

Functional Morphology of the Cephalopod Buccal Mass: A Novel Joint Type

Theodore A. Uyeno* and William M. Kier

University of North Carolina at Chapel Hill, Department of Biology, Chapel Hill, North Carolina 27599-3280

ABSTRACT The arrangement of the musculature and connective tissues of the buccal mass of the coleoid cephalopods *Octopus bimaculoides*, *Sepia officinalis*, and *Loliguncula brevis* was examined using dissection and histology. Serial sections in three mutually perpendicular planes were used to identify the muscles and connective tissues responsible for beak movements and stability and to describe their morphology and fiber trajectories. Four major beak muscles were identified: the anterior, posterior, superior, and lateral mandibular muscles. The anterior, posterior, and superior mandibular muscles connect the upper beak and the lower beak. Although the lateral mandibular muscles originate on the upper beak, they do not connect to the lower beak and instead insert on a connective tissue sheath surrounding the buccal mass. Examination of the fibers of the lateral mandibular muscles reveals that they have the organization of a muscular hydrostat, with muscle fibers oriented in three mutually perpendicular orientations. Although the beaks are capable of complex opening, closing, and shearing movements, they do not contact one another and are instead connected only by the musculature of the buccal mass. Based on the morphological analysis and observations of freshly dissected beaks undergoing the stereotyped bite cycle, the functional role of the beak muscles is hypothesized. The anterior and superior mandibular muscles are likely responsible for beak closing and shearing movements. The posterior mandibular muscle is likely also involved in beak closing, but may act synergistically with the lateral mandibular muscles to open the beaks. The lateral mandibular muscles may use a muscular-hydrostatic mechanism to control the location of the pivot between the beaks and to generate the force required for beak opening. The lack of contact between the beaks and the morphology of the lateral mandibular muscles suggests that the buccal mass of coleoid cephalopods may represent a previously unexamined flexible joint mechanism. The term “muscle articulation” is proposed here to denote the importance of the musculature in the function of such a joint. *J. Morphol.* 264:211–222, 2005. © 2005 Wiley-Liss, Inc.

KEY WORDS: joint; cephalopod; muscle; articulation; buccal mass; *Octopus bimaculoides*; beak; feeding

INTRODUCTION

Definitions and Characterizations of Joint Types

Two categories of animal joints are generally recognized: flexible and sliding joints (Wainwright et al., 1982; Alexander, 1983). Flexible joints are formed when a more pliant region connects two rigid

skeletal elements (termed links) (Fig. 1). Flexible joints are found in arthropods, such as the simple joints between the subsegments of the tarsus in the locust. They are also seen between the shell plates of chitons. Sliding joints are common in vertebrate skeletons and are characterized by two or more discrete links that contact and move relative to each other within the joint (Fig. 2). Force is transmitted from link to link through the joint and the range of motion is determined by the shapes of the articulating surfaces and the surrounding ligaments, tendons, and connective tissues.

Joints transmit force from one link to another throughout their range of motion. The forces transmitted are generated by the musculature during movement and antagonism, by reaction forces, and by gravity, and include compression, bending, torsion, and sometimes tension. Thus, an effective joint must be capable of allowing appropriate motion while safely transmitting a potentially diverse array of forces (McCarthy and Juskowitz, 2001).

The joint type described here is a specialized form of flexible joint in which the links are embedded in a mass of muscle and connective tissue. The muscle fibers may function as a muscular hydrostat (Fig. 3), in which fibers are arranged in a tightly packed three-dimensional array (Kier and Smith, 1985; Smith and Kier, 1989). In such an array, the contraction of muscle fibers oriented in one direction changes the shape of the array, creating deformation and movement and lengthening antagonistic muscle fibers running in another orientation. Thus, the muscle tissue in which the links are embedded must function as a joint while also generating the

Contract grant sponsors: American Microscopical Society; University of North Carolina Wilson Fund (to T.A.U.); National Science Foundation; Contract grant number: IBN-972707; Contract grant sponsor: DARPA; Contract grant number: N66001-03-R-8043 (to W.M.K.).

*Correspondence to: Theodore A. Uyeno, Department of Biology, CB#3280, Coker Hall, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3280. E-mail: uyeno@bio.unc.edu

Published online 23 March 2005 in
Wiley InterScience (www.interscience.wiley.com)
DOI: 10.1002/jmor.10330

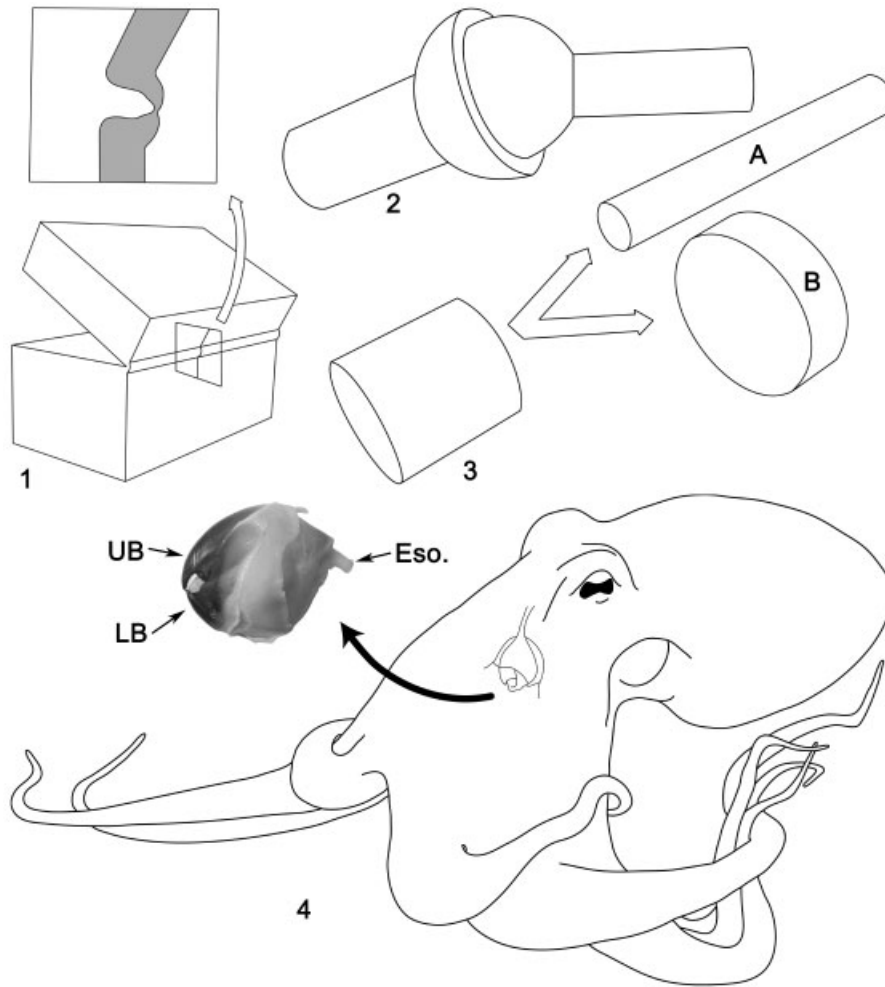


Fig. 1. A drawing of a box in which the base and lid are connected by a flexible joint. Note that the lid and base are formed of a single piece of material in which the hinge represents a thin connection that allows bending.

Fig. 2. A schematic drawing of a ball-and-socket style sliding joint. The terminal end of the right link is a sphere that fits within the cup of the left link. Such an arrangement allows rotation at the articulation while force is transmitted between links.

