SYMPOSIUM

Muscle Articulations: Flexible Jaw Joints Made of Soft Tissues

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Synopsis This study surveys animals that use soft tissues rather than rigid links to build jaw joints. Hard biting elements are useful; they are used in piercing or shearing during feeding and interactive behaviors and can directly impact survival and reproduction. The best understood biting systems include biting elements that are mounted on rigid jaw links that form a joint capable of transmitting the bite reaction forces. As such, jaws must incorporate joints that resist compression. Many jaw joints are "sliding joints", in which jaw links come into direct contact and the shape of the sliding contact surfaces dictates possible motions. There are, however, organisms that have biting elements on jaws that are made of flexible muscle and connective tissues. If arranged as a muscular hydrostat, in which multiple orientations of the muscle fibers may co-contract to provide turgid skeletal support, the multifunctional joint not only (a) provides the force to move the biting elements, but also (b) creates repositionable pivots and (c) transmits bite reaction forces. Such flexible joints, termed "muscle articulations", may be important to a number of soft-bodied animals. In this survey, we review the function of previously described muscle articulations: the joints found between inarticulate brachiopods' valves, cephalopods' beaks, the hooks of kalyptorhynch flatworms, and errant polychaetes' jaws. We also review the morphology, physiology, and feeding behaviors of the hagfish as a putative muscle articulation in an effort to understand how this jawless craniate is capable of biting with surprising force, seemingly without the benefit of any obvious method of opposing the force of the dental plate that is used to remove portions of food. Initial analysis suggests that a muscle articulation may be a key feature in coordinating head and body movements to provide the leverage needed for strong "bites".

Introduction

The ability to bite with hard teeth is a feature that has evolved independently in, and on several different occasions within, the Lophotrochozoa and the Ecdysozoa, the two main invertebrate lineages (Hochberg et al. 2015, this volume). This is not surprising considering the importance of biting to critical feeding and defensive behaviors in many of these animals. Indeed, the link between the morphology of the components of the biting system and the organism's ecology and evolution allows the features to be used as phylogenetic characteristics on which depend many important relationships of invertebrates (e.g., the importance of the jaw-like trophi in understanding the Gnathostomulida/rotifera–Acanthocephala relationship [Rieger and Tyler 1995], or the role of

the morphology of dental elements in the phylogenetic structure of the extinct conodonts [Lindström 1970]).

From a biomechanical point of view, biting or pinching is typically envisioned as the forceful occlusion of opposing tooth-elements in a way that allows suitably shaped teeth to effectively concentrate muscular contractile force in an appropriate manner: the use of grinding hypsodont teeth in grazing animals (Damuth and Janis 2011); the piercing of tough hides by saber teeth (Brown 2014); the shearing action that allows the blade-like teeth of barracudas to scissor through flesh (Grubich et al. 2008); or generating peak crushing strength by rock-crabs' claws (Palmer et al. 1999). Studies of the biting systems of vertebrates greatly outnumber those of

invertebrates. This may, in part, be due to a vertebrate-centric analysis of the function of jaw joints, but may also, in part, be due to the lack of a classification system that includes the soft-tissue joints of many soft-bodied invertebrates.

In this study, we first attempt to identify general features of biting systems. Second, we survey examples of invertebrates' joints with soft-tissue constructions in order to understand their position within an expanded classification. Third, we summarize the characteristics of muscular soft-tissue joints known as "muscle articulations". Fourth, we consider the craniate, yet invertebrate, hagfish's biting mechanism as a putative muscle articulation.

Features of the biting system

Vertebrates' biting systems are relatively well-described because (1) rigid jaws represent a simpler analysis than do deformable tissues, (2) analyses of vertebrates' biting systems are crucial in understanding the ecology and evolution of charismatic macrofauna, and (3) there are valuable medical benefits from understanding the biomechanics of our own jaws. The well-studied mammalian jaw is often simplistically modeled (e.g., Weijs 1980; Greaves 2012) as a two-dimensional, third-order lever (Fig. 1) that resembles a pair of forceps or pincers in which the jaw-closing force generated by the biting muscles (effort) is applied between the site where the teeth contact the food and the fulcrum (the mandibular joint). The result is that the mechanical advantage (the distance from the fulcrum to the muscle, divided by the distance from the fulcrum to the teeth) is less than one. This mechanical advantage indicates that the system is optimized for speed rather than optimized for force, or that the placement of the lever-effort, load, and fulcrum may be constrained by the skull's geometry. This simplistic view provides a scheme for defining a biting system. In surveying a variety of vertebrates' biting systems, including animals as varied as alligators (Erickson et al. 2003), mole-rats (Van Daele et al. 2009), horn sharks (Huber et al. 2005), cows (Radinsky 1985), and a variety of carnivores (Christiansen and Wroe 2007), we can identify four generally common features: teeth, rigid jaws, joints, and biting muscles. As we will see, these basic structural elements are also present in soft-tissue biting-systems and are defined as follows:

Teeth—Teeth are rigid elements that transmit bite force to the item being bitten. As such, the geometry of teeth closely match their function: grinding teeth often have broad surfaces that slide over one another and are formed of layers that wear differently, thereby maintaining optimal grinding characteristics (e.g., the grinding teeth of the extinct hadrosaur, Erickson et al. 2012); piercing teeth have reduced tip radii that more effectively concentrate force over a smaller surface area (e.g., the pointy occlusive "teeth" of some crustacean chelipeds, Brown et al. 1979). Generally, teeth tend to be stiff (high E or Young's modulus of elasticity) and therefore can be relatively brittle (low work to fracture) (Vogel 2013). Countering this, teeth are often made of composite materials (Waters 1980) that improve their durability (harder materials layered with flexible layers that reduce fracturing) and wear (roughness is maintained by layering heterogeneous materials). Teeth (or pincers, hooks, points, stylets, or jaws) in soft-bodied invertebrates are often the only rigid elements. They may be hardened and stiffened to a high degree by various means that include chemical crosslinking (e.g., the beaks of cephalopods, Miserez et al. 2008) and metal biomineralization (e.g., the copper jaws of bloodworms, Lichtenegger et al. 2003).

