

Evolution of Levers and Linkages in the Feeding Mechanisms of Fishes¹

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SYNOPSIS. The evolution of feeding mechanisms in the ray-finned fishes (Actinopterygii) is a compelling example of transformation in a musculoskeletal complex involving multiple skeletal elements and numerous muscles that power skull motion. Biomechanical models of jaw force and skull kinetics aid our understanding of these complex systems and enable broad comparison of feeding mechanics across taxa. Mechanical models characterize how muscles move skeletal elements by pulling bones around points of rotation in lever mechanisms, or by transmitting force through skeletal elements connected in a linkage. Previous work has focused on the feeding biomechanics of several lineages of fishes, but a broader survey of skull function in the context of quantitative models has not been attempted. This study begins such a survey by examining the diversity of mechanical design of the oral jaws in 35 species of ray-finned fishes with three main objectives: (1) analyze lower jaw lever models in a broad phylogenetic range of taxa, (2) identify the origin and evolutionary patterns of change in the linkage systems that power maxillary rotation and upper jaw protrusion, and (3) analyze patterns of change in feeding design in the context of actinopterygian phylogeny. The mandibular lever is present in virtually all actinopterygians, and the diversity in lower jaw closing force transmission capacity, with mechanical advantage ranging from 0.04 to 0.68, has important functional consequences. A four-bar linkage for maxillary rotation arose in the Amiiformes and persists in various forms in many teleost species. Novel mechanisms for upper jaw protrusion based on this linkage for maxillary rotation have evolved independently at least five times in teleosts. The widespread anterior jaws linkage for jaw protrusion in percomorph fishes arose initially in Zeiformes and subsequently radiated into a wide range of premaxillary protrusion capabilities.

INTRODUCTION

A central goal of functional morphology is to understand the transmission of force and velocity in musculoskeletal systems. Vertebrate musculoskeletal systems are often modeled by calculating the force and motion properties of a system from data on geometric conformation of muscles and bones. Recent modeling studies have focused on systems such as vertebrate jaws (Erickson *et al.*, 1996; Westneat, 2003), limbs (Biewener, 1989; Lutz and Rome, 1994), tongues and tentacles (Kier and Smith, 1985) and axial muscle (Westneat *et al.*, 1998; Azizi *et al.*, 2002). Biomechanical models are valuable in such studies because they provide a testable hypothesis of the relation between morphology and behavior, identify morphometric data with functional relevance, and promote exploration of functional variation in a comparative framework (Westneat, 1995).

The functional morphology of skull mechanisms in fishes has a long history due to broad interest in the high level of kineticism in fish skulls (Alexander, 1967; Elshoud-Oldenhave, 1979; Lauder, 1980, 1982; Liem, 1978, 1980; Osse, 1969; Waltzek and Wainwright, 2003; Westneat, 1991; Westneat and Wainwright, 1989). Cranial kinesis reaches extraordinary levels in many teleosts because there are 20 or more independently movable skeletal elements in the skull and many more in the pharyngeal apparatus. Schaeffer

and Rosen (1961) and Lauder (1982) traced the evolution of some of the key aspects of cranial kinesis in ray-finned fishes, but biomechanical modeling has not yet been used to examine fish skull evolution at this level. The dynamic motion of the teleost skull represents a challenge for the development of biomechanical models, and relatively few actinopterygian fishes have been analyzed with biomechanical modeling. Current models for fish skulls are based on the engineering theory of levers and linkages. The closing of the lower jaw of fishes has been modeled as a simple lever (Barel, 1983; Westneat, 1994; Wainwright and Richard, 1995) in a diversity of fish groups to compare feeding mechanics across taxa and during ontogeny. The lever mechanics of the lower jaw (Fig. 1) can also be analyzed as a more complex, dynamic system by including the geometry and properties of the adductor muscles that power jaw closing (Westneat, 2003).

Complex interactions between movable elements in the skull of fishes have been analyzed with linkage theory from mechanical engineering. For example, Anker (1974) proposed that lower jaw depression in teleosts may be modeled with a four-bar linkage mechanism in which the neurocranium, opercle, interopercle, and articular of the lower jaw were linked. Anker (1978) examined the action of this lower jaw depression mechanism during respiration. Muller (1987, 1989) used four-bar theory to propose mechanisms of hyoid depression and abduction in fishes, based on the connections between the skull, hyomandibula, hyoid, and sternohyoideus muscle. Westneat (1990) proposed that the mechanism of maxillary rotation was a four-bar linkage composed of suspensorium, palatine, maxilla, and coronoid portion of the lower jaw. Biome-

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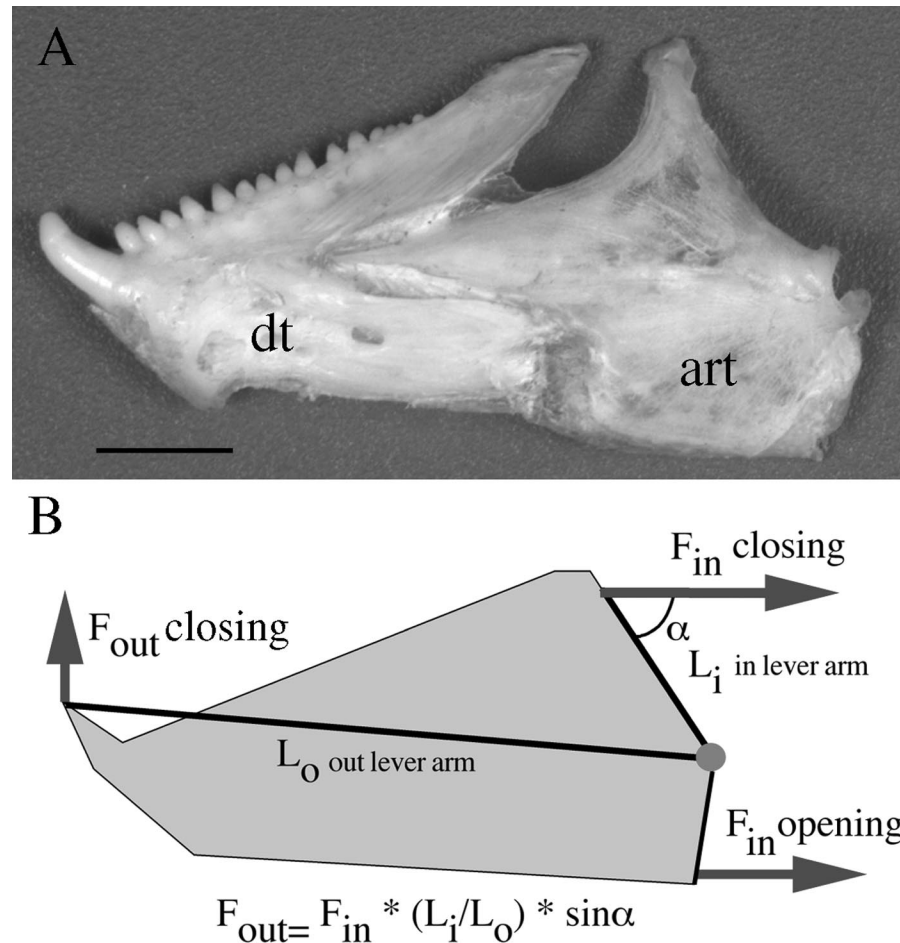


FIG. 1. Lower jaw lever mechanisms. (A) The mandible of a labrid fish, *Cheilinus trilobatus*, showing the dentary (DT) and articular (ART) bones that form the left jaw. (B) Lever mechanisms of jaw opening, showing in lever moment arms for opening and closing, the outlever arm of the jaw, and posteriorly directed arrows indicating input forces (F_{in}). The output force for the bite at the anterior tooth (F_{out}) is shown, with the equation for calculating output force ($F_{out, closing}$) as a function of mechanical advantage and muscle insertion angle. Adapted from Westneat (2003).

chanical models of fish jaws and skulls have the potential for testing hypotheses of mechanical design in a diversity of fishes, for developing ideas of functional transformation during growth and development, and for examining patterns of evolution in key functionally relevant characters in a phylogenetic context.

