Novelty Unlocks Morphological Diversity and Functional Opportunity for Fish Jaws

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Abstract

Morphological novelties that increase mechanical complexity create new axes for functional diversification and expand the evolutionary solutions to common problems. Intramandibular flexion is enabled by a novel joint between the two primary bones of the lower jaw and has spurred several specialized prey capture modes in fishes. We explore morphological, functional, and biomechanical implications of the intramandibular joint (IMJ) and its repeated independent origins across bony fishes. We offer a new scheme for classifying the incredible diversity of IMJ-associated lower jaw functional morphology based on commonly occurring postures. Additionally, we review documented functions permitted by intramandibular flexion and develop a simple biomechanical model to illustrate how changes in jaw morphology impact key functional traits and the capacity to modulate them. The unique attributes of IMJ-bearing fishes, we propose, have important consequences for how these feeding systems evolve. The replicated nature of the novelty further improves our ability to observe how various iterations on a similar adaptive theme may create divergent mechanical and evolutionary outcomes.

INTRODUCTION

Evolutionary novelties may facilitate access to new resources and can promote phenotypic and ecological diversification (Wainwright, 2007; Pigliucci, 2008). Intramandibular flexion, an additional source of mobility within the lower jaw system, has evolved various times in gnathostomes (Sampson and Witmer, 2007; Lee et al., 1999), including at least 10 (and likely many more) independent origins in fishes (Gibb et al., 2015). In these groups, lower jaw mobility is produced by (1) the ancestral quadratomandibular joint (QMJ) near the base of the angulo-articular bones (hereafter, the "articular") and (2) an intramandibular joint (IMJ) between the toothed dentary and the articular. The novelty is primarily characterized as an adaptation for bite-based feeding modes in species that feed on firmly attached benthic substrates (Konow et al., 2008; Gibb et al., 2015). Therefore, a key benefit of the IMJ is improved access to resources that are difficult for other species to secure. While the IMJ can be generally viewed as a convergent solution to a class of similar mechanical challenges, the reality is that fishes with this novelty boast a wide array of lower jaw mechanisms, differing in degree of flexion, directionality of movement, and sometimes even feeding mode.

The IMJ is present in various marine and freshwater fishes, with most documented origins in the diverse Percomorpha clade and at least one other in the distantly related characiform family, Distichodontidae (Vari, 1979; Konow et al., 2008; Gibb et al., 2015). The phylogenetic distribution of these lineages likely contributes to high diversity of IMJ-based feeding mechanisms. Consequently, the various manifestations of the novelty have led to a spectacularly diverse collection of lower jaw morphologies that vary with respect to relative length, shape, and associated dentition (Fig. 1). A particularly variable feature of IMJ systems is the articulation between the dentary and articular, which dictates the degree and nature of intramandibular flexion. The result is various augmented or altogether new functions not possible for other fishes (Gibb et al., 2015; Konow et al., 2008; Mihalitsis and Wainwright 2024; Martinez et al., 2024).

One outcome of the morphological and mechanical diversity of IMJ-bearing species is a broad range of diets across species (Fig. 1). The most common dietary strategy associated with the IMJ novelty is herbivory, but even this is partitioned among two main groups. First, there are consumers of turf algae covering hard benthic substrates (and sometimes the bacteria and detritus within it), including *Helostoma* (Ferry et al., 2012), *Girella* (Ferry-Graham and Konow, 2010), and *Ecsenius* (Ho et al., 2007). Some IMJ-bearing fishes brush particulate or epiphytic material from algae-covered surfaces, like *Ctenochaetus* (Purcell and Bellwood, 1993; Choat et al., 2002). Then, there are herbivores that feed on plants and macroalgae, like *Distichodus* (Martinez et al., 2022) and some species of *Centropyge* (Konow and Bellwood, 2011), *Siganus* (Zarco-Perello et al., 2024), and putatively IMJ-bearing *Naso* (Choat et al., 2002; Konow et al. 2008). Other biting specialists with IMJs feed on microphages on and within coral skeletons (many scarines; Bellwood and Choat 1990; Clements et al. 2017; Evans et al. 2023), on the corals themselves (select species from various IMJ-bearing reef lineages, like chaetodontids; Konow et al. 2017), and on sponges and tunicates (several pomacanthids; Konow and Bellwood 2005; Konow et al. 2008). Finally, while rare, there are also suction-feeders and planktivores, like *Nannocharax* (Martinez et al., 2024) and *Genicanthus* (Konow and Bellwood, 2011), which evolved from IMJ-bearing benthic biting ancestors. These highly varied diets challenge any notion that IMJs evolved within a limited ecological context.

