Initial stages of food ingestion by
Sepia officinalis (Mollusca: Cephalopoda)

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(With 1 plate and 2 figures in the text)

The cuttlefish ingests much skeleton from the crustaceans and fish it preys upon. The skeletal pieces are relatively large and their dimensions bear a close relationship to the length of the buccal mass and diameter of the oesophagus. The structures of the buccal mass are instrumental in the breakdown of prey and orientation of long pieces of skeleton to ensure their entry into the oesophagus. Many pieces of skeletal material present in the stomach contents still have attached muscles, showing that there is little, or no, external digestion. Skeletal material may be important for long-term maintenance of young *Sepia* in captivity.

Contents

Introduction

Sepia officinalis Linnaeus, 1758, feeds mainly on crustaceans, cephalopod molluscs and bony fish in the Ria de Vigo (Guerra, 1985), off the coast of Tunisia (Najai & Ktari, 1979), and elsewhere and less frequently on nemerteans and other prey (for reviews see Nixon, 1985, 1987*a*). The evidence comes largely from the examination of stomach contents. Their prey can be identified from the debris which includes pieces of exoskeleton from crustaceans, lenses, bones, otoliths and scales from fish, and lenses, beaks and sucker rings from sepioid cephalopods (Guerra, 1985).

The cuttlefish captures live, active and often relatively large prey. Crustaceans are caught by the tentacles or arms (Messenger, 1968), the mode of capture being determined by the size of the prey (Duval, Chichery & Chichery, 1984). To avoid injury, from the pincers of a crab for example, capture is swift and followed immediately by immobilization induced by cephalotoxin, secreted by the posterior salivary glands (Ghiretti, 1959; Koueta & Boucaud-Camou, 1986). An adult cuttlefish can take a prawn in 2 sec and paralyse it within 5 sec (Messenger, 1968). The then relaxed and harmless prey is bitten by the beak and reduced to a size suitable for ingestion, including the exoskeleton which is almost wholly devoured (Wilson, 1946; Messenger, 1968). The role of the digestive gland is of primary importance in the digestive processes of *S. officinalis*, both for enzyme

189

synthesis and absorption (Boucaud-Camou & Yim 1980; Boucaud-Camou & Boucher-Rodoni, 1983, Boucaud-Camou *et al.*, 1985). As yet little is known of the actions of the buccal mass in feeding and breakdown of prey.

The buccal mass lies at the centre of the base of the arms, and encases most of the beak, the exception being the sharp rostrum of the lower beak which protrudes (Clarke, 1986). The buccal complex includes the radula, lateral buccal palps and salivary glands. It lies within the buccal cavity and the lateral buccal palps lead back to the oesophagus. From the back of the buccal mass the oesophagus passes posteriorly to penetrate the central nervous system, which is largely enclosed in a cartilaginous cranium (Tompsett, 1939). The anatomical arrangement of the head of the cuttlefish implies some constraint on the size of particles that can pass along the oesophagus. Selected measurements of the cuttlefish and of hard debris in its stomach were made to allow some interpretation of the function of the buccal mass in feeding.

Materials and methods

Six *Sepia officinalis* Linnaeus, 1758, were caught in the Ria de Vigo, Spain, and their mantle lengths (ML) measured. The stomach was removed from each animal and the entire contents preserved in 4% formalin in sea water. The debris was examined with a binocular microscope and the pieces with the greatest length and diameter were measured and drawn in outline with the aid of a camera lucida attachment.

A further 7 specimens, also from the Ria de Vigo, were frozen shortly after capture. They were defrosted in tap water at room temperature. The mantle length, antero-posterior length of the buccal mass, and diameter of the oesophagus of each animal was measured. The entire contents of each stomach were examined as described above.

Two *Sepia officinalis* Linnaeus, 1758, captured in the Bay of Naples, Italy, were sectioned serially and stained for photomicroscopy. One specimen was newly hatched and the other a juvenile.

The antero-posterior length of the buccal mass, and the mantle length were measured in the additional 12 specimens, caught in the Bay of Naples, Italy, and off Plymouth, UK.

