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HISTORICAL TRANSFORMATION OF FUNCTIONAL DESIGN: EVOLUTIONARY MORPHOLOGY OF FEEDING MECHANISMS IN LORICARIOID CATFISHES

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Abstract.—The current hypothesis of relationship among the Loricarioidea (a diverse group of Neotropical catfishes) is used as the basis for a case study of historical transformation in the feeding mechanism in this monophyletic clade. The historical approach to functional morphology is discussed and is used in this analysis as a means of examining the evolutionary sequence of structure-function transformation. The distribution of structural novelties in the feeding mechanism and their functional correlates are mapped onto the current hypothesis of loricarioid phylogeny. Three major steps in the transformation of the feeding mechanism are identified. The first was the acquisition of highly mobile premaxillae in the lineage leading to the Callichthyidae, Astroblepidae, and Loricariidae. The second step occurred in the lineage leading to the Astroblepidae and Loricariidae: both families possess highly mobile premaxillae with new muscular insertions and movements that are independent of maxillary mobility. Another specialization at this level was the loss of the interoperculo-mandibular ligament and the acquisition of independent bilateral lower jaw mobility via loss of the tight connection between right and left sides of the lower jaws. The third major step occurred in the lineage leading to the Loricariidae. Further subdivision of the jaw adductor muscle resulted in an additional mesial subdivision with a direct muscle insertion onto the premaxillae. A neomorphic structure, the intermandibular cartilage plug (also shared by astroblepids) is specialized in loricariids with a direct attachment to the hyoid, resulting in an additional biomechanical linkage between the hyoid and mandible. A major trend in the evolution of the loricarioid feeding mechanism is the increase in the number of biomechanical linkages. This is hypothesized to be causally related to morphological and trophic diversity. Two explicit predictions are made testing the hypothesis that decoupling of primitively constrained biomechanical elements is related to increased morphological and functional diversity in descendant species. [Historical analysis; feeding mechanisms; evolutionary morphology; catfishes; biomechanics.]

The analysis of pattern and process in the transformation of organic design has been a major component of research in systematic and functional biology. Study of the constraints on the design of organisms arising from the interrelations of biological structures and the environmental forces experienced by organisms has characterized much of the field of functional morphology and biomechanics over the past 20 years (Gans, 1974; Wainwright et al., 1975; Gould, 1980; Lauder, 1982a; Roth and Wake, 1985). Key thrusts of this interest have been directed toward the inter-

pretation of morphology in terms of adaptation (Gans, 1960; Bock and Von Wahlert, 1965; Bock, 1980), and toward defining the morphological basis of adaptive radiation (Mayr, 1960; Stanley, 1968, 1975; Liem, 1973, 1980; Stebbins, 1973; Valentine, 1975; Lombard and Wake, 1977; Larson et al., 1981).

One area where functional morphologists have made little progress is in defining historical sequences by which character complexes of functional significance have been acquired. What historical sequences have lead to complex functional designs? How have *both* structural and functional novelties been acquired at successive hierarchical levels within a clade? Are there any general patterns to the way in which complex functional designs are

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acquired and transformed? These questions have received little attention, despite their importance to understanding evolutionary patterns and processes.

Two primary goals of an historical approach to the study of structure-function transformation are: (1) generation of historical hypotheses for the transformation of structure *and* function that are testable within a phylogenetic framework; and (2) discovery of general (emergent) patterns of structural and functional change. Interpretation of structure-function relations within a phylogenetic framework permits judgment of the degree to which an historical hypothesis of sequential acquisition of function is consistent with the nested hierarchy of structure (cladogram). Phylogenetic hypotheses stand independent of any hypothesis of functional transformation, and historical hypotheses may then be tested by examination of related monophyletic lineages. The discovery of general patterns emerges from the repeated observation, in different monophyletic clades, of similar historical consequences of particular intrinsic (structural) organizational properties of organisms. In this manner, an historical approach provides an opportunity to assess explanatory schema for the transformation of functional design.

In this paper, we present a case study in the historical analysis of a functional design: the feeding mechanism of loricarioid catfishes. We provide the results of a comparative analysis of functional design of the feeding mechanism and then compare these results to selected generalized representatives of outgroup clades. This procedure reveals the distribution of functional novelties within the Loricarioidea by mapping structure-function specializations onto the initial cladogram and allows determination of the historical sequence by which the specialized feeding mechanism was acquired. In addition, we discuss the implications of this case study for the possibility of discovering general patterns to morphological diversification (Lauder, 1981), and make explicit predic-

tions about patterns of form and function in loricarioid fishes.

LORICARIOID CATFISHES AS A CASE STUDY

The Neotropical loricarioid catfishes provide an exciting opportunity to examine the historical pattern of sequential acquisition of structural *as well as* functional novelties in a monophyletic clade. The phylogenetic hypothesis that serves as the basis for the present study is that first proposed by Baskin (1972) for the loricarioid catfishes and later discussed by Howes (1983b). According to this hypothesis, the Loricarioidea is a monophyletic group of catfishes (Siluroidei) with approximately 1,100 species and includes the families Loricariidae, Astroblepidae, Scoloplacidae, Callichthyidae, Trichomycteridae, and Nematogenyidae. In this paper, the term Loricarioidea is used in the sense of Baskin (1972), given superfamily status to conform with the classification of Fink and Fink (1981), and is not restricted to loricariids plus astroblepids (*sensu* Howes, 1983b). The hypothesis of relationship among loricarioid lineages is corroborated by morphological features other than those examined in this study, thus permitting a noncircular approach to the historical analysis of the feeding mechanism. The Siluroidei are considered monophyletic (Fink and Fink, 1981), and, with the exception of the Diplomystidae which appears to be the most primitive member of the siluroid clade (Fig. 1), interrelationships of the remaining catfish families (approximately 26) are largely unknown. However, the phyletic position of the siluroids within the ostariophysan fishes (Fink and Fink, 1981; Lauder and Liem, 1983) is well established.

Loricarioids exhibit great morphological as well as taxonomic diversity. Members of the group occupy a wide variety of habitats and trophic levels within Neotropical freshwaters. The Loricariidae (approx. 600 species) are primarily herbivorous, benthic algae scrapers, the Astroblepidae (approx. 50 species) are presumed

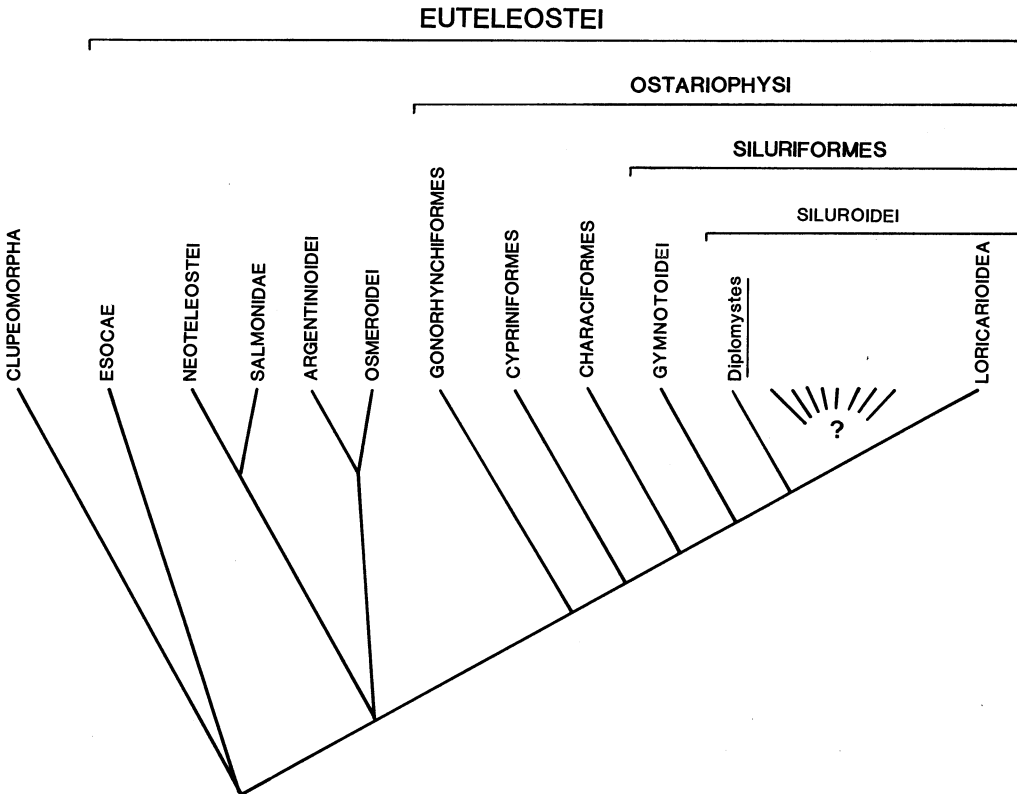


FIG. 1. Phylogeny of Euteleostei, modified from Fink and Weitzman (1982), Lauder and Liem (1983), and Rosen (1985). Within Siluroidei (catfishes), interrelations of 26 non-loricarioid families largely unknown.