The sheer diversity of IMJ-bearing fishes suggests that the novelty hardly limits phenotypic and trophic evolution, and could possibly promote it (e.g., Price et al. 2010). In this paper, we highlight some of the major axes along which these fishes have evolved. We first characterize common IMJ-themed morphotypes and summarize several of the novel functions previously described for these jaws. We then model two functional traits across different jaw shapes and explore the capacity of IMJ mechanisms to modulate those functions. Finally, we discuss some of the open questions regarding IMJ function and speculate on the evolutionary implications of the novelty.

MAJOR IMJ JAW TYPES

The highly varied morphologies of IMJ-bearing fishes reflect a collection of biomechanical systems that have evolved to acquire prey in surprisingly different ways. Two features immediately stand out as mechanically relevant modes of variation. First, the relative lengths of the rotating lever arms of the dentary and articular differ markedly across species (Table S1). Among those shown in figure 1, the dentary ranges from only 0.56 times the length of the articular (*Girella punctata*, Fig. 1I), to 1.79 times its length (*Ctenochaetus strigosus*, Fig. 1F). A second conspicuous pattern, one unique to IMJ-bearing fishes, is variation in the relative orientations of the dentary and articular. In Figure 1, the resting angle formed between the two lower jaw bones, measured ventrally, ranges from 72 degrees (*Helostoma temminckii*, Fig. 1E) to 204 degrees (*Chaetodon trifasciatus*, Fig. 1K). Importantly, differences in size and orientation create distinct starting postures for jaw movements, thereby influencing the outcome of mandibular kinesis (e.g., Martinez et al. 2024). Below, we introduce and define three commonly encountered postures in IMJ-bearing fishes.

Type 1, "Process in a pocket"

A common form of IMJ is characterized by an anteriorly projecting articular process (often triangular in shape) inserting into a concavity at the posterior of the dentary (Fig. 1, top row). The Type 1 posture is superficially similar to the ancestral lower jaw morphology present in non-IMJ-bearing fishes, though morphologically extreme versions exist (e.g., Fig. 1A). In these fishes, mobility at the IMJ is limited by a well-defined pocket on the dentary. Measurements of total potential flexion from fish shown in figure 1 (Fig. S1; Table S1), suggest that Type 1 fishes have the low intramandibular mobility (mean = 18 degrees ± 0.99 S.E.M.) compared to all other species (mean = 59 degrees ± 10.5 S.E.M.). Though, we caution that these estimates of flexion are based on skeletal anatomy (see Fig. S1) and do not account for soft tissues, which are likely to further constrain IMJ mobility. Species with a Type 1 posture have been shown to be force-modified coral excavators (Fig. 1A), substrate scrapers (Fig. 1 B&C), and biters of tough macroalgae (Fig. 1D) (Bellwood and

Choat, 1990; Choat et al., 2002; Ho et al., 2007; Clements et al., 2017).

Type 2, "Folded and free"

A subset of IMJ-bearing fishes displays a resting posture in which the dentary and articular form a loosely orthogonal angle with each other (~70-110 degrees; Table S1). This includes some of the most strongly modified lower jaw shapes in fishes (Fig. 1, middle row), with adaptations limiting impingement of bones and enabling greater freedom of motion about the IMJ. Anatomically, this is achieved by the expansion (Fig. 1E&F) or near loss (Fig. 1 G&H) of the pocket at the posterior margin of the dentary, contrasting the well-defined pocket that the articular firmly inserts into in non-IMJ bearing fishes. The soft tissues connecting and actuating jaw movements of Type 2 species are complex, though their function is highly understudied. In the family Distichodontidae, oral jaw movements are powered via several distinct subdivisions of the *adductor mandibulae* complex that enable independent control of the articular and dentary (e.g., Vari 1979; Martinez et al, 2024). A key consequence of the Type 2 posture is that jaw opening results in an unfolding of the mandibular bones, creating a novel form of lower jaw protrusion (Martinez et al., 2024), and in some cases facilitates extreme gape expansion (e.g., Ferry et al., 2012). While many species with this form of IMJ are highly skilled biters and scrapers, able to modulate their lower jaw angles to maintain contact with substrates (Ferry et al., 2012; Martinez et al., 2022), there are also speed-modified, suction-feeding invertivores (Martinez et al., 2024).

