

Teleostean Interrelationships, Morphological Function and Evolutionary Inference¹

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SYNOPSIS. Notions of functional and behavioral transformations among traits of similar organisms are *ad hoc* unless viewed within the context of a corroborated scheme of relationships of the taxa involved. For purposes of exposition a current best estimate of the interrelationships of the main groups of teleosts (as expressed by a branching diagram or cladogram) is used as a basis for evaluating the transformations of feeding and locomotor mechanisms. When the various states of these mechanisms are incorporated into the branching structure, the cladogram, when interpreted historically, specifies certain conceptual constraints such that, 1) specializations of the upper jaw first arose and proliferated before specializations of the paired fins, and 2) that fin spines arose only after changes in both feeding and locomotor mechanisms were well under way. These results are contrasted with familiar though unsupported adaptationist statements about the relative importance of locomotor and feeding mechanisms for the evolution of the spiny-finned teleosts (acanthopterygians)—a contrast between the interpretation of what happened as opposed to why it happened. The particular reasons *why* a given structure, function or behavior exists are unknowable and theories addressing such questions are untestable. Adaptationist arguments in general are framed in terms of forces external to the organism which impose a process of change that leads to good design. The concept of an external agency or process (such as selection) that can design structures or whole organisms to fit their environments, even when stated in rigorously biological language, are effectively the same, and almost as far removed from the empirical data, as the creationist argument for adaptation. To the extent that the empirical data of systematics are not allowed to constrain the evolutionary interpretation of functional anatomists, their explanation of historical change will be limited only by their own inventiveness and the gullibility of their audience.

The ways in which one views studies in evolution, phylogeny, morphological relationship and function depend on some definitions. By the word “evolution” I understand the general notion of a process of change through time; by “phylogeny” the temporal changes of biological systems prescribed by a genealogical nexus. By “morphological relationship” I understand a pattern of order in nature which can be expressed as a hierarchy of nested sets of structures and their ontogeny that describe the interrelationships of organisms; by “morphological function” the manner in which an organism behaviorally integrates and uses the structures in relation to parts of the environment. Knowledge of form and function is derived from empirical studies whose objectives are to describe observable patterns of things as they are.

This contrasts with the non-empirical studies of evolution and phylogeny which are, after all, about processes that are said to have taken place in the past.² There are thus two things that we do in considering evolutionary questions about groups of organisms. One is to study the way in which we think the organisms might be interrelated based on empirical study of their morphology, physiology, mechanical integrations and behaviors and to express such interrelationships in a branching diagram. The other is to interpret the branching diagram historically by assuming that the branching lines in the diagram reflect speciation events and ancestor-descendent connections. It is important to remember therefore that systematic research, which generates these diagrams, is concerned

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² From this comparison I exclude, however, the evolutionary biology of the population geneticist which has no known relevance to the origin of the natural hierarchy of organisms—assumptions to the contrary notwithstanding.

with the study of patterns, and that evolutionary research, if such could be said even to exist, is concerned with the assumption of a process. I see nothing objectionable in that assumption since the idea of a genealogical nexus is derived from empirical studies of heredity and ontogeny and adds a dimension of interest to systematics—I see nothing objectionable, that is, when historical interpretation is constrained by information about real properties contained in the branching diagram. Regrettably these empirical constraints are not always heeded, for the branching diagram tells us nothing whatever about *why* some teleosts have an upper jaw that is protrusile, or that the jaw arose from a non-protrusile one by some gradualistic or saltational process, or that the jaw confers a competitive advantage. What the branching diagram does tell us is that half or more of the teleosts have non-protrusile jaws, that there are several kinds of protrusility, and that one kind is a complex of integrated structural and functional features that uniquely characterizes a group of 8,000 or 9,000 species including the spiny-finned teleosts or acanthopterygians.

The Teleostei may be said to be a natural group (*i.e.*, monophyletic) because it is defined by unique features of the caudal fin supporting skeleton, the dermal components of the gill arch skeleton, and the mobility of the upper jaw bones (Patterson and Rosen, 1977). In living and fossil chondrosteans, in cladistians (*Polypterus* and *Erpetoichthys*) and the lepisosteid and amiid neopterygians the neural arches and spines in the tail region of the axial skeleton are relatively short and have their proximal ends restricted to their segmental location along the vertebral column or notochord (Fig. 1A). In teleosts (Fig. 1B) the ural neural arches are proximally and distally elongate, recumbent on the chordal axis, and their proximal ends extend forward to overlap three to four anterior vertebral segments. In the ventral gill arch skeleton sarcopterygians, cladistians, chondrosteans, and the lepisosteid and amiid neopterygians have a cluster of paired toothplates associated with the medial ba-

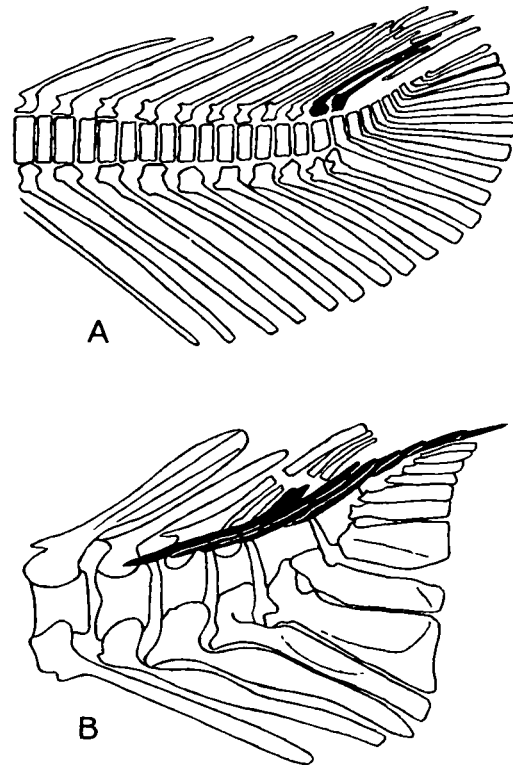


FIG. 1. Caudal skeletons. A, *Amia calva*, after Patterson (1973). B, *Leptolepis coryphaenoides*, after Patterson and Rosen (1977). The ural neural arches and spines in A and uroneurals in B are shown in solid black.

