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FISHES OF THE SUBORDER LABROIDEI (PISCES: PERCIFORMES): PHYLOGENY, ECOLOGY, AND EVOLUTIONARY SIGNIFICANCE

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ABSTRACT. We postulate that the Pomacentridae, Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic assemblage: the Labroidei. Four groups within the Labroidei can be defined as monophyletic assemblages on the basis of shared derived characters: the Pomacentridae, Cichlidae, Embiotocidae, and Labridae (which includes the Scaridae and Odacidae). The Pomacentridae is considered the primitive sister group of all other Labroidei; the Cichlidae is a sister group of embiotocids and labrids, and the Embiotocidae is a sister group of the Labridae. Labroids are characterized by (1) united or fused fifth ceratobranchials resulting in the formation of one functional unit; (2) a true diarthrosis between upper pharyngeal jaws and the basicranium without an intervening part of the transversus dorsalis anterior muscle; and (3) the presence of an undivided sphincter oesophagi muscle forming a continuous sheet. It is proposed that (1) the ecological and functional versatility of the trophic apparatus is correlated with a characteristic structural design, and that (2) this design has contributed to the dominant position of labroids in diurnal communities of tropical marine and lentic fresh waters.

INTRODUCTION

Liem and Greenwood (1981) have recently reviewed the comparative functional morphology of the pharyngeal jaw mechanism in acanthopterygian fishes. On the basis of functional considerations they have proposed that the Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic assemblage.

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Pharyngognathy, as expressed in the Cichlidae, has been correlated with several functional and ecological attributes which distinguish cichlids from most other Acanthopterygii. First, cichlids can mechanically process a broader range of food types (Liem, 1974). Second, they have greater feeding versatility (Liem and Osse, 1975; Liem, 1980) and hence a broadened fundamental niche (*sensu* Hutchinson, 1958, 1965). Finally, cichlids exhibit an extremely high species diversity, perhaps because extinction rates in changing environments are decreased (Liem, 1982). To test this hypothesis, evolutionary patterns in the Cichlidae must be compared with those of related fishes both more and less specialized with respect to pharyngeal jaw morphology. Such an analysis requires a thorough knowledge of phylogenetic relationships (Lauder, in preparation). In this paper we offer a revised hypothesis of the phylogenetic relationships of pharyngognath acanthopterygians first proposed by Liem and Greenwood (1981). New morphological evidence offered here and by Stiassny (1981, personal communication) requires the inclusion of the Pomacentridae in the monophyletic assemblage Pharyngognathi (*sensu* Liem and Greenwood, 1981), and a rearrangement of the Embiotocidae as the sister group of the Labridae instead of the Cichlidae. The resulting scheme of classification is as follows:

Suborder Labroidei

Family Pomacentridae

Family Cichlidae

Family Embiotocidae

Family Labridae (including Labridae, Odacidae, Scaridae)

The proposed phylogenetic relationships provide a basis for assessing patterns of change in the feeding apparatus, historical consequences of new feeding mechanisms, and the evolution of coral reef fish communities.

MATERIALS AND METHODS

Morphological studies were conducted with the aid of a Wild-M5 dissecting microscope and camera lucida. Clearing and staining followed the techniques of Taylor (1967). Scanning electron microscopy was conducted on an AMR-1000, and x-ray cineradiography of feeding labrids and cichlids was carried out using the Siemens Cineradiographic Unit at 150 frames sec⁻¹. The following material was examined:

Pomacentridae: *Abudefduf taurus* MCZ 42755, *Amphiprion xanthurus* MCZ 14852, *A. percula* MCZ 33399, *Dascyllus trimaculata* MCZ 14837, *D. albisella* MCZ 51671, *Eupomacentrus planifrons* MCZ 44745, *E. acapulcensis* MCZ 43961, *Pomacentrus littoralis* MCZ 5794, *Chromis atrilobatus* MCZ 44640.

Cichlidae: "*Haplochromis*" *leuciscus* MCZ 49517.

Embiotocidae: *Rhacochilus vacca* MCZ 57708, *Damalichthys vacca* MCZ 54333, *Cymatogaster aggregata* MCZ 57707, *Phanerodon furcatus* MCZ 54334, *Embiotoca jacksoni* MCZ 54332.

Labridae: *Tautogolabrus adspersus* uncat., *Tautoga onitis* uncat.; *Halichoeres bivittatus*, *Scarus croicensis*, *Sparisoma viride*, all MCZ acq. 1981-002-6.

Caribbean reef fishes were studied in Salt River Canyon and Tague Bay, St. Croix, U.S. Virgin Islands, and also studied at the Discovery Bay Marine Laboratory, Jamaica, W.I. Ecological classifications of reef fishes were based in part on observations made from the NULS-I Hydrolab during mission 81-8.

