Review

The fish tail as a derivation from axial musculoskeletal anatomy: an integrative analysis of functional morphology☆

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ABSTRACT

The adult morphology of the tail varies greatly among extant fishes despite sharing both ontogenetic similarities and the functional need to propel the body through a fluid medium. Both sharks (Chondrichthyes) and ray-finned fishes (Actinopterygii) control caudal fin musculature independently of axial body myomere activity to modify the stiffness and shape of their tails. For example, sharks and bony fishes possess different structural elements and muscles and move their tails in different ways, resulting in different locomotory hydrodynamic effects and a range of performance variables including speed and maneuverability. The stiffness of the heterocercal, lobate tail of the shark can be modulated during the tail beat resulting in nearly continuous thrust production. In contrast, the highly flexible tail of ray-finned fishes can be manipulated into many different shape conformations enabling increased maneuverability for these fishes. Consequently, the developmental, morphological, and functional derivation of the tail from the axial trunk has resulted in a diversity of form, the attributes of which may be of ecological and evolutionary significance.

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1. Evolution of the tail fin

As early as the Cambrian (approximately 530 mya), the chordate ancestors †*Pikaia* and †*Haikouichthys* exhibited some of the axial morphology we see in living fishes today. Both of these species were swimmers who had elongate bodies powered by myotomal muscle, the fossil preservation of which looks very much like the axial myomeres of living fishes (Shu et al., 1996, 2003; Morris and Caron, 2012). By the Devonian (approximately 420–350 mya), swimming vertebrates had evolved tails of many shapes and sizes. Evolution of a tapered caudal fin predates the evolution of jaws as evidenced by the anaspid †*Euphanerops longaevus* (Janvier and Arsenault, 2007). The rapid diversification of bony fishes continued with the development of fins supported by flexible rays; these fishes are known as the actinopterygians and make up approximately half of the vertebrate species we know to exist today (Near et al., 2012, 2013). And within this group, the 28,000 species known as Teleost fishes are united primarily by a synapomorphy of the skeletal morphology of their tail fins; specifically, the presence of a urohyal formed as an unpaired intramembranous bone (Patterson, 1968; Lauder and Liem, 1983; Arratia and Schultze, 1990; de Pinna, 1996).

Even a cursory survey of living fishes demonstrates the diversity in fish fin morphologies. Caudal fins, in particular, vary within and among species in shape, size, and structure (Fig. 1). For example, in the caudal fin, the number, length, width, ossification, segmentation, branching, and stiffness of fin rays that support the tail lobe differ among species (Lauder, 1989). Caudal fin shapes run the gamut of all imaginable conformations, ranging from nearly nonexistent in eel-like fishes, to rigid scythe-shaped in tunas and sharks, to large flexible deformable foils that would almost seem a hindrance to locomotion in some exotic goldfish. Variation in tail fin morphologies is noted to be a factor in sexual selection, functional specializations, and locomotor modalities (Affleck, 1950; Ameyaw-Akumal, 1975; Abou-Seedo, 1994; Hale, 1996; Arratia et al., 2001; Basolo and Alcaraz, 2003; Flammang, 2010). There are species-specific modifications to the morphology of the vertebrae; for example, structural modifications to the vertebral centra and spines are functionally important in extremely fast fishes (Long, 1992; Long and Nipper, 1996). However, there is surprisingly little diversity in the morphology of the vertebrae and myomeres along the long axis of the fish body (the trunk and peduncle, specifically) as compared to the morphology of the caudal fin skeleton (including fin rays) and musculature. The more anterior axial skeletal and muscular anatomy is far more similar among living and extinct fishes than is tail fin morphology. This raises the question: why are fish tail fins so diverse, while trunk morphology is comparatively not?

To examine the evolution and diversification of tail morphologies, several factors must be considered. It is important to understand the developmental processes of the trunk and tail to
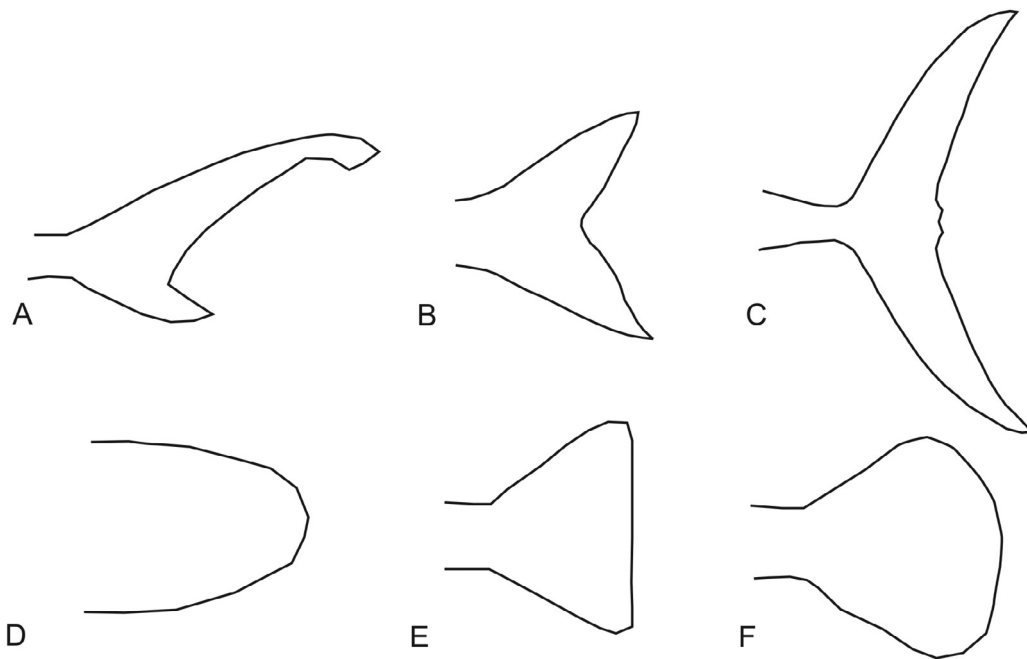
Fig. 1. Representative fish tail shapes: (A) heterocercal; (B) forked; (C) lunate; (D) eel-like; (E) truncate; (F) rounded.