Jaws—Jaws are structural supports that bear teeth. In the two-dimensional model (Fig. 1), the jaws represent the rigid forceps-like links or beams that are connected by a fulcrum or pivot to form the third-order lever. The jaws must bend as little as possible to maximize efficiency in transmitting the force generated by contraction of masticatory muscles to the teeth via the pivot. In humans, the mandible represents an extremely strong bone that is made rigid by its high percentage of compact bone (relative to the maxilla, Fanghänel et al. 2006) and has a high flexural stiffness, due to its large second moment of area (van Eijden 2000).

Rigid support of invertebrates' teeth is best described for arthropods (Manton [1964] provided a classic review of arthropods' mandibles). In exoskeleton mandibles, chelae, and other pincer-like structures, the teeth elements and the support-element of the rigid jaw are portions of a continuous hollow structure that is formed of a fibrous and globular protein-composite material (Vincent [2002] reviewed details of the material properties of arthropod cuticle).

In many soft-bodied invertebrates, the rigid tooth-support elements (jaws as defined here) are seemingly paradoxically made of soft contractile (muscle) tissue and materials that are strong in tension (e.g., connective tissues, basement membrane). For example, the radular teeth and odontophore of cephalopods are anchored to a pair of skeletal support elements known as bolsters (Messenger and
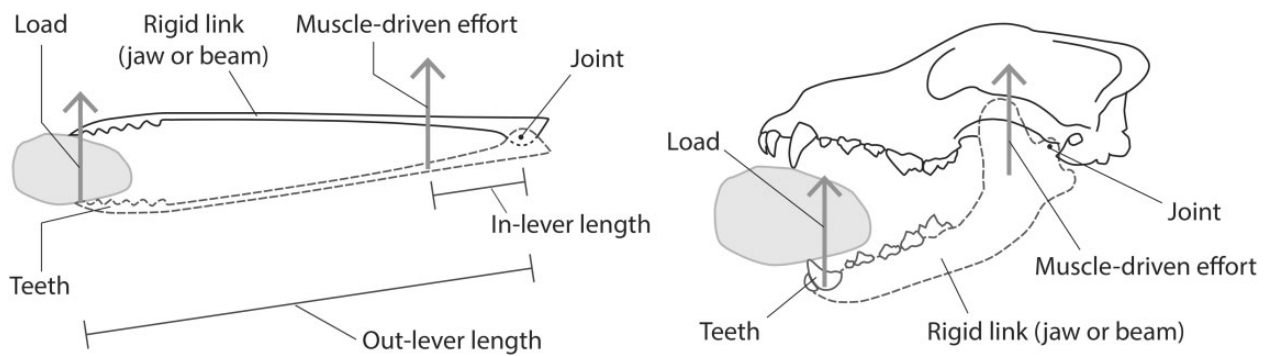
Fig. 1 Two biting systems modeled as two-dimensional, third order levers. On the left is a pair of pincer-like barbecue tongs being used to grasp a food item. The effort, in this case delivered by the grip of a hand, is located between the joint and the load where the teeth contact the food item. The arms of the tongs represent beams that must be rigid to efficiently transfer the force of the grip to the teeth. The joint must also be strong as it bears the compression resulting from the bite reaction forces. The mechanical advantage, calculated as the relatively short input lever length divided by a larger output lever length, is always less than one. On the right is a wolf skull, an analogous third order lever in which the force of contraction generated by the masticatory muscles represent the effort, the temporomandibular joint represents the pivot and the teeth that are driven into the food item are set into a rigid link represented by the mandible.

Young 1999). The bolsters are made of flexible muscle and connective tissues and yet can become stiff enough to deliver structural anchoring support when the intrinsic musculature is active. Messenger and Young (1999) noted that the bolsters are capable of providing rigid support because the fibers of the soft tissue are arranged as a muscular hydrostat.

Despite their non-rigid tissues, hydrostats provide structural support through the pressurization of internal fluid. This pressurization can result in a surprisingly turgid or "hard" structure (consider the increased firmness of the biceps brachii muscle when the elbow is flexed). The hydrostatic fluid may be encapsulated within a relatively large internal cavity (a classical hydrostat), or may be the fluid contents of the muscle fibers themselves (a muscular hydrostat). Muscular hydrostats (Kier and Smith 1985; Smith and Kier 1989) are composed of a tightly packed three-dimensional array of muscle fibers. The contraction of fibers oriented in one direction can change the shape of the overall muscle, create deformation and movement, and antagonistically lengthen muscle fibers running in other orientations.

The support that hydrostatic links can offer often is not as rigid as that generated by solid structures, but they provide adequate structure for many mechanisms: from humans' tongues to squids' tentacles. Indeed, constantly stiff or highly rigid beams may not always be optimal. While it is true that, ideally, stiff links are optimal for the transmission of force, Bayley et al. (2012) found that the ability to bend, and even buckle within special regions, helps prevent

catastrophic failure in locusts' jumping legs by absorbing energy when unexpected movements occur.

Joints—Joints, pivots, and fulcra are difficult to define. Aristotle, in perhaps the oldest biomechanical reference (*De Motu Animalium* c.330 BCE, Nussbaum 1986), defined joints as the elements within a mechanism that allow relative motions to occur between links and noted that they were critical for swimming, flying, and walking motions of limbs. This concept of a joint is notable in that it did not describe the construction of a joint; it simply defined joints as the area between links in which motion can occur.

