Chapter 7
Feeding in Jawless Fishes

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Abstract Hagfishes and lampreys are a peculiar minority of fishes that bite in the absence of jaws. Despite not being mounted to proper jaws, the dentition of hagfishes and lampreys can effectively incise the tissues of large marine animals. The jawless feeding mechanisms employed by hagfish and lamprey may prove insightful in our attempts to understand the evolutionary origins of jaw-driven feeding and, more broadly, the evolution of chordate feeding. These taxa appear to be descendants of the first chordates that possessed dentition, and thus potentially represent the earliest chordates to acquire prey through biting: the process of driving teeth into prey tissue by the means of a closed kinematic chain or loop. In this chapter, we demonstrate how hagfish and lamprey generate true biting movements and provide a comprehensive review of the anatomy and biomechanics of jawless feeding in both taxa.

7.1 Introduction to Jawless Feeding

7.1.1 Jawless Biting

The jawless fishes (agnathans) account for only 0.2% of extant craniates; these include the hagfishes (Order: Myxiniformes) and lampreys (Order: Petromyzontiformes). Though jawless feeding is rare in vertebrates, the feeding apparatuses of hagfishes and adult (post-metamorphic) lampreys are nonetheless effective. Their keratinous teeth can be driven into the tissues of exceedingly large food items, and carve out, or render, morsels with similar effect as produced by jawed biting movements (Clark and Summers 2007). Where most vertebrates bear teeth on opposable, pincer-like jaws, the teeth of hagfishes and lampreys are attached to the surface of

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eversible cartilaginous tooth plates, which are cyclically protracted and retracted to render and swallow pieces of food (Fig. 7.1a–d). The protraction and retraction of the tooth plates in hagfish is supported by an underlying basal plate or by the piston cartilage in lampreys. Many references for both taxa describe the tooth plates and their movements in terms of "rasping tongues". One may also draw general morphological and functional parallels between these agnathan tooth plates and their supportive cartilages to the form and function of molluscan radulae and their supportive odontophore (Fig. 7.1e).

Despite documented similarities in form and function of the hagfish and adult lamprey "rasping tongues" (Yalden 1985), these two groups employ considerably different approaches for rendering tissue. Lampreys use a prominent tooth-bearing oral disc that allows flesh-feeding (e.g., *Lampetra fluviatilis*) and hematophagous species (e.g., *Petromyzon marinus*) the ability to tightly adhere to the body surfaces of large and fast-swimming prey animals (Nichols and Tscherter 2011; Samarra et al. 2012). Once attached to the host, the lamprey employs cyclic protraction–retraction movements of its apicalis (or tooth plates) to draw blood and other tissues (Lanzing 1958; Hardisty and Potter 1971a). During this rasping movement, the drawing of blood is facilitated through the secretions from the buccal gland. The active component in these secretions is lamphedrin; an anticoagulant with cytolytic and hemolytic properties (Lennon 1954). Given the striking behavior of blood-sucking, predatory lampreys, the group, in general, is often referred to as ectoparasitic, however nonparasitic forms account for more than 50% (20 sp.) of the 38 extant lamprey species (Potter 1980; Renaud 1997; Gill et al. 2003). These nonparasitic species retain oral discs and tooth plates, albeit with reduced dentition, which are used for clinging onto surfaces like suction cups (Potter 1980; Gill et al. 2003).

With 78 recognized species (Fernholm et al. 2013), hagfishes are approximately twice as speciose as lampreys. Hagfishes are strictly marine and generally known to be opportunistic scavengers that feed on dead or dying vertebrates and invertebrates (Martini 1998; Auster and Barber 2006). There is little evidence for dietary diversity across species, and within species (e.g., *Eptatretus stoutii*), little evidence for ontogenetic dietary shifts (Clark and Summers 2012). However, recent observations of foraging behaviors in wild hagfishes of the genus *Neomyxine* suggest that some species are active predators on living free-swimming prey (Zintzen et al. 2011, Fig. 7.2). In contrast to adult lampreys, hagfishes cannot firmly adhere to surfaces because they lack oral suction discs. Despite this, hagfishes attempting to render tissue are capable of generating retractile forces similar to the biting forces produced by comparably sized gnathostomes (Clark and Summers 2007). Where predatory lampreys use their rasping tooth plates to create an ulcer for the purpose of feeding on blood and small bits of other tissues, hagfish tooth plates are used to carve or shear ingestible chunks of flesh from animal carcasses that are bigger than can be immediately swallowed. These tooth plates are also effective at grasping and intraorally transporting whole food items, such as polychaete worms and burrowing fish (Zintzen et al. 2011, Fig. 7.2).

An important difference between the feeding of hagfish and both parasitic lamprey and jawed vertebrates involves how these animals resist forces generated by
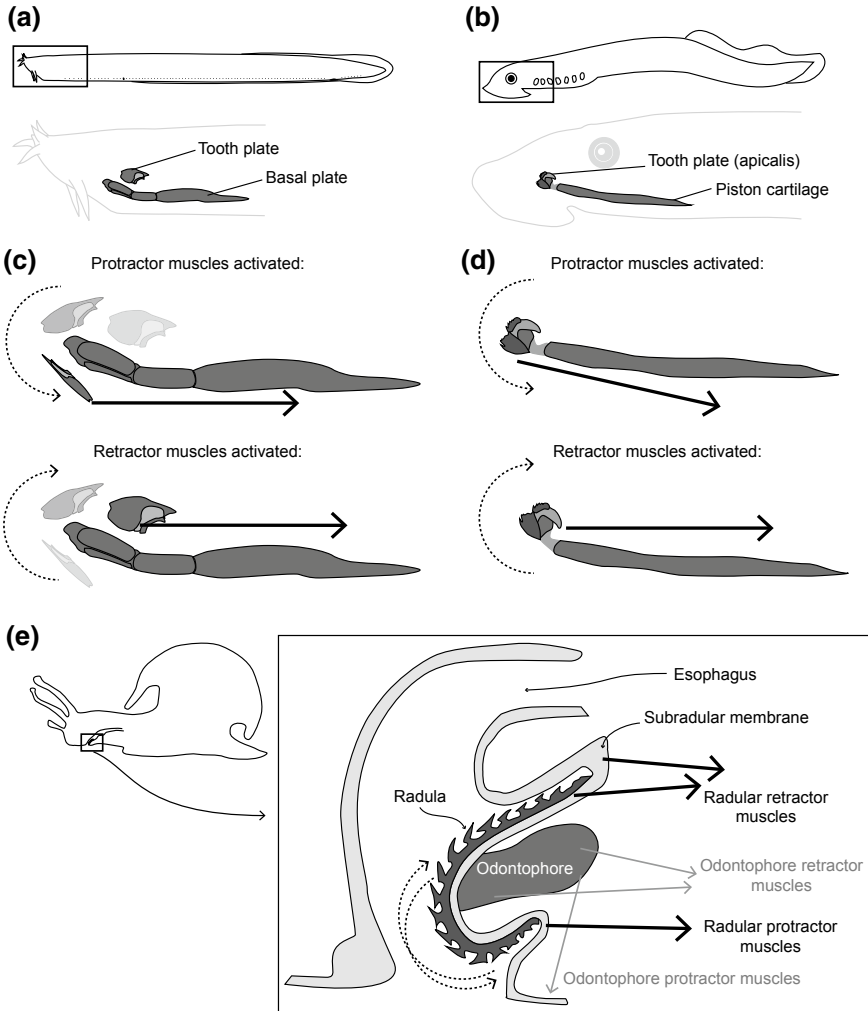
Fig. 7.1 Arrangement of dentition and supportive cartilages in the feeding apparatuses of hagfish and lamprey. The biting motions in these agnathan tooth plates relative to their supportive cartilages resemble the motions of a molluscan radula relative to its supportive odontophore. **a** Left lateral view of a hagfish (above) and a closer view of the head region (below) showing the position of the tooth plates and basal plate. **b** Left lateral view of an adult lamprey (above) and a closer view (below) of the apicalis and piston cartilage. **c** Left lateral view of tooth plate protraction (top) and retraction (bottom) movements relative to the basal plate in the hagfish feeding apparatus. Images from panels (**a**) and (**c**) were modified from Clark and Summers (2012). **d** Apicalis protraction (top) and retraction (bottom) relative to the piston cartilage in the feeding apparatus of an adult lamprey. **e** General arrangement and rasping motions of a molluscan radula relative to its supportive odontophore. Like the basal plate and piston cartilage of hagfish and lamprey, the molluscan odontophore bolsters the protractile–retractile movements of the radula (dentition). Images from panel (**e**) were modified from Brusca and Brusca (2003)
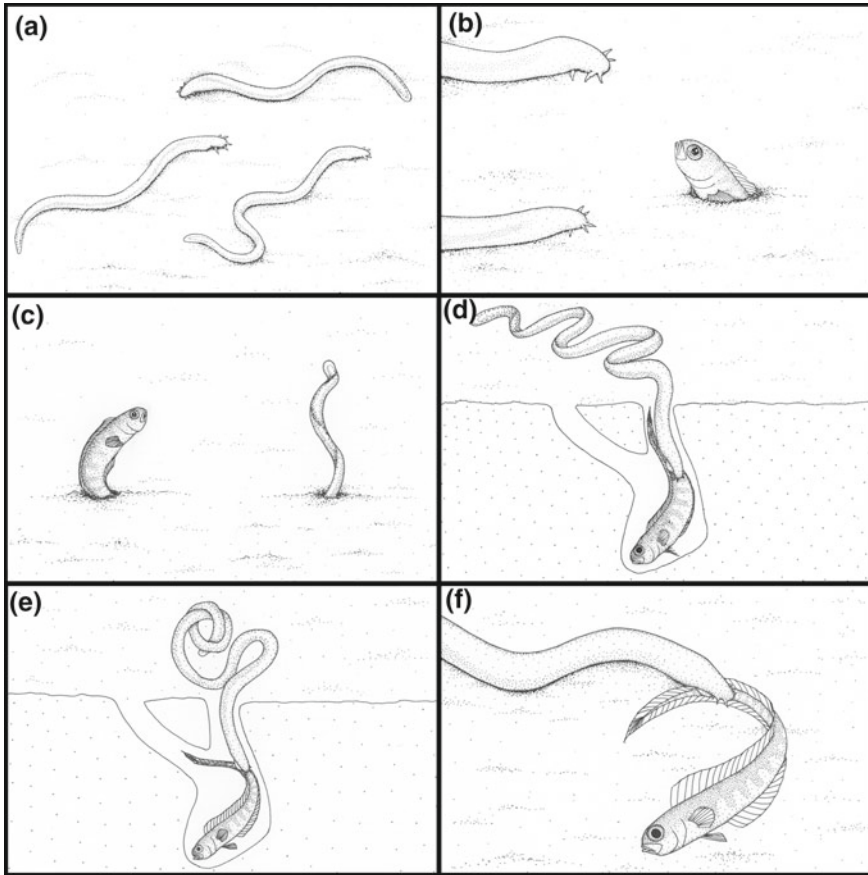
Fig. 7.2 Predatory behavior of a hagfish (*Neomyxine* sp.) on a red bandfish *Cepola haastii*. **a**, **b** Individual hagfishes actively searching for and identifying bandfish burrows. **c** A specimen of red bandfish attempting to exit the burrow when the hagfish enters. **d** The attack phase begins when the hagfish swims into the burrow and grasps the prey. Note the gyrations in the posterior region of the hagfish body during the attack. **e** The extraction phase begins with the formation of an overhand knot while the head of the hagfish remains in the burrow. **f** Manipulation of the body knot facilitates the extraction of the hagfish and grasped prey from the burrow. All images **a**–**f** were reproduced with the permission from Dr. Vincent Zintzen (*Source* Fig. 7.3 in Zintzen et al. 2011)

the dentition. Jawed vertebrates bite with teeth born on pincer-like beams that are connected by robust, compression-resistant jaw joints (Fig. 7.3a). This biting system forms a closed kinematic chain or loop, by which the skull, upper jaw, and dentition provide counteracting loads to the loads applied by the lower jaw and dentition. These applied biting forces and bite reaction forces, are transmitted along the upper and lower jaws to the jaw joints as compressive joint reaction forces. Parasitic lampreys use the adhering suction of their oral discs to close the kinematic chain, which counteracts the force applied by the apicalis to the prey's body wall (Fig. 7.3b). In the
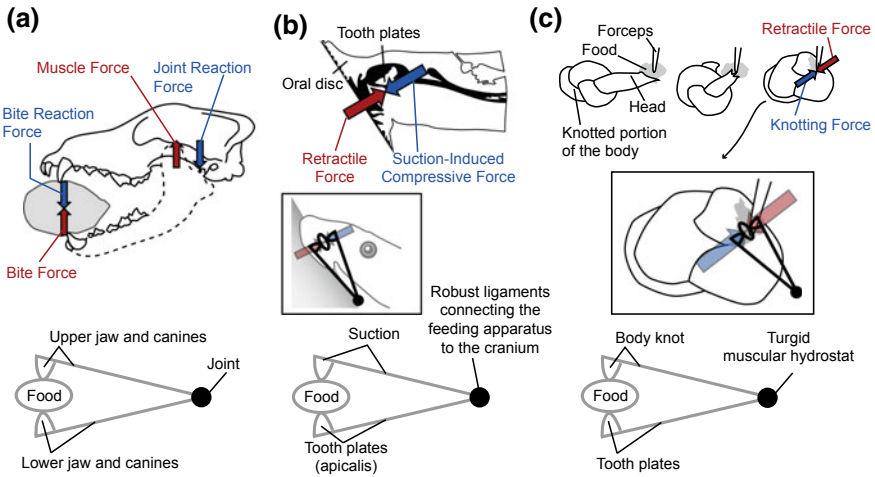
Fig. 7.3 Closed kinematic chains in the feeding apparatuses of jawed vertebrates (gnathostomes) and jawless fishes (agnathans). As with the jawed biting mechanism, the jawless feeding mechanisms of lampreys and hagfish (top images) can be decomposed to a pair of rigid links (resembling upper and lower jaws) joined at a compression-resistant joint (bottom images). These images demonstrate how hagfish and lamprey can employ biting mechanisms. **a** In this closed kinematic chain, the input force produced by the jaw muscles are transmitted along individual "links" in the chain that collectively form a closed loop. These individual "chain links" include (1) the applied muscle force spanning the jaw joint, (2) lower jaw, (3) lower teeth, (4) food, (5) upper teeth, (6) upper jaws and skull, and (7) back to the jaw joint. Also illustrated, are the applied forces in this system and their counterbalancing reaction forces. **b** When adhering to the body of a prey item, the lamprey is capable of driving its dentition into the food by means of a closed kinematic chain. The parasagittal section of the lamprey head (illustrated at the top) illustrates how the retractile force of the tooth plates (or apicalis) is counterbalanced by the compressive force of the lamprey's body (section modified from Hilliard et al. 1985). **c** Video image sequence (progressing from left to right) illustrating how the body knot of a hagfish can act like an opposing jaw to the tooth plates. As the stiffened body knot approaches and slides over and past the head, the rigid body applies a compressive knotting force against the food, which counteracts the tensile, retractile force (or jawless biting force) delivered by the tooth plates. Illustrations modified from Uyeno and Clark (2015)

lamprey feeding system, the counterbalancing suction-induced compressive loads and the apicalis-driven tensile loads are joined by prominent ligaments that connect the supportive piston cartilage to the robust cartilages of the cranium and branchial basket (Fig. 7.3b).