Fig. 3. A depiction of the action of a generalized muscular hydrostat. Muscular hydrostats are composed of a 3D arrangement of muscle fibers. A cylindrical muscular hydrostat such as the one depicted here may change shape due to the selective contraction of the muscle fibers of a given orientation, but it does not change volume significantly. For instance, change in shape such as that shown in A can be created by the contraction of fibers arranged radially or circumferentially. Change in shape such as that shown in B is created by contraction of longitudinal muscle fibers, i.e., fibers parallel to the long axis of the cylinder.

Fig. 4. A drawing of the position of the buccal mass within *Octopus bimaculoides*. The inset photo shows the left side of the buccal mass and the orientation of the buccal mass in the descriptions that follow: the dorsal surface is up, the ventral surface is down, the chitinous beaks (UB, upper beak; LB, lower beak) mark the anterior end of the buccal mass and the esophagus (Eso.) is posterior. Note that the beaks are in an opened position.

force that moves the links relative to each other. The term “muscle articulation” is proposed here to describe such a joint in which the muscle serves this dual function.

Cephalopod Buccal Mass Gross Morphology and Function

The buccal mass of the cephalopod studied in detail here, the California two-spot octopus *Octopus*

bimaculoides (Pickford/McConnaughey, 1949), and those of other cephalopods we examined, the common cuttlefish *Sepia officinalis* (Linnaeus, 1758) and the Atlantic brief squid *Lolliguncula brevis* (Blainville, 1823), show the characteristics of a muscle articulation because the upper and lower beaks (or “jaws” or “mandibles”) are embedded in muscles, do not articulate with one another (Kear, 1994), and are not connected by a flexible skeletal material. A

summary of the function and gross morphology of the buccal mass is provided below.

Octopus, squid, and cuttlefish, members of the subclass Coleoidea, are almost exclusively marine predators that have adapted to most marine habitats (Nixon and Young, 2003), including deep trenches and seamounts (Nesis, 1993) and even hydrothermal vents (Tunnicliffe et al., 1998). Coleoids feed on a wide range of prey including crustaceans, fishes, gastropods, bivalves, other cephalopods, polychaetes, ophiuroids, and foraminiferans (Nigmatullin and Ostapenko, 1976; Wells, 1978; Nixon and Budelmann, 1984; Nixon, 1987; Hanlon and Messenger, 1996; Nixon and Young, 2003). Members of the family Octopodidae (which includes the species genus *Octopus*) are mainly benthic (Nixon and Young, 2003). Feeding by octopods usually involves boring shells (Nixon, 1969, 1979a,b, 1980; Nixon et al., 1980; Nixon and Maconnachie, 1988), or piercing hard external skeletons, followed by injection of immobilizing saliva (Ghiretti, 1959, 1960; Cariello and Zanetti, 1977) and the manipulation and mastication of tissue into smaller pieces (Altman and Nixon, 1970; Kear, 1994).

Feeding is accomplished by the buccal mass. The buccal mass is a roughly spherical structure that lies just in front of the brain, within a sinus formed by the base of the arms (Boyle et al., 1979; Kear, 1994; Nixon and Young, 2003) (Fig. 4). The buccal mass is loosely attached within the sinus by the esophagus and the enclosing buccal membrane, a pigmented web of folded skin that is attached to the arms. The buccal membrane surrounding the beaks is folded into inner and outer lips (Nixon and Young, 2003). The exposed muscles of the buccal mass into which the beaks are embedded are covered by the buccal mass sheath, a thin, tough membrane of connective tissue and epithelium (Tanabe and Fukuda, 1999).

The buccal mass is composed of several structures. The upper and lower beaks are attached to each other by the mandibular muscles responsible for opening and closing. Both the upper and lower beaks are composed of a chitin-protein complex (Hunt and Nixon, 1981). The beaks are secreted by a single layer of tall columnar cells known as beccublasts. The beccublasts also attach the mandibular muscles to the beaks (Dilly and Nixon, 1976). Clarke (1962, 1986) described the morphology of the beaks and defined their descriptive terminology. The upper and lower beaks are roughly similar. Both beaks resemble U-shaped troughs in which the anterior portions are folded back upon themselves to create a biting surface and a hood (Fig. 5). The upper beak differs from the lower beak in possessing a pronounced hood, a sharp rostrum, and lateral walls of large surface areas, whereas the lower beak is characterized by exaggerated wings and a rounded anvil-like rostrum and jaw angle. The upper beak fits within the lower beak, creating an internal buccal cavity. This general form is seen even in the oldest

fossilized beaks from Carboniferous coleoids (Tanabe and Fukuda, 1999). Although the general form of the coleoid beak is similar among octopods, sepioids, and teuthoids, there are some consistent differences. Decapod (sepioid and teuthoid) upper beaks have relatively longer hoods and a larger space behind the hood but a smaller lateral wall area. Decapod lower beaks have more pointed rostra and shorter (the distance from the jaw angle to the posterior end of the crest) but deeper (the dorsoventral width) lateral walls (Kear, 1994).

Within the buccal cavity lies the buccal complex, which is comprised of the lateral buccal palps, salivary papilla, salivary glands, radula, and radular support system (Nixon and Young, 2003). The radular support system includes two cylindrical muscular hydrostatic bolsters that serve to anchor elements of the buccal complex and lower beak (Young, 1991; Messenger and Young, 1999). Thus, biting movements are generally characterized by the upper beak moving into contact with the lower beak.

The buccal mass is relatively free to swivel within the sinus, allowing for a large gape and even lateral movements. Even when dissected from the body, the beaks are capable of spontaneous biting cycles for up to 2 h after excision (Boyle et al., 1979). Young (1965, 1971), described the neural anatomy of the buccal mass and noted that the mandibular muscles were innervated by the inferior buccal ganglion, which in turn receives input through the interbuccal connective from the superior buccal lobe. Boyle et al. (1979) provided additional evidence that the musculature is controlled by the inferior buccal ganglion.

After the identification of a "mandibular muscle" by Young (1965), and the expansion of the nomenclature by Altman (unpubl. notes; see Kear, 1994) to include a superior, a lateral, and an inferior mandibular muscle, there have been two major functional descriptions of the cephalopod buccal mass.

Boyle et al. (1979) described two groups of muscles in the buccal mass of *Octopus vulgaris*: the paired lateral mandibular muscles and the superior mandibular muscle. They recorded electromyograms from various locations in the muscles of isolated buccal masses and observed activity during closing, but were unable to find locations of muscle activity during beak opening movements.

In a later study that focused on 23 species of coleoid cephalopods, Kear (1994) recognized an additional thin posteroventral layer of longitudinal muscle underneath the buccal mass sheath, and re-described the inferior mandibular muscle. Kear (1994) also studied the stereotypic movements of isolated buccal masses of *Eledone cirrhosa*, *Sepia officinalis*, *Loligo forbesi*, and *Alloteuthis subulata*. She described in detail the position of the beaks of *S. officinalis* and *A. subulata* during a full bite cycle. The bite cycle was defined as the movements of the beaks between five separate positions: 1) resting, 2) opening, 3) fully open, 4) closing, and 5) closed and