sibranchial copula to which the right and left arches attach, whereas in teleosts the basibranchial and basihyal cartilages are overlain by median toothplates (Fig. 2). In the upper jaw of sarcopterygians, cladistians, chondrosteans, and lepisosteid neopterygians, the maxilla and premaxilla (when the latter is present as a recognizable element) are sutured or otherwise joined immovably with the other bones of the cheek and snout (Fig. 3A). In amiids and a number of primitive fossil neopterygians the maxilla is movable, swinging downward on a hinge with the premaxilla when the mouth is opened (Fig. 3B). In teleosts, the maxilla and premaxilla are primitively firmly united and swing downward together on a premaxillary hinge with the ethmoid region (Fig. 3C). Patterson 1968a, 1973, 1975) and Nelson (1969a)

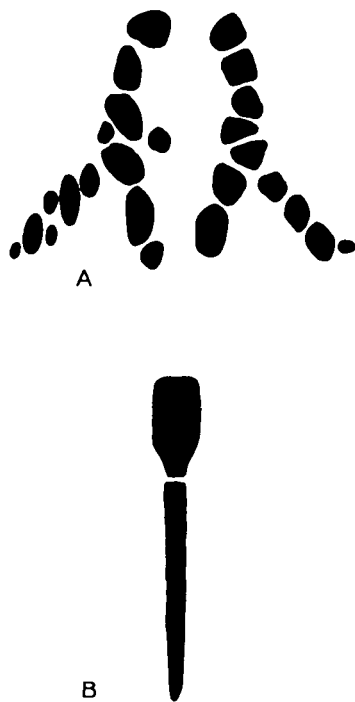


FIG. 2. Patterns of basibranchial tooth patches, after Nelson (1969a) A, *Polypterus* sp. B, *Elops lacerta*.

suggested a large number of other characters that might uniquely describe the teleosts but these are in need of additional study. For the present, however, the three features just discussed are unrefuted evidence of teleostean monophyly.

Since 1966 when Greenwood *et al.* reopened the general question of teleostean relationships a great amount of anatomical evidence has been discovered that disagrees with their original formulation of the problem. Compare, for example, the branching diagram of Greenwood *et al.* with the more detailed resolution of relationships shown in a cladogram which summarizes the past 15 years' work by a number of investigators (Figs. 4, 5). One way of appreciating the changes in concepts of relationship represented by these two diagrams is to depict the information contained in each in the same cladistic form. Accordingly the Greenwood *et al.* diagram may be represented as a simple branching structure (Fig. 4). When re-

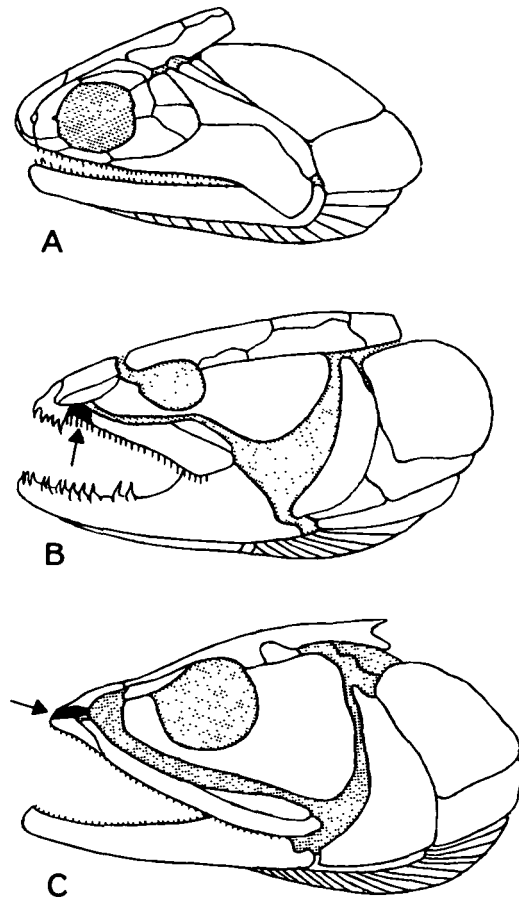


FIG. 3. Actinopterygian head skeletons, after Schaeffer and Rosen (1961). A, *Pteronisculus*. B, *Amia*. C, *Elops*. Individual infraorbital bones of cheekplate in B and C not shown. Arrows locate upper jaw hinge points (solid black). See Vrba (1968) for a description of the premaxillary hinge in *Elops*.

duced to just those taxa taken into consideration by Greenwood *et al.*, the cladogram based on newer data resolves 14 primary statements of relationship (Fig. 6, right). Of these 14, the Greenwood *et al.* scheme (Fig. 6, left) resolves only four, three of which include conflicts with the newer evidence (involving branch points 3, 9, 10, and 14). There have been many other changes in our understanding of relationships at still more detailed levels in the hierarchy but the comparison makes the point that much has changed in 15 years. What is not so apparent until a more de-

