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Scale-eating in characoids and other fishes

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Synopsis

Scale-eating is known for several unrelated fish groups, but few data are available on the habits of most species. General habits and feeding behavior of some lepidophagous characoids are presented and compared to other scale-eating species. The diversity of morphology, habits, and behavior of scale-eating fishes is great, and few patterns are shared by the specialized scale-eaters. Except for modified teeth, no morphological characteristic permits identifying a fish as a specialized lepidophage. Hunting tactics consist mainly of ambush, stalking, or disguise (aggressive mimicry). Scale-removal may be accomplished by a jarring strike with the snout, generally directed at the prey's flank, or by biting or rasping. The mode of scale-removal seems to reflect primarily the disposition of the jaws and the teeth. Scales are swallowed directly if taken in the mouth; if not, they are gathered as they sink, or picked up from the bottom. Scale-eating is probably a size-limited habit. Specialized scale-eaters rarely exceed 200 mm, most ranging near 120 mm. Some species eat scales only when young; most take other food items in addition to scales. Scale-eating habits probably arose from trophic or social behaviors. These are not mutually exclusive and, indeed, may have acted together during the evolution of lepidophagy. Suggested trophic origins include scraping epilithic algae, modified piscivory, and necrophagy. Social origins include intra- and interspecific aggressive behavior during feeding.

Introduction

Various fish species have adopted the habit of eating particular parts of other living fishes, including scales, skin, fins, gill filaments, blood, chunks of the body and even eyes (see Fryer et al. 1955, Roberts 1972, Curio 1976). Among these modes of mutilation, scale-eating is perhaps the most widespread, found in a number of fish species of several unrelated taxa from diverse habitats, in both freshwater and the sea.

Among the freshwater fishes, lepidophagous species have been found in five African genera of Cichlidae (Fryer & Iles 1972, Eccles & Lewis 1976,

Liem & Stewart 1976), seven genera of neotropical Characidae (Roberts 1970, Géry 1980, Goulding 1980), an Asian genus of Schilbeidae (Whitfield & Blaber 1978), one genus of Ariidae in Australasia (Roberts 1978), and at least three genera of neotropical Trichomycteridae (Baskin et al. 1980). The supposed scale-eating habits of *Oedemognathus* (Roberts 1970), gymnotiform Apterontidae, have yet to be confirmed. Among marine fishes, scale-eating is known mostly for juveniles. Lepidophagous species have been found in one genus of Ariidae in the W. Atlantic (Hoese 1966), one genus of Blenniidae in the tropical Pacific (Losey 1972a, 1978), two genera of Carangidae in the W. Atlantic

and Pacific (Major 1973, Sazima & Uieda 1980), two genera of Triacanthodidae in the Pacific (Mok 1978), one genus of Labridae in the tropical Pacific (Losey 1972b), one genus of Teraponidae in the Pacific (Whitfield & Blaber 1978) and two genera of Kyphosidae in the Pacific (DeMartini & Coyer 1981). Thus lepidophagous habits are presently known in at least five freshwater and seven marine fish families, mainly from tropical regions.

Lepidophagy is regarded as a derived, highly specialized habit, and scale-eating fishes are often morphologically and behaviorally specialized for feeding (e.g. Roberts 1970, Fryer & Iles 1972, Major 1973, Whitfield & Blaber 1978, Sazima 1980). In some instances it is associated with aggressive mimicry (Trewavas 1947, Sazima 1977), suggestive of its evolutionary complexity.

In this paper I present data on scale-eating in some neotropical characoid species and compare them mainly with African cichlids and some marine species. Most of the study sites and general procedures are described elsewhere (Sazima 1977, 1980, Sazima & Uieda 1980, Sazima & Machado 1982).

I will emphasize the relationships between morphology and behavior, and indicate patterns apparently common to most lepidophagous species. Also, I will indicate further study which may lead to a better knowledge of scale-eating and its evolution.

Scale-eating characoid genera

Characoids constitute the largest group of South American fishes, the number of species approaching one thousand (Géry 1977). The group has undergone extensive adaptive radiation resulting in an unparalleled diversity of diets and morphologies. The following genera are known to be specialized scale-eaters: *Roeboides*, *Exodon*, *Roexoexodon*, *Probolodus*, and *Catoprion* (Roberts 1970) and the recently described *Bryconexodon* (Géry 1980). Four representative scale-eating characoids are shown in Figures 1–4. A few *Serrasalmus* species (piranhas) practice lepidophagy to a certain extent, but rely mainly on fin-eating (Roberts 1970, Goulding 1980). *Roeboides* is the only polytypic genus of specialized scale-eaters, being widespread throughout the Neo-

tropics and present in almost all major river basins. The other lepidophagous genera are monotypic and have a more restricted range.

All specialized scale-eating characoid genera belong to the large family Characidae (including Serrasalminae). The classification and relationships of characids are insufficiently known to provide information on phyletic relationships of lepidophages. Most lepidophagous genera are placed in distinct tribes (e.g. Géry 1964, 1972, 1977, 1980). In contrast, genera such as *Roeboides* and *Exodon* have been placed together in the same subfamily, Characinae (e.g. Géry 1959, 1977, Roberts 1970), notwithstanding their different appearance (Fig. 1, 3). In fact, preliminary morphological and osteological studies by Naércio A. Menezes (personal communication) suggest that *Exodon* has more affinity with the Tetragonopterinae than with the Characinae, and this seems also to be supported by several aspects of its behavior (Sazima 1980). *Roexoexodon* is sympatric with *Exodon* in parts of its range, and in the Rio Araguaia, Goiás State, Brazil, they seem to be syntopic. The recently described *Bryconexodon* (Géry 1980) probably belongs to the same phyletic assemblage. *Probolodus* was described in the Cheirodontinae but some authors prefer to place it among the Tetragonopterinae (Roberts 1970, Géry 1980). It is clear that one of the most important steps in the study of the scale-eating habits in characoids rests in clarifying the systematic relationships among the species involved (Sazima 1980). The value of such a procedure is illustrated by the work of Liem & Stewart (1976) on the African cichlid *Perissodus*, and the predictions of Baskin et al. (1980) on scale-eating habits of trichomycterid catfishes.

Characteristics of scale-eating fishes

Morphology

Specialized teeth seem to be the only external feature characteristic of all scale-eating characoids. At least some teeth are directed forwards and point out of the mouth or are entirely external (Fig. 5–7). These teeth are stout with hypertrophied bases and

may be conical and mammiliform, or cuspidate. The outward pointing of the teeth appears unrelated to jaw length, total tooth number, cusp number or the presumed systematic relationships among species. Such a uniform adaptive response is almost certainly due to the relative simplicity of the mouth architecture as compared, for example, with the complex feeding apparatus of cichlids (Liem & Osse 1975). Certain teeth become modified early in juvenile life, e.g. the fourth dentary tooth of *Probolodus* (Fig. 7), which is clearly differentiated in 19 mm young (adults attain 110 mm). This tooth plays a key mechanical role during scale-removal as deduced from tooth wear and replacement (Roberts 1970) and from scale-removing behavior (Sazima 1980).