to be omnivorous, the Callichthyidae (approx. 250 species) feed largely on benthic invertebrates, while the Trichomycteridae (approx. 200 species) are mostly omnivorous but possess some parasitic members.

MATERIALS AND METHODS

Howes (1983b) examined the anatomy of the cranial muscles of loricarioid catfishes in detail and his work serves as the descriptive foundation for this study. With the exception of the monotypic Scoloplacidae, we examined preserved specimens of each of the loricarioid lineages for morphological data from jaw and hyoid myology and these data were compared to the morphology of selected members of each of the ostariophysan lineages (Fig. 1). In addition to myological dissection, alizarin-

and alcian-stained specimens were examined for each of the loricarioid lineages, including paratypes of *Scoloplax dicra* (Scoloplacidae), with the exception of the Nematogenyidae. A complete listing of material examined is presented in Appendix I.

Due to insufficient material for adequate dissection, it was not possible to examine the myology of *Scoloplax dicra*. This species was first described by Bailey and Baskin (1976), who concluded that it was allied with the loricarioid families Loricariidae, Callichthyidae, and Trichomycteridae. They provisionally placed it as a subfamily of the Loricariidae on the basis of a number of characters hypothesized to be derived for the family. We exclude *Scoloplax* from our functional analysis, but comment on its phyletic position within

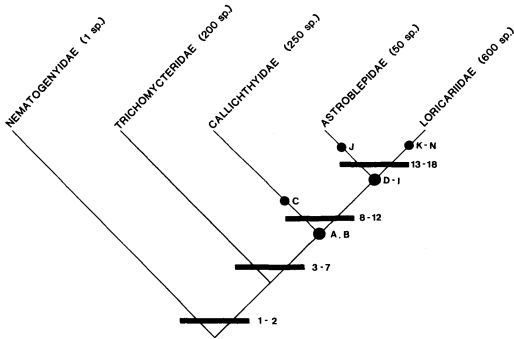


FIG. 2. Phylogeny of Loricarioidea. Numbered characters from Baskin (1972) and Howes (1983b); Lettered characters derived from this study and mapped onto cladogram supported by numbered characters. Characters listed in Appendix II.

the loricarioid clade based on new evidence presented here.

The functional interpretations of the morphological components of the feeding mechanism are based on comparative experimental studies of bone movement and muscle electrical activity in outgroup taxa (Lauder, 1982b, 1983, 1985), and preliminary data on the loricariid *Ancistrus*. Previous research has served to establish both the primitive morphological and functional attributes of the feeding mechanism for ray-finned fishes, teleosts, and euteleosts (Lauder, 1982b, 1983; also see Patterson, 1977; Patterson and Rosen, 1977; Rosen, 1982; Fig. 1).

RESULTS

Cladistics.—The phylogenetic relationships among the five loricarioid families are presented in Figure 2. Functional characters discovered in this study (designated by letters in Fig. 2) are mapped onto the initial cladogram of Baskin (1972), which is supported by the numbered characters.

The Loricarioidea is defined on the basis of a unique encapsulated swimbladder and integumentary teeth ("odontodes") on the fin rays and/or body (Fig. 2). Trichomycterids, callichthyids, astroblepids, and loricariids are united by the derived loss of the claustrum and intercalarium of the Weberian apparatus, and the presence of

odontodes on at least some opercular bones. Callichthyids share with loricariids and astroblepids an expanded pterotic-supracleithrum, which forms the lateral portion of the swimbladder capsule, a high degree of hypural fusion, type C hypurapophyses, and reduced number of caudal fin rays and caudal procurent rays. Loricariids share with astroblepids the sixth centrum fused to the Weberian complex, presence of a "connecting bone" between the transverse process of the second dorsal fin proximal radial and the distal end of the rib on the sixth centrum, a derived hypural fusion pattern, and an expanded ventral lip forming a sucker.

Bailey and Baskin (1976) considered *Scoloplax dicra* to be related to loricariids on the basis of: (1) integumentary teeth on fins and body; (2) encapsulated swimbladder; (3) lengthwise series of bony plates on dorso- and ventrolateral surfaces. They argued further for close relationship to the Loricariidae on the basis of shared lack of dorsal hypohyal and interhyal bones, presence of bifurcate neural spines, first rib on sixth centrum without parapophysis, and presence of the "connecting bone." However, trichomycterids also lack a dorsal hypohyal (Baskin, 1972), while *Nematogenys* and callichthyids both possess ossified dorsal and ventral hypohyals. Loricariids do in fact possess an interhyal, although it is reduced in size and tightly associated with the mesial face of the hyomandibula. Bifurcate neural spines are not unique to loricariids and *Scoloplax* (some amphiliids also possess them). *Scoloplax* lacks the expanded lower lip characteristic of astroblepids and loricariids. The pterotic-supracleithrum is only slightly expanded dorsally and the swimbladder capsule is entirely open laterally. The sixth centrum is not incorporated into the Weberian complex. Additional characters discovered in this study contradict placement of *Scoloplax* within the callichthyid-astroblepid-loricariid lineage, as discussed below. The exact placement of *Scoloplax* within the Loricarioidea remains uncertain, although available evidence (Fig. 2:

characters 1–7) suggests sister-group relationship to the clade composed of callichthyids-astroblepids-loricariids.

Results of a comparative analysis of jaw and hyoid myology are presented below. Functional morphology of the jaw muscles is presented first, progressing from primitive to derived across each taxon examined, followed by that for the hyoid musculature. Particular functional and morphological specializations revealed in this study are then mapped onto the initial cladogram shown in Figure 2.

Comparative myology.—In teleosts, the adductor mandibulae forms the outer muscle mass of the cheek and is variously subdivided in different groups. Following Winterbottom (1974), the outer dorsal division termed A1 has its insertion onto the maxilla, while A2 lies mesial to this and inserts onto the lower jaw. In primitive ostariophysans, the ventral adductor division inserts onto the maxilla or onto the ligamentum primordium (Fink and Fink, 1981:343). Vari (1979:317) stated that a lower jaw insertion for the outer part of the adductor is plesiomorphic for characoids. Howes (1983b:327) considered the plesiomorphic condition of the A1 adductor division in siluroids as that where the muscle inserts onto the lower jaw and lies lateral to the mandibularis nerve trunk.

Winterbottom (1974:231) stated that the path of ramus mandibularis V has at times been used, although unreliably, to identify subdivisions of the adductor. The homology of the subdivisions of this muscle is further complicated by the presence in some siluroids of an inner subdivision of an adductor, termed the retractor tentaculi, that inserts onto the maxilla and serves the base of the maxillary barbel. Because of its maxillary insertion, this muscle has been interpreted as A1 (Winterbottom, 1974). However, Howes (1983b; following Alexander, 1965) regarded this division as a derivative of the mesial adductor elements with a de novo attachment to the maxilla.

