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Symposium Summary: Evolutionary Patterns in Actinopterygian Fishes[1]

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SYNOPSIS. The actinopterygian fishes are an exemplary clade for the study of structural and functional evolutionary patterns. With over half of all vertebrate species, ray-finned fishes have diversified into a wide variety of habitats, and considerable progress has been made over the last fifteen years in understanding the genealogical relationships of actinopterygians. This symposium has contributed to our understanding of phylogenetic patterns in actinopterygians and to knowledge of the major structural and functional patterns in locomotor, auditory, trophic, and neural systems. A number of key areas for future research have been identified. (1) The relationships of "palaeonisciform" fishes, (2) the study of trends in feeding and locomotor systems within a phylogenetic context, (3) the identification of primitive patterns of pharyngeal jaw movement and steady and unsteady locomotor patterns in actinopterygians, (4) the homologies, identification, and functional significance of neural pathways in the telencephalon, and (5) the comparative study of form-function relations in the auditory system. The study of teleost fish biology has proceeded at the expense of data on primitive actinopterygians (*e.g., Polypterus, Polyodon, Acipenser, Lepisosteus, Amia*) which are especially important in the analysis of structural and functional patterns in ray-finned fishes.

The reconstruction of structural patterns provides the basis for interpreting evolutionary changes in function and for inferring mechanisms producing observed structural and functional patterns (see Eldredge and Cracraft, 1980). Structural similarities between taxa can be recognized and ordered into nested sets (cladograms) which indicate the historical sequence of structural change and the phylogenetic level at which evolutionary novelties were acquired in a clade. The degree to which evolutionary morphologists can make general statements about the historical pattern of evolutionary change in organisms depends directly on (1) the precision of the reconstruction of nested sets of structural patterns, (2) the ability to test historical hypotheses by searching for similar independently evolved patterns in several different monophyletic clades, and (3) the existence of general, emergent properties of structural and functional systems which transcend the particular (unique) sequence of evolutionary change in any one clade (Lauder, 1981).

Because of the importance of nested sets of structural features for general evolutionary interpretations, a key goal of this symposium was to summarize and contribute new information on structural patterns in the major morphological systems of actinopterygian fishes. As noted by Rosen, considerable progress has been made over the last fifteen years in the study of teleostean relationships, but it is only very recently that structural patterns in the feeding mechanism, ear, nervous system, and locomotor apparatus have begun to be interpreted in a phylogenetic context. Nieuwenhuys, for example, notes that all actinopterygians share a unique pattern of telencephalic development—eversion of the embryonic tube-shaped telencephalon to form hollow cerebral hemispheres—while several structures appear to be

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unique to teleost fishes, *e.g.*, the eminentiae granulares of the cerebellum.

Popper and Coombs describe the difference between hair cell orientation patterns in primitive actinopterygians and those of teleosts and stress the apparent evolutionary lability of both structural and functional aspects of the teleost auditory system. Evidence for lability is obtained by the lack of congruence between the distributions of various similarities in auditory structure and the currently accepted phylogenetic framework (see the papers by Patterson and Rosen) which is based on a different set of characters. In the actinopterygian feeding mechanism, a number of structural similarities have been identified which corroborate previous hypotheses of actinopterygian phylogeny: the change in origin of the pharyngohyoideus muscle and the occurrence of two biomechanically independent pathways governing mandibular depression.

In the study of actinopterygian locomotion, major progress has been made in deciphering the major structural changes since the important papers by Patterson (1968*a*, *b*), and the input of engineers and hydrodynamicists has provided a firm theoretical foundation for the analysis of locomotor function. However, any general conclusions about functional patterns in the evolution of actinopterygian locomotor systems must be tempered by the lack of data on primitive actinopterygians. Before conclusions on the nature of locomotion in teleost fishes can be formulated, it is essential to investigate fast-start capabilities, energetics, and steady swimming in primitive actinopterygians (*Polypterus, Lepisosteus, Acipenser, Polyodon, Amia*).