Type 3, "Aligned but adjustable"

A third common lower jaw configuration consists of species where the major axis of the articular and dentary are aligned (or nearly so), often elongate in shape (Fig. 1, bottom row). While some Type 1 species also display near alignment of mandibular bones (e.g., Fig 1

C&D), Type 3 is further distinguished by an enlarged dentary pocket allowing moderate to high levels of flexion at the IMJ (Table S1). Feeding kinematics are often such that both lower jaw bones rotate together during initial mouth opening, followed by isolated rotation of the dentary to either further expand the gape (e.g., some poeciliids; Gibb et al. 2008) or restrict it (e.g., pomacanthids; Konow and Bellwood 2005, 2011).

DIVERSE FUNCTIONAL OUTCOMES

Increased gape expansion

An increase in the maximum gape of the jaws is the most well-documented and likely the broadest use of intramandibular flexion among fishes. The function has been observed in fishes as phylogenetically, morphologically, ecologically disparate as kissing gourami and surgeonfishes (Ferry et al., 2012; Porter et al., 2015; Mackey et al., 2014; Purcell and Bellwood, 1993), where ventral rotation of the dentary about the intramandibular joint can dramatically increase gape size. These increased gapes permit a larger area across which the teeth can contact a food covered surface. For example, some poeciliids can rotate their dentary 90 degrees relative to the articular while substrate feeding (Gibb et al., 2008).

Improved force transmission during biting

An intuitive benefit of the intramandibular joint is modulation of the effective jaw length (i.e., the distance from the QMJ to a tooth biting an object) to improve force transmission. All else being equal, rotation at the IMJ can reduce the length of the lower jaw out-lever and elevate force transmission (Martinez et al., 2022; Westneat, 1994). Some of the clearest examples of augmented force transmission are the so-called nibblers in the genus *Girella*, which have a comparably short dentary (relative to the articular) but modest intramandibular flexion results in an increase in mechanical advantage (Fig. 1; Vial and

Ojeda 1990; Konow et al. 2008; Ferry-Graham and Konow 2010; Moran and Ferry 2014). The IMJ among *Girella* permits it to have nearly twice the jaw closing lever ratio as its close relative *Graus*, which bears comparable jaw adductors (Ferry-Graham and Konow, 2010).

Dynamic suspension - initial contact

In many IMJ-bearing species, the commencement of a biting strike requires direct contact between the oral jaws and a benthic substrate. Depending on the geometry of the surface or the angle at which the fish approaches it, intramandibular flexion can produce dynamic change in lower jaw length over small distances to ensure sufficient engagement of both jaws with the substrate (Gibb et al., 2015). In *Distichodus sexfasciatus*, when the upper jaw gains purchase on the substrate first, flexion at the IMJ will extend the dentary until the lower jaw tooth also meets the substrate (Martinez et al. 2022). In contrast, when the lower jaw engages first, it absorbs the contact and flexion shortens the jaw length until the upper jaw also engages (Supplemental video 1). A similar “shock absorption” function has been observed in acanthurid fishes (Mihalitsis et al., 2025*b*). It is also likely that these behaviors are mediated by fin braking (Higham, 2007; Perevolotsky et al., 2020). The net effect is improved mechanical compliance of the jaws as they contact the substrate.

Dynamic suspension - maintaining contact

A central challenge of consuming prey that is attached to the substrate is the ability to remove a large swath of food using a simple lever that only rotates along a fixed, curved path. The pincer-like nature of the simple lever system of most fish jaws transmits force effectively (Westneat, 1994) but is only able to directly contact the surface at a single distance from the substrate during jaw closing without supplemental motion of the fish’s body. Intramandibular flexion permits constant contact between the substrate and the jaws while allowing the body to remain stable in the water column (Gibb et al., 2008; Martinez et al., 2022). Documented most clearly in *Distichodus* and *Poecilia*, the active rotation of the dentary about the IMJ through the biting phase drags the jaws along the surface without requiring motion of the body. Increased duration of contact with the surface improves the quantity of prey accessible by a single biting strike, and the stability of the body may assist in predator vigilance during feeding bouts (Gibb et al., 2008; Konow et al., 2008). Furthermore, intramandibular flexion is predicted to improve the capacity of the jaw apparatus to accommodate the irregular structures that are ubiquitous in benthic habitats (Martinez et al., 2022).