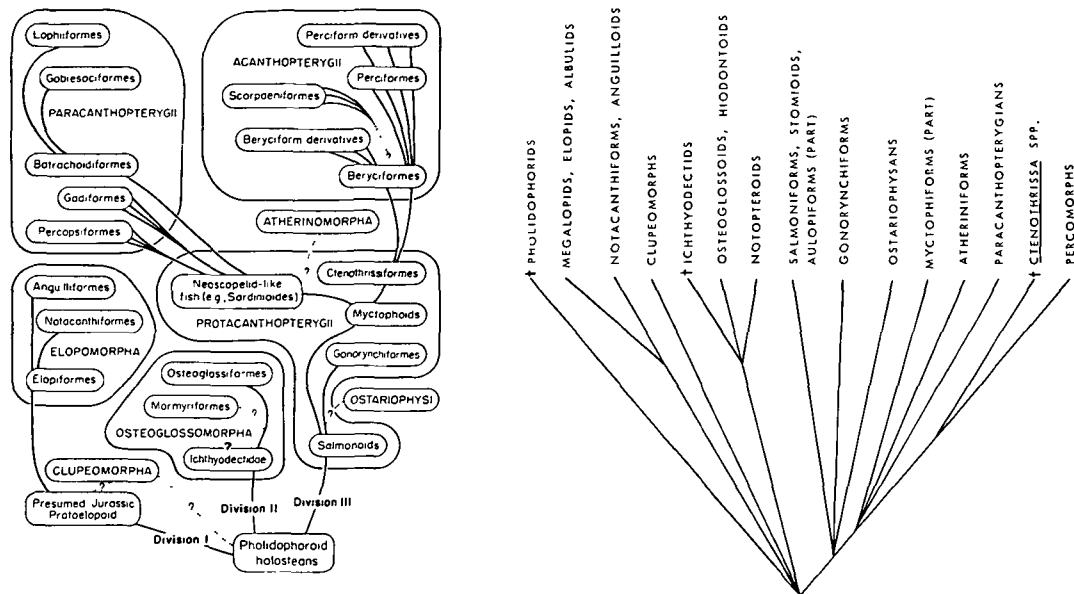


FIG. 4. Teleostean relationships. Left, as originally depicted by Greenwood *et al.* (1966), and right, that scheme transformed into a simple branching diagram. Group names at left are translated at right into modern taxonomic names.

tailed cladogram is examined (Fig. 5) is that there are still immense gaps in our knowledge of teleost relationships, especially within the Elopomorpha, Ostariophysi, and Euteleostei.

I do not propose to review here the technical anatomical details and cladistic argumentation that support the cladogram in Figure 5. The interested reader may refer to the published literature to become acquainted with the evidence (Nelson, 1967, 1968, 1969a, b, 1972a, b, 1973; Patterson, 1967a, b, 1968a, b, 1975; Greenwood, 1968, 1971, 1973; Rosen and Patterson, 1969; Rosen and Greenwood, 1970, 1976; Greenwood and Rosen, 1971; Rosen, 1971, 1973, 1974; Forey, 1973a, b; Greenwood *et al.*, 1973; Springer and Fraser, 1976; Patterson and Rosen, 1977; Fink and Weitzman, 1982). Instead I will ask you to indulge me this scheme so that we can get on with matters central to this symposium. Two of these matters concern locomotor and feeding mechanisms.

There is a popular notion that acanthopterygian fishes (the atheriniforms and percomorphs) represent a sort of pinnacle of teleostean evolution because of a supe-

riority in their maneuverability and diversity of feeding adaptations associated with the protrusile mouth. When such statements are made, what commentators usually have in mind is a very general concept (as drawn from such numerous sources as Gill [1893], Boulenger [1904], Jordan [1923], Regan [1929], Garstang [1931], Berg [1940], Matsubara [1955], Norman [1957], Danil'chenko [1964], Greenwood *et al.* [1966], McAllister [1968], Gosline [1971], Lindberg [1971], and Nelson [1976]) of a perchlike fish with a small number of vertebrae (24 or 25), two dorsal fins of which the first is spinous, three spines preceding the soft rays of the anal fin, a single spine preceding no more than five soft pelvic fin rays, no more than 15 branched rays in the caudal fin, scales armed posteriorly with small prickles or ctenii, armed opercular bones, pectoral fins that sit rather high on the sides near the fish's center of mass, pelvic fins with an anterior insertion under the pectorals, and a dentigerous premaxillary bone of great complexity that can be protruded and guided forward away from the snout by a long ascending process at the premaxillary