Hagfishes do not have an obvious method of closing this kinematic loop; if they simply press their tooth plates to a surface, the resulting effect would be to simply push themselves away from the carcass upon which they are trying to feed. To counteract this effect, hagfish employ their whole bodies to resist the pressure of their tooth plates: they swim forward as they are pressing their tooth plates to the food item and backward to tear off a sheared portion; or they press their bodies against burrow surfaces in the ground or within a carcass; or they form and manipulate body knots (Fig. 7.3c). Notably, hagfishes use the loops of the knot as leverage in order

to facilitate biting into whale carcasses and other oversized food items and generate enough force to defeat tough scaly body coverings with dense connective tissues (Clark and Summers 2012; Uyeno and Clark 2015). In the hagfish feeding system, a muscular hydrostat forms the compression-resistant joint between the counteracting retractile forces from the tooth plates and the whole body (Fig. 7.3c).

Despite their jawless condition, the feeding systems of hagfish and lampreys are indeed capable of generating compressive forces that counteract the tensile forces produced by their retracting tooth plates (Fig. 7.3b, c). This effect is similar to the bite reaction forces produced by the upper jaw and teeth of a mammal that counteracts the bite forces applied by the lower jaw and teeth (Fig. 7.3a). Like gnathostomes, hagfishes and post-metamorphic lampreys possess dentition that can be driven into objects through the use of a closed kinematic loop, which means, like gnathostomes, these jawless fishes possess a biting system. Here, we introduce the term "jawless biting" to refer to the retractile movements of the tooth plates of hagfishes and lampreys.

7.1.2   Natural History

Jawless fishes, or agnathans, were the most abundant vertebrates for over 140 million years until the end of the Devonian Period (approximately 360 million years ago) (Carroll 1988; Purnell 2002). During their 80 million-year coexistence with early jawed vertebrates, agnathans occurred in diverse forms. Ostracoderms, characterized by their rigid dermal body coverings made of bone and dentin, accounted for approximately 600 recognized species of the Paleozoic jawless fishes, with at least four distinct superclasses including the Pteraspidomorphi, Anaspida, Thelodonti, and the Osteostrachomorphi (Lingham-Soliar 2014). All species of these hard-bodied jawless fishes are known for possessing bony head and body armor covering a relatively unmineralized internal skeleton (Forey and Janvier 1993; Janvier 1993; Lingham-Soliar 2014). The general morphology of hagfishes and lampreys appears to have remained largely conserved since the Paleozoic. Conserved aspects of their morphology include: soft, flexible, and elongated bodies that lack paired fins, integuments that are devoid of scales, and their feeding apparatuses (Bardack 1991; Janvier 1993; Gess et al. 2006).

Most Paleozoic agnathan taxa are thought to be microphagous suspension feeders that used cilia to generate weak suction currents that were characterized by both low pressure and throughput relative to the powerful suction created by the rapid expansion of the buccal cavity in extant gnathostome fishes (Mallat 1984; Wainwright et al. 2015). Agnathan suspension feeding that involves relatively low-power suction currents continues to be used by larval forms of extant lamprey (Hardisty and Potter 1971b; Mallatt 1984). Macrophagy is known in a number of agnathans and related taxa; hagfishes (Dawson 1963), lampreys (Lanzing 1958), conodonts (Purnell 1993; Purnell and Donoghue 1997) and some thelodont fish species (van der Brugghen and Janvier 1993). Despite notable exterior differences between extinct and extant forms,

the jawless feeding mechanisms of these fossil macrophagous taxa were probably similar to those of adult lampreys and hagfishes (Purnell 1993; Goudemand et al. 2011).

7.1.3   Evolution of Chordate Feeding

Given the ancestral position of agnathans in the phylogeny of vertebrates, the jawless feeding mechanisms employed by hagfish and lamprey may provide insight into understanding the evolutionary origins of jaw-driven feeding and, more broadly, the evolution of chordate feeding. The evolutionary trend seems to be generally described as a transition from low-power suspension feeding that depends on ciliary action in basal chordates (e.g., urochordates and cephalochordates) to rapid, high-power suction in gnathostomes that is driven by a sudden drop in pressure induced by rapid expansion of the jaw and hyoid apparatus. Larval lampreys appear to use an intermediate approach, involving a feeding flow of moderate intensity produced by ciliary motion that is enhanced by the passive elastic expansion of an actively compressed buccal cavity in order to capture food particles from the water column (see Mallatt 1981). Extant agnathans appear to be descendants of the first chordates that possessed dentition, and thus potentially represent the earliest chordates to acquire prey through biting: the process of driving teeth into prey tissue through the use of a closed kinematic loop. Though histologically distinct and possibly phylogenetically independent from the enameloid teeth found in jawed vertebrates (Smith and Hall 1990; Smith et al. 1996), hagfish and lampreys can bite as forcefully as many jawed vertebrates. The keratinous dentition of these animals is highly effective in reducing large food items (Clark and Summers 2007). Biting is a prey-capture mode that has repeatedly evolved among jawed vertebrates, although it is second in frequency to suction feeding.

7.2   Jawless Feeding in Hagfishes

7.2.1   Biodiversity, Ecology, and Feeding Behaviors

Hagfishes are thought to have evolved over 500 million years ago and represent one of the most ancestral lineages of craniates (Forey and Janvier 1993). All species of hagfishes occur in demersal marine habitats, the depths of which may range from 10 m to 5000 m (Fernholm 1974; Martini 1998). Hagfishes feed on a diversity of prey such as; crustaceans, polychaete worms, cephalopods, various small fishes (Gustafson 1935; Wakefield 1990; Johnson 1994), hagfish eggs (Worthington 1905; Holmgren 1946), and the remains of larger marine vertebrates, such as mackerel sharks, sturgeon, birds, whales, and other marine mammals (Strahan 1963; Shelton

1978; Martini 1998). Hagfishes do not assemble in organized schools; however, when opportunities to feed on dead or moribund prey are presented, immense aggregations of hagfishes can result in spectacular feeding frenzies (Strahan 1963; Smith 1985; Martini 1998).

When feeding on large prey items, hagfishes couple cyclic protractions and retractions of their tooth plates with violent whole body movements including knotting (Clark and Summers 2012). During an en masse foraging event, such as feeding on a whale fall, individuals will often cluster themselves around an open wound and proceed to aggressively bite into the prey while employing body knotting, shaking, and twisting. In these situations, the hagfishes will frequently bump into and rub against one another but nonetheless continue to feed unperturbed. Also frequently observed during en masse feedings is the formation of slime aggregates on prey tissue. This is thought to be a possible deterrent for other marine scavengers (Martini 1998; Zintzen et al 2011).

Hagfishes are popularly portrayed as opportunistic scavengers on dead or dying marine animals, however, the diversity of their feeding niches is likely not fully characterized. Zintzen and colleagues (2011) have recently discovered that some hagfish species can actively hunt and capture living prey. Underwater video recordings revealed predatory behavior of a *Neomyxine* species hunting a burrowing Red Bandfish (*Cepola haastii*) (Fig. 7.2). These recordings showed several hagfishes searching for Red Bandfish burrows, with some individuals occasionally swimming into and out of burrows. This initial searching phase occurred during a relatively long time period (up to 118 min), while the subsequent attack and extraction phases lasted approximately 3 min. During the first minute of the attack, the hagfish drove its head (anterior third of the animal's total length) into a burrow and proceeded to violently shake and spin the free swimming two-thirds of its body. It is hypothesized that during this period in the attack, the hagfish was deploying its tooth plates for grasping the prey. This active period was immediately followed by a one-minute inactive period, during which it is hypothesized that the hagfish suffocated its prey with slime until the prey stopped moving (Zintzen et al. 2011). Following this period of inactivity was the extraction phase, which began with intense body movements followed by knot formation and manipulation. Less than 30 s later, the hagfish withdrew itself from the burrow with the Red Bandfish secured in its tooth plates (Zintzen et al. 2011).

7.3   Morphology of the Hagfish Feeding Apparatus

Myxinoid feeding morphology and behavior were initially observed by European zoologists in the mid to the late 1700s (Gunnerus 1766; Retzius 1790; Abildgaard 1792) and detailed anatomical descriptions have been known for more than a century (Ayers and Jackson 1901; Cole 1905, 1907; Dawson 1963). Morphological parallels are noticeable in the jawless feeding apparatuses of both hagfishes and

adult lampreys, which has raised the possibility of these taxa sharing a monophyletic origin as cyclostomes (Yalden 1985).

The jawless feeding apparatuses of lampreys and hagfishes are like those of jawed vertebrates in that they are comprised of teeth supported by stiff internal structural elements and powered by skeletal muscles (Clark and Summers 2007). In the feeding apparatuses of most gnathostomes, rigid tissues are represented by jaws that are predominantly composed of bone, while the stiffest elements in the jawless feeding apparatuses of hagfish (dentition and basal plate) and lampreys (dentition, piston cartilage, annular cartilage, and branchial basket) are made of unmineralized cartilage. Moreover, in hagfishes, these stiff elements are embedded in muscle and connective tissue that can account for up to 90% of the total mass of the feeding apparatus (Clark et al. 2010). However, the musculature itself is complexly arranged as a muscular hydrostat, and when activated, transforms the soft feeding apparatus into a surprisingly rigid structure that effectively accommodates forceful biting (Clark et al. 2010; Uyeno and Clark 2015).

In all hagfish species, the cylindrical feeding apparatus is located in the anterior 15–20% of the body's length and ventral to the esophagus (Fig. 7.4). In situ, the feeding apparatus is suspended dorsally from the diminutive cranial cartilages by delicate, sinuous arches of cartilage and thin sheets of muscle and connective tissues (Janvier 1993; Ziermann et al. 2014). Ventrally, the feeding apparatus is connected to the rectus muscle band (Fig. 7.5c), a component of the hagfish body wall musculature. When excised from the body, the feeding apparatus resembles a cylinder of muscle with a length roughly four times its width. The feeding apparatus from a 30 cm Atlantic hagfish can be casually described as looking almost exactly like a "Vienna sausage" (a short bite-sized sausage commonly served at parties in North America). Despite its soft tissue composition, and its lack of opposing jaw elements, the hagfish feeding apparatus is capable of creating strong shearing movements with its teeth (Clark and Summers 2007), especially when the tooth plate movements are supported by the leverage of coordinated whole body swimming and knotting movements (Uyeno and Clark 2015).

Despite the similarity in overall construction, the morphology of the feeding apparatuses is surprisingly diverse across species: variation can be observed in the relative size of the feeding apparatuses and in the total number of teeth (Fernholm 1998; Clark and Summers 2007). Comparison of cross-sectional areas of discrete muscles within the feeding apparatuses also shows marked variation between species, especially between Eptatretus and Myxinines (Clubb et al. 2019). In the following descriptions, we summarize a generalized overall construction of the feeding apparatus components (the basal plate, dentition, and musculature).