Although a number of biomechanical models have been proposed and tested, few fish groups in the huge radiation of actinopterygian fishes have been examined with modeling force and motion in mind. To promote evolutionary understanding of fish skull mechanisms, the present study surveys the morphology and biomechanics of feeding function in a broad sample of actinopterygian fishes from most major lineages. This work has three objectives: (1) present the morphological diversity of actinopterygian skulls from the perspective of biomechanical modeling, (2) present data on lever mechanics of actinopterygian ranging from *Polypterus* to Perciformes, and (3) trace phylogenetic changes in skull mobility and identify key events in the origin and evolution of the linkages that mediate jaw protrusion.

METHODS

Biomechanics of the mandible

The mandible of fishes is a classic 3rd-order lever for both opening and closing mechanisms, and the mechanism is present in virtually all actinopterygian fishes (Fig. 1). The fulcrum of the lower jaw is the quadrate/articular joint (Fig. 1B) about which the jaw rotates open and is pulled closed during feeding (Bar-el, 1983; Westneat, 1994, 2003). The outlever moment arm for jaw opening and closing is the distance from the jaw joint to the tip of the anterior-most tooth (Fig. 1). In comparisons among specimens with variable teeth or tooth damage, this outlever may be measured to the anterior tip of the jaw (Westneat, 1994). The inlever for jaw opening is the distance from the jaw joint to the site of attachment of the ligament (running from interopercle or hyoid) onto the posteroventral corner of the mandible. The mechanical advantage of jaw opening is the ratio of jaw opening inlever to outlever (Fig. 1). The origin and insertion of the adductor mandibulae muscles (often subdivided) onto the lower

jaw determine the moment arms for force transmission during jaw closing. For example, in a labrid fish, the A2 muscle inserts along the posterior edge of the coronoid process of the articular, and the A2 inlever moment arm is measured as the distance from the jaw joint to the dorsal muscle insertion point (Fig. 1B). The A1 and A3 subdivisions have their own lever advantages (Westneat, 2003). In this study, the simple mechanical advantage (lever ratio) is used, but it should be noted that this simple model of jaw closing force provides a useful comparative functional variable but it ignores the insertion angle of the adductor muscle, and thus overestimates force and underestimates velocity transmission for most fishes (Westneat, 2003).

Biomechanical computer models of all lever mechanisms were developed using Pascal language algorithms implemented in CodeWarrior 4.0 (Westneat, 2003) and are available from the author. The computer models accept morphometric data for the lengths of the inlever, outlever, and muscle lengths that attach to the lever (if available). Lever dimensions were measured for all fishes studied by analysis of digital photos and collection of coordinate data for the fulcrum and lever arms for both opening and closing mechanisms.

Linkage models of cranial kinesis

Complex motion in fish skulls occurs due to the presence of multiple levers and linkages that transmit muscle forces for cranial elevation, jaw rotation, maxillary motion, and upper jaw protrusion. Jaw linkages are surveyed broadly here in an effort to identify the origin and diversity of the linkage systems in fishes. The maxilla and premaxilla of many actinopterygians are immobile or move little, so protrusion models are not applicable. However, maxillary rotation is common among actinopterygians and is usually driven by a linkage connection between the mandible and the maxilla. Many lineages including the percomorphs and several groups basal to them have evolved more complicated linkage mechanisms in the anterior jaws that drive upper jaw protrusion (Westneat, 1990, 1994). Linkages are most often a variation on the percomorph anterior jaws linkage (Fig. 2) in which the lower jaw is the input link of a four-bar linkage involving the suspensorium (the fixed link), the palatine, nasal, or palatamaxillary ligament (the coupler link), and the maxilla (output link). In many taxa the opercular four-bar linkage (Fig. 2) aids in lower jaw depression. The action of the jaws linkage during cranial kinesis is to transmit ventral jaw rotation into maxillary rotation for the purpose of protruding the premaxilla forward toward the prey. During jaw closing, the linkage transmits force from jaw adductor muscles to the mandible and maxilla, and indirectly to the premaxilla for closing the mouth or delivering bite force.

Phylogeny, morphology and taxon sampling

The phylogeny for actinopterygian fishes used here is a composite of information taken from Coates (1999), Nelson (1994), Stiassny *et al.* (1996), and

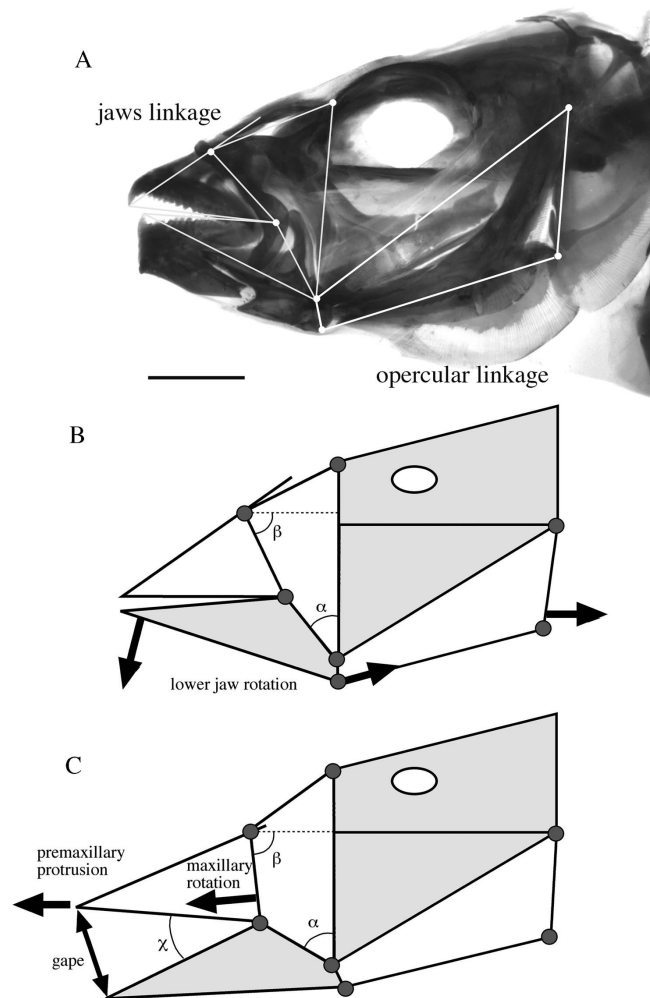


FIG. 2. Linkage mechanism of maxillary rotation and premaxillary protrusion in percomorph fishes. (A) Skull morphology of *Oxycheilinus digrammus*, a piscivorous labrid fish, with lines showing the geometry of the mandibular lever, the opercular 4-bar linkage, and the four-bar linkage that drives jaw motion. (B) The input motion that drives the linkage is ventral depression and rotation of the mandible (increase in angle α). (C) The output motions of the linkage are maxillary rotation (angle β), maxillary displacement ventrally, sliding and protrusion of the premaxilla, and increase in mouth gape and gape angle (angle χ).