Fink and Fink (1981) could not identify a separate A1 division in siluroids. In *Di-*

plomystes and *Nematogenys*, separate divisions of the adductor are not well differentiated and the insertion is largely or entirely onto the lower jaw (Howes, 1983a: 12). Within the Loricarioidea, the condition in *Trichomycterus* and *Henonemus* (Fig. 3) is most similar to the plesiomorphic condition in *Diplomystes* and *Nematogenys*. An inner division of A1 is only slightly separate anteriorly from the lateral mass and inserts onto the mesial face of the dentary and onto the connective tissue sheet which extends from the coronoid process of the dentary to the maxilla. The dorsal element lies mesial to the mandibularis nerve branch and would be termed A2 (following Howes, 1983b), with the portion lying lateral to the branch termed A1. There is no separate retractor tentaculi in those trichomycterids examined by us. In addition to the adductor, a simple broad muscle originates from the lateral ethmoid and inserts broadly onto the posterior aspect of the palatine. This muscle is homologous with the extensor tentaculi of other siluroids (Winterbottom, 1974; Howes, 1983b) and functions as the antagonist of the retractor tentaculi (Gosline, 1975).

As found in *Diplomystes* and other primitive catfishes (Lundberg, 1970), the premaxillae are attached to the neurocranium via lateral extensions of the mesethmoid. In most ostariophysans, including most catfishes, the premaxillae are only slightly mobile. The interopercle lies in series between the opercle and the lower jaw and is connected to the latter by a thick interoperculo-mandibular ligament. This morphology is consistent with the primitive halecostome biomechanical pathway for lower jaw depression (Lauder and Liem, 1983). Contraction of the levator operculi causes a dorsal rotation of the opercular series which is applied as a postero-dorsal force on the lower jaw via the interoperculo-mandibular ligament (Lauder, 1982b).

Members of the Callichthyidae show a number of specializations of the jaw musculature. In *Corydoras* (Fig. 4), the adductor is only slightly subdivided into dis-

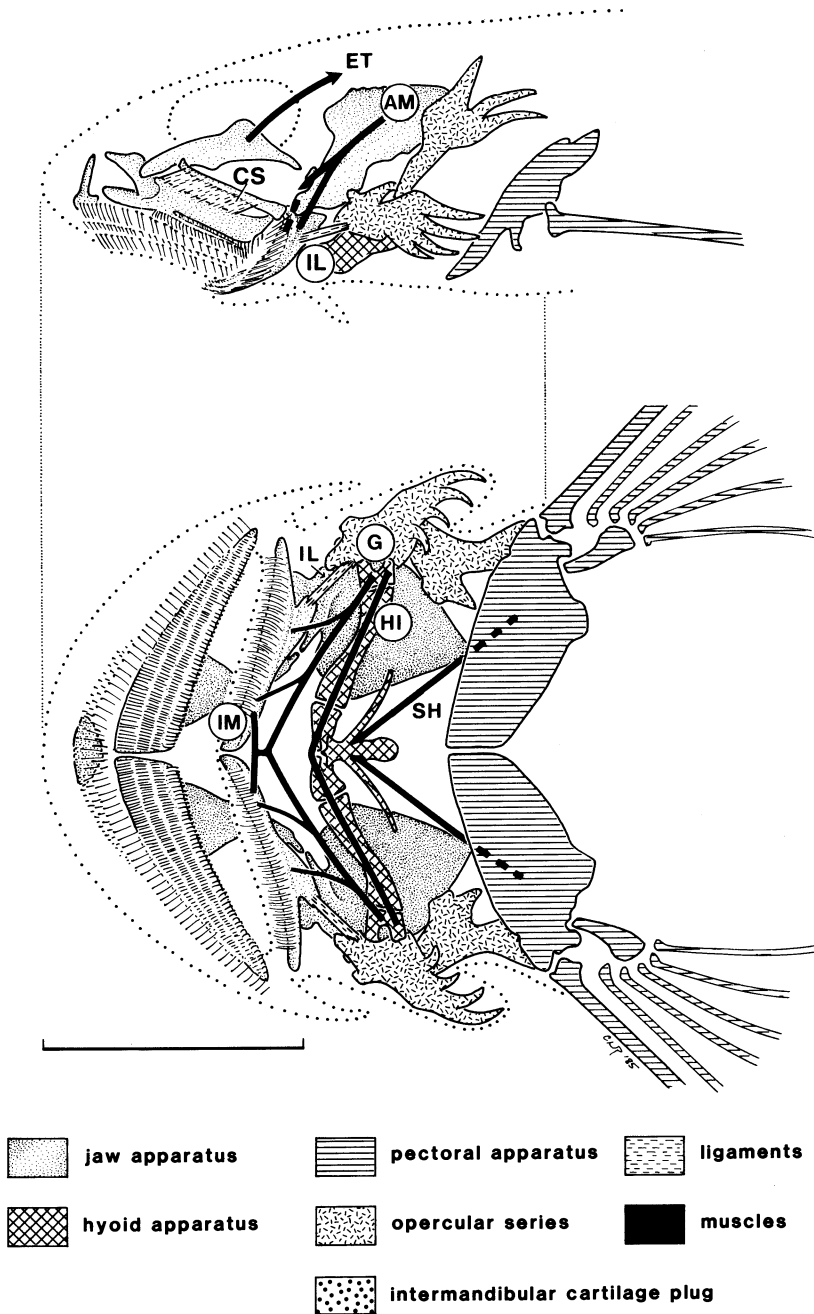


FIG. 3. Schematic illustration of functional components of feeding mechanism of *Henonemus* sp. (Trichomycteridae) FMNH 96624, in lateral (top) and ventral (bottom) views. Abbreviations for individual components as follows and apply to Figures 4-6 as well: (AM) adductor mandibulae; (C) muscle "C" of Howes (1983b); (CS) connective tissue sheet; (ET) extensor tentaculi; (G) geniohyoideus; (G1) geniohyoideus dorsal division; (G2) geniohyoideus ventral division; (HI) hyohyoideus inferioris; (IL) interoperculo-mandibular ligament; (IM) intermandibularis; (RP) retractor palatini; (RT) retractor tentaculi; (SH) sternohyoideus. Scale bar in Figures 3-6 equals 5 mm.

