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Dentition patterns among Pacific and Western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history

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Synopsis

The jaw dentition of fifteen species of Pacific and Western Atlantic chaetodontid butterflyfishes was examined in light of their feeding habits and phylogenetic relationships. The ancestral tooth pattern is typical of many of the butterflyfishes, and variations on this basic pattern involve changes in the arrangement, length and number of teeth, and tooth shape to a lesser extent. Many of the more derived conditions can be explained by simple changes in relative jaw shape and size. Despite what appears to be adequate time for evolutionary changes to occur between the Pacific and Western Atlantic faunas, many species retain the generalized tooth arrangement permitting efficient exploitation in a very generalized manner. However, Pacific species as a whole show more specialized morphologies for hard coral feeding than do Western Atlantic species. Cases of parallel and divergent evolution are identified between and among the two faunas. Most morphological change associated with feeding in butterflyfishes is confined to the anterior region of the head, and particularly a few key elements. Suggestions for future morphological studies on the chaetodontids are outlined.

Introduction

Feeding is an important biological role of the vertebrate head, and as such we expect to find morphological differences among species, particularly among species with divergent foraging strategies. Because the dentition and jaw structure of fishes appears to be evolutionary labile many studies have found good correlation between these parameters and foraging (Fryer & Iles 1972, Emery 1973, Greenwood 1974). Many of these differences are emphasized in sympatric populations of fishes that have undergone dramatic adaptive radiations, such as the African cichlid fishes.

Despite the fact that butterflyfish jaw dentitions look superficially alike, Hobson (1974) and Burgess (1978) described some differences, and I (Motta 1984, 1985, 1987, 1988) have elucidated major differences in shape, size, arrangement, number and even biochemical composition of their teeth that are related to how they forage.

In many cases we wish to interpret these differences or lack thereof, in an evolutionary context. While it is interesting to speculate about evolutionary changes that has occured in the feeding apparatus within certain taxa, it is most instructive to have an independently derived classification of the organisms upon which data can be superimposed. Blum's (1988, 1989) butterflyfish cladogram presents such a unique opportunity. With morphological data on fifteen species of Western Atlantic and Pacific butterflyfishes I can interpret my data on dentition patterns and jaw structure in an evolutionary context.

The chaetodontid butterflyfishes are a diverse group of circumtropical reef fishes (114 species, Burgess 1978) that derive their name from their bristle-like teeth (chaite = bristle, odon = teeth). The family is most speciose in the Indo-West Pacific, with diminishing species numbers with increasing distance from the area (Burgess 1978). In the Hawaiian Islands where this study was partly conducted there are approximately 20 species (Gosline & Brock 1960). In the Western Atlantic, particularly the Caribbean, there are seven species, five of which are primarily shallow water inhabitants (Hubbs 1963, Randall 1968). The biomass of butterflyfishes is also lower in the Caribbean-Eastern Pacific fauna as compared to the Indo-West Pacific fauna (Findley & Findley 1989).

Of all the Mid-Pacific forms already studied by me, only one species bridges the East Pacific barrier and is found on the west coast of North and Central America (*Forcipiger flavissimus*, Rosenblatt 1967, Burgess 1978). The Isthmus of Panama has separated the Pacific fauna from the Western Atlantic butterflyfishes for approximately two to five million years. None of the five Caribbean species studied here is found in the Pacific. Given this relatively long period of geographical separation and divergence of diets, this group provides an ideal opportunity to examine patterns in dentition that relate to foraging strategies and/or phylogenetic proximity among species.

Materials and methods

Feeding data

Diets and feeding habits of all the species are based on observations and gut content analyses by others (see Motta 1985, 1988, and below) and by field observations by myself. My observations are on adult specimens using SCUBA at Carrie Bow Cay and adjacent islands, Belize barrier reef; Port Royal Cays and Discovery Bay, Jamaica; south-west and north shore, St. Thomas; and Salt River canyon, St. Croix, U.S. Virgin Islands.

Species studied

Ten species of adult butterflyfishes were studied from the Hawaiian Islands and five from the Caribbean. These represent some of the most common and abundant species at the two locations. The diets and feeding behaviors of the Pacific species are detailed in Motta (1985, 1988) but are in brief: *Chaetodon miliaris* is an opportunistic zooplanktivore that feeds primarily on calanoid copepods; *C. trifascialis* is an obligate hard coral browser that is exclusively associated with *Acropora* corals (and therefore not very abundant in the Hawaiian archipelago); *C. auriga* is a benthic omnivore that tears off pieces of noncoralline and coralline invertebrates, particularly alcyonarians, polychaete worms, sea anemones, scleractinians and algae; *Chaetodon trifasciatus* browses on hard corals as does *C. ornatissimus* and *C. multicinctus*; *C. unimaculatus* is a facultative soft and hard coral grazer; *C. quadrimaculatus* is an omnivore that browses on algae, anthozoans, polychaetes and hydroids; *Forcipiger longirostris* is an inertial suction feeder on small invertebrates, mostly shrimps, feeding in crevices and between coral branches; and *F. flavissimus* is a predator grabbing and tearing pieces of larger, benthic noncoralline invertebrates.