ANALYSIS OF CHARACTERS

Definition of the Labroidei

We postulate that the Pomacentridae, Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic lineage, the Labroidei. A cladogram defining this group and expressing relationships among its major clades has been derived on the basis of three investigations: Liem and Greenwood (1981), Stiassny's analysis of the phylogenetic relationships of the Cichlidae (in which extensive out-group comparisons are described, Stiassny, 1981 and personal communication), and this study (Fig. 1).

All Labroidei share the following three derived characters: (1) junction or fusion of the two fifth ceratobranchial bones into a single unit, (2) diarthrosis between the upper pharyngeal jaws and the basicranium (Fig. 2 A-F; APU; Stiassny, personal communication), and (3) the presence of the sphincter oesophagi muscle as a continuous sheet, with no dorsal subdivision (Fig. 2; Stiassny personal communication). Within Perciformes, fused or joined lower pharyngeal jaws also occur among the Anabantidae (all), Kyphosidae (*Girella tricuspidata*), and Sciaenidae (*Pogonias chromis* and *Aplodinotus grunniens*). The pharyngeal jaw morphology and biting mechanisms of these fishes differ appreciably, however, from those of the Labroidei (Liem and Greenwood, 1981). Other acanthopterygians show some form of articulation between the upper pharyngeal jaws and the basicranium (e.g., Sparidae,

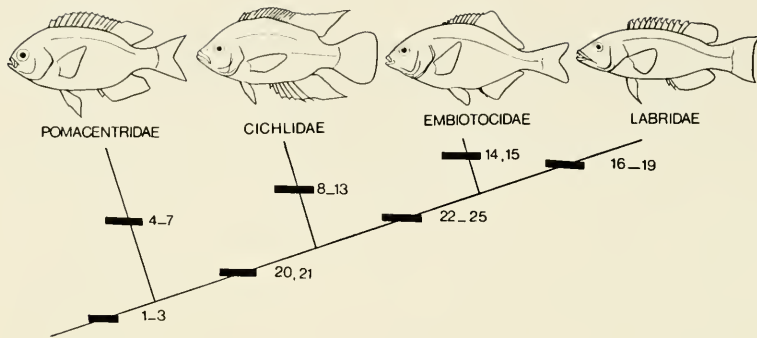


Figure 1. Cladogram illustrating interrelationships of the major labroid clades. Bars represent shared derived characters: (1) United or fused fifth ceratobranchials; (2) True diarthrosis between upper pharyngeal jaws and basicranium; (3) Undivided sphincter oesophagi muscle; (4) Strong sheet of connective tissue joining lower jaw with a ligament which inserts on the ceratohyal bone; (5) Nipple-like bony process on ventral surface of lower pharyngeal jaw; (6) Pharyngo-cleithral articulation of characteristic form; (7) Obliquus posterior dominant muscle to lower pharyngeal jaw; levator externus 4 and obliquus posterior vertically aligned on fourth epibranchial, separated by oblique aponeurosis or tendon; (8) Transversus dorsalis muscle subdivided into four parts; (9) Premaxillae and maxillae functionally decoupled; (10) Cartilagenous cap on anterior border of epibranchial 2; (11) Microbranchiospinae of characteristic form present on outer faces of second, third, and fourth gill arches; (12) A_2 and A_w portions of adductor mandibulae complex lacking major structural association; insertion of large ventral division of A_2 onto angulo-articular; (13) Head of epibranchial 4 distinctly expanded; (14) Intra-uterine development of young with strongly modified vascularized median fins; (15) Muscular sheet joining A_1 and $A_{2,3}$ portions of adductor mandibulae; (16) Levator posterior dominant muscle to the lower pharyngeal jaw, forming a force couple with the pharyngocleithralis muscle; (17) Toothplates of fourth pharyngobranchials absent (either lost or fused with pharyngobranchial 3), first pharyngobranchials absent or reduced; (18) Fourth epibranchials highly modified, articulating with upper pharyngeal jaws; (19) True pharyngo-cleithral articulation functioning as sliding and hinge joint; (20) Levator externus 4 is a continuous muscle joining prootic region to muscular process on lower jaw; (21) Predisposition for insertion of levator posterior muscle on lower pharyngeal jaw; (22) Loss of second pharyngobranchial toothplates; (23) First three branchial adductor muscles cover anterodorsal faces of the epibranchials; (24) Ligament connecting postmaxillary process of maxilla with anterior border of palatine and ectopterygoid; (25) Tooth rows arranged radially across the lower pharyngeal jaw, teeth located directly over the symphysis between left and right fifth ceratobranchials. LPJ toothplate composed of an anterior, small-toothed field and a posterior, large-toothed pavement replaced by addition along the rear margin of the LPJ.

