>	<i>F. longirostris</i>
Grabs and tears larger benthic noncoralline invertebrates with front or sides of jaw.	Obligate hard coral browser that nips at individual polyps.	Obligate hard coral browser that nips at individual polyps.	Opportunistic zooplanktivore that uses inertial suction feeding.	High speed inertial suction feeder on small invertebrates.
Tears noncoralline prey loose	Removes 1 polyp per bite.	Removes 1 polyp per bite.	-	-
Anteriorly directed, very prognathous, lateral gap, very small.	Anteroventrally directed, forcepslike, lateral gap, prognathous, small.	Anteroventrally directed, forcepslike, lateral gap, less prognathous, small.	Anteroventrally directed, less prognathous, tubular, laterally enclosed, moderate size.	Anteriorly directed, very prognathous, tubular, laterally enclosed, very small.
Protrudes upper and lower jaws when feeding.	Protrudes jaw when feeding.	Protrudes jaw when feeding.	Protrudes jaw when using suction.	Very pronounced upper and lower jaw protrusion during suction.
80	-	40	80	40
Very long with long ascending process.	Relatively short with moderate ascending process.	Relatively short with moderate ascending process.	Relatively short with moderate ascending process.	Very long with long ascending process.
Very long Numerous rows of recurved teeth that encircle mouth.	Moderate length. Teeth massed toward anterior to form a pad	Short Teeth massed toward anterior to form a pad	Short Reduced in number recurved teeth encircle mouth	Very long. Very reduced in number and distribution.
Very narrow	Small	Small	Moderate	Very narrow
4.8/short	5.5/moderate	-/moderate	5.2/moderate	very short
-	6.3	7.6	6.2	-

act intermediate or low velocity swimming movements may be carried out (Muller & Osse 1984). On the other hand, pipette suction feeding as seen in *F. longirostris*, has an even higher directional sensitivity due to the small size of the mouth aperture. Unlike *C. miliaris*, pipette suction feeders such as *F. longirostris* are morphologically restricted to only very small food items because of their small mouth (Muller & Osse 1984).

Summarizing the coral scrapers, *C. ornatissimus* has a very large mouth that is wider than tall, reduced upper jaw protrusion, so much so that an asymmetrical shovel-like mouth is formed, a very wide pad of brush-like teeth that do not encircle the mouth, particularly on its lower jaw with which it combs the coral surfaces. The other coral scraper *C. trifasciatus* also has an asymmetrical mouth with reduced protrusion and a wide brush-like pad of teeth, however, its mouth is not as large as the former, nor does the lower jaw protrude as much (Table 1), and it has fewer teeth than *C. ornatissimus* (Motta 1985). Concomitantly, the very specialized *C. ornatissimus* removes more coral tissue during its relatively slow bites (100 msec) than does *C. trifasciatus*. The relatively slow jaw action combined with repeated scraping of a particular coral area allows the teeth to effectively brush the coral tissue off the skeleton.

Such a scraping dentition has been reported by others (Alexander 1974, Norris & Prescott 1959). Barel (1983) found that decreased lower jaw lengths and reduced premaxillary protrusion, such as we see here, helped to contribute to a greater biting force in biting cichlids. The application of this large tooth pad and jaw as it combs the coral surfaces probably demands greater effort than many of the other biting types. Barel also found that epilithic algal scraping cichlids and oral shell-ing molluscivores have reinforced lower jaws and suspensoriums. An increased bite force in these fishes was in part allowed by an increased length of the primordial process of the lower jaw allowing greater leverage for part of the adductor mandibulae muscle. Although not quantified, the suspensoria and jaws of *C. ornatissimus* and of a lesser extent of *C. trifasciatus*, are massive, and the ascending processes of the dentaries are relatively large (Fig. 8, 12).