Comparative biomechanicists generally recognize two categories of animals' joints: sliding and flexible joints (Wainwright et al. 1982; Fig. 2). The best understood are the sliding joints (Fig. 2A). Formed by the physical contact between subsequent rigid links, they are thus capable of transmitting compressive forces that are loaded on joints by bite reaction forces (i.e., the forces that are equal and opposite to bite forces. This force is analogous to that which an anvil applies to the hammer during a strike). Reuleaux (1876) developed the modern engineering categorization of sliding (also known as kinematic) joints. He categorized them by the constraints that the shapes of the contacting surfaces impose on the relative motion of the links. The basic kinematic joints that are built with articulating surfaces are familiar to anatomists that describe rigid skeletal systems; e.g., the ball-and-socket-like condylar joints of crustacean locomotory limbs (Wootton 1999) or the nearly uniaxial hinge-like joint of humans' elbows
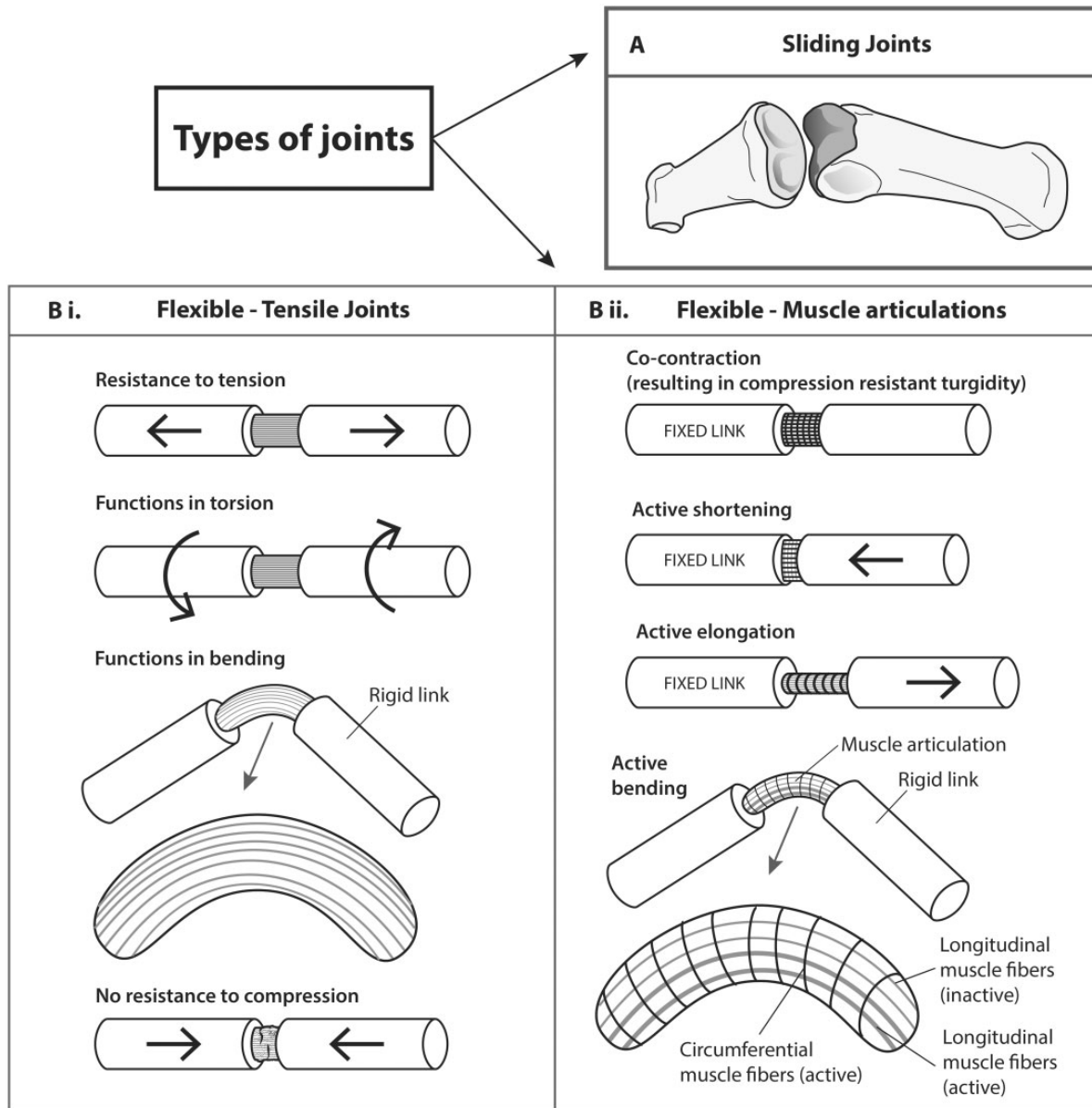
Fig. 2 Natural joints are divided into two classifications; Sliding joints and flexible joints. (**A**) Sliding joints often provide motion between rigid endo- and exoskeletal links. They efficiently transfer compressive reaction forces between links through abutting surfaces. The shapes of their articulating surfaces control the relative possible motions between the links. (**B**) i. Flexible tensile joints are formed by a flexible connection between adjacent links. They function well in tension and allow rotations in all directions, however this capacity for motion is lost if the joint is loaded in compression as the connection buckles and the edges of the links contact. ii. Muscle articulations are flexible joints in which the flexible connection is formed of active muscle, usually in the form of a muscular hydrostat, and dimension limiting connective tissue. Co-contraction of circumferential and longitudinal muscle fibers would result in no dimensional changes but the hydrostat would become turgid as its fluid contents pressurize, resulting in compression resistance. Active shortening results from contraction of longitudinal muscle fibers and passive lengthening of circumferential fibers. This occurs because the shape of the muscle would become short and wider in diameter as volume is fixed. Elongation occurs as the circumferential muscle fibers contract and passively elongates the longitudinal fibers. Bending movements are also possible by contracting circumferential muscle fibers and asymmetrically contracting the longitudinal fibers.