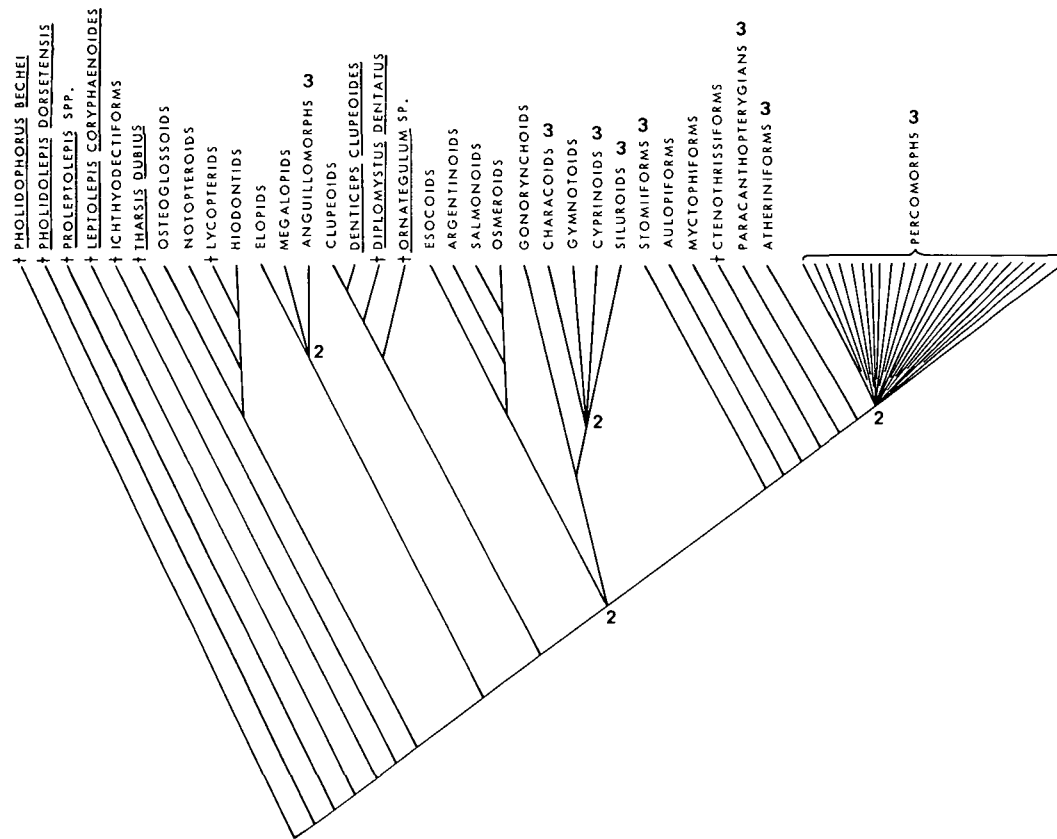


FIG. 5. Cladogram summarizing the results of the last 15 years of investigations of teleostean relationships. Number 2 indicates some major areas of unresolved relationships and, 3, some major questions about group composition.

symphysis. For each of these features, various adaptive roles have been proposed, and which, taken together, have been said to define an adaptively superior fish. In examining the notion that the perchlike fishes "represent the greatest focal point of fish evolution that exists today" (Gosline, 1968), what I propose to do is to proceed as if the cladogram of the Teleostei (Fig. 5), and the relationships it specifies of the acanthopterygians to other groups, is correct. On the branches of this depiction of relationships I shall then place various states of the locomotor and feeding mechanisms as these character states are known for the different taxa. Having done this, I will read the character state tree as if it were a record of biological history to see what might be learned. To minimize the

problem of homoplasies, the character state entered on a given branch or lineage on the cladogram will be the state of the character for the most primitive member of the lineage, a problem that of course does not arise in cases of branches representing single fossil species (branches one, two, four, and six). Thus, among Recent groups, the species of *Hiodon* are taken to represent the Osteoglossomorpha, *Elops* or *Megalops*, the Elopomorpha, *Percopsis*, the Paracanthopterygii, and so on.

First, however, some introductory remarks about paired fins and upper jaws. In chondrichthyans, sarcopterygians, cladians, chondrosteans and lepisosteids and amiid neopterygians the pectoral fins extend out horizontally from a ventral insertion on the girdle wall and the pelvic

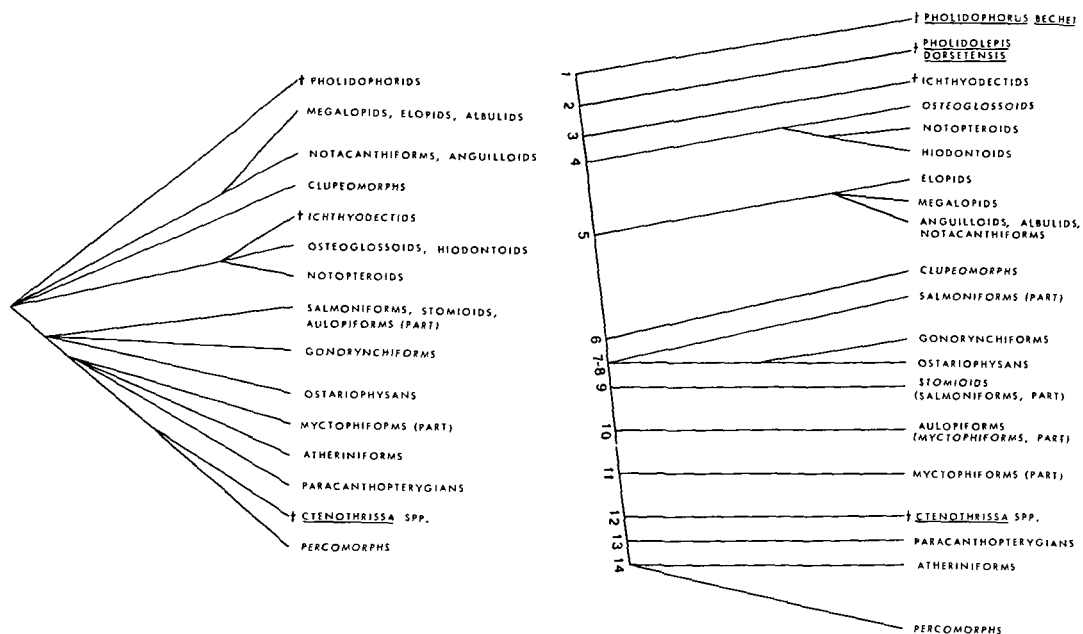


FIG. 6. The 14 taxonomic components included in the Greenwood *et al.* (1966) scheme (see Fig. 4) related according to current theories specified by the cladogram in Figure 5. Right, the 14 components related according to current theory. Left, the distribution of the same 14 components according to the 1966 scheme.