Gerreidae, *Pogonias*, *Aplodinotus*), but only in the Labroidei is there a true diarthrosis. In other perciforms a portion of the transversus dorsalis muscle or its aponeurosis passes between the apophyses of the upper pharyngeal jaws and basicranium (Stiassny, 1981).

Synapomorphies Characterizing the Pomacentridae

The damselfishes can be defined on the basis of four characters. (1) Stiassny (1981: 286) observed that "A strong sheet of connective tissue originates from the dorsal border of the bony ridge on the medial face of the lower jaw [dentary] and merges with a cylindrical ligament that passes posteriorly and inserts onto the ceratohyal bone." In other acanthopterygians she examined this ligament was wanting. The remaining three characters concern the structure of the lower pharyngeal jaw (LPJ). (2) The LPJ's of all pomacentrids we have examined bear on their ventral surfaces a pair of small nipplelike processes, which serve as the insertion sites for the pharyngohyoideus muscle. These processes are absent in all other acanthopterygians examined. (3) In primitive acanthopterygians there is no contact between the fifth ceratobranchial and the cleithrum. In most pomacentrids, however, the muscular processes of the LPJ abut upon the cleithrum and slide along it by means of articular facets. Two such facets may be present (e.g., *Pomacentrus littoralis*, MCZ 5794): a dorsal facet lying parallel to the dorso-ventral plane, and a ventral facet which is curved slightly outwards from this plane and may provide the LPJ with some lateral freedom of movement. Labrids, in contrast, have a true pharyngo-cleithral joint. The degree of pharyngo-cleithral articulation varies considerably among pomacentrids. Even when the two bones are closely related, the nature of the articulation differs from that seen in the Labridae (Liem and Greenwood, 1981). This difference is also reflected in the unique and complex shape of the muscular processes of the LPJ in pomacentrids, a feature related to their peculiar musculature (Figs. 2, 3). In some pomacentrids (e.g., *Microspathodon*) pharyngo-cleithral articulation appears to have been lost as part of a general reduction of the pharyngeal apparatus. (4) In pomacentrids, as in all more primitive perciforms, the fourth levator externus muscle (Fig. 2 A-F: LE₄) and levator posterior (LP) insert

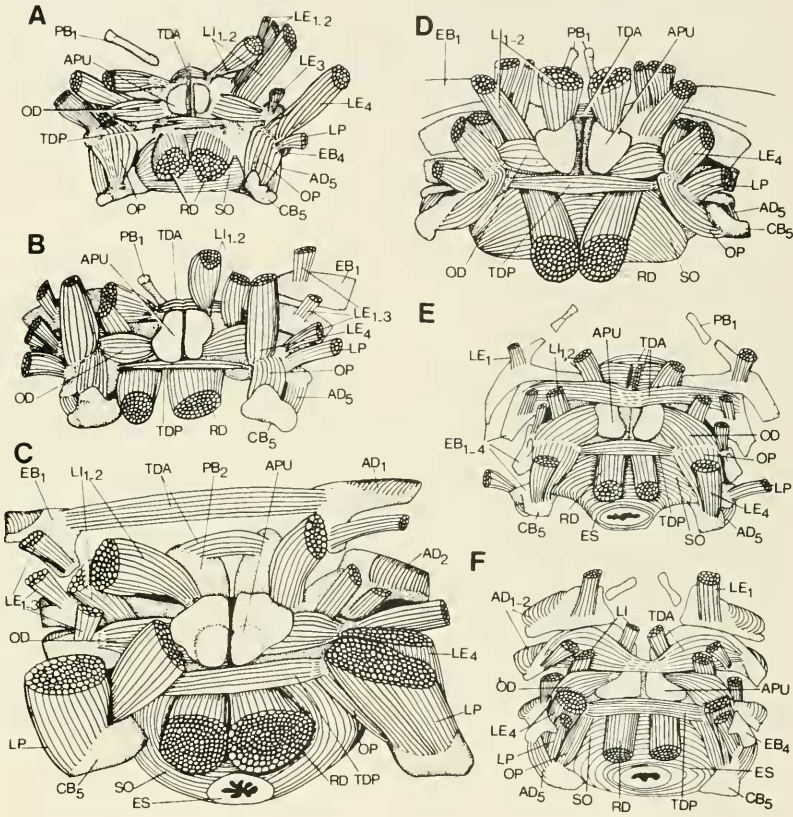


Figure 2. Dorsal aspect of the branchial musculature viewed from posterior to elucidate the muscles surrounding the esophagus and posterior branchial arches. A) *Pomacentrus littoralis*; B) *Abudefduf taurus*; C) *Tautoglabrus adspersus*; D) *Amphiprion xanthurus*; E) "*Haplochromis*" *leuciscus*; F) *Embiotoca jacksoni*.

