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The Buccal Apparatus of Recent and Fossil Forms

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PART M, CHAPTER 12: THE BUCCAL APPARATUS OF RECENT AND FOSSIL FORMS

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INTRODUCTION

Living Coleoidea are active and skilled predators whose diets consist mostly of crustaceans, mollusks, and bony fish, and can also include polychaetes, chaetognaths, siphonophores, and echinoderms. During their lifetime, coleoids may take a wide spectrum of prey: some will feed on the same species of prey but of increasing size; others, after reaching a particular size, change their prey species; some may take their own species, while some scavenge (Nixon, 1987, 1988a). Recent Coleoidea exhibit various methods of prey capture, usually due to the diverse morphology of their prey (Nixon, 1985).

The morphology of the buccal apparatus of living forms, and effects of surgical removal of one or more features, give some indication of its functions in prey capture and early stages of the digestive process. This may aid in studies of the buccal apparatus of fossil cephalopods, which can survive under special conditions of fossilization; this occurs mostly in ectocochleates, where the shell provides protection.

BUCCAL MASS

The buccal mass and its relationship with the whole animal can be seen in hemisections of three living coleoids: *Sepia, Alloteuthis,* and *Spirula* (see Nixon, 2011, fig. 7). It lies at the base of the brachial crown, and is a distinct, almost spherical mass, its shape determined by the chitinous upper and lower beaks (jaws, mandibles), which are largely encased in muscles. A buccal mass, with upper and lower beaks, is a constant feature, although the beaks may vary in shape and form; calcification may be absent or present (Nixon, 1988b, 1996; see Nixon, 2011, fig. 14–15). The buccal mass and its features have been described in Recent *Nautilus* (Messenger & Young, 1999) and several living coleiods (Nixon & Young, 2003). The beak of *Nautilus* is dense and black with white calcareous tips, whereas those of living coleoids are firm and range from translucent, pale amber to dense, impenetrable dark brown or black. They are composed of a chitin-protein complex in *Octopus vulgaris,* and analysis of three regions of the upper and lower beaks showed differences in the percentages of chitin and protein present (Table 1) (Hunt & Nixon, 1981). Mass spectrometric techniques

Table 1. Recent Coleoidea. The percentage of chitin and protein in chitinous structures of two coastal squids and an octopod (Hunt & Nixon, 1981).

Species	Structures	% Chitin	% Protein
Loligo vulgaris	Gladius	41.8	58.2
Octopus vulgaris	Upper beak		
	Rostrum	6.6	93.4
	Lateral wall	10.8	89.2
	Crest	7.5	92.5
	Lower beak		
	Rostrum	6.0	94.0
	Lateral wall	12.3	87.7
	Crest	7.8	92.2
	Radula	18.0	82.0
Alloteuthis subulata	Esophageal cuticle	7.4	92.6

Nixon, Marion. 2015. Part M, Chapter 12: The buccal apparatus of Recent and fossil forms. Treatise Online 69:1–30, 16 fig., 5 tables.

FIG. 1. Scanning electron micrograph of a hemisection of the buccal mass of the coastal squid, *Alloteuthis subulata* (120 mm mantle length) to show radula and other features within buccal cavity; *bec,* beccublasts; *eso,* esophagus; *l be,* lower beak; *lat buc palp,* lateral buccal palp; *man mus,* mandibular muscle; *r,* rostrum; *rad,* radula; *subm gl,* submandibular gland; *u be,* upper beak; *u lip,* upper lip; field width 3300 µm (see NIXON, 2011, fig. 13) (new).

revealed a chitin-protein composition in the beaks of *Nautilus belauensis*, and the Humboldt squid, *Dosidicus gigas;* however, analysis of comparable material of fossil taxa from Upper Cretaceous localities in North America and Japan showed no compounds from the chitin-polymer complex, but it did show the presence of aromatic compounds (GUPTA & others, 2008). The beaks form a cavity, which provides the space for the activity of the radula and its support system (NIXON, 1968; MESSENGER & YOUNG, 1999) (NIXON, 2011, fig. 13). The radula, a characteristic feature of Mollusca, is an elongated membrane bearing teeth and supported by muscles. Within the cavity are the lateral buccal palps and salivary glands; secretions of the latter aid the passage of whole prey and/or the breakdown of the prey into pieces small enough to enter and pass along the esophagus (Fig. 1). The esophagus has a cuticular lining of a chitin-protein complex (Table 1) (HUNT & NIXON, 1981). Four pelagic octopods, *Ocythoe tuberculata, Haliphron atlanticus*, *Tremoctopus violaceus,* and *Argonauta argo,* have a thick cuticle on the lateral buccal palps, and lining the esophagus, presumably to protect adjacent soft tissues including the circumesophageal lobes of the central nervous system (Nixon & Young, 2003).

The beaks are attached to the mandibular muscles of the buccal mass via a layer of tall columnar cells: the beccublast cells (Fig. 2). Three main groups of cells have been found on the upper beaks of *Octopus vulgaris* and *Alloteuthis subulata* (Dilly & Nixon, 1976b). The first group has cell-long fibrils, which may have contractile and/or tensile properties, and are attached to the complex trabeculae, which extend from the beccublast cells into the matrix of the beak, leaving imprints visible in scanning electron micrographs (see Nixon, 2011, fig. 16). At the other end, these cells are anchored to the beccublast-muscle cell interface, which is closely associated with muscles that move the beak. The second group of cells contain masses of endoplasmic reticulum, the cisternae of which are arranged along the long axis of the cell, and also dense granules that are probably the major source of the hard tissue of the beak. The third cell group contains a mixture of fibrils and secretory tissue (Dilly & Nixon, 1976b). Similar imprints have been found on the beak of the goniatite *Girtyoceras limatum* (Doguzhaeva, Mapes, & Mutvei, 1997), in living *Sepia esculenta,* and two ammonoids (Tanabe & Fukuda, 1999).

The muscles and connective tissues of the buccal mass of *Octopus bimaculoides, Sepia officinalis,* and *Lolliguncula brevis* have been examined to identify the mechanisms responsible for the complex opening, closing, and shearing movements of the beak (Uyeno & Kier, 2005). Anterior, posterior, superior, and lateral mandibular muscles connect the upper beak and lower beaks. However, the lateral mandibular muscles originate on the upper beak and insert on the connective tissue sheath surrounding the buccal mass, but do not connect with the lower beak. Notably, the upper and lower beaks do not make contact with each other, as the rostrum of the upper beak fits within that of the lower one. These authors considered that the buccal mass of coleoid cephalopods could represent a flexible joint mechanism and, to test their hypothesis, electromyography electrodes were implanted in muscles of the isolated buccal mass and the position of the beaks recorded (Uyeno & Kier, 2007). These results were consistent with the hypothesis that the lateral mandibular muscles were active when the beak opened, and it was concluded that the buccal mass of cephalopods forms a flexible joint in which the lateral mandibular muscles function as a muscular hydrostat and provide the force necessary to open the beaks (Kier & Smith, 1985).

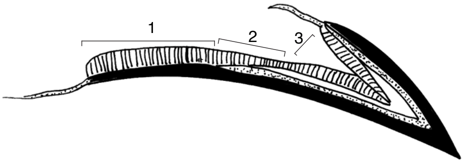

Fig. 2. Diagram of section through rostral region of upper beak of *Alloteuthis subulata,* showing major types of beccublasts; *1*, tall columnar cells, most having mainly secretory cytoplasmic contents with some fibrils; *2*, slightly shorter cells with mainly fibrillar and some secretory cells; *3*, mainly fibrillar cells (new).

The activity of the radula and its support system has been observed within the buccal cavity of *Octopus vulgaris,* after excising the rostrum of the upper and lower beaks (see Nixon, 2011, fig. 13), and recorded on cine film; drawings from single frames show some of the actions (Fig. 3; Nixon, 1968). The radula, and its teeth, its supporting system, and the lateral buccal palps, which lie on either side of the radula, follow a cycle of movements: as the radula moves towards the floor of the buccal cavity the lateral buccal palps move towards the midline and meet above the radula. The ribbon changes its form around the bending plane, and with each cycle of movement the teeth become erect and/or splayed laterally; as the bending plane is passed, the marginal teeth collapse medially towards the rachidian and lateral teeth (Nixon, 1968). Some indication of the function of the buccal apparatus comes

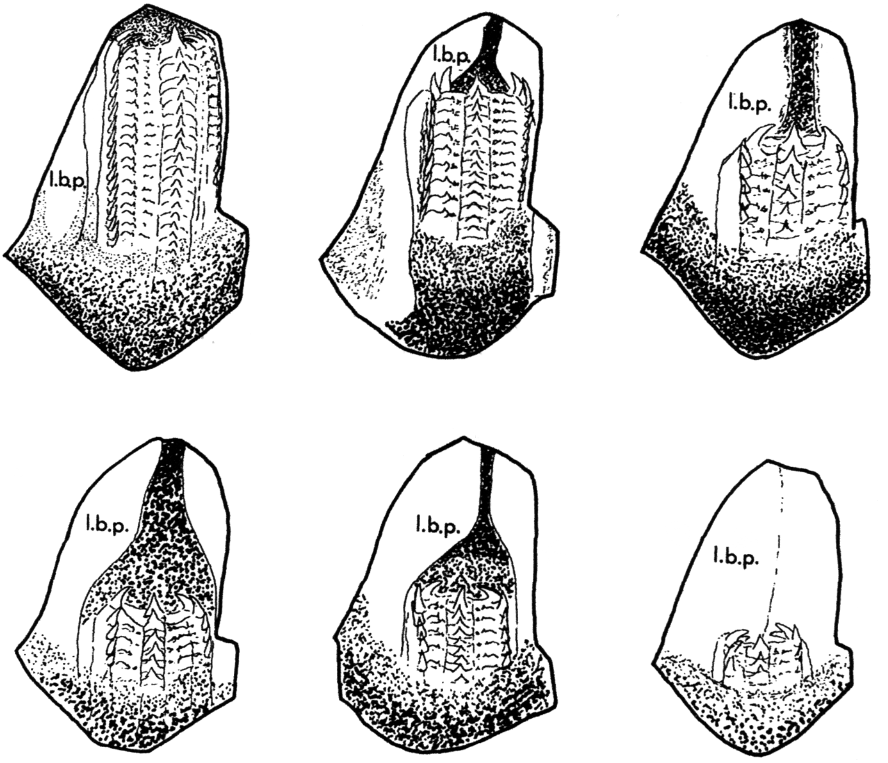

FIG. 3. Drawings of single frames from a cine film looking toward esophagus of octopod *Octopus vulgaris,* after removal of rostra of beaks to show lateral buccal palps *(l.b.p.)* and radula within buccal cavity; some phases of cycle of movements of structures have been illustrated; scale unavailable (Nixon, 1968).

from an experimental study of *Octopus vulgaris* in which the intake of food was measured before and after surgical excision of one or other of its chitinous parts: loss of the rostrum of the lower beak reduced the intake from crabs to 37%, of the upper beak to 69%, and of the radula to 86%, whereas the intake remained at or close to 100% in normal and control animals (ALTMAN & NIXON, 1970). This octopus can drill holes in mollusk shells after removal of part of its radula, but not after surgical removal of the papilla of the posterior salivary gland (NIXON, 1979, 1980; NIXON & MACONNACHIE, 1988).

