HOW MUCH CAN *CONUS* SWALLOW? OBSERVATIONS ON MOLLUSCIVOROUS SPECIES

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ABSTRACT

Feeding of three species of molluscivorous *Conus*, *C. textile*, *C. bandanus* and *C. omaria*, was studied in aquaria. *Conus* spp. are able to kill and remove from the shell prey larger than themselves. Also, *Conus* swallowed prey with weight up to half that of the predator. Estimates suggest that molluscivorous species of *Conus* are probably able to swallow prey with a shell volume reaching 85% of that of the predator, depending on the shape of the prey's body. It is confirmed that the thinning of the inner shell walls in *Conus* is connected with the ability to swallow voluminous prey. Digestion of prey occurs in both the oesophagus and stomach.

INTRODUCTION

Gastropods of the genus *Conus* are the best studied conoideans in respect of diet and prey capture mechanisms, and they are generally classified into three major dietary groups: vermivorous, piscivorous or molluscivorous (e.g. Kohn, 1983). Compared with other predatory gastropods, one of the unusual features of *Conus* is the size of the prey that they can swallow. *Conus* possess a radula consisting only of marginal hypodermic teeth that cannot be used for rasping or tearing the prey, and therefore they only swallow prey whole. The methods of attack and prey capture of different groups of *Conus* have been described in numerous publications and even videotaped (some videos of hunting *Conus* are available at http://biology.burke.washington.edu/conus/).

Piscivorous species can kill and swallow prey of a size similar to, or even exceeding, the length of their own shell (Kohn, 1956). Molluscivorous species, which feed on a wide range of gastropods, are of special interest, since they remove the prey's body from the shell prior to swallowing. Feeding of molluscivorous species of *Conus* has been described (Kohn & Nybakken, 1975; Schoenberg, 1981), but the authors mostly described the hunting patterns and diet of the predators, and did not address the question of how they manage to remove the prey from its shell and how they swallow it. The only published record is that of Kohn (2003), who described the progress of the prey and found the body of *Cantharus erythrostomus*, swallowed by *Conus victoriae*, intact in the posterior oesophagus and stomach nine hours after ingestion.

I was able to observe the feeding of several species of molluscivorous *Conus* in laboratory conditions (in the laboratory of Baldomero M. Olivera, University of Utah, Salt Lake City, USA and during the fieldwork at Panglao Island, Philippines, 2004). *Conus* were able to swallow surprisingly large prey. The objectives of this study were to estimate the size of prey that *Conus* can swallow, and to investigate the site where digestion of large prey items takes place.

MATERIAL AND METHODS

Experiments with feeding and prey size estimates were conducted during the Panglao 2004 Project expedition, organized by the Muséum National d'Histoire Naturelle, Paris, on the island of Panglao, Philippines. Three species of molluscivorous *Conus* (*C. textile* Linnaeus, 1758; *C. bandanus* Hwass in Bruguière, 1792 and *C. omaria* Hwass in Bruguière, 1792) were kept in aquaria with different species of other gastropods. The bottom of the aquaria was covered with several centimetres of sand with coral rubble and a permanent air flow provided. The water in the aquaria was partially changed daily.

Conus were quiescent for relatively long periods of time, sometimes up to two weeks. Regular checks (several times during the daytime) were conducted and, when hunting was observed, the time was recorded. Unfortunately, time recording was not accurate for night hunting, when observations were impossible. At different periods of time after swallowing prey, the snails were immobilized on ice and the shell then cracked and removed. The position of the ingested prey was determined by dissection and the specimens fixed in 80% ethanol for further studies.

Later the bodies of the predators were further dissected and the prey removed. The wet weights of predator and prey, excluding shell, were determined. The inner volume of the shell of the predator and the prey was measured in one case by completely filling it with water and weighing.

RESULTS

Hunting behaviour

Six hunting episodes were observed in Panglao and two more in the laboratory of the University of Utah. Hunting behaviour was similar in all observed cases and agreed well with the published accounts (e.g. Kohn, 2003). The snails responded to the presence of potential prey by extending their proboscis toward it (Fig. 1A). In most of our observations the prey had already been with predator for a long time in the aquaria without causing any response. The predator probed the prey's body with the proboscis and the injection of the tooth occurred. *Conus* then usually retracted the proboscis, leaving the tooth protruding from the prey. There was no preferential site on the foot for tooth injection. The prey usually reacted by violent shaking and partial or complete retraction within the shell. After some time, the body was extended and, depending on the size of the prey, *Conus* injected one or several additional teeth. From time to time the predator tested the prey with the proboscis or siphon (Fig. 1B). When the prey was finally immobilized (or dead), *Conus* held the shell of the prey with its foot, while the rostrum (extended rhynchostome lips) was attached firmly to the prey's body. Usually at this point the prey was completely overlain by the predator's body and shell