The position and wear of the teeth, as well as the relative length of the jaws, allow some predictions about the mode of attack and scale-removal. Thus, *Roeboides prognathus* and *R. paranensis* have a projecting upper jaw and many external teeth (Fig. 5). The foremost premaxillary and dentary teeth which point almost straight ahead are invariably worn and sometimes missing. These species seem to strike at prey mainly with their mouth closed (Sazima & Machado 1982). On the other hand, *Catoprion*, with protruding lower jaw has fewer, less projecting teeth and attacks prey with its mouth wide open. *Exodon*, with upper and lower jaws of almost equal length, has some external teeth pointed forwards and strikes at the prey either with its mouth open or closed. Although I have not observed living specimens of *Roeboides* and *Bryconexodon*, I predict from their jaw shape and dentition that the former can remove scales with its mouth closed whereas the latter probably has to open its mouth. In addition, the differential wear of teeth may indicate the right- or left-handedness of the individual, i.e. the tendency to remove scales from the prey using the right or left side of the mouth. I have observed this in *Roeboides prognathus* (D.L. Kramer has informed me of similar findings for *R. guatemalensis*).

Among the African scale-eating cichlids, there are numerous variations involving the form and disposition of teeth (Fryer & Iles 1972). The versatile cichlid mouth has permitted some remarkable

adaptations, such as jaws asymmetrically suspended to the right or to the left for striking the prey more effectively found in *Perissodus eccentricus* (Liem & Stewart 1976). In the other scale-eating fish groups the solutions vary from the presence of distinctive outer dentary teeth, tightly spaced, strongly hooked outwards and with spatulate tips, found only in juveniles of some species of the carangid *Oligoplites* and *Scomberoides* (Smith-Vaniz & Staiger 1973, Sazima & Uieda 1980, and Fig. 8) to the long rows of numerous needlelike teeth in the stegophiline catfishes (Baskin et al. 1980).

The size, shape and adherence of scales in scale-eating fishes is often discussed in relation to their feeding habits (Breder 1927, Roberts 1970, Whitfield & Blaber 1978, Sazima & Uieda 1980). Reduction in scale-size seems to be common in most scale-eaters; the assumption is that small and adherent scales reduce intraspecific scale-eating. We have found that *Roeboides prognathus*, *R. paranensis*, *Probolodus heterostomus*, *Exodon paradoxus* and *Catoprion mento* are all capable of removing scales from conspecifics, apparently with the same ease with which they obtain scales from usual prey species (Sazima 1980, Sazima & Machado 1982, personal observations). In *P. heterostomus* I found conspecific scales in 4 out of 69 stomachs examined. My observations on characoids suggest that scale characteristics of these fishes do not actually prevent intraspecific scale-eating, although they may help to reduce damage when attacks actually occur. Behavioral avoidance is probably a major factor which reduces scale-loss or damage during intraspecific encounters (Sazima 1980). On the other hand, in the carangid *Oligoplites saurus* the deeply embedded, needlelike scales and leathery skin actually does prevent damage to skin in cases of intraspecific (misdirected?) attacks during the pursuit of schooling prey (Sazima 1980).

An additional possible explanation for small, adherent scales is the role they may play in preventing damage from retaliatory actions of the prey. Several predators exhibit counter-adaptations to the defensive actions of their prey (Curio 1976), and it must be noted that scale-eaters may attack prey larger than themselves (Breder 1927, Sazima 1980), against which they have few defenses other than

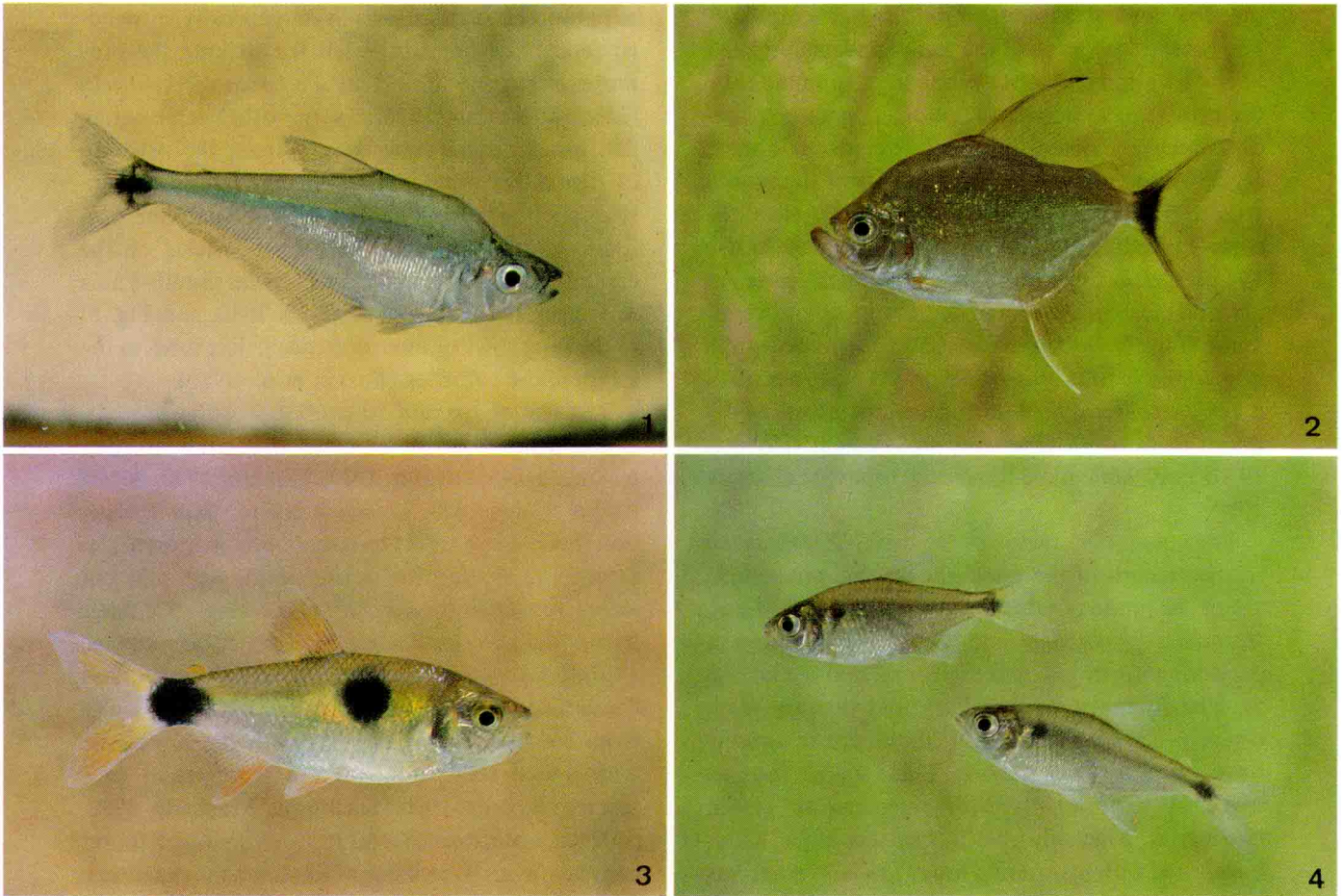


Fig. 1-4. Four representative species of scale-eating characoid fishes: (1) *Roebooides prognathus*, 72 mm standard-length; (2) *Catoprion mento*, 61 mm; (3) *Exodon paradoxus*, 59 mm (note 'twin-spot' pattern); (4) *Probolodus heterostomus*, about 30 mm, shown with its usual prey *Astyanax fasciatus* (upper).

their agility. In a few instances I have observed *Probolodus* being chased by a previously attacked *Astyanax*. Although it usually evaded the pursuer, sometimes the *Probolodus* was overcome and bitten, without, however, resulting in damage to its skin (Sazima 1980).