Johnson and Patterson (1993). The skulls of 35 species (Table 1) of actinopterygian fishes were obtained from museum collections to represent an initial survey of functional diversity of feeding in ray-finned fishes. Specimens were either dried skeletons or were cleared and stained using the enzyme technique of Taylor and Van Dyke (1985) with chemical concentrations and reaction times tailored for each batch of specimens. Digital images for quantitative analyses and figures were captured using a Wild M3Z stereomicroscope or a light table, both equipped with a digital camera. Digital images were analyzed using QuickImage (J. Walker), a customized version of NIH Image 1.62, on an Apple Macintosh G4 computer.

TABLE 1. Mechanical advantage for opening and closing of the lower jaw in 35 species of fishes from throughout the actinopterygian phylogeny.

Genus	Species	MA open	State	Genus	Species	MA close	State
<i>Strongylura</i>	<i>incisa</i>	0.030	0	<i>Strongylura</i>	<i>incisa</i>	0.040	0
<i>Lepisosteus</i>	<i>osseus</i>	0.045	0	<i>Lepisosteus</i>	<i>osseus</i>	0.051	0
<i>Gymnothorax</i>	<i>javanicus</i>	0.052	0	<i>Hiodon</i>	<i>alosoides</i>	0.117	0
<i>Hiodon</i>	<i>alosoides</i>	0.057	0	<i>Atractosteus</i>	<i>spatula</i>	0.121	0
<i>Polypterus</i>	<i>senegalus</i>	0.062	0	<i>Harpadon</i>	<i>nehereus</i>	0.138	0
<i>Aulostomus</i>	<i>chinensis</i>	0.074	0	<i>Osteoglossum</i>	<i>bicirrhosum</i>	0.140	0
<i>Scomber</i>	<i>scombrus</i>	0.075	0	<i>Cheilio</i>	<i>inermis</i>	0.140	0
<i>Harpadon</i>	<i>nehereus</i>	0.077	0	<i>Hydrolycus</i>	<i>scomberoides</i>	0.165	0
<i>Oncorhynchus</i>	<i>tshawytscha</i>	0.083	0	<i>Atherinomorus</i>	<i>lacunosus</i>	0.205	0
<i>Elops</i>	<i>saurus</i>	0.084	0	<i>Elops</i>	<i>saurus</i>	0.207	0
<i>Sardinella</i>	<i>aurita</i>	0.086	0	<i>Arapaima</i>	<i>gigas</i>	0.212	0
<i>Sphyraena</i>	<i>barracuda</i>	0.086	0	<i>Gymnothorax</i>	<i>javanicus</i>	0.227	1
<i>Esox</i>	<i>lucius</i>	0.089	1	<i>Esox</i>	<i>lucius</i>	0.228	1
<i>Arius</i>	<i>felis</i>	0.090	1	<i>Stephanoberyx</i>	<i>monae</i>	0.229	1
<i>Arapaima</i>	<i>gigas</i>	0.092	1	<i>Oncorhynchus</i>	<i>tshawytscha</i>	0.233	1
<i>Osteoglossum</i>	<i>bicirrhosum</i>	0.094	1	<i>Micropterus</i>	<i>salmoides</i>	0.246	1
<i>Hydrolycus</i>	<i>scomberoides</i>	0.097	1	<i>Gadus</i>	<i>morhua</i>	0.248	1
<i>Cheilio</i>	<i>inermis</i>	0.100	1	<i>Epinephelus</i>	<i>itajara</i>	0.252	1
<i>Polymixia</i>	<i>lowei</i>	0.115	1	<i>Amia</i>	<i>calva</i>	0.269	1
<i>Atherinomorus</i>	<i>lacunosus</i>	0.120	1	<i>Scomber</i>	<i>scombrus</i>	0.271	1
<i>Atractosteus</i>	<i>spatula</i>	0.131	1	<i>Sphyraena</i>	<i>barracuda</i>	0.278	1
<i>Cyprinus</i>	<i>carpio</i>	0.132	1	<i>Polymixia</i>	<i>lowei</i>	0.285	1
<i>Apteronotus</i>	<i>macrolepis</i>	0.141	1	<i>Pterois</i>	<i>volitans</i>	0.285	1
<i>Micropterus</i>	<i>salmoides</i>	0.142	1	<i>Sardinella</i>	<i>aurita</i>	0.306	1
<i>Amia</i>	<i>calva</i>	0.143	1	<i>Serrasalmus</i>	<i>rhombeus</i>	0.310	1
<i>Gadus</i>	<i>morhua</i>	0.143	1	<i>Cyprinus</i>	<i>carpio</i>	0.331	1
<i>Stephanoberyx</i>	<i>monae</i>	0.150	2	<i>Arius</i>	<i>felis</i>	0.347	2
<i>Holocentrus</i>	<i>adscensionis</i>	0.154	2	<i>Holocentrus</i>	<i>adscensionis</i>	0.350	2
<i>Platichthys</i>	<i>stellatus</i>	0.161	2	<i>Platichthys</i>	<i>stellatus</i>	0.351	2
<i>Cyttopsis</i>	<i>rosea</i>	0.195	2	<i>Aulostomus</i>	<i>chinensis</i>	0.363	2
<i>Serrasalmus</i>	<i>rhombeus</i>	0.199	2	<i>Polypterus</i>	<i>senegalus</i>	0.421	2
<i>Epinephelus</i>	<i>itajara</i>	0.227	2	<i>Balistes</i>	<i>vetula</i>	0.433	2
<i>Pterois</i>	<i>volitans</i>	0.238	2	<i>Apteronotus</i>	<i>macrolepis</i>	0.476	2
<i>Chlorurus</i>	<i>sordidus</i>	0.290	2	<i>Cyttopsis</i>	<i>rosea</i>	0.505	2
<i>Balistes</i>	<i>vetula</i>	0.331	2	<i>Chlorurus</i>	<i>sordidus</i>	0.680	2

* MA is the ratio of inlever to outlever of the mandible (after Westneat 1994). Species are ranked from lowest MA (fastest) to highest MA (most forceful), with discrete character states shown.

RESULTS AND DISCUSSION

The central findings of this study are (1) that the variation seen in mandibular lever geometry has direct implications for functional diversity in ray-finned fishes and shows extensive convergence throughout actinopterygian phylogeny, (2) that a phylogenetic trend of increasing skull kinesis in ray-finned fishes can be modeled as changes in lever and linkage biomechanics, and (3) that premaxillary protrusion linkage mechanisms have evolved independently at least five times in teleosts.