Closing the jaws while protruded

Quantified only among marine angelfishes (family Pomacanthidae), the intramandibular joint permits gape closure while the upper jaws are fully protruded (Konow and Bellwood, 2005). This mechanism differs substantially from most other substrate-feeding modifications of the intramandibular joint. Here, the dentary and articular rotate together during mouth opening, in a manner similar to non-IMJ bearing fishes, but gape closure is achieved from isolated dorsal rotation of the dentary to bite the prey. The expression of this novel function in pomacanthids is highly conserved, yet it still gave rise to a high level of dietary diversity across the group (Konow and Bellwood, 2011). Though this function has only been described in pomacanthids, a variant may occur in some picking poeciliids that also have upper jaw protrusion (Hernandez et al., 2008; Gibb et al., 2008).

Enhanced lower jaw protrusion

Upper jaw protrusion is present in a majority of living fishes, driven by rotation of the lower jaw, to which upper jaw bones are ligamentously connected (Bellwood et al., 2015). Within this general scheme, various combinations of cranial morphologies and kinematic mechanisms produce anteriorly directed movements of upper jaws (Motta, 1984). While given less emphasis in the literature, mandibular depression during gape expansion also generates a form of protrusion (see Waltzek and Wainwright, 2003), resulting in the displacement of the distal end of the lower jaw away from the head. Depending on the resting orientation of the jaw, this protrusion can be anteriorly or ventrally directed. In IMJ-bearing fishes with the Type 2 lower jaw (Fig. 1, middle row), additional extension of the dentary can be generated by rotation around the IMJ, supplementing movement of the entire mandible rotating at the QMJ. In *Nannocharax* (Fig. 1F), IMJ flexion increases protrusion of the lower jaws away from the head by 25% (Martinez et al., 2024). This novel function of the lower jaws is particularly important in IMJ-bearing species with limited or no ability to protrude their upper jaws (such as distichodontids and some biting acanthurids).

FUNCTIONAL AUGMENTATION AND MODULATION

Model setup and simulated jaw movements

Changes in the geometry of biological linkage systems have important implications for mechanical function and evolutionary diversification (Westneat, 1994; Alfaro et al., 2004; Martinez and Sparks, 2017; Muñoz et al., 2018). In both non-IMJ and IMJ-bearing fishes, morphological diversity of jaw linkages has been attributed to differences in force transmission, displacement, speed, and overall kinesis (Westneat, 1994; Wainwright et al., 2004; Ferry-Graham and Konow, 2010; Martinez and Wainwright, 2019). As discussed above, various augmented (or altogether novel) capabilities have been described in fishes with IMJs. Though, less attention has been given to the direct functional consequences of different linkage geometries in IMJ-bearing jaws, or the capacity within a single jaw configuration to modulate those functions (Ferry et al., 2012; Porter et al., 2015; Martinez et al., 2022). Here, we devise a simple modeling framework to explore the effects of mandibular linkage geometry on two key functions of feeding systems, jaw protrusion and closing mechanical advantage.

Inspired by the functional abilities of fishes with a folded or Type 2 jaw posture, we created five models differing only in the relative lengths of their mandibular links (Fig. 2A). Type 2 fishes were used due to overall similarities in the nature and directionality of their jaw movements and for the ability of some species to perform a novel form of lower jaw protrusion (Martinez et al., 2024). The observed range of Type 2 dentary lengths from figure 1, expressed as a proportion of articular length, vary from approximately 0.8-1.8 (see Table S1). These values represented the extreme morphologies of our models, with three evenly sampled values in between. With this setup, all articular links were equal to 1, and all included angles at the IMJ set to 50 degrees. We opted to keep the IMJ angle constant to isolate the effect of relative lengths of jaw links on function.

