

Caudal Fin Locomotion in Ray-finned Fishes: Historical and Functional Analyses¹

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SYNOPSIS. Over the last 20 years, considerable progress has been made in quantifying the movement of the body during locomotion by aquatic vertebrates, and in defining the role of axial musculature in producing these kinematic patterns. Relatively little is known, however, about how specific internal structural features of the axial system in fishes affect body kinematics, and how such structural and functional features have changed during evolution. The major theme of this paper is that historical, phylogenetic patterns in the axial musculoskeletal system need to be integrated with experimental and functional data in order to understand the design of the locomotor apparatus in vertebrates. To illustrate this proposition, the evolution of the tail in ray-finned fishes is presented as a case study in phylogenetic and functional analysis of the vertebrate axial musculoskeletal system. Traditionally, the evolution of the tail in ray-finned fishes has been viewed as a transformation from a primitively heterocercal (functionally asymmetrical) tail to a homocercal tail in which the axis of rotation during locomotion was vertical, generating a symmetrical thrust. Both phylogenetic and functional approaches are used to examine this hypothesis. Major osteological and myological features of the tail in ray-finned fishes are mapped onto a phylogeny of ray-finned fishes to discern historical sequences of morphological change in the axial musculoskeletal system. A key event in locomotor evolution was the origin of the hypochordal longitudinalis muscle, the only intrinsic caudal muscle with a line of action at an appreciable angle to the body axis. This muscle originated prior to the origin of a caudal skeleton bearing both hypaxial and epaxial fin ray supports. The hypochordal muscle is proposed to be a key component of the axial musculoskeletal system that allows most fishes to modulate caudal function and decouples external morphological symmetry from functional symmetry. Experimental data (strain gauge recordings from tail bones, and electromyographic recordings from intrinsic and extrinsic caudal muscles) corroborate this interpretation and suggest that functional symmetry in the tail of ray-finned fishes is not predictable from skeletal morphology alone, but depends on the activity of the hypochordal longitudinalis muscle and on locomotor mode. The homocercal teleost tail may thus function asymmetrically.

INTRODUCTION

The study of aquatic locomotion has received more attention over the last 20 years than any other aspect of vertebrate functional morphology. Numerous recent books and symposia have dealt with the mechanisms by which vertebrates move through the water (*e.g.*, Gray, 1968; Aleyev, 1969; Webb, 1975; Wu *et al.*, 1975; Blake, 1983). In part because of their extraordinary taxonomic and locomotor diversity, ray-finned fishes (Actinopterygii) have provided key examples for the analysis of locomotor movements and data used to test theoretical hydrodynamic models of

aquatic propulsion. The analysis of fish locomotion has served as a primary example for the analysis of how environmental demands constrain organismal design (Weihs, 1989). The dense and viscous aquatic medium places severe constraints on the functional design of propulsive systems, and both theoretical models of these constraints and the experimental demonstration of design limitations have used ray-finned fishes as a model system.

There are three areas in which particularly significant progress has been made in the analysis of fish locomotion. First, the kinematics of aquatic propulsion has been extensively studied and these data have been used to test theoretical models of body movement (Gray, 1933*a, b*; Bainbridge, 1963; Lighthill, 1971; Weihs, 1973; Webb, 1978*a*; Videler and Hess, 1984). Major categories of locomotor mode have been

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defined on the basis of kinematic patterns such as the well-known anguilliform, tuniform, and ostraciiform locomotor classes (Breder, 1926; Webb, 1975; Lindsey, 1978). Secondly, the role of the myotomal musculature and skin fiber systems in producing body deformations has been the subject of continuing study (Bone, 1966, 1978, 1988; Johnston, 1980; Wainwright, 1983) and the mechanisms by which muscle contractions act to bend the body have been analyzed. Thirdly, an important set of functional and design constraints have been identified by Webb (1978*a, b*). He has shown that the functional requirements for high performance in steady, continuous locomotion are in conflict with demands for high accelerations (unsteady locomotion).

Despite this progress in the area of biomechanics and functional morphology of aquatic propulsion in fishes, there are major conceptual avenues that have yet to be explored. For example, almost no progress has been made in synthesizing the results from biomechanical and functional studies with historical, phylogenetic analyses. In addition, almost nothing is known about the functional significance of morphological features in the axial musculoskeletal system that have been used by systematists to define lineages of ray-finned fishes.

The major theme of this paper is that historical patterns in the axial musculoskeletal system of fishes need to be integrated with experimental and functional data: there has been no synthesis of experimental and phylogenetic research so necessary to a general understanding of the evolution of structure and function in the axial musculoskeletal system. Without a synthesis of historical and functional data, it will not be possible to understand the design of vertebrate locomotor systems. The aim of this essay is to illustrate this point and provide a case study of *both* functional and phylogenetic analysis of the locomotor apparatus. It is beyond the scope of the paper to consider all aspects of locomotor structure and function. Rather, I will concentrate on presenting a case study of a classical system: evolution of the tail in ray-finned fishes.

PHYLOGENY AND BIOMECHANICS OF THE CAUDAL FIN: A CASE STUDY

Nearly every investigator who has discussed the evolution of vertebrates has commented on the caudal fin of ray-finned fishes (Actinopterygii). Caudal fin evolution has become a textbook case of structural and functional modification in vertebrates, and is used to illustrate how changes in external morphology have occurred and had important functional consequences (*e.g.*, Goodrich, 1930; Jollie, 1972; Romer and Parsons, 1986). Further emphasizing the importance of this system, many investigators have attributed the diversification of teleost fishes into over 23,000 species, by far the largest clade of vertebrates, to their locomotor abilities. Gosline (1971, p. 34) for example, notes that "The perfection of caudal locomotion has probably been the single greatest achievement of the teleostean fishes," and Lund (1967, p. 216) comments that "the versatility of the teleostean caudal skeleton was a very important factor in the rapid radiation of teleosts during the Mesozoic."

Exactly what are the changes that are proposed to have occurred in the actinopterygian caudal skeleton? Primitive ray-finned fishes possess a heterocercal tail in which the notochord and vertebral elements extend into the upper (dorsal) tail lobe (Fig. 1B). The fin rays and the supporting skeletal elements thus attach to the ventral surface of vertebral axis. This morphological arrangement is proposed to have generated an epibatic (lift) force as the tail was swept from side to side (Affleck, 1950; Alexander, 1967; Aleyev, 1969). The heterocercal tail morphology is viewed as both structurally and functionally asymmetrical in that the tail is formed primarily out of hypaxial structures, and the direction of thrust produced by the tail does not pass through the vertebral axis. The inclined angle of fin rays with respect to the vertical and the upturned vertebral axis defines an oblique line of fin ray oscillation (Fig. 1B, C).

It is important at this point to clearly distinguish between epaxial and hypaxial structures in the caudal fin, and the terms

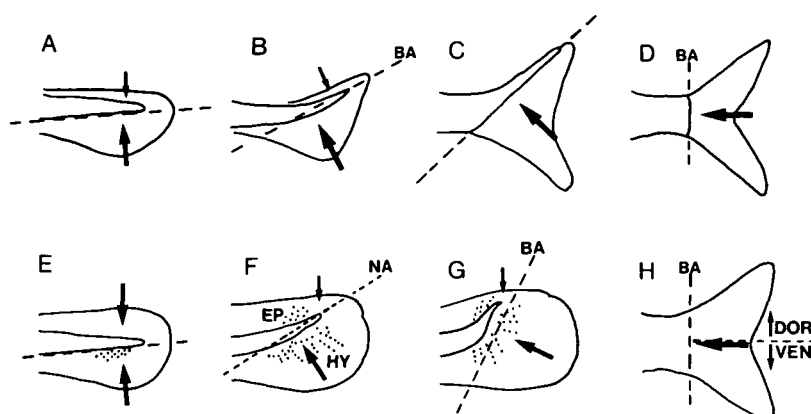


FIG. 1. Figure of homocercal and heterocercal tails and lines of bending based on Affleck (1950). A–D. Four diagrams of different external tail morphologies showing some of the variation in tail shape within ray-finned fishes. E–H. Diagrammatic sequence of tail ontogeny in a teleost fish. The dashed line indicates the line of bending (BA) of the tail as proposed by Affleck (1950). The homocercal tail (D and H) is proposed to have a vertical line of bending. Shapes A, B, and C represent heterocercal tails with an oblique line of bending. The arrows indicate the directions and relative magnitudes of thrust produced by the dorsal and ventral tail lobes as proposed by Affleck (1950). Note the distinction between the developing epaxial (EP) and hypaxial (HY) components of caudal structure on either side of the notochordal axis (NA) shown in F, and the dorsal (DOR) and ventral (VEN) lobes of the tail shown in H.