A large range of jaw mechanisms is revealed as one moves from *Polypterus* to Perciformes (Fig. 3). Many independent evolutionary transitions occur from feeding systems with high force transmission to those specialized for speed of jaw motion. Biomechanical estimates of jaw closing force transmission (mechanical advantage) range across an order of magnitude from 0.04 to 0.7 (Table 1). Each major group of actinopterygians appears to have members with fast and members with forceful jaw mechanics, suggesting that convergent evolution of jaw function is likely to be the rule at both higher levels and at species levels of gen-

erality. This diversity of mechanical design and emergent pattern of convergence is likely driven by the alternative requirements for force and speed associated with a strategy for biting vs. strategies for suction feeding (Alfaro *et al.*, 2001) and the high frequency of switching between these strategies among species (Westneat, 1995).

The evolution of kinesis in the jaws of fishes is a story of increasing mobility among jaw bones and the origin of linkage mechanisms enabling maxillary and premaxillary motion at several different points in actinopterygian phylogeny (Fig. 3). A linkage for maxillary rotation originated in Amiiiformes and persists throughout many teleost species. This mechanism operates by transferring ventral mandibular rotation into anterior maxillary rotation via a ligamentous coupling that was described by Lauder (1979, 1980), and warrants additional linkage modeling. This mechanism is modified in many lineages by addition of new elements such as a rotational palatine or nasal and associated ligaments that confer increased dorsal maxillary rotational and translational mobility. Kineticism of the maxilla is the precursor to premaxillary protrusion

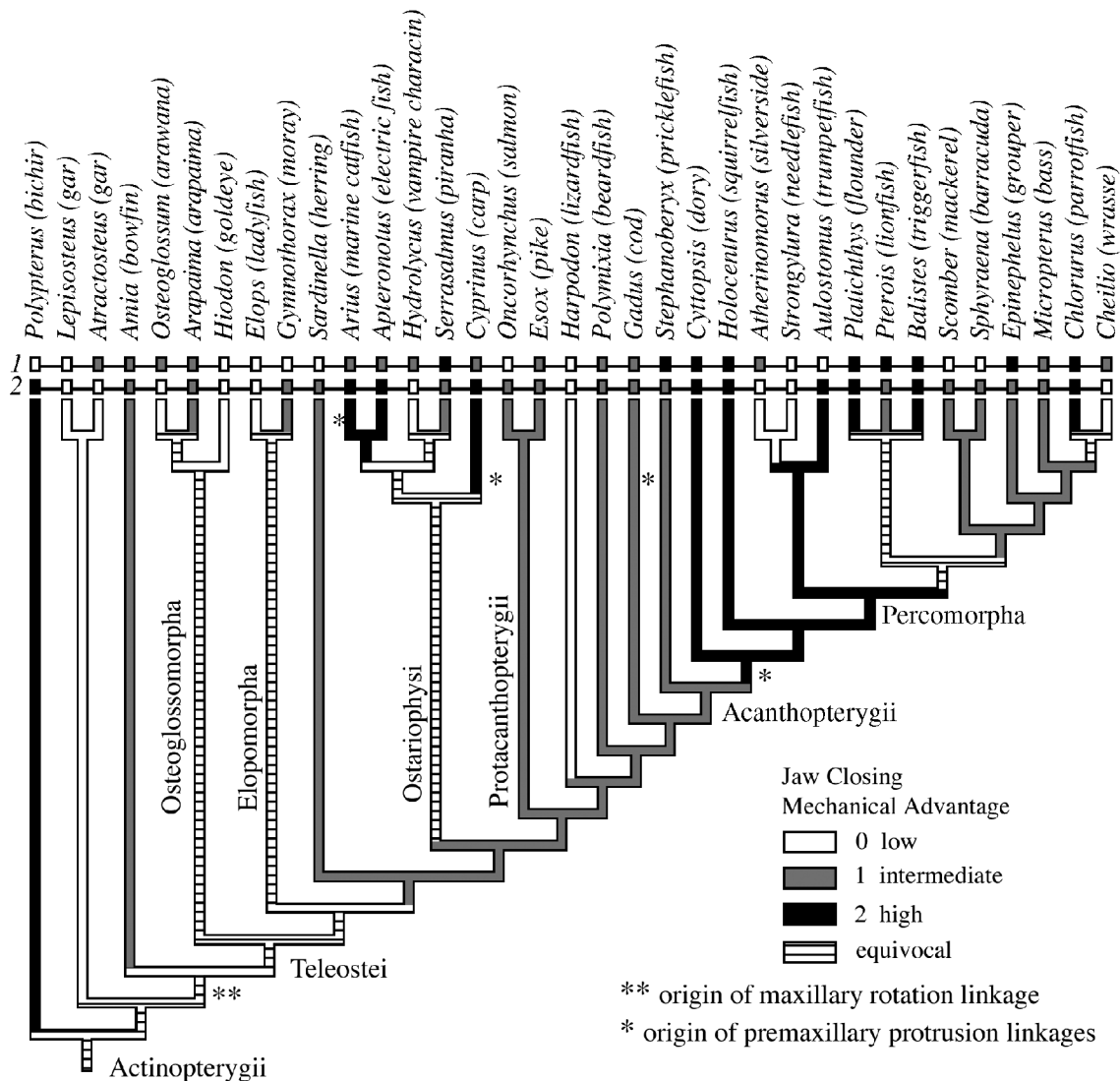


FIG. 3. Evolution of jaw lever mechanical advantage in 35 species of actinopterygian fishes. Phylogeny is a composite tree based on Coates (1999), Nelson (1994), Stiassny *et al.* (1996), and Johnson and Patterson (1993). Two characters are optimized on the phylogeny, character 1 is jaw opening mechanical advantage (with tip states only shown) and character 2 is jaw closing mechanical advantage (with tip states and branch shading illustrated). Low MA jaws emphasize velocity and high MA jaws transmit relatively more force. Phylogenetic origin of the maxillary rotation linkage (**) and 4 of at least 5 origins of premaxillary protrusion (*) are indicated on the tree topology.

which is a hallmark of feeding and evolutionary diversity in fishes.

Premaxillary protrusion mechanisms have evolved at least five times among major groups of ray-finned fishes (Fig. 3). Using the phylogenetic hypotheses of Johnson and Patterson (1993), it can be shown that these independent evolutionary events are functionally convergent, in that upper jaw protrusion occurs, but that the musculoskeletal mechanics underlying each type of protrusion mechanism are different. Many of the cyprinid fishes (minnows and carps) have upper jaw protrusion, via mechanisms described by Alexander (1966) that involve a rotational and twisting maxilla. The loricariid catfishes have independently evolved a highly mobile premaxilla associated with algae scraping (Schaefer and Lauder, 1986). Subsequent

clades on the actinopterygian tree such as salmonids, esocids, aulopiform and stomiiform fishes lack upper jaw protrusion but most retain a mobile maxilla. A novel, highly kinetic mechanism of maxillary and premaxillary protrusion evolved in the lampridiform fishes at the base of the acanthomorphs (Fig. 3), in which both maxilla and premaxilla are largely free of the neurocranium and are pulled forward and ventrally during jaw opening. This is found in an extreme form in *Stylophorus chordatus*, which has one of the most extremely protrusible mouths among fishes (Pietsch, 1978).