BEAKS OF RECENT CEPHALOPODA

OWEN (1832) gave the first illustration of the upper and lower beaks of *Nautilus* after examining the buccal mass of the first living *Nautilus pompilius* brought to England. He noted the black, horny, beaks and their similarity to those of the parrot, but differing in that the rostral region of the lower beak encases that of the upper beak, and named the major regions internal and external laminae. The extreme tip of the upper beak is white, calcareous, dense, and resembles an arrowhead, and OWEN (1832, p. 21) conjectured that “certain fossils called Rhyncholites . . . . as appertaining to the Cephalopoda.” His study confirmed that these fossils had formed the calcareous tip of fossil nautilids. The beaks of Recent *Nautilus* are chitinous and their tips calcitic, the lower beak has a delicate calcareous covering termed the conchorhynch (TEICHERT, MOORE, & ZELLER, 1964). The rhyncholite and the concorhynch usually carry several rows of denticles on their oral surfaces in both fossil and living *Nautilus* (SAUNDERS & others, 1978).

The beak of a giant squid, *Architeuthis,* was found within the buccal mass when it was washed ashore in the Kattegat in 1853 and taken to STEENSTRUP, who gave a short description of it to The Natural History Society (1855), although illustrations of the beaks and details of his nomenclature did not follow until 1898. He termed the anterior projecting tip, the rostrum; the larger interior horny plate, the palatal plate; the smaller outer part, the frontal part; the upper internal part forming the floor of the cavity, the gular plate; the lower outer horny plate, the mental part; and the prolongations extending from the frontal part to the most anterior region of the gular plate, the wings (VOLSØE, KNUDSEN, & REES, 1962). After examining the buccal apparatus from several giant squids, *Architeuthis,* and isolating the beaks, VERRILL (1879, p. 204) adopted the nomenclature that was "essentially that used by Professor Steenstrup." NAEF (1921) described the beaks of a coleoid and termed the tip of the upper beak the biting process, and the backward extension, the outer plate. CLARKE (1962, 1986) listed the names given by these early authors to features of the beaks together with new terms that he introduced; the main features are shown with their nomenclature in Figure 4. The upper beak has a rostrum, which is usually sharp and pointed with a downward curve and its anterior tip quite hard (Fig. 1). The outer side of the rostrum expands toward the posterior end of the beak to form the hood, and the inner side expands posteriorly to form the lateral walls and the crest. At each side of the hood is the wing, which is small in the upper beak. From the beak angle to the wing is the shoulder; this region usually forms a cutting edge and shows wear. The features of the lower beak are essentially the same as those of the upper beak, but they differ in their relative sizes. The rostrum of the lower beak is broader than that of the upper beak, which it accommodates when the beaks are closed. The hood is shorter from front to back in the lower beak than in the upper beak. The lateral walls are nearly flat and meet together at the crest, and the wings are notably much more developed than in the upper beak and extend beyond the free edges of the lateral walls. It was found that the lower beaks have features which allow the identification of cephalopods from isolated beaks recovered from the stomachs of predators, such as cetaceans (CLARKE, 1980, 1996), seals (KLAGES, 1996), seabirds (CROXALL & PRINCE, 1996), and fishes (SMALE, 1996). Furthermore, CLARKE (1980, 1986) demonstrated that measurements of isolated lower beaks made it possible to estimate the mantle length and body weight of coleoids

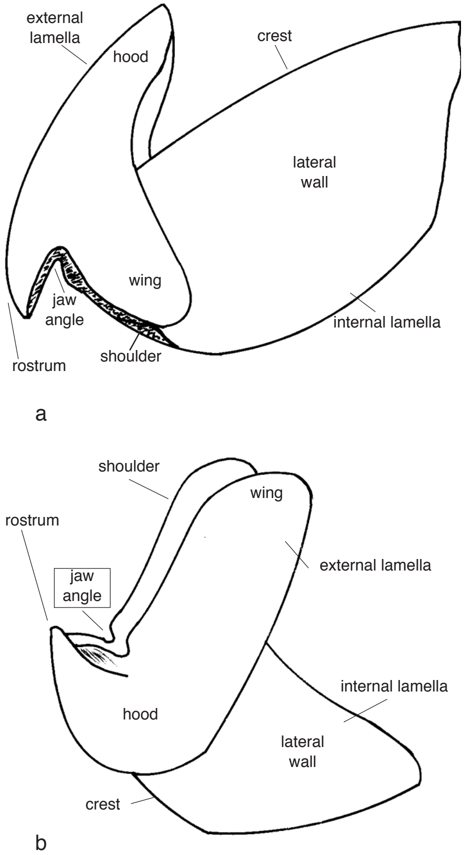

FIG. 4. Drawings illustrating main features of isolated upper *(a)* and lower *(b)* beaks of giant squid *Architeuthis,* with 208 cm mantle length; nomenclature follows CLARKE (1962, 1986) (new).

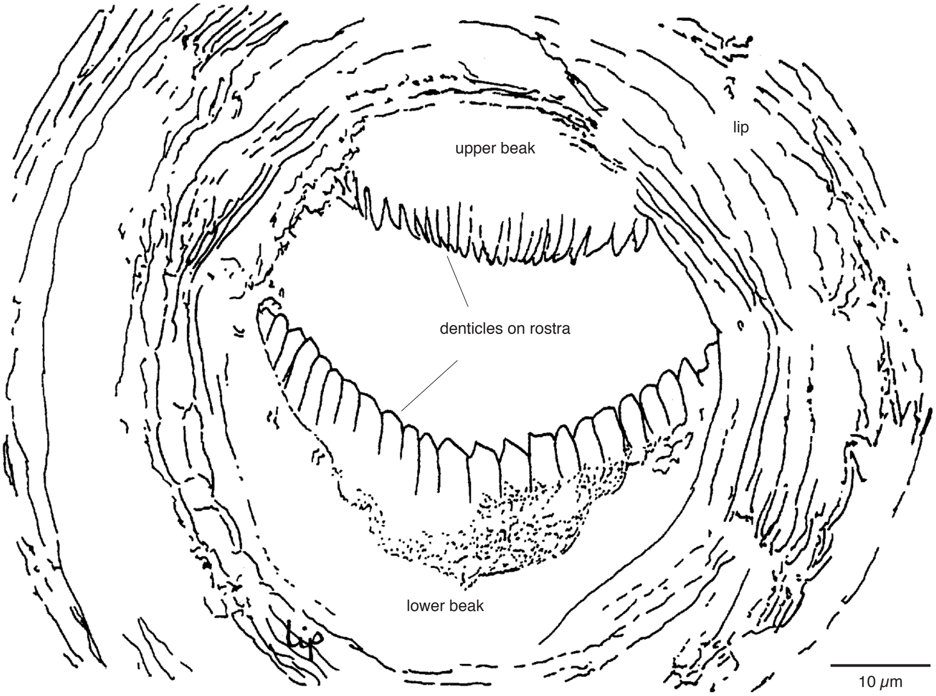

FIG. 5. Drawing from a scanning electron micrograph of mouth of newly hatched *Octopus vulgaris,* seen from in front, to show lips and rostrum with denticles on oral edge of upper and lower beaks (Nixon & Mangold, 1996).

ingested by predators and calculate their biomass. In their morphometric analysis, NEIGE & DOMMERGUES (2002) found that differences in coleoid beak shape reflect phylogenetic relationships.

The shape and form of the upper and lower beaks of the giant squid *Architeuthis* and coastal octopod *Octopus vulgaris* are shown in Figure 4. The lower beak of the coastal squid, *Loligo forbesi* (see NIXON, 2011, fig. 15), and the lower beak of many living cephalopods were illustrated by CLARKE (1962, 1980). In 1986, CLARKE provided stereoscopic pictures of the lower beaks of 113 genera of cephalopods, some represented by several species. CLARKE and MADDOCK (1988) suggested that the lower beak of the early coleoid developed from a beak similar in shape to the chitinous part of the lower nautiloid beak. Their brief analysis indicated a close relationship between the following pairs of families: Loliginidae and Sepiolidae; Architeuthidae and Thysanoteuthidae; Octopoteuthidae and Lepidoteuthidae; Onychoteuthidae and Pholidoteuthidae; and Enoploteuthidae and Lycoteuthidae. Fewer similarities were found among other families.

The beaks of coleoid paralarvae and hatchlings are often translucent and pale in color, but the rostral tips may be dark, and from here the darkening process spreads progressively over the hood and lateral walls to the wings, but the distribution and density varies. This darkening process was followed in the beaks of 18 species of Mediterranean cephalopods, and differences were found in the distribution of the pigmentation between species (MANGOLD & FIORONI, 1966), and in ontogenetic series of *Octopus vulgaris* (NIXON, 1969, 1973), *Psychroteuthis glacialis* (GROEGER, PIATKOWSKI, & HEINEMANN, 2000), and *Todaropsis eblanae,* for which a scale for the darkening process was

Table 2. Stomach contents of fossil Coleoidea and Ammonoidea species; in addtion to *Dorateuthis syriaca* Woodward, 1883*,* stomach contents are known from numerous species of fossil Coleoidea.

Coleoidea	Crop or Stomach Contents
Late Cretaceous	
Dorateuthis syriaca	Fish remains, whole vertebrae, large rib segment (Lukeneder & Harzhauser, 2004).
Ammonoidea	Buccal Cavity Contents
Late Cretaceous	
Baculites sp.	Fragments of isopods adult and juvenile, planktotrophic gastropod shell, and crustacean fragments (Kruta & others, 2011).
Ammonoidea	Crop or Stomach Contents
Early Jurassic	
Hildoceras levisoni	Jaw apparatus of small ammonites. Calcitic debris resembling echinoderm stereom; another specimen has aragonitic shell debris (Lehmann & Weitschat, 1973; Riegraf, Werner, & Lörscher, 1984).
Hildoceras serpentinum	Small aptychi (Riegraf, Werner, & Lörscher, 1984).
Harpoceras falciferum	Mostly pereiopods of small decapod crustaceans, rarely abdomens or telsons of the same crustaceans. Crustaceans (dead or exuviae?) remains often concentrated in densely packed balls, 10–50 mm diameter, and even filling much of body chamber indicating storage potential (Jäger & Fraaye, 1997).
Arnioceras sp.	Foraminiferans and ostracod shells (Lehmann, 1972).
Ammonoidea	Crop or Stomach Contents
Triassic	
Svalbardiceras spitzbergense	Many fragments of ostracods (Lehmann, 1985).

constructed (Hernandez-Garcia, 2003). The beaks also thicken progressively during life in all species, especially at the rostral-edge and shoulder (Clarke, 1980). Changes in the beaks have been followed during growth from embryo to maturity in *Octopus vulgaris*; at embryo stage XVII–XVIII, the beaks are translucent but subsequently darken (Nixon, 1969, 1973); and the oral surfaces of the upper and lower beaks of hatchlings have denticles (Fig. 5), which Boletzky (1971) noted on the beaks of teuthoids and octopods, and are also present in the pigmy squid, *Idiosepius* (Adam, 1986). The denticles are retained while the young octopuses are pelagic and living in the plankton, but the oral denticles are lost or resorbed by the time they settle on the sea bed and their beaks have distinct, thickened rostral tips. The denticles aid the young to capture and feed on larval crustaceans, such as shrimps and crabs, when in the plankton (Nixon & Mangold, 1996).