Abbreviations: AD, adductor branchialis; APU, apophysis of upper pharyngeal jaw (third pharyngobranchial); CB₅, fifth ceratobranchial (lower pharyngeal jaw, LPJ); EB, epibranchial; ES, esophagus; LE, levator externus muscle; LI, levator internus muscle; LP, levator posterior muscle; OD, obliquus dorsalis muscle; OP, obliquus posterior muscle; PB, pharyngobranchial; RD, retractor dorsalis muscle; SE, sphincter oesophagi muscle; TDS, transversus dorsalis anterior muscle; TDP, transversus dorsalis posterior muscle.

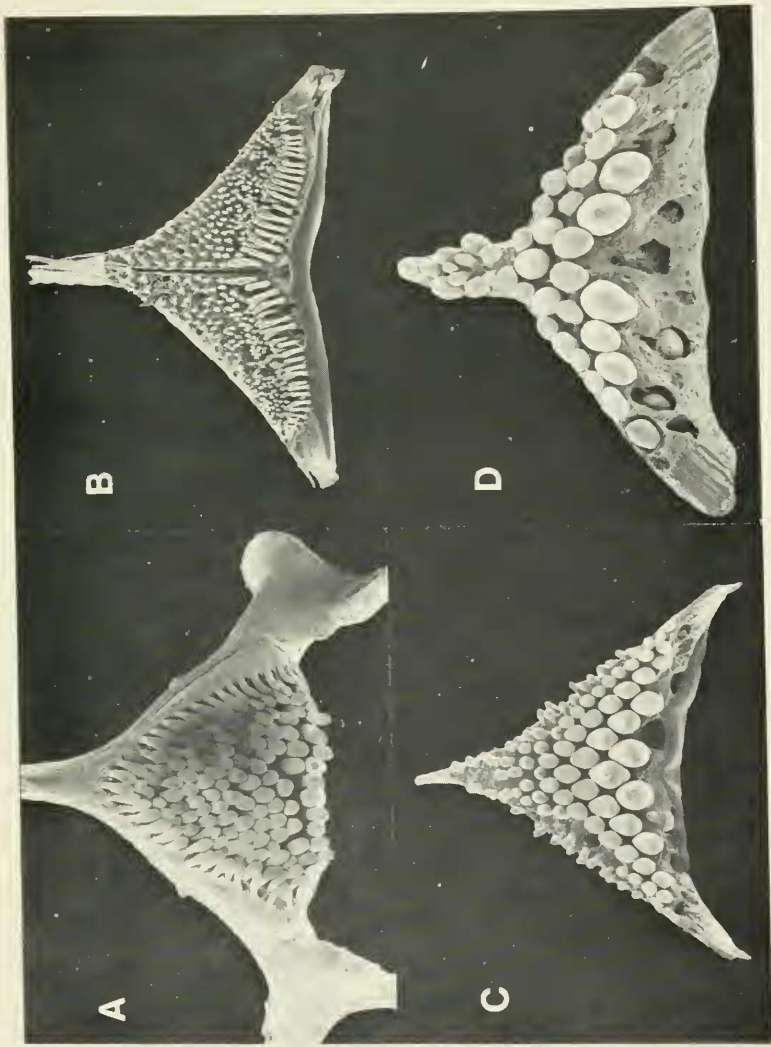


Figure 3. Scanning electronmicrographs of lower pharyngeal jaws of Labroides (anterior is up on the page). A) Pomacentridae: *Pomacentrus littoralis*, a Pacific coral reef fish; B) Cichlidae: *Hemittilapia oxyrynchus*, from Lake Malawi, East Africa; C) Embiotocidae: *Cymatogaster aggregata*, from the Pacific coast of North America; D) Labridae: *Tautoga onitis*, from the Atlantic coast of North America.

on the dorsal aspect of the fourth epibranchials (Liem, 1974). However, the pomacentrid LE_4 (Fig. 2A,B,D) splits near its insertion site on the fourth epibranchial (EB_4). The larger head inserts near the insertion site of LP, while a smaller medial head joins an oblique aponeurosis that runs anteromedially along the border of EB_4 . The obliquus posterior (OP) is the major muscle operating the posterior region of the LPJ. The OP muscle runs between the broad dorsal flange of each muscular process and the flange along the EB_4 just below the insertion site of LE_4 (Fig. 2A, B, D). Here the LE_4 and OP muscles are separated by the oblique aponeurosis. Thus the sites of origin and insertion for OP in pomacentrids are the same as the other acanthopterygians, but the extremely close relationship between LE_4 and OP on the fourth epibranchial is a derived character. The aponeurosis is present in all pomacentrids examined, and it clearly separates the fibers of the LE_4 from those of the OP. Nevertheless, the insertions for the two muscles are extremely close together, a condition which seems to foreshadow the muscular sling of cichlids and other Labroidae. There is a broad flange on EB_4 to receive LE_4 , and the posterior flanges on EB_4 and the fifth ceratobranchial (CB_5) are vertically aligned. Between them, and possibly contributing to the mechanical linkage between the two, is the stout dorsal portion of CB_4 . Thus, while the muscles of the LPJ in pomacentrids still originate and insert on the same bones as in non-labroid acanthopterygians, the geometry of these insertions has been modified in a characteristic fashion. The resulting condition may represent a primitive counterpart to the cichlid muscular sling (Liem, 1974).