Using the starting configurations above, we applied rotational movements to the jaw links across two simulated phases of movement, mouth opening and closure (i.e., biting). We followed observations on the directions and extent of jaw rotation in Type 2 species (Martinez et al., 2022, 2024). For mouth opening, we applied a total of 30 degrees of clockwise rotation to the articular link and 20 degrees of counterclockwise rotation to the dentary link, each distributed across 10 stages. Lower jaw protrusion was measured from the opening phase as the distance of the distal end of the dentary (the anteriormost lower jaw tooth) to the proximal end of the articular (the QMJ) between final and starting linkage configurations. We note that this differs from lower jaw protrusion measured in Martinez et al. (2024), which was determined relative to stable reference points on the skull (not available in our linkage models). For jaw closing, we started with the final configuration from jaw opening, applying 10 degrees of counterclockwise rotation to the articular and 20 degrees of counterclockwise rotation to the dentary. We measured jaw closing mechanical advantage (MA) at each stage of the simulated model movements, as the ratio of in-lever to out-lever lengths. Based on adductor muscle insertions in a pair of Type 2 species (Martinez et al., 2022, 2024), we set the in-lever in all models at 0.75 (three quarters of the way along the articular). We note that although we kept the in-lever at a constant proportion of articular length for simplicity and ease of model comparisons, actual species are expected to display diversity in muscle insertion locations, which will impact in-lever lengths. The out-lever was the distance from the origin of the articular link (QMJ) to the distal end of the dentary (anterior tooth). Finally, we calculated mean MA across motion stages and the degree of MA modulation as the range of values experienced by a linkage across closing movements. MA modulation is a consequence of intramandibular flexion; independent rotation of the dentary from the articular results in dynamic change in lower jaw out-lever length during feeding movements. We predicted that different starting linkage shapes would produce different levels of MA modulation despite applying identical rotation to the links.

Biomechanical outcomes of IMJ configurations

The results from our models show that different jaw geometries, paired with IMJ flexion, will produce varying levels of lower jaw protrusion during gape opening (Fig. 2B). There was a positive, but saturating, increase in lower jaw protrusion in mandibles with increasing relative dentary size. Across all five models, lower jaw protrusion showed a 36.6% increase from lowest to highest. Research has shown that the ability to protrude the lower jaw can aid in both substrate feeding and open water suction (Martinez et al., 2022; 2024).

A commonly noted functional attribute of IMJs is their role in tuning or modulating mechanical advantage (MA) of the lower jaw system for increased force production during substrate biting (Hernandez et al., 2008; Konow et al., 2008; Ferry-Graham and Konow, 2010; Gibb et al., 2015). Simulated biting movements revealed that mean jaw closing MA increased at smaller relative dentary lengths, representing a 58.6% increase across the five linkages considered here (Fig. 2C, gray points). This is opposite from the trend observed for jaw protrusion, possibly reflecting the trade-off between displacement and force production (Westneat, 1994). Differences in linkage geometry also had implications for the capacity of jaw systems to modulate MA (Fig. 2C, vertical bars). Jaw systems with greater mean MA values also exhibited greater modulation in MA values within a given biting movement, showing a 77.5% increase in modulation across models.

These results highlight the role of morphological variation of IMJ jaw systems in producing disparate functional outcomes. Still, we emphasize that this exercise represents only a single set of jaw rotations and other inputs will produce different functional results. Thus, both morphological differences across species and behavioral modulation within species could be important sources of functional variation.

A MECHANISM FOR PROMOTING FUNCTIONAL OPPORTUNITY

Past research has raised questions about whether the IMJ reduces the capacity of fishes to consume prey from the water column (Gibb et al., 2015). Indeed, a majority of the novel functions enabled by the IMJ convey advantages well suited to remove prey from the benthos. A key feature of this argument is the trade-off between motion and force (Westneat, 1994), such that traits of force-modified jaws used for grazing, scraping, or picking prey from the substrate are antagonistic to successful suction feeding (Westneat, 1994; Hernandez et al., 2008; Ferry-Graham and Konow, 2010; Konow et al., 2008). However, the potential of the IMJ to enhance jaw protrusion (Fig. 2A) and increase gape size suggests that some functions may be conducive to suction feeding, which relies on rapid expansion of the head and jaws (Lauder, 1980). Our linkage simulations and recent work documenting the IMJ in a suction feeder (Martinez et al., 2024) demonstrate that IMJ-enabled functions may be more transferable than previously thought. On the other hand, some planktivores that evolved from IMJ-bearing, biting ancestors (e.g., *Genicanthus* and some *Naso* species) display suppressed mobility at the IMJ (Konow et al., 2008). Thus, the utility of the IMJ for suction feeding is likely context-specific or contingent on the ancestral jaw system.