Further up the actinopterygian tree, *Polymixia* lacks premaxillary protrusion and this genus occupies a key position as the sister-group to a major sister-pair of large clades, the Paracanthopterygii and Acanthopterygii. At

least one origin of upper jaw protrusion occurs in each of these lineages. Most paracanthooids lack premaxillary protrusion, but some cods have weak protrusion and the anglerfishes of the family Antennariidae have fairly extensive jaw protrusion used in conjunction with their dorsal fishing lures. The most widespread anterior jaws linkage used for premaxillary protrusion in fishes is that of the acanthopterygians. This mechanism appears to be absent or reduced in *Stephanoberyx* (at the base of Acanthopterygii according to Johnson and Patterson, 1993) but arose initially in Zeiformes (the dories), which have a rotational palatine link that frees the maxilla to translate and rotate, and an ascending premaxillary process that enables the premaxilla to slide anteriorly and downward. This mechanism is present in most acanthopterygians and most major groups of percomorphs, and has been modified in many lineages to enhance upper jaw motion.

The biomechanics of jaw function have not been studied in many clades of ray-finned fishes, although behavioral observations and/or kinematic data have been published for representatives of many lineages. Below I briefly review our knowledge of feeding mechanisms and present some new data on lever and linkage mechanisms in some of the major taxa of interest to an exploration of functional evolution in fishes.

Basal actinopterygians

The basal ray-finned fish lineages represented by the living *Polypterus*, *Lepisosteus* and *Amia* (Fig. 4) provide estimates of ancestral states for the evolution of feeding systems in ray-finned fishes. Lauder (1980) investigated the feeding mechanisms of these three genera and showed that they feed primarily by rotating the skull dorsally, dropping the lower jaw, and employing hyoid depression to generate suction. Lower jaw rotation is generated in all three taxa by retracting the hyoid and exerting a posterior force on the opening inlever of the mandible via the mandibulohyoid ligament (Lauder, 1980). Recent work on feeding in sturgeon (Carroll and Wainwright, 2003) shows that these basal actinopterygians share hyoid-mediated jaw depression, but have a unique jaw protrusion mechanism, convergent with sharks, that employs jaws that are independent of the neurocranium.

The mechanical advantage of jaw opening ranges from 0.045 in *Lepisosteus osseus* and 0.06 in *Polypterus senegalus*, to 0.14 in *Amia calva* (Table 1). *Amia* possesses a double jaw opening mechanism, as it also has an interoperculo-mandibular ligament for transmission of jaw opening force via the opercular series (Lauder, 1980). This ligament inserts on the jaw slightly dorsal to the insertion of the mandibulohyoid ligament, so its mechanical advantage is slightly lower (about 0.13).

No anterior jaws linkage for maxillary or premaxillary motion is present in *Polypterus* or gars, because the maxilla and premaxilla are not independently mobile. However, *Amia calva* is the most basal living fish

that has maxillary rotation via a linkage system powered by lower jaw rotation. The maxilla has a dorsal rotational joint with the neurocranium, which allows it to swing anteriorly (Lauder, 1980). As the mandible rotates ventrally, the force and motion of this rotation is transmitted to the maxilla via the maxillomandibular ligament and the connective tissue fascia that joins the lower jaw and maxilla (Fig. 4C). This is a novel four-bar linkage mechanism in which the suspensorium and skull form the fixed link, the mandible is the input link, the maxillomandibular ligament is the coupler link, and the maxilla is the output link. The geometry and rotation of this linkage were calculated by Lauder (1979) and the linkage modeling of this system warrants further investigation in both *Amia* and in many teleosts.

The mechanics of jaw closing are highly variable in basal actinopterygians. The homologues of the adductor mandibulae complex are detailed in Lauder (1980), and their mechanical advantage for jaw closing force ranges across an order of magnitude from *Lepisosteus osseus* (0.05) to *Polypterus senegalus* (0.42). This means that *L. osseus* transmits only 5% of adductor muscle force at the jaw tip, whereas *P. senegalus* transmits up to 42% of muscle force to the jaw tip for biting. Conversely, *L. osseus* multiplies jaw muscle speed by a factor of 20, and *P. senegalus* by a factor of just 2.4, illustrating the trade-off between force and speed in jaw lever systems.

Osteoglossomorphs, elopomorphs, and clupeomorphs

The three basal teleost clades are extraordinarily diverse in jaw morphology, skull mechanics and feeding habits. Among these clades are such diverse forms as arawanas, knifefishes, mormyrids, eels, tarpon, and herring. Few studies have examined the functional morphology of feeding in these groups, with several notoptyerids (Sanford, 2001a; Wainwright *et al.*, 1989) of the osteoglossomorphs and *Megalops* (Grubich, 2001) of the elopomorphs the only subjects of detailed kinematics and EMG research. These basal teleost clades thus represent a critical region of the phylogeny (Fig. 3) for evolutionary study of feeding mechanisms.

The present survey includes six taxa in this region of the phylogeny, which show low and intermediate mechanical advantages of the jaw indicating feeding systems largely designed for speed. Among the osteoglossomorphs, *Osteoglossum*, *Arapaima* and *Hiodon* have relatively low (fast) opening and closing mechanical advantage, reflecting their strategy of rapid strikes on mostly evasive prey. *Osteoglossum* (Fig. 4D) has a particularly long jaw designed for rapid motion, and most notoptyerids (not described here) appear to have long, fast jaws as well. Elopomorphs are a large group with about 600 species, including tarpon, ladyfish, and a large number of eel families. *Elops* and *Gymnothorax* also have low or intermediate jaw mechanical advantages (Table 1; Fig. 3), and the role of a fast bite in the moray eel *Gymnothorax* is readily apparent from the toothy morphology (Fig. 4E). Eels