These species are all distributed in the tropical Indopacific as far east as the Hawaiian Islands, except for the two long-nosed forms. *Forcipiger longirostris* the distribution of which is still not resolved but is found as far east in the Pacific as the Tuamotus, and *F. flavissimus* which is found as far east as the west coast of Mexico (Burgess 1978, Thomson et al. 1979, J. Briggs personal communication). *Chaetodon miliaris* is endemic to the Hawaiian Islands (Burgess 1978).

There is not as much data on the diets and feeding habits of the Caribbean species. *Chaetodon capistratus* the most common Caribbean butterflyfish, is a browser tearing one polyp loose per bite, primarily exposed (expanded) polyps. It uses slight rapid forward lunges and occasionaly lateral jerks of the head to capture its prey. Prey preference varies with location but includes gorgonians, scleractinians, zoantharians, polychaetes, anemones, and other small amounts of animal matter (Randall 1967, Birkeland & Neudecker 1981, Gore 1984, Lasker 1985, Motta personal observation).

Chaetodon striatus uses lateral jerks of the head and slight forward lunges during its prey capture. Randall (1967) found polychaete worms and anthozoans to predominate the gut contents, accompanied by a small amount of unidentified crustaceans, and mollusc eggs. Kaufman & Ebersole (1984) classed it as an invertebrate specialist. Therefore, this species apparently browses mostly on sessile non-scleractinian invertebrates, mostly by grabbing and tearing its prey.

The data on *C. sedentarius* is likewise depauperate. Based on my observations, and Randall's (1967) gut content data on three specimens, it appears to be very generalized in diet. It mostly grabs and tears small, sessile, non-scleractinian invertebrates, but also takes scleractinian and gorgonian polyps, algae, small motile invertebrates such as shrimp, and may often feed on plankton. It too uses slight forward lunges and lateral swipes of the head.

Chaetodon ocellatus uses lateral swipes a great deal, as well as forward lunges. Aiken (1975) reports that it feeds mostly on polychaetes, echinoderm tube feet, amphipods, algae, unidentified crustaceans and unidentified eggs. It also appears to primarily feed by grabbing and tearing its sessile prey.

Chaetodon aculeatus is a highly selective predator grabbing and tearing polychaetes, crustaceans, and eggs, oftentimes with very rapid forward lunges. However, it also browses tentacles from tubeworms, and pedicellariae and tubefeet from echinoids (Randall 1967, Birkeland & Neudecker 1981, personal observation). Similar to *C. auriga* and *F. flavissimus* it spends considerable time searching for its prey in rubble, and in-and-around ledges and holes.

These five species are distributed throughout the Western Atlantic Ocean from South America partially up the east coast of North America, and are generally found throughout the Caribbean. They are not found in the Pacific Ocean and do not bridge the Isthmus of Panama (Burgess 1978, J. Briggs personal communication).

Dentitions

The tooth bearing premaxillae and dentaries were removed and cleaned briefly in 5% sodium hypochlorite solution in an ultrasonic cleaner. These bones and the teeth of the ten Pacific species are detailed in Motta (1985, 1988) and butterflyfish tooth structure is given in Motta (1984). The dentaries of all species were illustrated with a camera lucida. Tooth rows on five to ten individuals of each species were counted in the symphysial region of the upper and lower jaw. In species without discrete tooth rows visible, the jaws were cleaned until all the teeth were removed by dissolving their collagenous attachment, and the tooth pedicel rows counted on the jaw.

Cladistics

The cladogram is that of Blum (1988, 1989) and includes only those species investigated here. Blum's cladogram encompasses many more species than presented here, and is based on a parsimony analysis of 34 variable features of osteology and soft anatomy, coded as 50 binary and two multistate unordered characters. These include ten post cranial, seven branchial, and 17 skull characters. Pomacanthids are used as the first outgroup, and the second outgroup contains *Drepane*, ephippids, scatophagids, and the Acanthuroidei.

Results

The dentitions of the ten Pacific species are detailed and illustrated in Motta (1985, 1988). The dentaries of all species, with the tooth arrangement, is illustrated in Figure 1. The premaxillae of these species have similar tooth arrangements to the dentaries. The dentition patterns of the 15 species examined can be grouped into the following