Among the characoid scale-eaters, the body shape does not appear to reflect any particular adaptation to scale-eating. For instance, the deep body of *Catoprion* (Fig. 2) is the rule among the serrasalmine characoids, as is the somewhat elongated

body and anal fin of *Roebooides* among Characinae. On the other hand, genera such as *Exodon*, *Bryconexodon* and *Probolodus* have a body shape like those found in most tetragonopterine characins (Fig. 3, 4, 11).

The color pattern of some scale-eating fishes has occasionally been discussed in relation to their feeding habits (Roberts 1970, Whitfield & Blaber 1978). The translucent body of some species of *Roebooides* may favor undetected stalking of their prey (Sazima & Machado 1982). The similarity of

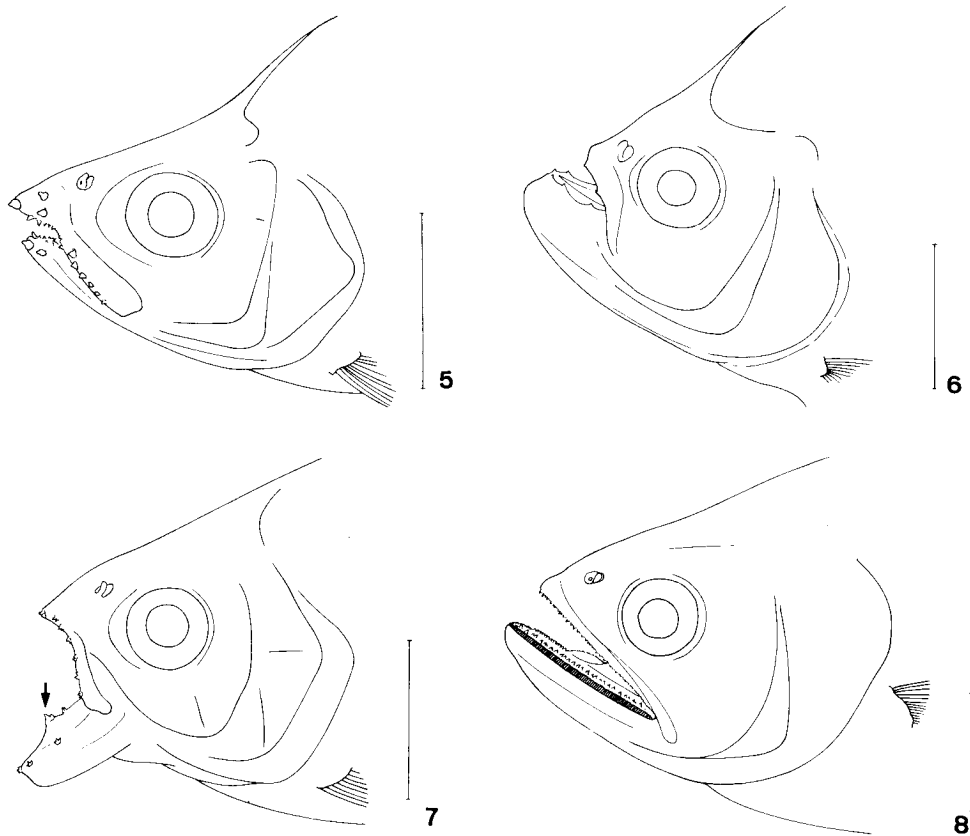


Fig. 5-8. Heads of three characoid and one carangid species of scale-eating fishes to show jaw proportion and teeth types and arrangement (vertical scales are 10 mm): (5) *Roebooides prognathus*, with projecting upper jaw and external, forwards directed, mamilliform teeth (after Sazima & Machado 1982); (6) *Catoprion mento*, with prognathous jaw and few, outwards pointing tricuspid teeth; (7) *Probolodus heterostomus* showing the few, forward directed tricuspid teeth – note prominent position of the fourth dentary tooth (arrow); (8) *Oligoplites palometa*, a carangid, with outer dentary teeth tightly spaced and hooked outwards.

Probolodus heterostomus to *Astyanax fasciatus* (Fig. 4) favors its schooling with this habitual prey species (Sazima 1977, 1980). The 'twin-spot' pattern of *Exodon paradoxus* (Fig. 3) is an exception among scale-eating fishes and has no counterpart among Characidae in general. This is an aggressive and robust schooling species and its dentition is strong and sharp. (It is the only specialized scale-eater I have observed which bites resolutely when handled.) Fishes with such characteristics sometimes possess clearly recognizable intraspecific signal-marks, e.g. reddish belly associated with deep body in *Serrasalmus nattereri* (Markl 1972). The color pattern of *E. paradoxus* may be primarily related to social, intraspecific interactions (Sazima 1980), as already recognized by Lowe-McConnell (1964). Facts suggest-

ing a relation between these body marks and scale-eating will be discussed later.

In summary, scale-eating is characterized by a wide variety of morphological patterns. Aside from dentition, there is no single external feature which characterizes a 'scale-eating type' among the specialized lepidophagous characoids (and perhaps other scale-eating taxa too). The absence of morphological characterization becomes increasingly important when one realizes that to feed on scales, a fish need not necessarily have specialized dentition. Some species of the generalized and omnivorous characoid genus *Astyanax* have been found to ingest scales (Nomura 1975). To recognize the scale-eaters, one has to study feeding habits and behavior.