Synapomorphies Characterizing the Cichlidae

Six characters clearly distinguish the Cichlidae as a monophyletic assemblage: (1) The transversus dorsalis muscle is subdivided into four parts (Liem and Greenwood, 1981; Fig. 2E:TDA). (2) The premaxillae and maxillae of all cichlids are functionally decoupled; i.e., premaxillary protrusion can be regulated independently from motion of the maxillae by means of multiple mechanical pathways (Liem, 1978, 1979). Four additional characters have been described by Stiassny (1981): (3) There is an extensive cartilaginous cap on the anterior border of EB_2 (*Cichla ocellaris* being the exception). (4) Microbranchiospinae of characteristic form are present on the outer

faces of the second, third, and fourth gill arches. (5) The A_2 and A_w portions of the adductor mandibulae complex have lost a major structural association, and there is an insertion of a large ventral division of A_2 onto the angulo-articular. (6) The head of EB_4 is distinctly expanded.

Synapomorphies Characterizing the Embiotocidae

Two characters are considered synapomorphies for the Embiotocidae. (1) All embiotocids are fully viviparous fishes, which deliver large, well-developed young. The males have a small intromittent organ derived from anal fin rays. The young are usually closely packed in the ovarian sacs which function in the fashion of a uterus. Monophyly of the embiotocids can be established on the basis of the highly specialized mode of "intra-uterine" development with its associated structural, physiological, and behavioral features, involving spatulate extensions of the webs of median and caudal fins, each with a rich blood supply (Webb and Brett, 1972). (2) Stiassny (1981) has found a small sheet of parallel muscle fibers arising from the anteromedial region of the A_1 part of the adductor mandibulae muscle and inserting upon the dorsal aponeurosis of A_{2+3} part of this muscle.

Synapomorphies Characterizing the Labridae

The families Labridae, Odacidae, and Scaridae have been recognized as close relatives within the Labroidei (Greenwood *et al.*, 1966). Here the three groups are recognized as a single family, the Labridae, since the monophyletic nature of this assemblage is strongly indicated by both morphological and functional characters. (1) The levator posterior muscle (Fig. 2C:LP) is the dominant muscle of the LPJ, forming a force couple with the pharyngocleithralis externus muscle (Liem and Greenwood, 1981). (2) The toothplates of the fourth pharyngobranchials are absent (either lost or fused with pharyngobranchial 3; Stiassny, 1981), while the first pharyngobranchials are absent or reduced. (3) The fourth epi-branchials are highly modified and of characteristic form, articulating with the upper pharyngeal jaws (Yamaoka, 1978, 1980; Gobalet, 1978). (4) There is some form of physical contact between the LPJ and the cleithrum in all members of the clade (Liem and Greenwood, 1981).

The posterior face of the muscular process on each side of the LPJ bears an articular facet, which fits against a small fossa on the cleithrum. The mechanics of this joint are quite complex. Cine-radiography of the LPJ in *Tautogolabrus adspersus* during mastication shows that there is a biphasic pattern involving both a hingelike and a sliding movement. The dynamics are reminiscent of those in the human temporo-mandibular joint. At rest and during the bite the LPJ is in close contact with the cleithrum and exhibits the pattern of a hinge-joint. During protraction the LPJ slides down and forward, using the anterior face of the cleithrum as a track. The morphology of the pharyngocleithral joints of odacids and scarids is basically similar to that of labrids, though the support system is stronger, and it is unknown whether the LPJ disarticulates during protraction. The condition in odacids and scarids overlaps broadly with that of the Labridae. *Cryptotomus roseus* is a scarid with a labridlike LPJ; both it and *Nicholsina denticulata* have many wrasselike features (see Gobalet, 1980 for comparative discussion of *Nicholsina*). *Pseudodax mollucanus* is a labrid with a scaridlike LPJ (Bleeker, 1862).

Interrelationships Among the Labroidei

The relationships proposed here differ from those of previous investigators (Greenwood *et al.*, 1966; Nelson, 1967; Liem and Greenwood, 1981) in three important ways. The Pomacentridae is considered the primitive sister group of other Labroidei. The Embiotocidae is postulated to be the sister group of the Labridae, and not the Cichlidae. Finally, the Labridae, Scaridae, and Odacidae are united in a single family, Labridae, to reflect striking similarities in their morphological as well as functional specialized features (Fig. 1).