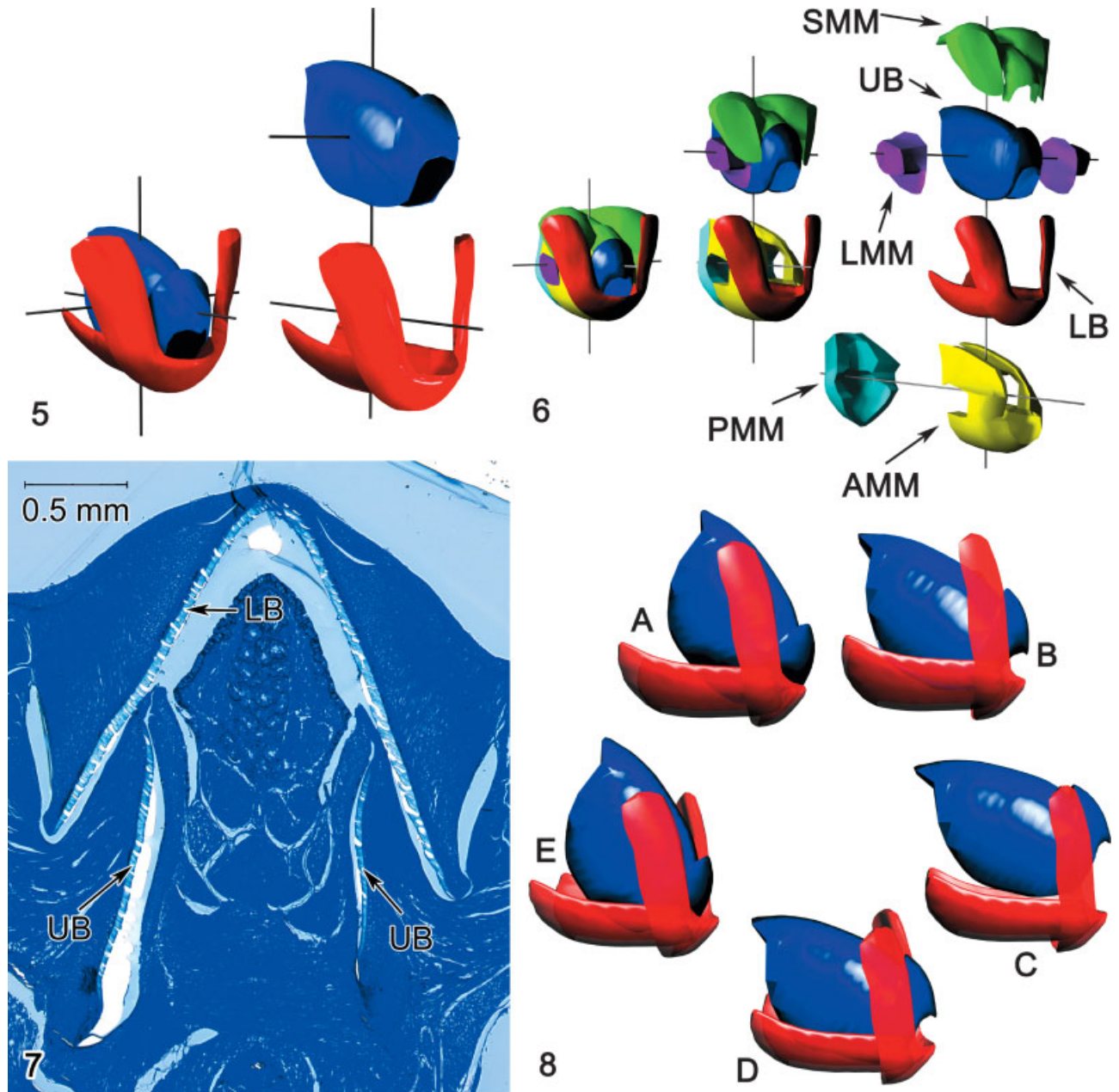


Fig. 5. A computer rendering of the upper (blue) and lower (red) beaks of *Octopus bimaculoides*. The left pair shows how the upper beak fits within the lower beak. The right pair shows the upper beak separated from the lower. Both sets are pictured in a front right quarter view.

Fig. 6. A series of computer renderings of three sets of beaks of *Octopus bimaculoides* with attached mandibular muscles. The left set shows the muscles attached to the beaks. The center set shows the upper and lower beaks separated with the mandibular muscles originating on the respective beaks. The right set shows the beaks and mandibular muscles separated. The color convention is as follows: the lower beak (LB) is red, the upper beak (UB) is dark blue, the superior mandibular muscle (SMM) is green, the lateral mandibular muscles (LMM) are purple, the anterior mandibular muscle (AMM) is yellow, and the posterior mandibular muscle (PMM) is light blue.

Fig. 7. Micrograph of a frontal section of the buccal mass of *Lolliguncula brevis*. The anterior is towards the top of the micrograph. The section is at a level where both the lower beak (LB) and upper beak (UB) are visible in the same plane. The lateral walls and the crest of the lower beak are cut obliquely. The lower edges of the left and right lateral walls of the upper beak are also visible. This is as close together as the upper and lower beaks were observed; they do not contact one another. Brightfield microscopy of 3.0- μ m thick glycol methacrylate section.

Fig. 8. Diagram illustrating movement of the upper beak (blue) with respect to the anchored lower beak (red), of *Octopus bimaculoides*, during a stereotypical bite cycle (description follows Kear, 1994). Position A, resting; B, opening; C, fully open; D, closing; E, closed and retracted.

retracted. During this cycle, she noted that the axis of rotation of the upper beak during biting movements varied and thus was not restricted to a single location. Like Boyle et al. (1979), she also stimulated various locations of the musculature electrically and observed that closing of the beaks was elicited in response to stimulation at most locations. Electrical stimulation of the area near the inferior buccal ganglion elicited an entire bite cycle. Only simultaneous stimulation near the centers of the paired lateral mandibular muscles resulted in a strong opening movement (Kear, 1994). It is unclear, however, how the lateral mandibular muscles generate force to open the beaks.

The goal of this study was to analyze, in detail, the morphology of the musculature and connective tissues of the buccal masses of *Octopus bimaculoides*, *Sepia officinalis*, and *Lolliguncula brevis* in order to explore the roles of the various muscles in beak movements and muscle articulations.

MATERIALS AND METHODS

Four adult specimens of *Octopus bimaculoides* (70–99 g wet weight), obtained from the National Resource Center for Cephalopods (Galveston, TX), were quickly and lightly anaesthetized using 2.5% ethanol in seawater (O'Dor et al., 1990). After the specimens were relaxed, the buccal masses were removed and placed in small bowls containing aerated seawater chilled to 17°C. The endogenous bite cycles performed by the excised buccal masses were observed and the entire buccal masses were then immediately fixed for at least 48 h in buffered formalin in seawater (10% v/v; Kier, 1992). One specimen was dissected to identify major features of the buccal mass musculature (such as discernable muscle divisions, overall shape, and origins and insertions). During the dissection, digital photographs and measurements were taken of the beaks and muscles to provide data for a 3D model. Fixation weakens the beccublast connection between the beaks and the musculature, thus facilitating the removal of the beaks in larger specimens prior to embedding. The remaining buccal masses were reserved for histological processing. The larger buccal masses without beaks were dehydrated, embedded in paraffin (Paraplast Plus, Monoject Scientific, St. Louis, MO), and serially sectioned at 10 µm, one each in transverse, parasagittal, and frontal planes. The sections were stained using Milligan's Trichrome stain and Picro-Ponceau with Hematoxylin stain on alternate slides (Kier, 1992) and examined by brightfield and polarized light microscopy. The former location of the beaks was apparent in the sections because the beccublasts could be observed lining the space formerly occupied by the beaks. Particular attention was focused on documenting muscle fiber trajectories. Those fibers with trajectories potentially arranged as a muscular hydrostat were defined as a single muscular functional unit. A 3D model of the muscles and connective tissues was constructed using 3D modeling software (Anim8or, <http://www.anim8or.com>). The basic shape of the beak and muscles was drawn using digital photographs of the dissection and then outlines were digitized for manipulation by the software. The dimensions of the model were then adjusted by matching ~300 points on the model to measurements of corresponding points in the dissected buccal mass. For comparative purposes, the buccal masses of five specimens of the cuttlefish, *Sepia officinalis* (280–440 g wet weight) were examined with serial sections in transverse, frontal, and parasagittal planes using the procedures described above. The beaks of the brief squid, *Lolliguncula brevis* (18–24 g wet weight), were small and thin enough to section without removing them from the buccal mass. Therefore, the intact buccal masses of six specimens were dehydrated, embed-

ded in glycol methacrylate plastic (JB-4, Structure Probe, Inc., West Chester, PA), and serially sectioned at 3 µm in transverse, parasagittal, and frontal planes. Every tenth section was collected and stained using Toluidine blue stain (2% Toluidine blue O (C.I. 52040) in 2% sodium borate; modified from Burns, 1978).