Behavior

There are few descriptions of scale-eating behavior. About 10 out of the 50 or more known lepidophagous species have been observed actually removing scales of the prey, and these observations have mostly been made on fishes in aquaria. The only studies containing field observations on scale-eating characoids dealt mainly with the general aspects of fish communities (Zaret & Rand 1971, Kramer 1978 for *Roeboides guatemalensis*). I have found lepidophagous characoids in sites ranging from muddy inlets in sizeable rivers (Fig. 9) to very clear pools in small, sluggish creeks (Fig. 10). In scale-eaters, vision seems to be the main sense employed to detect and orient approach to the prey, as well as to attack it and evade possible retaliation. With few exceptions, characids are diurnal and have well developed eyes. *R. prognathus* increases its predatory activity at dusk (Sazima & Machado 1982) and *R. guatemalensis* exhibits crepuscular or even nocturnal predatory behavior (D.L. Kramer, personal communication). Species of this genus have a network of pores on the head, called pit lines (Géry 1966), which I suspect are sensitive structures which allow perception of prey at a distance, a function comparable to that suggested for the branch of the laterosensory canal in

the premaxillary of the characoid *Acestrorhynchus* (Menezes 1969). A *Roeboides prognathus* placed in a 50 l tank with one or two prey fishes, removed scales from them in muddy water with visibility not greater than 20 mm (maximum depth at which a white 50 mm long object remained visible), while it did not molest a conspecific, as indicated by stomach contents analysis (Sazima & Machado 1982).

Scale-eating fishes often approach their prey using concealment or mimicry. *Catoprion mento* may stalk or ambush its prey using clumps of waterweeds as cover (Fig. 10). The translucency of *Roeboides prognathus* and *R. paranensis* may conceal their approach (Sazima & Machado 1982). *Roeboides* and *Catoprion* may also linger close to the prey, behaving as if 'not interested' in the prey (sensu Curio 1976) and thereby attack from close quarters. I have also observed this subtle behavior in young *Serrasalmus spilopleura* and *S. marginatus*, two 'mutilating' characoids. The use of harmless fish species as a 'cover' to approach a prey may be one of the predatory tactics of *Probolodus* schooling with *Astyanax fasciatus*. (A similar hunting tactic is used by the skin- and mucus-eating blennioid *Plagiotremus azalea*, which swims 'concealed' within schools of the labrid *Thalassoma lucasanum*, Hobson 1968.) In addition, *Probolodus* and species of the cichlid genera *Corematodus* and *Perissodus* are

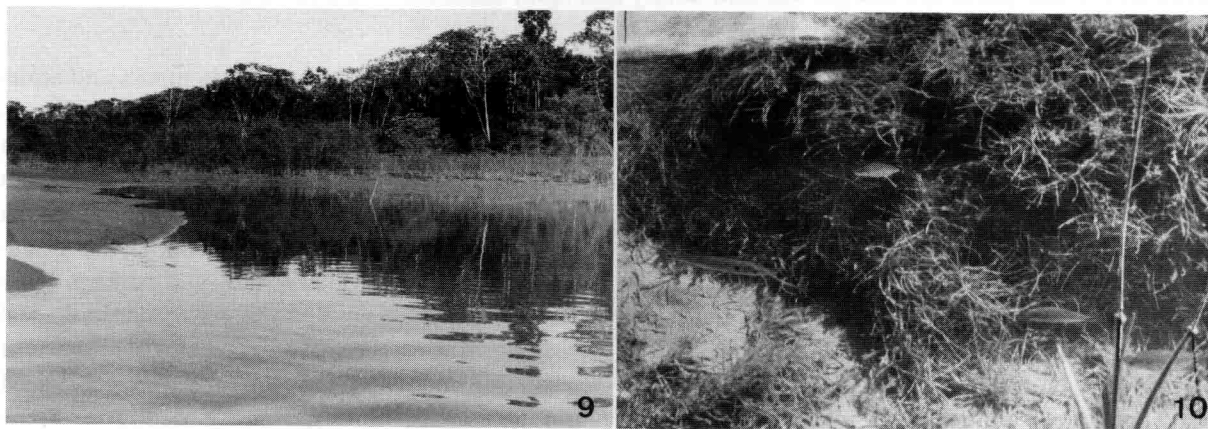


Fig. 9. Inlet in the Rio Cuiabá, near Cuiabá, Mato Grosso State, Central Brazil. The often muddy waters of this river harbor three species of *Roeboides*, which may occur syntopically.

Fig. 10. Fishes in a clear pool of a small creek in the Pantanal region near Poconé, Mato Grosso State, Central Brazil. A specimen of *Catoprion mento* appears near the centre of the picture; one *Acestrorhynchus altus* is on the left, below and two *Astyanax bimaculatus* are visible on the right lower corner. Note abundant aquatic vegetation.

aggressive mimics of their prey fish (Trewavas 1947, Sazima 1977, Brichard 1978). By having the prey's appearance (e.g. Fig. 11), they can maneuver to a convenient attacking position. The cichlid *Perissodus microlepis* poises in midwater near rocky slopes, waiting to strike at the unwary victims (Brichard 1978). The carangids *Scomberoides* and *Oligoplites* are open water fishes which often school together with their intended prey (Major 1973, Sazima & Uieda 1980). Young *O. saurus* are greenish and silvery and may adopt the color tone and posture of their intended victims (Sazima & Uieda 1980). On the other hand, young *O. palometa* have a yellowish phase with two dark bars and seem to stalk and ambush prey among marsh grass and other aquatic vegetation. At least one exception to these subtle or deceptive modes of approach is known: *Exodon paradoxus* rushes towards the prey, seemingly without subterfuges (Roberts 1970, Sazima 1980). This uncommon tactic, together with its schooling habits and unique color pattern suggests that *Exodon* may be a group predator similar to the conspicuously patterned teraponid *Terapon jarbua* which also schools when attacking the prey (Whitfield 1979). This teraponid attacks intermittently from behind, thus maintaining the element of surprise (Whitfield & Blaber 1978).

The actual attack varies little among the lepidophagous characoids. Usually, the predator strikes at the flank of a prey from a perpendicular or posterior oblique position (Fig. 12–14). Strikes of *Roeboides prognathus* and *Exodon paradoxus* are mostly caudad (Fig. 13); such a thrust removes scales more easily than one directed against the free edge of scales (Sazima & Machado 1982). *Catoprion mento* strikes most frequently at a right angle to the prey's flank (Fig. 12), maximizing scale-removal by the wide open mouth. A single well directed strike by *Catoprion* removes several rows of scales, leaving a neatly denuded spot on the side of the prey. Field observations indicate that *Catoprion* is actively avoided by its prey. The scale-removing strike of the specialized lepidophagous characoids is jarring and the prey is frequently displaced by the force of impact (Fig. 16). Moreover, most favor attacks on moving fish. The escape reflex of the prey adds to the impact of the strike and this, accompanied in some predators by a lateral head jerk as it bites, helps furnish the force needed to dislodge the scales. After the first attack, the scale-eaters do not follow the prey for a great distance.