Chief evidence for the proposed primitive sister-group relationship of the Pomacentridae to other Labroidei is found in the osteology and myology of the LPJ. In the Cichlidae, Embiotocidae, and Labridae, the LE₄ and (in general) LP muscles insert on the LPJ. The LE₄ and LP muscles of Pomacentridae insert on the fourth epibranchials, which represents the primitive condition in the Perciformes. Aerts and Verraes (1982) have demonstrated that the LE₄ of the cichlid *Haplochromis elegans* (and presumably, other cichlids as well) is actually a composite of LE₄ plus a large medial head of the obliquus posterior muscle, the two fusing during

development. This condition is never fully developed in Pomacentridae (Fig. 2A, B, D: OP, LE₄). Obliquus posterior (OP) is the dominant muscle to the LPJ while LE₄ remains a separate muscle, though it is large, and is aligned with the OP. The result is that the two muscles together bridge the gap between prootic and LPJ, meeting across the fourth epibranchial, where they are separated by an aponeurosis (Fig. 2A, B, D: OP, LE₄).

Four derived characters establish sister-group relationship between the Embiotocidae and Labridae. (1) These groups have lost the second pharyngobranchial toothplates (Nelson, 1967; Stiassny 1981). (2) The first three branchial adductor muscles cover the anterodorsal faces of the epibranchials (Stiassny, 1980 and Fig. 2C, F: AD₁₊₂). (3) A ligament connects the postmaxillary process of the maxilla with the anterior border of the palatine and ectopterygoid (Stiassny, 1980). (4) Tooth rows are arranged radially across the LPJ, with teeth located directly over the symphysis between left and right fifth ceratobranchials. The LPJ toothplate is composed of two fields: an anterior field (often lost in durophages), and a posterior field bearing the large cardinal teeth used in crushing or grinding. New cardinal teeth are added only to the rear margin of the LPJ, forming a conveyor-like pavement with greatest wear toward the front (Fig. 3; see also Embiotocidae: *Damalichthys vacca*; Labridae: *Pseudodax mollucanus*; all scarids).

The phylogeny proposed in Figure 1 assumes that similarities in pharyngeal dentition between the Labridae and Embiotocidae on the one hand, and Pomacentridae on the other, are homoplasies. In cichlids the LPJ toothplate is divided into left and right regions, with the largest teeth arranged in two main rows parallel to the symphysis, and there are no teeth located directly over the symphysis. This is clearly the primitive condition, since (a) the LPJ of labroids is derived from two separate fifth ceratobranchial bones, and (b) this condition is displayed in those non-labroid perciforms possessing fused or joined fifth ceratobranchials. In pomacentrids, as well as in embiotocids and labrids, the teeth cross the plate in a radial series and there are teeth located directly over the symphysis. As a sole synapomorphy for pomacentrids, embiotocids, and labrids this character seems too tentative. It appears independently in the Beloniformes, another group with fused lower pharyngeal jaws, which is clearly unrelated to the Labroidei (Collette, 1966). Pharyngocleithral joints appear in both the Pomacentridae and the

Labridae, but are clearly dissimilar in form. Thus in terms of the specialized osteological and myological characters discussed above, the pharyngeal jaws of the Cichlidae, Embiotocidae, and Labridae resemble each other much more closely than any one of these groups resembles the Pomacentridae.

Independent investigations (Stiassny, 1981; Liem and Greenwood, 1981, and this study) have resulted in very similar hypotheses of labroid phylogenetic relationships. Stiassny (1981, personal communication) has based her studies primarily on soft-tissue characters, while we have concentrated on functional and osteological characters. The relationships postulated in Figure 1 deviate drastically from previous schemes. This is mainly because important new osteological, dental, and myological evidence has emerged.

DISCUSSION

Ecology of the Labroidei

The new phylogenetic scheme of the Labroidei has important implications for our perception of the ecology and functional morphology of this group. The gradal nature of former classifications obscures relationships and thereby masks evolutionary sequences, ecological diversity, and changes in functional patterns. To illustrate this point we will briefly discuss some of the implications of the new phylogeny for ecological concepts as they pertain to the Labroidei.

Labroidei as defined here unites at least 1,470 species (some 5 to 10 percent of living fishes) that are extremely diverse ecologically. Nevertheless, the majority of labroids occur within one general type of environment: warm, slow-moving water with abundant habitat structure. Tropical marine reefs are densely populated by pomacentrids and labrids. These are joined by embiotocids on temperate Pacific reefs. All four clades figure prominently in aquatic macrophyte forests such as grass beds, kelp beds, algal reefs, or heavily vegetated pond and stream edges. Relatively few labroids are abundant in pelagic, soft-bottom, or strictly lotic assemblages.