“dorsal” and “ventral” that are often applied to caudal structures. Epaxial and hypaxial refer to structures that originate developmentally from above and below the notochordal axis respectively (Fig. 1; Whitehouse, 1910). These terms are *not* synonymous with dorsal and ventral, which refer to the positions relative to a horizontal axis through the middle of the body. As fin rays in most fishes develop from hypaxial tissues (Fig. 1), they are properly referred to as hypaxial structures. Only a few components of the caudal skeleton are epaxial in origin. Teleost fish tails, however, have roughly equal dorsal and ventral lobes; some hypaxial fin rays thus articulate with epaxial endoskeletal elements.

The homocercal tail of teleost fishes is externally symmetrical (Fig. 1D). Both epaxial and hypaxial derivatives contribute to the internal caudal skeleton, and the axis of rotation is proposed to be vertical: fin rays oscillate about a vertical axis where they join the skeletal supports within the tail. The functional result of the external symmetry and vertical axis of rotation is purportedly that the direction of thrust produced by the tail passes through the vertebral axis, and does not generate lift

forces (Aleyev, 1969). Olson (1971, p. 534) exemplifies this view: “Evolution in the actinopterygians proceeded through successive stages to a reduced heterocercal tail, found in subholosteans and some holosteans, and to a strictly homocercal condition in which the tail fin is symmetrically disposed as in many teleosts. Functionally, the fin so produced is isobatic, with the thrust being entirely forward.” It is important to note that this external symmetry is not mirrored by the internal skeletal structure: epaxial and hypaxial components of the tail are not mirror images, but the asymmetrical caudal skeleton does support externally symmetrical fin rays.

Considerable significance has been attached in the literature to the evolutionary transformation within ray-finned fishes from the primitive heterocercal condition to the teleost homocercal shape (Patterson, 1968; Nybelin, 1973), and one of the dominant arguments is that the homocercal tail is more efficient than the heterocercal tail. As Affleck (1950, p. 365) comments, “Because the fin of a homocercal tail swings about a vertical axis it is more efficient as part of the propulsive unit than the fins of a heterocercal tail.” Patterson (1968, p.

233) proposed that teleost fishes had an advantage in locomotion because of "the increased efficiency in horizontal swimming of a fish in which both lobes of the tail are equal in area and in flexibility, in which the axis is not upturned, and in which the tail swings about a vertical rather than an oblique axis . . ." Gosline (1971, pp. 35–36) concurs, stating that a teleost fish "can swing both caudal lobes back and forth synchronously, both lobes generating a directly forward force."

It is critical to note several features of the proposed differences between heterocercal and homocercal tails. First, actual functional differences between these two tail types in ray-finned fishes have not been demonstrated *in vivo*. Secondly, the precise sequence of structural modification of the heterocercal tail into the homocercal tail has not been documented. Thirdly, virtually all analyses have focused on the skeletal system, and have ignored the intrinsic caudal muscles that might function to modify the position of the fin rays and caudal skeleton. And, fourthly, all workers have discussed caudal function in ray-finned fishes during continuous locomotion, and have not addressed the possibility that caudal morphology may reflect functional demands imposed by *both* continuous locomotion and fast-start accelerations.

The purpose of the case study of caudal evolution in ray-finned fishes presented below is to address these unresolved issues in more detail. Specifically the following questions will be considered. (1) What is the precise historical sequence of modification of the caudal skeleton *and* musculature in ray-finned fishes? (2) Does the homocercal tail of teleosts actually function symmetrically as has been assumed? In other words, does external symmetry imply functional symmetry? (3) Does the function of the homocercal teleost tail change between continuous locomotion and fast-start accelerations?

PHYLOGENETIC PATTERNS TO CAUDAL STRUCTURE

Historical analysis

By what specific historical sequence was the functional design of the homocercal

teleost tail produced? Did modifications to the epaxial portion of the tail occur prior to those in the hypaxial portion, and how did the ability of teleost fishes to alter the area of the caudal fin evolve? Historical sequences such as these can be resolved by mapping structural features of the caudal musculoskeletal system onto a previously established phylogeny. Figure 2 summarizes the results of such a procedure, and the phylogeny used is based on work summarized by Lauder and Liem (1983). The following discussion will analyze the sequence by which musculoskeletal novelties in the caudal skeleton and musculature were acquired at successive phylogenetic levels, starting with the basal (primitive) condition for ray-finned fishes. In this way, an explicit historical sequence can be reconstructed by which the complex design of the homocercal tail was built up.

Primitive ray-finned fishes such as *Cheirolepis* (Pearson, 1982) and *Moythomasia* (Gardiner, 1984) had a strongly heterocercal tail in which the hypaxial lobe appears to have had no intrinsic musculature. There is no contribution of the epaxial skeleton or myotomes to caudal fin structure. Based on the attachment of the most superficial lateral myotomal fibers (often designated as the *lateralis superficialis* muscle, a portion of which is shown in Fig. 8) to the head of the fin rays in almost all extant ray-finned fishes, it is parsimonious to assume that *lateralis superficialis* in early ray-finned fishes also attached to the heads of the fin rays and was capable of affecting at least minor changes in fin ray position. The tail of *Polypterus*, the most primitive living actinopterygian (Figs. 2, 3), is specialized with respect to other lower ray-finned fishes in having a diphyrcercal morphology with both epaxial and hypaxial lobes. Dissections of *Polypterus* reveal that the lateral myotomes thin posteriorly to attach to the heads of the caudal fin rays (Fig. 3). There is no differentiation of superficial and deep caudal musculature in *Polypterus* and no separation of distinct intrinsic muscles.