Other relationships are important between the attack behavior and the morphology or general habits of a species. When several *Exodon* attack a group of prey fish, their 'twin spot' pattern darkens to its maximum, and they stand out unmistakably

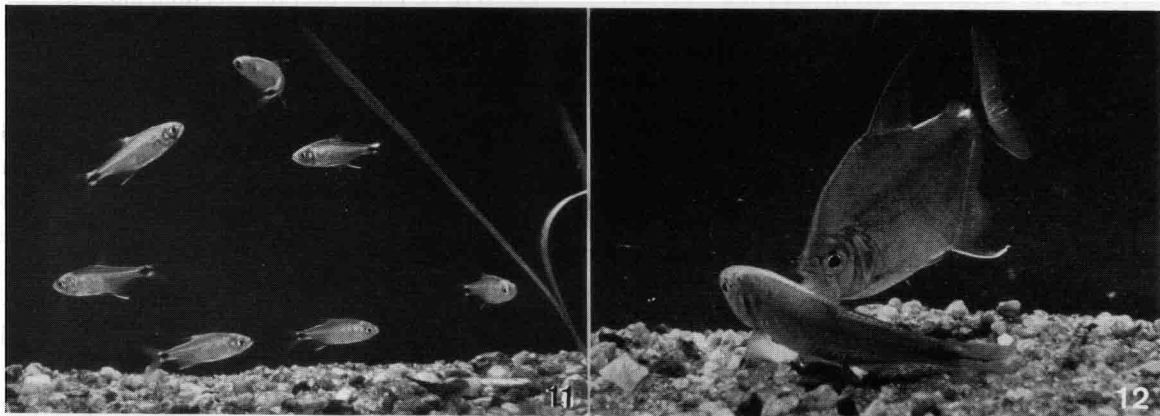


Fig. 11. Interactions in a mixed group of *Probolodus heterostomus* and *Astyanax fasciatus*. The uppermost fishes are *Probolodus* aiming a charge at an *Astyanax*; the lowermost ones are *Astyanax*, one chasing the other.

Fig. 12. Scale-removing attack of *Catoprion mento* towards *Astyanax* prey. The wide mandible can remove several rows of scales in a single strike.

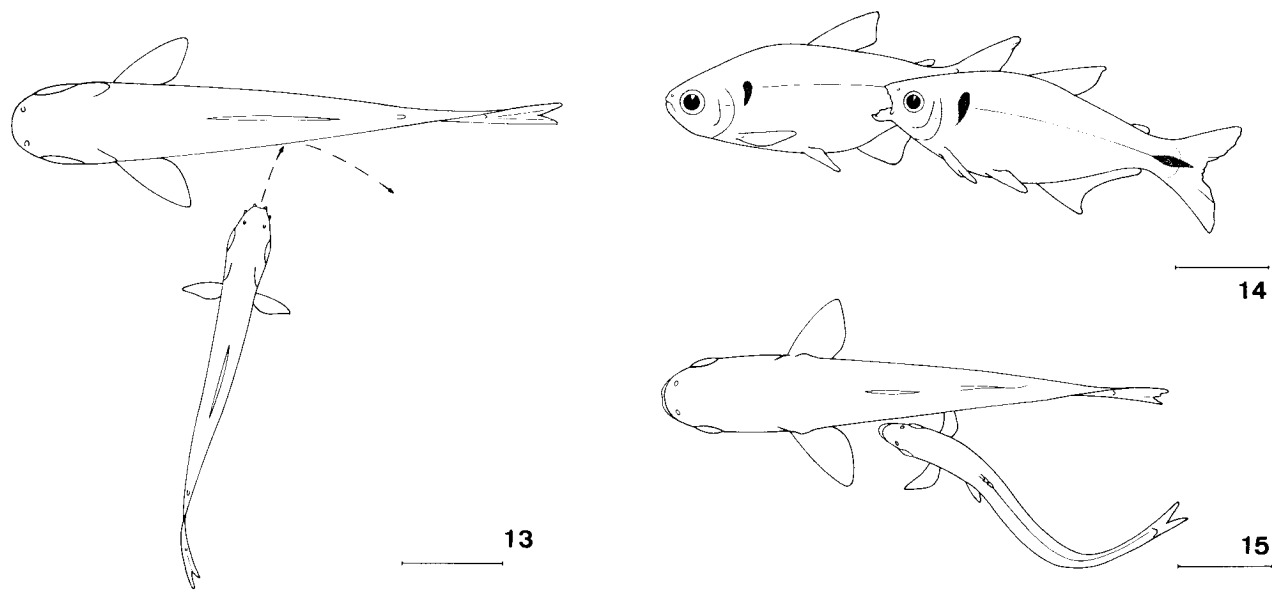


Fig. 13–15. Scale-removing attacks of two characoid and one carangid species (horizontal scales are 20 mm); (13) *Roeboides prognathus* attacking a *Tetragonopterus argenteus* – the predator commonly strikes at the prey with its mouth closed and directs the thrust caudally (after Sazima & Machado 1982); (14) *Probolodus heterostomus* biting the flank of *Astyanax fasciatus* – this fish follows the prey and strikes mainly from behind; (15) young *Oligoplites saurus*, a carangid, positioned to strike at the flank of a *Mugil curema* – the wave-like posture is characteristic, and scales are removed with the side of the mandible (redrawn from Sazima & Uieda 1980).

among the milling prey. This possibly allows *Exodon* to easily discriminate the attacked fish and may reduce intraspecific attacks. The oblique, latero-posterior charge of *Probolodus* (Fig. 14) is consistent with its schooling habits and mimetic pattern: *Astyanax* cannot easily discriminate a fish so positioned, and field observations suggest that they mistake the predator for a following companion (Sazima 1980). The cichlid *Corematodus* probably also uses its resemblance to the prey fish to position itself before closing its jaws over the tail of the victim and rasping off the scales as the prey flees (Trewavas 1947, Fryer & Iles 1972). The carangids *Scomberoides* and *Oligoplites* curve the body into an 'S' posture (Fig. 15) and, with the mouth open, strike at the prey's body with the side of the mandible (Major 1973, Sazima & Uieda 1980). This posture is believed to be a requisite both for positioning the mouth so that the teeth can be inserted under the scales (Major 1973) and for providing the force necessary to dislodge the scales (Sazima & Uieda 1980). On two occasions I have

observed an individual of *O. saurus* touching the belly of the intended victim with its pectoral fin before the actual scale-removing strike. Physical contact with the host preceding actual feeding seems to be important for cleaning and mucus- and scale-eating activity by the labrid *Labroides dimidiatus* (Losey 1978, 1979).

The dislodged scales are swallowed immediately if taken in the mouth, or gathered as they sink, a behavior which appears in all scale-eaters studied to date. After a strike, *Roeboides*, *Exodon* and *Probolodus* often turn about to pick up the falling, dislodged scales. Scales on the substrate are visually sought and ingested after lifting them with the snout (Fig. 17) sometimes hours after the initial attack.