The buccal mass forms a notable proportion of the embryo and its length can be expressed as a percentage of the mantle length in living coleoids; this diminishes with growth (see Nixon, 2011, fig. 12). The length of the buccal mass of some ammonoids was related to the shell diameter (Morton & Nixon, 1987; Nixon, 1988a). Jäger and Fraaye (1997) examined the diet of *Harpoceras falciferum* and summarized the remains present in the crop/stomach of some other well-preserved ammonites (Table 2). The buccal mass of the coleoid *Dorateuthis syriaca* forms 6.2% of the mantle length, and the crop or stomach of this fossil was found to include entire vertebrae and large rib segments from fish too large to ingest (Table 2). Thus it had reduced the fish to pieces small enough to pass along the esophagus; well-digested material, chyme, is present in a sac near the stomach (Fig. 6) (Lukeneder & Harzhauser, 2004).

The prey of living coleoids is varied: small prey is ingested whole and larger prey reduced to small pieces. Debris in the stomach is often identifiable to genus and sometimes species (Tanabe & others, 2008). The coleoids feed

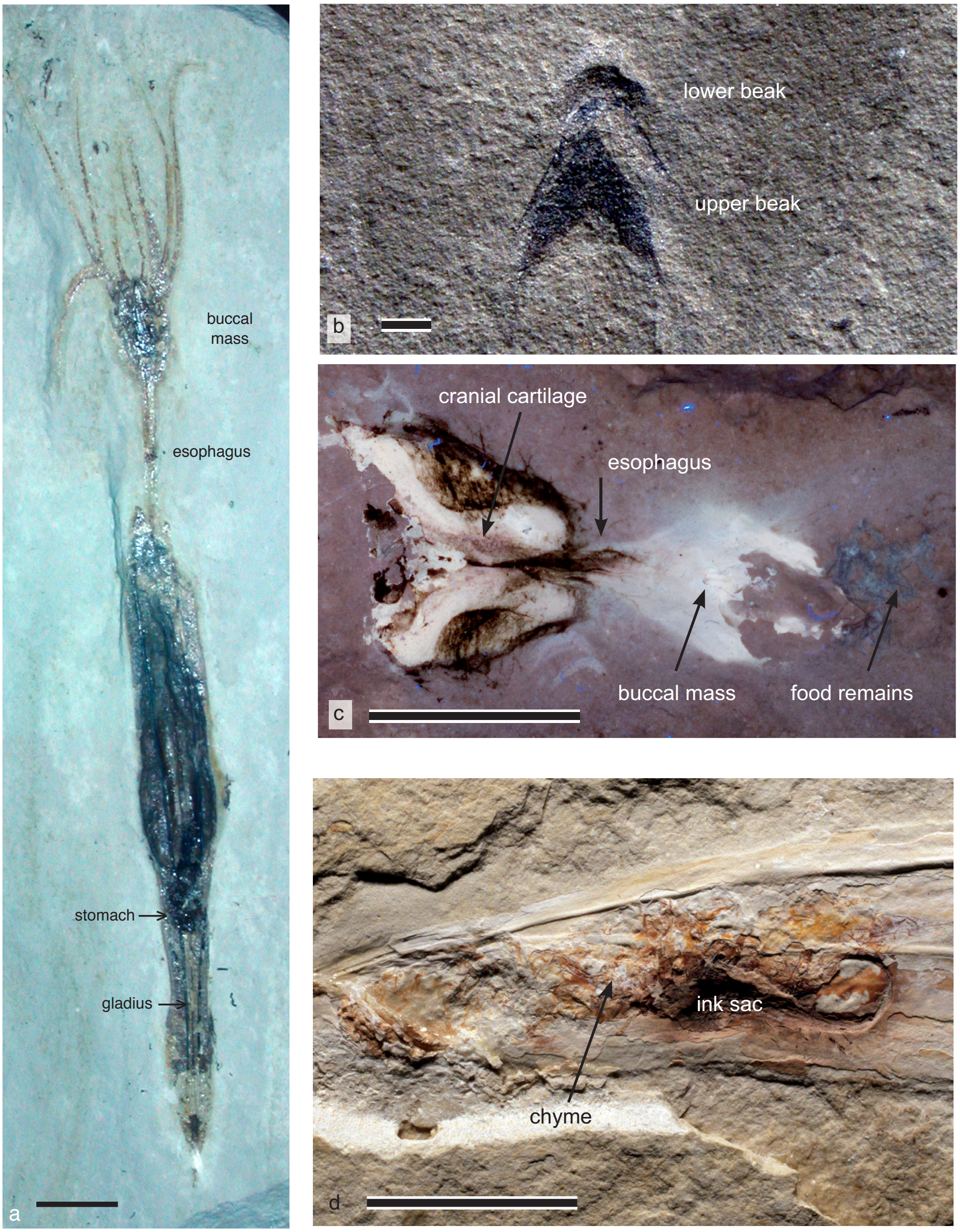

Fig. 6. Examples of Late Cretaceous coleoids with remains of the digestive system; *a, Dorateuthis syriaca,* NHMW 1998z0105 (Naturhistorisches Museum Wien, Austria), upper Santonian, Sahil Alma, Lebanon, whole specimen, gladius length 97 mm, showing buccal mass, esophagus, and stomach containing food remains, scale bar, 10 mm (adapted from Lukeneder & Harzhauser, 2004); *b, Glyphiteuthis libanotica,* CRE034, upper Cenomanian–upper Santonian, Hakel and Hadjoula, Lebanon, dorsal view of upper and lower beaks, scale bar, 1 mm (Fuchs & Larson, 2011b); *c–d, Dorateuthis syriaca,* BHI5579 (Black Hills Institute, Hill City, South Dakota, USA), enlarged view of cranial cartilage *(c)* and posterior region *(d),* scale bars, 10 mm (adapted from Fuchs & Larson, 2011b).

Table 3. Recent Coleoidea. Material identified in the crop or stomach of wild-caught specimens.

Recent Coleoidea	Crop or Stomach Contents
Decabrachia	
Spirulida	
Spirula spirula	Whole copepods and ostracods, and others half-digested (Nixon & Young, 2003).
Teuthoidea	
Myopsida	
Loligo forbesi	Fish vertebrae, lenses, otoliths, scales, coleoid beaks (Martins, 1982).
Loligo opalescens	Prey in fragments, including fish scales, eyes, vertebrae, bones, dismembered crustaceans, and crania; beaks, radulae, suckers from squid of same species (Fields, 1965).
Oegopsida	
Ommastrephes sloani	Remains of fish, crustaceans, mollusks including *Ommastrephes sloani* (Okutani, 1962).
Moroteuthis ingens	Teleost fish, mostly myctophids; cephalopods, squids; crustaceans, small amphipods and copepods (Phillips, Jackson, & Nichols, 2001).
Chiroteuthis imperator	Remains of fish, crustaceans, and squid; and spectra of micronektonic organisms (Kubota, Koshiga, & Okutani, 1981).
Gonatus fabricii	Juveniles took zooplankton, copepods, euphausids, a few pteropods, and subadults-amphipods. (Nesis, 1965).
	Juveniles fed on amphipods, isopods, probably also prawns and mysids. Vertebrae, ribs, fin rays, scales, and lenses from the fish, capelin, *Mallotus villosus;* a change of prey took place and adults took a larger percentage of fish and cephalopods, and fewer crustaceans (Kristensen, 1984).
Octobrachia	Crop or Stomach Contents
Octopoda	
Incirrata	
Octopus vulgaris	Crustaceans including Brachyura, Anomura, Natantia, Isopoda, Stomatopoda, Ostracoda, Amphipoda (Nigmatullin & Ostapenko, 1976).
	Scale worms (Budelmann & Nixon, 1984).
Bolitaena sp.	Whole small copepods, bitten flesh from arms and other parts of smaller bolitaenids (Nixon & Young, 2003).
Japetella diaphana	Crustaceans, calanoids, euphausids and decapods, chaetognaths, mollusks, and fishes (Passerella & Hopkins, 1991).
Argonauta boettgeri, A. argo	Heteropods, pteropods; small fish have severed heads and flesh eaten; also feeds on gonads of jellyfish (Nesis, 1977; Beebe, 1926; Clarke & Herring, 1971; Heeger, Piatkowski, & Möller, 1992).
Tremoctopus violaceous	Small fish, crustaceans, jaws and spicules of polychaetes (Nixon & Young, 2003).
Ocythoe tuberculata	Crustaceans, and bite-size pieces taken from sardines (Nixon & Young, 2003).

mostly on crustaceans, fish, and mollusks, and to a lesser extent on echinoderms, polychaetes, siphonophores, chaetognaths, and other invertebrates (Table 3) (Nixon, 1987). A review of the early life of *Octopus vulgaris* showed that its newly hatched young are planktonic and prey upon zooae of crustaceans of increasing size until the octopus settles on the sea floor, where it feeds on young crabs (Nixon & Mangold, 1996). Secretions of the salivary glands include a toxin, cephalotoxin, which immobilizes a crab in less than

30 seconds (Ghiretti, 1959, 1960). External digestion also occurs in *Octopus vulgaris,* as a crab retrieved 90 seconds after capture cannot be pulled apart, but after 27 minutes is easily dismembered, although it is limited to the arthrodial membrane and musculo-skeletal attachment mechanisms, as the exoskeleton separates at the joints and the muscles can be withdrawn from the appendages (Nixon, 1984). Paralarvae of *Octopus vulgaris* left only whole empty skeletons of zooae belonging to three species of crab (Hernandez-Garcia, Martin, & Castro, 2000). Subsequently, this species increases the variety and size of its prey with growth (Smale & Buchan, 1981), and shows temporal and regional differences in feeding habits (Hatanaka, 1979). The features of the digestive system of *Octopus vulgaris* suggest it is sophisticated in its mode of capture and breakdown of its prey.