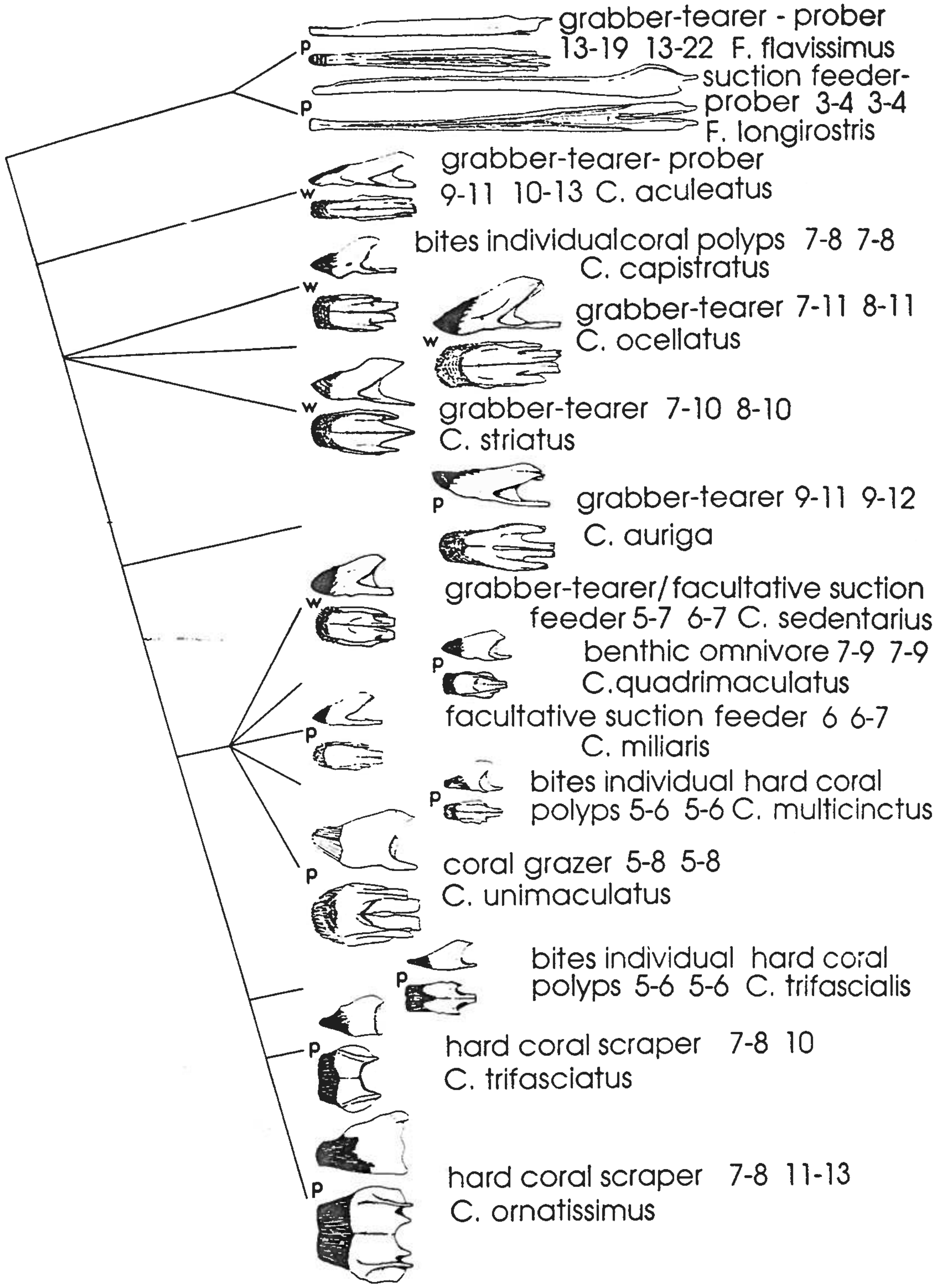

Fig. 1. Left lateral and dorsal view of the dentary of fifteen species of Pacific and Western Atlantic butterflyfishes arranged in a cladogram representing the relative degrees of relatedness. The extent and distribution of the jaw teeth are indicated as well as the summarized feeding behavior for each species. Number of symphysial tooth rows in the premaxilla (left) and dentary (right) is indicated for each species beside the feeding behavior (p – Pacific species, w – Western Atlantic species).

general categories:

1. Teeth in distinct rows with the more lingual teeth being shorter, finer, and more villiform: and more labial teeth more spatulate such that a gradation exists. Teeth lie on the ascending process of the dentary and the descending process of the premaxilla, so that the teeth encircle the mouth. Included are: *C. aculeatus, C. auriga, C. capistratus, C. quadrimaculatus, C. miliaris, C. ocellatus, C. sedentarius, C. striatus,* and *C. unimaculatus.*

2. Teeth in distinct rows with the more lingual teeth being shorter, finer, and more villiform, and more labial teeth more spatulate such that a gradation exists. Teeth do not lie on the ascending process of the dentary and descending process of the premaxilla, otherwise, teeth do not encircle the mouth. *C. multicinctus* is included in this category.

3. Teeth lie in very few distinct rows, mostly on the anterior edges of the jaws. The teeth are all short, villiform, and oriented approximately dorsoventrally, however, lingual teeth are slightly shorter than more labial ones. This includes *F. longirostris*.

4. Teeth lie in numerous distinct rows, groups of rows forming externally visible bands. The short, villiform teeth encircle the mouth, lying on the ascending process of the dentary and the descending process of the premaxilla, and are mostly oriented in a dorsoventral direction. Lingual teeth are only slightly shorter than more labial ones which are slightly more spatulate and longer. This includes *F. flavissimus*.