The species that grasp and tear their prey exhibit convergence in form. *C. auriga* has numerous rows of very recurved teeth that encircle the mouth (Motta 1985), as well as a large lateral gap (Fig. 1). It grasps its prey with either the anterior or lateral parts of the mouth. Its very prognathous jaw, due to its long jaw bones, is used for probing in crevices (Table 1). Morphological parameters such as tooth bearing width and internal diameter of the mouth are, however, not significantly different from *C. quadrimaculatus* and *C. miliaris* (Fig. 3, 10). The other species that grasps and tears its prey, *F. flavissimus*, is also morphologically specialized for grasping and tearing its prey. It has a very small mouth with a large lateral gap (Fig. 1). The numerous, hooked teeth encircle the jaw like *C. auriga* (Fig. 9, 11, 12). It too grasps its prey with the anterior or lateral parts of the mouth. Goldschmid et al. (1980), Goldschmid (1982), Goldschmid & Kotschal (1981, 1985), Kotschal & Goldschmid (1983) and to some extent Lindquist & Dillaman (1986) found that semi-circular jaws suggest an omnivorous diet with emphasis on sessile organisms, while beak-like jaws indicate an emphasis on vagile organisms such as crustaceans and polychaetes. Capturing prey with a sideways movement of pincer-like jaws, such as in these two species, may prevent a backward flow of water due to the predator approaching the prey head on, and therefore, allow the predator to capture these vagile prey (Muller & Osse 1984). Jaw protrusion is also relatively rapid in these species (20 msec for *C. auriga* and 30 msec for *F. flavissimus*) which is important in the rapid capture of their vagile prey. In many cases the polychaete worms were observed to retract and escape predation faster than the fishes were able to capture them.

The coral browsing species *C. multinctus* and *C. trifascialis* both nip individual polyps with their anteriorly massed teeth. In both species the teeth do not lie on the descending process of the premaxilla and the ascending process of the dentary, otherwise, they do not encircle the jaw (Motta 1985, and Fig. 9). Nipping is always done with the anterior portions of the teeth. Both species have a rather prognathous jaw with a forceps-like mouth (Fig. 1). Their mouths are both relatively small (Fig. 3)

correlated with their small prey, and the tooth bearing widths are narrow and not significantly different (Fig. 10). The skulls are rather delicate (Fig. 8).

Lastly, *C. unimaculatus* grazes on soft and hard corals breaking off pieces of the skeleton along with the soft tissue. It does this by vigorously lunging at the coral. It has a very robust head and jaw in comparison to the other species (Fig. 8). The jaws are massive as well as the teeth (Fig. 9, 11, 12), and massed towards the anterior. Like the coral scraping species, it has a large mouth (Fig. 3) with a wide tooth bearing area (Fig. 10).

In terms of the gut length, a crude indication of their intestinal adaptations to their prey, the very specialized, obligate coral feeders *C. ornatissimus* and *C. trifasciatus* have the longest guts. Harmelin-Vivien & Bouchon-Navaro (1983) correlated a global repletion index for numerous species of butterflyfishes (Table 1). The index is based on the weight of the entire alimentary canal and that of the fish, and gives some indication of the relative importance of the guts in relation to the total weight of the fish. Surprisingly, they found that the index increases with coral feeding, as physiologically, corals represent more of a vegetable food than an animal food due to the large amount of symbiotic algae. *C. ornatissimus* and *C. trifasciatus* had very high values, as they have long intestines (Fig. 14). These species consume large quantities of coral tissue (see introduction). Both *C. multicoloratus* and *C. quadrimaculatus* supplement their diets with algae, the latter more so (Hourigan unpublished, Tricas 1985, Motta personal observation). Their intestines are not significantly different in length from *C. auriga*, *C. trifascialis*, and *C. unimaculatus* (Fig. 14). Strangely, *C. trifascialis* appears to feed exclusively on hard coral polyps, but does not have a relatively long gut (Fig. 14), or a high global repletion index (Harmelin-Vivien & Bouchon-Navaro 1983). Perhaps unlike the scraping species, it takes such a small mass of tissue per bite (one polyp) that the gut is not as accentuated as that of *C. ornatissimus* or *C. trifasciatus*.