BEAKS OF FOSSIL FORMS

An experiment followed the decay and fossilization of nonmineralized tissue of whole specimens of Recent coleoids, namely the squids *Alloteuthis subulata* and *Loligo forbesi*, and the sepiolid *Sepiola atlantica,* in sea water (Kear, Briggs, & Donovan, 1995). Degradation was recorded for periods from one day to fifty weeks, and the material examined, or sampled, at intervals. The process occurred at comparable rates in the soft tissues. After ten weeks, a few sucker rings remained recognizable, and after fifty weeks, the beaks, parts of the radulae, crystals, and a mass of semi-liquid tissue survived. Disintegration of muscles was rapid and ultrastructural details lost in less than two days, although the tunic layers, intramuscular connectives, and the collagenous component of the muscle survived longer. Cells of the crest area of the upper beak retained some fine structure for more than four weeks, and in scanning electron micrographs the fibers appeared to insert directly onto the beak and seemed to form clumps 70–100 µm in diameter. Within these clumps were smaller bundles, 10 µm in diameter, which could mimic the beccublast cells in *Alloteuthis* and *Octopus* (Dilly & Nixon, 1976b) (see Nixon, 2011, fig. 16). The beaks survived with little alteration throughout the experiment. Individual fibers, about 2 µm, probably represent the fibrillar phase of the beccublast cells, rather than the mandibular muscles, and their survival may reflect their structural nature and the protected position of the buccal mass. The beaks, radulae, suckers, gladii, lenses, and statoliths proved more decay resistant (Kear, Briggs, & Donovan, 1995), the first four being chitin-protein complexes (Table 1) (Hunt & Nixon, 1981). Several well-preserved Jurassic genera were examined: in *Mastigophora* the ultrastructure was seen in a continuous series of tissues from the outer tunic, through the mantle and gladius, to the muscular sheath of the digestive gland (see Nixon, 2011, fig. 28); and in *Belemnotheutis* the radial and circular muscle, the outer collagenous tunic, and the supporting meshwork of intramuscular fibers were preserved (Kear, Briggs, & Donovan, 1995; and see Nixon, 2011, fig. 28).

The buccal mass of fossil Cephalopoda can survive under special conditions of fossilization, but the beaks and radulae usually remain obscured by the mandibular muscles. Beaks of Nautiloidea (Saunders & Richardson, 1979) and Ammonoidea (Lehmann, 1967, 1981) occur most often, and those of Coleoidea rarely (Lukeneder & Harzhauser, 2004). The earliest record of a beak from a fossil coleoid was found by Quenstedt (1858) in a quarry near the village of Nusplingen, Germany, who preliminarily assigned it to *Plesioteuthis prisca* (Fig. 7a–c). The same specimen was examined by Naef (1922); it has a sharp rostrum darkened at the tip, a hood, deep lateral walls, and a long crest, and resembles the upper beak of living coleoids.

Jurassic

Well-preserved fossil coleoids were discovered in the Moltrasio Limestone Formation, lower Sinemurian, Lower Jurassic, in Osteno, Italy, some with partially preserved soft tissues; line drawings illustrate an upper and lower beak (Garassino & Donovan,

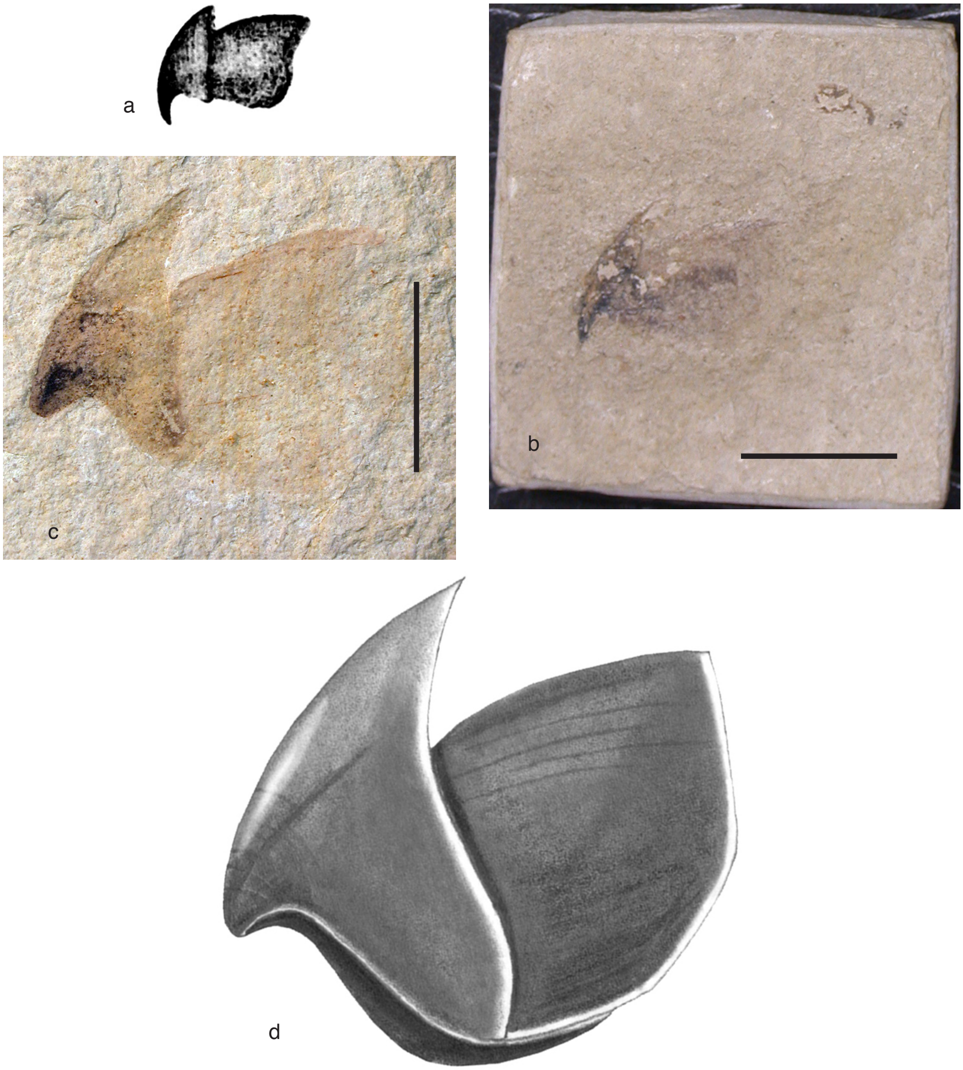

FIG. 7. Fossil isolated upper beaks of *Plesioteuthis prisca,* Upper Jurassic lithographic limestone slates, Nusplingen, southwestern Germany; *a,* drawing (Quenstedt, 1858); *b,* original specimen of QUENSTEDT (1859), GPIT QU1885 (Geological Paleontological Institute, Tübingen) scale bar, 2 cm (new, photographs courtesy of Dirk Fuchs); *c, ?Plesioteuthis prisca*, SMNS64603 (Staatliches Museum für Naturkunde, Stuttgart), scale bar, 1 cm (Klug & others, 2005, fig. 8A–B); *d,* reconstruction of specimen in part *c* (adapted from reconstruction in Klug & others, 2005, fig. 12B).

2000). More than 20 coleoid beaks have been recovered from the Nusplingen Quarry, Germany, Upper Jurassic (Kimmeridgian), and the finds included lower beaks and upper beaks (Fig. 8). In addition, a pair of associated structures was found and interpreted as a lower and upper beak of one individual, possibly *Trachyteuthis hastiformis,* with gladius (KLUG & others, 2005). From the same site, a new specimen was identified as *Plesioteuthis prisca*, and comprised an upper beak with a gladius *in situ*, thus linking a specific form of beak to the species (Fig. 7d). This made reconstruction of the upper and lower beaks possible (KLUG, SCHWEIGERT, & DIETL, 2010) and shows

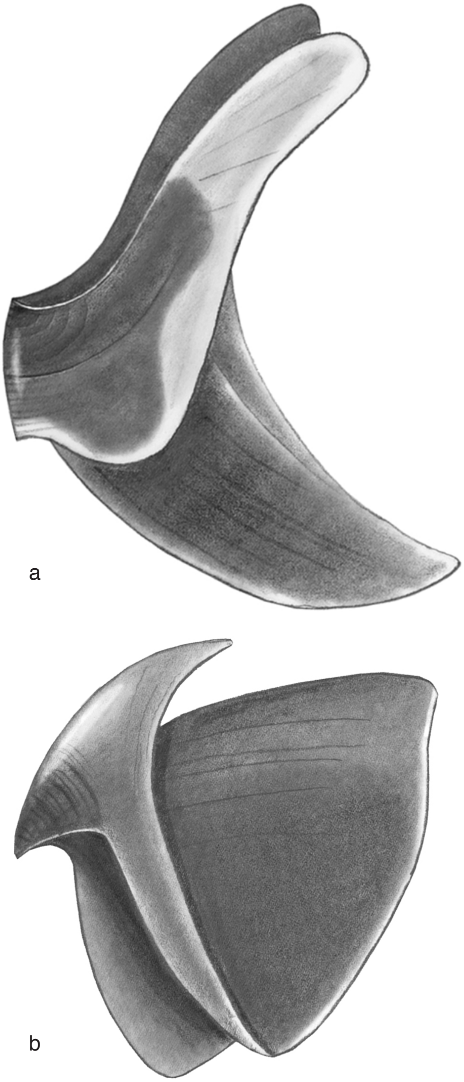

FIG. 8. Reconstructions of beaks; *a, Trachyteuthis,* lower beak; *b, Leptotheuthis,* upper beak (Klug & others, 2005, fig. 11B, 12A).

the upper one to be like that illustrated by QUENSTEDT in 1858 (Fig. 7a).

From the same formation at Nusplingen, four forms of lower beak and three of upper beaks were found. Their morphology and the association of beak pairs with a gladius characteristic of *Trachyteuthis hastiformis* allowed taxonomic assignment of the two beak forms (Fig. 9) (KLUG & others, 2005).

FIG. 9. *Trachyteuthis hastiformis*, SMNS 65478 (Staatliche Museum für Naturkunde, Stuttgart, Germany), Jurassic, Germany, upper beak in lateral view, and lower beak from above, ×1.5 (Klug & others, 2005).

The length of the lateral wall of one lower beak measures 29 mm, and of the upper beak 20 mm, the gladius being 268 mm. The lower beak displays the remains of the lateral wall and the hood. The rostrum and hood of the upper and lower beaks are darkened, but this fades posteriorly. The upper beaks of other specimens of the same species, including the largest one, have smoothly rounded rostral tips; from these new specimens it became possible to reconstruct both beaks (KLUG & others, 2010).

One large, complete, specimen from the same formation in the Nusplingen quarry was identified as *Leptotheuthis gigas.* It comprised a pair of fins, gladius, head, small eyes, funnel, and several arms, including cirri, all readily visible, although the beaks are faint (Fig. 10). An isolated upper beak, tentatively assigned to the same genus because of its large size, has a length of 19 mm and height of 27 mm, but as it had settled at an oblique angle it is distorted; the rostrum is stout and darkened in some parts (KLUG & others, 2005).