5. Teeth are mostly massed towards the anterior, spatulate, and approximately the same length, however, there are a few more lingual teeth that are shorter and more villiform. Examination of the tooth pedestals with the teeth removed reveals, as in all the other species examined, that the teeth actually lie in distinct rows grouped into bands. However, because the tooth tips lie in approximately the same transverse plane, they appear as an anteriorly massed pad. Teeth 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. This includes *C. ornatissimus, C. trifascialis,* and *C. trifasciatus*.

The species within the group-one category are, however, not entirely similar. Some of the species have very few rows of teeth, *C. unimaculatus* and *C. miliaris* for example, and others have more tooth rows, *C. aculeatus* and *C. auriga*. The peripheral teeth of *C. unimaculatus*, a grazer that damages the coralline portion of the coral skeleton, are extremely robust. The orientation of the teeth also varies among these species.

In the series *C. auriga, C. aculeatus*, and *F. flavissimus* the tooth pedestals become increasingly dorsoventrally directed as the dentigerous or tooth bearing portion of the jaw becomes more longitudinally oriented. Furthermore, the teeth lie further up the ascending process of the dentary (Fig. 1), and further down the descending process of the premaxilla. In essence, these jaws become increasingly depressed, the ascending and descending processes less pronounced, such that the tooth bands become visible when viewed from above as illustrated on the dentaries. Tooth bands are visible on all of the species when the teeth are removed, but it becomes increasingly evident as the teeth become more dorsoventrally oriented.

Choosing four common points on the dentaries of three very disparate jaw types from *C. quadrimaculatus, C. ornatissimus*, and *F. flavissimus* emphasizes the anatomical differences. *Chaetodon quadrimaculatus* has seven to nine discrete rows of teeth in the dentary. These teeth are attached to tooth pedestals (Motta 1984) that lie in rows grouped into bands (Fig. 2). The dentigerous surface of the jaw lies approximately in a transverse plane, with the pedestals projecting in the longitudinal direction. The more dorsal teeth are shorter and finer in this species, whereas the more ventral teeth are longer and thicker. Because the pedestals lie on above the other in the transverse plane, the more dorsal teeth (the short and fine ones) do not extend as anterior as the ventral ones, and distinct tooth rows are visible dorsally.

Chaetodon ornatissimus has 11 to 13 tooth rows on the dentary and the teeth appear as an anteriorly massed pad. The same four reference points on this jaw (Fig. 2) show that the jaw is foreshortened, and the anterior tooth bearing surface is sloped such that the dorsal surface overhangs the ventral surface. The result is that even though the more dorsal

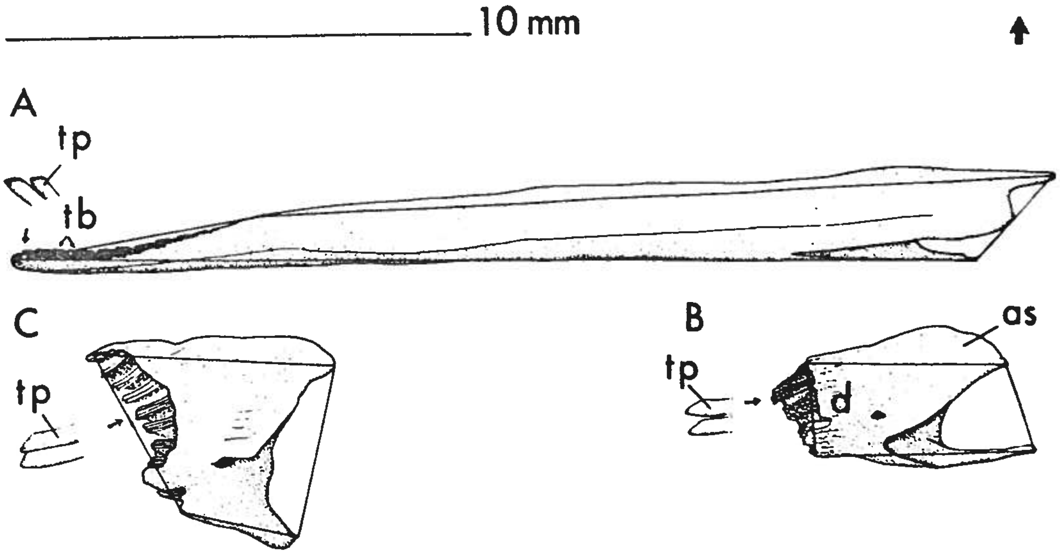

Fig. 2. Dentaries of three representative butterflyfishes with the teeth removed. Four common points on each bone are connected to indicate the relative shape changes in the jaw types. Representative tooth pedestals are enlarged: A – *F. flavissimus;* B – *C. quadrimaculatus;* C – *C. ornatissimus.* Arrow in upper right indicates dorsal (as – ascending process of dentary, d – dentigerous area of jaw, tp – tooth pedestals).

teeth are somewhat shorter and finer, they lie approximately as far anterior as the more recessed ventral teeth and all the teeth then form a pad with all the tooth tips lying at about the same location. Tooth rows are not evident when viewed dorsally.