7.3.1   Basal Plate

The basal plate is formed of several cartilaginous structures that together represent the most robust of cartilages in the cranial skeleton and in the whole animal. Situated
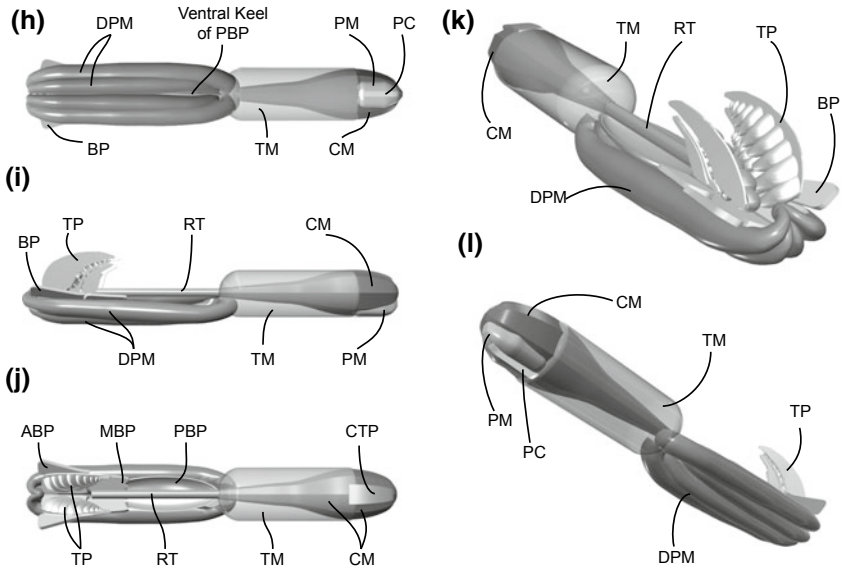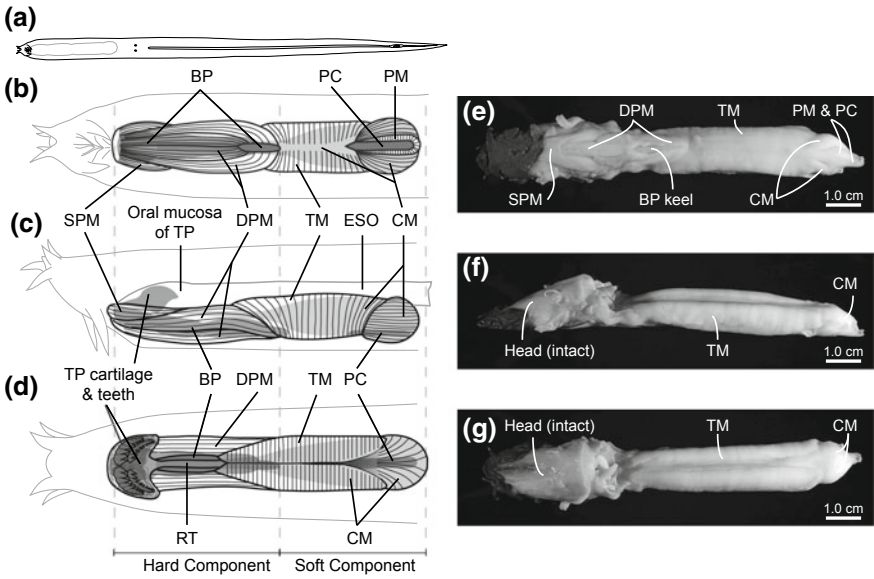
◄**Fig. 7.4** Morphology of the hagfish feeding apparatus. (**a**) Ventral view of a specimen of Atlantic hagfish *Myxine glutinosa* with the position of the cylindrical feeding apparatus outlined. Magnified ventral (**b**), left lateral (**c**), and dorsal (**d**), views of the feeding apparatus showing the anterior and posterior hard and soft components, the position of the esophagus, the variable and complex orientations of muscle fibers, and the arrangement of the retractor muscle (lighter shading) relative to the tooth plates and cartilage (darker shading). To the right of these illustrations are photographs of the feeding apparatus of a Pacific hagfish *Eptatretus stoutii* from ventral (**e**), left lateral (**f**), and dorsal (**g**) views with the esophagus removed and the head intact. BP, basal plate; DPM, deep protractor muscle; ESO, esophagus; PC, perpendicularis cartilage; PM, perpendicularis muscle; CM, clavatus muscle; RT, retractor tendon; SPM, superficial protractor muscle; TM, tubulatus muscle; TP, tooth plates. **h–j** Three-dimensional illustrations of the hagfish feeding apparatus with the tooth plates (TP) in the retracted position. Illustrations are presented in ventral (**h**), left lateral (**i**), dorsal (**j**), anterior-three-quarter (**k**), and posterior-three-quarter (**l**) views to demonstrate the cylindrical shape and the complexity in the arrangements of muscle and connective tissues. In all drawings, the tubulatus muscle (TM) is semitransparent to show the deeper clavatus muscle (CM). Note that the PM and posterior fibers of the TM are connected to the perpendicularis cartilage. In contrast, connections between the CM and PC are absent. ABP, anterior basal plate; BP, basal plate; CTP; connective tissue patch (the insertion for the PM fibers); MBP, middle basal plate; PBP, posterior basal plate. Anatomical illustrations **a–d** were modified from Clark et al. (2010) with permission. Photo credits **e–g** Mr. Luke Clubb

at the base of the cranial skeleton, the basal plate provides attachment sites for feeding musculature and supports the protraction–retraction movement of the tooth plates. This composite structure can be divided into anterior, middle, and posterior segments, and when summed, the length of these cartilages (i.e., basal plate length) constitutes the anterior 40–50% of the feeding apparatus (Figs. 7.4 and 7.5).

When we manipulate excised basal plates, we observe that the connections between these subdivisions allow the basal plate to conform to specific shapes. Both anterior and middle basal plates, which are sagittally subdivided into bars, resemble vertebrate hyaline cartilage and have been referred to as type I cartilage (Wright et al. 1984, 2001). The anterior basal plate consists of a pair of medial bars and a pair of lateral bars, which connect with the two bars of the middle basal plate (Fig. 7.5a, b). The articulations between these subdivisions in the anterior and middle basal plates can give the basal plate a trough-shaped cross-section that provides a supportive platform for the tooth plate movements and respective feeding musculature (Fig. 7.5d) (Cole 1905; Dawson 1963). It is possible that the suture-like joints within and between the anterior and middle basal plate can enable the basal plate to undertake some changes in shape (Uyeno and Clark, Personal Observations). The anterior and middle basal plates are the only parts of the feeding apparatus with cartilaginous connections to the cranial cartilages. Labial cartilages, which articulate with cartilages in the tentacles and palate, project from the anterolateral margins of the lateral bars of the anterior basal plate (Fig. 7.5a, b) (Cole 1905). Branchial arch cartilages, which project from the posterolateral margins of the middle basal plate, connect with the cartilages in the palate (Fig. 7.5a, b) (Cole 1905).

Posterior segments of hagfish basal plates bear a more tendinous appearance than a hyaline cartilage appearance, and thus are referred to as type II cartilage (Wright et al. 1984, 1998). In contrast to the anterior and middle segments, the posterior basal plate
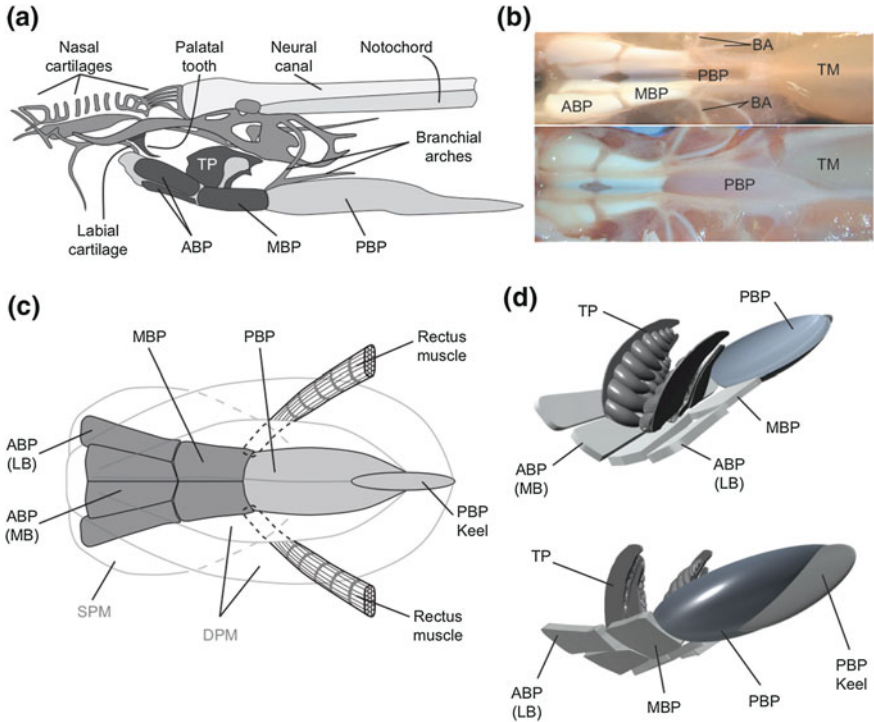
Fig. 7.5 Morphology of the cranial skeleton and basal plate in the hagfish. **a** Illustration of the cranial skeleton of a hagfish from left lateral view. Note the thin, sinuous morphology of the labial and branchial cartilages that connect the basal plate to the remaining cranial cartilages. The darkest shaded tissues: the palatal tooth, tooth plates, anterior, and middle basal plates, represent the most rigid of tissues in the head and whole animal. **b** Photographs of the basal plate of a Pacific hagfish *Eptatretus stoutii* from dorsal view (anterior is left). These photos show the anterior, middle, and posterior divisions of the basal plate and its connection with the branchial arches (**BA**). In contrast to the anterior and middle divisions, the posterior basal plate resembles tendon or elastic cartilage more so than hyaline cartilage, and is considerably less stiff and more flexible. Photographs of the tubulatus muscle (TM) intact (top) and cut (bottom) demonstrate the attachment of the TM to the dorsolateral surfaces of posterior basal plate. **c** The ventral surface and keel of the basal plate provides the origin for the protractor muscles and one of the three major axial muscles, the rectus muscle. **d** 3D drawings of the basal plate and retracted tooth plates from anterior-three-quarter (top) and posterior-three-quarter (bottom) views. Note that the arrangements of the anterior and middle basal plate cartilages produce a trough-shaped cross-section, and on the ventral surface, the convexity and prominent keel of the more flexible posterior basal plate supports the protractor muscles. ABP, anterior basal plate; DPM, deep protractor muscle; LB, lateral bar; MBP, middle basal plate; MB, medial bar; PBP, posterior basal plate; SPM, superficial protractor muscle; TP, tooth plates

is less stiff, lacks subdivisions, and is relatively elongate, narrow, and tapers caudally (Fig. 7.5). The length of the posterior basal plate accounts for the posterior 50–60% of the basal plate length. Although the posterior basal plate does not articulate with any cranial cartilages, it retains a trough-shaped transverse cross-section and provides attachment sites for some of the major feeding muscles (tubulatus and deep protractor muscles). Located on the dorsal surface of the posterior basal plate is a central longitudinal groove, above which the retractor tendon is positioned at rest and when the dentition is protracted. On the ventral surface of the posterior basal plate is a prominent longitudinal keel, which provides attachment for the deep protractor muscles (Fig. 7.5d). The posterior and lateral surfaces of the posterior basal plate provide attachment sites for the anterior fibers of the tubulatus muscle.

While we have not been able to record direct, in situ visualizations of basal plate motions in a freely behaving hagfish, we hypothesize that the arrangement of basal plate cartilages and associated musculature described above likely permits some deformation of the basal plate. This ability to deform may enhance the possible motions of the dentition. For example, protraction and retraction of molluscan odontophore are known to facilitate the radular movements (Padilla 2004; Mikhlina et al. 2015) (Fig. 7.1e). Morphological variation between the anterior and posterior halves of the basal plate coupled with the presumptive differences in material properties could bear some important functional ramifications. Presumably, this would be much like the associated color and stiffness gradients occurring in cephalopod beaks are hypothesized to attenuate biting stresses (Miserez et al. 2008). In the case for the hagfish feeding apparatus, the posterior basal plate could buffer the transmission of stresses from the most rigid of tissues (teeth and anterior/middle basal plate) to the most flexible tissues (visceral, muscle, and connective tissues).

7.3.2 Dentition

The tooth plates, a bilaterally symmetric series of teeth and supportive cartilages, represent the most dynamic structure in the hagfish feeding apparatus. Individually, the tooth plates bear two rows of dentition supported by two pairs of cartilages divided into anterior and posterior arches (Fig. 7.6). The anterior arch, which supports the dentition, is larger and more flexible than the posterior arch. Dentition of the tooth plates is supported by the anterior cartilaginous arch, which is fenestrated for the transmission of dental nerves, or *nervus dentalis*, and the attachment of connective tissues (Cole 1905). The deep protractor muscle, originating from the ventral surface of the basal plate, inserts onto the leading edge of the anterior arch. The smaller but stiffer posterior arch is the attachment site for the retractor muscle tendon (Cole 1905). The differential stiffness in the anterior and posterior tooth plate arches parallels the different muscle forces and stresses exerted by the retractor and protractor muscles on the tooth plates during feeding (Clark and Summers 2007).

Projecting from the anterior arch of the tooth plates are two rows of smooth, curved, non-serrated keratinous teeth, which are sometimes referred to as "horny
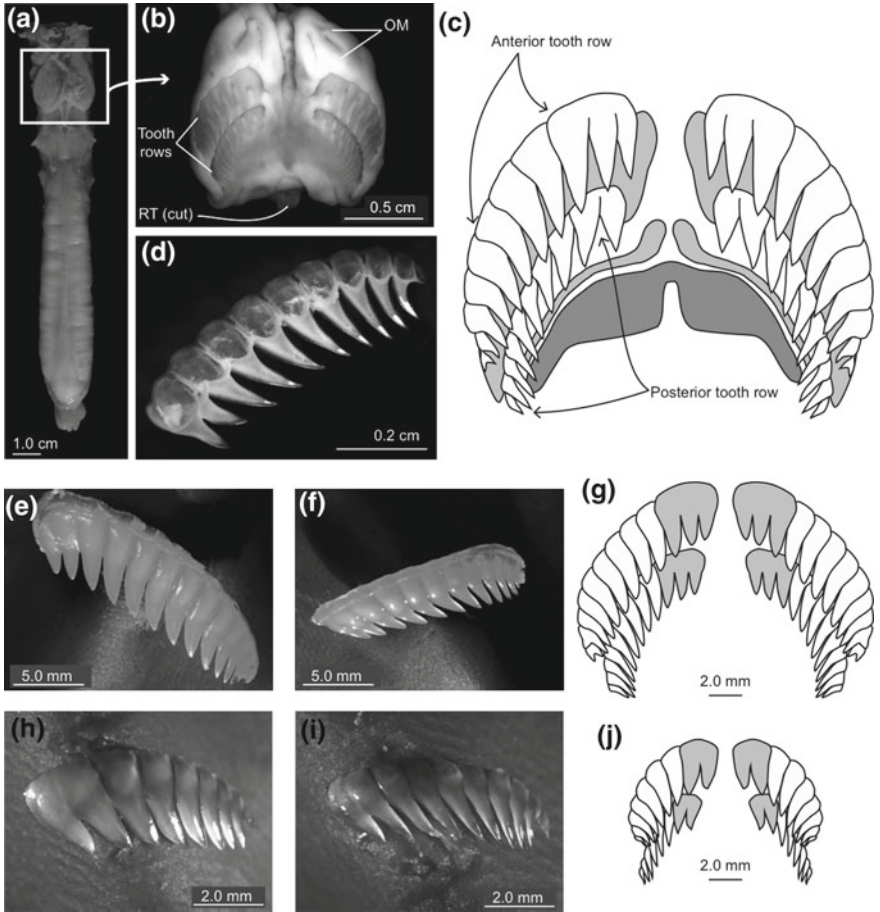
Fig. 7.6 Dentition of the hagfish. **a** Photograph of the feeding apparatus of a Pacific hagfish *Eptatretus stoutii* in dorsal view, with the white box indicating the position of the tooth plates. Photo credit: Mr. Luke Clubb. **b** Magnified photo of the tooth plates excised from the feeding apparatus of an Atlantic hagfish *Myxine glutinosa*. **c** Illustration of the anterior and posterior tooth rows and supportive cartilages (in gray) in the tooth plates of *E. stoutii*. **d** Posterior tooth row from *M. glutinosa* rotated to demonstrate its hollow morphology (e.g., gray surfaces are internal). **e–j** Diversity in the dentition of hagfishes, exemplified in *Eptatretus cirrhatus* and *Myxine limosa*. Magnified photos of the anterior (**e**) and posterior (**f**) tooth rows removed from the tooth plates of a specimen of *E. cirrhatus*. **g** Illustration of the teeth of *E. cirrhatus* highlighting the total tooth number and fusion patterns of the medial teeth (shaded) in both anterior and posterior tooth rows. Total tooth numbers and fusion patterns vary across different species of hagfishes (Fernholm 1998). Magnified photos of the anterior (**h**) and posterior (**i**) tooth rows from the tooth plates of *M. limosa*. (J) An illustration of the dentition of *M. limosa* demonstrates the smaller size and total number of teeth relative to the dentition of *E. cirrhatus*. Also indicated by the illustrations are the 2–2 tooth-fusion patterns in the anterior–posterior medial teeth of *M. limosa* (**J**) compared with the 3–3 tooth-fusion patterns of *E. cirrhatus* (**g**)