Modes of life exhibited by marine labroids differ characteristically from those of sympatrically occurring non-labroid and functionally intermediate forms. We illustrate these patterns with data from a coral reef fish assemblage observed in Salt River Canyon, St. Croix, U.S. Virgin Islands (Table 1). The 137 species

Table 1. Relationship between functional morphology of the pharyngeal jaws and potential anti-predator mechanisms for 137 species of coral reef fishes observed during visual censuses in Salt River Canyon, St. Croix, U.S. Virgin Islands (Kaufman and Ebersole, in preparation).

Potential Anti-Predator Mechanisms	Functional Morphology of Pharyngeal Jaws		
	Primitive	Intermediate	Labroid
Non-territorial	O = 52	O = 10	O = 5
Non-schooling	E = 33.74	E = 18.09	E = 15.16
Not heavily armed	X ² = 9.88	X ² = 3.62	X ² = 6.81
Heavily armed	O = 16	O = 17	O = 0
	E = 16.62	E = 8.91	E = 7.47
	X ² = 0.02	X ² = 7.35	X ² = 7.47
Territorial or Schooling	O = 1	O = 10	O = 26
	E = 18.64	E = 9.99	E = 8.37
Not heavily armed	X ² = 16.69	X ² = 0.00	X ² = 37.13
	X ² = 88.98, <i>p</i> < .001		

O = observed frequencies for numbers of species in each category.

E = expected frequencies.

X² = Chi-square value within cell.

X² = total Chi-square.

observed during two series of replicated visual censuses (Kaufman and Ebersole, in preparation) were divided into three categories according to pharyngeal jaw functional morphology: (1) primitive, with pharyngeal jaws unspecialized for mastication; (2) intermediate forms exhibiting some, but not all of the features found in Labroidae (as discussed below in greater detail); and (3) labroids. The species were also placed into three other categories related to strategies for avoiding predation (refuging): (1) non-territorial and non-habitually schooling species, both unarmed; (2) strongly territorial and habitually schooling species, both unarmed; and (3) species armed with frank defensive mechanisms (toxin, venom, dermal armor, enlarged spines), or which live inside corals, sponges, invertebrate tests, and boreholes. It was postulated that trophic mechanisms and refuging strategies would be interrelated. Table 1 provides evidence of highly significant relationship between "pharyngeal jaw" and "anti-predation" categories (X² = 88.98; *p* < .001). A detailed list of the species and their categorizations can be obtained from the authors.

The data in Table 1 suggest that there are characteristic modes of life for coral reef labroids. Most of them both feed and refuge on the reef. They are not heavily armed. They are, for the most part, either territorial or schooling. Territorial labroids defend a general area as a multipurpose territory rather than occupying one specific hole or cavity as do many inquiline gobies, blennies, or jawfishes (Opisthognathidae). The residents exclude potential competitors for food, hiding places, and mates, as well as species that threaten the integrity of the territory (Low, 1971; Thresher, 1976; Kaufman, 1977, 1979; Potts, 1977; Williams, 1979, 1980; Ebersole, 1977; Lobel, 1980). Even the schooling and planktivorous labroids are strongly reef-associated, utilizing benthic cover as the ultimate means of escape from predators. In summary, members of the Labroidei generally rely on the reef for refuge, exploiting those foods which are, or can be made available without travelling over long distances. There is an exception to this pattern. Adults of the larger species (such as the huge Caribbean parrotfishes *Scarus guacamaia* and *S. coelestinus*) sometimes forage or migrate to and from the reef as individuals. For these fishes, large size alone may be a sufficient deterrent against predators.

Other reef-dwelling fishes exhibit modes of life that contrast with those of the labroids. The non-labroid category in Table 1, including such fishes as berycoids, apogonids, serranids, and lutjanids, consists of both diurnal and nocturnal predators which stalk small soft-bodied prey. The intermediate pharyngeal jaw category is dominated by two groups: armed fishes that feed on the reef by day and rest on the reef at night, and unarmed fishes that feed off-reef at night and shelter on the reef during the day. The heavily armed plectognaths, chaetodontids, and acanthurids comprising the bulk of the first group together exploit almost as broad a range of foods as the labroids. Individually, however, they exhibit functional limitations related to gape, mouth position, jaw mobility and pharyngeal jaw mechanics that should seriously limit feeding versatility in comparison to that of similar-sized pomacentrids or labrids. This is reflected in what is known of their diet (e.g., Randall, 1967; Hobson, 1974; Reese, 1975). Relatively few of these species enhance their own local food supply by defending feeding territories (possibly *Acanthurus sohal*, Vine, 1974; *Chaetodon trifascialis* [formerly *Megaprotodon strigangulus*], Reese, 1975). The nocturnal

off-reef predators (e.g., Pomadasyidae) prey chiefly on small benthic invertebrates.