(Bottlang et al. 2000). These basic joints are constructed, whether natural or man-made, to safely limit the six possible degrees of freedom (i.e., the orthogonal axes about which one link can rotate or translate relative to the other) and the range of motion.

Flexible joints were described by Wainwright et al. (1982) and Alexander (1983) as a thin region within

an otherwise continuously rigid element (Fig. 2B). The thin region serves as a joint by deforming and allowing relative motion of the adjacent rigid portions. Alexander (1983) noted that the distal intertarsal joints of locusts' legs are flexible joints. The thin intertarsal membranes allow rotation along all three axes (three degrees of rotational freedom), but the joint seems to only function during tension; when the locust hangs from the claws on its distal limb. When loaded in compression, however, the membranes buckle, the rigid portions of the exoskeleton abut against each other, and the joint ceases to function. We refer to this type of joint as a tensile flexible joint, as it functions only in tension and buckles under compression. Because of this mode of failure, tensile flexible joints are not suitable for biting systems in which bite reaction forces load the joint in compression.

There is, however, a second type of flexible joint: the titular ''muscle articulation'' (Fig. 2C). In this type of joint, the occluding elements of the biting mechanism are connected by a joint made of deformable muscle and connective tissues that often are arranged as a classical or muscular hydrostat. Unlike tensile flexible joints, the flexible tissues of muscle articulations can bear compressive loads by generating hydrostatic structural support. Thus, muscle articulations form a joint that can transfer bite reaction force from one link to the other without buckling. Because muscle articulations use the turgidity of pressurized fluid to bear compressive loads, these joints typically incorporate a classical or muscular hydrostat that provides skeletal support.

Muscles used in biting—biting force is generated by contractile tissue. Typically this tissue is formed of muscle fibers (with a great diversity of form in invertebrates) (Hooper and Thuma 2005; Hooper et al. 2008) or organizations of sarcomeres within muscle cells. There are also a number of non-muscular contractile mechanisms that should not be overlooked by functional morphologists investigating novel mechanisms found in invertebrates. These mechanisms, reviewed by Vogel (2013), may include osmotic devices, hydration/dehydration engines, and intracellular molecular mechanisms that include polymerization of tubulin and interactions of non-sarcomeric actin and myosin microfilaments. Regardless of the mechanism, the forceful occlusion of the teeth results in bite reaction forces that must be borne by a compression-resistant joint.

Contracted muscles must be passively elongated to their original resting length to divaricate the jaws preparatory to the next biting motion. This passive elongation is often facilitated by antagonizing musculature arranged in ways that expand gape. It important to note, however, that antagonists are not always muscular; this force may instead be provided by tensile elements (that can easily be missed in histochemical preparations that differentiate only muscle) that control changes in shape (such is the case in the length limiting medial band of the kalyptorhynchs' hook support presented below or in the helical tensile wrapping of the bodies of many vermiform organisms). This force may also be provided by the release of elastic energy stored during biting (e.g., by bending a stiff beam, such as the limb of an archery bow, or by stretching an elastic material such as a collagenous tendon or a basement membrane). Investigators describing novel systems of biting should also note that use of relatively small muscles is possible if there is a mechanism that amplifies power through an elastic storage mechanism. If muscular contractile force can be used to store energy elastically over a relatively long period and this energy can be rapidly released, then the output of power can be quite high. As an example, trap-jaw ants (Larabee and Suarez 2014) use a combination of springs and latches to generate much faster and more powerful closures of the jaw than is expected from direct production of force by muscles.

We propose that, regardless of the details of how the biting system is constructed, the functionality of four fundamental components—teeth, jaws, joints, and muscles—must be met. In soft-bodied animals, these requirements may be fulfilled in unique ways. First, teeth may be the only permanently stiff and hard material incorporated into the organism's body. Second, jaws may not be made of rigid materials, but instead may provide hydrostatic support. Third, the jaw joint may not be a sliding-type joint and may instead be a flexible-muscle-articulation type of joint. Fourth, in addition to providing biting force, muscles may also form pivots and generate structural support.

Case studies

To better characterize the multiple roles of muscles in the function of muscle articulations, we review four invertebrate examples.

Octopuses' beaks—a strong compression-bearing joint that can relocate its pivot point

Octopuses have parrot-like beaks with piercing tips and edges that can be used in scissor-like shearing. The occluding surfaces of the upper and lower beaks are made of heavily cross-linked chitin and are thus stiff and hard. The beaks are embedded within a set

of mandibular muscles that form a buccal mass. The beaks do not articulate within the buccal mass to form a sliding-type joint; instead the embedded portions of the beaks become less cross-linked and are quite thin and flexible where they are connected to the musculature through the becublast cells that secrete the beak's material (Miserez et al. 2008).

The upper beak bears an inverted U-shaped transverse cross-section and thus has a saddle-shaped appearance. The lower beak has an inverted saddle-shape with slightly wider lateral walls, such that the upper beak fits within the lower one (Fig. 3A). This overlap of lateral walls disallows the formation of a sliding joint because there are no contacting surfaces that can be loaded in compression to resist bite reaction forces. Instead, the upper beak is capable of five degrees of freedom (Uyeno and Kier 2007); it is capable of pitch, yaw, and rolling rotational motions relative to the stationary lower beak and the upper beak can also translate toward and away from the lower beak and forward and backwards (side-to-side motions are limited by the overlap of the lateral walls). Indeed, when following the beaks through a bite-cycle in order to identify an axis of rotation, one notices that instantaneous pivot points can be located anywhere within a region (Fig. 3A).