Forcipiger flavissimus has a lenghtened jaw and with almost a longitudinally oriented tooth bearing surface (Fig. 2). In this case the tooth pedestals are oriented in a more dorsoventral direction, and because the teeth are all of approximately the same length, the 13 to 22 rows of teeth form a dorsoventrally oriented pad of short, villiform teeth. The tooth bands are now visible when viewed dorsally.

Discussion

The structure of butterflyfish teeth has been described in detail elsewhere (Motta 1984, 1985, 1987, 1988). Basically they are comprised of a form of dentine partly covered by an enameloid substance (Orvig 1977, Poole 1971). Each tooth has a shaft with a pulp cavity, and a tooth cap capped with iron (Motta 1984, 1987). Jaw teeth are borne on the premaxilla and dentary in a region referred to as the dentigerous area. Burgess (1978) noticed three distinct patterns of tooth arrangement in butterflyfishes. The most common arrangement is a series of discreet tooth rows. The others are a series of tooth bands (a band being composed of more than one row in close apposition) or a single anterior band. I recognize five categories of tooth pattern in these 15 species. The most common arrangement is a series of discreet tooth rows, showing marked gradation from more villiform, smaller, and shorter teeth in the lingual region, to more spatulate teeth labially. In fact, in all the butterflyfishes examined, the more lingual teeth are smaller and more villiform, although there might be fewer of these teeth in some species.

The functional teeth are all attached to bony pedestals (Motta 1984). The pedestals are in turn arranged in discreet bands in all species although the bands might not be visible externally in some species. In the majority of species with discrete rows of teeth visible, the pedestals lie in a plane that is not quite transverse on the jaw bone, that is, the dentigerous surface is approximately transverse (*C. quadrimaculatus*, Fig. 1). Blum (1988) also found that in most chaetodontids and outgroup taxa, the descending process of the premaxilla is toothed, and the angle between the ascending and descending processes is approximately 90 degrees.

The teeth of the different rows are of different length, such that viewed from the gape one sees discreet rows of teeth and not bands. Because the more dorsal teeth on the dentary are shorter, and their pedestals lie approximately in a transverse plane with the other pedestals, there caps lie more lingual to the other teeth, and so forth for the other rows, such that discrete rows are formed. The same arrangement applies to the premaxilla teeth.

The majority of the species in this type 1 category (see results) have teeth encircling the mouth, that is, teeth lying on most of the descending process of the premaxilla, and on most of the ascending process of the dentary. Other dentition patterns are variations on this arrangement. *Chaetodon multicinctus* varies from this pattern somewhat by not having teeth on most of the ascending and descending processes. In butterflyfishes with primarily a single anterior band of teeth forming a pad, *C. ornatissimus* for example, the dentigerous area of the jaws may be sloped such that the more medial or inner portion lies more anterior than the more outer or distal portion (Fig. 1). There still exist tooth rows and tooth bands, but the shorter inner or proximal teeth lie approximately as far anterior as the longer, more distal teeth because their pedestals lie more anterior than those of the larger teeth. In this way of pad of teeth is formed that has all the teeth with their caps approximately as far anterior as each other, and the tooth rows are not visible externally. This is seen in *C. ornatissimus*, *C. trifasciatus*, and less so in *C. trifascialis*.

In the series *C. ocellatus, C. auriga, C. aculeatus*, and *F. flavissimus*, the dentigerous area becomes increasingly sloped towards the longitudinal, or frontal plane. *Forcipiger flavissimus* has 13 to 22 rows of teeth in four mid-sagittal bands, the teeth all point approximately dorsoventrally, and the more lingual teeth are still slightly shorter and finer (Motta 1988) (Fig. 1). In this species the tooth bands are visible along with the tooth rows, and the dentigerous area is lengthened.

These arrangements are all variations on a theme, rows of teeth arranged into bands. What varies is the three dimensional arrangement of the teeth, relative length of the teeth, number of teeth, and tooth shape to less extent. Unlike the African cichlid fishes that display a range of tooth types (conical, bicuspid, tricuspid) (Fryer & Iles 1972, Greenwood 1974, Liem & Osse 1975), the butterflyfish tooth type is remarkably constant despite the various specializations.

By lengthening the jaw bones and reorienting the tooth pedestals dorsoventrally during the evolution of the species, *F. flavissimus* for example, has formed numerous rows of recurved teeth that lie in bands (Fig. 1). This species has a relatively large lateral slit in the gape, one that is lined with numerous rows of teeth. This jaw can effectively grasp and hold its worm-like prey. The two long-nosed forms, *C. aculeatus* in the Western Atlantic, and *F. flavissimus* in the Pacific both have similar diets of sessile non-scleractinian invertebrates such as worms, and they both have similar jaw morphologies and dentitions. These two species are ecological equivalents (Pianka 1975) as they fill similar ecological niches in different independently evolved faunas.