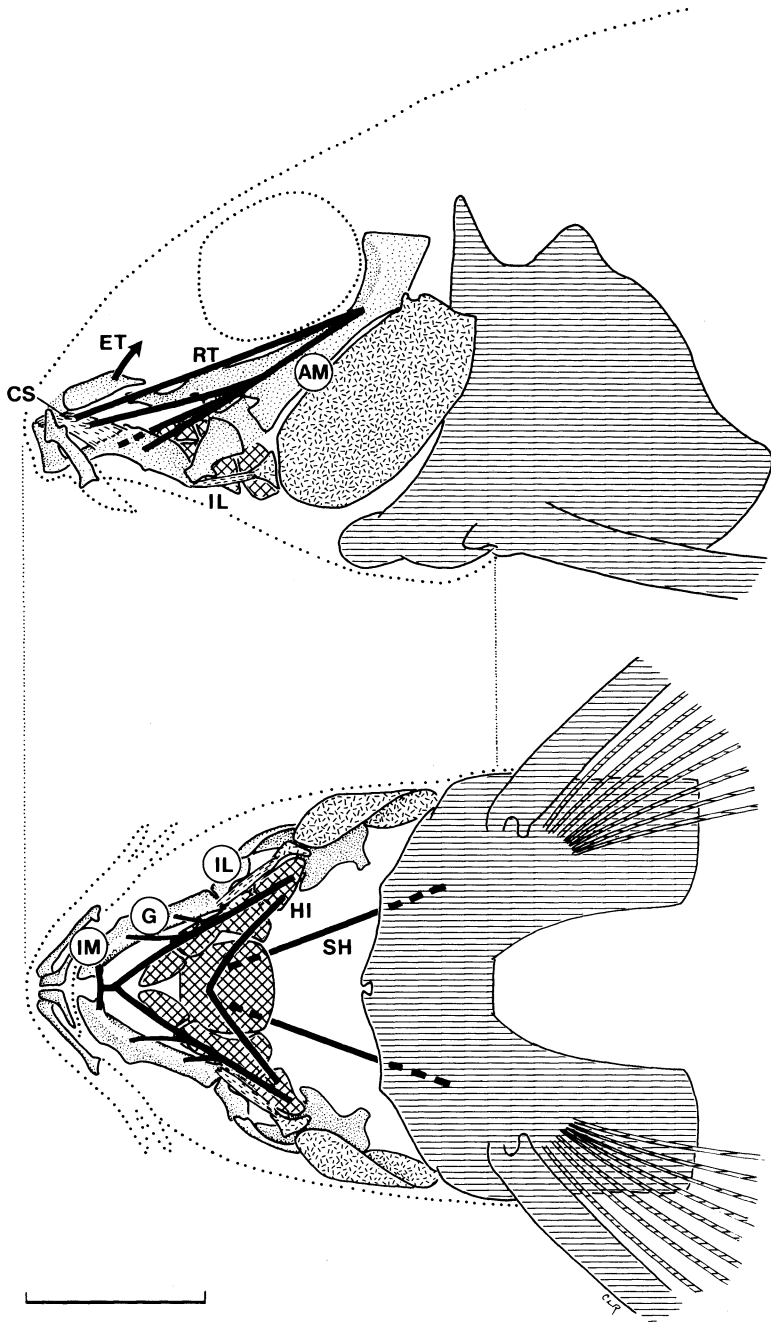


FIG. 4. Schematic illustration of functional components of feeding mechanism of *Corydoras aeneus* (Callichthyidae), FMNH 54832. For abbreviations, refer to Figure 3.

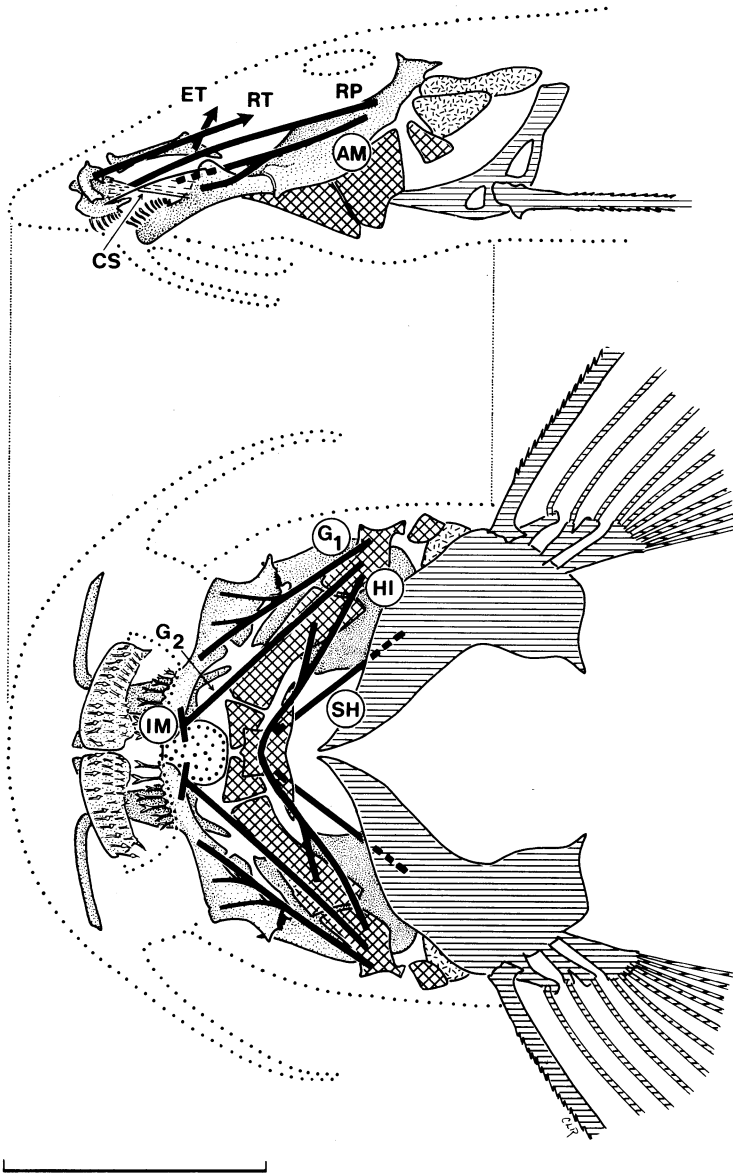


FIG. 5. Schematic illustration of functional components of feeding mechanism of *Astroblepus boulengeri* (Astroblepidae), FMNH 96626. For abbreviations, refer to Figure 3.

tinct A1 and A2 sections. A dorsal division (retractor tentaculi) originates from the hyomandibula and inserts on the connective tissue sheet extending from the coronoid process to the maxilla and premaxilla. Unique among catfishes and shared by all members of the Callichthyidae, Astroblepidae, and Loricariidae, are the

highly mobile premaxillae, which are ligamentously attached to the mesethmoid (ethmoid-premaxillary hinge joint of Howes, 1983b). In most callichthyids, the premaxillae are reduced in size and both upper and lower jaws lack dentition. The ventral adductor division originates primarily from the preopercle and inserts

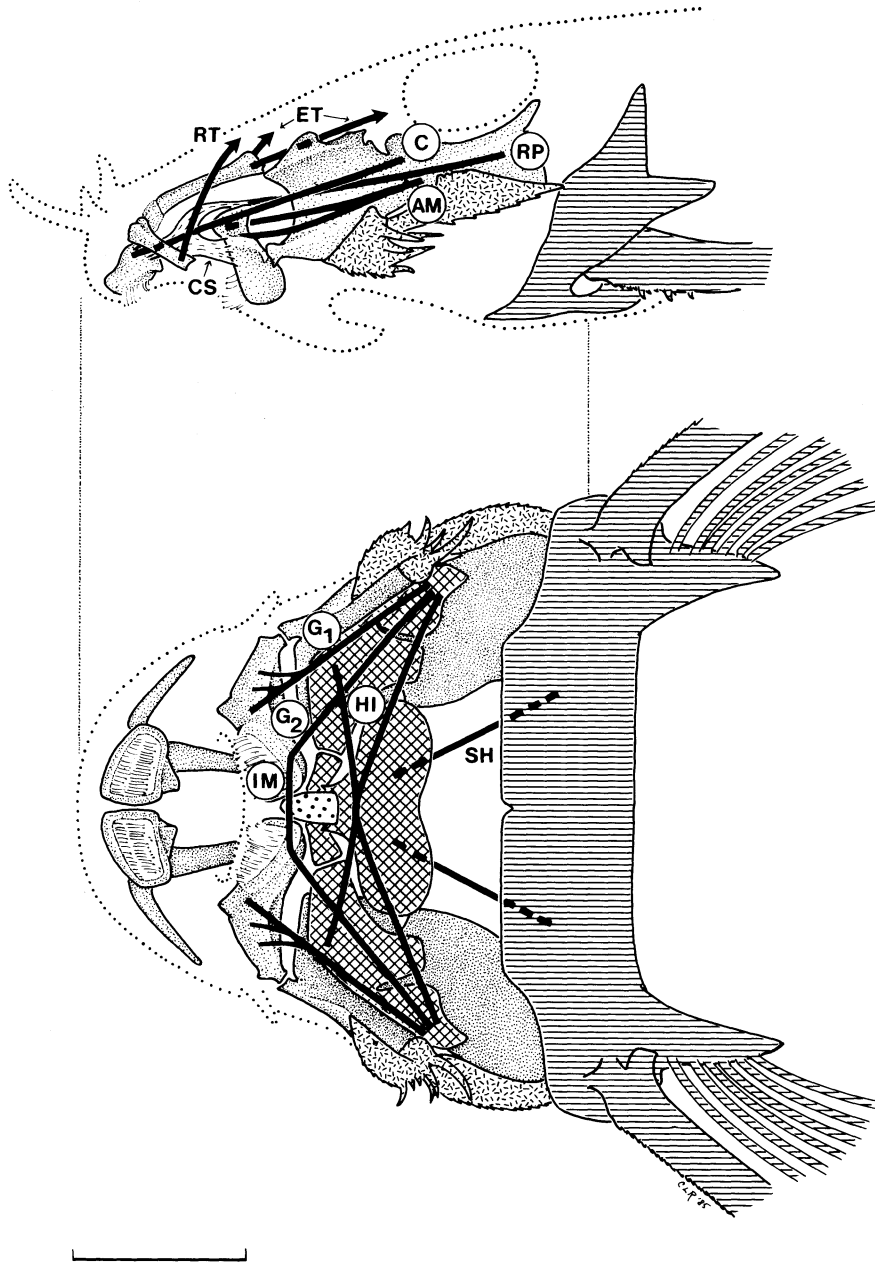


FIG. 6. Schematic illustration of functional components of feeding mechanism of *Ancistrus* sp. (Loricariidae), FMNH 96629. For abbreviations, refer to Figure 3.