The motions of the upper beak relative to the lower one are powered by the mandibular muscles. A morphological description of the musculature (Uyeno and Kier 2005) and a subsequent functional analysis (Uyeno and Kier 2007) note that there is a muscle group with the fibers appropriately oriented for creating forceful biting movements (i.e., closure of the beak). There is also a muscle group with fibers oriented in a way that provides effective antagonistic beak-opening movements. However, one muscle group, the lateral mandibular muscles, resembles a solid cylinder of muscle with fibers in all three mutually perpendicular orientations (Fig. 3A). This muscular hydrostat is thought to become turgid, thereby fixing the point of upper-beak rotation within the pivot area. It is also thought to enlarge the gape of the mouth by changing geometry and translating the upper beak away from the lower beak. Thus, in cephalopods' articulations of beak muscles, muscle not only generates biting force, but also aids in providing the antagonistic opening force, provides skeletal support, and resists compression to form the pivot of the joint.

Valves of inarticulate brachiopods—a muscle articulation with a classical hydrostat that is not a jaw

The inarticulate brachiopod bears two elongate shells that do not form an interlocking tooth hinge-joint (as do articulate brachiopods). Instead the valves are separated by a coelomic space that is surrounded by muscles that connect the valves at varying angles (Trueman and Wong 1987; Fig. 3B). Pressurization of this space constitutes a classical hydrostat that resists compression and thereby forms a hinge between the valves. This flexible hinge is important for their mode of feeding. Inarticulate brachiopods bury themselves with the tips of their valves extended a short way out of the sediment where they generate filter-feeding currents with their lophophore. A fleshy pedicle with an internal hydrostatic space anchors the body by inflating. The simple fluid-filled space within the pedicle does not allow enough control to actively "worm" the animal backwards into the substrate. Instead, the valves are used in a scissoring/digging motion to tunnel down into the substrate, make a U-turn and arrive at the surface in the correct feeding position (Trueman and Wong 1987; Fig. 3B). The multiple degrees of freedom allowed by the joint supports complex scissoring motions of the valves (Savazzi 1991; Fig. 3B). This muscle articulation is notable as it is not a biting system *per se*, although the flexibility of these motions by the valve resembles the behaviors of other muscle-articulation biting systems. It is also notable because the muscle articulation relies on a classical fluid-filled coelom rather than upon a muscular hydrostat.

Hooks of kalyptorhynch flatworms—a miniature muscle articulation that uses tensile elements

Meiofaunal kalyptorhynch flatworms of the genus *Cheliplana* bear two stout hooks on the ends of muscular hook-supports or tongues (Karling 1961; Smith et al. 2015, this volume) The hooks and supports represent the terminal elements of a proboscis that can be hydraulically everted and grasp prey found in the minute interstices between grains of sand. Once prey is caught, it is transferred to a posterior pharynx. The hooks, therefore, are not strictly analogous to teeth as the proboscis and mouth are not associated.

Uyeno and Kier (2010) described the hook-supports as a muscle-articulation type of joint (Fig. 3C), as they function as microscopic muscular hydrostatic links that rigidly support the hooks, create the compression-resistant joint, and generate bite-force. Uyeno and Kier (2010) noted that the actin-rich material at the center of the hook-supports were oriented perpendicular to its long axis, an orientation inappropriate for the shortening of the hook-supports during contraction. Instead, their contraction is thought to reduce the hook-support's
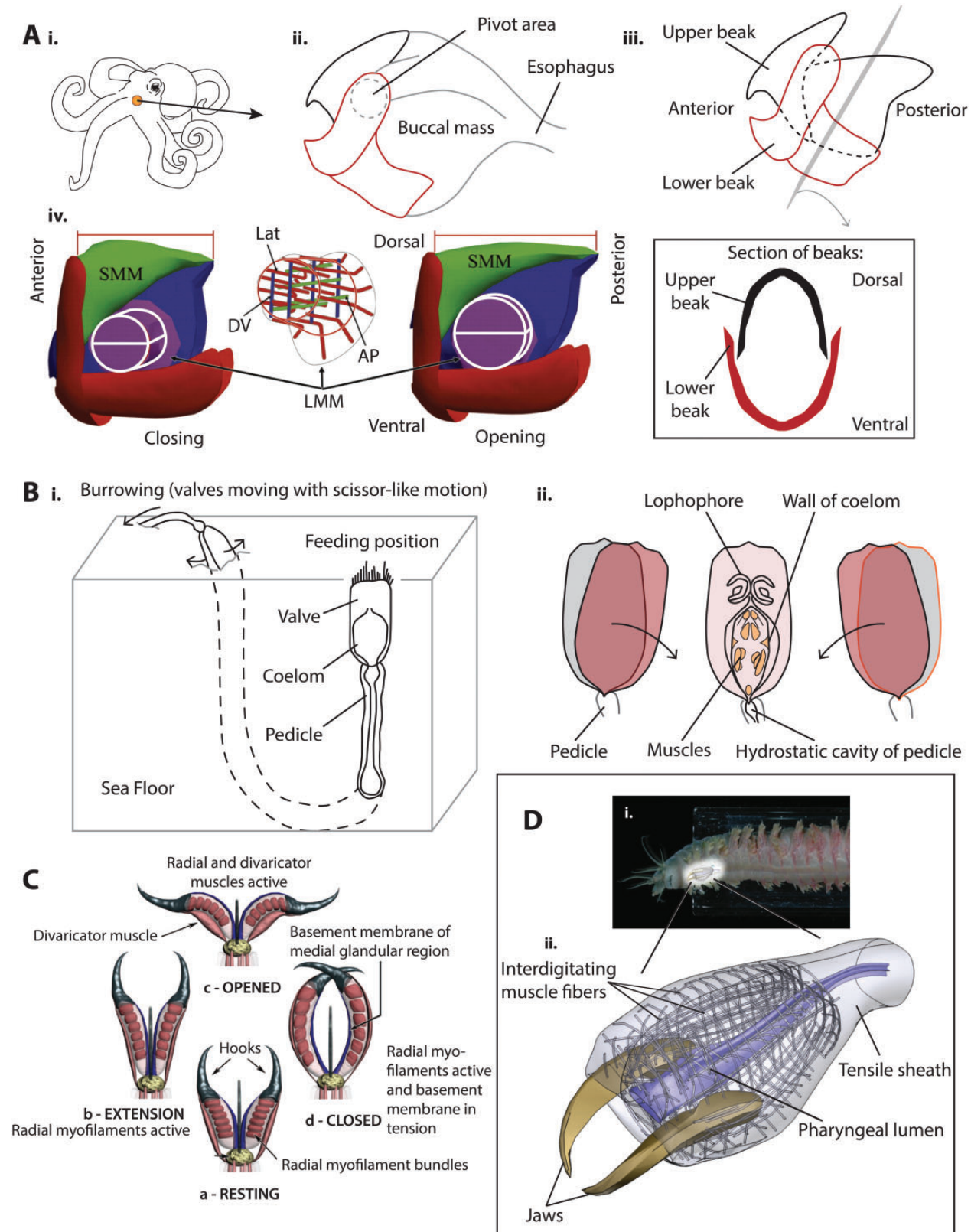
Fig. 3 Case studies: four examples of invertebrate muscle articulations. (**A**) The octopus buccal mass muscle articulation: i. Position of buccal mass within the octopus. ii. The upper and lower beaks are embedded in the musculature of the buccal mass. iii. The saddle-like upper and lower beaks fit within each other. As the walls overlap, there are no sliding joint surfaces within this biting system. iv. The major closing muscle of the buccal mass is the superior mandibular muscle (SMM). Its contraction brings the enlarged wings of the red lower beak toward the blue upper beak in a closing motion. The major opening muscle is the lateral mandibular muscle (LMM). This