In the Chondrostei (Figs. 2, 4), numerous hypaxial fin rays attach to small cartilages ventral to the notochord, and no

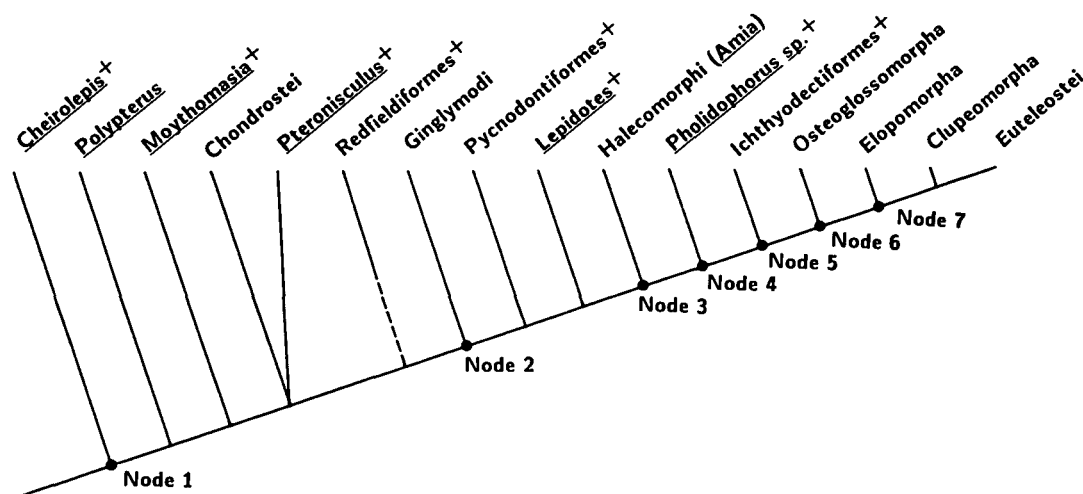


FIG. 2. Phylogenetic relationships of the major clades of ray-finned fishes (Actinopterygii). Taxa marked with a "+" contain no living species. This phylogeny is based on work summarized in Lauder and Liem (1983), notably Patterson (1973, 1977, 1982), Patterson and Rosen (1977), Wiley (1976), and Schaeffer and McDonald (1978), as well as Gardiner (1984). Taxa derived from Node 1 = Actinopterygii; taxa derived from Node 3 = Halecostomi; taxa derived from Node 4 = Teleostei. Using this phylogeny as a basis, morphological novelties in the axial musculoskeletal system were identified at successive phylogenetic levels. Those features primitive for ray-finned fishes, and thus present at Node 1 are: the absence of intrinsic caudal musculature, lateralis superficialis muscle attached to the heads of the caudal fin rays, heterocercal tail, posterior haemal spines directed posteroventrally. Locomotor characters present at the other nodes on the cladogram are: Node 2: hypurals on posterior caudal vertebrae oriented anteroposteriorly, epurals present (Schultze and Arratia, 1986) but not supporting dorsal fin rays, weakly developed hypochordal longitudinalis muscle, distinct superficial and deep intrinsic caudal muscle layers, large flexor ventralis muscle; Node 3: epaxial interradialis and supracarinalis posterior muscles present, well-developed hypochordal longitudinalis; Node 4: ural neural arches modified into uroneurals (but not expanded into supporting elements for dorsal fin rays), expansion of posteriorly directed haemal spines; Node 5: caudal skeleton has only two ural centra (*vs.* three or more primitively), expanded uroneurals, posterodorsally located epurals (epaxial elements) serving to support dorsal fin rays; Node 6: seven hypurals (*vs.* eight or more primitively), hypochordal longitudinalis muscle originates from the ventral hypurals (and not from the vertebral column), hypaxial interradialis and infracarinalis posterior muscles present; Node 7: only two uroneurals extend anteriorly past second ural centrum.

intrinsic caudal muscles are present. Tendons from the posterior myotomes extend posterodorsally along the notochord and attach to connective tissue overlying the notochord and tail cartilages.

In the Ginglymodi (gars and their relatives; Wiley, 1976) there are no epaxial supports for caudal rays, but well developed hypural bones (modified haemal spines) are present and support the caudal fin rays (Fig. 5). At this phylogenetic level (Fig. 2: Node 2) distinct superficial and deep intrinsic caudal musculature is present. Gars also have a weakly developed hypochordal longitudinalis muscle (Fig. 5: HL). This muscle originates on the caudal vertebrae and extends posterodorsally to insert on the first dorsal fin ray. This muscle is

the first intrinsic caudal muscle to differentiate phylogenetically in ray-finned fishes and it occurs in clades retaining the primitive heterocercal tail condition (Fig. 2: between Nodes 2 and 3). The hypochordal longitudinalis in gars is a differentiated division of a large intrinsic ventral flexor muscle which extends broadly from the vertebral column posteroventrally to insert on and between the heads of the fin rays (Fig. 5: FV). The ventral flexor muscle spans the entire lateral surface of the hypural bones between the vertebral column and fin ray heads, and is subdivided into many bundles running nearly parallel to the hypurals; the hypochordal longitudinalis is merely a particularly well differentiated dorsal component of the flexor

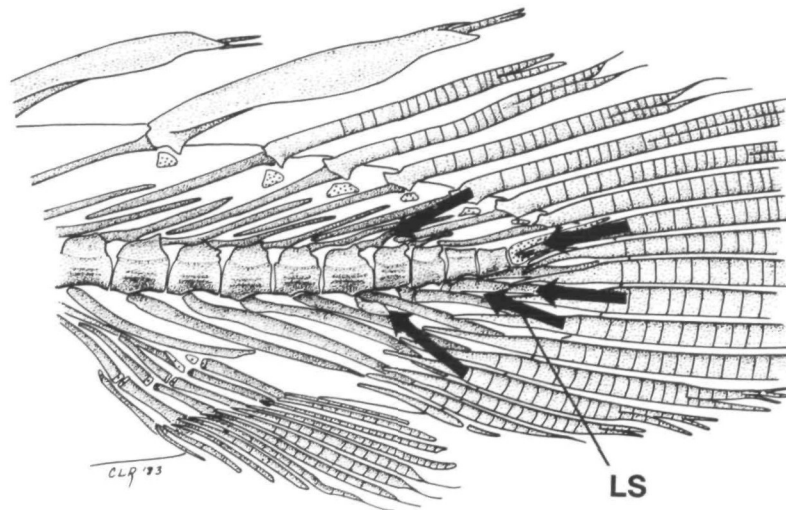


FIG. 3. Caudal skeleton and musculature of *Polypterus senegalus*. In this and Figures 4, 5, and 6, black lines indicate major muscles and their lines of action. Note the specialized symmetrical tail with caudal fin rays being supported by both epaxial and hypaxial skeletal elements. *Polypterus* lacks intrinsic caudal musculature and shares with other primitive ray-finned fishes the condition of having the lateralis superficialis (LS) myotomal fibers attaching to the heads of the fin rays (black arrows).

ventralis. There is considerable muscle fiber exchange between the muscle bundles composing the flexor ventralis, while the hypochordal longitudinalis is separated from the flexor ventralis by a distinct fascial plane. In gars, the hypochordal longitudinalis forms an angle of about 30° with the horizontal precaudal body axis, similar to the angle formed by the ventral fiber bundles of the flexor ventralis (Fig. 5: HL, FV). Superficial to the flexor ventralis is a broad lateralis superficialis muscle attaching to the heads of the caudal fin rays.

The Halecostomi (Fig. 2: Node 3) of which the Halecomorphi (*Amia* and fossil relatives) is the primitive sister clade, pos-

sess several morphological novelties in the caudal region. The hypochordal longitudinalis muscle is well developed (Fig. 6) and differentiated from the surrounding superficial and deep intrinsic caudal musculature. The hypochordal longitudinalis lies at an increased angle to the vertebral column relative to the ginglymod condition, inserting on the dorsal fin rays at about a 75° angle. The hypochordal longitudinalis originates from the posterior caudal vertebrae and narrows posterodorsally to tendons which insert on the first three dorsal fin rays (Fig. 6: HL). As in gars, there is a large deep flexor ventralis that covers the hypurals laterally and is subdivided into

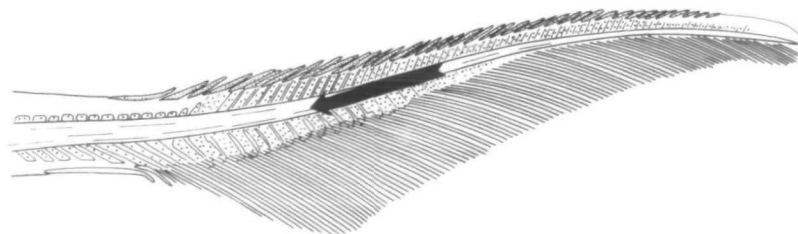


FIG. 4. Caudal skeleton and musculature of *Acipenser stellatus*. Note that there are no intrinsic caudal muscles. The lateral body myotomes condense posteriorly to a series of long tendons that run along the notochord (black arrow). The fin rays in this heterocercal tail are hypaxial structures.