Results

The stomach contents

The state of the debris in the stomach of each specimen and the type of prey present is shown in Table I. Material was found in the stomachs of all but two specimens, both of which were mature females with eggs. Crustacean material was present in 10 of the 11 remaining cuttlefish, fish in five, parts of a cephalopod in one, and unidentified eggs in three (Table I). Crustacean exoskeleton debris in the stomach contents was found to be soft in two cuttlefish, both had been frozen: the crustaceans were presumably in a state of ecdysis when eaten. The exoskeleton in the stomach contents preserved in formalin was not noticeably soft although this solution does result in dissolution of calcium.

The parts of crustaceans found in the cuttlefish stomachs included appendages, elytra and packets of gill leaflets (Table I, Fig. 1). Some of the appendages were broken or fractured, but the joints of several had remained intact with the arthrodial membrane in place. Muscles were often found to be still attached to the exoskeleton within the appendages. Packets of gill leaflets were present.

TABLE I

*Measurements of the 13 **Sepia officinalis** examined and the type of prey and the state of their remains present in each stomach*

ML (mm)	Sex	Ant.-post. length buccal mass (mm)	Oeso-phagus diameter (mm)	Remains found in stomach				State of remains
				Crustacean	Fish	Cephalopod	Eggs	
Formalin fixed								
82	♀			+	+		+	crustacean exoskeleton fragments, appendages with intact muscle inside, joints and arthrodial membranes intact; fish scales
116	♂			+		+		large pieces of a sepioid including fractured upper and lower beak devoid of soft tissue, skin still present, most sucker rings lost; small pieces of crustacean exoskeleton
132	♀			+	+			crustacean remains, some separation of joints but others including muscles still *in situ*, gill lamellae
150	♀			+	+		+	a few pieces of crustacean exoskeleton; fish vertebrae with muscles adhering
177	♀				+			fish remains as a large mass of tissue with bones and skin
180	♀			+				crustacean fragments some with muscle still attached
Frozen								
17·5	♀	3·5	0·5	+				mass of small pieces largely of crustacean appendages, pink in colour; the exoskeleton was soft when pressed
64	♂	13·0	1·1	+				very little present, exoskeleton remains pale pink; exoskeleton was soft when pressed
68	♀	13·0	1·5	+			+	filled with mass of small eggs with embryo developing; a few pieces of crustacean exoskeleton
113	♀	22·0	2·0	+	+			crustacean exoskeleton; bones from fish, scales and one otolith; material was a grey compacted mass
150	♀	27·0	3·0					stomach empty (mature, with eggs)
157	♀	29·0	3·0					stomach empty (mature, with eggs)
185	♀	29·6	3·0	+				dense mass, brownish red material mostly crustacean appendages; exoskeleton was hard when pressed (mature with eggs)