Most of these dentition patterns could be accomplished by simple proportional changes in the jaw length and orientation of the tooth pedestals. Using a coordinate system similar to that of Thompson (1961) whereby four coordinates are outlined for each jaw, the relative depression of the dentary and reorientation of the dentigerous area is emphasized (Fig. 2).

Greenwood (1974, 1984) found that what differences there are in jaw shape among the Lake Victoria *Haplochromis* cichlid fishes are attributed to allometric growth changes. The generalized oral dentition among haplochromines in Lake Victoria and elsewhere comprise an outer row of unequally bicuspid teeth backed by two or three rows of smaller, tricuspid teeth. Departures from this pattern are principally by changed relative proportions in shape, in number, in differentition of cusp pattern, and in the pattern of tooth distribution in the jaws. None of these changes seem to involve macromutations or other extraordinary evolutionary events (Liem & Osse 1975). Similar to the coral scraping butterflyfishes *C. ornatissimus* and *C. trifasciatus*, there is a trend among the epiphytic algal-scrapers of Lake Victoria for increase in the inner tooth rows and a tendency for the inner teeth to match the outer teeth (Greenwood 1984).

The most plausible vicariance model of Caribbean and Eastern Pacific fish faunas implies that butterflyfishes of the two regions were at once congruent. This original Eastern-Pacific-Caribbean track was fragmented (Rosen 1975). The butterflyfish fauna of the Eastern Pacific and Caribbean were separated at latest, during the rise of the Isthmus of Panama some two to five million years ago (Woodring 1966, Vawter et al. 1980, Futuyma 1986). The new world landmass constitutes a barrier that is virtually complete as witnessed by the fact that there are probably less than a dozen shore fishes common to the tropical waters on both sides of the isthmus (Briggs 1961). Damselfishes on both sides of the isthmus have been shown to have considerable genetic differentiation despite little morphological change (Gorman et al. 1976, Gorman & Kim 1977), and the presence of so called geminate pairs of fishes, Atlantic and Pacific fishes which are morphologically close but different species, indicates the degree of genetic divergence possible. However, distinct morphological changes can occur in a much shorter time period; the explosive speciation of the African lake cichlid fishes took place in the geologically short time span of 750000 years (Greenwood 1984). Greenwood (1974, 1984), Liem & Osse (1975), and Liem (1970) have argued that relatively simple allometric changes such as these might be relatively rapid in the evolutionary time frame. In part, the evolutionary success of the haplochromine cichlid fishes in the African lakes could be due to the relatively simple and rapid adaptive modifications of their cranial anatomy (Greenwood 1974).

As most of these Pacific butterflyfishes, with the exception of *F. flavissimus*, are Indopacific in distribution and not found in the eastern Pacific, their time of separation from the Western Atlantic fauna is most likely more than two to five million years. Blum (1988, 1989) has provided a hypothesis of phylogenetic relationship for these 15 species (Fig. 3). This permits discussion of the evolutionary changes in the dentition as discrete events in the phylogeny of chaetodontids.

Based on outgroup comparisons (Blum 1988, personal communication) the ancestral butterflyfish dentition might be best exemplified by *C. capistratus*, *C. ocellatus*, or *C. striatus*. This type of dentition is characterized by setiform teeth: tooth caps unicuspid and slightly spatulate; four to five fold differences between the most labial and lingual teeth; teeth at about 30 degrees from the horizontal; three bands of tooth rows along the medial symphysis with three overlapping rows in the most labial band. The ancestral condition is exemplified by the majority of the species examined here: *C. capistratus*, *C. ocellatus*, *C. striatus*, *C. sedentarius*, *C. quadrimaculatus*, and *C. miliaris* (category 1 of results).

If this is the case, parallel evolution in dentition patterns and jaw form has occured among *F. flavissimus*, *C. aculeatus*, and *C. auriga* with their apomorphic elongated jaw bones, reorientation of the tooth rows in a more dorsoventral direction, and numerous rows of teeth that encircle the mouth. This dentition and jaw structure is suited for probing in crevices, and grasping and tearing their prey (Motta 1985, 1988). I previously indicated that this implies convergent evolution (Motta 1988), but it is better described as parallel evolution. Ideally, convergent evolution involves cases in which similar phenotypes have evolved by different developmental pathways (Futuyma 1986), or it can be defined as the production of a set of similar phenotypic characteristics in phylogenetically unrelated organisms subject to similar abiotic or biotic agents on natural selection (Cody & Mooney 1978). On the other hand, parallel evolution refers to independent developmental modifications of the same kind. Whereas, related species have similar developmental programs, parallelism is frequent among closely related species (Futuyma 1986).