The fishes attacked probably escape without much harm and recover. (Under aquarium conditions missing scale-rows of *Astyanax* spp. and *Carassius auratus* regenerate in about three to four weeks.) Thus scale removal is less serious to prey fish than fin-clipping, practiced by many *Serra-*

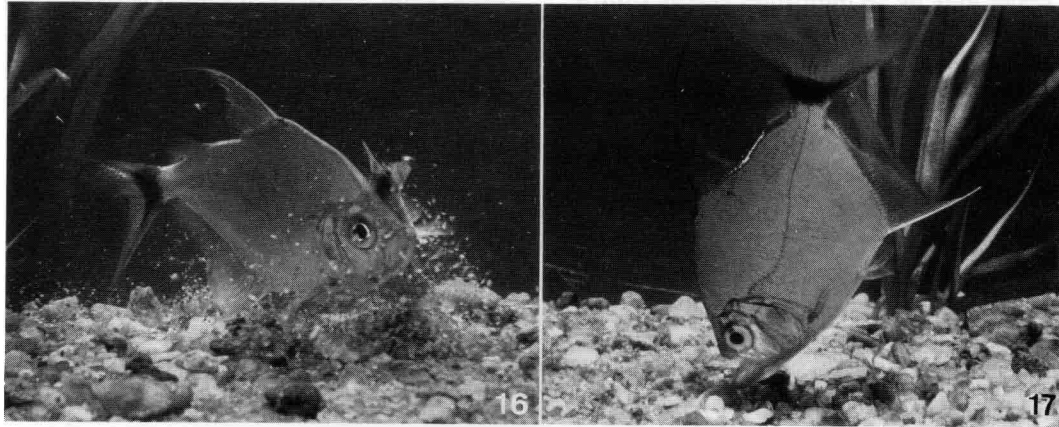


Fig. 16–17. *Catoprion mento* completing a scale-removing strike on *Astyanax*, showing the prey displaced by the force of the impact (16); *Catoprion mento* seeking for fallen scales, lifting them from the substrate with its wide mandible (17).

salmus species, for a crippled fish is more vulnerable to other predators. Although scale- or fin-eating can be regarded as a parasitic mode of feeding, I consider it predation because of the tactics used.

Prey choice

Most scale-eating fishes attack prey as large as, or larger than, themselves (Breder 1927, Hoese 1966, Major 1973, Whitfield & Blaber 1978, Sazima 1980, Sazima & Uieda 1980). The limits probably are determined by the size of the removed scales (Whitfield & Blaber 1978), as the mouth and esophagus of the predator must be able to engulf them, and by the ability of the scale-eater to approach its victim and to retreat, if necessary (Marlier & Leleup 1954, Whitfield & Blaber 1978, Sazima 1980). Scale-eaters remove scales from diverse fish species (Major 1973, Mok 1978, Whitfield & Blaber 1978, Vieira & Géry 1979, Sazima 1980). Among characoids *Probolodus* preys mostly on *Astyanax* and, to a lesser extent, on *Curimatus* (Sazima 1977). Cichlid species are rarely attacked (Sazima 1977, 1980). *Roeboides prognathus* takes scales mostly from tetragonopterines, *Astyanax* and *Tetragonopterus*, but cynopotamines may also be attacked (Sazima & Machado 1982). In the field, I observed *Catoprion* attacking only *Astyanax bimaculatus*, a ubiquitous fish in the habitat of the former at Poconé, Mato Grosso State

(Fig. 10). Vieira & Géry (1979) listed anostomids, hemiodids, and possibly curimatids as prey of *Catoprion* in the Rio Curuá-Una, Pará State. Under aquarium conditions, characoids accept almost every scale-bearing species presented to them, including goldfish *Carassius auratus* (Sazima 1980). Predator preferences (Hoese 1966, Fryer & Iles 1972, Sazima 1977, Sazima & Machado 1982) probably reflect prey attributes such as abundance, spatial and temporal distribution, specific behavior, and the ease of scale removal.

No characoid scale-eater was ever seen removing scales from dead fish, or even freshly killed ones, in aquaria experiments (Sazima 1980). On the other hand, the carangid *Oligoplites saurus* habitually eats scales from dead fish under aquarium conditions. This suggests that *Oligoplites* is to a certain extent a scavenger and that scavenging may have been one of the ways which led to lepidophagy in this genus (Sazima & Uieda 1980).

Dietary specialization

Scales probably must be complemented by other kinds of food. Whitfield & Blaber (1978) provided the calorific value of scales from *Mugil cephalus* ($= 2 \text{ cal mg}^{-1}$), a mugilid fish preyed on by the teraponid *Terapon jarbua*. Fish scales contain 40–85% protein (van Oosten 1957), but data on their nutritive value are entirely lacking. The mucus

covering scales may be an important energy source for scale-eaters, as suggested for the cleaning labrid, *Labroides phthirophagus* (Gorlick 1980). Fish mucus is rich in protein (Wessler & Werner 1957) and lipids (Lewis 1970). Probably no scale-eating characoid feeds exclusively on scales, a possible exception being *Roebioxodon* (Roberts 1970, Knöppel 1972). *Roeboides* also ingests arthropods and fishes (Zaret & Rand 1971), and *Probolodus*, *Bryconexodon* and even *Exodon* take insects and plant material, including leaves, seeds, and algae (Roberts 1970, Knöppel 1972, Sazima 1977, 1980, Géry 1980, Sazima & Machado 1982). *Catoprion* eats insects and plant material, but has a distinct preference for scales when adult (Vieira & Géry 1979). Such a shift from a diversified diet to an almost entirely lepidophagous one as the fish grows, has also been noted for species of *Roeboides* (Roberts 1970, Sazima 1980, Sazima & Machado 1982).

The capacity of scale-eating characoids to take food items other than scales may be important. I examined a seemingly healthy adult *Probolodus heterostomus* with most of its teeth worn out and some in the process of replacement, its stomach containing only plant material and insects. Other scale-eating fishes also take alternative food items (Marlier & Leleup 1954, Greenwood 1965, Hoese 1966, Fryer & Iles 1972, Major 1973, Sazima & Uieda 1980, Whitfield & Blaber 1978). A few species, such as the cichlids *Perissodus straeleni* and *Corematodus* spp., and the triacanthodid *Tydemania navigatoris*, seem to subsist solely on scales (Trewavas 1947, Marlier & Leleup 1954, Fryer & Iles 1972, Mok 1978).

Scale-eating appears to be a size-limited behavior. Some scale-eating fishes, such as the carangid genus *Oligoplites*, cease lepidophagy, concomitantly with changes in dentition, as they grow (Major 1973, Smith-Vaniz & Staiger 1973, Sazima & Uieda 1980). Moreover, several African cichlids increasingly complement their diet with small fishes (Marlier & Leleup 1954, Fryer & Iles 1972). Perhaps it is no coincidence that scale-eaters rarely exceed the length of 200 mm and that most range near 120 mm (Roberts 1970, Fryer & Iles 1972, Mok 1978, Sazima 1980). Lower size limits occur too; *Probolodus* at length of about 19 mm takes

scales from *Astyanax* of similar sizes (Sazima 1980).

In the stomach of lepidophagous fishes, the ingested scales become eroded and coalescent; in the intestine, they are reduced to a structureless pulp (Roberts 1970, Whitfield & Blaber 1978, Sazima & Machado 1982). The digestive transit time varies according to the species (Sazima 1980). As far as I know, no one to date has investigated the physiology of digestion in scale-eating fishes.