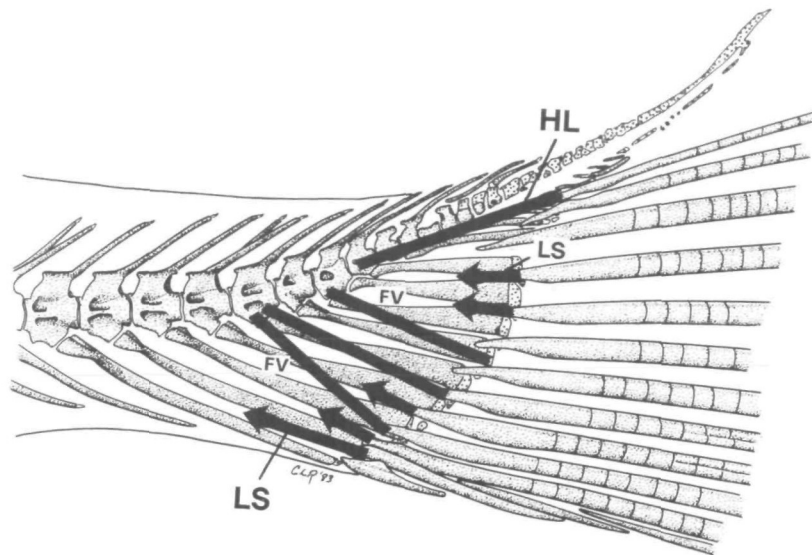


FIG. 5. Caudal skeleton and musculature of *Lepisosteus oculatus*. Note the lateralis superficialis fibers (LS) attaching to the fin rays (arrows) and the extensive flexor ventralis (FV). Selected fiber bundles of the flexor ventralis are diagrammatically indicated by black lines. The hypochochordal longitudinalis (HL) is a distinct division of the flexor extending from the vertebral column to the dorsal fin rays.

distinct bundles. Lateralis superficialis muscle fibers attach to the fin ray heads and cover the flexor ventralis in lateral view (Fig. 6: LS). The morphology of the hypochochordal longitudinalis muscle in *Lepisosteus* and *Amia* indicates that it differentiated from the flexor ventralis, and not directly from the myotomes as has been suggested (Winterbottom, 1974, p. 290).

Two related novelties in the musculature of the dorsal portion of the caudal fin also occur at this phylogenetic level (Fig. 2: Node 3). Interradialis muscles are present between the dorsal fin rays and a supracarinalis posterior muscle (Winterbottom, 1974) extends from the posterior base of the dorsal fin to attach to the upper caudal fin rays (Fig. 6: IR, SCP). These two sets of muscles are antagonistic to each other and allow expansion, stabilization, and contraction of the dorsal caudal fin rays; caudal fin area can thus be modified. There are no ventral interradians or infracarinalis posterior muscles present at this phylogenetic level.

At the next phylogenetic level (Fig. 2: Node 4), a major innovation occurs in the caudal skeleton. As first adduced by Pat-

erson (1968), the Teleostei are defined by the presence of elongate ural (tail) neural arches called uroneurals. These elements provide the first major stiffening component of the epaxial portion of the caudal skeleton, but at this hierarchical level do not support fin rays posteriorly.

Significant expansion of the epaxial support in the tail occurs at the next phylogenetic level within the Teleostei (Fig. 2: Node 5; Table 1). The uroneurals of ichthyodectiform fishes are expanded to form supports for the dorsal fin rays, and epural bones provide added stiffening of the upper caudal lobe (Patterson, 1968, 1973). There has also been a reduction in the number of vertebral centra in the tail region at this level.

Living teleost clades (Fig. 2: Node 6) share further modifications of the intrinsic caudal musculature not found in *Amia* (Figs. 7, 8). Both epaxial and hypaxial carinal muscles are present, and both epaxial and hypaxial interradians muscles occur. The hypochochordal longitudinalis has a new origin from ventral hypural bones (not from the vertebral column), and this condition is maintained within the vast majority of

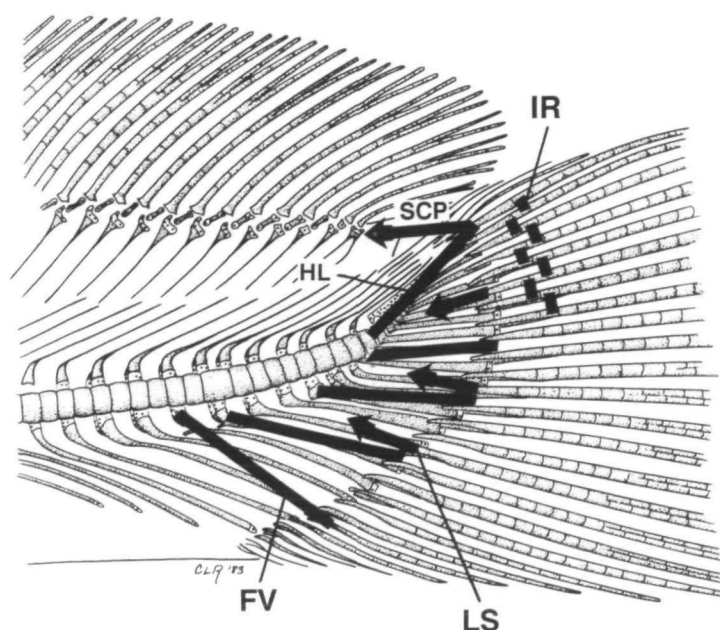


FIG. 6. Caudal skeleton and musculature of *Amia calva*. Note the interradialis muscles (IR) on the dorsal fin rays only, and the supracarinalis posterior (SCP) attaching to the upper fin rays. An extensive deep flexor ventralis (FV) is present as is the lateralis superficialis (LS).

teleost fishes (Fig. 8). The hypochordal longitudinalis is a very conservative muscle phylogenetically, showing relatively little variation within teleosts and maintaining its origin from the hypurals and its tendi-

nous insertion onto the most dorsal three or four fin rays in taxa as divergent as osteoglossomorphs, ostariophysans, and percomorphs (Nursall, 1963; Cowan, 1969; Liem, 1970; Winterbottom, 1974; Lauder,

TABLE 1. Evolution of function in the caudal musculoskeletal system of ray-finned fishes. Nodes in the first column refer to Figure 2. See text for discussion.

Phylogenetic level	Major proposed functional characters	Number of intrinsic caudal muscles*
Actinopterygii (Node 1)	Caudal fin ray movement coupled to myotomal contractions	0
Ginglymodi + Halecostomi (Node 2)	Lateral bending of caudal fin rays independent of myotomal contraction	2
	Less muscular control of dorsal than ventral caudal fin rays in the medio-lateral plane	
Halecostomi (Node 3)	Ability to modulate caudal area in the sagittal plane using dorsal caudal rays	4
	Increased muscular control of dorsal fin rays via the hypochordal longitudinalis	
Teleostei (Node 4)	Stiffening of epaxial portion of the caudal skeleton	7
Ichthyodectiformes and living teleost clades (Node 5)	Further stiffening and support for the epaxial portion of the caudal skeleton	7+
Living teleost clades (Node 6)	Control over caudal fin area complete, with acquisition of ability to move both dorsal and ventral fin rays in the sagittal plane	7+
	Ability to modulate dorsal fin ray stiffness increased by alterations in hypochordal longitudinalis origin and insertion	

* For specific muscles at each phylogenetic level see caption for Figure 2.