Similarly, the dentition and jaws of *C. multicinctus* and *C. trifascialis* show parallelism. These species are obligate hard coral browsers that nip one polyp per bite, and both have small jaws with teeth that are massed towards the anterior (Motta 1985, 1988). Most of the teeth are similar in length, but more so in *C. trifascialis*, and there are no teeth on

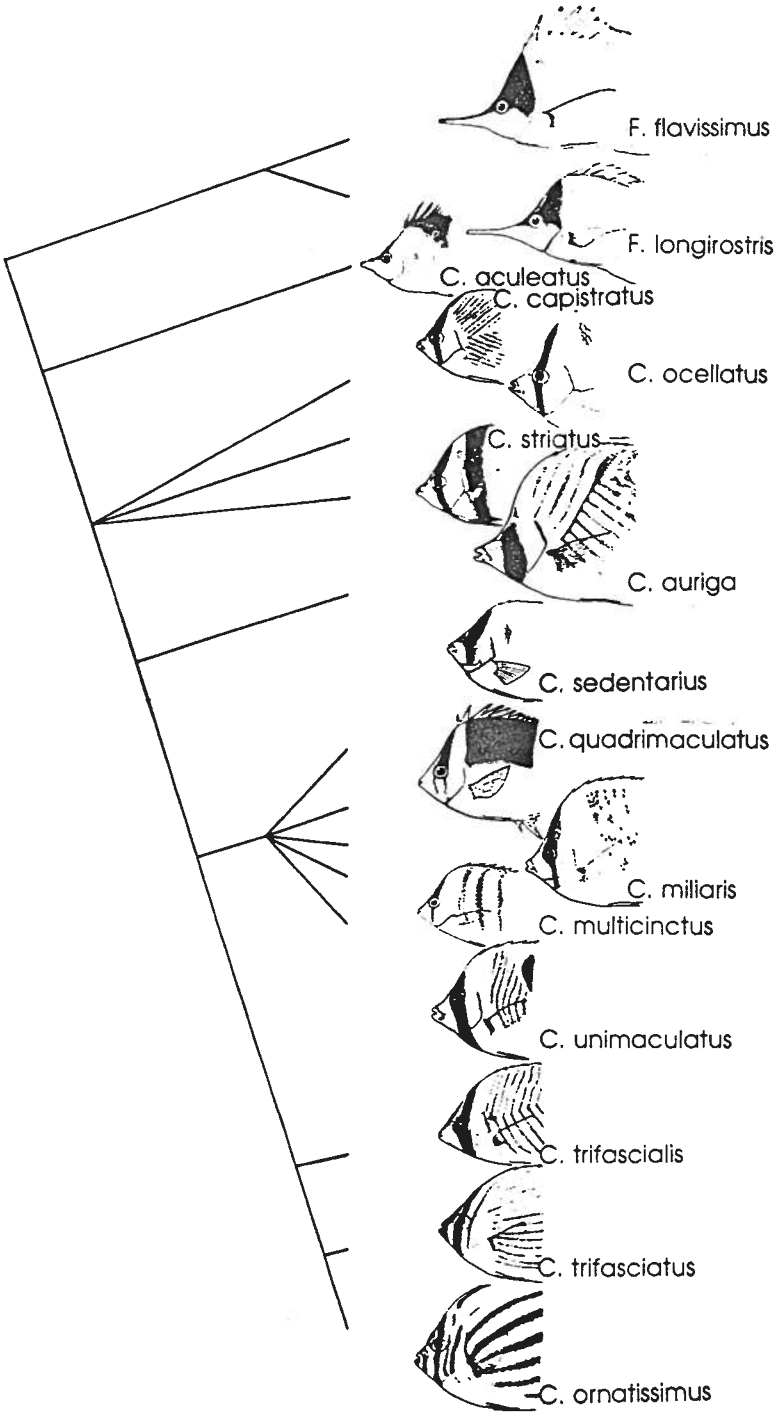

Fig. 3. The relative degrees of relatedness of some Hawaiian and Western Atlantic butterflyfishes based on thirty four morphological characters (see text for explanation). The heads are illustrated with the mouth in the relaxed position. *Forcipiger flavissimus* and *F. longirostris* are sister species. The group comprised of *C. sedentarius*, *C. quadrimaculatus*, *C. miliaris*, *C. multicinctus*, and *C. unimaculatus* are monophyletic. Likewise, *C. trifascialis*, *C. trifasciatus*, and *C. ornatissimus* are believed to be monphyletic. *C. trifasciatus* and *C. ornatissimus* are almost certainly sister subgenera (S. Blum personal communication).

most of the ascending process of the dentary and the descending process of the premaxilla.

The robust peripheral teeth of the coral grazing *C. unimaculatus* (Motta 1985, 1988) is an autapomorphic character that apparently is not shared with any other butterflyfish. The dentition pattern of teeth massed towards the anterior to form a pad with fewer teeth on the ascending process, such as on *C. trifascialis*, *C. trifasciatus*, and *C. ornatissimus* (Fig. 1) is synapomorphic. However, the sister species (Blum 1988, personal communication) *C. trifasciatus* and *C. ornatissimus* have a highly derived synapomorphic shovel-like mouth (Motta 1985, 1988) that is suited for combing corals to remove soft tissue.

The sister species *F. flavissimus* and *F. longirostris* have undergone divergent evolution in their dentition, with the latter being specialized for high speed inertial suction feeding on small, suspended invertebrates (Motta 1988).