cross-sectional area and thus increase its length. This assumes the constant volume of the hook-supports and that the dimension perpendicular to the contraction of the musculature is constrained (i.e., the supports get longer rather than simply becoming thin). The elongation of the hook-supports is antagonized by lateral muscular elements that run from the base to the hook-bearing tip. The co-contraction of these two muscular elements may result in the lateral rotation of the hook (Fig. 3C). No medial muscular elements were identified and tensile elements were hypothesized to play a role in limiting changes in the medial length of the hook-support to produce inward bending or ''biting'' motions. Smith et al. (2015, this volume) have completed the morphological characterization of this muscle-articulation by performing an ultrastructural analysis and describing the medial tension-bearing element of the hook-support-like tongues in an unarmed schizorhynchid proboscis.

Kalyptorhynch proboscides suggest that muscle-articulation-type joints can be effectively miniaturized and that smaller biting systems may use tensile elements instead of contractile ones. Indeed, the use of collagens and other tensile proteins represent potential savings in volume and reduce the metabolic cost associated with maintenance of active muscle.

Errant polychaetes' jaws—a jaw joint with complex orientations of fibers

The biting system of the phyllodocidan polychaetes consists of zinc-biomineralized (Lichtenegger et al. 2003) left and right jaws embedded within a pharyngeal bulb on either side of a muscular mouth and pharynx (Pilato 1968a, 1968b). The pharyngeal bulb is an eversible structure such that the jaws are normally not visible. The hydraulically everted bulb functions as a muscle-articulation type of joint (Uyeno and Kier 2014) that allows the exposed jaws to forcefully swing open and closed through a wide horizontal arc. The jaws may also make small lateral translations and lengthwise rotations.

Unlike the other muscle articulations, there are few discrete bands of muscles with direct origins and insertions (Fig. 3D). Instead, the pharyngeal bulb musculature surrounding the jaws and pharyngeal lumen seems to be made of a solid block of muscle composed of interdigitating muscle fibers oriented in many different directions. It is, however possible to develop functional postulates for various orientations of fibers based on their function as a muscular hydrostat (see Uyeno and Kier [2014] for details). For instance, radial fibers that connect the pharynx's luminal surface to an external bulb-sheath may tend to reduce the thickness of the bulb and widen the pharyngeal lumen. Multiple orientations of fibers located at the esophageal end of the bulb, if co-contracted, may serve as a hard anchor for muscle-fiber orientations that open and close the jaws. Similar to the kalyptorhynch condition, it is important to note the function of tensile elements. In this case, the collagenous fibers of the extracellular matrix, arranged as contra-rotating helices that form a superficial sheath surrounding the pharyngeal bulb, may function to constrain the bulb's volume, and therefore its overall shape. Clark and Cowey (1958) described the function of such crossed-fiber tensile wrappings. Investigators of novel biting systems may find polarized light or phase-contrast imaging useful in visualizing important non-muscular, tensile elements.

Fig. 3 Continued

muscle is a complex muscular hydrostat with mutually perpendicular lateral (lat), dorso-ventral (DV), and antero-posterior (AP) muscle fiber orientations. These different orientations of muscle fibers contract with various activation patterns to allow the shape of the LMM (as outlined in white) to approximate a long skinny cylinder in the closing beak and to become shorter and fatter and thus push the upper beak away from the lower in an opening motion. (Figure reproduced with permission from The Company of Biologists Ltd; Uyeno and Kier 2007). (**B**) i. Inarticulate brachiopods do not burrow with their pedicle, thus they dig a U-shaped path using scissor-like motions of their valves to arrive at their feeding position (illustration modified from Trueman and Wong 1987). ii. The valve motions are generated using a muscle articulation that pressurizes the coelom to generate a compression resistant joint. This allows side-to-side and opening-closing motions between the valves (illustration modified from Hyman [1959] and Savazzi [1991]). (**C**) A sequence of movements of the grasping hooks of the Kalyptorhynch flatworm (*Cheliplana* sp.). The center of each hook support contains radial myofilament bundles that contract to extend the hooks (b). Co-contraction of the lateral divaricator muscle causes an opening motion (c). If the radial myofilament bundles contract and lengthen the hook support further than is permitted by the basement membrane of the medial glandular region, then the hook supports curve inward resulting in a hook closing motion (d). (Figure reproduced with permission from The Biological Bulletin, Uyeno and Kier [2010]). (**D**) i. The pharyngeal bulb of the ragworm *Alitta virens* (Sars 1835) is composed of a complex interdigitation of muscle fiber orientations contained between the pharyngeal lumen and the external tensile sheath. The jaws are mounted on either side of the mouth. The musculature supports the jaws, produces opening and closing force, and resists the compression of the bite reaction forces. ii. The position of the bulb in the living animal (photo courtesy of Dr W.M. Kier).