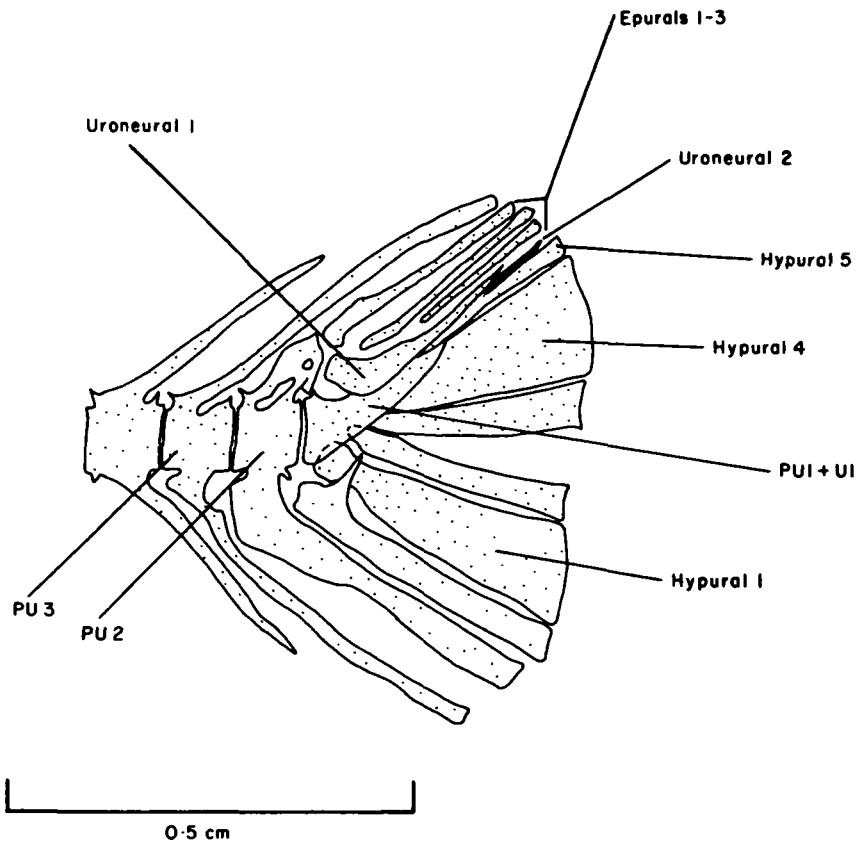


FIG. 7. Caudal skeleton of *Lepomis gibbosus*. This morphology is typical of a generalized percomorph teleost caudal skeleton (Gosline, 1961). Note the posteriorly directed (and expanded) hypurals, the three epurals, and the two small uroneural bones. The uroneurals are considerably smaller than those present in early teleosts (e.g., at Node 6 in Fig. 2). Note that the only true epaxial elements in this homocercal caudal fin are the uroneurals and epurals; these support relatively few dorsal fin rays. The strain gauge results presented in Figure 9 were recorded on hypural four. From Lauder (1982). Abbreviations: PU_{1-3} , preural centra one to three; U_1 , ural centrum one.

personal observations). Taxa that have a truly symmetrical internal caudal skeleton such as some scombroids (Fierstine and Walters, 1968) have lost the hypochordal longitudinalis muscle. Within the Teleostei, modifications of the caudal skeleton are common and include fusion of the hypural bones and reduction and fusion of epurals and uroneurals. In most teleost fishes the hypurals have expanded and are oriented posteriorly, supporting fin rays both above and below the precaudal vertebral axis (Fig. 7).

This procedure of mapping morphological novelties in the axial musculoskeletal system onto a phylogenetic hypothesis has

allowed the definition of a precise historical sequence of structural transformation. The key general morphological results of this procedure are (1) that the hypochordal longitudinalis muscle differentiated *prior* to the origin of a homocercal tail in teleost fishes, (2) that the first intrinsic caudal muscles were associated with the ventral fin rays, (3) that the hypochordal longitudinalis is derived from the dorsal portion of the flexor ventralis muscle, (4) that true external tail symmetry (homocercy) in teleost fishes is a result of novel internal skeletal supports (epural and uroneural bones) for dorsal fin rays, and (5) that musculature involved in expanding and con-

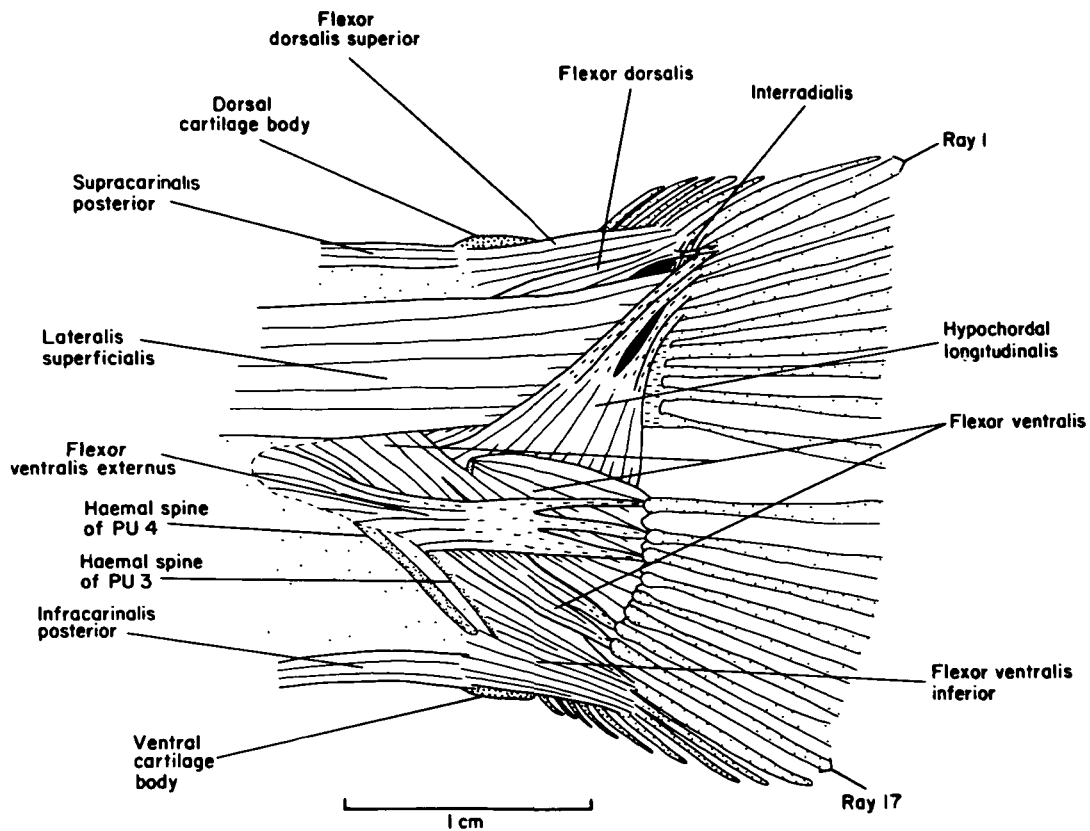


FIG. 8. Caudal musculature in *Lepomis macrochirus*. This lateral view of the middle and deep muscle layers shows the typical condition in the tail of a percomorph teleost with a homocercal tail. The ventral portion of the lateralis superficialis muscle has been removed to show the deeper musculature. The illustrated dorsal portion of this muscle passes under the hypochordal longitudinalis to attach to the heads of the dorsal fin rays. Note the presence of both epaxial and hypaxial carinal muscles, and the hypochordal longitudinalis muscle. This muscle is the only intrinsic caudal muscle that connects ventral and dorsal components of the caudal skeleton. From Lauder (1982).

tracting the caudal fin rays (thus allowing modulation of caudal area) evolved in two steps, the first changes occurring in the dorsal region, with subsequent modifications in the ventral aspect of the fin.