The facultative zooplanktivore *C. miliaris* has a slightly shorter gut which correlates with the predominance of animal matter (calanoid copepods)

in the diet, and *F. flavissimus* and *F. longirostris* have the shortest intestines, which is further correlated with the amount of animal rather than plant material in the diet.

The amount of iron covering the caps of various butterflyfish teeth has also been correlated with their diet (Motta 1987). Similar to the above, *C. ornatissimus* is found to have one of the highest iron concentrations on the tooth tips. The iron has been shown to harden the teeth and resist abrasion in other vertebrates and invertebrates (Motta 1987). A highly significant difference has been found in iron concentrations between the coral feeding *C. ornatissimus*, *C. kleinii*, *C. trifasciatus*, and *C. multicoloratus*, which have high iron concentrations, and the following species that feed more on soft-bodied prey – *F. longirostris*, *F. flavissimus*, and *C. quadrimaculatus* – which have low iron concentrations.

The four-bar linkage model is a mechanical model of the levator operculi jaw opening mechanism that is used in the initiation of jaw opening in virtually all teleost fishes. It can be used to predict the efficiency of the lowering of the mandible (Liem 1980b). A high kinematic coefficient k implies that the velocity of the jaw opening mechanism is transmitted more efficiently, while a lower k implies that force is transmitted more efficiently (Anker 1974, Barel et al. 1975, 1977). With a high k , a large rotation angle of the mandible results from a small rotation angle of the gill cover (Anker 1974). The efficiency coefficients very generally correlate with the size of the food, with predators on large prey having a low k (therefore a force efficient jaw), and predators on small prey having a high k (therefore a kinematic efficient opercular apparatus) (Barel et al. 1975). High k values may also be an indicator that jaw movements are transmitted very efficiently, enhancing the velocity of mandibular depression, which has a pronounced effect on inertial suction for instance (Liem 1980b). In African cichlid fishes, piscivores have high values of k ranging from 5 to 17, while algae scrapers and invertebrate pickers have relatively low values of k ranging from 2.5 to 4 (Liem 1980b).

It has been correctly argued that comparing k without accounting for the interspecific variation in

skull width that occurs in the coronal plane is invalid, because comparing four-bar linkage systems means little if we cannot account for this variation (anonymous). However, in butterflyfishes there is little lateral variation in the compressed head dimensions among species, permitting at least, approximate comparisons of k .

In contrast to algae scrapers investigated by Liem (1980b), *C. ornatissimus*, the very specialized coral scraper, has the highest kinematic coefficient (9.1). This species uses the lower jaw almost exclusively. A high k implies that if the levator operculi muscle is similar in length and size among species, which it appears to be, then for a comparable angular movement of the operculum, the angular excursion of the mandible will be greater than in the other species. This is apparently what occurs (Fig. 8). Although the angle of the maximally open mouth (measured to the center of the open mouth and noting that the upper jaw only protrudes slightly in this species) is only significantly greater to that of *C. unimaculatus* which has a low k (Fig. 7), the angle made by the mandible is actually greater than in most of the species. The lower jaw of *C. ornatissimus* pivots through a large angle to lie anterior to that of most of the other species (Fig. 4). Therefore, a high k permits this large angular excursion, and consequently a very asymmetrical mouth that can be applied to the coral surfaces for scraping.

Chaetodon unimaculatus has a long (Fig. 6), robust mandible and feeds by vigorously lunging and biting off coralline tissue. A power-efficient mechanism is therefore most likely necessary to initiate jaw opening, and this species has the lowest k value of 4.4. The remainder of the species have intermediate k values ranging from 5.1 to 7.6, such that little definitive can be said of the measurements. My overall opinion on the four bar-model and k values is that the model at present is too simplistic, and to better understand and interpret such results we need information on at least the size, insertion, and contraction speed of the levator operculi, mandible mass and angular excursion, and the role of other muscles in assisting jaw opening.