Remains from bony fish included vertebrae, ribs, fin rays, scales and otoliths (Table I, Fig. 1). Muscles often adhered to bones; fins were sometimes intact with chromatophores still recognizable in the skin. Many of the fish bones in the stomachs were long and sharp.
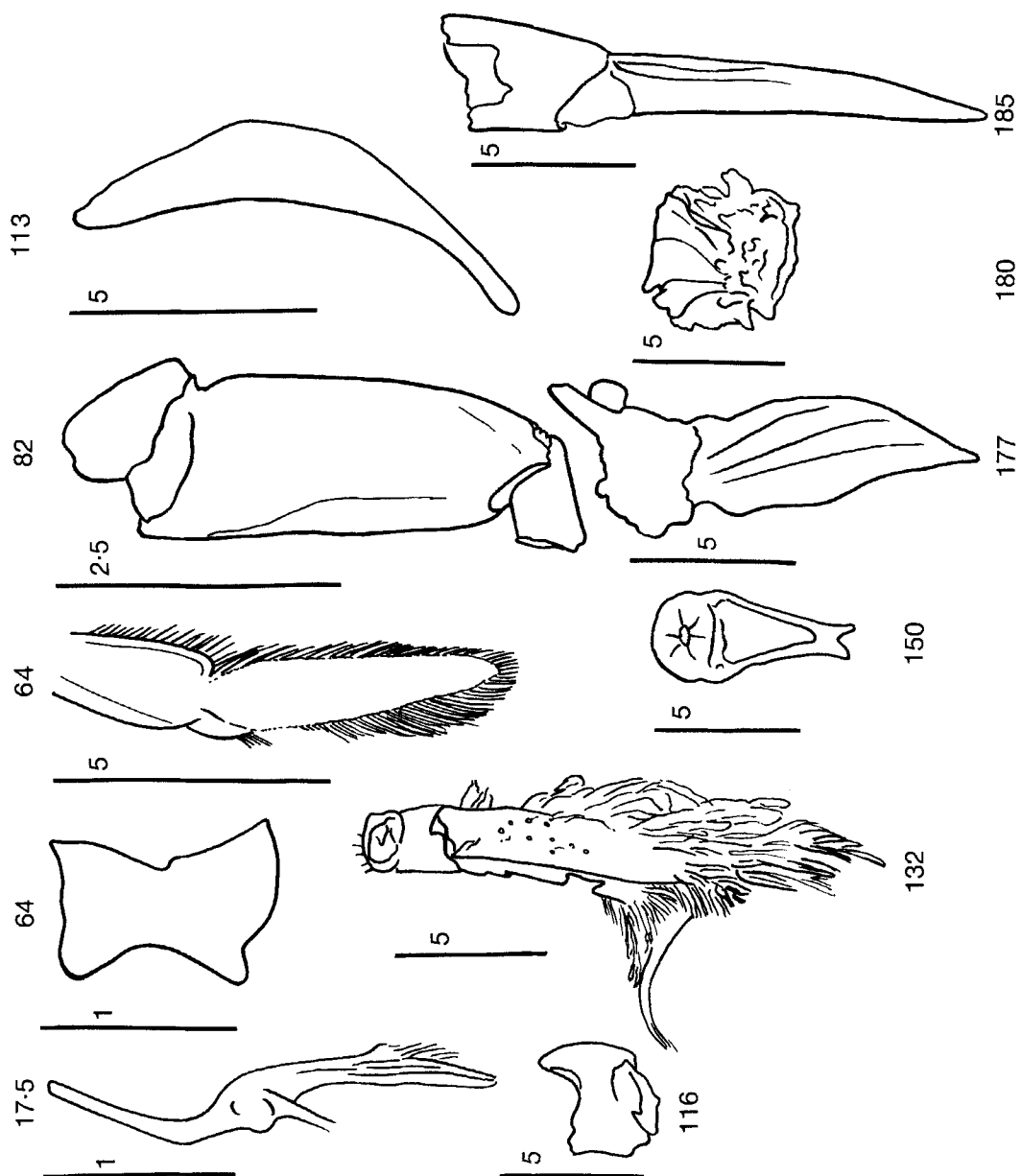
FIG. 1. Outline drawings of the largest piece of skeleton found in each stomach examined. The mantle length of the cuttlefish is given in mm above or below each. The scale bar is in mm.
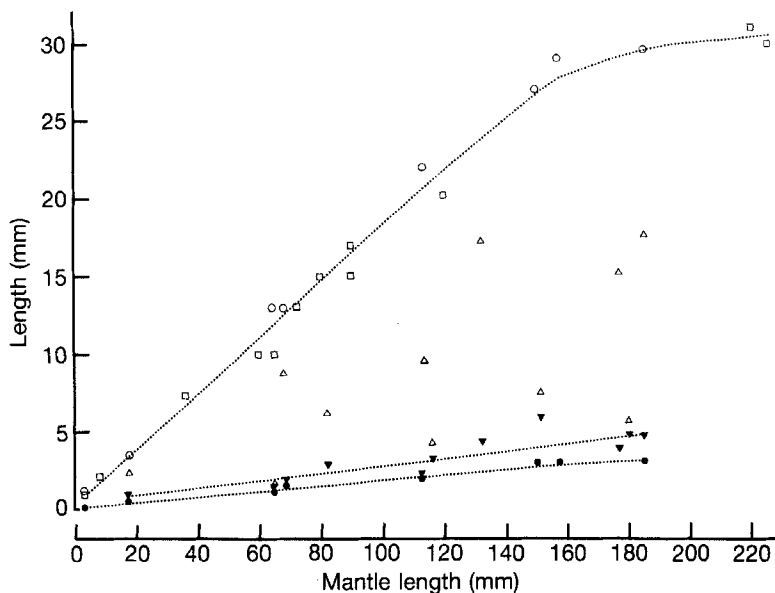
FIG. 2. The antero-posterior length of the buccal mass (O) and additional measurements of specimens from Italy and U.K. (□), the diameter of the oesophagus (●), and the maximum length (△) and diameter (▼) of the largest piece of skeletal material in each stomach is plotted against the mantle length of the cuttlefish.