cusps" or "horny teeth" in the literature (Fig. 7.6). In a given species, the total number of the teeth from the posterior row of the tooth plates are usually less than or equal to that in the anterior row. Depending on the species, the total number of teeth on the tooth plates from an individual can vary from 26 teeth (e.g., in *M. paucidens*) to 70 teeth (e.g., in *E. carlhubbsi*) (Fernholm 1998). The dentition on both rows of the tooth plates are progressively longer and broader in the medial direction and progressively shorter and narrower in the lateral direction (Clark and Summers 2012). On both anterior and posterior rows, the largest teeth are usually fused as pairs or trios. The shape of the teeth somewhat resembles the grasping dentition of piscivorous sharks and teleosts, and while the total number and fusion patterns of the dentition in the anterior and posterior rows vary across species (Fernholm 1998), the general morphology (e.g., sinuous shape and smooth surface devoid of serrations) of these teeth appears to be conserved (Fig. 7.6e–j).

Situated in the roof of the mouth immediately anterior to the resting or retracted tooth plate is a single posteriorly curved tooth called the palatal tooth (Fig. 7.5a), which is usually larger than any of the dentition on the tooth plates. The anatomical position of the palatal tooth relative to the tooth plates, coupled with characteristic head depression movements, enable the palatal tooth to function like a ratchet in that precludes the kickback or expulsion of food during intraoral transport as the tooth plates are repeatedly protracted and retracted after food is ingested (Clark and Summers 2007).

7.3.3 Feeding Musculature

The cylindrical hagfish feeding apparatus can be divided into an anterior "hard component" and a posterior "soft component" (Fig. 7.4). The basal plate and tooth plates are situated in this region, the hard component represents the more dynamic and rigid portion of the feeding apparatus. The bulk of the major feeding musculature is complexly arranged as a muscular hydrostat in the soft component (Clark et al. 2010; Clubb et al. 2019). The muscles described here (i.e., the ones that predominantly control tooth plate protraction and retraction motions) can be referred to as the major feeding muscles; all of which are innervated by the trigeminal nerve (Lindström 1949). In the following descriptions, we collectively use the terminology presented by Clark et al. (2010).

7.3.3.1 Protractor Muscle Group

The musculature that powers protraction of the tooth plates occurs in the relatively rigid anterior portion of the hagfish feeding apparatus. The Deep Protractor Muscles (DPM), or *Musculus protractor dentium profundus* (Cole 1907), originates from the ventral surface of the posterior basal plate and inserts onto the leading edge of the anterior cartilaginous arch of the tooth plates. The DPM possesses four tubular-

shaped heads (a pair of lateral heads and a pair of medial heads) with longitudinally arranged fibers that span the length of the muscle. Each head of the DPM retains a conserved cross-sectional shape through its length, and connects with its skeletal origins and insertions via short tendons. The Superficial Protractor Muscles (SPM), or *M. protractor dentium superficialis* (Cole 1907), originates from the ventral surface of the posterior basal plate and inserts onto the oral mucosa anterior to the tooth plates. From a ventral perspective of the feeding apparatus, this thinner sheet of muscle becomes visible as its fibers sweep along and over the lateral and anterior surfaces of the DPM (Figs. 7.4 and 7.5c).

7.3.3.2   Retractor Muscle Group

Three muscles comprise the soft component of the feeding apparatus: (1) a retractor muscle (also known as the *M. retractor mandibuli* (Ayers and Jackson 1901), the *M. longitudinalis linguae* (Cole 1907), or the *M. clavatus* (Dawson 1963; Clark et al. 2010; Clubb et al. 2019)), (2) a vertical muscle (also known as the *M. perpendicularis* (Cole 1907; Dawson 1963; Clark et al. 2010), and (3) a sphincter muscle (also known as the *M. constrictor musculi mandibuli* (Ayers and Jackson 1901), the *M. copulo-copularis* (Cole 1907), or the *M. tubulatus* (Dawson 1963; Clark et al. 2010; Clubb et al. 2019)). The smallest muscle, the *M. perpendicularis* (PM), possesses vertically oriented fibers packed within the mid-sagittal plane of the posterior 30% of the *M. clavatus* (CM). Overlying the PM are the semi-longitudinally arranged fibers of the CM. The anterior 65–75% of the CM is enveloped within an overlying array of circular fibers of the *M. tubulatus* (TM) (Fig. 7.4). Within this region of overlap, the CM progressively tapers in the anterior direction where it connects to the long, narrow retractor tendon at the anterior portion of the TM that interconnects with the posterior basal plate. This morphology has most recently been reviewed in Clubb et al. (2019).

7.4   Biomechanics and Functional Morphology of Hagfish Feeding

Hagfishes are capable of forcefully and dynamically driving teeth into food items, despite a number of features that seem maladapted to forceful biting (Clark and Summers 2007). First, the hagfish feeding apparatus (HFA) is predominantly constructed of deformable muscle and connective tissues, and thus does not depend on stiff bones connected by joints. Second, the teeth of a hagfish come in the form of tooth plates, which, in effect, represent one half of a jaw. How can a hagfish forcefully use its teeth without having an opposing jaw element to crush and shear against? Third, the deformable biting system of a hagfish is mounted in the head of a similarly deformable body that can be easily be maneuvered in tight spaces (see

Freedman and Fudge 2017). Indeed, with a flexible body, hagfish can vigorously tie themselves into a number of different knots. Is not such flexibility a shortcoming? Engineers that design man-made biting systems (e.g., Jaws of Life, table saws, etc.) strive to create housings that support the biting bits as rigidly as possible so that force generated can be directed to the biting surface rather than wasted in deforming the housing. The analysis of this seemingly contradictory relationship between form and function depends on understanding the biomechanics of the feeding apparatus movements and also the complex and integrated body movements.

7.4.1 The Hagfish Feeding Mechanism

The bite produced by a hagfish can be decomposed to a cyclical three-step process: First, the tooth plates are protracted from the mouth. Second, the teeth are pressed into the food item. Third, the tooth plates, along with rendered bits of food, are retracted into the mouth (Fig. 7.7). While it is difficult to separate the forces generated within and outside the feeding apparatus, the strong biting force of a hagfish is likely generated by a combination of retractor muscle activity in the feeding apparatus and coordinated body movements.

At rest, the retracted tooth plates are folded along their longitudinal axis and the left and right halves of the tooth plates resemble the covers of a book resting on its spine. Thus, the left and right rows of teeth are brought together like pages between the tooth plate covers such that the teeth point posteriorly (Fig. 7.8). The retracted tooth plates are covered by the soft oral mucosa contiguous with the esophagus (Figs. 7.4c and 7.6b). During protraction, the left and right halves of the tooth plates rotate laterally as the tooth plates protracted from the mouth. The end of the protraction phase is marked by the book cover-like halves of the tooth plate in an "open book" position that results in the rows of teeth oriented towards the food item. Protraction is coupled with simultaneous unveiling of the oral mucosa that exposes the teeth, and when the tooth plate is maximally protracted and unfolded, teeth apices point anteriorly in preparation for appropriate contact with the food item (Fig. 7.8). As retraction begins, the teeth are driven into and then become hooked on the food item. The rest of the retraction phase is marked by the tooth plates folding medially as they return into the mouth with dismembered food items in tow (Fig. 7.8). Upon entering the mouth, oral mucosa envelopes the tooth plates, which unhooks the food from the teeth and then works the food into the esophagus. The dislodging of captured food items from the tooth plates is also aided by the palatal tooth and cyclic head depression—elevation movements during subsequent protraction–retraction cycles (Clark and Summers 2007).

Rotation of the tooth plates about the distal end of the basal plate resembles a simple pulley, and modeling the mechanism as a pulley has allowed us to generate predictions for the retractile forces of hagfishes (Clark and Summers 2007, 2012). If this simple pulley system were to be modeled in static equilibrium, the magnitude of the input force would equal the magnitude of the output force, therefore, the amount
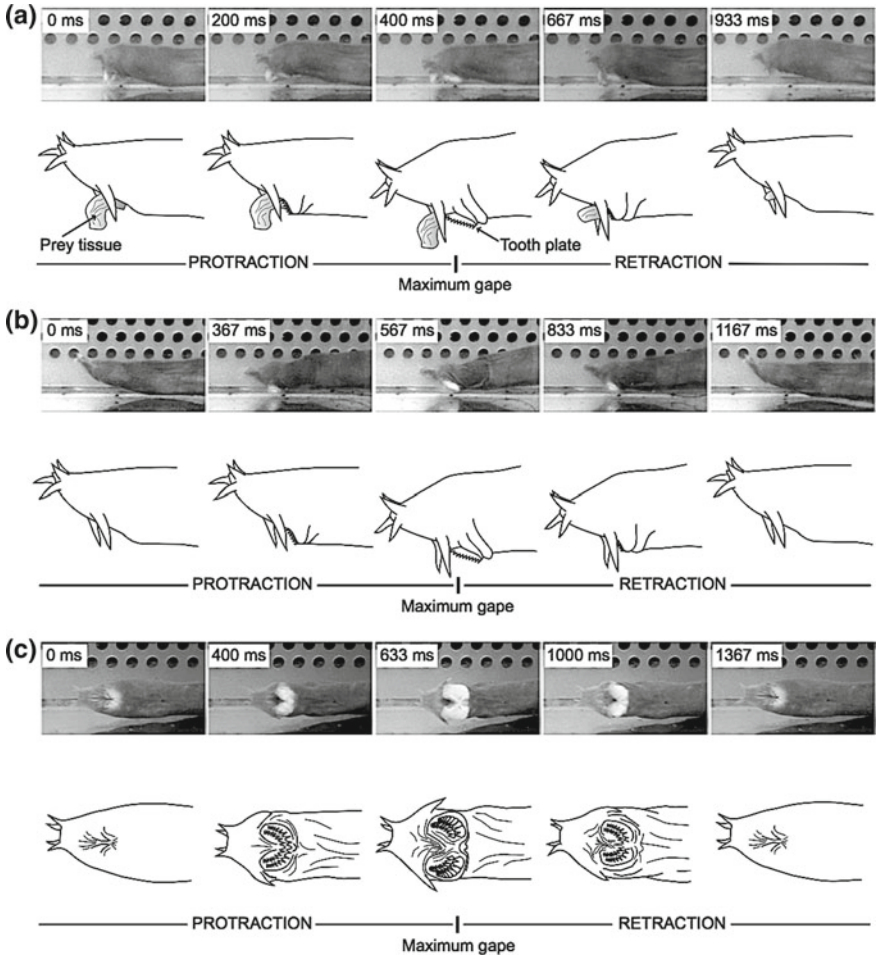
Fig. 7.7 Video image sequences and illustrations of the protraction–retraction cycles (bite cycles) in the Atlantic hagfish *Myxine glutinosa*. (**a**), Left lateral view of a hagfish gape cycle during the capture phase, when food is grasped and being engulfed. (**b**), Left lateral view of a hagfish bite cycle during the intraoral transport phase, which commences once food is swallowed. (**c**). Ventral view of the bite cycle during transport. Note, in ventral view, the bilateral unfolding of tooth plates as they exit the mouth during protraction, followed by the medial folding as they are retracted. The time at each event is indicated in the upper left corner of each video image. This figure was modified from Clark et al. (2010) with permission
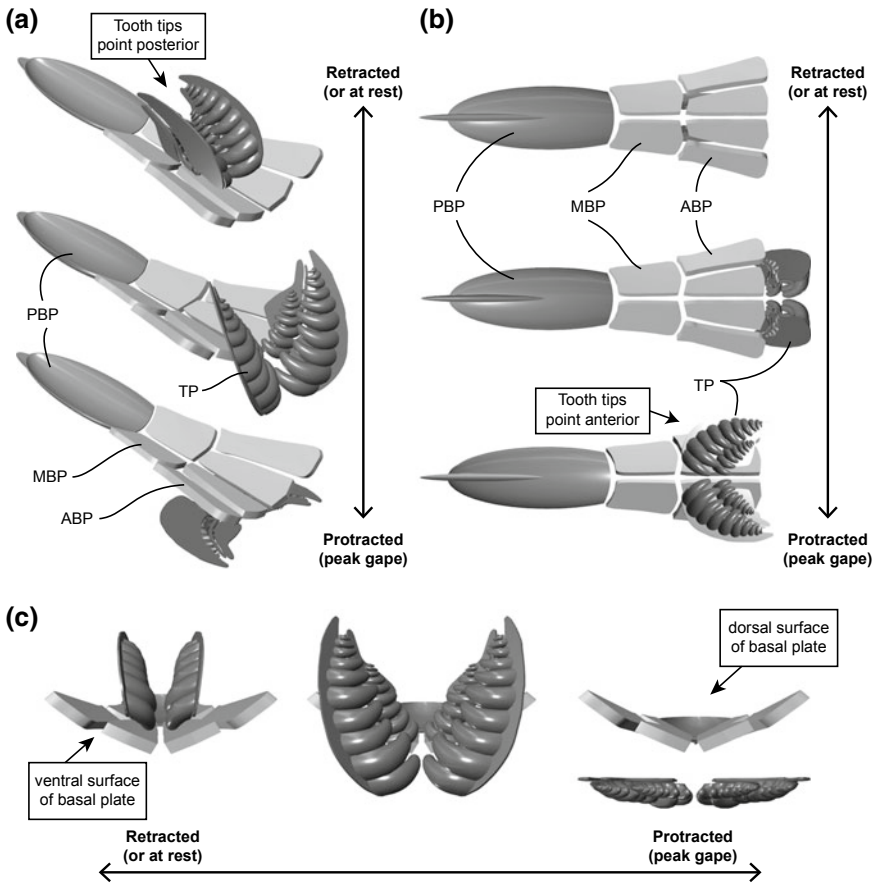
Fig. 7.8 Three-dimensional drawings of the tooth plate protraction–retraction cycles relative to the supportive basal plate in anterior-three-quarter view (**a**), ventral view (**b**) and frontal view (**c**) Note that in all views, the bilateral halves of the protracting tooth plates begin to part and unfold, like an opening book. When the tooth plates are maximally protracted, the apices of the teeth point in the anterior direction. Conversely, when the tooth plates are retracted, the halves of the tooth plates fold medially and the apices of the teeth point in the posterior direction when the tooth plates are fully retracted