The relationship between the pharyngeal dentition and the feeding habits of six species of butterflyfishes is not clear (Motta 1985) and therefore,

not pursued further. Examination of the gill rakers on a superficial level reveals patterns that do not always conform to the arrangement as presented in Figures 11 and 12. The planktivorous *C. miliaris*, the grazing *C. unimaculatus*, and *C. auriga* that grasps and tears pieces of non-coralline sessile invertebrates, have the longest gill rakers. Long, closely spaced gill rakers with better developed spines 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 act as a sieve, separating food from other material (Alexander 1974, Lagler et al. 1962). While this seems intuitively clear for the facultative zooplanktivore, *C. miliaris*, it is not clear for *C. auriga*. Perhaps the longer rakers in this species and in *C. unimaculatus* prevent the relatively large particles from escaping through the gills, and prevent damage to these tissues by calcareous fragments in *C. unimaculatus*.

The species that scrape large quantities of masticated tissue, *C. ornatissimus* and *C. trifasciatus*, have very short rakers that lack spines. Scraping the coral tissue may produce a bolus of tissue and mucus that is relatively large and unlikely to pass through the gill rakers, necessitating only short rakers. Greenwood (1974) postulated a similar hypothesis for cichlid phytoplankton feeders that entangle their prey in mucus boli. Robotham (1982), Sibbing & Uribe (1985) and others have suspected mucus entrapment of prey during feeding but the relationship to gill rakers is still not clear, and using inter-raker measurements as an estimate of prey capture success should be used with caution (Wright et al. 1983).

The coral-polyp pickers *C. trifascialis* and *C. multicinctus* both have short and somewhat spiny rakers, as do the long-nosed butterflyfishes *F. longirostris* and *F. flavissimus*. The functional significance of these is not clear. Hyatt (1979) noted that there is a lack of critical evidence relating gill raker numbers, length and spacing to food type or size. For instance, plankton feeders do not always possess well developed gill rakers (Hyatt 1979, Suyehiro 1942). Kapoor et al. (1975) found that gill raker equipment may vary in fishes with identical modes of feeding. Rather than continue adaptationist 'storytelling' (Gould & Lewontin 1979), these data are

presented to demonstrate that raker gross morphology is not simply related to prey size or type in these butterflyfishes and further research is necessary before conclusions can be drawn.

Evolutionary trends

If the phylogenetic relationships of these butterflyfishes according to Blum (personal communication) is accepted (Fig. 15), certain trends emerge. Evolutionary convergence in the feeding morphologies has apparently occurred in the more distantly related *F. flavissimus* and *C. auriga*. Both species show morphological and behavioral adaptations for grasping and tearing their prey. Likewise, the coral browsing and nipping *C. trifascialis* and *C. multincinctus* show convergence in their dentition and jaw structure. The suction planktonic feeders *C. miliaris* and *F. longirostris* have also converged on a form suited for inertial suction feeding. However, this implies that the sister species *F. flavissimus* and *F. longirostris* have diverged in terms of their feeding morphology and behavior to some extent, despite their overall gross similarity. Despite being more closely related to each other than to the remaining species, the group comprised of *C. quadrimaculatus*, *C. miliaris*, *C. multincinctus* and *C. unimaculatus* show a diverse range of morphological and behavioral adaptations for feeding. Finally, the sister species *C. trifasciatus* and *C. ornatissimus* show morphological similarity because they are closely related.

Feeding guilds and functional morphology

Numerous researchers have classified fish feeding habits into guilds such as herbivory, carnivory, omnivory and the like (Hobson 1968, Vivien 1973, Hiatt & Strasburg 1960, Randall 1967, Smith & Tyler 1973). Smith (1978) summarized the many classifications by feeding guilds. While this approach might be useful from an ecological standpoint, Smith & Tyler (1973) questioned it, stating that how and where a fish feeds are more important than what it eats. Fish are notably opportunistic in