RESULTS

Morphology of the Beaks and the Mandibular Muscles

Orientations and abbreviations. The following descriptions and images rendered from the 3D computer model are based on analyses of the buccal mass of *Octopus bimaculoides*. The morphology of the beaks and mandibular muscles of *Sepia officinalis* and *Lolliguncula brevis* were similar and all significant differences are noted below.

Although the long axis of the esophagus of benthic octopods is normally vertical, the isolated buccal mass is described here with the long axis of the esophagus horizontal, making the orientation of the buccal mass identical to that of pelagic cephalopods, such as *Sepia officinalis* and *Lolliguncula brevis*. Thus, the rostra are anterior and the esophagus is posterior (Fig. 4). The upper and lower beaks occupy a dorsal and ventral position and each is bilaterally symmetrical about the sagittal plane.

Four mandibular muscles are recognized here: the paired left and right lateral mandibular muscles, the anterior mandibular muscle, the posterior mandibular muscle, and the superior mandibular muscle (Fig. 6).

Upper and Lower Beak

The upper and lower beaks of the species examined here do not articulate with each other. Figure 7 is a frontal section from the lower quarter of the buccal mass of *Lolliguncula brevis* showing the lower and upper beak lateral walls. No contact was observed between these lateral walls. Instead, the upper and lower beaks slide by each other. The only points at which the beaks make contact are at the occlusion of the rostra and jaw angles (i.e., those surfaces that are used for shearing food).

The beaks of the three coleoids examined in this study are similar in overall morphology. The beaks of *Sepia officinalis* (a sepioid) and *Lolliguncula brevis* (a teuthoid) are less robust than those of the octopod *Octopus bimaculoides*. The rostra of *O. bimaculoides* are much less pointed than those of *S. officinalis* and *L. brevis* and the lower beak rostrum of *O. bimaculoides* is especially well rounded. The lower beak of *O. bimaculoides* has relatively large lateral wings that provide large surfaces for muscle attachment. The hood of the upper beak of *O. bimaculoides* is relatively shorter and broader than that of *S. officinalis* and *L. brevis*.

By observing the movements of the portions of the beaks not embedded in tissue during the stereotypical buccal mass bite cycles and comparing sections

of buccal masses that have been fixed in different positions, we can identify the positions of the beaks within the buccal mass during the bite cycle. The bite cycle of the isolated buccal mass of *Octopus bimaculoides* is very similar to that described by Kear (1994) for *Sepia officinalis* and *Alloteuthis subulata*. We did not observe and could not evoke bite cycles in the freshly dissected buccal masses of

Lolliguncula brevis. Figure 8 shows a summary of the orientations of the beak of *O. bimaculoides* at each step in the bite cycle.

Lateral Mandibular Muscle

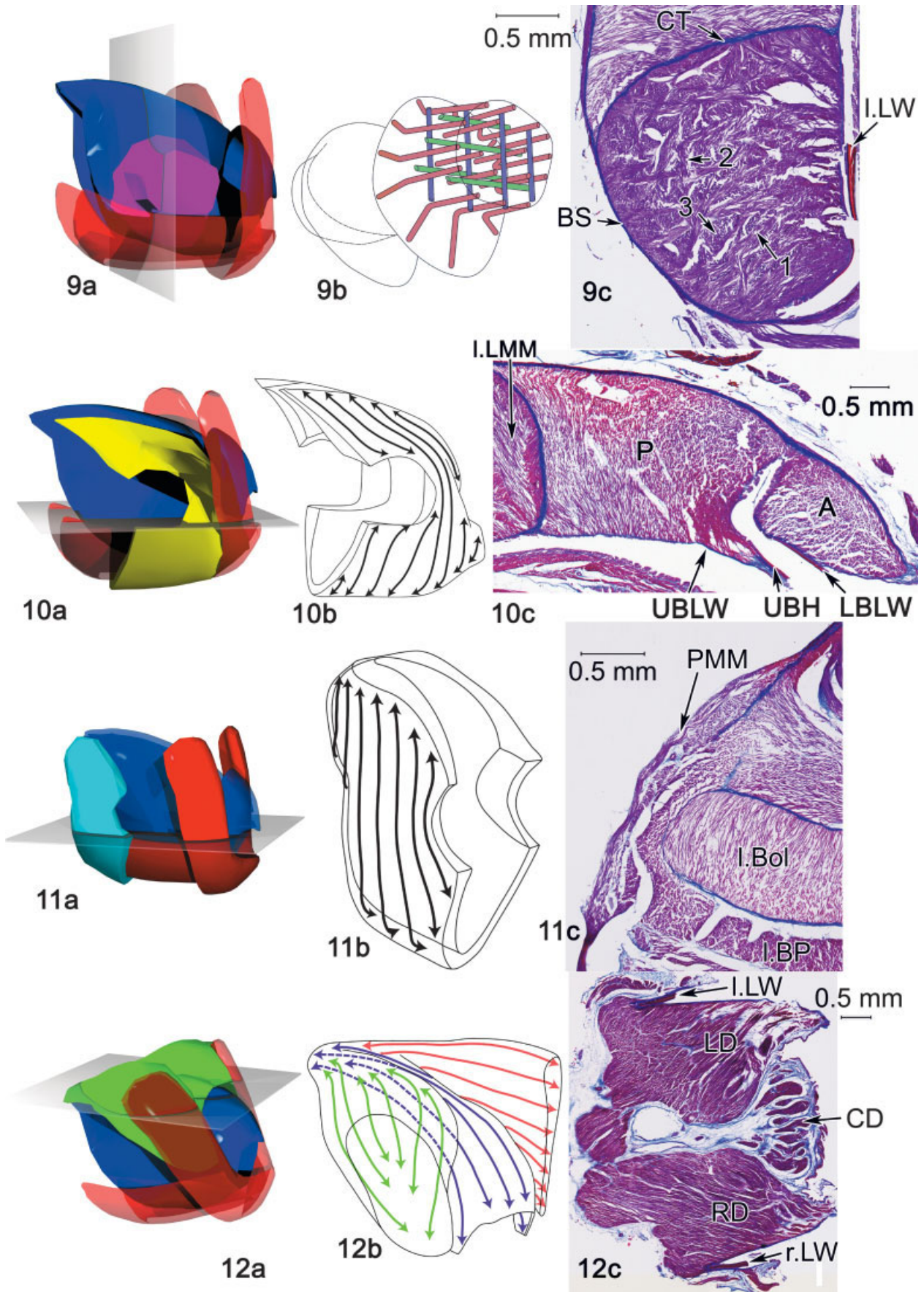
Gross morphology. The symmetrical left and right lateral mandibular muscles are robust cylin-