of force produced by the protractor and retractor muscles would equal the amount of force applied by the tooth plates during protraction and retraction (Fig. 7.9). Thus, the retractile force of the hagfish tooth plate equals the maximum isometric force production (e.g., assuming 100% recruitment of motor units) of the retractor muscle (*M. clavatus*). In these studies, the physiological cross-sectional area of the *M. clavatus* (CSA_{CM}) was determined using the methods described in Powell et al. (1984), by dividing the product of the *M. clavatus* mass (M_{CM}) and the cosine of the
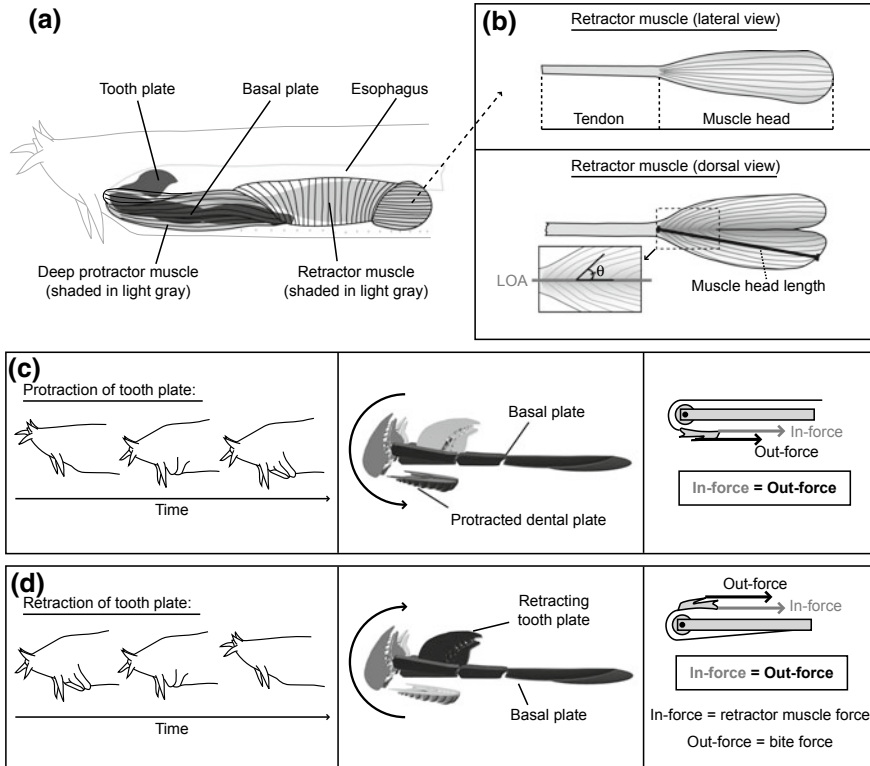
Fig. 7.9 The feeding mechanism of the hagfish can be modeled as a simple pulley. **a** Left lateral view of a hagfish head with the feeding apparatus highlighted to show the muscles that pull directly on the tooth plates. **b** The retractor muscle possesses a bipennate fiber arrangement and inserts onto the posterior margin of the tooth plate with a long narrow tendon, granting this muscle some resemblance to a human gastrocnemius muscle. LOA, line of action; θ, pennation angle. Kinematic profiles of protraction (**c**) and retraction (**d**) of the tooth plates, by which the forces acting on the tooth plates relative to the basal plate (middle) can be modeled with the simple pulley method (right). Images have been modified from Clark and Summers (2012)

pennation angle (θ) by the product of muscle's density (ρ) and muscle fiber length (=L_{CM}).

$$CSA_{CM} = (M_{CM}\cos\theta)(\rho\, L_{CM})^{-1}$$

The maximal isometric force production of the *M. clavatus* (F_{CM}) was calculated as the product of the CSA_{CM} and the specific tension of white muscle in hagfishes (K), which was substituted with the specific tension of elasmobranch *Scyliorhinus canicula* (L. 1758) white muscle (Lou et al. 1999). When applied to the static pulley, the force generated by the retractor muscle equals the retractile force (*sensu* Clark and Summers 2007) or jawless biting force in a hagfish.

$$Jawless\ biting\ force = F_{CM} = CSA_{CM}\,K$$

Bite force is a significant measurement for feeding performance, as the force production relates to the hardness and size of the food that can be managed. These measurements are indicative of the morphology of the feeding apparatus, prey handling times, and more broadly, the natural diet and ecology of a species (Wainwright 1987; Hernandez and Motta 1997; Herrel et al. 2001; Huber et al. 2005; Herrel and Gibb 2006). Hagfishes can bite as forcefully as many fishes and tetrapods, and they do so in the absence of a stiff, robust internal skeleton and pincer-like jaws. The theoretical retractile forces of 30–40 cm long specimens of Atlantic and Pacific hagfish are approximately 7.0 N and 10.0 N, respectively (Clark and Summers 2007). In an ontogenetic series of *E. stoutii* Pacific hagfish (*TL* range = 17.0–61.5 cm), the biting forces theoretically range from 3.0 N to >20.0 N (Clark and Summers 2012). When dissected from the feeding apparatus, the *M. clavatus* and tendon looks like a human *M. gastrocnemius* and Achilles tendon. The bipennate fiber arrangement of the clavatus muscle relative to its line of action grants it the capability to contract with greater force but less speed than comparable muscles (e.g., *M. protractor dentium profundus*) with longitudinal fiber arrangements. Furthermore, the long, narrow retractor tendon, which transmits the clavatus muscle force to the tooth plates, is as strong and stiff as gnathostome tendons (Summers and Koob 2002). These properties of the hagfish feeding apparatus grant it the capacity for handling a variety of possible food items, and renders it especially useful for grasping and transporting sizable chunks of flesh.

7.4.2 Tooth Plate Kinematics During Feeding

The feeding bouts of hagfishes can be divided into four general stages: identification, positioning, ingestion (capture) and intraoral transport; all of which have been observed in the wild (Zintzen et al. 2011) and in laboratory settings (Clark and Summers 2007). Hagfishes rely on olfactory and tactile stimuli for identifying possible food items. Identification involves an independent movement of the barbels (or tentacles) as they contact the food. Simultaneously with or immediately following identification, the mouth is positioned onto or next to the food, followed by ingestion, which occurs when the tooth plates are repeatedly protracted and retracted until the food is engulfed (Fig. 7.7a). Once ingested, additional protraction–retraction cycles are used to facilitate the swallowing or intraoral transport of the food (Fig. 7.7b, c).

Two-dimensional kinematics of tooth plates in hagfishes have been described in *M. glutinosa* Atlantic hagfish and in *E. stoutii* Pacific hagfish (Clark and Summers 2007). In this study, animals were presented with thin rectangular samples of squid mantle in order to stimulate tooth plate movements in the absence of excessive body movements and knotting. Despite differences in phylogenetic origins, the relative size of the feeding apparatuses (Fig. 7.10a, b), and bite force production, the kinematic profiles of the tooth plates were similar in both *M. glutinosa* and *E. stoutii* (Fig. 7.10c, d). The duration of each protraction–retraction cycle, or bite cycle, were approximately one
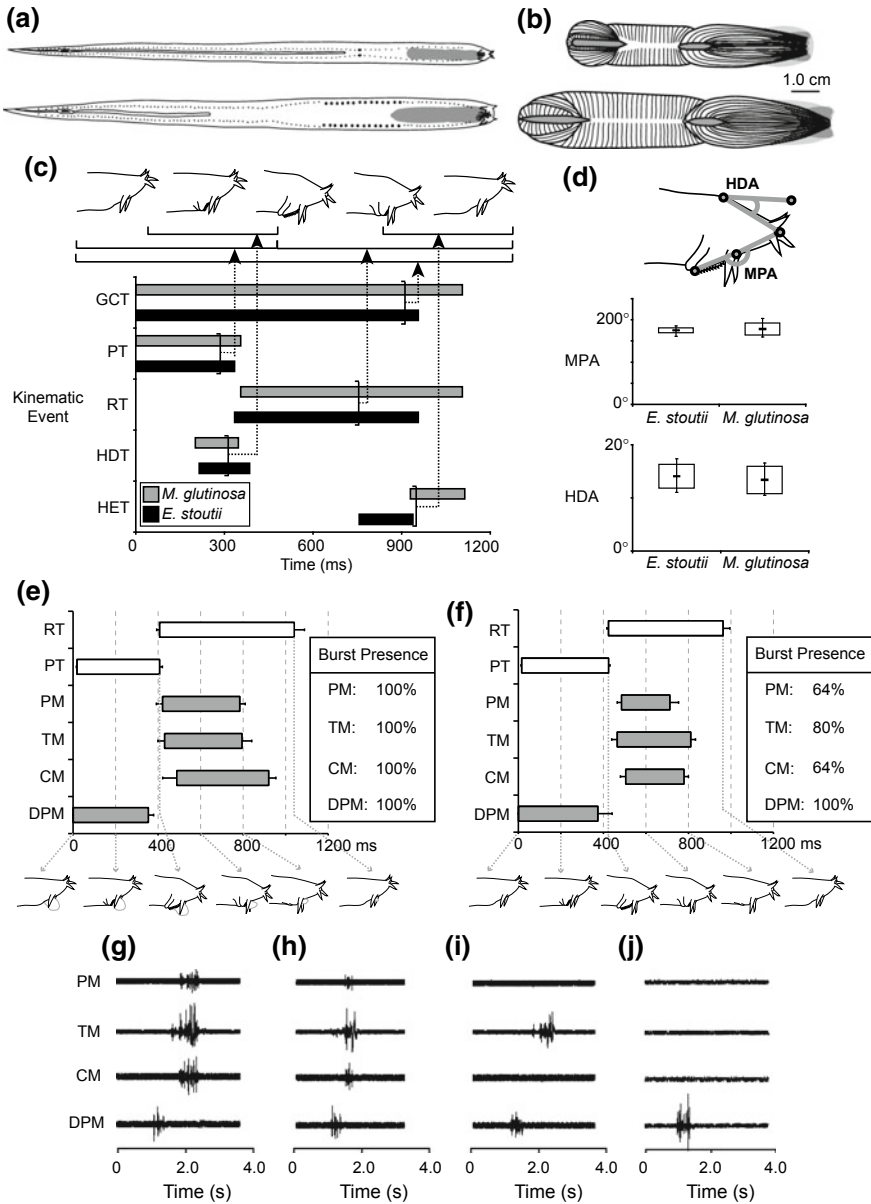
second, with tooth plate protraction and retraction accounting the initial third and latter two-thirds of the bite cycle. Stereotypic cranial movements like head depression and elevation were also similar between both species (Fig. 7.10d).