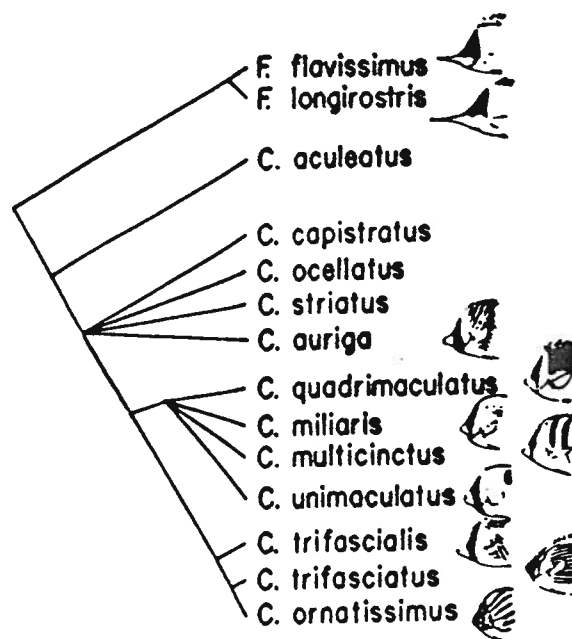


Fig. 15. The relative degrees of relatedness of some Hawaiian and Western Atlantic butterflyfishes based on thirty morphological characters (only five directly related to feeding). *Forcipiger flavissimus* and *F. longirostris* are sister species. The group comprised of *C. quadrimaculatus*, *C. miliaris*, *C. multincinctus* and *C. unimaculatus* are monophyletic. Likewise, *C. trifascialis*, *C. trifasciatus* and *C. ornatissimus* are believed to be monophyletic. *C. trifasciatus* and *C. ornatissimus* are almost certainly sister subgenera, and *C. ornatissimus* is one of the most morphologically derived butterflyfishes shown here (S. Blum personal communication).

their feeding, and the general impression is that how they feed tells much more than what they eat. Van Oijen et al. (1981) has noted that the classification of fishes into trophic groups is not consistent. It can be based on the systematic position of the food item (molluscivores), on the size (ontogenetic stage) of the food (paedophages), or on the location of the food (periphyton versus phytoplankton). Witte (1984) notes that morphologically, most trophic groups are recognized by a particular facies. A facies and its constituent structures is related more to the way food is collected than to the food type itself, as with oral shelling or pharyngeal crushing of molluscs. Barel (1983) found no simple relation between food and the feeding apparatus in cichlid fishes. This is the result of at least two factors: the feeding function is not necessarily the

only demand determining the structure of the feeding apparatus, and the functional significance of the feeding apparatus is to be understood in mechanical terms and food categories are subordinate to that. Kaufman & Ebersole (1984) likewise questioned the validity of exclusively classifying fishes by trophic guilds. They believe that much about the organization of fish assemblages can be understood by focusing on morphological and behavioral features in relation to the microtopographic features of the environment.

In the butterflyfishes examined, the compressed head and body shape may in part be determined by the swimming mode and an anti-predatory role, and not only by feeding. Chaetodontids are specialized for maneuvering and slow swimming, which in turn might be related to feeding on non-evasive, concentrated food sources (Webb 1984). Secondly, the functional significance of the butterflyfish feeding apparatus can probably be best understood in terms of their feeding mechanics, especially when we categorize the species investigated as nippers, scrapers, suckers, and biters and tearers. Otherwise, how they eat may be more important than what they eat, in terms of understanding the function and evolution of the feeding apparatus.

This study, and those such as Witte (1984) on African cichlids indicate that more in-depth studies of fish communities can reveal more specializations and species segregation than previously revealed. Witte showed that the four basic trophic groups in Lake Victoria – piscivores, insectivores, zooplanktivores, and molluscivores – show greater separation under close examination. The corallivorous butterflyfishes for example, show separation in terms of the corals they feed on (Reese 1975, Motta 1980 and others), temporal and spacial separation (Hobson 1968, Hourigan unpublished), as well as in terms of how they feed on the corals (scrapers, nippers, browsers, grazers), and related to the latter, the biomass of tissue removed.