Fig. 9. **a:** A right rear quarter view of the right lateral mandibular muscle in *Octopus bimaculoides* (the rostra are pointing to the right). The right lateral mandibular muscle, shown in purple, is roughly cylindrical and flared at its base. The transparent plane indicates the section plane of the micrograph shown in **c**. **b:** A right rear quarter view of the lateral mandibular muscles without the beaks showing the orientations of muscle fibers of the right lateral mandibular muscle. The red fibers originate on the lateral wall of the upper beak and extend laterally towards their insertion on the buccal sheath. Those fibers at the edges of the lateral mandibular muscle curve because the medial surface is larger than the lateral surface. The blue fibers are oriented dorsoventrally. The green fibers are oriented anteroposteriorly and therefore have an orientation perpendicular to the other two sets of fibers. **c:** Micrograph showing a transverse section of the left lateral mandibular muscle at its thickest part. The left margin of the lateral mandibular muscle is left in the image. The dorsal surface is towards the top. A portion of the left lateral wall of the upper beak (l. LW) and the buccal sheath (BS) are visible. The lateral mandibular muscle appears round as the beaks were removed and the lateral mandibular muscles are contracted. Note that there are three orientations of muscle fibers. Some fibers (1) are oriented laterally (visible as horizontal fibers in the plane of section) extending from the lateral wall (l. LW) to the buccal sheath (BS). Additional fibers (2) are oriented in the plane of section in a dorsal-ventral orientation. Fibers oriented in an anterior-posterior direction (3) are visible in transverse section. Note that these numbered fiber orientations correspond to the colored fiber orientations in **b** (1 = red, 2 = blue, 3 = green). Brightfield microscopy of 10- μ m paraffin section stained with Milligan's Trichrome.

Fig. 10. **a:** A right rear quarter view of the anterior mandibular muscle in *Octopus bimaculoides* (the rostra are pointing to the right). The anterior mandibular muscle (yellow) is a broad muscle that partially fills the space within the upper beak hood and completely fills the space within the lower beak hood. The transparent plane identifies the section plane of the micrograph shown in **c**. **b:** A right rear quarter view of the anterior mandibular muscle without the beaks. Arrows indicate the trajectory of muscle fibers. The fibers of the anterior mandibular muscle run in a roughly parallel direction from their origin on the lateral walls of the lower beak, around the anterior edge of the lateral mandibular muscles, to the lateral walls of the upper beak. **c:** Micrograph showing the left half of a frontal section of the middle of the buccal mass of *Octopus bimaculoides*. Anterior is towards the right. The section is at a plane just below the midline of the buccal mass. The left lateral wall of the lower beak (LBLW), the left side of the hood of the upper beak (UBH) and the beccublasts that attach to the left lateral wall of the upper beak (UBLW) are visible. Two portions of the anterior mandibular muscle are visible. The anterior part (A) lies anterior to a crease formed by the proximity of the lateral wall of the lower beak to the hood of the upper beak. The posterior part (P) lies between this crease and the left lateral mandibular muscle (l. LMM). Note that along most of the cross section of the anterior mandibular muscle the fibers are cut in cross section, denoting a dorsoventral orientation. The posteriormost fibers, however, show a more oblique orientation as they are following the anterior edge of the contracted left lateral mandibular muscle (l. LMM). Brightfield microscopy of 10- μ m paraffin section stained with Milligan's Trichrome.

Fig. 11. **a:** A right front quarter view of the posterior mandibular muscle in *Octopus bimaculoides* (the rostra are to the right). The posterior mandibular muscle (light blue) covers the posterior opening of the upper and lower beak and anchors the structures within the buccal cavity. The transparent plane identifies the section plane of the micrograph in **c**. **b:** A right front quarter view of the posterior mandibular muscle without the beaks showing the trajectory of muscle fibers. The fibers of the posterior mandibular muscle are similar to those of the anterior mandibular muscle, in that they run in a roughly parallel direction from their origin on the lateral walls of the lower beak to the lateral walls of the upper beak. They differ, however, in curving around the posterior edges of the lateral mandibular muscles. **c:** Micrograph of the left half of a frontal section from the lower half of the buccal mass of *Octopus bimaculoides*. Posterior is towards the left. The posterior mandibular muscle (PMM) is the thinnest mandibular muscle. The fibers of the posterior mandibular muscle are oriented in the plane of this section. They interdigitate with the muscles of the organs of the buccal cavity and with the mandibular muscles. Note the left bolster (l. Bol) and the muscles of the left buccal palp (l. BP) that fill the buccal cavity. The spaces between the posterior mandibular muscle and the organs of the buccal cavity are artifacts. Brightfield microscopy of 10- μ m paraffin section stained with Milligan's Trichrome.

Fig. 12. **a:** A right front quarter view of the superior mandibular muscle in *Octopus bimaculoides* (the rostra are pointing to the right). The superior mandibular muscle (green) is the largest muscle that connects the upper and lower beaks. The transparent plane identifies the section plane of the micrograph in **c**. **b:** A right front quarter view of the superior mandibular muscle without the beaks showing the three divisions. The green arrows show the trajectories of the muscle fibers of the right division. These fibers originate within the posterior central division and insert on the right lateral wing of the lower beak. The trajectories of the fibers in the central division are indicated by blue arrows. These fibers originate and insert along the entire crest of the upper beak. The left division is symmetrical with the right division. The red arrows represent muscle fiber directions within the left division. The left division fibers also originate on the posterior central division, but insert on the left lateral wing of the lower beak. **c:** Micrograph of a frontal section of the dorsal portion of the buccal mass of *Octopus bimaculoides*. The anterior is to the right. The micrograph shows the left (LD) and right (RD) divisions of the superior mandibular muscle extending from the midline out to their insertion points on the left (l. LW) and right (r. LW) lateral wings of the lower beak. The central division (CD) of the superior mandibular muscle that exists between the hood and crest of the upper beak is also shown. The space surrounded by blue connective tissue in the center of the section is the area once occupied by the crest of the lower beak (removed). Brightfield microscopy of 10- μ m thick paraffin section stained with Milligan's Trichrome.



Figures 9–12.

ders of muscle tissue that are surrounded by connective tissue. The lateral mandibular muscles have their origin on the lateral walls of the upper beak and a somewhat smaller insertion on the surrounding connective tissue (Fig. 9a). The lateral mandibular muscles of *Lolliguncula brevis* and *Sepia officinalis* are relatively smaller in volume with respect to the size of the beaks than those of *Octopus bimaculoides*. The 3D reconstruction of the right lateral mandibular muscle shown in Figure 9a illustrates a shape that corresponds to the partially opened position of the beak bite cycle. Comparing similar sections taken from buccal masses of *L. brevis* that were fixed in different stages of the bite cycle revealed that the shape of the lateral mandibular muscles changes during movement. From the position illustrated in Figure 9a (which corresponds to the "opening" position in Fig. 8B), the diameter of the lateral mandibular muscles increase and the length of the muscles (measured from the origin to the insertion) decrease as the gape of the beaks widens. As the beaks close, the lateral mandibular muscles become longer and thinner. The lateral mandibular muscles are longest and thinnest when the beaks are in the closed and retracted position and the lateral mandibular muscles are displaced anteriorly by the anterior mandibular muscle and posterior mandibular muscle. Figure 9c is a photomicrograph of a transverse section taken through the middle of the buccal mass. The lateral mandibular muscle in this image appears spherical because all orientations of fibers within the muscle are contracted and the support usually offered by the beaks to hold the shape of the lateral mandibular muscle is not present. Also apparent in this photomicrograph (Fig. 9c) is the separation of the lateral mandibular muscles from surrounding muscles by a sheet of connective tissue.