KLUG and others (2010) described the first belemnitid beak discovered, *Hibolithes semisulcatus,* also from Nusplingen; it is a typical coleoid beak without evidence of a calcified rostrum as in nautiloids. Compared with coexisting gladius-bearing coleoids, both the upper

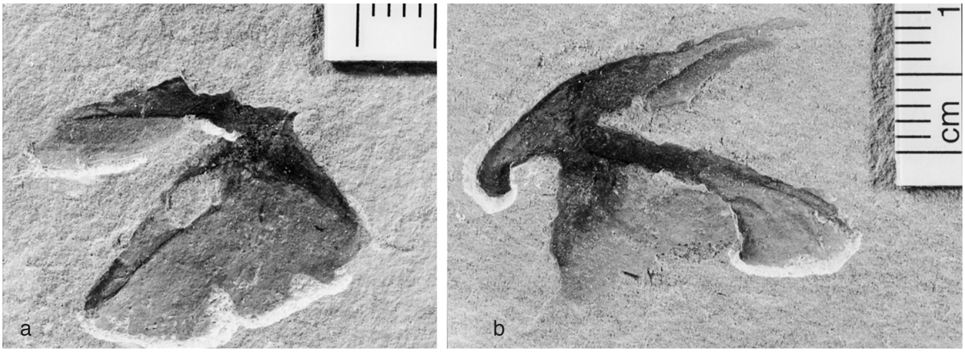

FIG. 10. *Leptotheuthis gigas,* SMNS 64923 (Staatliche Museum für Naturkunde, Stuttgart, Germany), Jurassic, Germany; *a,* lower and *b,* upper beak in oblique lateral views from moderately preserved specimen, scale in mm (Klug & others, 2005).

and lower beaks of *Hibolithes* have a much more pointed rostrum, similar to Recent Decabrachia.

Cretaceous

The buccal mass is frequently preserved in the Upper Cretaceous Lebanon Limestones, but coleoid beaks are poorly known (FUCHS & LARSON, 2011a, 2011b). A specimen of *Dorateuthis syriaca,* Plesioteuthidae NAEF, 1921, Upper Cretaceous, Sahil Alma, Lebanon, has preserved soft tissues (Fig. 6a). The buccal mass has a well-defined beak, 6 mm in length, that curves to an anterior apical point. Behind the buccal mass, the esophagus emerges and leads to the stomach, both of which have a chitin lining; the stomach contains only fish remains, including entire vertebrae and large rib segments from prey too large to be ingested whole (Table 2). The amount of food debris indicated it to be a voracious feeder. There is a region, slightly overlapping the stomach, with well-digested fragments, or chyme; this specimen has a gladius 97 mm in length (LUKENEDER & HARZHAUSER, 2004, 2005). FUCHS and LARSON (2011a) examined further specimens of *Dorateuthis syriaca,* from the Cenomanian-Santonian Plattenkalks of Lebanon, that included the buccal mass, esophagus, and in some specimens a distinct cord, which passes through the cephalic cartilage (Fig. 6c). The position of the stomach is sometimes indicated by an accumulation of chopped fish, and one specimen preserves the cuticular lining of the stomach. The division of the stomach into two parts is confirmed and another specimen has a long band of undigested fish remains between the anterior mantle and the stomach.

Marine deposits from the North Pacific, Hokkaido, and Vancouver Island Upper Cretaceous yielded isolated and well-preserved upper and lower beaks (TANABE, HIKIDA, & IBA, 2006; TANABE & others, 2008; TANABE & HIKIDA, 2010). The specimens occurred individually in calcareous concretions and retain their original shape and form; they are composed of black carbonate apatite (TANABE & others, 2008). Comparison of the lower beaks of fossil and living forms, especially the posteriorly projected inner lamella and the absence of an anterior calcareous tip, made it possible to refer the fossil beaks to the Coleoidea, *Nanaimoteuthis jeletzkyi,* family uncertain, and to *Paleocirroteuthis haggarti* and *P. pacifica,* suborder Cirrata (TANABE & others, 2008; TANABE, 2012). A calcareous nodule, collected from Kamikinenbetsu Creek, Hokkaido, the Upper Cretaceous (Turonian) of Japan (TANABE, HIKIDA, & IBA, 2006) contained an upper beak, 33 mm in length, with a well-developed lateral wall, and a sharply pointed rostrum, 18.2 mm in length. The genus and species to which the beak belongs has been assigned to Coleoidea,

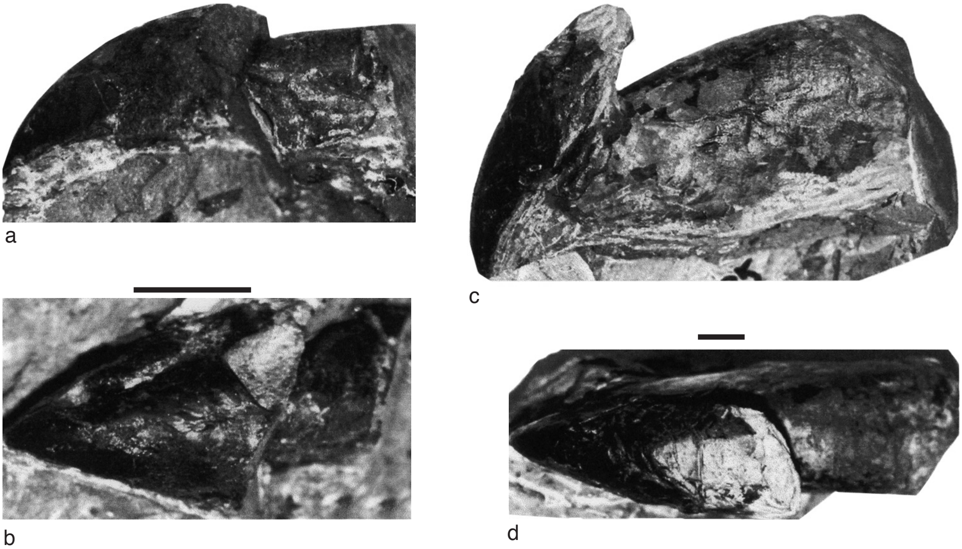

FIG. 11. *a–b*, genus and species indeterminate (MM 28665, University Museum, University of Tokyo), middle Turonian, Obira, northwestern Hokkaido, Japan, incomplete upper jaw, left lateral *(a)* and dorsal *(b)* views, scale bar, 10 mm; *c–d*, *Yetzoteuthis gigantus* (NMA-335, Nagasaki Museum Natural History), Teuthida, Campanian, Nakagawa, northern Hokkaido, Japan, left lateral view of an almost complete upper beak *(c)* and dorsal view *(d)*, scale bar, 10 mm (Tanabe, Hikida, & Iba, 2006).

but order and family uncertain, and genus indeterminate (Fig. 11a–b).

A nodule recovered from Wakkawenbetsu Creek, Upper Cretaceous, Campanian, of Hokkaido, Japan, revealed an almost complete upper beak of black horny material. The beak is 97 mm in length, with a lateral wall 22.5 mm in length; the rostrum is sharply pointed, the hood is 56.2 mm in length, and the wing is well developed, with a length of 50.4 mm. Its size is comparable with that of the living giant squid, *Architeuthis* sp., and it was placed in the Teuthida, Oegopsida, but of uncertain family, as a new species, *Yetzoteuthis gigantus* TANABE, HIKIDA, & IBA, 2006 (Fig. 11c–d).

A concretion from the Upper Cretaceous, lower Campanian, from Vancouver Island, Canada, contained a lower beak with a large outer lamella and relatively short inner lamella; both are of a black material, probably originally of chitin (Fig. 12a). The hood covers 75% of the crest when viewed in profile. The rostrum is distinct, with a point. The maximum length of the beak is 54.0 mm. By comparing the diagnostic features of the lower beaks of living cephalopods it was possible to place the fossil with the Coleoidea, order Vampyromorpha, and assign it to a new species, *Nanaimoteuthis jeletzkyi* TANABE & others, 2008, family uncertain. TANABE and HIKIDA (2010) described a new species, *Nanaimoteuthis yokotai*, Upper Cretaceous, Turonian, from two lower beaks found in Hokkaido, Japan, and placed in the Vampyromorpha. The inner and outer lamellae are of equal length, and the maximum length is 63.7 mm; this is larger than that of *N. jeletzkyi,* indicating a larger body size. Lower beaks of *Nanaimoteuthis* and *Paleocirroteuthis,* 38–110 mm maximum length, are also large compared with those of living vampyromorphs and cirrates, respectively.

In the same formation, another concretion was found containing a lower beak. The beak has a large, thick outer lamella covering 65% of the crest in profile; the inner lamella is longer and presumably both were originally of chitin. The rostrum has a sharp tip and the beak angle

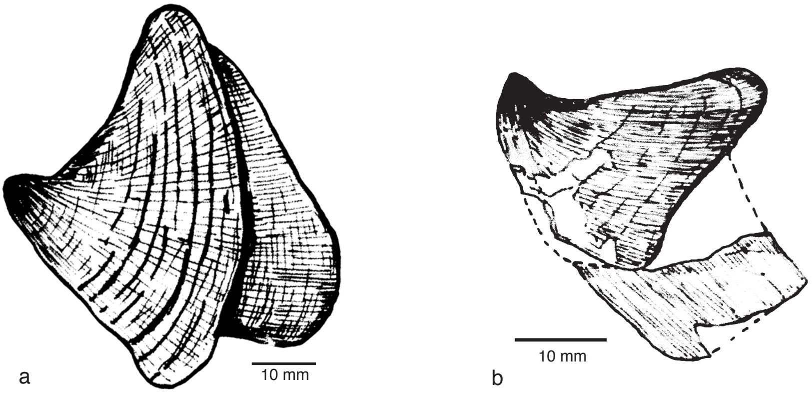

FIG. 12. Lower beaks of fossil Coleoidea. *a, Nanaimoteuthis jeletzkyi*, CDM 2006.1.1 (Courteney and District Museum and Paleontology Center, Vancouver Island, Canada), Cirrata, lower Santonian, Hokkaido, Japan, right lateral view (Tanabe & others, 2008); *b, Paleocirroteuthis pacifica*, CDM 2006.2.1, Cirrata, lower Campanian, Pender Formation, (Tanabe & others, 2008).

is obtuse. Comparison of the lower beak of this fossil with those of living forms led to its assignment to a new genus and species, *Paleocirroteuthis pacifica* (Fig. 12b), and a second specimen with similar features to *Paleocirroteuthis haggarti*, both species of the order Octopoda, suborder Cirrata (TANABE & others, 2008).

Miocene

One upper beak and three lower beaks of sepiolid coleoids, from the middle Miocene, were collected in Voslau, Austria. The upper beak, 4.1 mm in length, is poorly preserved and consists of the rostrum, crest, and parts of the hood (Fig. 13a). The rostrum and hood are largely pigmented, with only the posterior edges being clear but yellowish; the crest is amber colored and lacks dark pigmentation. In the best preserved of the three lower beaks, the rostrum, hood, and almost complete wings survive, although the posterior edge of the hood-wing complex shows damage (Fig. 13b). The rostrum and a narrow area close to the beak angle displays darkening, whereas the wings and crest are pale. The rostral edge is nearly straight with a small tip, and the narrow, elongated wing broadens toward the inner end. The general features of the upper and lower beak are coleoidlike and considered to show similarity with those of modern decabrachian sepiolids (HARZHAUSER, 1999).

RADULA

Recent Coleoidea

The radula is a characteristic feature of the buccal apparatus of the phylum Mollusca. The morphology and histology of the buccal masses of living coleoids—*Sepia, Heteroteuthis, Alloteuthis; Teuthowenia, Leachia, Vampyroteuthis, Cirrothauma,* and *Octopus*—were described by NIXON and YOUNG (2003). The radular apparatus of living *Nautilus,* its ontogeny, breakdown, and resorption of the radular teeth, was described by MESSENGER and YOUNG (1999).