Functional hypotheses

The phylogenetic sequence of structural modification in the caudal musculoskeletal apparatus outlined above provides data on which to frame hypotheses of the evolution of function. This is an important aspect of the interplay of historical and functional analyses: phylogenetic patterns suggest explicit functional hypotheses. Proposed functional changes at successive hierarchical levels on the cladogram of Figure 2 are

outlined in Table 1. Primitively within the Actinopterygii, caudal fin ray movement was coupled to myotomal contraction due to the lack of distinct intrinsic caudal muscles. Caudal fin ray stiffness and position were presumably not greatly alterable during locomotion except as a direct consequence of myotomal contraction. At the level of the Ginglymodi (Fig. 2: Node 2), independent control of caudal fin ray motion was achieved with the origin of the large flexor ventralis muscle. This muscle allows lateral bending and control of fin ray motion independently of actions of the lateralis superficialis muscle.

At the next level (Fig. 2: Table 1: Node 3) the first ability to modulate caudal fin

area occurs. Only the epaxial pair of antagonistic muscles (interradialis and supracarinalis posterior) is present, indicating that the ventral fin rays were less capable of adduction and abduction. Thus, although the ability to control caudal fin ray movement in a medio-lateral direction is best developed for the ventral fin rays, the ability to adduct and abduct the fin rays in the sagittal plane develops first in the dorsal fin rays.

At Nodes 4 and 5 (Fig. 2; Table 1) the dorsal fin rays receive their first epaxial skeletal supports, and the posteriorly directed haemal spines (hypurals) are expanded, marking the transition from the primitive heterocercal fin to a homocercal shape. Finally, at Node 6, caudal fin area is alterable by movements of both dorsal and ventral rays as the hypaxial interradialis and carinal muscles are present. At this level, the hypochordal longitudinalis also acquires an origin from the hypurals and attachments to the first four dorsal fin rays.

The historical sequence of hypochordal longitudinalis muscle origin and the discordance between structural modifications in the dorsal and ventral parts of the tail suggests an important function for the hypochordal muscle in locomotion. The externally symmetrical teleost homocercal tail is internally asymmetrical and the dorsal fin rays are not supported either by skeletal elements or by flexor musculature to the extent of the ventral fin rays. As the tail is swept from side to side, the dorsal edge will tend to trail the leading ventral edge. This should be especially true in clades possessing well-developed ventral flexors but weakly developed hypochordal longitudinalis muscles such as the gars (*Ginglymodi*). The phylogenetic development of the hypochordal longitudinalis is correlated with increasing epaxial support for the dorsal fin rays (Fig. 2; Table 1). This muscle may thus function to stiffen the dorsal tail margin and generate a flatter tail surface that is not inclined to the horizontal during locomotion. Under this hypothesis, the hypochordal longitudinalis muscle is essential for homocercal tail *function* as even the externally symmetrical

arrangement of caudal fin rays does not by itself counter internal structural asymmetry. A broader implication of this idea is that teleost fishes should be able to modulate their tail function by controlling the level of activity in the hypochordal muscle. If the hypochordal muscle is used during locomotion, then the tail should function symmetrically. If the hypochordal muscle is not activated, then the tail should function asymmetrically and the dorsal margin is predicted to trail behind the ventral as the caudal fin sweeps from side to side. This would tend to twist the caudal skeleton so that the posterior edge of the dorsal hypurals was bent to the side opposite to that which the tail is being moved.

FUNCTIONAL MORPHOLOGY

Introduction

In order to provide quantitative experimental data bearing on the function of the homocercal tail in ray-finned fishes and to test the above hypotheses, I conducted a two-part experimental analysis designed to address the following questions. (1) Does the homocercal teleost tail actually function symmetrically? (2) Does the teleost tail change from symmetrical to asymmetrical function depending on locomotor mode? (3) Is the hypochordal longitudinalis muscle used during locomotion and is activity in this muscle correlated with symmetrical tail function? By symmetrical tail function, I mean that the caudal fin is generating forces oriented anteroposteriorly and that the dorsal lobe of the tail is functioning in concert with the ventral and not trailing behind or generating less propulsive force.

The first set of experiments was designed to address questions (1) and (2) above. If one could directly measure bending in hypural bones, then an indication of how the caudal fin was being used during different locomotor behaviors could be obtained. Such measurements were made by implanting a strain gauge onto hypural number 4 and directly assessing the pattern of hypural deformation during both continuous locomotion and fast starts. Measurement of caudal muscle function was accomplished by electromyographic recordings of both myotomal and intrinsic

muscles (such as the hypochordal longitudinalis) during both continuous locomotion and fast starts.

Both of these approaches have been applied to the caudal fin of sunfishes (family Centrarchidae). While this group of teleost fishes is phylogenetically derived within the Teleostei, these fishes constitute an excellent system within which to gather experimental data and test initial explanatory hypotheses of caudal function. A great deal of continued research is clearly needed to extend these experimental results to other ray-finned clades.

Strain gauge analysis

Patterns of hypural deformation during locomotion were studied in *Lepomis gibbosus* (Lauder, 1982). The caudal skeleton (Fig. 7) has five posteriorly oriented hypural bones with hypurals one and four being the largest. Two uroneurals and three epurals form the epaxial components of the skeleton (Fig. 7). In lateral view, the musculature of the caudal fin (Fig. 8) is typical of the teleost homocercal condition (Nursall, 1963; Winterbottom, 1974; Lauder, 1982). A large lateralis superficialis and its aponeurosis cover the intrinsic muscles laterally (the ventral portion of the lateralis and the aponeurosis have been removed in Fig. 8) and attach to the heads of the fin rays. Infra- and supracarinalis posterior muscles attach to cartilage elements anterior to the ventral and dorsal procurrent rays. The hypochordal longitudinalis muscle originates mainly from hypural one and narrows to four tendons that insert on dorsal fin rays one to four (Fig. 8).

Rosette strain gauges were bonded to one side of hypural four (Fig. 7) in four specimens (see Lauder [1982] for details of the experimental procedures used) in order to measure the pattern of bone deformation during locomotion. Rosette strain gauges measure bone deformation along three axes simultaneously and thus allow the calculation of the principal strain angle and an estimate of the loading situation. Fishes bearing the strain gauges were allowed to swim freely in an aquarium for recordings of bone strain during continu-

ous locomotion, and were startled into rapid accelerations for fast-start recordings.

Figure 9 shows the results of the strain recordings on hypural four. During fast-start accelerations, the principal strains are oriented parallel and perpendicular to the body axis (Fig. 9: FS). These data are consistent with a loading pattern of lateral bending with no twisting of hypural four about its attachment to the caudal vertebrae. This pattern is the expected one if the caudal fin is functioning symmetrically. The bone strain found during continuous locomotion is quite different from the fast-start pattern, however (Fig. 9: CLC, CLI). The axes of compression and tension as the tail is swept from side to side are inclined at an angle of 35° to the horizontal. This indicates that the homocercal tail is functioning asymmetrically and that the dorsal hypurals and tail lobe are contributing less force to propulsion than the ventral lobe. The observed deformation pattern would be produced if the posterodorsal corner of hypural four (the site of fin ray attachment) were lagging behind the rest of the caudal skeleton as it was moving laterally. The angles of deformation of the hypural were identical for both tail motion to the right and left (Lauder, 1982) indicating that strain gauge implantation was not affecting the strain pattern.