Fiber orientation. The orientation of lateral mandibular muscle fibers varies as a function of position. Many fibers run parallel to the long axis of the muscle from their origin to insert on the buccal mass sheath or the connective tissue sheet that surrounds the muscle (the red fibers in Fig. 9b). When these fibers are relaxed and elongated, they follow a curve from their attachment at the origin on the beak so that the lateral mandibular muscles taper from origin to insertion. Contracted fibers of this orientation can be seen in the photomicrograph of Figure 9c as extending from the space formerly occupied by the upper beak lateral wall to the buccal mass sheath. A smaller number of fibers are arranged in planes perpendicular to the long axis of the cylinder. These fibers can be seen in Figure 9c as either transversely sectioned fibers (depicted in Fig. 9b as the green fibers) or as fibers oriented in the plane of the section (depicted in Fig. 9b as the blue fibers) and perpendicular to the more numerous fibers that run parallel to the long axis of the lateral mandibular muscles.

Anterior Mandibular Muscle

Gross morphology. The anterior mandibular muscle originates on the lateral walls and, as a thin layer, on the crest of the lower beak and follows the curve of the crest dorsally (Fig. 10a). It is also firmly attached to the overlying buccal sheath. The anterior mandibular muscle extends dorsally along the lower beak lateral walls and then across the gap between the upper and lower beaks to its insertion adjacent to the crest on the lateral walls of the upper beak. The anterior mandibular muscle is not oriented in a straight trajectory between the origin and insertion points; however, as the lateral mandibular muscles are located on the lateral walls of the upper beak, between these two locations. Therefore, as depicted in Figure 10b, the anterior mandibular muscle takes a curving path around the connective tissue sheet surrounding the lateral mandibular muscles to insert on the upper beak lateral walls. In all the cephalopods observed in this study, the borders between the anterior mandibular muscle and the central division of the superior mandibular muscle are difficult to define within and near the hood of the upper beak, but can be recognized by differences in muscle fiber orientation. The borders between the anterior mandibular muscle and posterior mandibular muscle on the lower beak crest are also defined by differences in muscle fiber orientation as there are no connective tissue divisions at these borders. Comparisons of sections of buccal masses with the beaks in different positions reveal that the anterior mandibular muscle shortens dorsoventrally with a corresponding increase in thickness during beak closing.

Fiber orientation. As shown in Figure 10b, the anterior muscle fibers of the anterior mandibular muscle follow a direct course as they extend from their origin along the lateral walls of the lower beak to their insertion on the upper beak or the buccal sheath. The fibers ventral to the lateral mandibular muscles, however, must curve anteriorly and either insert on the sheet of connective tissue that encloses the lateral mandibular muscles or, if their position is sufficiently anterior, continue to curve around the anterior edge of the lateral mandibular muscles and insert high on the lateral walls of the upper beak. The anterior mandibular muscle fibers that lie dorsal and posterior to the lateral mandibular muscles also have a curved trajectory, as they originate on the lateral mandibular muscle connective tissue sheet and then curve posteriorly towards their insertion high on the upper beak lateral wall. The curvature of the anterior mandibular muscle fibers around the lateral mandibular muscle can be seen in Figure 10c, a photomicrograph of a frontal section through the left half of the anterior mandibular muscle and left lateral mandibular muscle. The dorsoventrally oriented fibers of the anterior mandibular muscle are cut in transverse section along most

of the cross-sectional area of the muscle. As the lateral mandibular muscle is contracted, it is displacing the fibers of the anterior mandibular muscle that curve around its anterior out of a dorsoventral orientation and these anterior mandibular muscle fibers are thus cut obliquely. Many of the fibers that originate on the ventral surface of the lower beak lateral walls extend towards, and insert on, the buccal mass sheath and are thus cut in longitudinal section in Figure 10c. In *Octopus bimaculoides* there is a small number of anterior mandibular muscle fibers situated near the lower edge of the lateral mandibular muscles that originate on the lateral mandibular muscle connective tissue sheet and extend into the anterior mandibular muscle along a path that is perpendicular to the majority of the other anterior mandibular muscle fibers.

Posterior Mandibular Muscle

Gross morphology. The posterior mandibular muscle is the smallest and thinnest of the four mandibular muscles. It is a thin sheet of fibers that originates on the crest of the lower beak and inserts on the upper beak lateral wall inferior to the crest (Fig. 11a). The slightly thicker anterior portion of the posterior mandibular muscle curves around the lateral mandibular muscles. The posterior of the posterior mandibular muscle forms the posterior wall of the buccal cavity as it extends from the end of the lateral walls of the lower beak up to a level just below the esophagus. As such, it connects to the structures that occupy the cavity within the beaks. The posterior mandibular muscles in *Sepia officinalis* and *Lolliguncula brevis* appear relatively thicker than that of *Octopus bimaculoides* with respect to upper beak length.

Fiber orientation. The fiber orientation of the posterior mandibular muscle is primarily dorsoventral, except where the anterior portion of the posterior mandibular muscle curves around the lateral mandibular muscles (Fig. 11b). It is difficult to distinguish the posterior mandibular muscle from the anterior mandibular muscle where they both originate on the crest of the lower beak. The border is distinguished by tracing the fibers up to the lateral mandibular muscles and comparing their trajectories. The posterior mandibular muscle fibers follow the posterior contours of the lateral mandibular muscles. Beyond the edge of the upper and lower beak lateral walls, the posterior mandibular muscle fibers interdigitate with the muscle fibers of the buccal palps, the bolsters, and the radula retractor muscles to enclose the buccal cavity. The photomicrograph of Figure 11c is a frontal section of the posterior mandibular muscle enclosing the buccal cavity showing its relative size and connection to the structures of the buccal cavity. The level of the section is just below the point where the esophagus exits from the buccal mass.

Superior Mandibular Muscle

Gross morphology. The superior mandibular muscle (Fig. 12a) is a robust dorsal muscle that lies above the level of the esophagus. It originates primarily as a central division along the crest of the upper beak. Its origin includes the entire area of the upper beak crest as well as a large area within the hood. Extending from their origins on the central division and the dorsalmost portions of the upper beak lateral walls are two robust left and right divisions that extend to their insertion on the left and right wings of the lower beak. The gross morphology of the superior mandibular muscle is similar in *Octopus bimaculoides*, *Lolliguncula brevis*, and *Sepia officinalis*. The cross-sectional areas of the left and right divisions of the superior mandibular muscle are relatively large compared with the posterior mandibular muscle and anterior mandibular muscle. As the beak closes and retracts, the left (Fig. 12b, shaded red) and right (Fig. 12b, shaded green) divisions of the superior mandibular muscle shorten and increase in cross-sectional area. Observations of isolated *O. bimaculoides* buccal masses during beak closure and retraction show the left and right divisions of the superior mandibular muscle becoming so short and thick that they contact each other over the dorsal surface of the central division (Fig. 12b, shaded blue).

Fiber orientation. Muscle fibers in the right (Fig. 12b, green arrows) and left (Fig. 12b, red arrows) divisions run approximately straight from their origins in the central division and along the dorsal edges of the upper beak lateral wall, to their insertion on the lower beak wings. The muscle fibers within the central division (Fig. 12b, blue arrows) originate along the entire surface of the upper beak crest and follow an anterior-posterior trajectory. Figure 12c is a photomicrograph of a frontal section of the dorsal portion of the buccal mass in which the superior mandibular muscle is somewhat contracted. The superior mandibular muscle can be seen here extending from the central division below to its insertion points on the left and right lateral wings of the lower beak. The central division can also be seen in this section as fibers, between the two lateral divisions, extending into the region between the hood and crest of the upper beak.