fins arise just in front of the anus near the posterior end of the abdominal cavity. These positional relations are therefore taken to be the primitive ones for gnathostomes. Pectoral fins with a higher insertion on the side and pelvic fins with a more anterior insertion on the abdomen are taken to be derived. As discussed by Breder (1926), Harris (1927), Alexander (1967) and others, the pectoral fin of teleosts can vary in position from the primitive ventral one to an insertion above the midlateral scale row. Similarly, the pelvic fin can vary in position from near the anus to an insertion directly under the pectoral fin insertion, and even farther forward in some very specialized conditions. In general, the pectoral can occur high on the side while the pelvic fin retains a posterior insertion, but when the pelvic inserts anteriorly under the pectoral fin the pectoral insertion is always somewhat higher on the side than in the primitive state. For simplicity four states of the pectoral insertion (Fig. 7, P_1 – P_4) are specified as ventral and horizontal or obliquely downward in ori-

entation (P_1), near the ventral body wall and oriented obliquely upward (P_2), just below a midlateral position (P_3), and at or slightly above the midlateral position and oriented horizontally or obliquely upward (P_4). Four states of the pelvic insertion (Fig. 7, V_1 – V_4) are given as nearer the anus than the pectoral fin insertion (V_1), midway between the anus and the pectoral insertion (V_2), just behind the level of the pectoral insertion (V_3), and below the pectoral insertion with a strong ligamentous or bone-to-bone contact between the pelvic and pectoral girdles (V_4).

To these different states of the pectoral and pelvic fins may be added some information on the development of fin spines, rigid supports at a fin's leading edge. Again, four conditions are specified (Fig. 8). In actinopterygian fishes fin spines primitively are absent and this is also true of each of the major groups of teleosts (osteoglossomorphs, elopomorphs, clupeomorphs, and euteleostean). The primitive condition is represented by the symbol S_1 . In S_2 one or more spines occur in

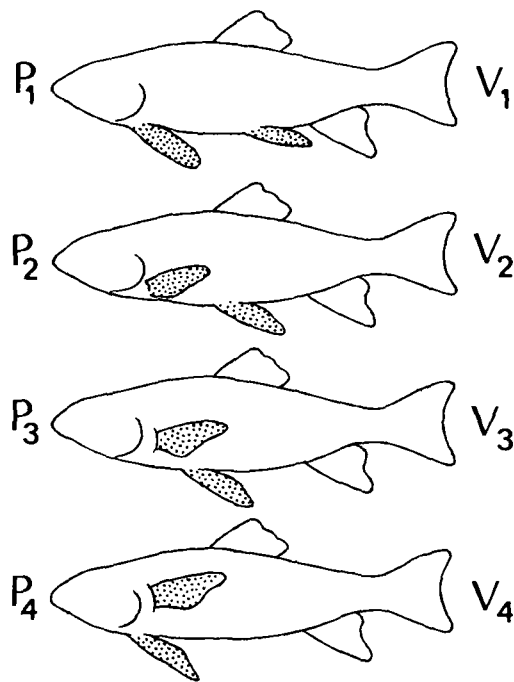


FIG. 7. Representation of different pectoral and pelvic fin positions in teleostean fishes, diagrammatic.

the dorsal fin. In S_3 spines are present in the dorsal and anal fins. In S_4 spines are present in the dorsal, anal and pelvic fins.

As suggested earlier with respect to the teleostean upper jaw the primitive condition is simply to have the premaxilla joined firmly to the maxilla on a butt joint so that abduction of the maxilla causes a corresponding rotation of the premaxilla on its ethmoid hinge; this is designated as state J_1 (Fig. 9). This primitive arrangement is found in such Mesozoic teleosts as *Pholidophorus bechei*, *Pholidolepis dorsetensis* and in *Proleptolepis*. In other teleosts the posterolateral or alveolar arm of the premaxilla fills a notch on the anteroventral surface of the maxilla (J_2). An exaggeration of this condition, in which the alveolar arm extends backward for up to half the length of the maxilla, occurs together with a large, medially concave, symphyseal process lateral to a median rostral cartilage and forms an articular surface for a maxillary hinge (J_3). In a fourth state (J_4) the premaxilla also has an ascending process medial to the articular process and a still

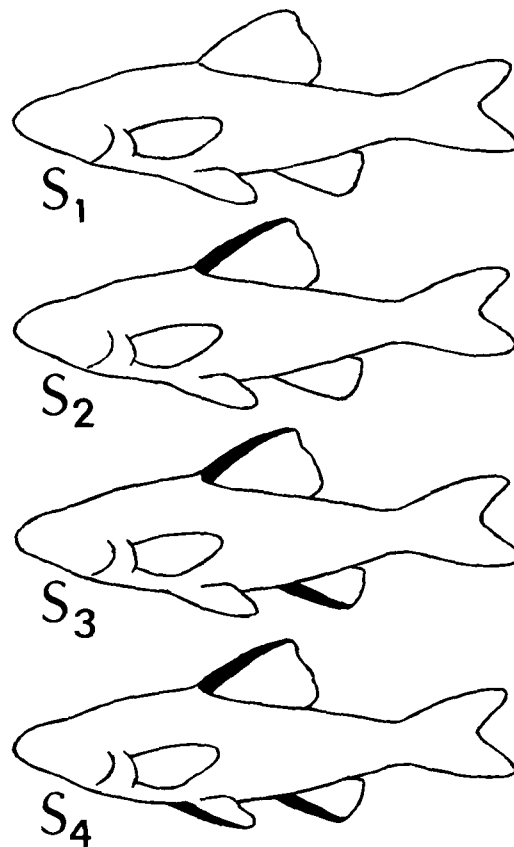


FIG. 8. Representation of fin spine occurrences in teleostean fishes, diagrammatic.