Definition of a muscle articulation

Muscle articulations are a type of flexible joint in which the flexible component is made of contractile muscular and tensile tissue. The muscular tissue in these joints is multifunctional: It must (1) generate biting force; (2) form a joint that does not buckle while bearing compressive loads; and (3) form rigid structural links that serve as jaws and bolsters. To serve these functions, the soft tissues are often organized as a classical or muscular hydrostat. Muscle articulations may represent an important type of joint as such an arrangement may allow a larger range of motion and greater number of degrees of freedom than a more conventional articulated joint. This gain in flexibility and diversity of movement, however, may require increasingly complex neuromuscular control.

Muscle articulations may be a more common biomechanical feature than previously recognized, as they have now been described in several soft-bodied invertebrate phyla; molluscs, brachiopods, annelids, and platyhelminthes. Because only four muscle articulations have been described so far, further investigations into biting systems should be undertaken. It should be noted that muscle articulations may not necessarily function in biting systems, as these joints may be useful anywhere a flexible, yet compression-resistant, joint is needed. (Indeed, human-engineered muscle articulations may be valuable as a multifunctional robotic end-effector.)

The hagfish's feeding system—a putative mechanism

The biomechanics of the unique feeding system of hagfish has not yet been fully characterized, but preliminary analyses suggest that it may depend on the function of a muscle articulation. Its description may expand the diversity of muscle articulations as well as better define the characteristics of that type of joint. Indeed, this system may be a good test of the definition of a muscle articulation as hagfishes have no opposable jaws. With seemingly only one half of a biting system, this arrangement would suggest that they cannot pinch or grasp food in a forceful bite. However, Clark and Summers (2007) have documented that hagfish deliver strong bites using a single dental plate and are capable of forcefully tearing flesh from tethered food items. Kinematic analysis of frames of video recorded during feeding bouts suggests that coordinated movements of the head and body allow for a more forceful bite than may be delivered by using recurved teeth in a shearing

motion. It is our hypothesis that the other half of the hagfish's biting system does exist; a muscle articulation represents a joint within the head that simultaneously allows the dental plate to be both supported and positioned so that the force generated by integrated body movements can be leveraged for an opposing ''bite''.

Hagfish feeding without whole-body movements involves procuring foods through cyclic protraction and retraction of the dental plate. First, the protracting dental plate's bilaterally symmetric arrangement of keratinous teeth is everted and opened like a paper folder and subsequently drawn into contact with the food. Grasping of food continues as the maximally protracted dental plate and associated food are retracted into the mouth. As the dental plate retracts and the folds close, the teeth begin to lay flat medially, which further secures the food as it enters the mouth. Rigid tissues (teeth and a few unmineralized cartilages) are positioned in the anterior half of the cylindrically shaped hagfish's feeding apparatus (Fig. 4A). In this rigid component, the dental plate is positioned above a robust basal plate. Protractor and retractor muscles allow the dental plate to rotate over the anterior margin of the supporting basal plate (Clark et al. 2010). The basal plate is also maneuverable and thus positions the dental plate, in a manner similar to that of the radula/odontophore in molluscs.

The posterior soft component of the feeding apparatus is a muscular hydrostat formed of a sheath of circumferential muscle fibers surrounding a retractor-muscle core made of longitudinal fibers. The functional complexities of this three-dimensional arrangement of muscle fibers have perplexed comparative anatomists for more than a century (Müller 1839; Fürbringer 1875; Cole 1907; Dawson 1963; Clark et al. 2010). There are two postulates of muscle-function during biting (Fig. 4B). First, the sliding core hypothesis (*sensu* Fürbringer 1875) suggests that the circumferential fiber-sheath may generate peristaltic motions that protract and retract a stiff retractor-muscle core. Second the core-wedge hypothesis (*sensu* Dawson 1963) describes a rigid, conic wedge-shaped retractor-muscle core that is forced rearward as the circumferential fiber-sheath contracts and increases in length while decreasing in diameter.