Ecomorphological hypothesis

Numerous factors can influence a predators' prey utilization, among them are behavior and morphol-

ogy. One of the main premises of the ecomorphological hypothesis is that morphology is closely reflective of diet, and morphological resemblance between species is proportional to dietary resemblance and overlap (Findley & Black 1983, Grossman 1986). Based on the ecomorphological hypothesis we should be able to predict patterns in the ecology of individuals, populations, or species assemblages from the morphological characteristics (Wiens & Rotenberry 1980). Some studies on foraging behavior and morphology of birds and bats have found a close relationship between feeding ecology and morphology (Miles et al. 1987, Miles & Ricklefs 1984, Findley & Black 1983, Karr & James 1975, Cody & Mooney 1978), while others have found little correlation between morphology and diet (Wiens & Rotenberry 1980).

Studying an assemblage of twenty species of stream fishes, Moyle & Senanayake (1984) found that morphological specialization is associated with dietary and/or microhabitat specialization. However, using a set of a-priori morphological characters derived from previous studies of functional morphology, Felley (1984) found poor correspondence between ecological niche differences and morphology in cyprinids. An a-posteriori set revealed by factor analysis for a subgroup of cyprinids was more predictive. Liem (1980a) and Kotrschal (unpublished) have questioned the assumption that morphological specialization necessitates ecological specialization. They found that apomorphic species of fishes they studied are very generalized in prey choice and prey handling. The cichlid *Cichlasoma minckleyi* is polymorphic with a papilliform and a molariform type that exhibit vastly different trophic morphologies, yet Liem & Kaufman (1984) found that their feeding patterns are virtually identical.

Schmitt & Coyer (1982) found that disparate foraging behaviors were a much better indicator of the relative differences in diets between two surfperches than was external morphology. Grossman (1986) also found that behavior is more important than feeding morphology in determining prey utilization in 16 species of an intertidal marine fish assemblage. He found that morphological similarity was a poor predictor of dietary similarity, a

result in opposition to the ecomorphological hypothesis.

If the ecomorphological hypothesis applies to this butterflyfish assemblage, then firstly I would expect the more morphologically specialized species to have more specialized diets and vice versa; this relationship generally holds. The morphologically specialized coral scrapers *C. trifasciatus* and *C. ornatissimus*, and nippers *C. multincinctus* and *C. trifascialis* feed almost exclusively on coral tissue, although they may feed on a wide variety of corals and take some other non-coraline prey (Reese 1975, Motta 1980, unpublished, Hourigan unpublished, Tricas 1985, Bouchon-Navaro 1986). However, the species that are morphologically specialized for grasping and tearing, *C. auriga* and *F. flavissimus*, take a very wide range of prey from scleractinian corals to algae. Polychaete worms predominate in the diet of *F. flavissimus* at Moorea, and vermetid worms appear to predominate at Kona, Hawaii (Motta unpublished). Bouchon-Navaro (1986) found *F. flavissimus* to have one of the most generalized diets of the butterflyfishes they studied in the Johdanian coast and Moorea Island. *Chaetodon auriga* seems to take mostly scleractinians at Moorea (Harmelin-Vivien & Bouchon-Navaro 1983) and polychaete worms at Hawaii (Motta 1980, unpublished). What is consistent is not what prey is taken, but rather how the prey are taken.

The grazing *C. unimaculatus* is also quite labile in its prey choice although it prefers scleractinian corals (see introduction). The more morphologically generalized species *C. quadrimaculatus* and *C. miliaris* have the widest repertoire of prey choice as the ecomorphological hypothesis would predict. Along with *F. flavissimus*, Bouchon-Navaro (1986) also found *C. quadrimaculatus* to have one of the most generalized diets. However, all of these species are noticeably opportunistic in their feeding, and almost all have been observed to abandon their preferred prey and feed exclusively on abundant plankton sources for up to a few days (Motta 1980). Therefore, similar to the observations of Liem (1980a) and Kotrschal (unpublished) the very morphologically specialized species can be very generalized in their prey choice, what is more

consistent at least in terms of their benthic feeding, is how they capture the prey rather than what prey is taken.