The radula is a chitin-protein complex (Table 1), and, in Recent Cephalopoda, is an elongated ribbon bearing teeth that are regularly arranged to form transverse and longitudinal rows (Fig. 14). The radula is formed within the radular sac (RAVEN, 1958), which lies at the back of the buccal mass and below the esophagus (see NIXON, 2011, fig. 13). Teeth are added to the ribbon continuously by odontoblasts, which lie at the blind end of the radular sac; the rachidian (central) tooth is formed first, followed by the teeth on either side in mediolateral order (WILLIAMS, 1909). The ribbon is wider and the teeth larger as they emerge from the radular sac and the radula proceeds forward to the front of the radular complex, where it turns acutely

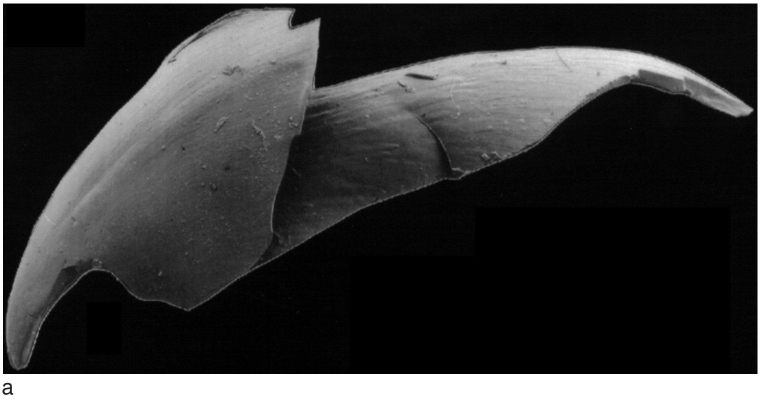

FIG. 13. Sepiolida, middle Miocene, Voslau, Austria; *a*, NHMW 1999z0050/0001 (Museum of Natural History, Wien, Austria), upper beak, lateral view, ×33; *b*, NHMW 1999-z0050/0050/0002, lower beak, oblique lateral view, ×27 (Harzhauser, 1999).

and ventroposteriorly at the bending plane (Fig. 1) (see NIXON, 2011, fig. 13). The teeth emerging from the sac are larger than the preceding ones; this is illustrated in the oegopsid squid, *Teuthowenia megalops* (DILLY & NIXON, 1976a), and the coastal octopod, *Octopus vulgaris* (NIXON, 1968). As the radula approaches and passes the bending plane, the teeth may display wear and degradation; it terminates near the subradular gland (Fig. 1) and the teeth lost or resorbed, presumably as a result of the action of the enzymes secreted by the gland (NIXON, 1998b).

The elements in each transverse row are repeated in number, shape, and form in the preceding and succeeding rows and are named from the center to the periphery (Table 4). The radula of Recent Nautiloidea is wide, and each transverse row has thirteen elements; these comprise the rachidian tooth with, on each side, two lateral teeth, a marginal tooth and marginal plate, and a second marginal tooth and plate; the number of elements is constant (Fig. 15a). If the two outer elements on each side are omitted, then the names for the central nine elements can be retained for those radula of fossil

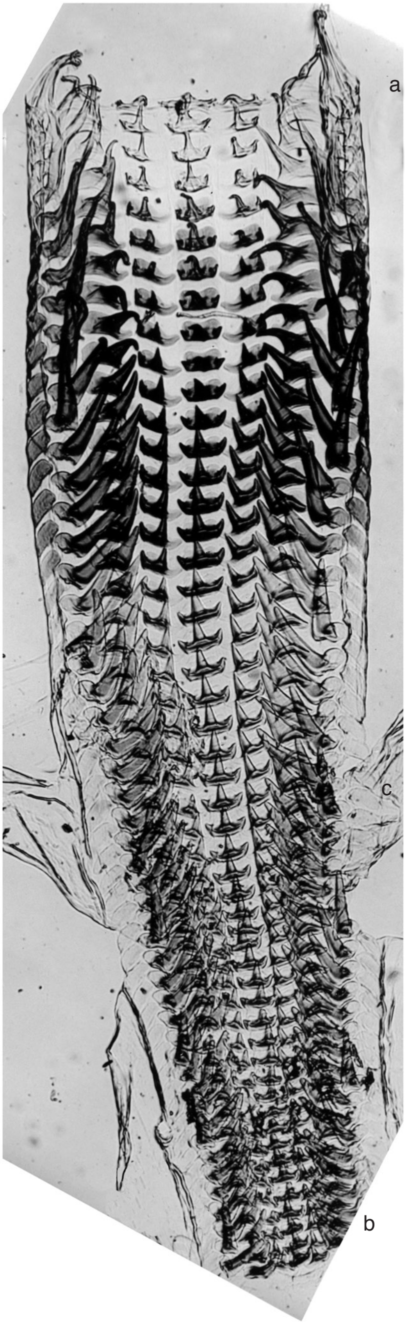

FIG. 14. Recent *Loligo vulgaris*, a coastal squid, mantle length 250 mm, weight 75 g; radula has been isolated and flattened and is 7.91 mm long, with fifty-one transverse rows of teeth; *a*, newly formed teeth within and just beyond radula sac; *b*, distal end of radula with oldest and smallest teeth; *c*, region of the bending plane (new).

TABLE 4. The names and abbreviations for the radular elements in a single row of teeth; radichian (central) tooth, with the lateral teeth, marginal teeth, and marginal plates on one side of the ribbon (Nixon, 1995, 1998b).

Radular element	Abbreviations
Rachidian (central) tooth	R
Lateral tooth 1	L1
Lateral tooth 2	L2
Marginal tooth 1	M1
Marginal plate 1	MP1
Marginal tooth 2	M2
Marginal plate 2	MP2

and living Coleoidea (Fig. 15b–d), namely a rachidian tooth, two lateral teeth, one marginal tooth, and one marginal plate on each side; the marginal plates may be present or absent, depending upon the species. There are some exceptions. For example, in *Spirula spirula,* the radula is vestigial (KERR, 1931), but notably the lateral buccal palps bear a very thick cuticle with numerous stout teeth (NIXON & YOUNG, 2003). Several species of the genus *Gonatus* have only five teeth in each transverse row (SARS, 1878; KRISTENSEN, 1981b), and in some deep-sea octopods the radula may be present, reduced, or absent (G. L. VOSS, 1988b). Radular teeth exhibit wear as they reach and pass the bending plane (Fig. 14). The ribbon and its elements terminate as they reach the subradular organ (YOUNG, 1965) in which there are cells formed from modified odontoblasts (odontoclasts). These cells act to dissolve the elements of the radula and absorb the debris (resorbtion) in the subradular sac; they were described in *Nautilus* and *Octopus* by MESSENGER and YOUNG (1999). The nomenclature makes it possible to represent the elements of the radula of Cephalopoda by a formula, using abbreviations for each tooth and marginal plate (Table 4); such a formula permits comparisons and allows modifications to represent other features of the teeth as they are recognized (NIXON, 1995).

Three types of radula are recognized among extant coleoids (Fig. 15b–d). The most

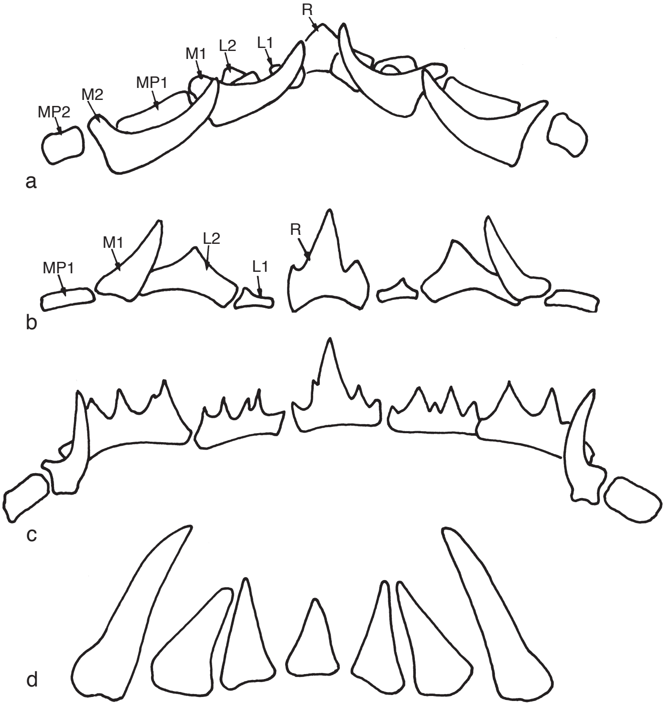

FIG. 15. Recent Cephalopoda; teeth present in one transverse row of radula of *a*, *Nautilus* (Nautiloidea), *b*, *Octopus,* Octopoda (heterodont), *c*, *Japetella,* Octopoda (ctenodont), and *d*, *Sepia,* Sepioidea (homodont); see Table 4 for explanation of abbreviations (adapted from Nixon, 1995).

common is the heterodont radula, in which there is an ectocone (cusp) on the mesocone, or main cusp, of the rachidian tooth, and usually also on the first lateral teeth. The second is the homodont radula, in which the teeth have but a single cusp, and the third is the ctenodont radula, in which all of the teeth are multicuspid. In the heterodont radula of some octopods, the mesocones of the rachidian teeth bear ectocones whose position alters in a sequential manner. This phenomenon was observed in the 19th century but only described in the 20th century by ROBSON (1925), who recognized two forms that he termed symmetric and asymmetric seriation. In symmetric seriation, ectocones occur on one mesocone, then on the following third and fifth ones, continuing in the same order. In asymmetric seriation, successive rachidian teeth have ectocones on either side of the mesocone, and their position is repeated in groups; the ectocones shift downward and outward on the mesocone of a series of rows until becoming outermost, when the series begins again (NAEF, 1923). Seriation was considered by ROBSON (1925) to be unique among Octopodinae but has since been found in four species of a small pygmy squid, *Idiosepius* (ADAM, 1986).

Fossil Radulae

The first radula recognized to belong to a fossil cephalopod was that of *Glaphyrites (Eoasianites),* a Permian ammonoid, which has nine elements in each transverse row (Table 5) (CLOSS & GORDON, 1966; CLOSS, 1967). Radulae were then sought in other Ammonoidea (LEHMANN, 1981, 1990; KLUG & JERJEN, 2012); most of those found so far have seven teeth and two marginal plates (although in some it is not certain whether they are present or absent). A partial reconstruction of an orthocerid radula, *Michelinoceras,* indicates seven teeth in each transverse

Table 5. Formulae for the elements of the radulae of some living and fossil forms; see Table 4 for abbreviations.