The proportion of other food items ingested, relative to scales, can provide a useful measure of the degree of specialization of a given scale-eating species. Stomach contents of 21 specimens of *Roeboides prognathus* taken at one site in the Rio Cuiabá, Mato Grosso State, were composed exclusively of scales, except for a few insects in five of them. In contrast, stomachs of 14 syntopical, comparably sized individuals of *R. bonariensis* contained insects in the same proportion as scales, with six of them having no scales at all. It seems that *R. bonariensis* has a more diversified diet, which agrees with its less modified jaws and teeth compared to *R. prognathus* (Sazima 1980). In the characid subfamily Acestrorhynchinae a trend towards piscivory was found in the most specialized species as defined by changes in dentition, cranial architecture, and body plan (Menezes 1969). A similar trend possibly occurs within the genus *Roeboides*, in which forms such as *R. bonariensis* seem to be the least specialized (near the ancestral, *Charax*-like stock?), whereas forms like *R. prognathus* appear the most specialized (Sazima 1980).

The evolution of scale-eating habits

Trophic origin

Several hypotheses have been proposed to explain the evolution of scale-eating in fishes, and all of them involve a trophic origin: scraping of epilithic or epiphytic algae, removal of epibionts or ectoparasites, modified and 'degenerated' forms of predation or piscivory, and necrophagy (Fryer et al. 1955, Greenwood 1965, Géry 1969, Fryer & Iles 1972, Whitfield & Blaber 1978, Whitfield 1979, Sazima & Uieda 1980, Sazima & Machado 1982).

Scale-eating African cichlids are said to have evolved both from herbivorous and carnivorous ancestors (Fryer et al. 1955, Greenwood 1965, Fryer & Iles 1972, Liem & Stewart 1976). Fryer et al. (1955) proposed an intermediate step toward lepidophagy, starting from algae-scraping behavior, through the grazing of epibionts on the bodies of other fishes. A 'modified piscivory' has also been proposed by some authors, although none has suggested what kinds of paths might have led to scale-eating. Of two closely related species of *Docimodus*, one has fin-eating habits whereas the other is a skin- and scale-eater (Eccles & Lewis 1976). The fact that some scale-eaters can be caught on lines baited with pieces of fish (Fryer & Iles 1972), however, does not contribute much to the argument for 'modified piscivory', inasmuch as feeding on small fishes is usual in certain size classes of scale-eaters.

Modified piscivory was also suggested by Géry (1964, 1969, 1972) for *Catoprion* and *Exodon*. For *Catoprion*, modified piscivory seems to be a reasonable mechanism, once accepting its phyletic affinity with the piranhas, Serrasalminae (Géry 1972, 1977). Most species of *Serrasalmus*, especially when young, feed mainly on fins or chunks of the body of other fishes. The species *S. elongatus* always appears to specialize on fin- and scale-eating (Roberts 1970, Goulding 1980). Some aspects of the hunting and scale-eating behaviors of *C. mento* are in many ways similar to those of some piranhas, and this seems to lend support to such an idea. However, as the evolution of particular habits is difficult to trace using exclusively behavioral data, phyletic studies are needed to help. At present the affinities between the Serrasalminae (piranhas) and the related Myleinae (pacus) are poorly understood and *Catoprion* may be a specialized offshoot of a group which evolved carnivorous as well as herbivorous habits.

The possible relationship between scale-eating, together with other 'mild' forms of mutilation, and the cleaning habit have been already pointed out (Losey 1978, 1979, DeMartini & Coyer 1981). The labrid *Labroides*, a well known cleaner, may forage on scales and mucus (Losey 1972b, Gorlick 1980), and the young of two kyphosid species engage in cleaning as well as scale-feeding (DeMartini &

Coyer 1981). Scale-feeding in the carangids *Oligoplites* and *Scomberoides* probably is also related to occasional cleaning habits (Smith-Vaniz & Staiger 1973, Sazima & Uieda 1980), for one behavior might lead to the other — cleaning and scale- or mucus-eating are extremes on a behavioral continuum (DeMartini & Coyer 1981). For *Oligoplites*, necrophagy was proposed as an alternative (or complementary) origin for scale-eating (Sazima & Uieda 1980). Removal of scales from dead fishes has not been observed in lepidophages other than *O. saurus*. I suspect that some of the scales reported in *Arius cleptolepis* (Roberts 1978) might have been ingested in this manner, as I observed young individuals of other two ariids, *Netuma barba* and *Genidens genidens*, removing mucus and scales from dead fish (Sazima 1980).

Mucus-eating may have been the ancestral feeding behavior of the scale- and even blood-feeding trichomycterids. *Ochmacanthus reinhardtii* was reported feeding on this nutritious secretion (Roberts 1972) and *Branchioica bertonii*, aside from taking blood in the gill chambers of *Pseudoplatystoma* spp., were observed behaving as if they were rasping mucus from the body surface of these hosts (Machado & Sazima 1983). I have found specimens of *Pseudostegophilus maculatus* with their stomachs filled with mucus along with some characoid scales. Mucus seems to be of major importance in the diet of some ariids, blenniids, labrids, and even young cichlids (Hoese 1966, Hobson 1968, Losey 1972a, 1972b, 1978, Noakes 1979, Gorlick 1980, Sazima 1980).

Social origin

It seems logical to seek the origin of a given feeding habit in other seemingly related modes of feeding. Nevertheless, this will not necessarily be the case, for some specialized modes of feeding have almost certainly originated from other, qualitatively different behaviors (Eibl-Eibesfeldt 1970, Curio 1976). This seems to be the case for at least *Probolodus heterostomus* and *Exodon paradoxus*, for which I suggest here a primarily social origin for their specialized, scale-eating habits, i.e. intra- and interspecific aggression. As seen earlier, there is

evidence that both species are related to the Tetragonopterinae, and it is certain that some *Astyanax* species occasionally consume scales. Let us examine the agonistic behavior of some tetragonopterines for the possible origins of scale-eating habits.

Many *Astyanax* species are inquisitive schooling fishes which feed opportunistically on almost anything edible. Aggressive encounters between individuals in the school are frequent and consist mainly of short chases and bites (sometimes accompanied by displays such as undulatory swimming). Occasionally in these conflicts a few scales are dislodged by the attacking fish, which may then ingest them. This behavior is frequent in *Astyanax bimaculatus*, *A. fasciatus* and *A. scabripinnis* and, indeed, appreciable amounts of *Astyanax* scales may be consumed by the two former species (Nomura 1975). Breder (1927) commented upon the aggressiveness of *A. ruberrimus* and noted that most individuals bear wounds or scars resulting from bites.