Most of the functions described for IMJ-bearing fishes represent planar rotations in the dorsoventral direction. A major axis of motion not well understood is an IMJ's capacity for mediolateral flexion. Such movements could facilitate increased buccal expansion or enhance lateral jaw bending, used by some fishes to extract substrate-attached prey from complex structures (Mihalitsis et al., 2025*a*,*b*). In the Moorish idol (*Zanclus cornutus*) and its surgeonfish (acanthurid) relatives, lateral rotation between the dentary and articular permit the left and right dentaries to slide relative to each other at their medial symphysis (Mihalitsis et al., 2025*a*). Lateral bending of the oral jaws has also been observed in *Distichodus* while removing vegetation from the substrate, and was coincident with intramandibular flexion (Martinez et al., 2022). Moreover, IMJ-bearing species differ in intermandibular mobility (i.e., between left and right sides of the jaw), with some containing a flexible jaw symphysis joined by soft tissues, and others possessing a completely fused symphysis. These variants are expected to impact the extent and nature of jaw modulation when interacting with substrates and prey, but further work is needed on this topic.

The overall outcome of IMJ diversity is an expansion of the functional potential of the jaw apparatus. There is not simply one convergent mechanism associated with the various iterations of the IMJ, but a collection of jaw systems that perform a range of functions. Within individual IMJ-bearing lineages, there is no definitive signal as to whether the novelty facilitates (Price et al., 2010) or constrains (Konow and Bellwood, 2011; Konow et al., 2017) subsequent diversification, but a common trend is the ability of these fishes to interact with their prey in new ways. Our understanding of the consequences of the IMJ is clearly incomplete. Additional research on this rare but consequential novelty will undoubtedly lead to the discovery of additional lineages possessing it and to new functions yet to be described.

Data availability

Code used for this paper will be made available on Dryad upon acceptance.

Figure Captions

Figure 1. A sample of the morphological diversity of fishes with documented or putative intramandibular joints. Images show the lower jaws of fishes from micro-CT scans, each with a segmented articular (blue) and dentary (yellow). Biomechanical linkages are superimposed on each image (purple lines), with flexion points (circles) shown at the quadratomandibular joint (QMJ) and intramandibular joint (IMJ). Jaws are organized by proposed postural morphotypes, including Type 1 ("process in a pocket"), Type 2 ("folded

and free"), and Type 3 ("aligned but adjustable"). The primary diet item of each species is provided, based on published sources listed in Table S1.

Figure 2. Simulated movements of hypothetical IMJ-based jaw linkages. (A) Five linkage configurations were constructed to represent the range of relative articular ("a") and dentary ("d") lengths in Type 2 species shown in figure 1. Linkage joints (IMJ and QMJ) are shown as dots, and each model was scaled to have an articular length of 1 and an included angle of 50 degrees. (B) Peak protrusion of models increased nonlinearly with longer dentaries during simulated jaw opening movements. (C) In contrast, mean jaw closing mechanical advantage (MA) decreased in longer dentaries, as did the range of values expressed during closing movements (i.e., MA modulation).