We postulate that feeding versatility was a chief factor in shaping the characteristic modes of life exhibited by marine labroids; i.e., schooling or territorial behavior with a strong reliance on the reef for both food and shelter. Trophic mobility can be one key to survival when spatial mobility is limited by a high risk of predation. The antithesis of this strategy, rarely exhibited by labroids, is to reduce the risk of predation by adopting some active defensive mechanism.

Labroids play a disproportionate role in determining the distribution and abundance of benthic organisms in tropical marine hard-bottom communities (Randall, 1961, 1974; Ogden and Lobel, 1978; Brock 1979). In part this is due to broad-spectrum feeding capabilities (hard-shelled invertebrates, coral rock, coral, algae). Many labroids locally manipulate the substratum and its occupants to suite their own needs (Brawley and Adey, 1977; Kaufman, 1977, 1979; Wellington, 1981). This constitutes a patchy disturbance to sessile invertebrates (Kaufman, 1977; Connell, 1978) and could be a principal factor regulating food abundance for other reef organisms.

*Labroid Phylogeny and the Evolution of
Acanthopterygian Feeding Mechanisms*

When the cichlid pharyngeal jaw mechanism was first described, it appeared to represent an abrupt breakthrough in the acanthopterygian feeding mechanism, radically different from anything known in the cichlids' presumed ancestors (Liem, 1974). Subsequent radiation seemed to involve little modification of the basic feeding mechanism (Fryer and Iles, 1972; Greenwood, 1974). The new hypothesis on the genealogical relationships of the Labroidei presented here requires that these views be revised considerably.

One erroneous hypothesis was that the pharyngeal jaw complex is unique to cichlids; present evidence rejects such a hypothesis (Liem and Greenwood, 1981). Many features present in cichlids are present in Labroidei. Second, there was thought to be a large morphological and functional gap between cichlids and their primitive (ancestral) counterparts; there is not. The apparent gap was an artifact of insufficient data, now bridged by primitive labroids and certain non-labroid perciforms. Aerts and Verraes (1982) have shown that during the ontogeny of a cichlid (*Astatoti-*

lapia elegans) the LE_4 splits into a lateral and a medial head. The medial head of LE_4 unites with the medial head of the OP, thus establishing a functionally as well as a structurally uninterrupted muscle between the prootic and the muscular process of the LPJ, i.e., a compound LE_4 . The characteristic arrangement of LE_4 and OP in pomacentrids (e.g., *Pomacentrus littoralis*, Fig. 2) resembles those early ontogenetic stages in cichlids before the compound muscle is formed. The Pomacentridae is clearly primitive, however, in terms of the origins and insertions of LE_4 and OP. Thus the Pomacentridae is intermediate between the more derived labroids (cichlids, embiotocids, and labrids) and other perciforms.

Other perciforms which approach the labroid condition in one or more respects are morphologically (and perhaps phylogenetically) intermediate between labroids and primitive perciforms. The anabantoids, Kyphosidae, and Sciaenidae have fused or joined pharyngeal jaws in some members. The fifth ceratobranchials of the Gerreidae and Pomadasyidae (especially *Anisotremus surinamensis*) have no true bony junction, but are in some species very tightly bound together by strong ligaments. Certain Sciaenidae (e.g., *Pogonias chromis*, *Aplodinotus grunniens*) and Gerreidae have an articulation between the upper pharyngeal jaws and the basicranium although it is not as well developed as in labroids. The shell-cracker centrarchid *Lepomis microlophus* and the molluscivorous Carangidae (*Trachinotus* spp.) have broad, hypertrophied lower pharyngeal jaw elements which meet closely at the midline (Kaufman and Ono, in preparation). Nearly all of these morphologically intermediate forms feed habitually on hard-shelled benthic invertebrates in addition to a wide variety of other organisms, both hard and soft. Selection favoring a broader, more inclusive diet could have been a major factor in the early evolution of labroids. This hypothesis can not be tested without first developing a better picture of perciform phylogeny. However, the presence of so many intermediate forms (one of which may represent the primitive sister group of the Labroidei) and the intermediate characteristics displayed in Pomacentridae, indicate that advanced acanthopterygian pharyngeal jaws are the result of a series of morphological changes. There was no single "adaptive breakthrough" (*sensu* Simpson, 1944, 1953; Liem, 1974).

In summary, this new model of labroid relationships will permit us to examine the nature of evolutionary change in a structurally complex mechanical system. Judging from the great ecological diversity of labroids, it seems that their specialized pharyngeal jaw apparatus has greater structural potential and functional flexibility than that of its more primitive counterparts. The more precise labroid phylogenetic scheme will allow us to determine if there is a general relationship between design versatility and historical patterns of morphological change.

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