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