Cephalopod flesh was in ill-defined chunks: some suckers had separated from the tentacular club, and the beak was in at least nine fragments, but devoid of adhering tissue (Table I, Fig. 1). No vestiges of cuttlebone were found but dissolution had probably already taken place as the material had been stored in formalin. Guerra & Castro (unpubl. obs.) have found cuttlebone, statoliths and lenses of *Sepia* in the stomachs of other specimens of cuttlefish.

Some of the pieces of exo- and endoskeleton amongst the stomach contents were found to have muscles still attached and *in situ*. In other pieces of debris the musculo-skeletal attachments had broken and the skeleton was devoid of adhering muscles.

Relationship between the size of skeletal material in the stomach and the anterior region of the predator's digestive tract

Figure 1 illustrates some of the variety in form, size and sharpness of ingested skeletal material found in the stomachs of 11 cuttlefish.

In Fig. 2 the length and diameter of the largest pieces of skeleton found in each stomach are plotted against the mantle length of the predator.

The antero-posterior length of the buccal mass of seven cuttlefish captured in Vigo, together with a further 12 specimens caught elsewhere, are also plotted against the mantle length in Fig. 2. The buccal mass continues to increase in length until a mantle length of about 150 mm is reached, and thereafter its growth slows markedly. The diameter of the oesophagus from the seven cuttlefish from Vigo, and of the newly-hatched animal shown sectioned in Plate Ia, is plotted
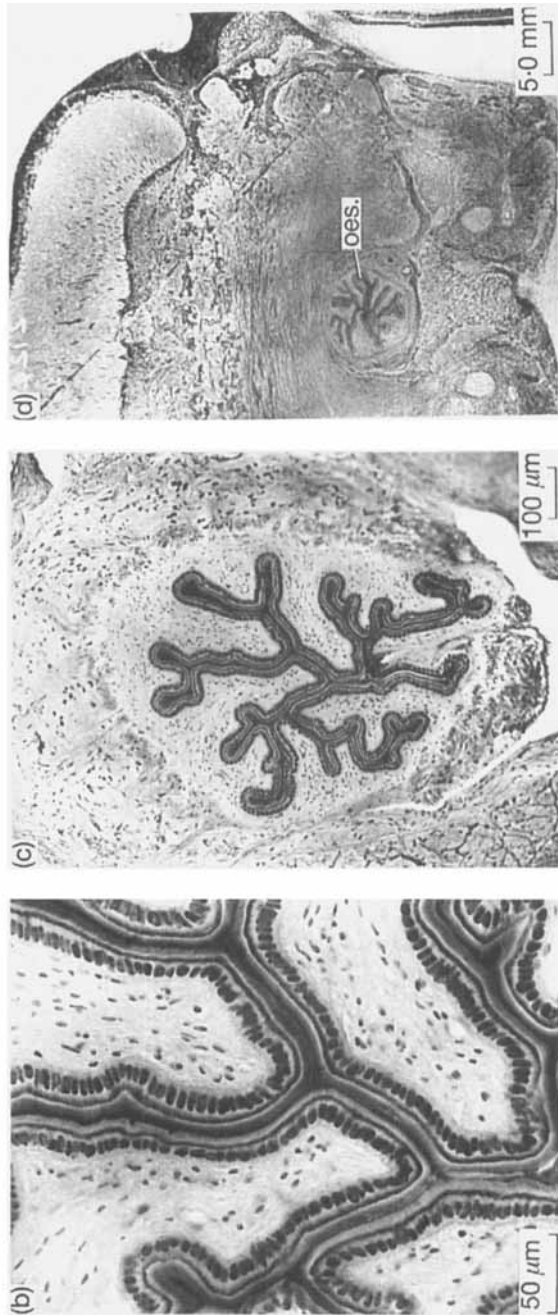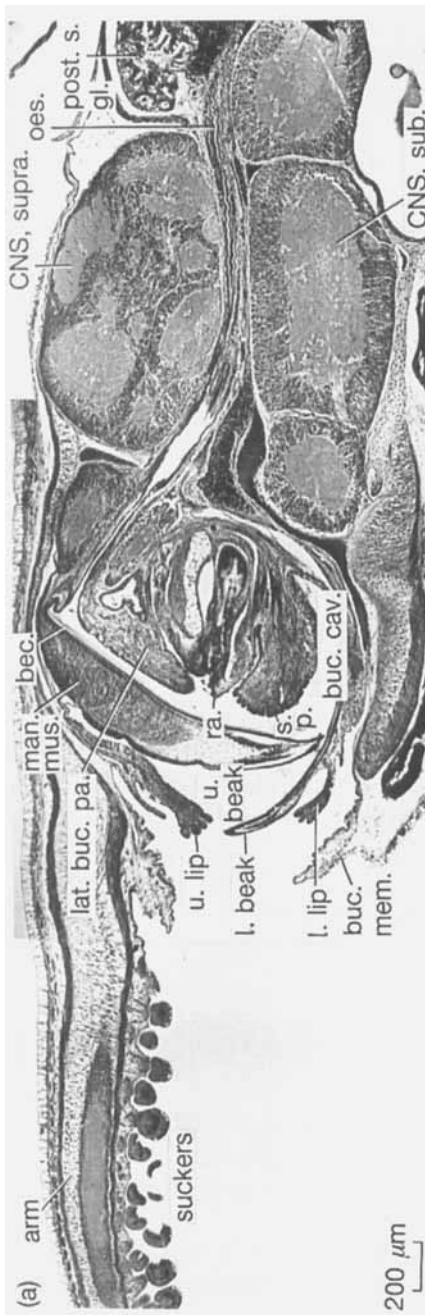
PLATE 1. (a) Sagittal section of head of newly-hatched *Sepia officinalis* to show buccal mass, buccal complex, oesophagus and central nervous system (haematoxylin and eosin). bec., beccublast; buc. cav., buccal cavity; buc. mem., buccal membrane; CNS, sub., suboesophageal mass of central nervous system; CNS, supra., supraoesophageal mass of central nervous system; l. beak, lower beak; l. lip, lower