Among the species there is also a range in number of tooth rows in addition to the shape, size, and distributional differences of the teeth. The most specialized suction feeder *F. longirostris* has a greatly reduced dentition typical of plankton feeding fishes (Gregory 1933, Suyehiro 1942, Lagler et al. 1962, Davis & Birdsong 1973, Emery 1973, Alexander 1974) although the reasons for this are not entirely clear. Both *C. miliaris* and *C. sedentarius* are very generalized feeders taking a wide range of prey types, and both are facultative inertial suction feeders on plankton, *C. miliaris* more so. Both of these species have about five to seven rows of teeth in each jaw.

The two obligate coral browsers *C. multicinctus* and *C. trifascialis* that nip individual hard coral polyps also have few tooth rows which is correlated with the very small jaws (Motta 1988) that form pincher-like mouths. *Chaetodon capistratus* has a broader diet, removing individual stony and soft coral polyps along with a variety of other prey, and its dentition is more pleisiomorphic compared to the very specialized Pacific hard coral feeders. On the other extreme, the species that browse on sedentary, non-scleractinian invertebrates by grabbing and tearing them loose, *F. flavissimus*, *C. aculeatus*, *C. ocellatus*, *C. striatus*, and *C. auriga*, have an increase in tooth row number, forming numerous distinct rows of teeth that are often more dorsoventrally oriented. These teeth encircle the mouth and allow them to hold onto their vagile prey (Motta 1985, 1988). Elongation of the jaws and dentigerous area may accompany the increase in tooth row number.

Butterflyfish diversity diminishes from the Indo-Pacific, with 30 species in the Marshall and Marianas Islands for instance (Schultz et al. 1953), 20 in the Hawaiian Islands (Gosline & Brock 1960), and seven in the Western Atlantic (Hubbs 1963, Randall 1968). There is a greater diversity of dentition and jaw morphologies among the Pacific species examined than among the Western Atlantic species, but this could be an artifact of the greater number of species in the Pacific. If a random sample had only examined five Pacific species, *C. auriga*, *C. quadrimaculatus*, *C. miliaris*, *C. multicinctus*, and *C. unimaculatus* for example, then the morphological diversity would have been little greater than that exemplified by the Western Atlantic species.

The five common Western Atlantic species investigated here have been isolated from the ten Pacific species for a considerable period of time, long enough for distinct morphological changes to occur. If the selection pressures associated with feeding are similar in the Pacific and the Western Atlantic butterflyfish faunas, then I would expect ecomorphological convergence between them, similar to that found in other vertebrates, for example birds from different continents (Karr & James 1975, Cody 1975, Cody & Mooney 1978), and desert lizards (Pianka 1975, Cody & Mooney 1978). However, I would expect to find differences under varying selection pressures, for example, alcyonacian soft corals are more represented in the diet of some of the Caribbean species examined, whereas hard scleractinian corals are proportionaly more important in the diet of some of the Pacific species.

There appears to be greater morphological specialization for feeding on hard corals in the Pacific, with the nipping jaws of *C. multicinctus* and *C. trifascialis*, the scraping jaws of *C. ornatissimus* and *C. trifasciatus*, and the robust jaws and teeth of the coral grazing *C. unimaculatus*. However, feeding on sessile non-coralline invertebrates such as tubeworms, pieces of echinoids, and the like, appears to pose similar evolutionary pressures in both faunas, and beak-like jaws for probing in crevices and numerous rows of short, dorso-ventrally oriented teeth have evolved to a greater and lesser extent in *C. ocellatus, C. auriga, C. aculeatus,* and *F. flavissimus*. However, despite at least two to five million years of separation, many of the species retain an ancestral dentition that is extremely versatile, permitting efficient exploitation of the benthos and the plankton. In these cases it appears that behavior determines dietary preference more than feeding morphology.

Butterflyfishes are remarkably consistent in body form. The morphological variation that exists is mostly in cranial anatomy, particularly the anterior regions of the feeding apparatus. Greenwood (1974, 1981) similarly found that most of the adaptive radiation in the Lake Victoria haplochromine cichlids occurs chiefly in the cranial anatomy and is developed through simple morphological transformations involving differential growth patterns in the various skull regions, coupled with similar changes in the jaws and suspensorium. Relatively simple changes in dentition, accompanied by other changes in a few key elements of the head such as the premaxilla and dentary (Motta 1985, 1988) have resulted in a diversity of feeding types among the butterflyfishes.

Future morphological research on butterflyfish feeding adaptations should expand the investigation on comparative osteology and myology of other species to reveal if and how the neurocranium as a whole has responded to these evolutionary changes, and further interspecific comparisons should be made on the cranial feeding adaptations. Further studies are needed to reveal whether my studies on 15 species have exhausted the major morphotypes in the group, or if there is additional diversity in the feeding structures. Another area that needs to be thoroughly explored, is the ecomorphological hypothesis that butterflyfish feeding and morphology are intimately related. Using various morphological parameters that appear to be directly related to feeding (Motta 1985, 1988), a multispecies study using principal component analysis and cannonical correlation should be made to investigate the relationship between feeding morphology and feeding ecology (Motta 1988).

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