◀**Fig. 7.10** Interspecific variation in the hagfish feeding apparatus, exemplified in *Myxine glutinosa* and *Eptatretus stoutii*. **a** Ventral views of *M. glutinosa* (top) and *E. stoutii* (bottom) of similar *TL* with their feeding apparatuses shaded to indicate position in the head. **b** Ventral views of the feeding apparatuses from a *M. glutinosa* (top) and a *E. stoutii* (bottom) of similar *TL*. Note the significantly robust morphology in *E. stoutii* relative to *M. glutinosa*. Despite these discrepancies, kinematic time variables (**c**) and angular variables (**d**) of both *M. glutinosa* and *E. stoutii* are similar between these species. GCT gape cycle time; HDA, head depression angle; HDT, head depression time; HET, head elevation time; MPA, maximum protraction angle; PT, protraction time; RT, retraction time. Images in (**c**, **d**) have been modified from Clark and Summers (2007). **e**–**j** Muscle activity in the hagfish feeding apparatus. **e** Composite block diagram showing kinematic time variables (PT and RT) and the relative onsets, durations, and offsets of activation in the major feeding muscles of hagfish during the capture phase of feeding. Muscles include: the perpendicularis muscle (PM), clavatus muscle (CM), tubulatus muscle (TM), and the deep protractor muscle (DPM). The inset showing burst presence, indicates that during capture phases, all muscles studied were activated during each protraction–retraction cycle. **f** Block diagram showing the relative timing of kinematic events and muscle activation events during the intraoral transport phase of feeding. Note that the burst presence in the PM, CM, and TM decline when ingested food is being swallowed. **g** Raw electromyographic recordings (EMGs) show muscle activity patterns during a single gape cycle occurring in the capture phase. Raw EMGs from the first (**h**), second (**i**) and third (**j**) gape cycles of the intraoral transport phase demonstrate the progressive decline in burst presence from the retractor muscles once food is ingested. Images have been modified from Clark et al. (2010)

7.4.3 Muscle Activity in the Hagfish Feeding Apparatus

The soft component of the hagfish feeding apparatus (HFA) appears to function as both an actuator for the tooth plate and a skeletal support system for the retractor muscle pulling on the tooth plate. The soft component of the HFA is a cylindrical muscular hydrostat consisting of a three-dimensionally complex arrangement of connective tissues and muscle fibers with circular, bipennate (semi-longitudinal), and vertical orientations (Fig. 7.4) (Clubb et al. 2019). Clark et al. (2010) discovered that co-contraction of all three muscles comprising the hydrostat is what supports the *M. clavatus* as it pulls the tooth plates in the mouth (Fig. 7.10e–j). Synchronized video and electromyographic data from *M. glutinosa* Atlantic hagfish show that the *M. clavatus*, *M. tubulatus* (sphincter muscle), and *M. perpendicularis* stay inactive during protraction but fire when the tooth plates retract. These data also demonstrate that elastic recoil of the stretched retractor tendon, muscle, and connective tissues initiates the retraction of the tooth plates. This is evident from the absence of electrical activity during the initial 10–50 ms of tooth plate retraction (Fig. 7.10e, f). Instead of a bony or cartilaginous skeleton, the retractor muscle's force production is supported by the hydrostatic pressures generated by the activated *M. tubulatus*, and *M. perpendicularis*.

Simultaneous activation of the *M. tubulatus*, and *M. perpendicularis* effectively stiffens the origin of the retractor muscle, and therefore through pressurized myoplasm, transforms the soft component of the HFA into a rigid skeletal origin for the retractor muscle (Clark et al. 2010). The increased turgidity of this muscular hydrostat successfully resists deformations from applied loads, and thus facilitates the transmission of muscle-generated retractile force to the tooth plates.

Synergism from these three muscles occur during the capture phase, however, the muscle activity in the hydrostat progressively decreases when food is transported intraorally (Fig. 7.10g–j). This progressive reduction to absence of bursts from the *M. clavatus*, *M. tubulatus*, and *M. perpendicularis* during retraction in the intraoral transport phase also indicates the use of passive elastic recoil mechanisms (Clark et al. 2010). During the bite cycles associated with swallowing, the release of the strain energy stored during protraction suffices for retracting the tooth plates (Clark et al. 2010). Passive retraction like this has recently been observed in the feeding apparatuses of *E. stoutii* electrically stimulated to maximally protracted states (Fuerte-Stone et al. 2016).

7.4.4   Jawless Biting Versus Jawed Biting

The broader goal of the research conducted by Clark and Summers (2007) was, from the perspective of a jawless feeding system, to assess possible functional and selective advantages of jaws. By comparing biting force production, gape size, and biting speed of hagfishes with previously published data on various gnathostomes, Clark and Summers (2007) demonstrated that neither forceful bites nor large gapes are novelties presented by a jawed feeding apparatus. Despite their considerably soft and jawless condition, hagfishes are capable of generating as much biting force as a jawed vertebrate of similar size. The 180° gape angles achieved with maximally protracted tooth plates (Fig. 7.10d) enable hagfish to ingest large food items. Other than a few species of snakes and fishes, large gape angles as such are rarely implemented for prey capture among gnathostomes (Clark and Summers 2007). Delivering forceful bites and apprehending food with large gapes are beneficial for the rapacious foraging habits commonly observed in wild specimens (e.g., en masse feeding on a large carcass).

The speed at which the bite is delivered, however, appears to be a major functional innovation allowed by jaws (Clark and Summers 2007). The parameter of feeding that hagfishes appear to fall short is the bite cycle or gape cycle time. At 1000 ms, the protraction–retraction cycle of the hagfish is an order of magnitude longer than any previously published gnathostome bite cycle time. The sluggishness of the hagfish bite can be attributed to its feeding mechanism and, perhaps, to its feeding ecology.

Under a given amount of force, the amount of displacement and mechanical work achieved by a concentrically contracting muscle would be significantly enhanced if the muscle were to span one or multiple joints in a rigid lever or linkage system. These features are obvious in the gnathostome biting apparatus, which can be modeled as third-class levers or four-bar linkages typically geared to increase closing velocity at the expense of force (Frazzetta 1962; Muller 1987; Westneat 1990, 2004). The arthrodire placoderms, known for biting with heavy dermal cranial armor, likely avoided the problem of sluggishness by moving their heavy mouthparts with four-bar linkages geared for high kinematic transfer efficiencies (Anderson and Westneat 2007). Joints and rigid links are absent in the hagfishes, and even if modeled as a

pulley, the hagfish feeding apparatus neither amplifies the speed nor the force of the end effector (tooth plates) as in the levers or linkages (Clark and Summers 2007). The slower delivery of bites from hagfish is nonetheless suitable for a diet consisting of dead or dying animals, in which the pressure of apprehending elusive prey is relieved. However, faster gape cycles could facilitate the predatory habits noted in *Neomyxine* (see Zintzen et al. 2011). Lampreys and even some extinct agnathan lineages possibly rely on a similar mechanism for feeding like the hagfish (e.g., Janvier 1993; Yalden 1985), and thus could be faced with the same limitations for producing rapid bites.

7.4.5 No Joints? No Problem!

Many vertebrate biting systems can be represented by a simple mechanism including rigid upper and lower jaws that bear teeth anteriorly and are connected to each other posteriorly through a joint (Fig. 7.3a). Between the teeth and joint are jaw-adducting muscles that originate on the upper jaw and insert on the lower one. In this pincer-like organization, food is placed between the teeth, the jaw adductor muscles generate a force that is transmitted along the lower jaw to the lower teeth, which apply pressure (*sensu* Gignac and Erickson 2015) to the food that is subsequently transferred to the upper teeth, upper jaws, and jaw joints. In this closed kinematic chain, the upper jaws apply an opposing bite reaction force to the lower jaws (Newton's Third Law). Less obviously, unless one suffers from a temporomandibular joint disorder, there is also an equal and opposite reaction force that loads the joint in compression (Fig. 7.3a). This mechanism represents a closed kinematic chain, in which the food rests on the teeth of the lower jaw, the lower jaw is connected to the upper jaw through a compression-resistant joint and the teeth of the upper jaw makes contact with the food. If the joint was not able to resist compression, or did not exist, then muscular contraction would simply result in bringing the loose ends of the jaws together rather than breaching the food.

If one considers the hagfish feeding apparatus as simply an upper jaw with anteriorly pointing teeth, it can be simply modeled as a spear or spade. Perhaps the momentum of the forward swimming hagfish could be enough to drive the teeth into the prey, however, a model like this does not explain the strong retractile force that hagfishes can produce in order to tear off chunks of flesh. The hagfish mechanism must overcome two separate problems: (1) the feeding apparatus must be made into a rigid jaw structure, despite being composed of compliant muscle and connective tissue, and (2) the hagfish must create both an ad hoc temporomandibular-like joint and a lower jaw in order to close the kinematic chain. The musculature of the HFA is responsible for generating the force needed to move the tooth plates, while providing the structural stiffness needed to support the teeth as they are driven into the food. The first task, a muscle providing motive force, is quite conventional and depends on muscles pulling on tendons. However, the second and less obvious task depends on the muscle and connective tissues in the HFA to be arranged as a muscular hydro-

stat that becomes turgid and thus provides the rigid structural support needed to effectively use the tooth plate.

Muscular hydrostats are densely packed, three-dimensionally complex arrangements of muscle tissues that are composed of two or more muscle fiber orientations (Kier and Smith 1985). Fiber orientations may be arranged antagonistically to cause deformations, or, when co-contracting, may pressurize their myoplasm and lend a turgidity to the overall structure. This form of structural support contrasts the endo- and exoskeletal systems of vertebrates and arthropods that make extensive use of rigid links. A simple example of a muscular hydrostat may be a cylinder composed of longitudinal muscle fibers contained within a wall of circumferential fibers. If the longitudinal muscle fibers contract while the circular fibers are relaxed, the entire cylindrical structure becomes shorter and fatter because no changes in volume are occurring. Conversely, the cylinder becomes longer and narrower when the longitudinal muscles relax and the circular muscles contract. Alternatively, simultaneous contraction of the two orientations of fibers results in pressurization of the cylinder rather than any shape change. Muscular hydrostats can also be comprised of more than two muscles or connective tissue fiber orientations and the fibers may be oriented radially, helically, circumferentially or at any oblique angle depending on the required function (Kier and Smith 1985; Smith and Kier 1989).

EMG data from *M. glutinosa* reveal that these muscles relax during protraction of the tooth plates but simultaneously contract when the tooth plates are retracted (Clark et al. 2010; Fig. 7.9e–j). The co-contraction of these muscles effectively stiffens the soft component of the HFA, which (1) provides a necessarily rigid skeletal origin or anchor for the clavatus muscle that also facilitates the transmission of forces from the muscle to the tooth plates and (2) transforms the previously soft, deformable feeding apparatus into a turgid, deformation-resistant cylindrical block, or link, that stabilizes the motions of the tooth plates relative to the motions of the basal plate and whole body. This resistance to deformation by compressive bite reaction forces associated with tooth plate retraction and body movements precludes the feeding apparatus from buckling or collapsing while ingesting food. This resistance effectively counterbalances the retractile forces of the teeth and closes the kinematic loop in the hagfish feeding mechanism, like an anvil does to a hammer (Fig. 7.3c).

The ability of this soft feeding apparatus to simultaneously employ the functional roles as an actuator and stabilizer of tooth plates resembles the control strategies used by many forcefully biting, soft-bodied invertebrates. We hypothesize that the functionality of the missing parts of the hagfish biting system (e.g., second jaw and joint) is supported by the complex muscular hydrostat that is the posterior soft tissue component of the hagfish feeding apparatus (Clubb et al. 2019). This muscular hydrostat must function as (1) the force generator for movement, (2) a rigid structure that allows the tooth plate to be supported, and (3) a joint that allows the teeth to be positioned so that the force generated by integrated body movements can be leveraged for an opposing bite (Uyeno and Clark 2015). These multiple functions of a muscular hydrostat may be a commonly recurring functional motif in soft-bodied invertebrate morphology and are known as "muscle articulations." A fascinating example of a muscle articulation is the one associated with upper and lower beaks of cephalopods

(Uyeno and Kier 2005, 2007). In contrast to the better-understood "sliding joints" occurring in many animals with rigid skeletons, in which the articulating surfaces of the rigid links (e.g. upper and lower jaws) are in direct contact with one another (Wainwright et al. 1982), muscle articulations are a type of "flexible joint" in which muscle and connective tissues arranged as multifunctional muscular hydrostats form a repositionable joint or pivot area between two disconnected rigid links (Uyeno and Clark 2015). Muscle articulations are multifunctional because they provide the force to move the biting elements, create the joint interconnecting the rigid links, and transmit bite reaction forces (Uyeno and Clark 2015).

7.4.6 Body Knotting in Hagfishes

When a hagfish struggles to procure food with simple retraction or rearward swimming, it employs whole body knotting to close the kinematic loop and generate the necessary "biting" force. Here, perhaps counterintuitively, the extremely flexible body of the hagfish becomes an adaptation to creating leverage through the formation and deft manipulation of body knots (Fig. 7.11a). Elongate, limbless, gape-limited aquatic vertebrates are known for integrating head movements with body movements for reducing prey size or handling exceedingly tough prey. Knotting behaviors have evolved independently in hagfishes (Jensen 1966; Uyeno and Clark 2015), pelagic sea snakes *Pelamis platurus* (Pickwell 1971), and in some species of moray eels (Miller 1987; Barley et al. 2015), and considering its prevalence in hagfish feeding, body knotting may represent an ancestral vertebrate strategy for consuming oversized prey.

Possible adaptations for knotting in hagfishes include a flexible, elongate body comprising a complex arrangement of body wall (body core) muscles and an incomplete vertebral column devoid of vertebrae; all of which are enveloped in a loose skin (Clark et al. 2016). The axial muscles of hagfishes include two distinct segmented muscle groups (the parietal and rectus muscles) positioned deep to a superficially overlapping unsegmented oblique muscle (Cole 1907; Jansen and Andersen 1963; Vogel and Gemballa 2000; Clark et al. 2016) (Fig. 7.11b). These arrangements of body core muscles grant a large range of motion by enabling a hagfish to twist its body along its longitudinal axis, bend its body bilaterally and dorsoventrally.