Questions (1) and (2) raised at the start of this section can now be answered. These results clearly indicate that the homocercal teleost tail does function asymmetrically during slow steady swimming and that tail function does change with locomotor mode (fast starts). Internal skeletal asymmetry appears to have a major role in caudal function during normal steady swimming. It is not necessarily true that a homocercal tail functions symmetrically, and one must now question proposals of increased caudal efficiency in homocercal tails during continuous locomotion.

What is causing the shift in caudal function between fast starts and continuous locomotion? The hypochordal longitudinalis muscle is ideally placed to cause such a change in strain pattern. The line of action of the hypochordal muscle crosses

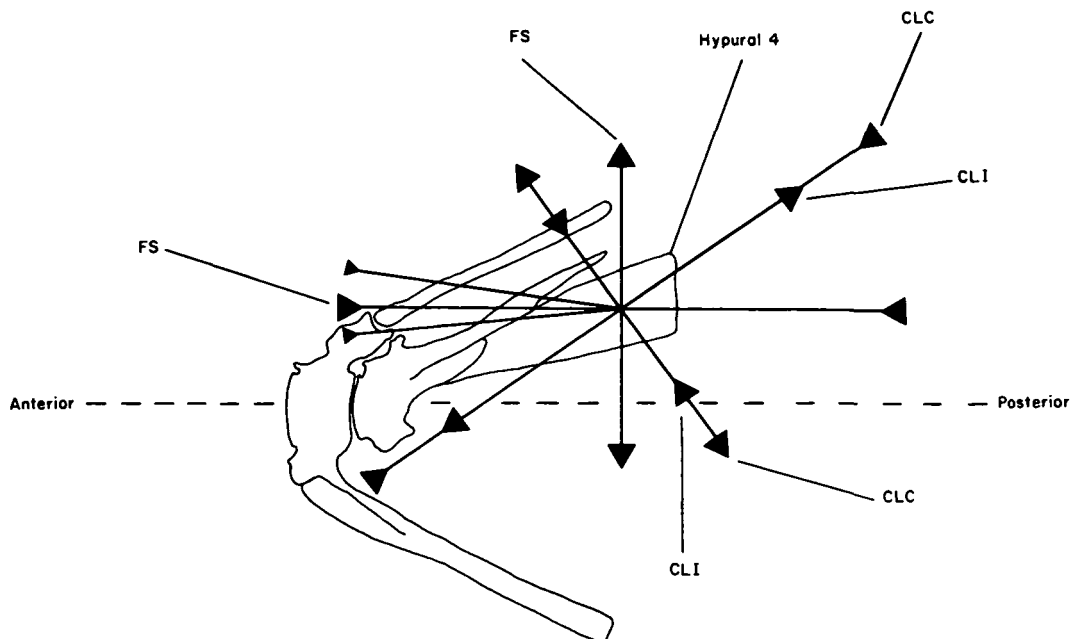


FIG. 9. Orientation of the strain patterns on hypural four recorded during both continuous locomotion (CL) and fast-start accelerations (FS). The direction of the arrowheads indicates tensile or compressive strains, and the relative length of the perpendiculars reflects the ratio of compressive to tensile strain on hypural four. Note that during fast starts the axes of deformation are oriented parallel and perpendicular to the body axis, while during continuous locomotion the strain axes are inclined at about a 30° angle to the horizontal. From Lauder (1982). Abbreviations: CLC, continuous locomotion, data from contralateral tail strokes (movements of the tail to the side on which the strain gauge was *not* attached); CLI, ipsilateral data during continuous locomotion.

the posterior edge of hypural four to attach to the four dorsal fin rays. Activity of this muscle during locomotion would bend the posterodorsal edge of hypural four anteroventrally and thus rotate the obliquely inclined strain shown in Figure 9 dorsally towards the horizontal. This hypothesis predicts that the major difference between symmetrical function during fast starts and asymmetrical tail function during continuous locomotion is due to differential activity in the hypochordal longitudinalis muscle.

Electromyographic analysis

This prediction (and question (3) raised at the start of this section) was tested by recording muscle electrical activity during locomotion in the bass (*Micropterus salmoides*; three specimens) and the pumpkinseed sunfish (*Lepomis gibbosus*; two specimens). Muscles from which activity patterns

were obtained include deep portions of the midbody myotomes, myotomal segments in the caudal peduncle, and the hypochordal longitudinalis and flexor dorsalis intrinsic caudal muscles. In order to provide an indication of tail movement, a small unipolar electrode was implanted subcutaneously in the posterodorsal aspect of the caudal peduncle at the point where the dorsal fin rays attach to the epural bones. An impedance converter (see Lauder and Shaffer [1985] for details) was used to pass a high-frequency signal between this electrode and a metal plate on the side of the flow tank. As the tail moved from side to side, the impedance between the tail electrode and the metal plate changed, providing a direct measure of tail oscillation. Recordings were made as fishes swam in a flow tank (28 by 18 cm working section, designed following the plans in Vogel and LaBarbera [1978]). At slow speeds, bass

and pumpkinseed swam continuously using body and caudal fin propulsion. At high flow velocities (above 0.8 m/sec) fishes were unable to maintain their position and resorted to a burst and glide locomotor pattern. These bursts involved rapid accelerations and were used to assess caudal muscle function during near maximal exertion. Fishes could use the burst and glide pattern only for 10–30 sec before becoming exhausted.

Figure 10 shows representative data from four muscles during locomotion in the bass. As expected from the strain gauge recordings, the hypochordal longitudinalis has only an extremely low level of activity, even during high-speed continuous locomotion. However, during rapid accelerations, the hypochordal longitudinalis is strongly active (Fig. 10: HL) and is repeatedly used as the bass attempts to maintain its position in the flow.

DISCUSSION AND PROSPECTUS

The historical and functional analyses presented here provide a basis for reinterpreting the evolution of the caudal axial musculoskeletal system in ray-finned fishes, and suggest many further lines of inquiry. The experimental data make clear that the view that the homocercal teleost tail functions symmetrically must be questioned. The pattern of homocercal tail function in teleost fishes (at least those studied experimentally) strongly depends on the presence of electrical activity in the hypochordal longitudinalis muscle. The intrinsic muscles of the tail cannot be ignored as they have in past discussions of caudal fin function and evolution.

The historical, phylogenetic analysis indicates that the hypochordal longitudinalis muscle originated as a division of the flexor ventralis (a hypaxial muscle) and that the ability to alter the area of the caudal fin was achieved first for the dorsal fin rays