onto both the lateral (A1) and mesial (A2) aspects of the anguloarticular as well as onto the connective tissue sheet, with a dorsal extension that is confluent with the tendinous insertion of the connective tis-

sue sheet onto the premaxilla. Callichthyids have retained the undifferentiated extensor tentaculi as well as the interoperculo-mandibular ligament.

A large number of specializations char-

acterize the lineage leading to the Astroblepidae + Loricariidae. Astroblepids (Fig. 5) and loricariids (Fig. 6) share a large straplike retractor tentaculi which has its origin shifted to the lateral ethmoid, completely separate from A1 and A2, inserting directly onto the maxilla. Members of both taxa share with callichthyids the highly mobile premaxillae, which are broad and distinctly cup-shaped in the former two taxa. The following discussion highlights differences in jaw myology between astroblepids and loricariids.

Astroblepus retains the primitive siluroid connective tissue sheet between lower and upper jaws. However, the anterior aspect of this sheet is confined to an insertion onto the premaxilla rather than to the premaxilla + maxilla, correlated with the direct connection of the retractor tentaculi with the maxilla (Fig. 5). The A1 and A2 subdivisions of the adductor are only slightly differentiated anteriorly in *Astroblepus*, where the ventro-lateral portion inserts onto the lateral face of the anguloarticular and the dorso-medial portion inserts onto the dorsal and mesial face of the anguloarticular as well as to the connective tissue sheet. Astroblepids share with loricariids a de novo subdivision of the adductor, lying mesial to A1 and A2 (retractor palatini of Howes, 1983b). This muscle originates from the dorsal part of the hyomandibula and inserts onto the connective tissue sheet at the premaxilla. In *Astroblepus*, there are two separate bony elements ventral to the opercle. The median element is the interopercle and the antero-ventral element is the expanded interhyal element of the hyoid arch. However, the interoperculo-mandibular ligament is absent.

In the Loricariidae, this trend toward further subdivision of the adductor complex is continued (Fig. 6). In addition to the retractor palatini, which loricariids share with astroblepids, loricariids possess a mesial subdivision that has a tendinous insertion onto the premaxilla (muscle "C" of Howes, 1983b). In contrast to Howes, we find no element in *Astroblepus* that can be considered homologous with muscle "C"

in loricariids. In addition, the extensor tentaculi has become subdivided in loricariids, with a separate dorsal and ventral insertion onto the palatine (muscles "E" and "F" of Howes, 1983b). Loricariids share with astroblepids the loss of the interoperculo-mandibular ligament. However, in loricariids the homologue of the interopercle cannot at present be identified.

In discussing the hyoid muscles of loricariids, we include those muscles between the pectoral girdle and the hyoid arch and between the hyoid and lower jaw. Trends in the evolution of these muscles in loricariids have involved subdivision, shifts in muscle orientation, and related osteological specializations. Viewed within the phylogenetic context, these changes can be characterized in terms of multiple biomechanical pathways and increased complexity of design.

The Trichomycteridae (Fig. 3) represent the primitive siluroid arrangement of the hyoid musculature as found in *Diplomystes* and *Nematogenys*. The sternohyoideus is a relatively large, straplike muscle lying dorsal to the remaining hyoid muscles. Its origin is from the anterior face of the pectoral girdle and it inserts onto the dorsal and posterior aspects of the urohyal. Ventral to these muscles is the large hyohyoideus inferioris which extends between the ceratohyal and epihyal to a midline raphe, ventral to the urohyal. The geniohyoideus extends between the hyoid and the lower jaw. It originates from the epihyal and ceratohyal and inserts onto the postero-medial aspects of the dentary, making a broad contact with the fibers of the opposite side. Lying anterior to this juncture is the small intermandibularis, whose individual fibers cannot be easily distinguished from those of the geniohyoideus. Right and left halves of the lower jaws are slightly separate at the midline, yet retain the tight ligamentous attachment. The mandibulo-hyoid ligament is present in all siluroids examined and extends from the epihyal to a posterior anguloarticular process.

In general, three distinct biomechanical pathways are present in the hyoid region. Hyoid retraction is accomplished by con-

traction of the sternohyoideus. Hyoid depression and elevation are mediated by the hyohyoideus inferioris, along with the sternohyoideus. Finally, lower jaw depression could be achieved by contraction of the geniohyoideus and contraction of the sternohyoideus, transmitted to the lower jaw via the mandibulohyoid ligament.

The condition of the hyoid musculature in callichthyids is also relatively unspecialized (Fig. 4). The geniohyoideus inserts along the entire mesial face of the dentary. The fibers of the right and left sides of the hyohyoideus inferioris make a very broad contact at the midline. The morphology of the head in callichthyids is relatively more compressed and less depressed as compared to trichomycterids; the shape and extent of the sternohyoideus in callichthyids reflects this difference.

A large number of specializations of the hyoid musculature, relevant osteology, and associated functional morphology are uniquely shared among loricariids and astroblepids (Figs. 5 and 6). In both groups, the geniohyoideus has become differentiated, with a dorso-lateral segment having a broad origin on the epihyal and inserting directly onto the lower jaw. A smaller ventral segment originates from the epihyal and inserts onto a large spherical cartilaginous plug, situated between and attached to the right and left halves of the lower jaws and extending posteriorly to the hypohyals (Fig. 5). In loricariids, the ventral geniohyoideus subdivision inserts onto the ventral lip tissue, ventral to the cartilage plug. In both astroblepids and loricariids, neither subdivision of the geniohyoideus meets at the midline as they do in all other catfishes (Howes, 1983b). Astroblepids and loricariids share a specialized laterally bifurcate hyohyoideus inferioris, with its anterior division originating from the anterior part of the ceratohyal and a larger posterior division originating from both the epihyal and ceratohyal.

The intermandibularis extends across the fleshy base of the lower lip mesially from the dorsal subdivisions of the geniohyoi-

deus. In loricariids, the intermandibularis is continuous across the mandibular juncture anterior and ventral to the cartilage plug. But in astroblepids, the intermandibularis is divided into right and left halves which insert directly onto the intermandibular cartilage plug. The cartilage plug in loricariids is directly attached to the hypohyals at the midline. In astroblepids, the plug makes no direct attachment to the hypohyals. In both groups the right and left sides of the lower jaws are widely separate at the midline.

The significant functional consequence of these morphological specializations is the increase in number of biomechanical pathways controlling jaw and hyoid movement. The wide separation between right and left sides of the lower jaw, along with independent insertions of right and left sides of the geniohyoideus, strongly suggests the potential for independent mobility of the two halves of the lower jaw (Howes, 1983b). The relation of the cartilage plug to the lower jaws allows for greater mobility than is possible with the primitive tight ligamentous connection.

Due to the direct attachment of the cartilage plug to the hypohyals, loricariids possess an additional functional couple between the hyoid and mandibular arches that is unique among catfishes. In addition to the simultaneous depression of both halves of the lower jaws, potentially achieved through coordinate contraction of both sides of the geniohyoideus, in loricariids the lower jaws can be depressed simultaneously via contraction of the sternohyoideus through its linkage to the lower jaws by means of the intermandibular cartilage plug. This coupling is in addition to, but distinct from the mandibulohyoid ligament couple.