The comparably slack skins of hagfishes likely enhance the flexibility of the predominantly decoupled body core (Clark et al. 2016; Freedman and Fudge 2017). This can easily be demonstrated by experimenting with sheath-core constructed ropes designed to possess different amounts of sheathing for cores of a fixed length and radius (Fig. 7.11c). Through these manipulations of rope sheath looseness, it is clear that the looser sheathed models are regularly flexible while tauter-sheathed ropes bear more flexural stiffness (Clark et al. 2016). Like the taut skins of other fishes, the skins of hagfishes are strong and stiff anisotropic biological composites; however, in contrast to other fish skins, the skins of hagfishes are more compliant to stresses
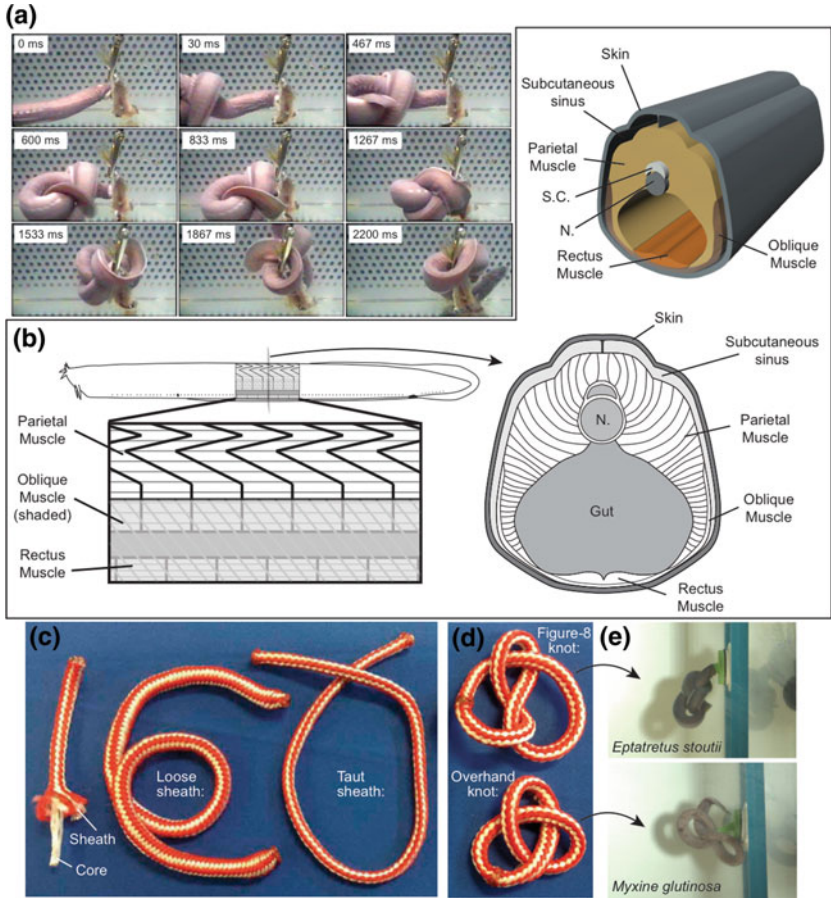
Fig. 7.11 Body knot formation and manipulation in hagfishes. **a** Video image sequence of a specimen of *Eptatretus stoutii* feeding on tethered food. Note that the formation of the knot begins in the caudal end of the hagfish, and once formed, the knot is slid towards the head and pressed against the food surface to leverage an ingestible piece of food. **b** The loose skin and complex axial musculature of hagfish. (Left) Lateral view of a hagfish with its body core muscles enlarged to show variable fiber arrangements of the three muscle groups: the parietal, rectus, and oblique muscles. (Right) Transverse section of a *E. stoutii* (approximately at 50%*TL*) showing how the superficial sheet of unsegmented oblique muscle overlaps with the segmented rectus and parietal muscles. (Right-top) Anterior-three-quarter view of a hagfish body segment (three-dimensional drawing) to illustrate the loose skin and arrangement of muscle tissues comprising the body wall (body core). N, notochord; SC, spinal cord. **c** Sheath-core constructed ropes can serve as models for the hagfish body, with the core of the rope representing the animal's body core, and the rope's sheath representing the animal's skin. Loose sheathed ropes (ropes with extra sheathing) are regularly flexible in contrast to ropes with tauter sheathes. **d** Two styles of knots commonly observed in hagfishes include the figure-eight (top) and trefoil, or overhand knot (bottom). **e** Video images of a *E. stoutii* (top) and a *M. glutinosa* (bottom) employed figure-eight and overhand knots, respectively. The hagfishes in these videos are employing body knots to free their heads secured within custom rubber membranes. Video images in (**a**) have been modified from Clark and Summers (2012). The two-dimensional drawings in (**b**) and the rope photos (**c**, **d**) have been modified from Clark et al. (2016). Austin Haney (VSU) provided the images in (**e**)

and strains applied in the circumferential direction. This discrepancy is proposed to facilitate the torsional movements required for the knotting (Clark et al. 2016).

To date, there are few studies that investigate the biomechanics and functional morphology associated with body knotting in hagfish (but see Haney et al. 2016). However, a large number of studies tangentially describe the function of body knotting based on qualitative observations (Jensen 1966; Zintzen et al. 2011; Clark and Summers 2012; Uyeno and Clark 2015; Glover and Bucking 2015; Clark et al. 2016). Generally, these functions fall into three categories: (1) Enhancing the retraction of the tooth plates while feeding on firmly tethered food (Clark and Summers 2012) and for extracting burrowing prey (Zintzen et al. 2011), (2) Removing potentially suffocating mucous from the body (Jensen 1966; Fudge 2001; Lim et al. 2006), and (3) Escaping predatory attacks (Jensen 1966). Knotting can be elicited in specimens restrained to rubber membranes (Haney et al. 2016), and by using this approach, we have been able to document the diversity in knotting kinematics across species in our laboratories (Fig. 7.11d, e).

Despite being relatively thinner and longer than *E. stoutii*, *M. glutinosa* typically requires more time to form and manipulate knots does not bend its body into loops with small radii. As such, *M. glutinosa* usually produce and manipulate simple loops or overhand knots, while specimens of *E. stoutii* regularly form figure-eight knots or even more complex knots (Fig. 7.11d, e). A possible reason for differences in body stiffness (at least behaviorally) may be because the skin is built differently between the two species: while transverse skin sections in both species show a great amount of connective tissue, *E. stoutii* skin shows additional fibers that stain in a manner consistent with muscle (Patel et al. 2017). Furthermore, different knotting behaviors might be attributed to the variation in the material properties of the skins between these species (Patel et al. 2017). Preliminary analyses of knotting events of both species suggest some commonalities in the form of underlying movements that, together, form all loops and knots. We hypothesize that these may represent motor primitives and believe that further studies on this matter are required as a development of complex body movements through control of a relatively small set of motor primitives may be an efficient method of controlling a long sinuous body that may deform in three-dimensional space at any position.

7.5 Jawless Feeding in Lampreys

7.5.1 Introduction

The jawless feeding mechanisms of lampreys can also give us some insight into the evolutionary trends of early vertebrate feeding. A notorious image of a foraging lamprey might be an adult parasitic species (e.g., *Petromyzon marinus* Sea lamprey) firmly attached to a fish or an aquarium glass wall (Fig. 7.12a). Adult *P. marinus* use keratinous teeth mounted on a "rasping tongue" like the hagfish feeding apparatus

to bite into large food items, however, in addition to biting, the lamprey feeding apparatus generates the suction required to adhere to the prey's body. Sea lampreys are highly recognized for their invasion of the North American Great Lakes and for their impact on endemic fishes at the individual and population levels (e.g., Smith and Tibbles 1980). There is a substantial literature on the gut contents of lamprey (e.g., Farmer 1980) and on the bite marks produced by parasitic lamprey on various prey (e.g., King 1980), however, studies on the functional morphology and biomechanics of lamprey feeding are comparably minimal.

Among the earliest descriptions on the form and function of feeding and breathing in adult lampreys came from Dawson (1905a, b). Subsequent efforts to characterize the feeding morphology of lamprey included postulates for function (Reynolds 1931; Lennon 1954; Lanzing 1958; Gradwell 1972; Hilliard et al. 1985). The ability for lamprey to firmly cling to surfaces has inspired studies on intraoral pressure fluctuations during suction and ventilation (Gradwell 1972), during vibration-induced startle responses (Currie and Carlsen 1988), and during feeding (Kawasaki and Rovainen 1988). Within the past 30 years, advances in our understanding of the functional morphology and biomechanics of adult lamprey feeding came from efforts by Hilliard et al. (1985), Kawasaki and Rovainen (1988), Rovainen (1996), and Renaud et al. (2009).

7.5.2   Feeding in Larval Lampreys

Lampreys have adopted different life history and feeding strategies to the hagfishes (Hardisty and Potter 1971a). Hagfishes only occur in marine environments and undergo direct development (Martini 1998), while lampreys develop as larvae, called ammocoetes, in freshwater environments for five to seven years (Hardisty and Potter 1971b). Most of the predatory, or parasitic lampreys are anadromous, taking on their post-metamorphic adult feeding habits in open-water marine environments. Following up to two years of this predatory stage, the lampreys migrate back to freshwater environments to spawn (Hardisty and Potter 1971b). Nonparasitic adults do not feed and remain in freshwater where they eventually spawn. Adults of all species die after mating (Hardisty and Potter 1971a, b).

Ammocoetes burrow into the substrate and expose their heads during feeding. The feeding apparatus of ammocoetes bears more resemblance to the urochordates and cephalochordates than to adult lampreys. Instead of using teeth, all species of larval lamprey possess oral and branchial cilia that are used for suspending food particles via mucous cords, which are subsequently pulled into the gut via ciliary action. This ciliary action is facilitated by a moderate suction that draws water to the mouth. Mallatt (1981) posited that the dual-pump model for teleost ventilation (Hughes and Shelton 1958) also applies to larval lampreys, though in the case of larval lamprey, the expansion of the mouth is achieved by releasing elastic strain energy stored in the wall of the actively compressed oropharyngeal cavity. Urochordates and cephalochordates draw in water via pharyngeal ciliary action but do not use cyclic
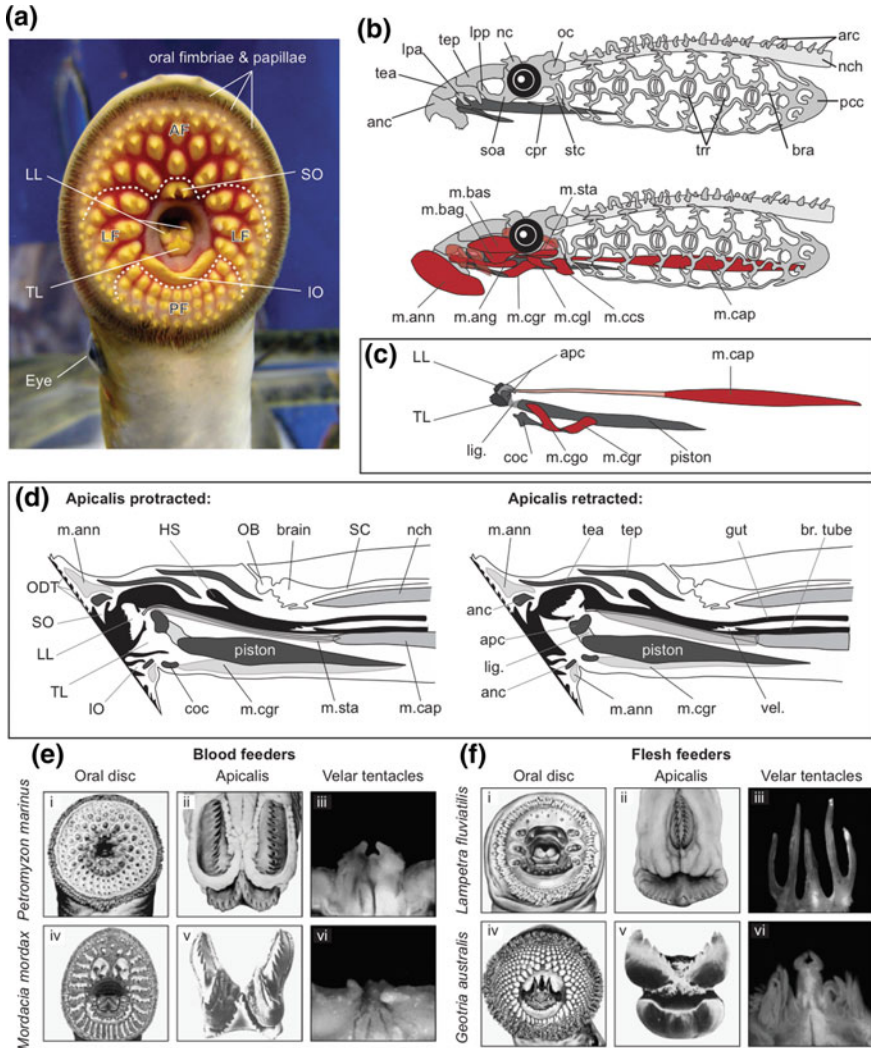
◄**Fig. 7.12** The form and function of lamprey feeding. **a** Photograph of a post-metamorphic sea lamprey (*Petromyzon marinus*) attached to an aquarium wall showing the dentition of the oral disc and apicalis (Photo credit: Andrea Miehls). Names and arrangements of teeth: AF, anterior field; IO, infraoral lamina; LF, lateral field; LL, longitudinal lingual laminae; PF, posterior field; SO, supraoral lamina; TL, transverse lingual lamina. **b** Left lateral views of the cranial skeleton of the lamprey (*Lampetra fluviatilis*) with musculature removed (top) and with major feeding muscles included (middle). Names of cartilages: anc, Annular cartilage; arc, arcualia; bra, branchial basket; cpr, cornual process; lpa, anterior lateral plate; lpp; posterior lateral plate; nc, nasal capsule; nch, notochord; oc, otic capsule; pcc, pericardial cartilage; soa, subocular arch; stc, styliform cartilage; tea, anterior tectal cartilage; tep, posterior tectal cartilage; trr, trematic ring. Names of muscles: m.ang, annuloglossus; m.ann, annularis; m.bag, basilaroglossus; m.bas, basilaris; m.cap, cardioapicalis; m.ccs, constrictor cornualis superficialis; m.cgr, copuloglossus rectus; m. cgl, cornuoglossus; m.sta, styloapicalis. **c** Left lateral view of the dentition, cartilage, and muscles in the "rasping tongue" of a lamprey (*L. fluviatilis*). apc, apical cartilage; coc, copular cartilage; lig, piston ligament; m.cgo, copuloglossus obliquus **d** Left lateral views of a lamprey (*Geotria australis*) sectioned in the mid-sagittal plane to illustrate the position of the apicalis in protracted (left) and retracted states (right). HS, hydrosinus; OB, olfactory bulb; SC, spinal cord; ODT, oral disc teeth; vel, velum; br. tube, branchial tube. **e**, **f** Comparative feeding morphology in blood-feeding and flesh-feeding lampreys, illustrating variation in the oral disc (i, iv), apicalis (ii, v), and velar tentacles in ventral view (iii, vi). Anatomical illustrations and photos were modified from Miyashita (2012) (**b**, **c**), Hilliard et al. (1985) (**d**), and Renaud et al. (2009) (**e**, **f**)

pumping of the branchial (pharyngeal) cavity for generating feeding currents, though ascidians (urochordates) can reject food by compressing the pharyngeal wall (Orton 1913).