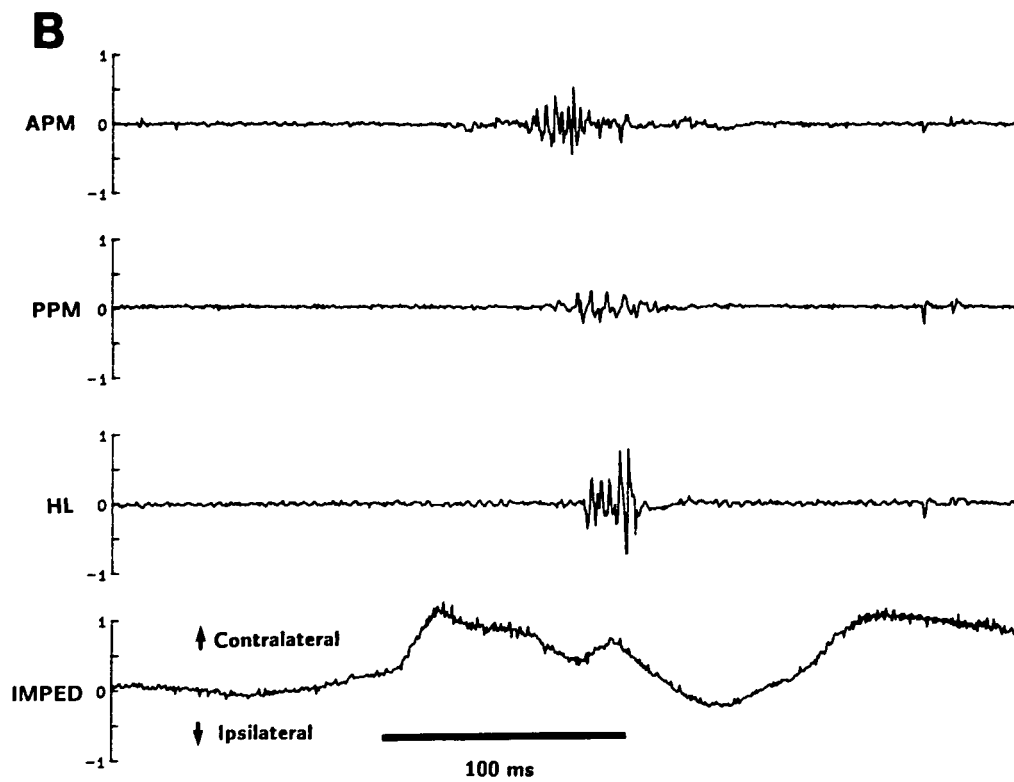
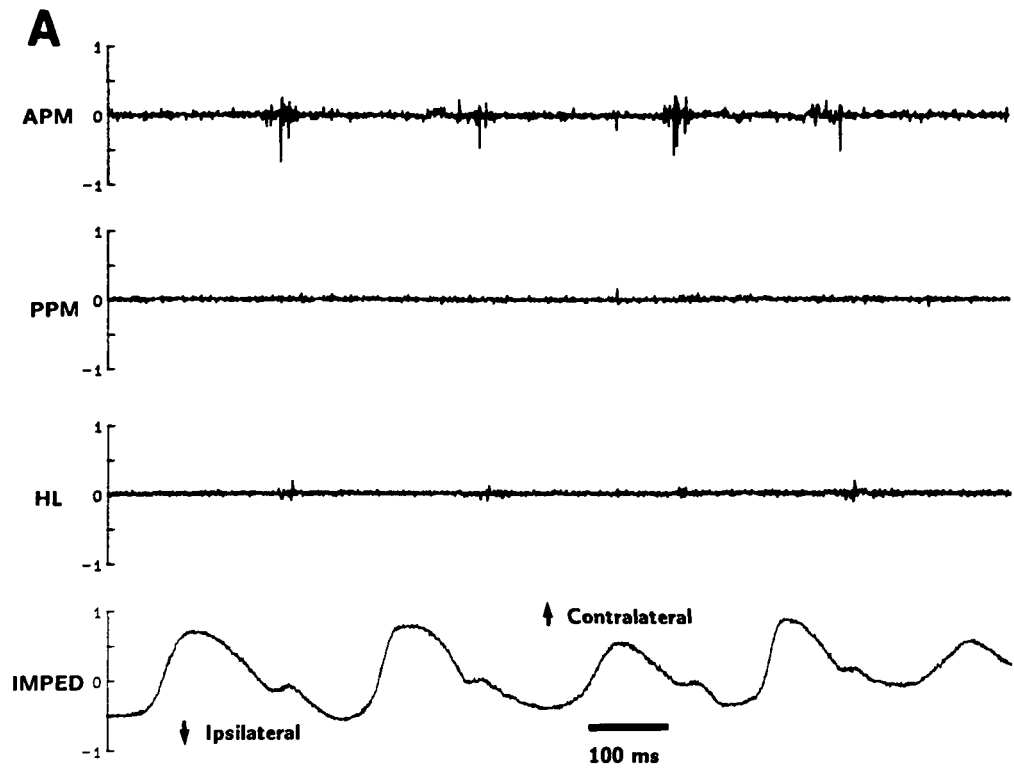
(Fig. 2: Node 3; Fig. 6). Only later did the capability of altering the area of the ventral portion of the caudal fin evolve. Furthermore, there is a clear historical relationship between the origin of internal epaxial supports and modifications of the hypochordal longitudinalis muscle origin and insertion.

A synthesis of both the phylogenetic and functional approaches to the axial musculoskeletal system of ray-finned fishes suggests a number of avenues for further research. A much broader base of comparative experimental data is necessary to further test the generality of the hypothesis that the hypochordal longitudinalis muscle plays a major role in determining the functional properties of the caudal fin. Marshall (1971, pp. 30–31) has also suggested that the hypochordal longitudinalis muscle is integral to caudal fin kinematics, but his hypotheses have yet to be tested. Quantitative electromyographic data are needed from the intrinsic caudal and myotomal musculature in *Polypterus*, *Lepisosteus*, and *Amia* as well as for primitive teleosts such as osteoglossomorphs. Data such as these would permit functional consequences of structural features to be mapped as characters onto the phylogenetic hypothesis (Fig. 2) much more precisely than can now be done. It is clear that one cannot explain the complexity of intrinsic caudal musculature in teleost fishes on the basis only of steady swimming and burst and glide locomotion. Considerable research will need to be done on maneuverability and use of the caudal fin in dynamic stability before the full significance of intrinsic muscle complexity will become apparent.

The exact role of the hypochordal longitudinalis muscle in mediating tail function needs detailed investigation, both by precise correlative studies of tail kinematics in relation to hypochordal longitudi-

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FIG. 10. Representative electromyograms from locomotion in the bass (*Micropterus salmoides*). Upper panel: recordings from fast continuous swimming. Lower panel: recordings from a rapid acceleration (burst). Note the increase in amplitude of the hypochordal longitudinalis muscle during fast starts. Vertical scale is in $\mu V \cdot 10^2$. Abbreviations: APM, anterior peduncular myotome; HL, hypochordal longitudinalis muscle; IMPED, impedance trace of tail position (see text); PPM, posterior peduncular myotome.



nalis muscle activity, and by experimental manipulations. For example, the tendons of the hypochordal longitudinalis could be severed at their attachments to the dorsal fin rays, and the effect on caudal function observed. If the view presented here is correct, eliminating the hypochordal longitudinalis should reduce fast-start performance without substantially modifying the efficiency of continuous locomotion. Eliminating the hypochordal longitudinalis is predicted to cause the dorsal fin rays to trail the ventral rays during fast starts and produce an asymmetrical thrust during rapid acceleration. Aleyev (1969, 1977), Bainbridge (1963), and Marshall (1971) have all noted that the dorsal and ventral fin rays in the teleost tail may exhibit different kinematic patterns, but the consequences of these observations have never been pursued, especially with respect to the possibility that hypochordalis muscle might be causally implicated in caudal fin kinematics.

The results presented here raise the question: exactly what is a homocercal tail? Since the sunfish tail, exhibiting the classical homocercal shape, has been shown to function asymmetrically, then the definition of a homocercal tail should only apply to external shape, referring specifically to equal dorsal and ventral fin ray lobes in the tail. Internally, there is considerable structural asymmetry, and neither dorsal/ventral nor epaxial/hypaxial components are mirror images of each other. There is nothing about the external shape of the caudal fin *alone* that enables us to predict its functional properties. Function and locomotor performance will be a consequence of the interaction of external shape, internal skeletal morphology, and the design and relative activity of intrinsic caudal musculature.

Any morphological system has a history that must be taken into account if we are to fully understand the relationship between form and function. Without understanding the historical patterns that have led to current structures, we risk mistaking correlations between present-day structures, environments, and functions for a causal relationship. Determining causal

interrelationships of form and function requires an historical analysis (Lauder, 1989). The axial musculoskeletal system of ray-finned fishes is no exception: functional and phylogenetic approaches are mutually illuminating. Yet such a combined approach is still in its infancy, and a more general understanding of vertebrate axial musculoskeletal systems awaits the synthesis of historical and functional information.

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