know whether they are regulated by the same patterning and positioning modules or if they are independently organized. Anatomical differences in skeletal and muscular morphologies in tails result in functional differences in terms of how the tail fin will interact with the fluid environment. And as a result, different tail fin morphologies will exhibit specific performance traits which may be selected for under varied ecological circumstances.

2. Development of the tail

As in all vertebrates, the fish tail bud begins to form immediately following gastrulation, followed by a pattern of extension, protrusion, and eversion away from the yolk cell. The post-anal axial body of fish larvae is extended posteriorly and both somites and fin folds are symmetrical about the longitudinal axis (Fig. 2). However, within three days after hatching, this axial symmetry is lost as the ventral portion of the developing tail grows rapidly, displacing the notochord at an angle dorsally (Potthoff et al., 1988; Bird and

Fig. 2. Embryonic filetail catshark (*Parmaturus xaniurus*) of unknown age. (B) is a magnified image of the inset in (A). The first and second dorsal (d1 and d2, respectively), anal (a) and caudal (dorsal lobe, cd; ventral lobe, cv) fins have all formed, but a dorsal remnant of the median fin fold (mff) still remains.

Mabee, 2003; Britz and Johnson, 2005; Hilton and Johnson, 2007). This shift in axis orientation, aided by the migration of trunk neural crest cells (Smith et al., 1994), precipitates the formation of a caudal nerve plexus (Ishikawa and Iwamatsu, 1993; Schneider and Sulner, 2006), distinct muscle groups unlike the trunk myomeres, and cartilaginous or bony skeletal elements supporting the developing caudal fin (Bird and Mabee, 2003).

The tail region in fishes develops via mechanisms that are distinct from those of the head and the trunk (Kanki and Ho, 1997; Griffin et al., 1998; Ahn and Gibson, 1999; Kimelman and Griffin, 2000; Morin-Kensicki et al., 2002; Holley, 2006). In fact, the tail has its own organizing center which acts independently of the dorsal organizer in larval zebrafish, *Danio rerio* (Agathon et al., 2003). Median fin patterning is regulated by *Hox* genes; expression boundaries in *Hox* groups 1–11 designate the anterior 17 somites in larval zebrafish as "trunk" and the remaining 14 posterior caudal somites as "tail" (Mabee et al., 2002). Further evidence supporting the tail region as a developmental entity separate from the trunk is the way *shh* and *bmp2b* modify bone patterning in the tail fin differently than in the more anterior axial skeleton (Quint et al., 2002).
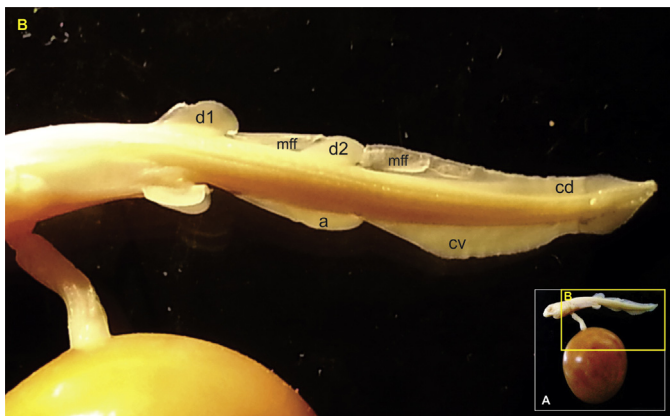
3. Anatomy of the tail

The axial body of living fishes is supported by serially arranged vertebral elements which possess dorsal and ventral projections known as the neural and haemal arches, respectively. The "M"-shaped myomeres are anteriorly and posteriorly facing cones of muscle which attach to several vertebrae and their spines in series such that contraction of one myomere will manipulate the position of multiple vertebrae via a complex arrangement of myoseptal tendons (Winterbottom, 1974; Lauder, 1980; Koob and Long, 2000; Gemballa et al., 2003). This trunk morphology is conserved among fishes. However, in examining the evolution of tail fin morphologies of living fishes, there is a trend of increasing complexity of the structure of the tail relative to that of the trunk over time (Flammang and Lauder, 2009; cf. Fig. 3). In sharks and early actinopterygian fishes, the vertebral elements and myomeres curve dorsally into the tail (Gemballa, 2004). In both groups of fishes, with the exception of