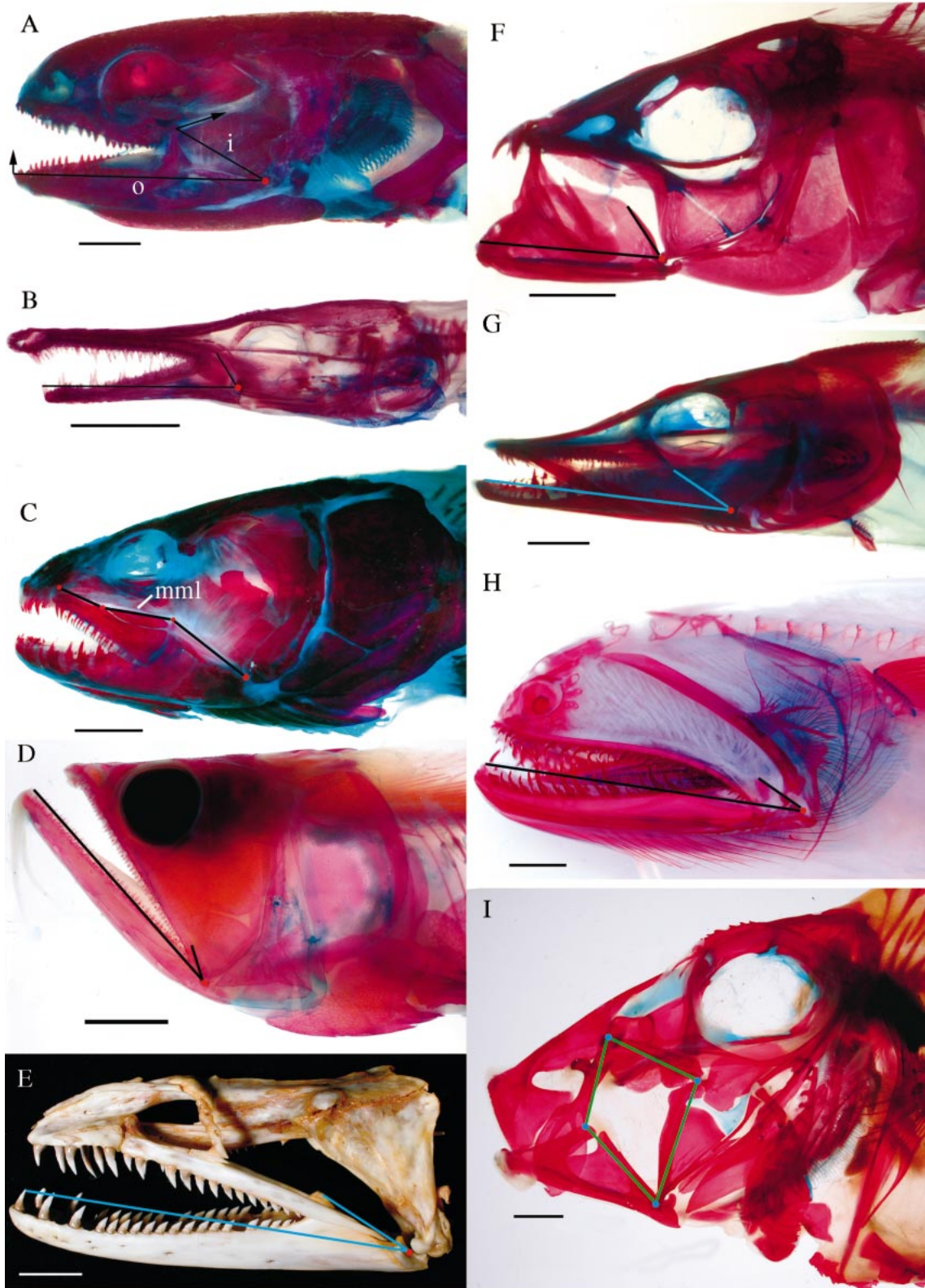


FIG. 4. Skull diversity, mandibular lever variation, and linkage structure in actinopterygian fishes. (A) The bichir, *Polypterus senegalus*, illustrating a simple mandibular lever with input (i) and output (o) lever arms. (B) Lever dimensions of the alligator gar *Atractosteus spatula*. (C) The bowfin, *Amia calva*, illustrating the 3 movable elements in the four-bar linkage for maxillary rotation; mml, maxillomandibular ligament. (D) Lever dimensions of the arawana, *Osteoglossum bicirrhosum*. (E) Lever dimensions of the moray eel, *Gymnothorax javanicus*. (F) Lever dimensions of the clupeid *Sardinella aurita*. (G) Lever dimensions of the northern pike, *Esox lucius*. (H) Lever dimensions of the bombay-duck, *Harpadon nehereus*. The earliest clade to show an anterior jaws four-bar linkage with a rotational palatine that powers protrusion is the dorids illustrated by (I) the rosy dory, *Cyttopsis rosea*. Scale bar = 5 mm.

show a large range of strategies however, including a number of marine eels with short crushing jaws that are likely more specialized for force production. Lastly, most clupeomorphs (herrings, sardines and relatives) are planktivores with relatively low mechanical advantages of the mandibular levers (Fig. 4F).

Significant premaxillary protrusion does not occur in any of these fishes. However, most of these fishes retain a rotational maxilla, powered by the linkage that transmits lower jaw rotation during jaw opening and retracted by adductor mandibulae muscle contraction during jaw closing. Maxillary rotation plays a key role in forming the mouth tube for suction feeding in many osteoglossomorphs, functions in transmitting actual bite force of predatory teeth in many eels, and forms the funnel for plankton capture in clupeomorphs. No detailed functional morphology of the ligamentous connection between the mandible and maxilla has been performed, although this study found a maxillomandibular ligament in all cleared and stained species examined. Thus it appears that the linkage for maxillary rotation that originated in *Amia* has been retained in many teleost lineages. Some of the most important areas of future research on fish feeding mechanics are the need for study of the evolution of feeding behavior in basal teleosts, analysis of linkage mechanisms in these diverse fishes, and study of maxillary linkage design.

Ostariophysans

An attempt to treat ostariophysan feeding diversity in a broad survey such as this is necessarily superficial, but illustrated representatives from each of the major lineages begin to depict the range of structure and function in this group that contains over 25% of living fishes. Previous work on feeding mechanisms in catfishes (Schaefer and Lauder, 1986, 1996; Herrel *et al.*, 2002), cyprinids (Alexander, 1966; Ballintijn *et al.*, 1972) and Characiformes (Lauder, 1981; Janovetz, 2002) show extensive intra-clade variability in feeding morphology and behavior. This diversity is reflected in the wide range of different skull morphologies in the group (Fig. 5). However, few of the 2,700 cypriniforms, 1,400 characiforms, or 2,500 catfishes and electricfishes have been examined from the perspective of feeding biomechanics.

The cypriniform fishes (minnows, carps, suckers) generally possess a protrusible premaxilla with a short ascending process that slides along the neurocranium, influenced by its attachments to the maxilla and to a single midlateral ossification called the kinethmoid (Alexander, 1966). The skull of the carp (Fig. 5A) shows the forceful lower jaw and protrusible premaxilla characteristic of the clade. The Characiformes includes a number of species well known for their feeding habits, including the piranhas and the vampire characin or “payarra” (Fig. 5B). Upper jaw protrusion is absent or rare in characins, but their lower jaw levers exploit a large range of force and velocity capabilities. This is illustrated by the comparison of the forceful

Serrasalmus jaw with the fast jaw of *Hydrolycus* (Table 1).

Catfishes have a wide feeding repertoire from predatory suction feeders and herbivores to parasites and wood-eating species. Schaefer and Lauder (1986, 1996) performed the most complete functional and evolutionary analysis of catfish feeding structures, identifying multiple increases in biomechanical complexity in loricarioids. A key trend among the loricarioids is increased premaxillary mobility that is controlled by maxillary motion and in some taxa by novel muscle subdivisions that insert on the premaxilla (Schaefer and Lauder, 1986). Many catfishes are accomplished suction feeders with high volume expansion of the buccal cavity and fast jaws, whereas other taxa maximize bite force (Herrel *et al.*, 2002). This is certain to be reflected in the lever and linkage mechanisms of the jaws, but this area of inquiry remains largely unexplored. The single catfish species (*Arius felis*) measured here (Fig. 5C) had an intermediate opening advantage and a forceful closing mechanism (Table 1).