Indeed, a theme echoed by many of the participants in this symposium is the lack of comparative data from primitive actinopterygians. For the most part, investigators have chosen to examine a few teleost species and have largely neglected the potentially important comparative basis provided by primitive forms. This lack of comparative information on functional (and in some cases, structural) patterns severely constrains interpretations of the evolution of functional systems. In addition, the analysis of primitive living ray-finned fishes not only allows more confident reconstruction of functional patterns in fossil forms, but also, when compared to elasmobranchiomorphs, actinists, and lungfishes, permits the identification of those structural and functional patterns that are unique to ray-finned fishes. Hypotheses about functional significance, selection pressures, or historical patterns of change depend critically on the distributional pattern of the features under examination, and data from primitive actinopterygians form a crucial part of determining character distributions. Areas in which data from primitive actinopterygians (*i.e.*, non-teleosts) are particularly needed include (1) pharyngeal jaw structure and function, (2) kinematics and energetics of steady and unsteady swimming, (3) behavioral and physiological correlates of auditory structure, and (4) ascending and descending neural pathways in the telencephalon. Data on the respiratory and visual systems (areas not covered in this symposium) are also badly needed.

In addition to contributing to understanding general evolutionary patterns of form and function, the experimental analysis of form in actinopterygians has enabled design tradeoffs and compromises to be identified which greatly aid in inferring functional patterns in extinct taxa, in explaining deviations from "optimal" performance, and in providing a conceptual framework for the study of limitations and versatility in the evolutionary transformation of form and function. Webb, for example, in a series of experiments on fast-start performance and steady swimming in teleosts (summarized in Webb, this symposium) has shown that the design requirements for hydrodynamically efficient steady swimming conflict with those for unsteady swimming (also see Lighthill, 1969, 1970). Recognition of these alternative design requirements gives new insight into functional correlates of form in fishes which can alter their body profiles by changing fin area, and permits quantitative comparison of locomotor performance relative to an external standard.

Conversely, the demonstration of an increase in structural complexity in the feeding mechanism of actinopterygian fishes, and the correlation between structural diversity and the number of biomechanical pathways governing a function, provides an indication of general structural properties that may permit morphological versatility. The recognition of both compromises and structural and functional versatility in an historical framework depends on an analysis of patterns at various levels in actinopterygian phylogeny and on the existence of a corroborated hypothesis of relationship.

Because of the rapid progress since the publication of Greenwood *et al.* (1969) in reconstructing actinopterygian phylogeny, ray-finned fishes provide an excellent group in which to test hypotheses and theories in structural biology and examine the relationship between form and function. The degree of structural and taxonomic diversification in actinopterygians and the existence of multiple corroborated monophyletic clades allows testing of hypotheses about structural and functional evolution to a degree not possible in many other clades. One goal of this symposium has been to stress the dramatic increase in our knowledge of ray-finned fishes and to call attention to the potential usefulness of this clade in testing hypotheses in evolutionary morphology. Throughout actinopterygian evolution there have been repeated episodes of reductive evolution, paedomorphosis, and changes in complexity of organization which could provide the basis for an examination of general historical patterns resulting from structural and/or functional compromises. Only by bridging the gap between experimental analyses and the study of patterns of character distribution can new and general scientific ideas emerge. It is our hope that this symposium will provide the basis of such cooperation and that historical factors will play an increasingly important role in the examination and explanation of form and function in fishes.

REFERENCES

Eldredge, N. and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process.* Columbia Univ. Press, New York.

Greenwood, P. H , D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:339–456.

Lauder, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. Paleobiology. 7:430–442.

Lighthill, M. J. 1969. Hydromechanics of aquatic animal propulsion—a survey Ann. Rev. Fluid Mech. 1.413–446.

Lighthill, M. J. 1970. Aquatic animal propulsion of high hydrodynamic efficiency. J. Fluid. Mech. 44:265–301.

Patterson, C. 1968*a*. The caudal skeleton in lower Liassic pholidophorid fishes. Bull. Br. Mus Nat. Hist. Geol. 16:201–239.

Patterson, C. 1968*b*. The caudal skeleton in Mesozoic acanthopterygian fishes. Bull. Br. Mus. Nat Hist. Geol. 17:47–102.