lip; lat. buc. pa., lateral buccal palp; man. mus., mandibular muscle; oes., oesophagus; post. s. gl., posterior salivary gland; ra., radula; s. p., salivary papilla; u. beak, upper beak; u. lip., upper lip. (b) and (c) Transverse section of oesophagus, its cuticular lining and underlying tall columnar cells (haematoxylin and eosin). (d) Transverse section through head of a juvenile showing the central nervous system encircling the oesophagus (oes.) (Cajal).

against the mantle length (Fig. 2). The diameter of the oesophagus shows a steady increase in size, again until a mantle length of 150 mm is attained, after which it remains almost constant.

The maximum length of hard material was less than the antero-posterior length of the buccal mass, but much greater than the width of the oesophagus (Fig. 2). The diameter of skeletal material was, however, equal to or slightly greater than that of the oesophagus. The size of skeletal material present in the stomach contents tends to show a progressive increase in size in relation to the mantle length of the predator (Fig. 2).

The buccal mass and oesophagus

Plate Ia shows the arrangement of the buccal mass, oesophagus and central nervous system in a newly hatched *Sepia officinalis* in sagittal section. The buccal mass is spherical, its shape being determined by the firm beaks and the associated mandibular muscles. The beaks have distinct rostra which protrude forward and are relatively sharp. The circular lips surround the rostra of the beaks. Within the buccal cavity is the buccal complex, formed by the lateral buccal palps, the radula, the salivary papilla and glands. The lateral buccal palps extend from the front of the buccal cavity back to the oesophagus, and bear small teeth on their antero-medial surfaces.

Plate Id, a transverse section through the head of a juvenile, shows the oesophagus closely surrounded by the central nervous system. The oesophagus is deeply folded and has a cuticular lining (Plate Ic). The cuticle, secreted by the underlying tall columnar cells is approximately 10 μm in the juvenile (Plate Ib).