Buccal Mass Connective Tissue Sheath

The buccal mass is enclosed by a sheet of connective tissue fibers that are oriented in the plane of the sheath. Fiber orientations in the sheath vary as a function of location. The fibers of the sheath surrounding the lateral mandibular muscles show preferred orientation in the dorsoventral direction. The orientation of the connective tissue fibers overlying the divisions of the superior mandibular muscle varies, but a significant proportion of the fibers are

aligned along the long axis of the superior mandibular muscle divisions. The connective tissue associated with the beccublasts within the hoods of the upper and lower beaks show three orientations. Two orientations are mirror images of each other, running from left posterior to right anterior and vice versa. Most of the fibers, however, are arranged perpendicular to the long axis of the beaks, extending from the left side to the right. The fibers are highly birefringent and have the staining properties of collagen. The buccal mass sheath is continuous with the connective tissue sheath surrounding the lateral mandibular muscles as well as with the connective tissue associated with the beccublasts. Frontal or parasagittal sections show that the buccal mass sheath varies in thickness with the thickest portions found in anterior areas of the upper and lower beaks where the buccal mass sheath is continuous with the beccublast connective tissue.

DISCUSSION

The two rigid beaks do not contact one another, but are instead associated with, and embedded in, four muscle groups and the entire structure is enclosed in a connective tissue sheath. How does this musculature and connective tissue generate the complex beak movements during biting and manipulation of food? How is the force required for movement and muscular antagonism transmitted if the beaks are not in contact with one another? To answer these questions, movements of the beaks during a bite cycle can be analyzed in the context of the origin, insertion, and fiber trajectories of the muscles to predict whether a given muscle is shortened or elongated in a given phase of the bite cycle, and how force is transmitted during movement.

The same relative stereotypic motions of the beaks were observed here for isolated buccal masses of *Octopus bimaculoides* (Fig. 8) as were observed for the coleoid cephalopods investigated by Boyle et al. (1979) and Kear (1994). The movements of the beaks during this consistent bite cycle were therefore used to determine the distance between origins and insertions of the four muscle groups of the buccal mass. As the contraction of a muscle may result in a decrease in distance between the origin and insertion, a change in these distances suggests muscle activity. The hypothesized muscle activities during a bite cycle based on this analysis are summarized in Table 1.

The lateral mandibular muscles (Fig. 9) are hypothesized here to function in opening movements and in creating a pivot around which the upper beak can rotate relative to the lower beak. In *Octopus bimaculoides*, the lateral mandibular muscles include an extensive network of muscle fibers oriented perpendicular to the fibers extending from origin to insertion, and may thus function as muscular hydrostats (Kier and Smith, 1985). Since the lateral man-

TABLE 1. Summary of hypothesized muscle activity during the bite cycle of the coleoid buccal mass

	Mandibular muscles			
	Lateral	Anterior	Posterior	Superior
Closed		✓		✓
Opening	✓		✓	
Opened	✓		✓	
Closing			✓	✓
Retracted		✓		✓

A check mark indicates activity of the muscle during that phase of the cycle. These beak positions correspond to those illustrated in Figure 8. A, Closed; B, Opening; C, Opened; D, Closing; E, Closed.

dibular muscle can be considered to be essentially constant in volume, contraction of the perpendicular fibers will elongate the other fibers and vice versa, providing a potential mechanism for antagonism of the two fiber orientations and the control of shape change in the lateral mandibular muscle. The contraction of the fibers of the lateral mandibular muscle that extend from origin to insertion will likely cause the buccal mass sheath to move medially towards the lateral wall of the upper beak and, because it is essentially constant in volume, the diameter of the lateral mandibular muscle will increase and lengthen the fibers of perpendicular orientation. This shape change in the lateral mandibular muscle may displace the anterior mandibular muscle, the posterior mandibular muscle and the lateral divisions of the superior mandibular muscle and move the upper beak away from the lower beak. Thus, the lateral mandibular muscles may be responsible for elongation of the other muscles. This proposed function is consistent with earlier observations by Kear (1994), who elicited opening by stimulation at the location of the lateral mandibular muscle. Contractions of the anterior mandibular muscle and the posterior mandibular muscle around the circumference of the lateral mandibular muscles may re-elongate the lateral mandibular muscles to their resting length. In addition, the extensive network of fibers perpendicular to the long axis in the lateral mandibular muscles of *O. bimaculoides* may also play a role in re-elongation of the lateral mandibular muscle. Also, simultaneous contraction of the perpendicular fibers and the parallel fibers of the lateral mandibular muscle may provide a means of increasing the stiffness of the muscle so that it can function as a pivot around which movement can occur.

The muscle fibers of the anterior mandibular muscle probably function in closing the upper and lower beak, but two different movements are possible. If no other muscles are active, anterior mandibular muscle contraction probably functions to bring the two beaks together in a shearing motion that moves the upper beak posteriorly with respect to the lower beak. Simultaneous activity of the lateral mandibu-

lar muscles may provide a pivot, and since the anterior mandibular muscle fibers are curved around the lateral mandibular muscles, anterior mandibular muscle contraction causes the rotation of the rostrum of the upper beak into the rostrum of the lower beak during closing.

The posterior mandibular muscle may also function in two ways, depending on the activity of the other muscles. When contracting alone, it probably brings the upper and lower beaks together. When contraction of the posterior mandibular muscle occurs simultaneously with activity of the lateral mandibular muscles, opening of the beak may occur; the fibers of the posterior mandibular muscle connect the two beaks posterior to the lateral mandibular muscles so that if the lateral mandibular muscles serve as a pivot, contraction of the posterior mandibular muscle will bring the posterior portions of the beaks together, thereby causing the rostra to rotate apart. Indeed, in the previous study by Kear (1994), simultaneous electrical stimulation of the musculature defined here as posterior mandibular muscle and lateral mandibular muscle resulted in beak opening. In *Sepia officinalis*, the posterior mandibular muscle is relatively thicker in cross section and therefore may contribute more force to the opening and closing motions than does the posterior mandibular muscle of *Octopus bimaculoides*.

The superior mandibular muscle most likely closes the beaks. Contractions of the robust rami move the upper beak in a ventral-anterior direction and bring the biting surfaces of the beaks together. The simultaneous activation of the superior mandibular muscle and the posterior mandibular muscle may be responsible for the closed and retracted position that Kear (1994) described as the resting position (Fig. 8A).

The following is a summary of the differences between morphological description, terminology, and functional roles proposed here and those of Boyle et al. (1979) and Kear (1994). Boyle et al. (1979) identified two muscles, the superior mandibular muscle and lateral muscles which incorporated the anterior mandibular muscle, posterior mandibular muscle, and lateral mandibular muscles. They noted that the superior mandibular muscle and several areas of the lateral muscles were active during closing. They suggested that opening was at least partially passive.

Kear (1994) described four muscles, the superior mandibular muscle, the inferior mandibular muscle (which incorporated the anterior mandibular muscle and portions of the posterior mandibular muscle), the thin sheet of longitudinal muscles below the buccal sheath (which incorporated the posteroventral portion of the posterior mandibular muscle), and the lateral mandibular muscles (which incorporated the lateral mandibular muscles and portions of the anterior mandibular muscle and posterior mandibular muscle that spanned the beaks). Kear

(1994) identified the lateral mandibular muscles as functioning as a pivot, and the superior mandibular muscle as providing most of the closing force with the inferior mandibular muscle providing for a closing-shearing action. The contraction of the posterior portions of the lateral mandibular muscles was proposed for opening movements.

There are several novel insights in the current study. The lateral mandibular muscles are here recognized as muscular hydrostats and are therefore capable of opening the beaks on their own as well as acting as an antagonist for the other mandibular muscles. The posterior mandibular muscles may also aid in opening the beaks in the manner described by Kear (1994) of her lateral mandibular muscles. The superior mandibular muscle probably closes the beaks by drawing the rostra closer together, while the anterior mandibular muscle probably closes the beaks while retracting the upper beak relative to the lower one. These proposals are consistent with the electromyographical recordings and stimulation experiments of Boyle et al. (1979) and Kear (1994).