	Genus	Formula	Reference
Fossil Cephalopoda			
Unnamed coleoid	coleoid	R+L1+L2+M1+MP1+MP2	Doguzhaeva, Mapes, & Mutvei, 2010a
Donovaniconida	*Saundersites illinoisiensis*	R+L1+L2+M1+MP1+MP2	Doguzhaeva, Mapes, & Mutvei, 2010a
Nautiloidea			
Nautilida	*Paleocadmus herdinae*	R+L1+L2+M1+MP1+M2+MP2	Saunders & Richardson, 1979
Nautilida	*Paleocadmus pohli*	R+L1+L2+M1+MP1+M2+MP2	Saunders & Richardson, 1979
Ammonoidea			
Goniatitida	*Girtyoceras limatum*	R+L1+L2+M1+MP1	Doguzhaeva , Mapes, & Mutvei, 2010a
Goniatitida	*Glaphyrites (Eoasianites)*	R+L1+L2+M1	Closs & Gordon, 1966
Ammonitida	*Eleganticeras*	R+L1+L2+M1	Lehmann, 1981
Ammonitida	*Dactylioceras*	R+L1+L2+M1	Lehmann, 1981
Ammonitida	*Arnioceras*	R+L1+L2+M1	Lehmann, 1981
Ammonitida	*Aconeceras trautscholdi*	R+L1+L2+M1+MP1	Doguzhaeva & Mutvei, 1992
Ammonitida	*Baculites* sp.	R+L1+L2+M1+MP1	Kruta & others, 2011
Recent Cephalopoda			
Nautiloidea	*Nautilus*	R+L1+L2+M1+MP1+M2+MP2	Nixon, 1995
Spirulidea	*Spirula spirula*	Teeth absent from radula	Kerr, 1931
Oegopsida	*Thysanoteuthis rhombus*	R+L1+L2+M1	Naef, 1923
Oegopsida	*Teuthowenia megalops*	R+L1+L2+M1+MP1	Dilly & Nixon, 1976a
Oegopsida	*Gonatus fabricii*	R+L1+M1	Sars, 1878; Kristensen, 1981b
Myopsida	*Loligo vulgaris*	R+L1+L2+M1+MP1	Adams, 1954
Sepioidea	*Sepia officinalis*	R+L1+L2+M1	Robson, 1924
Vampyromorpha	*Vampyrotheuthis infernalis*	R+L1+L2+M1	Pickford, 1949
Octopoda, Cirrata	*Grimpoteuthis*	R+L1+L2	G. L. Voss, 1988b

row (Mehl, 1984). An unidentified orthocone, from the Upper Ordovician Soom Shale, has four or five elements, although other elements may have been obscured during fossilization, but no marginal plates are present (Gabbott, 1999). Two isolated radulae from Mazon Creek, upper Carboniferous, closely resemble those of Recent *Nautilus,* although they could not be related directly to the nautiloids present. A ten-armed squid was present, including its radula, together with another individual (Saunders & Richardson, 1979), and both have been redescribed (see below) (Doguzhaeva, Mapes, & Mutvei, 2010a). The radula of endocochleate cepahlopods has little chance of surviving the process of fossilization in the absence of an external shell. Currently, the radulae of both fossil coleoids so far described (Doguzhaeva, Mapes, & Mutvei, 2010a) have eleven elements in each transverse row (Fig. 16; Table 5). A radula has been exposed in one belmnoid, *Acanthoteuthis,* Upper Jurassic, Fossillagerstatte, southwestern Germany (Klug & others, 2011), and it resembles those of Recent Coleoidea. The paucity of coleoid radulae in the fossil record makes it useful to include the formulae of those of Nautiloidea, Orthocerida, and Ammonoidea currently known, allowing comparison between some Recent and fossil forms (Table 5). In the early stages of coleoid evolution, a radula with eleven elements (seven teeth and four plates) may have been derived from the nautiloid radula, which has thirteen elements (seven teeth, four marginal teeth, and four marginal plates) by resorbtion or loss of marginal tooth 2 (Fig. 15).

Two fossils from Mazon Creek, Illinois, United States, Carboniferous, Middle Pennsylvanian, were assigned to the *Jeletzkya douglassae* by Saunders and Richardson in 1979, but new data on the morphology of the shell, radula, arm hooks, mantle muscle tissue and traces of ink in two specimens (PE

32521 [holotype], PE 20808 [paratype]), led Doguzhaeva, Mapes, & Mutvei (2007) to redescribe them as *Saundersites illinoisiensis,* Donovaniconidae, order Donovaniconida. This is the earliest coleoid radula yet described, and each transverse row has eleven elements with two adjacent marginal plates on each side of the teeth (Fig. 16a; Table 5). The shell length of PE 32521 is 56 mm, the radula about 3.5 mm long and 2.5 mm wide, with some thirty transverse rows of teeth visible. The central, rachidian tooth, distinguished by its position in a transverse row and symmetrical shape, is about two and a half times shorter than the marginal teeth; it has a broad, stout basal region, and triangular upper part with an apical point. On either side of the seven teeth there are two adjacent marginal plates, with marginal plate 1 adjacent to marginal tooth 1 (Fig. 16a). The lateral teeth are poorly preserved and cannot be described in detail. The marginal tooth is tall, curved backwards and its apex pointed, the basal portion is wide.

A concretion, recovered from the Eudora Shale, Oklahoma, United States, upper Carboniferous, Missourian, is known only from its radula, arm hooks, and possible debris of cranial cartilage, and is unnamed (Doguzhaeva, Mapes, & Mutvei, 2010a). Some parts of the radula are more completely preserved than others. There is a symmetrical, rachidian tooth with a broad, stout, basal portion, and an upper part that is triangular, with an angle of 35 degrees, and reaches an apical point. On either side there appear to be two, slightly taller lateral teeth, and two, tall, asymmetrically curved marginal teeth with apical points. This radula has 11 elements in each transverse row with 2 adjacent marginal plates on each side of the teeth (Fig. 16b; Table 5).

DRILLING AND FEEDING IN RECENT AND FOSSIL OCTOPODS

Cavities made by living octopuses in the exoskeletons of their prey are ovoid to subcircular in shape, with a diameter of 0.8 to 4.0 mm on the surface that tapers to 0.3 to 1.57 mm at the point of penetration (Nixon & Maconnachie, 1988). Living "species of several genera of octopus occupy the summit of the trophic pyramid as top carnivore of marine benthic communities throughout the world's seas and oceans" (Bromley, 1993, p. 167).

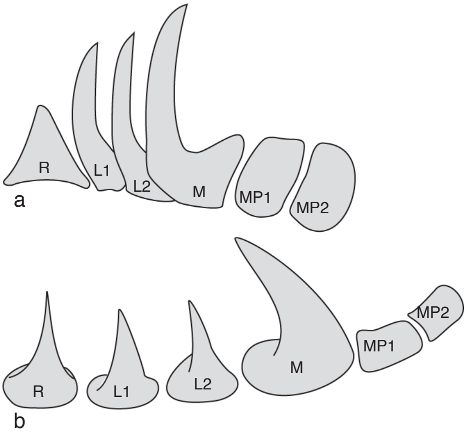

Fig. 16. Fossil Coleoidea, rachidian (central) tooth *(R)* and those of the right side of a transverse row of teeth of radulae; see Table 4 for explanation of abbreviations; *a*, unnamed coleoid, PE20808 (Field Museum of Natural History, Chicago), upper Carboniferous, Eudora Shale, Oklahoma, USA; *b*, *Saundersites illinoisensis,* PE 32521 (Field Museum of Natural History, Chicago), upper Carboniferous (Moscovian), Mazon Creek, Illinois, USA (adapted from Doghuzhaeva, Mapes, & Mutvei, 2007, 2010a).

The steps taken from first sighting the prey to capture and ingestion can be followed in the species for which there is most available evidence, *Octopus vulgaris.* It detects its prey visually (Boycott, 1965), and a juvenile octopus can reach it in 3.8 seconds in the laboratory (Maldonado, 1963). The captured prey is enveloped within the interbrachial web and held by the arms and suckers (Boycott, 1965). Tens of thousands of morphologically distinct receptors are present on each sucker, including chemo- and mechanoreceptors (Graziadei, 1964, 1971), as well as numerous putative receptors on the slender terminal tips of the arms (Nixon & Young, 2003, fig. 31.7). The muscles of the arms and suckers (Graziadei, 1971) manipulate the prey into a position in which the octopus can attempt to open a bivalve or withdraw the body of a gastropod. *O. dierythraeus* will also initially attempt to pull a bivalve apart and spend more energy to access the flesh quickly before it will drill (Steer & Semmens, 2003). If *O. vulgaris* fails to gain access, then it sites the buccal mass over the musculo-skeletal attachments of the prey (Nixon & Maconnachie, 1988; Fiorito & Gherardi, 1999), as does *O. rubescens* (Anderson, Sinn, & Mather, 2008). *O. vulgaris* preys on crustaceans, which it will drill over or close to the large adductor muscle of the chela (Mather & Nixon, 1995), or drill their joints (Altman & Nixon, 1970); another octopod, *Eledone cirrhosa*, will puncture the eye (Grisley, Boyle, & Key, 1996).

After penetrating the exoskeleton, the saliva from the paired posterior salivary glands, which lie behind the head, can be introduced through the duct. The saliva includes a toxin, cephalotoxin, which rapidly subdues the prey (Ghiretti, 1959, 1960; Songdahl & Shapiro, 1974; Cariello & Zanetti, 1977). The paired anterior salivary glands, in the lateral buccal palps, secrete mucus (Gennaro, Lorincz, & Brewster, 1965) and other substances including hyaluronidase (Romanini, 1952), One, or both, sets of glands, together with the radula and radular complex, are involved in excavating the prey.

The microstructure of the molluscan shell is formed of calcite prisms (Mohs scale of hardness 3), aragonite tablets (Mohs scale of hardness 3.5–4), and organic matrix. It is well organized when the fracture face is seen at high magnification in a scanning electron microscope (SEM). Ambrose, Leighton, and Hartwick (1988, p. 491) suggested "that *Octopus dofleini* employs chemical dissolution of the shell during drilling." After being subjected to the actions of the octopus's saliva, radula, and radular complex, the fracture surface of the shell shows disorganization, dissolution and etching of the tablets and prisms when seen at high magnification with the SEM (Nixon, Maconnachie, & Howell, 1980).

Hydrophones recorded sounds from *Octopus vulgaris* that were attributed to its drilling activities (Arnold & Arnold, 1969; Wodinsky, 1969). The radular teeth at and beyond the bending plane are often worn (Nixon, 1998b), indicating their involvement in drilling, at least in the early stages. However, the radula is often too wide to reach the bottom of the cavity and penetrate the shell (Nixon, 1979), but the eversible tip of the posterior salivary gland—with its many chitinous denticles, 40 µm in height at the tip, and small denticles, 15 µm in height, packed around its base—could complete the excavation (Nixon, 1979, 1980). However, these denticles are not as hard as the prisms and tablets of the molluscan shell (chitinous radulae of topshells and winkles have a hardness of 2.0–2.5 on Moh's scale (Crothers, 2001) and may produce vibrations rather than sounds from the interaction of either the muscle attachments or the prisms and tablets.

The shape and form of the holes drilled by living octopuses in the exoskeletons of their prey have a number of characteristic features, some being visible in the light microscope, but examination at very high magnification with a SEM is necessary to confirm that the activities are due to octopods. These features result from the actions of the radular complex and salivary glands on the mineral and organic material of the exoskeletons of mollusks and crustaceans (Nixon & Maconnachie, 1988), and include the following.