The hypothesis also states that species with similar morphologies should possess similar diets. This is true for some species; *C. ornatissimus* and *C. trifasciatus* both have similar jaw and head morphologies and both browse scleractinian coral tissue by scraping. In fact, the choice of coral species and the relative number of bites on each coral is almost identical for both species in Hawaii (Motta 1980). Similarly, *C. multincinctus* and *C. trifascialis* have similar morphologies and browse individual coral polyps where they co-occur, such as in the Marshall Islands. However, as a group, the coral feeders that have similar diets have very different morphologies, that is, different morphological strategies for dealing with coral tissue. The browsing nippers (*C. multincinctus* and *C. trifascialis*), browsing scrapers-biters (*C. ornatissimus* and *C. trifasciatus*), and the grazing *C. unimaculatus* as a group have very different morphologies. In this respect the data do not support the ecomorphological hypothesis. The grasping and tearing species *C. auriga* and *F. flavissimus* have very different gross morphologies but similar diets, although their dentitions are similar in form.

These data do not particularly support the hypothesis that feeding morphology is a good predictor of what these butterflyfish feed on, rather, they predict how they feed. Therein might lie one of the reasons there has not been good fit to the hypothesis in some organisms. The ecomorphological hypothesis states, in part, that morphology and prey type are closely related. I believe that in some cases morphology is more related to how an organism feeds rather than to what it feeds on. Miles et al. (1987) and Miles & Ricklefs (1984) found that morphology is a good predictor of foraging substrate and how passerine birds maneuver during feeding. Secondly, researchers often measure parameters such as interorbital length, weight of the fish, and the like (Schmitt & Coyer 1982). I believe that these may be very distantly related to prey choice and lead to lack of correlation with diet. This might be why Findley & Findley (1985) found no relationship between morphology, diet, and

coexistence in Pacific and Caribbean butterflyfishes. They used morphological characters from the work of Burgess (1978) including mostly overall body measurements such as fin lengths, number of fin rays, and only a few of the 29 characters used were anything approaching structures directly related to feeding. My study indicates that measurements such as jaw shape, mouth width, prognathousness of the jaw, amount and speed of jaw protrusion, and particularly dentition patterns, may be better correlates, as indeed some others have found (Grossman 1986, Moyle & Senanayake 1984). Such parameters as the angle of the open mouth to the longitudinal axis of the body (the angle of jaw protrusion in most cases) seems only distantly related to prey choice. There are multiple evolutionary solutions to dealing with a particular prey type, such as coral tissue for example, and searching for an optimal or sole morphological strategy might be misleading. I propose that in some cases we test the ecomorphological hypothesis in terms of a close fit between feeding morphology and prey handling (how the organism feeds), rather than what it feeds on.

Evolutionary plasticity of the feeding apparatus

In my analysis of the jaws of six species of butterflyfishes (Motta 1985) I postulated as has Greenwood (1974, 1984), Liem & Osse (1975), and Liem (1970), that differences in jaw morphology might be accomplished by relatively simple changes in a few structural elements (premaxilla, dentary, dentition) that would be relatively rapid in the evolutionary time frame. Strauss's (1984) findings that apparent adaptational changes in African cichlid heads can best be explained by simple allometric relationships, supports the contention that differences among haplochromines are the result of subsequent changes in relative growth rates. Small heterochronic changes in development may lead to notable differences in form among species, even when the allometries remain constant or nearly so (Frazetta in Strauss 1984). A similar mechanism is believed to result in the polymorphic forms of the cichlid *Cichlasoma minckleyi* with its two distinct

trophic morphologies (Liem & Kaufman 1984). In these ten species of butterflyfishes, relatively minor changes in certain key elements, such as the premaxilla and dentary in particular, as well as structures such as the dentition, have led to a variety of trophic morphologies. In fact, relatively simple changes in a few elements can radically alter the jaw opening lever mechanism and change the kinematic coefficients (Liem 1980b). These concepts deserve further study.

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