longer alveolar arm with an expanded part on the dorsal edge (post-maxillary process); the maxilla, now completely excluded from the gape of the open mouth, has a more complex anterior hinge with the premaxillary articular process and its muscular control (by the adductor mandibulae) is in general more complex than in conditions J_1 to J_3 . Also in the third and fourth states, the ethmoid hinge of the premaxilla is a rather loose connection and is represented by a set of ligaments running from the articular process to either the head of the maxilla or the ethmoid region. In a fifth state (J_5) the ascending premaxillary process is two or more times the height of the articular process and the premaxilla can be pulled away from the snout (*i.e.*, can be protruded) by abduction of the lower jaw and can be returned to rest by

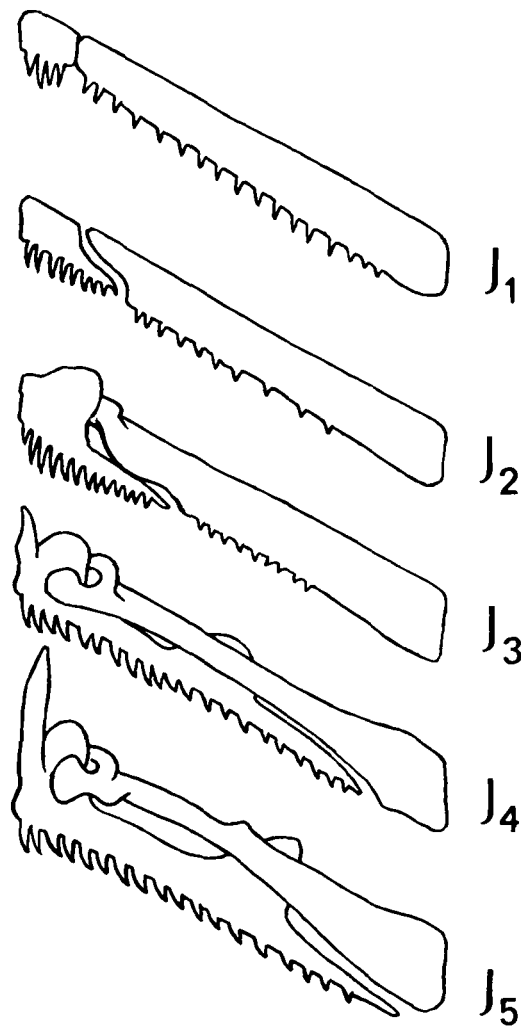


FIG. 9. Representation of types of associations between the two upper jaw bones of teleostean fishes, diagrammatic. In the primitive condition, J_1 , premaxilla to the left, maxilla to the right in series; in the most derived condition, J_5 , the two bones are in tandem.

the action of the adductor mandibulae on the maxilla (see Rosen, 1973, pp. 412–420, 442–452, 455–473 and Table 1 for descriptions of various morphological conditions).

Each of the four paired fin character states, the four states of fin-spine development, and the five upper jaw character states are entered on the branches of the cladogram (Fig. 10). In this diagram the primitive states are represented by white

rectangles and increasingly derived states by rectangles of increasing black content.

Clear trends, or character-state transformations, are evident in each of the four characters. Starting from the top row of rectangles, in the pectoral fin, the primitive state (P_1) is characteristic of branches 1 through 12 on the cladogram (Fig. 10). P_2 occurs on branches 13 to 15, and P_3 and P_4 in the more apomorph positions 16 to 19. The exceptional P_4 in the pectoral fin character would be rated as an autapomorphy of branch 17 (atherinomorphs). In the pelvic fin the transformation is essentially the same except for a reversal at branch 17 or a convergence at 16. In spine development, the transformation from the primitive state (S_1) begins at branch 14 (S_2). S_3 characterizes 15 and 16, and S_4 , 17 to 19. The first derived state of the upper jaw, however, begins all the way back at branch 4 (J_2), transforms to J_3 at branch 12, to J_4 at branch 13, and to J_5 at branch 19.

Similar transformations are repeated within sections of the Teleostei. For example, among osteoglossomorphs (branch 7), the pectoral position, which is primitive in *Hiodon*, occurs in a derived state in the very specialized mormyroid fishes. In clupeomorphs (branch 9), the cladistically plesiomorphous *Denticeps* has the primitive pelvic position, but the other clupeomorphs have a V_2 or V_3 state of the character. Among paracanthopterygians (branch 16) the plesiomorphous percopsiforms have condition V_3 but the apomorphous gadiforms have V_4 , and some have an even more derived pelvic position anterior to the pectoral girdle. Likewise in spine development, dorsal spines (S_2) occur in apomorph groups of elopomorphs (notacanth) and among ostariophysans (some cyprinoids and siluroids), and strongly protrusile upper jaws, differing from those of percomorphs, occur in several groups of ostariophysans.