In current studies, the proposed functions of the various beak muscles are being tested experimentally. Since isolated beaks spontaneously undergo apparently normal cycles of biting, electromyograms can be recorded from the muscles of the beak while monitoring movement. This will allow a definitive test of the predictions of muscle activity (Table 1) proposed here.

This analysis of the cephalopod buccal mass has identified what may be a previously unrecognized joint mechanism, here termed a "muscle articulation." Other examples of such muscle articulations may occur in the feeding and locomotory structures in other invertebrates. For instance, kalyptorhynch flatworm hooks (Karling, 1961), nereid polychaete jaws (Pilato, 1968), and inarticulate brachiopod valves (Trueman and Wong, 1987) appear to have the characteristics of muscle articulations because the rigid elements are not in contact and are embedded in muscle. Future studies of these mechanisms are planned in order to explore the possibility that muscle articulations may be common in invertebrates and to identify the principles of their function.

ACKNOWLEDGMENTS

We thank Mr. M.H.M. Niessen for assistance with histology, Dr. J.T. Thompson for discussions and assistance, and Dr. T.T. Uyeno and Dr. J.G. Carter for constructive edits of this work.

LITERATURE CITED

Alexander RMcN. 1983. *Animal mechanics*, 2nd ed. Oxford, UK: Blackwell Scientific.

- Altman JS, Nixon M. 1970. Use of the beaks and radula by *Octopus vulgaris* in feeding. *J Zool (Lond)* 161:25–38.
- Boyle PR, Mangold K, Froesch D. 1979. The organization of beak movements in *Octopus*. *Malacologia* 18:423–430.
- Burns WA. 1978. Thick sections: techniques and applications. In: Trump BF, Jones RT, editors. *Diagnostic electron microscopy*, vol. 1. New York: John Wiley & Sons. p 146–149.
- Cariello L, Zanetti L. 1977. α - and β -cephalotoxin: two paralyzing proteins from posterior salivary glands of *Octopus vulgaris*. *Comp Biochem Physiol* 57(C):169–173.
- Clarke MR. 1962. The identification of cephalopod “beaks” and the relationship between beak size and total body weight. *Bull Br Mus (Nat Hist)* 8:421–480.
- Clarke MR. 1986. *A handbook for the identification of cephalopod beaks*. Oxford, UK: Clarendon Press.
- Dilly PN, Nixon M. 1976. The cells that secrete the beaks in octopods and squids (Mollusca, Cephalopoda). *Cell Tissue Res* 167:229–241.
- Ghiretti F. 1959. Cephalotoxin: the crab-paralysing agent of the posterior salivary glands of cephalopods. *Nature (Lond)* 183:1192–1193.
- Ghiretti F. 1960. Toxicity of octopus saliva against Crustacea. *Ann N Y Acad Sci* 90:726–741.
- Hanlon RT, Messenger JB. 1996. *Cephalopod behaviour*. Cambridge, UK: Cambridge University Press.
- Hunt S, Nixon M. 1981. A comparative study of protein composition in the chitin-protein complexes of the beak, pen, sucker disc, radula and oesophageal cuticle of cephalopods. *Comp Biochem Physiol* 68(B):535–546.
- Karling, TG. 1961. Zur morphologie, entstehungsweise und Funktion des Spaltrüssels der Turbellaria Schizorhynchia. *Arkiv För Zoologi* 13:253–286.
- Kear AJ. 1994. Morphology and function of the mandibular muscles in some coleoid cephalopods. *J Mar Biol Assoc UK* 74:801–822.
- Kier WM. 1992. Hydrostatic skeletons and muscular hydrostats. In: Biewener AA, editor. *Biomechanics (structures and systems): a practical approach*. New York: IRL Press at Oxford University Press. p 205–231.
- Kier WM, Smith KK. 1985. Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool J Linn Soc* 83:307–324.
- McCarthy JM, Joskowitz L. 2001. Kinematic synthesis. In: Antonsson EK, Cagan J, editors. *Formal engineering design synthesis*, 1st ed. Cambridge, UK: Cambridge University Press. p 321–362.
- Messenger JB, Young JZ. 1999. The radular apparatus of cephalopods. *Philos Trans R Soc Lond (B)* 354:161–182.
- Nesis KN. 1993. Cephalopods of seamounts and submarine ridges. In: Okutani T, O’Dor RK, Kubodera T, editors. *Recent advances in cephalopod fisheries biology*. Tokyo: Tokai University Press. p 365–373.
- Nigmatullin CM, Ostapenko AA. 1976. Feeding of *Octopus vulgaris* Lam. from the northwest African coast. *ICES CM 1976/K: Shellfish and Benthos Committee* 6:1–15.
- Nixon M. 1969. Growth of the beak and radula of *Octopus vulgaris*. *J Zool (Lond)* 159:363–379.
- Nixon M. 1979a. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia* 18:431–443.
- Nixon M. 1979b. Has *Octopus vulgaris* a second radula? *J Zool (Lond)* 187:291–296.
- Nixon M. 1980. The salivary papilla of *Octopus* as an accessory radula for drilling shells. *J Zool (Lond)* 190:53–57.
- Nixon M. 1987. Cephalopod diets. In: Boyle PR, editor. *Cephalopod life cycles*, vol. 2. Comparative reviews. London: Academic Press. p 201–219.
- Nixon M, Budelmann BU. 1984. Scale-worms — occasional food of *Octopus*. *J Mollusc Stud* 50:39–42.
- Nixon M, Maconnachie E. 1988. Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. *J Zool (Lond)* 216:687–716.
- Nixon M, Young JZ. 2003. *The brains and lives of cephalopods*. Oxford, UK: Oxford University Press.
- Nixon M, Maconnachie E, Howell PGT. 1980. The effects on shells of drilling by *Octopus*. *J Zool (Lond)* 191:75–88.
- O’Dor RK, Pörtner HO, Shadwick RE. 1990. Squid as elite athletes: locomotory, respiratory, and circulatory integration. In: Gilbert DL, Adelman WJ, Arnold JM, editors. *Squid as experimental animals*. New York: Plenum Press. p 481–503.
- Pilato G. 1968. La muscolatura dei Policheti. II. Muscolatura del bulbo faringeo di *Perinereis cultrifera* (Grube). *Arch Zool Ital* 53:169–187.
- Smith KK, Kier WM. 1989. Trunks, tongues and tentacles: moving with skeletons of muscle. *Am Sci* 77:28–35.
- Tanabe K, Fukuda Y. 1999. Morphology and function of cephalopod buccal mass. In: Savazzi E, editor. *Functional morphology of the invertebrate skeleton*. New York: John Wiley & Sons. p 245–262.
- Trueman ER, Wong TM. 1987. The role of the coelom as a hydrostatic skeleton in lingulid brachiopods. *J Zool Lond* 213:221–232.
- Tunncliffe V, McArthur AG, McHugh D. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv Mar Biol* 34:352–442.
- Wainwright SA, Biggs WD, Currey JD, Gosline JM. 1982. *Mechanical design in organisms*. Princeton, NJ: Princeton University Press.
- Wells MJ. 1978. *Octopus: physiology and behaviour of an advanced invertebrate*. London: Chapman and Hall.
- Young JZ. 1965. The buccal nervous system of *Octopus*. *Philos Trans R Soc Lond (B)* 249:27–43.
- Young JZ. 1971. The anatomy of the nervous system of *Octopus vulgaris*. Oxford, UK: Clarendon Press.
- Young JZ. 1991. The muscular-hydrostatic radula supports of *Octopus*, *Loligo*, *Sepia* and *Nautilus*. *J Ceph Biol* 2:65–93.