Protacanthopterygii through Aulopiformes

Relationships between the protacanthopterygian orders Esociformes, Salmoniformes, and Osmeriformes and the next clades up the tree, Stomiiformes, Aulopiformes, and Myctophiformes remain the subject of debate (see Nelson, 1994). The feeding mechanics of pike (Fig. 4G) and salmon have been examined by functional morphologists (Lauder and Liem, 1980; Rand and Lauder, 1981; Sanford, 2001b), but no information is available on the other lineages in this central region of the actinopterygian tree. All of these taxa appear to have the typical mechanisms of lower jaw depression, cranial elevation, and maxillary rotation found in basal teleosts. These taxa all apparently lack premaxillary protrusion, although no detailed functional analyses have been performed to test for protrusion. Among these fishes a number of modifications in the length of the mandible occur that impact mechanical advantage. The jaw mechanisms of the pike and salmon measured here show a fast opening lever for the salmon and intermediate mechanical advantages for both opening and closing in the pike (Table 1; Fig. 3). Stomiiformes, an assemblage of interesting toothy deep water forms, often with long jaws, are not represented in the present data set. The aulopiform species in the data set, *Harpadon*, the bombay duck (Fig. 4H) has a long mandible with many teeth and mechanical advantage values that favor speed (Table 1).

Lampridiformes and Polymixia

The lampridiform fishes (opahs, tube-eyes, ribbon and oar-fishes) have extraordinarily protrusible jaws due to the loss of ligamentous connections of the maxillary head to the neurocranium, allowing both maxilla and premaxilla to be pulled forward and ventrally with the mandible (Pietsch, 1978). Their phylogenetic position is near the base of the acanthomorphs (Olney *et*

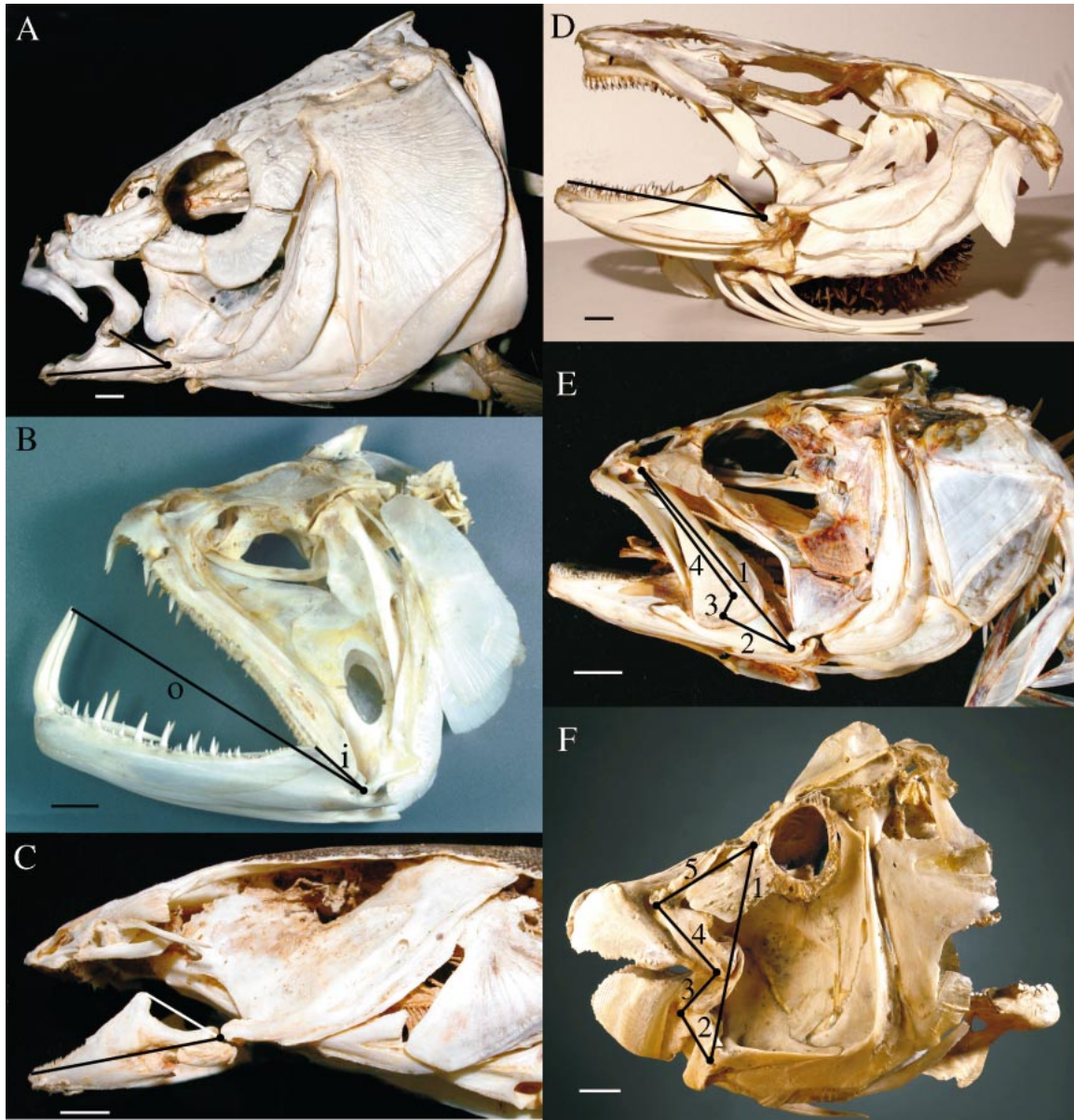


FIG. 5. Skull diversity, mandibular lever variation, and linkage structure in actinopterygian fishes. Skull and jaw lever dimensions of the ostariophysan fishes (A) carp, *Cyprinus carpio*, (B) vampire characin, *Hydrolycus scomberoides*, with inlever (i) and outlever (o) labeled, and (C) catfish *Arius felis*. (D) Lever dimensions of the cod *Gadus morhua*. (E) Skull of the large-mouth bass, *Micropterus salmoides*, with diagram of four-bar linkage for maxillary rotation; 1, fixed link; 2, articular input link; 3, maxillomandibular ligament coupler link; 4, maxillary output link. (F) The parrotfish *Scarus guacamaia*, with a novel five-bar linkage for control of upper and lower jaws; 1, fixed link; 2, articular input link; 3, dentary coupler link; 4, maxillary output link; 5, palatine and palatamaxillary ligament coupler link. Scale bar = 10 mm.

al., 1993). No data is available on their lever or linkage geometry at this time, but as one of five origins of protrusion in teleosts they warrant further analysis. *Polymixia*, the beardfish (Table 1), may belong in the Beryciformes but recent work suggests that it is the sister-group to the paracanthopterygian plus acanthopterygian clades (Johnson and Patterson, 1993). If this taxon provides the outgroup state for jaw mechanics in the huge radiations of fishes in the paracanthopterygian, acanthopterygian, and percomorph crown lineages, those states are intermediate mechanical advantage for both jaw opening and closing levers (Table 1;

Fig. 3). Also, in contrast to lampridiform fishes, *Polymixia* has little or no upper jaw protrusion, and instead has the typical basal teleost mechanisms of cranial elevation, jaw depression, and linkage for maxillary rotation.