These independent instances of a seemingly regular pattern of character transformations suggest, therefore, that there exist unidirectional relationships among the different locomotor and the different feeding mechanisms. The suggestion is re-

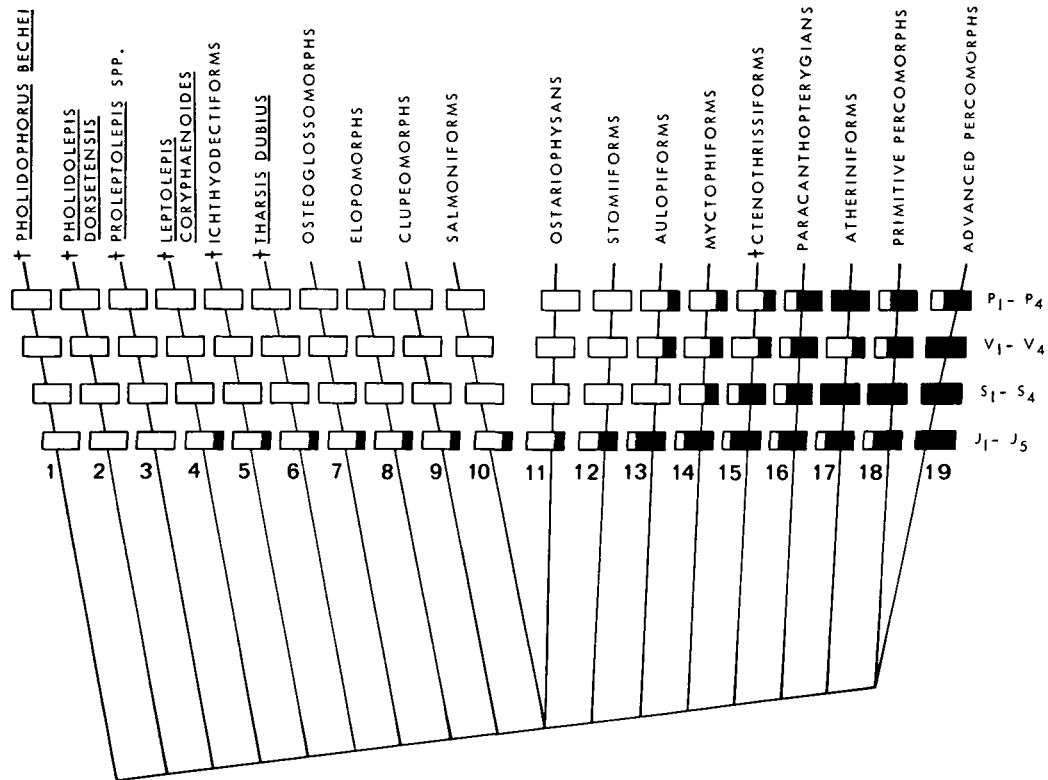


FIG. 10. A character-state tree of pectoral and pelvic fin positions, fin spine occurrences, and upper jaw types based on a simplified depiction of the cladogram of teleostean interrelationships in Figure 5.

jected, however, by observations of several kinds of reverse transformations that are consistent with ontogenetic data or with a number of most parsimonious cladistic solutions to the relationships of the taxa within the Myctophiformes (branch 14), Paracanthopterygii (branch 16), Atherinomorpha (branch 17), Melamphaidae (a component of branch 18), and Perciformes (branch 19). Some examples are: the pectoral transformation series $P_4 \rightarrow P_3 \rightarrow P_2$ and pelvic transformation $V_2 \rightarrow V_1$ in atherinomorpha (Rosen and Parenti, 1981); the ontogenetic shift posteriorly of the pelvis ($V_3 \rightarrow V_2$) in the melamphaidae (Ebeling, 1962); the absence of fin spines in cladistically apomorphic myctophiforms (Rosen, 1973), paracanthopterygians (Rosen and Patterson, 1969) and atherinomorpha (Rosen and Parenti, 1981); and the absence of fin spines and protrusibility of the upper jaw in various apomor-

phous groups of perciforms. One might reasonably argue, because this analysis is at a very superficial level and assumes the correctness of the initial cladogram of the Teleostei, that a more detailed study of each of the locomotor and feeding morphologies would mitigate the severity of the polarity reversals shown by the last few examples. This might very well be so especially in view of the number of still unanswered questions about teleostean relationships. But some of the reversals provide so far ontogenetically and cladistically uncontradicted empirical constraints that must be acknowledged in any general functional and evolutionary interpretations of these morphological systems.

When interpreted historically with respect to the main features of the fins and upper jaw, the cladogram tells us (1) that changes in jaw mechanics first arose, and in some cases proliferated, in teleosts with

a primitive fin arrangement and morphology, (2) that the euteleostean jaw mechanism was fairly well advanced before pectoral and pelvic positions shifted, and (3) that fin spines arose only after an initial shift in paired fin orientation and specialization of the jaw. Thus a theory about the evolution of the protrusile jaw should not require a subsidiary theory about a correlated change in fin position. And, because of the reversals of pelvic fin position and fin-spine development in fishes with a derived pectoral fin orientation, a theory about the evolution of the pectoral should not require subsidiary theories about correlated changes in pelvic position and fin spines. The branching diagram therefore specifies a variety of permissible combinations of certain independent mechanisms for feeding and locomotion but has nothing to say about what, if anything, is prohibited. It is simply an interpretation of *what* did happen. Why it happened that way is another question—a question that so far has seemed answerable only in terms of some notion of purpose such as improvements in engineering design or better adaptations for use of the environment's resources.