Discussion

The hard particles found in the stomach contents of the cuttlefish include pieces that have been 'bitten' from the prey. Many pieces although long are nevertheless shorter than the antero-posterior length of the buccal mass. The beak is the only structure available capable of reducing crustaceans to a size that can enter the buccal cavity and then pass along the oesophagus. The beak of *Sepia officinalis*, a chitin-protein complex (Hunt & Nixon, 1981), is secreted by beccublasts (Plate Ia) (Dilly & Nixon, 1976). As the animal grows the chitin 'becomes thicker and stiffer than in most squids' and the jaw edge of the lower beak is 'often worn' (Clarke, 1986).

The disparity between length and diameter of severed pieces of skeleton found amongst the stomach contents must necessitate orientation within the buccal cavity so that it can enter the oesophagus. This must occur either as the material is taken into, or while it is within, the buccal cavity. The rhythmical activity of the structures of the buccal complex (Nixon, 1968; Boyle *et al.*, 1979) is presumably instrumental in ensuring the orientation and passage of food material towards and into the oesophagus. Once there, the material is carried along the oesophagus by peristaltic movement (Andrews & Tansey, 1983). Peristalsis of isolated preparations of the oesophagus is even stimulated by cephalotoxin, increasing tonus and contractions (Ghiretti, 1960). Similar action *in situ* would facilitate the passage of food towards the stomach.

The cuticle lining the oesophagus, a chitin-protein complex (Hunt & Nixon, 1981), is of α-chitin (Rudall, 1965; Rudall & Kenchington, 1973). This lining presumably provides some protection, especially for the soft tissues of the encircling central nervous system, during the passage of sharp particles of food. And yet protection is not complete in *Octopus vulgaris* since setae from polychaetes do occasionally pass into the brain, after penetrating the cuticle (Nixon & Budelmann,

1984). The relationship demonstrated between the diameter of skeletal material and of the oesophagus itself suggests a further possible function. The cuticle may prevent excessive expansion of the oesophagus, and act to limit the size of the material passing into and through it to the stomach.

Muscles are often attached and even retained within crustacean appendages, and on ribs and other bones of fish, when in the stomach of the cuttlefish. This shows that little, or no, external digestion takes place, as breakdown of the musculo-skeletal attachments occurs after the food reaches the stomach. The breakdown may result from the action of enzymes secreted in the saliva (Koueta & Boucaud-Camou, 1986) and taken into the stomach with the food. The saliva of *Octopus vulgaris* is instrumental in the breakdown of muscle attachments to the exoskeleton of crabs *before* the food enters the mouth (Nixon, 1984); and by implication in *Eledone cirrhosa* as prey could not be identified (Boyle, 1986) and led to the development of a serological technique (Boyle, Grisley & Robertson, 1986).

The source of calcium for the cuttlebone is not known but may come from the diet and/or the sea water. Amongst extant cephalopods, *Sepia*, *Spirula* and *Nautilus* are the only ones to possess calcified shells, internal or external. Small crustaceans, some whole and others in fragments, have been found in stomachs of *Spirula* (Kerr, 1931; Young, 1977). Sterols in this cephalopod are also present in pelagic crustaceans with similar migration patterns (Ballantine, Roberts & Morris, 1981). *Nautilus* has a heavily calcified external shell, and feeds on crabs, lobsters and shrimps and also scavenges (see Nixon, 1987a, b). The crop may weigh up to 25% of the body weight (Wells, 1986) and often contains relatively large pieces of skeletal material (see Fig. 2 in Nixon, 1987b). Calcium is present in sea water but it seems probable that at least some of the mineral for the cuttlebone is of dietary origin, and Wells (1986) suggests that the latter may be the source for the *Nautilus* shell. In other shelled molluscs, protein and calcium are both essential components of the diet for the formation of calcium deposits (see Wilbur, 1964). Experimental studies are, however, needed to follow calcium uptake before we can be certain of the source in the cuttlefish. In young *Sepia officinalis*, chamber formation does decrease with starvation (Boletzky, 1974), suggesting that at least some of the calcium comes from the diet. The possible importance of skeletal material in the diet of young *Sepia* should be considered during long-term maintenance under artificial conditions.

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