Paracanthopterygii

Functional morphologists have not investigated feeding biomechanics in the large assemblage of taxa in the Paracanthopterygii (including percopsiforms, brotulas, cods, anglerfishes, etc.), with the exception of work on antennariids by Pietsch and Grobecker

(1987). None of these interesting forms have been examined for major feeding modifications with respect to mechanical design of levers and linkage systems of the jaws. However, some of these animals are spectacularly bizarre in their feeding systems, particularly the anglerfishes and deep-sea forms with lures and massive jaws filled with teeth that will provide some exciting functional morphology and mechanical analysis. The frogfishes have developed significant jaw protrusion (Pietsch and Grobecker, 1987), and some of the cods, including *Gadus* (Fig. 5D) show slight premaxillary protrusion. If this ability is confirmed in cods with functional analysis it would represent a 6th origin of upper jaw protrusion in teleosts. *Gadus morhua* shares an intermediate state for both jaw levers with *Polymixia* below it on the phylogeny of Figure 3. Exploration of jaw mechanics throughout the diverse paracanthopterygian clades will be necessary to properly polarize this node for comparison with acanthopterygians.

Acanthopterygii and percomorphs

The higher-level phylogeny of the Acanthopterygii, the teleost crown group of over 13,000 species, remains a subject of debate (Johnson and Patterson, 1993; Parenti, 1993; Stiassny, 1986), particularly in regard to the basal acanthopt clades and the positions of the mullets and silversides. In Johnson and Patterson's (1993) phylogeny, the first three clades off the backbone of the tree are Stephanoberyciformes, Zeiformes, and Beryciformes. *Stephanoberyx* has a forceful jaw opening lever and an intermediate closing advantage, while both *Cyttopsis* (a zeiform) and *Holocentrus* (a beryciform) have forceful jaws (Table 1; Fig. 3). *Stephanoberyx* has little or no upper jaw protrusion, but the condition of Zeiformes is striking. Zeids such as *Cyttopsis* (Fig. 4I) have a mechanism for extreme upper jaw protrusion with an extended ascending process of the premaxilla, a highly rotational maxilla, and a palatine element that rotates on its proximal articulation with the suspensorium to allow increased maxillary mobility. Zeiform fishes have previously been placed with the percomorphs and even as sister to the Tetraodontiformes (Rosen, 1984), but if the proposed relatively basal acanthomorph position of the Zeiformes is maintained, then the zeiform mechanism may be the origin of the highly protrusive four-bar linkage mechanism of the anterior jaws described for percomorphs (Westneat, 1990). This mechanism of jaw protrusion is retained in a similar or modified form in Beryciformes, most of the Smegmamorpha (silversides, mullets, etc.), Pleuronectiformes, and most Perciformes. Alternatively, if the atherinomorphs are at the base of the percomorphs (Parenti, 1993), then the jaw protrusion mechanism found in members of this group would represent the origin of the percomorph-type jaws linkage.

Percomorph fishes have modified the jaws and feeding mechanism in an astonishing number of ways for feeding on every prey type imaginable. The smeg-

mamorph clade of Johnson and Patterson (1993) forms a basal sister-group to the remaining percomorphs (Fig. 3). The atherinomorph and mugilimorph groups retain the mechanisms of maxillary rotation and jaw protrusion of basal acanthomorphs, modifying them in various ways among species for a benthic-feeding, surface-feeding, or planktivorous way of life. Silversides tend to have fast jaws for plankton capture (*Atherinomorus*; Fig. 3) and the needlefish *Strongylura* beats the long-nose gar by a nose for the fastest jaw lever in fishes (in the current data set), with an opening mechanical advantage of 0.03 and closing advantage of 0.04 (Table 1). Representing the Gasterosteiformes in the current data set, the trumpetfish *Aulostomus* has the unusual combination of a fast opening lever and forceful closing lever (Fig. 3).

Relationships among the Pleuronectiformes, Scorpaeniformes, Tetraodontiformes, and Perciformes are largely unresolved at higher levels, but the feeding mechanics of these groups have received extensive attention from functional morphologists. More is known about feeding biomechanics in perciform groups such as cichlids (Liem, 1978, 1980; De Visser and Barel, 1998), labrids (Westneat, 1995), and centrarchids (Wainwright and Lauder, 1992) than most other clades, although few of these studies used biomechanical modeling as a basis for comparing species. The taxa selected from these groups for analysis here (Fig. 3) show a range of mechanical designs for the jaw levers, including forceful levers in *Platichthys*, *Balistes*, and *Chlorurus*, fast opening or closing levers in *Cheilio*, *Scomber*, and *Sphyraena*, and intermediate or mixed jaw advantages in *Pterois*, *Epinephelus*, and *Micropterus*. Linkage designs are equally diverse, with groupers, bass, and wrasses sharing a highly protrusible anterior jaws linkage, the mackerel and barracuda having reduced or lost premaxillary protrusion, the triggerfish also losing premaxillary protrusion in favor of a powerful bite, and most flounders showing asymmetry in linkage design on the two sides of the head (Gibb, 1997). Linkage systems vary widely among these taxa, from the simple maxillary linkage of the large-mouth bass (Fig. 5E) to the five-bar linkage of some parrotfishes (Fig. 5F). Patterns of gain, loss, and functional modification of the key levers and linkages in these diverse fishes are almost entirely unexplored.

CONCLUSIONS

The evolution of fish feeding systems is a history of change in multiple mechanical systems that raise the head, drop the lower jaw, expand the hyoid, and protrude the upper jaw. Tracing the evolution of change in these functional units has long been the goal of functional morphologists (Lauder, 1982; Ferry-Graham and Lauder, 2001) and the analysis offered here adds the perspective of quantitative biomechanical modeling to this goal for just a few of these mechanical units. Using this approach, a survey of jaw lever function across a diversity of actinopterygian fishes

shows a clear pattern of convergence on similar mechanical design across disparate phylogenetic groups. For example, the long jaws of gar and needlefish arose independently and give these disparate taxa the most velocity specialized mandibles yet measured in fishes. Similarly, the three species in each column of Table 1 with the most forceful jaw levers all come from clades in different regions of the actinopterygian tree (Fig. 3). An important conclusion of this study is that jaw mechanics show patterns of diversification and convergence at these higher levels that are similar to patterns seen among diverse species groups within families (Westneat, 1995).

Complex connections between muscles, tendons, and bones can often be modeled using linkage theory from mechanical engineering. Several linkage models have been proposed in fishes (Anker, 1974; Muller, 1989; Westneat, 1990, 1991) but the potential for exploration of linkage design has barely begun. The present study concludes that the mechanism of maxillary rotation described by Schaeffer and Rosen (1961) and Lauder (1979) is a four-bar linkage system that warrants further modeling, as it is retained throughout most teleost fishes. This basic mechanism is modified in numerous clades for increased maxillary mobility by adding rotational palatine, nasal, or ligamentous connections dorsally. Combining phylogenetics with observation of upper jaw protrusion ability shows that premaxillary protrusion has evolved multiple times. Development of linkage models and testing model predictions with live animal behavior in multiple clades who have independently evolved premaxillary protrusion will add a new dimension to our understanding of the evolutionary history of fish feeding mechanisms.

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