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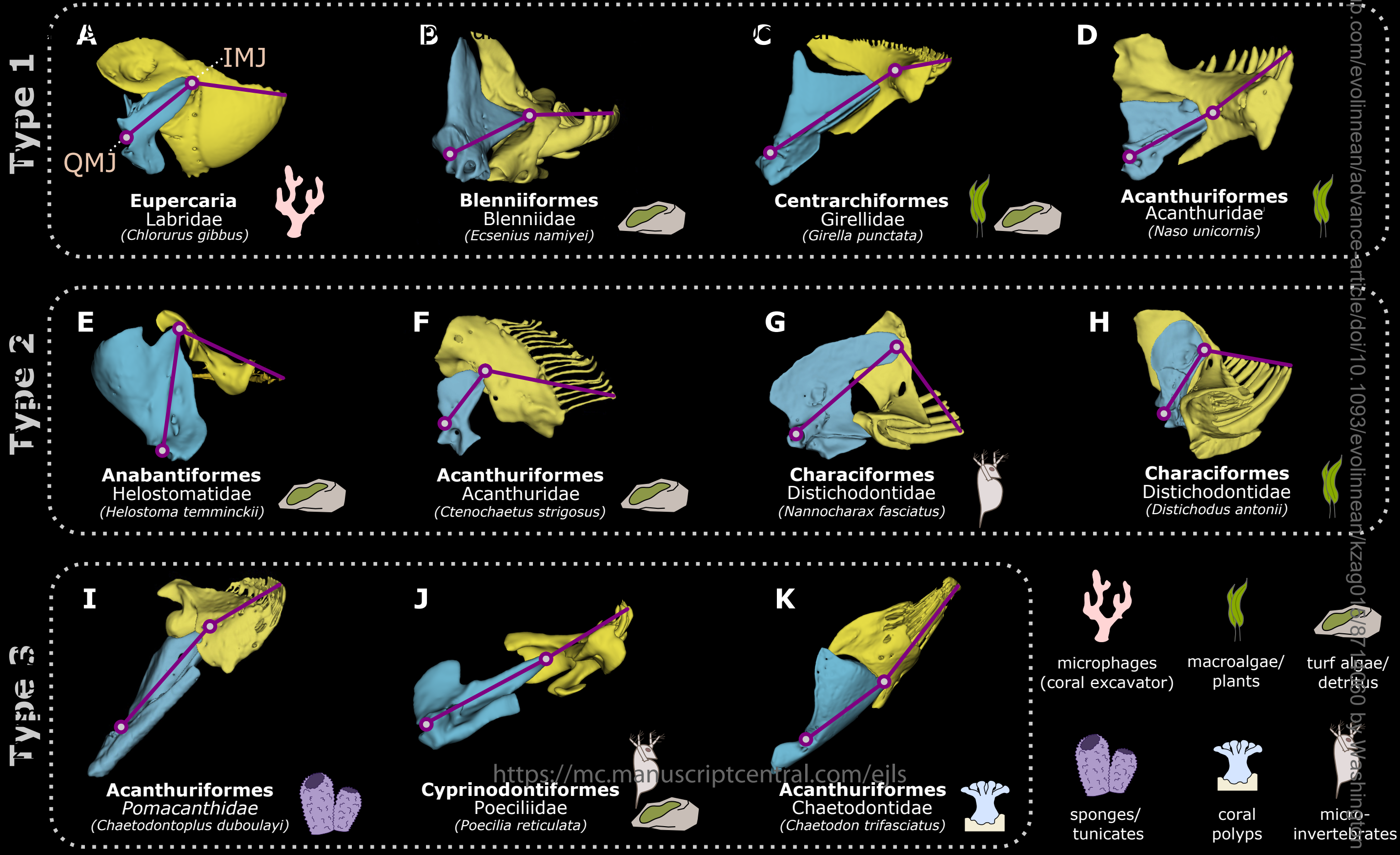
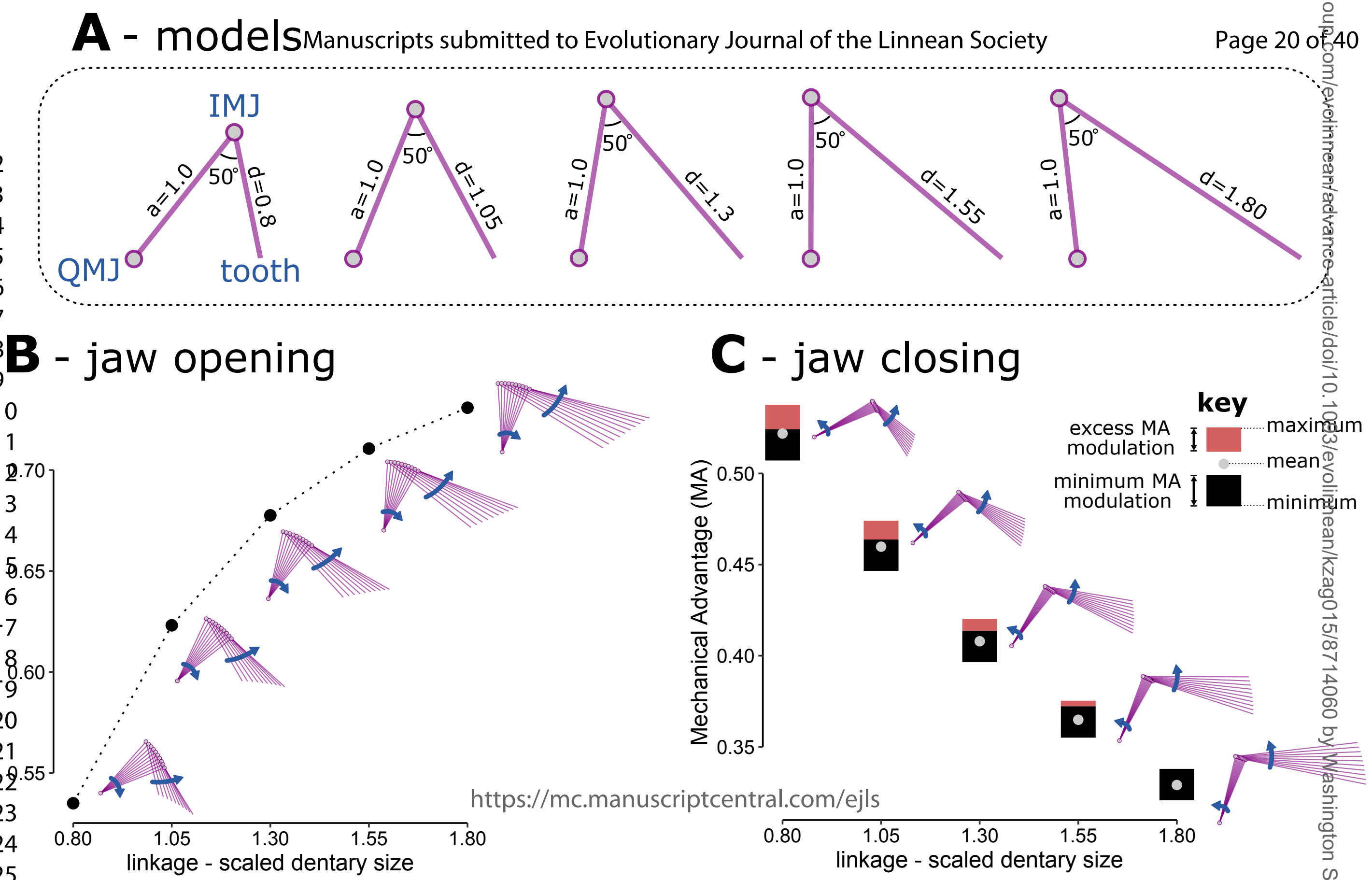