Correlated with the expanded lower lip forming a sucking disk is the expansion of the hyohyoideus inferioris in loricariids and astroblepids. The sternohyoideus mediates dorso-ventral hyoid depression, with pivot points at the interhyals and some amount of flexure at the hypohyal juncture. Hyoid depression results in a reduction of pressure in the oro-branchial

chamber. Loricariids are further specialized in having the antero-dorsal surface of the ceratohyal greatly expanded, forming a broad surface for the origin of the hyohyoideus inferioris. The laterally bifurcate inferioris may be specialized for greater flexibility in modulating hyoid elevation as antagonists of the sternohyoideus. Loricariids and astroblepids continue to respire while maintaining continuous suction pressure at the oral disk (Alexander, 1965).

Although astroblepids also possess a laterally bifurcate hyohyoideus inferioris, there is no corresponding antero-dorsal expansion of the ceratohyal as in loricariids. Several other unrelated catfishes possess laminar bone that extends across the cartilaginous junctions between hyoid arch elements. In loricariids, the hyoid arch is further strengthened against flexure and lateral bending by the rigid suture between the epihyal and ceratohyal elements. Some loricariid taxa (e.g., *Chaetostoma*) also possess a direct bony connection between the epihyal and ceratohyal elements.

DISCUSSION

Mapping the distribution of structural novelties on the current hypothesis of loricarioid phylogeny (Fig. 2) allows for the direct assessment of the historical sequence of acquisition of structural and functional patterns in the transformation of a complex biological design: the feeding mechanism. Both structural novelties and their functional correlates in the feeding mechanism are mapped into the initial cladogram. This procedure reveals features primitive for the Siluroidei as well as specializations in hyoid and mandibular morphology at successive hierarchical levels within the Loricarioidea.

In order to avoid circularity, we have not used the results of this analysis to strengthen the initial phylogenetic hypothesis presented in Figure 2 for the Loricarioidea. However, many characters have been discovered that do corroborate the

initial hypothesis and could be incorporated into future phylogenetic analyses.

Historical sequences and functional design.—A detailed listing of the significant morphological novelties and their hypothesized functional correlates in the evolution of the loricarioid feeding mechanism is presented in Table 1. This discussion will focus only on a few of the key novelties at each hierarchical level.

Based on outgroup analysis, primitive loricarioids possessed adductor musculature that appears to conform to the primitive condition for teleost fishes (Winterbottom, 1974; Lauder, 1982b). The adductor mandibulae is not differentiated into distinctly separate divisions, the premaxillary bones of the upper jaw are relatively immobile, the geniohyoideus muscle is undifferentiated, the right and left halves of the lower jaw are firmly attached to each other anteriorly, and an interoperculo-mandibular ligament is present (Table 1). This functional design is one with relatively few mechanical degrees of freedom: the upper jaw has limited mobility; the two halves of the lower jaw have limited independent mobility; and jaw muscles show few differentiated parts potentially capable of independent function.

The mechanics of the feeding mechanism also appear to be similar to those of primitive teleosts (Lauder, 1982b, 1985). Lower jaw depression is mediated by the two primitive mechanisms: (1) the hyoid linkage via the mandibulohyoid ligament; and (2) the opercular linkage via the interoperculo-mandibular ligament (Fig. 3; IL).

The first step in the transformation of functional design in the loricarioid feeding mechanism was the acquisition of mobile premaxillae in the lineage leading to the Callichthyidae, Astroblepidae, and Loricariidae (Fig. 4, Table 1). The absence of mobile premaxillae in *Scoloplax* contradicts its presumed phylogenetic placement with callichthyids, astroblepids, and loricariids in the Loricarioidea. In callichthyids there is no muscle with a unique insertion onto the premaxilla. Although

TABLE 1. Summary of historical sequence by which complex design of loricarioid feeding mechanism was built up. Structural features and their functional significance listed at each successive hierarchical level in loricarioid clade.

Level of generality	Structure	Functional consequence of structure	
Loricarioidea (plesiomorphic condition)	1 Undifferentiated adductor mandibulae	1 Limited functional differentiation	
	2 Premaxillae firmly attached to cranium	2 Little mobility of upper jaws relative to cranium	
	3 Undifferentiated geniohyoideus		
	4 Tight ligamentous connection between right and left halves of lower jaws	4 Unilateral lower jaw mobility only	
	5 Interoperculo-mandibular ligament present	5 Operculo-mandibular functional couple mediating lower jaw depression	
Callichthyidae + Astroblepidae + Loricariidae	6 Ethmoid hinge joint: premaxillae not firmly attached to cranium	6 Highly mobile upper jaws	
	7 Dorsal extension of lateral adductor mass onto connective tissue sheet	7 Transition step to direct muscle insertion onto upper jaws	
Astroblepidae + Loricariidae	8 Retractor tentaculi present, with direct insertion onto maxilla	8, 9 Movement of maxilla independent of premaxilla	
	9 Connective tissue sheet without attachment to maxilla		
	10 Novel acquisition of retractor palatini; its insertion onto premaxilla via connective tissue sheet	10 Indirect muscle insertion onto upper jaws	
	11 Loss of interoperculo-mandibular ligament	11 Loss of opercle couple for lower jaw depression	
	12 Lower jaws without tight ligamentous attachment at midline	12-14 Independent bilateral lower jaw mobility	
	13 Novel acquisition of cartilage plug	13 Novel mandibulo-hyoid functional couple	
	14 Bilateral subdivision of geniohyoideus	14 Bimodal biomechanical pathway for lower jaw movement	
	15 Bilateral bifurcation of hyo-hyoideus inferioris		
	Loricariidae	16 Cartilage plug with direct attachment to hyoid arch	16 Novel biomechanical couple between lower jaw and hyoid arch; hyoid movement mediates lower jaw depression
		17 Novel acquisition of muscle "C", with direct insertion onto premaxilla	17 Direct muscle control over upper jaw movement

the premaxillae are mobile, movement is limited to that mediated by the retractor tentaculi which inserts onto the connective tissue sheet attached to the premaxilla. This is a retention of the primitive siluroid arrangement. The dorsal extension of

the lateral adductor mass onto the connective tissue sheet in callichthyids could be considered a transitional step toward a direct muscle insertion onto the premaxilla.

The second major step in the transformation of the feeding mechanism was

achieved in the lineage leading to astroblepids + loricariids (Table 1). The retractor tentaculi developed a sole insertion onto the maxilla, and the connective tissue sheet lost its attachment to the maxilla (Figs. 5 and 6). Correlated with this was the acquisition of a muscular attachment of a mesial subdivision of the adductor complex (retractor palatini) to the mobile premaxilla via the connective tissue sheet. Thus, the presumed common ancestor of loricariids and astroblepids had a premaxilla whose mobility was independent of movements of the maxilla.

Another major specialization at this stage was the loss of the interoperculo-mandibular ligament which mediates lower jaw depression in all other catfishes and in the vast majority of the approximately 25,000 species of halecostomes as well (Lauder, 1982b). Possibly related to this was the acquisition of independent bilateral mobility of the lower jaws (Table 1). The two halves of the lower jaw are no longer firmly tied to each other in the midline at this phylogenetic level and, thus, are potentially capable of independent movement. The fact that the lower jaws in *Scoloplax* are firmly united at the midline contradicts its placement within the Loricariidae (sensu Bailey and Baskin, 1976).

Also at the astroblepid + loricariid level, differentiation of the geniohyoideus has resulted in greatly increased complexity in mandibulo-hyoid morphology (Figs. 5 and 6; G1, G2). The primitively single geniohyoideus on each side (Fig. 4; G) has split into two parts. The dorsal geniohyoideus subdivisions, through coordinated contraction, could mediate simultaneous depression of the lower jaws. In addition, a neomorphic structure, the midline cartilage plug (Figs. 5) lies between the hyoid and mandible, although it does not have a firm attachment to the hyoid. The ventral division of the geniohyoideus attaches both to the lower jaw and to the cartilage plug. Although there is currently no experimental evidence that the geniohyoideus muscle subdivisions are capable of independent contraction, their distinct

nature and the decoupling of the right and left halves of the lower jaw strongly indicate the possibility of independent motion of the right and left sides of the lower jaw (Howes, 1983b).