The difference between what might have happened in evolution as compared with why it happened is illustrated by another simple example involving the presence of a "lure" on the snout of lophiiforms or anglerfishes. This structure consists of a movable, basal, supporting rod on the tip of which there is a differentiated part to which other fishes are attracted when the "lure" is moved. A fish that approaches this "lure" closely might be eaten by the anglerfish. Two kinds of statements have been made about the origin of this structure that have to do with proximate and ultimate causes. The proximate cause is the ontogenetic migration forward of the anterior dorsal fin spines onto the head; the anterior-most spine ends up on the snout retaining a modified dorsal spine musculature that permits the spine to be moved about in a way that happens to attract other fishes. But one might choose to describe the origin of this anomalous dorsal spine position—in fishes that

have been variously characterized as "these tiny freaks of the sea" (by Jordan, 1905) or the "most grotesque of all teleosts" (by Romer, 1966)—in terms of the adaptive advantage of this phenotype. Not long ago Lewontin (1978) grudgingly admitted the futility of searching for these ultimate causes, these "why did it happen" questions, but pleaded nonetheless that some things just cry out for explanation: "... it must be feasible to make adaptive arguments about swimming appendages [and] this in turn means that in nature the *ceteris paribus* assumption must be workable." These things that cry out, like things that go bump in the night, can be given plausible, or at least non-mysterious and therefore soothing, causal interpretations. *What* happens to the anglerfish dorsal fin spine during ontogeny can, and has been, described in some detail, but plausible, soothing stories about *why* it happened serve only to conceal that the singular historical process, this mystery, can not be studied empirically. Thus, in the original cladistic example, one might ask if fishes with $P_3V_4S_4$ and J_5 (the percomorphs) can operate more efficiently, and outcompete, those with $P_1V_1S_1$ and J_2 (cladistically primitive teleosts)? Or, do the two kinds of fishes just represent alternative solutions to the problems of swimming and feeding? Obviously both types of fishes feed and swim effectively or they would not be here, and, viewed historically, one type preceded the other in time. But if one type is better than the other, how might this be judged—by increased taxonomic diversity, number of individuals, kinds of ecologies inhabited, or foods eaten? There are probably at least as many species of non-percomorphs as percomorphs in as many different ecologies, eating as many kinds of foods; and non-percomorphs such as benthic and pelagic ostariophysans (in freshwater), and clupeomorphs and stomioids (in seawater), certainly predominate in number of individuals. It is furthermore known to every aquarist that fishes with a primitive fin arrangement have behavioral and locomotor abilities like those of percomorphs. What we seem to mean by "better," therefore, is differentiated, either by

becoming simpler or more complex—that is, by changing into something new. The observation that a fish with a certain type of mouth can eat coral polyps carries no assurance that a fish with a different type can not do so. The observation does not, in other words, carry with it the implication that the first type of fish is *uniquely* suited to this role.

The real advantage of pursuing functional morphological studies on animals, or the parts thereof, is that the nature of organic diversity can become known in more detail. Such studies therefore increase our character discrimination. But the idea that inevitably evolution results in functionally better systems is simply a derivative of the human reason for causing transformations, be they of political systems or automotive brake systems. Notice, however, that a transformation also explains a functional alternative, *i.e.*, a new attribute or capability that enables some original function to be served in the same way. The idea that “new” equals “better” is really just a manifestation of our own social philosophy transformed into a biological principle known as Darwinism. We have purposes and objectives and nature must also. It was Darwin’s original idea, still represented today somewhat disguised, “that every detail of structure . . . was of some special, though unrecognized, service.”³ It is a principle that invites the evolutionist to become free from empirical constraints. Thus Alexander (1967) has boldly declared that “studying fish design involves trying to understand the structure of fish in terms of selective advantage” and proposed that fin “. . . spines have probably evolved largely as defense against predators” and that the “. . . deep bodies and large fins which make typical acanthopterygians so maneuverable . . . are advantageous . . . among vegetation in lakes, or in coral reefs.” Romer (1966) characterized $P_3V_4S_4J_5$ fishes as “a major upward step in teleost history,” and had little hesitation in identifying which features were

mainly responsible: “But more important . . . in the evolution and success of acanthopterygians than spine development or mouth changes was a radical change in methods of locomotion” involving paired fins. With such comments we pass from the realm of what happened to why it happened—even when it would be more honest to avoid the pretense of knowledge and simply profess ignorance. Huxley (1938) explained why he thought we must take the extra step: “if we repudiate creationism, divine or vitalistic guidance, and the extreme forms of orthogenesis, as originators of adaptation, we must (unless we confess total ignorance and abandon for the time any attempts at explanation) invoke natural selection [*i.e.*, the adaptationist argument].” Of Huxley, Macbeth (1974) asked: “Why use the word *must*?” Some earlier remarks of Popper’s (1962) capsulates an answer: “There exists no law of evolution, only the historical fact that plants and animals change, or more precisely, that they have changed. The idea of a law which determines the direction and character of evolution is a typical nineteenth-century mistake, arising out of the general tendency to ascribe to the ‘Natural Law’ the functions traditionally ascribed to God.”

I imagine that the empirical limitations imposed by systematists will continue to go unnoticed in the evolutionism of some functional anatomists. If so, what will constrain their explanations of how and why? There seem to be only two limiting factors: proximately, their own inventiveness, and ultimately, the gullibility of their audience.

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³ Quotation from Darwin (1871) who had then repudiated this earlier point of view.

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