Type 1
A
IMJ
QMJ
Eupercaria
Labridae
(Chlorurus gibbus)
B
Blenniiformes
Blenniidae
(Ecsenius namiyei)
C
Centrarchiformes
Girellidae
(Girella punctata)
D
Acanthuriformes
Acanthuridae
(Naso unicornis)
Type 2
E
Anabantiformes
Helostomatidae
(Helostoma temminckii)
F
Acanthuriformes
Acanthuridae
(Ctenochaetus strigosus)
G
Characiformes
Distichodontidae
(Nannocharax fasciatus)
H
Characiformes
Distichodontidae
(Distichodus antonii)
Type 3
I
Acanthuriformes
Pomacanthidae
(Chaetodontoplus duboulayi)
J
Cyprinodontiformes
Poeciliidae
(Poecilia reticulata)
K
Acanthuriformes
Chaetodontidae
(Chaetodon trifasciatus)
microphages
(coral excavator)
macroalgae/
plants
turf algae/
detritus
sponges/
tunicates
coral
polyps
micro-
invertebrates


A - models
IMJ
a=1.0
50°
d=0.8
QMJ
tooth
a=1.0
50°
d=1.05
a=1.0
50°
d=1.3
a=1.0
50°
d=1.55
a=1.0
50°
d=1.80
B - jaw opening
peak protrusion
0.70
0.65
0.60
0.55
0.80
1.05
1.30
1.55
1.80
linkage - scaled dentary size
C - jaw closing
key
excess MA modulation
minimum MA modulation
maximum
mean
minimum
Mechanical Advantage (MA)
0.50
0.45
0.40
0.35
0.80
1.05
1.30
1.55
1.80
linkage - scaled dentary size