Aggressive behavior in *Astyanax* may intensify during and after feeding activities, seemingly because search for food increases the chance and the duration of the encounters between the members of the school. Such a correlation has previously been recognized in animals other than fish (Curio 1976). Moreover, tetragonopterine characins often congregate in schools of mixed species, or even genera (Lowe-McConnell 1975), and aggressive scale-eating behavior may sometimes be directed against fishes other than conspecifics. Were this to have repeatedly occurred in crowded, food-limited populations, seemingly ideal conditions for the initial evolution of scale-eating would have been created. It seems that from the 'mild' scale-eating practiced by some *Astyanax*, very few evolutionary steps are necessary to arrive at the specialized, habitual lepidophagy found in *Probolodus heterostomus* and *Exodon paradoxus*. Both species have general habits similar to those of some *Astyanax* species and are also quarrelsome towards conspecifics and other fish (Sazima 1980). The agonistic displays of *Probolodus* exhibited at the sudden approach of another fish in the school, as well as the unique 'twin spot' pattern of *Exodon*, probably have appeared as aggression-reducing devices during the evolution of lepidophagous habits, thereby reducing intraspe-

cific scale-eating (Sazima 1980).

Two important conditions for the acquisition of lepidophagy via aggressive behavior as envisioned here are that agonistic encounters increase in feeding occasions and that attacks are occasionally directed towards individuals of other species in the mixed schools (both observed in *Astyanax*). Another point of importance is the propensity to ingest the scales dislodged during aggressive encounters, as some fishes do not make use of them, whereas *Astyanax* swallow the scales and digest them to a certain extent. The origin of scale-eating in *Probolodus* and *Exodon* via aggressive behavior in an *Astyanax*-like ancestor may presently be accepted as a probable mode of evolution of this feeding behavior for these two genera. Phyletic studies on *Probolodus*, *Exodon*, *Bryconexodon*, *Astyanax* and other seemingly related characids may provide an additional test for this interpretation. (Of course, there still remains the alternative of an exclusively trophic origin.)

Intraspecific aggression might also provide an alternative explanation for the origin of scale-eating in *Catoprion mento*, a serrasalmine. Although this may seem unduly speculative, it seems relevant in this context to quote Greenwood (1965) who, in discussing the evolution of scale-eating habits of the African cichlid *Haplochromis welcommei*, wrote: 'If the derivation of the lepidophagous species from algae-grazing ancestors be accepted, there is still one major step unexplained: what stimulus led the proto-lepidophages to seek food from the surface of other fishes?' One possible answer is aggressive behavior. Most cichlids exhibit aggressive, territorial behavior (Eibl-Eibesfeldt 1970, Fryer & Iles 1972), and some of their agonistic encounters might result in biting and scale-removal. I have observed captive individuals of two unidentified species of herbivorous myleine characids chasing, biting and swallowing the dislodged scales of conspecifics. A herbivorous species adapted to graze on hard substrates, such as a number of African 'mbuna' species, could very well dislodge and ingest some scales in attack situations. From this origin, scale-removal and ingestion may be perfected to constitute a habitual mode of feeding dislinked from its original social context.

Table 1. Behavioral characteristics, feeding habits and suggested origin of lepidophagy, in various scale-eating fishes.^a

Species ^b	Social habits	Hunting tactic	Scale-removal behavior	Main food items	Suggested origin for scale-eating
CHARACIDAE					
<i>Roeboides prognathus</i> (plain color, young translucent)	Solitary, rarely in small groups	Ambushes or stalks	Strikes at the flank of prey, mainly with mouth closed ^c	Scales, insects, fishes	Ingestion of scales during unsuccessful attack to prey; Picking up epibionts
<i>Exodon paradoxus</i> (twin spot pattern)	Schooling (in homotypic groups)	Rushes toward prey, in group	Strikes at the flank of prey, with mouth closed, or bites ^e	Scales, insects	Intra- and interspecific aggressive behavior; Opportunistic foraging on various substrates
<i>Probolodus heterostomus</i> (aggressive mimic)	Schooling (mainly in mixed groups, together with prey)	Approaches under disguise	Strikes from behind, with mouth open and bites ^d	Scales, insects, plant material	As above
<i>Catoprion mento</i> (plain color)	Solitary, rarely in twos	Stalks, or ambushes, frequently with use of plant cover	Strikes at the flank of prey almost in a right angle and bites ^d	As above	Modified predation; Aggressive behavior
CICHLIDAE					
<i>Corematodus shiranus</i> (aggressive mimic)	Solitary, but joins prey's schools	Approaches under disguise	Closes its jaws over the tail of prey ^e (inferred)	Scales only	Modified predation
<i>Perissodus straeleni</i> (aggressive mimic)	As above	As above	Pushes its mouth against the back of prey ^f	Scales, fishes	Modified predation; Grazing on epibionts; Aggressive behavior
GARANGIDAE (young only)					
<i>Oligoplites saurus</i> (plain color)	Solitary, or in small groups	Swims together with prey, sometimes under disguise	Strikes with the side of mandible parallel to the flank of prey ^g	Scales, invertebrates, fishes	Opportunistic foraging on other fishes ('cleaning'); Necrophagy
<i>Oligoplites palometa</i> (barred pattern)	Solitary	Stalks, frequently with use of cover	As above	As above	As above
TERAPONIDAE					
<i>Terapon jarbua</i> (striped pattern)	Schooling	Schools and lunges at prey	Presses open jaws against the prey's body ^h	Scales, invertebrates, fishes, plant material	Modified predation; Modified parasite removal
BLENNIIDAE					
<i>Plagiotremus azalea</i> and <i>P. laudandus</i> (aggressive mimics)	Solitary, but may join schools of other, similar fishes	Ambushes or stalks, frequently under cover or may disguise among other, similar fishes	Strikes from behind and bites at the prey's fins	Skin, scales, mucus	Opportunistic foraging on other fishes

^a Sources: Trewavas 1947, Marlier & Leleup 1954, Géry 1964, 1969, Hobson 1968, Roberts 1970, Fryer & Iles 1972, Losey 1972a, Sazima 1977, 1980, Brichard 1978, Whitfield & Blaber 1978, Whitfield 1979, Sazima & Uieda 1980, Sazima & Machado 1982, present paper.

^b The geographical distribution of these species is: Characidae – S. America (freshwater); Cichlidae – Africa (freshwater); Carangidae – W. Atlantic; Teraponidae – Indo-Pacific; Blenniidae – Pacific.

^c Teeth conical or mamilla-like, some external and pointed almost straight ahead.

^d Teeth tricuspid, with median cusp greatly developed and pointed outwards.

^e Teeth small, oblique crowned pointed, and arranged in file-like series.

^f Broad, laminar and strongly recurved teeth.

^g Outer dentary teeth hooked outwards, with spatulate tips.

^h Teeth conical, the outer series larger than the inner, the latter forming a broad band.

I suggest that scale-eating habits may be initiated, or facilitated, by two types of causes: trophic or social. These may be complementary, rather than mutually exclusive, although their relative importance can — and probably does — vary from situation to situation. The behavioral link provided by aggression may help explain some of the steps needed for the evolution from a given, more 'orthodox' feeding habit, to a predominantly lepidophagous one. This may be especially true for such new, opportunistic groups, as were the characoids over the course of their adaptive radiation. Since scale-eating arose in diverse, independent evolutionary lines among the various fish groups, many behavioral alternatives have certainly been involved in the establishment of this feeding habit (Table 1).

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