7.6 Morphology of the Lamprey Feeding Apparatus

Most of our understanding of the morphology of the post-metamorphic lamprey feeding apparatus comes from parasitic species. The lamprey feeding apparatus is born on a cartilaginous cranial skeleton significantly more elaborate than the cranium of hagfishes (Fig. 7.12b), and the biting and suction achieved with both an oral disc and a tooth plate necessitates more muscles (e.g., Hilliard et al. 1985; Ziermann et al 2014; Miyashita 2015). Along with a piston cartilage and apicalis, major structures of the lamprey cranium involved in feeding include the annular cartilage, copula cartilage, branchial basket and pericardial cartilage (Hilliard et al. 1985). The relatively robust and numerous cartilages in the lamprey head form the rim of the oral disc (e.g., annular cartilage), drive biting movements (e.g., piston and apical cartilages), and support the muscle-generated forces during suction and retraction of the apicalis.

7.6.1 Oral Disc

A unique feature to the lamprey feeding apparatus is the oral disc, which facilitates attachment to a prey's body. Throughout the surface of the oral disc are numerous keratinous teeth arranged in left and right lateral fields, anterior fields and posterior fields (Hubbs and Potter 1971) (Fig. 7.12a). During attachment, the teeth of the oral disc become embedded in the host like athletic cleats that work to prevent slippage along the prey's body. Oral fimbriae and papillae are soft, filamentous structures lining the periphery of the oral discs in all lampreys (parasitic and nonparasitic), excluding species from *Mordacia*. These mucus-secreting soft tissue projections develop during metamorphosis and appear to have sensory functions (Lethbridge and Potter 1979; Khidir and Renaud 2003). Furthermore, mucus secretion around the rim of the oral disc has been proposed to aid in suction by producing a seal at the mouth (Lethbridge and Potter 1979). The oral disc is structurally supported by the annular cartilage and its movement or shape changes are largely controlled by the associated annularis muscles (Dawson 1905b) (Fig. 7.12b).

7.6.2 Apicalis and Piston Cartilage

The tooth plates of a lamprey, or apicalis, can be observed from the oral aperture located at the center of the oral disc (Fig. 7.12a). Like the tooth plates of hagfishes, the apicalis bears serially arranged keratinous teeth that can be driven into prey tissue by cyclic protraction and retraction (Fig. 7.12c, d). The apicalis comprises a single transverse lingual lamina positioned anterior to a pair of longitudinal lingual laminae. In some species, the teeth on the transverse and lingual laminae are serrated and like the teeth on the oral discs, the teeth on the apicalis are diverse across species and appear to be functionally associated with diets (Potter and Hilliard 1987; Renaud et al. 2009).

When the apicalis is cyclically protracted and retracted during feeding, its transverse lamina is most effective at puncturing the prey's integument while the paired longitudinal laminae, which bilaterally unfold and medially fold like hagfish tooth plates, intraorally transport blood and fleshy tissues to the gut (Hilliard et al. 1985). Underlying the apicalis, oral and gut cavities, is the supportive piston cartilage: a robust, elongate cone-shaped structure spanning between the oral aperture and the branchial basket. The piston cartilage of lamprey supports the movements of the apicalis and the piston cartilage itself, like molluscan odontophore and hagfish basal plates, can be protracted and retracted (Fig. 7.1). However, in contrast to the anatomically decoupled tooth plates and basal plates of hagfish, the apicalis of lamprey is directly attached to the head of the piston cartilage by a stiff, fibrous piston ligament (Hilliard et al. 1985) (Fig. 7.12c, d).

7.6.3   Major Feeding Muscles

The feeding behaviors of lamprey include stereotypic movements of the oral disc, tooth plates, pharynx (oral cavity), and velum (Hilliard et al. 1985; Kawasaki and Rovainen 1988); all of which are controlled by muscles innervated by branches of the trigeminal nerve (Lindström 1949). Described here are the major components of the lamprey feeding apparatus involved in the protraction and retraction movements of the apicalis and piston cartilages. Particularly useful references for the anatomy of these muscles include the investigations conducted by Hilliard et al. (1985), Miyashita (2012), and Ziermann et al. (2014). The research conducted by Hilliard et al. (1985) included functional postulates based on anatomical descriptions (gross dissection and histology) and manipulations of the feeding apparatus from euthanized specimens of Southern Hemisphere Lamprey *Geotria australis*. Particularly beautiful anatomical illustrations of the lamprey feeding apparatus can be obtained from Miyashita (2012).

The primary apicalis retractor muscle of a lamprey, the *M. cardioapicalis*, resembles the clavatus muscle of a hagfish in that it is connected to the apicalis by a long narrow tendon. In contrast to the clavatus muscle, the cardioapicalis muscle is born on a relatively robust pericardial cartilage, which forms the posterior surface of the branchial basket, and the associated sphincter muscle (*M. constrictor glossae profundus internus*) is substantially reduced relative to the robust tubulatus muscle of hagfishes and only encircles a portion of the cardioapicalis muscle and piston cartilage (Hilliard et al. 1985; Miyashita 2012; Ziermann et al. 2014). Constriction of the sphincter muscle is hypothesized to aid in protracting the piston cartilage (Hilliard et al. 1985). A putative synergist for the *M. constrictor glossae profundus* is the *M. constrictor cornualis superficialis*, which links the paired cornual processes adjacent to the posterior region of the piston and runs under the piston cartilage like a sling (Hilliard et al. 1985; Ziermann et al. 2014) (Fig. 7.12b).

Additional protractor muscles of the piston cartilage include the *M. annuloglossus* and *M. copuloglossus rectus* (Hilliard et al. 1985). The *M. annuloglossus* spans between the annular cartilage and piston cartilage, and the *M. copuloglossus Rectus* spans from the posterior end of copula cartilage to the piston cartilage. The *M. copuloglossus obliquus*, which originates from the posteroventral side of the copula and inserts onto the head of the piston, was originally hypothesized to be a retractor of the piston cartilage (Hilliard et al. 1985). However, in *Ichthyomyzon unicuspis* the *M. copuloglossus obliquus* appears to be a protractor of the piston (Kawasaki and Rovainen 1988). The large *M. basilaris* that overlaps many of the cranial muscles are also hypothesized to support the piston cartilage. The anteroventral extension of the *M. basilaris* that inserts onto the lateral posterior surface of the piston head (Hilliard et al. 1985), and likely functions in the expansion or compression of the oral cavity (Kawasaki and Rovainen 1988).

7.7 Biomechanics and Functional Morphology of Lamprey Feeding

The efforts of Hilliard et al. (1985) and Kawasaki and Rovainen (1988) include the most recent and important contributions to our understanding of the functional morphology and biomechanics of feeding in adult lamprey. Hilliard et al. (1985) provided a detailed anatomical description of the feeding apparatus musculature of *G. australis* with associated functional hypotheses. Kawasaki and Rovainen (1988) conducted experiments on live specimens of *Ichthyomyzon unicuspis*, which included observations of apicalis movements and suction pressure measurements synchronized with EMG recordings from the *M. basilaris*, *M. annularis* and branchial muscles during feeding. A helpful review of the feeding and breathing in lamprey can be obtained from Rovainen (1996).

7.7.1 Protraction and Retraction of the Apicalis

The adult lamprey feeding apparatus can generate biting movements through the cyclic protraction and retraction of the apicalis. These biting movements of the "rasping tongue" are coupled with biting and suction of the toothy oral disc being applied to the prey's body. Retractile forces from the *M. cardioapicalis* are transmitted to the apicalis by a long narrow tendon and supported by the pericardial cartilage. Protraction appears to be driven by the activity of the *M. copuloglossus rectus* and *M. copuloglossus obliquus* and the ligamentous linkages between the copula, piston, and apical cartilages (Kawasaki and Rovainen 1988).

Protraction–retraction cycles of the tooth plates in lampreys appears to be more restricted than the tooth plate movements of hagfishes. The limited motion of the tooth plate in adult lampreys can be attributed to the robust piston ligament connecting the tooth-bearing apical cartilage to the anterior edge of the supportive piston cartilage (Hillard et al. 1985; Fig. 7.12c, d). In the hagfish feeding apparatus, the tooth plates are free to move relative to the basal plate (see Clark and Summers 2007). Through manipulation of euthanized specimens of *G. australis*, Hillard et al. (1985) showed that the retraction of the tooth plates occurs during the protraction of the piston cartilage, and vice versa.

7.7.2 Feeding Modes of Parasitic Lampreys

Parasitic lampreys feed on blood and other tissues from a larger living host, typically a bony fish (Hardisty and Potter 1971a; Khidir and Renaud 2003). Lampreys use their toothed oral discs (or suckers), "rasping tongues," and volumetric fluctuations in the buccal (oral) and pharyngeal cavities to adhere to prey (Reynolds 1931; Lanzing 1958; Kawasaki and Rovainen 1988). The feeding morphologies and natural diets

of parasitic lampreys are diverse, and their feeding modes have been categorized as flesh-eating (Genera: *Ichthyomyzon*, *Petromyzon*, and *Mordacia*), blood-eating (Genera: *Eudontomyzon*, *Lampetra*, *Lethenteron*, *Geotria*), intermediate or blood-and-flesh-feeding (Genera: *Entosphenus* and *Tetrapleurodon*), and carrion-feeding (*Caspiomyzon wagneri*) (Potter and Hilliard 1987; Rovainen 1996; Renaud et al. 2009).

The relationships between feeding morphologies and phylogenetic patterns have been investigated by Hubbs and Potter (1971), Potter and Hilliard (1987), Salewski et al. (1995), Gill et al. (2003) and Renaud et al. (2009). Recent efforts by Renaud et al. (2009) provide an excellent description of the relationships between the diet and morphology of the dentition, buccal glands and velar apparatus in parasitic lamprey (Fig. 7.12e, f). Blood-feeding lampreys (e.g., *Petromyzon* and *Ichthyomyzon*) possess larger buccal glands than the flesh-feeding *Lampetra*, *Lethenteron*, *Eudontomyzon* and *Geotria*, which probably reflects the increased dependence that blood-feeding species have on anticoagulants (Renaud et al. 2009). Larger velar tentacles in flesh-feeding lamprey species relative to blood-feeding species are proposed to be useful in preventing larger food items from entering the branchial tube. In blood feeders, like *P. marinus* and *Mordacia* sp., the relatively narrow teeth born on the transverse lingual lamina and longitudinal laminae are proposed to be adaptations for rasping holes, while the stouter dentition in flesh feeders like *Lampetra fluviatilis* and *G. australis* are proposed to facilitate gouging tissue from the prey's body (Renaud et al. 2009; Fig. 7.12e, f).

7.7.3 Adhesion to Prey

Once a lamprey finds a place to cling to, it actively applies its oral disc, or sucker, onto the substrate until it successfully adheres to it. Manipulation of the sucker is achieved through contractions of the annularis muscle. Attachment of an adult lamprey to a substrate involves a vacuum created in the sucker cavity and oral (or buccal) cavity, accompanied by movements of the apicalis, piston, oral disc and whole body (Dawson 1905b). In addition to rasping and tearing flesh, the retracted apicalis appears to function like a valve between the oral cavity and sucker cavity, and prevents water in the oral cavity from leaking back into the sucker cavity (Kawasaki and Rovainen 1988). Thus, in addition to rasping and tearing flesh, the apicalis forms an intermittent seal between the sucker and oral cavity (Rovainen 1996). The velum functions like another valve that directs water flow from the oral cavity to the branchial tube or to the gut. If velar apparatus blocks passage of fluid to the branchial tube, the fluid will be directed to the esophagus. Separation of water flow enables a foraging parasitic lamprey to breathe while actively biting into the prey with its apicalis. Once attached to a substrate, water in the oral cavity and hydrosinus can be pressurized by constriction of the pharyngeal and basilaris muscles to flow into the branchial tube or into the esophagus (Reynolds 1931; Kawasaki and Rovainen 1988). Active muscle-generated expansion of the oral cavity induces a vacuum that draws

fluid into the mouth. This expansion of the oral cavity can occur with relaxation of the apicalis (during pumping) or with maximal protraction of the apicalis (during feeding). During feeding, cyclic protraction reaction of the apicalis does not impede suction (Kawasaki and Rovainen 1988; Rovainen 1996).

7.8 Conclusions

Because the jawless condition represents the primitive feeding apparatus for vertebrate animals, the biomechanics and functional morphology of jawless feeding in hagfishes can bear some insight into the selective and functional advantages of jaws (see Clark and Summers 2007). These studies also provide an informative perspective on the evolutionary trends in the form and function of feeding across the chordates, especially during those crucial transitional steps from suspension feeding with cilia to suction and biting with proper jaws. Despite their poor fossil record, some of the feeding mechanisms employed by many extinct taxa (e.g., conodonts and thelodonts) may be explained by careful observations and studies on the jawless feeding mechanisms of extant hagfishes and lampreys. There appears to be more diversity in the morphology and biomechanics of knotting and feeding across species that previously thought, given the progressive increase in the number of species and the advancements in our understanding of the phylogenetic relationships between hagfish species (see Fernholm et al. 2013).

Hagfish are jawless fishes that use the muscular hydrostatic function of their feeding apparatus to create turgid structural support for their everted tooth plates (Clark et al. 2010; Clubb et al. 2019). When extra biting force is needed to procure a grasped food item, hagfishes can use their flexible bodies to create an ad hoc joint and lever system. The joint connects the feeding apparatus to loops of body knot that are then pressed against the food item (Uyeno and Clark 2015). This body contact with the food item creates a closed kinematic loop that can then be used to generate leverage needed for forceful bites. With a significantly more elaborate cartilaginous cranium, the biting system of the adult predatory lamprey might not rely on muscular hydrostatics for achieving motive and structural support for inducing a bite within a closed kinematic loop, and furthermore, are not known for creating and manipulating body knots. Instead, the biting forces and movements of the apicalis appear to be supported by the robust cranial, branchial and pericardial cartilages, and counterbalanced by the suction and dentition on the oral disc.

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