1. The drill holes are usually associated with the region of attachment of muscles to the exoskeleton; the myostracum in bivalves, the spire and area close to the columella in gastropods (often on the opercular side); and in shells in which the columella is short or absent and the final whorl is large, distribution is random.
2. The innumerable receptors of the arms and suckers (Graziadei, 1964, 1971) are presumably involved in the location of drill sites.
3. Holes drilled in crustaceans: in carapace, 0.4–1.0 mm to 0.7–2.0 mm, on the internal and external surfaces, respec-

tively (Guerra & Nixon, 1987); in the chelae 0.1–0.8 mm to 0.5–1.8 mm, on the internal and external surfaces, respectively (Mather & Nixon, 1995). Another octopod, *Eledone cirrhosa,* punctures the eye of its crustacean prey (Grisley, Boyle, & Key, 1996).

4. The surface is ovoid or subcircular, with or without a lip, sometimes surrounded by a sheen.
5. The external surface although small, 0.21–1.57 mm, is larger than the penetration point, 0.26–0.73 mm.
6. The walls slope, with the angle depending on thickness or the mineral and structural form of the shell, and may be stepped.
7. The properties of the mollusk shell are important in determining the shape, form, and size of the cavities drilled.
8. Effect of the radular teeth, radula complex, and saliva, on the exoskeletons of mollusks and crustaceans, is visible with the light microscope, but it can only be confirmed with the SEM.

Cavities Drilled by Fossil Octopods

The characteristic features of cavities drilled by Recent octopods in mollusk shells and crustacean exoskeletons are closely similar to those found in fossils from the Early Miocene, Pliocene, and Pleistocene. The habits of octopods, as well as the organs involved in all of the processes from capture to ingestion (described above), must have been established early.

There are two major groups of fossils, trace fossils and body fossils. Trace fossils "are structures produced by the activity of organisms in unconsolidated sediment or hard sediments" (Bromley, 1981, p. 55) and represent an interaction between organisms and their substrates.

The exoskeletons of fossil mollusks and crustaceans have been found with small cavities, and these have been termed trace fossils or ichnofossils. Those with cylindrical holes and straight sides were named *Oichnus simplex* Bromley, 1981, and the ones that are ovoid in shape at the surface and taper to the point of penetration were named *Oichnus ovalis* Bromley, 1993.

A collection of 267 disarticulated valves of the lower Eocene bivalve *Venericor clarendonensis* included 38 specimens that had been penetrated by holes (0.70 mm to 2.14 mm diameter on the surface, tapering to 0.48 mm to 1.83 mm at the entry point), concentrated over musculo-shell attachment sites (Todd & Harper, 2011). Numerous shells of *Pecten jacobaeus* from the Pliocene have an ovoid cavity at the surface, 0.46 mm by 0.74 mm, which tapers to 0.17 mm by 0.27 mm at the point of entry (Bromley, 1993).

Pliocene sessile acorn barnacles were examined, and a drill hole found with an outer diameter of 0.74 by 0.46 mm and penetration hole of 0.27 by 0.17 mm (Klompmaker, Portell, & Karasawa, 2014). Many scallops from Plio-Pleistocene shell beds have holes of 0.80 mm to 1.60 mm on the surface, mostly located between ribs on the so-called upper left valve, opening directly into the adductor myostracum (Harper, 2002). Comparison of the features present in cavities drilled by living octopuses in mollusk shells, visible with the light and at very high magnification in the SEM, shows that the effects of the radula, radular complex and salivary glands are strikingly different from those on fracture surfaces (Nixon, Maconnachie, & Howell, 1980). Notably, the cavities found in fossil shells have features that are closely similar to those in the shells drilled by living octopuses, and thus the internal organs of Recent octopods were almost certainly present and functional in the fossil ancestors of octopods.

DISCUSSION

The description and subsequent reconstruction of the beaks of ammonoids since the 1960s indicate variation in the presence or absence of calcitic parts, shape and form, and size differences between the upper and lower beaks (Lehmann, 1981; Tanabe & Fukuda, 1999). The upper and lower beaks are visible in the fossil coleoid, *Dorateuthis syriaca* (Lukeneder & Harzhauser, 2004).

From Nusplingen, Germany, specimens with upper and lower beaks, which represent the Nautiloidea, Ammonoidea, and Coleoidea, have been described and reconstructed (Klug & others, 2010). Beaks of ammonoids, from the Carboniferous to the Cretaceous, are best known, and exhibit differences in shape and form, size, presence or absence of associated calcitic structures, inner lamella shorter or longer than outer lamella; most of these changes appear to occur in the lower beak, notably the disparity in length between the upper and lower beak (Lehmann, 1981, 1990; Nixon, 1996; Tanabe & Fukuda, 1999). In some ammonites, the lower beak is notably larger than the upper beak and a calcified protective covering is present in a few, for example *Hildoceras.* It is feasible that these ammonites could have ingested a large volume of seawater only to expel the fluid from the buccal cavity later, and retain the prey.

Electron micrography of fossil cephalopods has revealed muscle tissues (e.g., Kear, Briggs, & Donovan, 1995). The muscle scars of *Aconeceras* indicate strong retractor muscles to the head and funnel, and small scars a complex muscular system (Doguzhaeva & Mutvei, 1991, 1993). The spherical buccal apparatus with the beak, esophagus and crop/stomach are visible in *Dorateuthis syriaca* (Fig. 6b) (Lukeneder & Harzhauser, 2004), and the cephalic cartilage, and cuticular wall of the stomach, recognized in further specimens (Fuchs & Larson, 2011a; Lukeneder & Harzhauser, 2004). Such special conditions for preservation of soft parts occur in the lithographic limestone, Upper Jurassic, Kimmeridgian, of Nusplingen Quarry, Germany (Klug & others, 2010); Upper Cretaceous, upper Santonian, in Sahil, Lebanon (Lukeneder & Harzhauser, 2004); and in Upper Cretaceous, upper Cenomanian, of Hâqel and Hâdjoula, Lebanon, (Fuchs & Larson, 2011b; Fuchs, Bracchi, & Weis, 2009).

The morphology of the buccal mass, muscle attachments, and secretory tissue, is little known because of the rarity of preservation of soft tissues in fossils, making morphological changes difficult to ascertain since these tissues leave little or no trace. In the living coleoids *Octopus bimaculoides, Sepia officinalis,* and *Loliguncula brevis*, three muscles (the anterior, posterior, and superior mandibular muscles) connect the upper and lower beaks, and the lateral mandibular muscles originate on the connective sheath surrounding the buccal mass but do not connect with the lower beak (Uyeno & Kier, 2005, 2007). Attachment of mandibular muscles to the beak of living coleoids is via a layer of beccublast cells, which leave imprints (see Nixon, 2011, fig. 16) (Dilly & Nixon, 1976a); similar imprints have been found on the beaks of the ammonites *Girtyoceras* (Doguzhaeva, Mapes, & Mutvei, 1997), and *Gaudryceras* (Tanabe & Fukuda, 1983, 1999).

Clarke (1962, 1980, 1986) found that the lower beaks of living coleoids have characteristic features useful for identification. However, Clarke and Maddock (1988, p. 123) commented that "no great differences in the food are known which would seem likely to account for the differences in lower beak shape;" the capture of prey by the tentacles, and its breakdown by the cutting or shearing actions of the beaks is probably similar amongst most squids (see Table 3). The salivary glands of several cephalopods, including *Octopus vulgaris*, secrete a toxin, cephalotoxin, which subdues captured crabs (Ghiretti, 1959, 1960), and an enzyme, which acts to separate the exoskeleton so that only soft tissues are ingested (Nixon, 1984). Experimental evidence indicates that loss of the rostrum of the lower beak reduces food intake (Altman & Nixon, 1970).

Survival of the crop and/or stomach and their contents in some fossils suggest predatory habits. The beak of the coleoid, *Dorateuthis syriaca* (Fig. 7b), has sharp rostra, reminiscent of living coleoids, and its prey is relatively large as the crop/stomach contents include whole vertebrae and long rib segments (Table 2) (Lukeneder & Harzhauser, 2004, 2005). Living coleoids prey mostly on crustaceans, fish, and cephalopods and their young ingest whole small prey (Table 3). Ammonoids took small prey and ingested it whole (Table 2).

The esophagus of the open-sea octopods, *Japetella diaphana*, *Tremoctopus violaceous, Argonauta argo, Haliphron atlanticus,* and *Ocythoe tuberculata* is wide, with a relatively thick lining of chitin, sometimes even laminated (Nixon & Young, 2003). Such a lining presumably acts to protect the digestive tract and the surrounding central nervous system from sharp exoskeletal material. The thin chitin lining of the esophagus of *Octopus vulgaris* usually protects the surrounding tissues, but serial sections of brains included setae from the polychaete *Hermione hystrix;* setae were also found near the brain and between the digestive tract and posterior salivary gland duct (Budelmann & Nixon, 1984).

The radulae of eighty-three living cephalopods have been examined; these specimens represent only about 8% of the currently known 650 living species. In the radulae of the following Recent forms, there are three elements in the octopod *Vosseledone charrua,* five in *Gonatus fabricii* (Kristensen, 1981b), and up to thirteen elements in others. In a very small number, the radula is vestigial or absent: for example, the spirulid *Spirula spirula* and the cirroctopod *Cirrothauma murrayi* (Nixon, 1998b). At present, between seven and thirteen elements have been found in the radulae of just twenty cephalopods (Fig. 16; Table 5); this represents only a miniscule percentage of the group (Nixon, 1996). Doguzhaeva, Mapes, and Mutvei (2007) suggested that the eleven elements in early Carboniferous coleoids may have been inherited from the monoplacophoran radula or the archaic radula of early cephalopods. The most persistent of the radula, through fossil and living forms, is the rachidian tooth, which is the first to develop in the radular sac (Raven, 1958). Such changes in the elements of the radula could have been inherited from the monoplacophoran radula or the archaic radula of early cephalopods. Changes may have occurred by the addition of a marginal tooth between the two marginal plates, or by loss or resorption of the second marginal tooth. The latter is perhaps more likely, as *Octopus vulgaris* has a subradular gland, which lies at the end of the radula and acts to loosen, or resorb, teeth as they reach the end of the ribbon (Nixon & Young, 2003). A later step may be either the fusion of the two adjacent marginal plates, or the loss or resorption of one, but until there is further evidence uncertainty remains.

Changes during growth of living cephalopods are apparent in the shape and form of the beak, and in the number, shape, and form of the elements of the radula. Factors involved in these developments may include the mode of capture, availability, and diverse morphology of the prey, which is either ingested whole or reduced to pieces small enough to enter the esophagus. Whether modifications of the mouthparts and/or digestive tract are due to diet, or to other factors, is uncertain in Recent coleoids, and more obscure in fossil forms. The soft tissues identified among fossil specimens, including stomach contents, provide evidence of diet as well as morphological changes. Lukeneder and Harzhauser (2005, p. 06376) commented that this "calls for putting more emphasis on soft part morphologies of exceptionally well-preserved specimens in future studies."

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