Electromyographic data from *Myxine glutinosa* reveal that the muscles of the sheath and the retractor-core co-contract during retraction of the dental plate and are inactive during protraction (Clark et al. 2010). Thus, when activated, the turgid sheath-muscle may function as a stiff supportive anchor
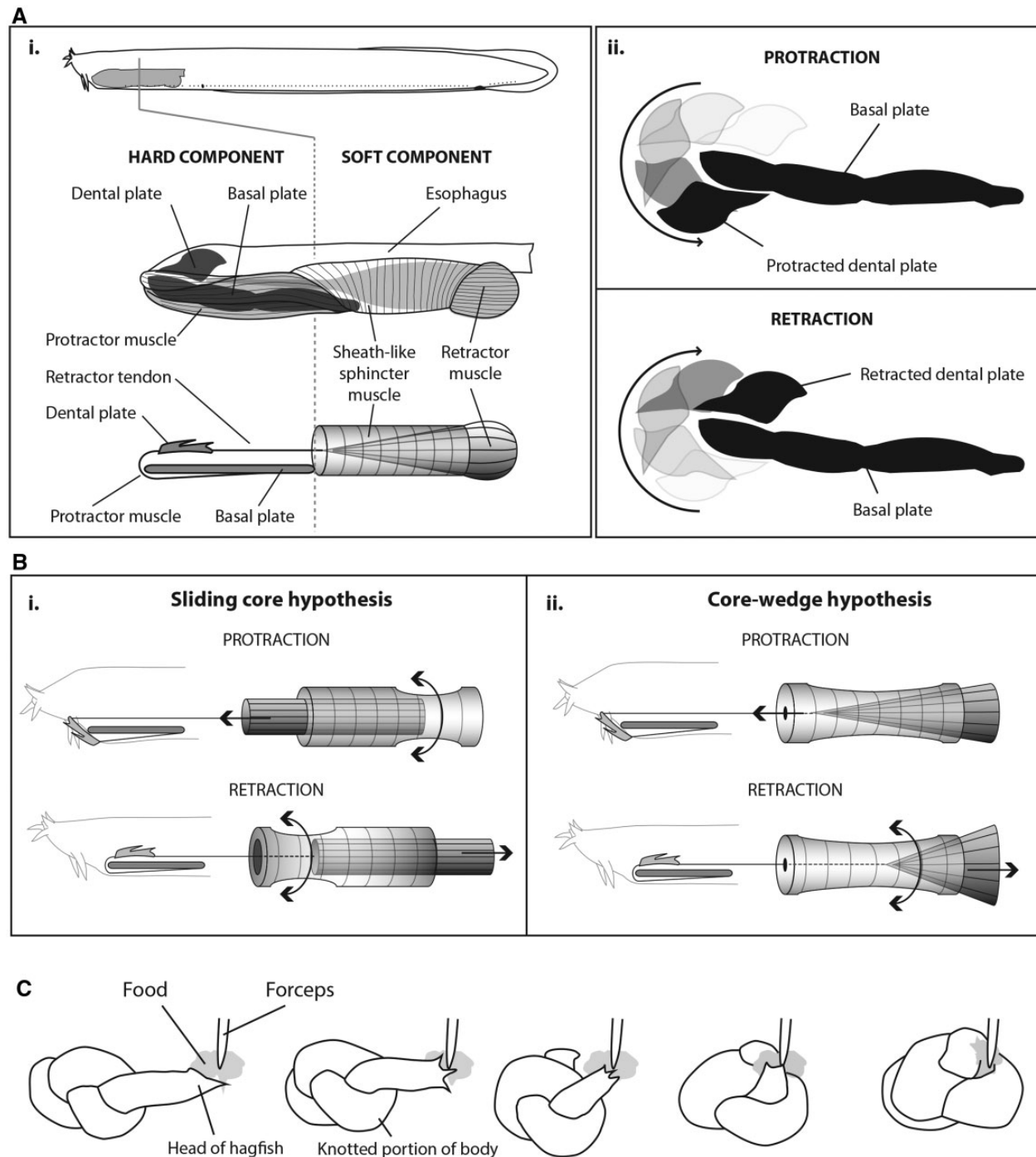
Fig. 4 Form and function of the hagfish feeding apparatus and knotting behaviors. (**A**) Morphology of the hagfish feeding apparatus and the mechanics of dental plate movements: i. The feeding apparatus (shaded organ shown within the animal and below in both an anatomically correct illustration and in a mechanical sketch) is composed of a hard component (featuring a dental plate and a cartilaginous basal plate) and a soft component (featuring the major biting musculature). ii. Dental plate protraction and retraction movements are supported by the underlying basal plate (Figure reproduced with permission from Elsevier, Clark et al. 2010). (**B**) There are currently two hypotheses for function of the soft component during protraction and retraction movements: i. In the sliding core hypothesis the sheath-like sphincter muscle contracts in a peristaltic motion around a core-like retractor muscle, thereby driving both protraction and retraction of the dental plates. ii. In contrast, the core-wedge hypothesis predicts that retraction occurs when the conical wedge-shaped retractor muscle is squeezed out of the surrounding sheath-like sphincter muscle. (**C**) A sequence of video frames (the behavior progressing from left to right) illustrates the manipulation of an anteriorly moving body knot in a hagfish. Note that the knot is passed toward the head after the food item has been engaged by the dental plates. As the knot nears the head, the head appears to disappear within a loop of the knot. This surrounding loop is used to form a stable platform that presses against the food item. This leverage is then used by the head to forcefully tear a portion of fish away from the forceps tether.

for the retractor-core muscle. This muscular hydrostatic structural support helps anchor a muscular articulation-type joint; however, the functional details of the connection between the soft and rigid components are unclear, particularly in the connection's role in positioning the dental plate while providing compression-resistance for the basal plate during feeding. Hagfish employ body-knotting behaviors that enhance biting force (Clark and Summers 2012). In *Eptatretus stoutii*, *E. springeri*, and *M. glutinosa*, a tight figure-eight knot (Clark and Uyeno, personal observations) is formed in the posterior body and then slid toward the head so that a loop is pressed against the surface of the food (Fig. 4C). The knotted body produces a stable platform that resists bite reaction forces and an *ad hoc* lever that enhances force applied to the dental plate. As such, the action of the dental plate, the angle of the body, and the ability of the body to form and manipulate knots that form a lever, are crucial parameters of "biting" force.

The hagfish's feeding mechanism may be a muscle articulation. It is formed of an array of soft tissues that allows rigid teeth to apply substantial force to food items with complex and diverse motions. However, whereas other muscle articulations represent a joint between two permanently rigid components, the hagfish's muscle articulation may be unique in that it may connect a permanently rigid component to a flexible body that generates support only when needed.

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