The third stage in the transformation of the feeding mechanism occurred in the Loricariidae (Fig. 2, Table 1). The dorsal subdivision of the geniohyoideus makes a direct insertion onto the lower jaw, which has become shortened, broadened, and ventromedially rotated as compared to the condition in astroblepids (compare Figs. 5 and 6). Further subdivision of the adductor complex continued with the development of an additional mesial subdivision (muscle "C" of Howes, 1983b) with direct tendinous insertion onto the highly mobile premaxilla. Although astroblepids share with loricariids the loss of the interoperculo-mandibular mechanical linkage, loricariids have acquired a novel couple between the hyoid and lower jaw via the cartilage plug which has a direct attachment to the hyoid. Loricariids thus have two novel independent biomechanical pathways for controlling movement of the lower jaws. Direct attachment of the right and left halves of the dorsal division of the geniohyoideus, in addition to the ventral division, allow for full development of independent bilateral mobility of the lower jaws. A thick flap of skin on the postero-dorsal margin of the opercle in loricariids permits only limited lateral mobility of the opercle. The opercular articulation on the hyomandibula, which permits both lateral and dorso-ventral movements of the opercle in the vast majority of actinopterygian fishes, is further specialized in several loricariid taxa where lateral flexure of the opercle serves to erect the cheek spines characteristic of several genera (e.g., *Ancistrus*, *Chaetostoma*, *Panaque*).

Within the loricarioid lineage, then, a number of novel specializations of the feeding mechanism—not known elsewhere within the 25,000 species of ray-finned fishes—have occurred, and the phylogenetic distribution of these novel-

TABLE 2. Comparison of number of described species, geographic distribution, habitat, and trophic information for five loricarioid families treated in this study.

	Nematogenyidae	Trichomycteridae	Callichthyidae	Astroblepidae	Loricariidae
Number of species	1	200	250	50	600
Distribution	Central Chile	South America, Panama, Costa Rica	South America, Panama	Andean South America, Panama	South America, Panama, Costa Rica
Habitat	Unknown	Substrate burrows, rock crevices, high altitude streams	Pools, streams	Torrential streams	Pools, streams, large rivers; shallow and deep water, mountain streams
Trophic characteristics	Unknown	Generalist omnivores	Aquatic insect larvae, detritus	Generalist omnivores	Detritus, periphyton, aufwuchs

ties on the cladogram (Fig. 2) indicates a specific historical sequence to the structural transformation. Overall, it is possible to say that modifications to the upper jaw occurred prior to those of the lower jaw in the evolution of the clade (Table 1), and that there is a clear trend within loricarioids towards increased biomechanical independence of functional components in the feeding mechanism.

Within the Loricarioidea two main functional specializations occur that are related to the morphological modifications described above: algae scraping by the jaws, and the ability to attach the body to the substrate with an oral sucker. Using the mouth to attach to the substrate undoubtedly involves a host of jaw specializations that may be quite different from those required for algae scraping. Unfortunately, there are no good functional analyses of the biomechanics of substrate attachment and, in the absence of such studies, it is difficult to identify those specializations within the Loricarioidea that are related to substrate attachment versus substrate feeding. A key goal of future research should be to identify the functional conflicts (if any) between feeding on and attaching to substrates, in relation to the pattern of structural modification in the jaws discussed above.

Evolution of the Loricarioidea.—The five

lineages within this clade exhibit considerable taxonomic, morphological, and ecological diversity. Unfortunately, surprisingly little is known of the ecology of members of the Loricarioidea (i.e., Lowe-McConnell, 1963, 1975; Knoppel, 1970; Zaret and Rand, 1971; Saul, 1975; Moodie and Power, 1982; Arratia and Menu Marque, 1984; Power, 1984; this information is summarized in Table 2). Field observations (Power, 1984; pers. comm.) suggest that many loricariid taxa are trophically segregated specialists at scraping algae from different microhabitats and substrate types (e.g., *Otocinclus* from leaf surfaces, *Chaetostoma* from rocks, *Panaque* from wood surfaces). Variations in tooth morphology across loricariid genera support this contention.

One possible correlate of the development of increased complexity in the number of muscle attachments to the upper jaws in loricariids is an increased refinement and plasticity in motor control of jaw movements in feeding on varied and irregular surfaces. Multiplicity in motor control may be further developed by the acquisition of the new hyoid-mandible linkage via the intermandibular cartilage plug. The loss of obligate maxillary movements during upper jaw motion may be seen as a specialization for algae scraping.

Direct muscle attachments to mobile

TABLE 3. Comparison of number of biomechanical pathways in feeding mechanism of ray-finned fishes at different hierarchical levels primitive to Loricariidae.

Hierarchical level	Number of biomechanical pathways ^a	
	In upper jaw ^b	In lower jaw and hyoid
Actinopterygii (ray-finned fishes)	0	1
Teleostei (teleost fishes)	0	2
Ostariophysi	0	2
Siluroidei (catfishes)	0	2
Loricarioidea (loricarioid catfishes)	0	2
Callichthyidae + Astroblepidae + Loricariidae	3	2
Astroblepidae + Loricariidae	4	6
Loricariidae	5	7

^a Bilaterally symmetrical pathways treated as one unless bones they affect are not firmly attached at midline.

^b Exclusive of indirect effects of epaxial muscles.

premaxillary bones might thus be considered as a morphological innovation worthy of special consideration as a key innovation (Liem, 1973; Larson et al., 1981), as increased control of upper jaw movement might be causally related to trophic specialization. However, callichthyids have highly mobile premaxillae, but no direct muscle attachments. Trichomycterids have relatively immobile premaxillae, yet have diversified to a similar extent. Therefore, highly mobile premaxillae alone cannot be justified as a key innovation. Similarly, loricariids and astroblepids both possess new muscular attachments to the highly mobile premaxillae, yet astroblepids fall far short of the dramatic adaptive radiation of the Loricariidae. Loricariids also greatly exceed all other loricarioids in terms of diversity of jaw and teeth size and shape.

Structural hypotheses and historical morphology.—One type of general hypothesis that has been proposed concerning the evolution of structural patterns is that "primitive members of a morphologically diverse monophyletic lineage possess functional, structural, or morphogenetic networks which have a greater number of

independent (decoupled) elements as compared to similar networks in closely related but less morphologically diverse monophyletic lineages" (Lauder, 1981:437). This could be called the *decoupling hypothesis*. According to this view, a phylogenetic increase in the number of biomechanical components (as by the decoupling of primitively constrained elements) in a morphological system is related to morphological and functional diversity because of the increased possibility for change and novel connections between independent components in a complex system. An increase in constructional flexibility is also expected to correlate with the acquisition of new functions. This hypothesis falls under the class of structural hypotheses classified as *relational hypotheses* by Lauder (1981).

The results of this case study lend general support to the decoupling hypothesis in historical morphology (Vermeij, 1973; Lauder, 1982a). As shown in Table 3, there is a clear increase in the number of biomechanical pathways in the feeding system in both the upper and lower jaws as compared to outgroup taxa at several phylogenetic levels. Trends in the evolution of the Loricarioidea have involved the decoupling of primitively constrained systems (relatively immobile premaxillae and lower jaw symphysis), an increase in the number of functional (biomechanical) linkage systems (direct muscle attachments to the premaxillae), and an increased multiplicity of biomechanical pathways controlling functional components in the feeding mechanism.

However, if this structural hypothesis is to be useful, we must generate explicit predictions that can be tested by future research. The nature of these predictions, as in all relational hypotheses in structural morphology, will be a comparison between a clade possessing a particular morphological feature (such as decoupling of two biomechanical pathways), and the sister taxon to this clade. For each set of clades compared, the decoupling hypothesis predicts that the species in the clade charac-

terized by the primitive possession of a decoupled biomechanical pathway will show increased variation of shape or function as compared with species in the sister clade.

Based on this case study, a number of predictions can be made concerning the functional design of the feeding mechanism within the Loricarioidea and will serve to make the abstract concept of the decoupling hypothesis more concrete. The loricarioid clade as a whole can be used to produce two tests of the hypothesis that decoupling primitively linked (or constrained) biomechanical elements is related to increased morphological and functional diversity in descendant species.

First, we predict that the diversity of upper jaw movement patterns and the range of muscle function within the callichthyid + astroblepid + loricariid lineage (Group 1) will be greater than in the primitive sister lineage (Trichomycteridae; Group 2). This prediction is based on the fact that group 1 possesses three more biomechanical pathways in the upper jaw than group 2 (Table 3). Testing the prediction that variation will be greater in group 1 requires quantifying the diversity of muscle activity patterns during feeding by species in the two groups.

Secondly, we predict that the diversity of lower jaw movement and muscle activity patterns during feeding within the astroblepid + loricariid lineage will be greater than in the primitive sister lineage, the Callichthyidae. This prediction is based on the increase in number of biomechanical pathways from 2 to 6 (Table 3) at the astroblepid + loricariid hierarchical level. A related prediction at this phylogenetic level is that the diversity of tooth shape, premaxillary shape, and lower jaw shape should be greater in species within the astroblepid + loricariid lineage than in the Callichthyidae. This prediction is based on an expected correlation between structural and functional diversity in the upper and lower jaw. We also expect greater diversity of upper and lower jaw shapes and mobilities within the Loricariidae than in the Astroblepidae.

Testing these predictions would involve quantifying the diversity of bone and tooth shapes within the test lineages, and testing for increased variance in the predicted clade versus its primitive sister taxon. Such testing falls easily within the realm of currently available analytical procedures and techniques.

We believe that the significance of these predictions for research in historical and functional morphology is twofold: (1) Functional analysis has permitted the generation of hypotheses about diversity of shape and function in clades that allow subsequent morphometric and functional research to proceed in an hypothesis-testing manner. Rather than using experimental and multivariate techniques simply to describe patterns of variation in the form and function of organisms, these approaches can now be used to refute or corroborate a priori predictions of the historical hypotheses outlined above. (2) The combined approach of phylogenetic analysis and functional morphology has provided nontrivial hypotheses about the evolution of design in a major group of vertebrates. It is our hope that future research on this and other case studies will provide the quantitative data required to evaluate predictions and to generate new explicit hypotheses about organismal design and its historical component.

Quantification of the diversity of bone movement patterns, muscle activities, trophic ecology, and bone shape within monophyletic clades is not an easy task. Yet, general structural hypotheses about form and function need to be tested if progress is to be made in determining the extent of historical regularity to the evolution of design.

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- tumidus*, 37030, 1 CS; *Notropis spilopterus*, 96620, 2 CS; *Zacco platypus*, 43700, 1.
- Characiformes*.—*Astyanax bimaculatus*, 96621, 3 CS; *A. fasciatus*, 76374, 1; *Distichodus rostratus*, 50311, 1; *Hoplias malabaricus*, 84281, 1; *Stethaprion erythroptus*, 96622, 2 CS.
- Gymnotoidei*.—*Apteronotus* sp., 96040, 2; *Eigenmannia virescens*, 85550, 3 CS; 95981, 2; *Hypopomus artedi*, 70075, 2 CS; *Sternopygus macrurus*, 50191, 1.
- Siluroidei*.—Diplomystidae: *Diplomystes viedmensis*, 58004, 1 CS. Doradidae: *Hemiodoras carinotus*, 53192, 1. Scoloplacidae: *Scoloplax dicra* PARATYPES, UMMZ 198967C&S, 2 CS. Nematogenyidae: *Nematogenys inermis*, 96108, 2. Trichomycteridae: *Acanthopoma bon-di*, 96623, 5 CS; *Henonemus* sp., 96624, 2 CS; *Pseudostegophilus nemurus*, 96625, 1, 1 CS; *Trichomycterus oroyae*, 41047-52, 6; *T. sp.*, 96618, 1 CS. Callichthyidae: *Callichthys callichthys*, 50068, 1; *Corydoras aeneus*, 54832, 3 CS; *C. paleatus*, 69994, 2; *C. punctatus*, 69548, 1 CS; *Hoplosternum magdalenae*, 84055, 1. Astroblepidae: *Astroblepus boulengeri*, 96626, 2 CS; *A. festae*, 96627, 1, 1 CS; *A. grivalvae*, 96628, 1 CS; *A. longifillis*, 70017, 3 CS; *A. simonsii*, 84655, 1, 2 CS. Loricariidae: *Ancistrus chagresi*, 84604, 3, 3 CS; *A. sp.*, 96629, 5; *Hypostomus madiera*, 84145, 3 CS.

APPENDIX II

Characters Used to Construct Cladogram
(Fig. 2)

Numbered characters are those from Lundberg and Baskin (1969), Baskin (1972), and Howes (1983b). Characters designated by letters are those derived from this study of the feeding mechanism; these characters were *not* used to generate the cladogram and have been mapped onto the cladogram in order to examine historical patterns involving the feeding mechanism. (1) encapsulated swimbladder; (2) odontodes (integumentary teeth) on pectoral fin spine; (3) loss of claustrum and intercalarium; (4) loss of ductus pneumaticus; (5) loss of transformator process of tripus; (6) superficial ossification on ventral surface of Weberian vertebrae, extending over the joint with basioccipital; (7) odontodes on opercle; (8) pterotic-supracleithrum expanded, forming lateral swimbladder capsule; (9) hypural fusion pattern $PH+1+2;3+4+5$; (10) type "C" hypurapophyses; (11) reduced number of principal and procurrent caudal-fin rays; (12) odontodes on all fin-rays; (13) rib on sixth vertebra with double articulation to the centrum; (14) "connecting bone" between distal end of second dorsal-fin basal to lateral end of rib on sixth vertebra; (15) mouth forming sucking disk; (16) hypural fusion pattern $PH+1+2;3+4+5+UN$; (17) sixth vertebra incorporated into Weberian complex; (18) transverse process of first anal-fin pterygiophore expanded laterally.

(A) highly mobile premaxillae; (B) adductor mandibulae subdivided, with mesial division inserting onto premaxilla via connective tissue sheet; (C) premaxillae reduced, loss of dentition; (D) intermandib-

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APPENDIX I

Materials Examined

Listed by FMNH catalogue number unless otherwise specified. All specimens dissected; catalog number, and number examined (per lot) are indicated. "CS" designates cleared and stained material. AMNH = American Museum of Natural History, FMNH = Field Museum of Natural History, UMMZ = University of Michigan, Museum of Zoology.

Gonorhynchiformes.—*Chanos chanos*, AMNH 87984, 1 CS; *Gonorhynchus abbreviatus*, 63856, 1.

Cypriniformes.—*Barbus altianalis*, 62935, 1; *B. sachi*, 76948, 1 CS; *Botia macracanthus*, 76298, 1; *Carpiodes*

ular cartilage plug present; (E) geniohyoideus subdivided and separate at midline, with a dorsal division inserting onto lower jaws and a ventral division inserting onto ventral lip tissue; (F) hyohyoideus inferioris bifurcate laterally; (G) adductor mandibulae subdivided, retractor palatini inserting onto the premaxilla via the connective tissue sheet; (H) origin of retractor tentaculi shifted anteriorly to lateral ethmoid, insertion directly onto maxilla; (I) loss of in-

teroperculo-mandibular ligament; (J) intermandibularis separate at midline, inserting onto cartilage plug; (K) intermandibular cartilage plug with direct connection to hypohyals at midline; (L) ceratohyals expanded, sutured with epiphyals; (M) adductor mandibulae subdivided, muscle "C" present, inserting directly onto premaxilla; (N) extensor tentaculi subdivided.