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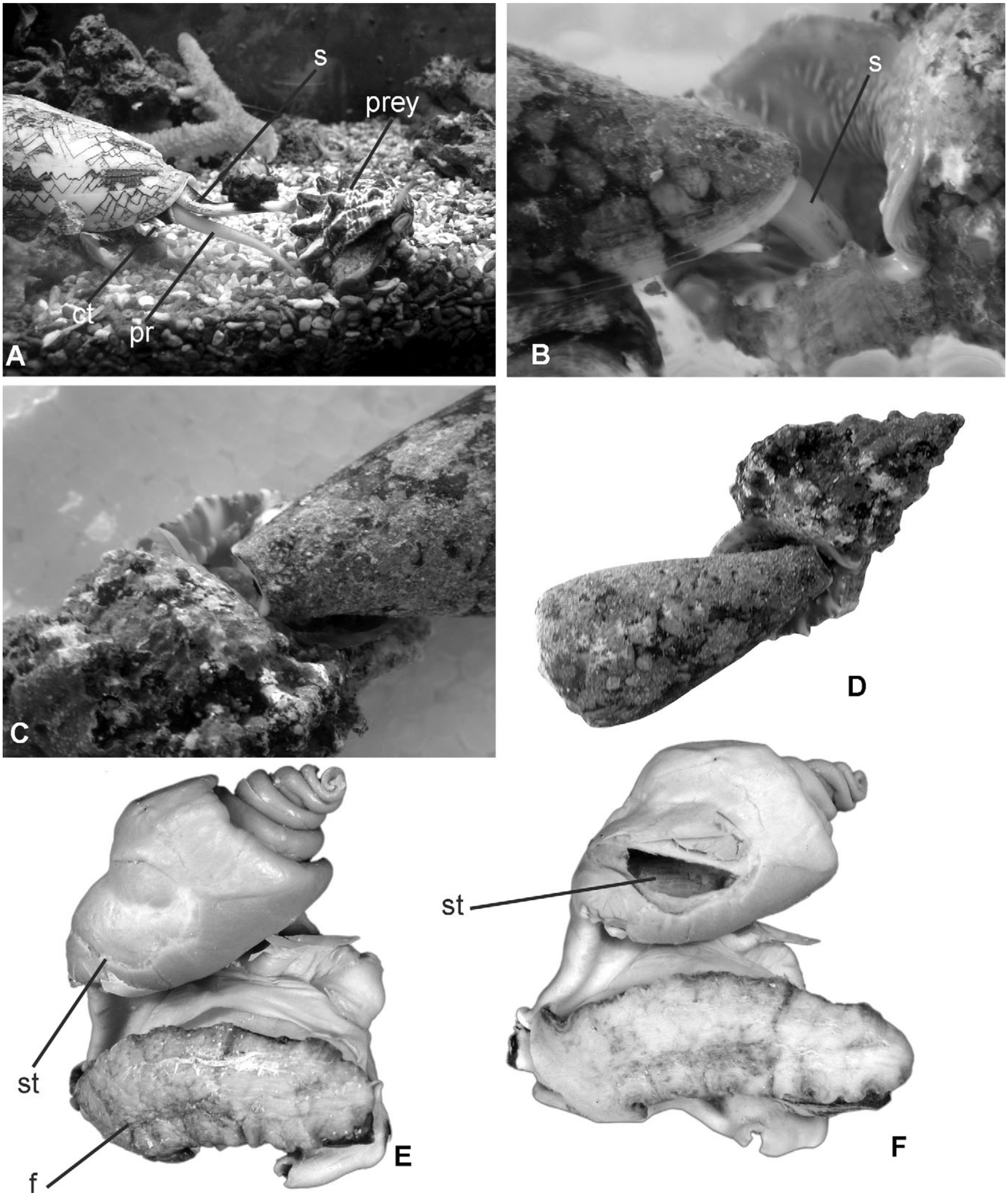

Figure 1. A. *Conus textile* hunting a *Vasum muricatum* in aquarium (photo courtesy of L. Mironov). **B.** *Conus bandanus* probing body of immobilized *Tutufa rubeta*. **C, D.** *Conus bandanus* pulling out body of *T. rubeta* from shell. **E, F.** *Conus bandanus* (shell length 93 mm) with body of prey, *Oliva amethystina*, in the stomach. **F.** External wall of stomach of predator with body of prey removed to show extremely swollen inner volume of stomach. Abbreviations: ct, cephalic tentacle; f, foot; pr, extended proboscis; s, siphon; st, stomach.

(Fig. 1C, D) and both remained immobile for a long period of time, from minutes to hours. At this point, no observations on the *Conus* actions were possible. Eventually it moved away, leaving the shell of the prey completely empty. An operculum (if present) was usually removed from the prey's foot and either remained in the empty shell, or was found on the bottom of the aquarium.

Feeding episodes of Conus bandanus

(1) A specimen of shell length 76 mm stabbed a bursid *Tutufa rubeta* (Röding, 1798) (shell length 82 mm) during the night (moment of stabbing not seen), was disturbed in the morning and positioned itself again on the prey aperture around 11.30 h. The *C. bandanus* remained on the prey aperture for the next 7.3 h (Fig. 1C, D). At 18.50 h the *Conus* suddenly released the prey, the body of which was halfway out of the aperture. On examination, a single tooth was found in the margin of the foot. The prey was returned to the aquaria but the *Conus* did not return to it, and at 20.45 h when examined, it was loose and intact within the shell, but with the operculum separated from the foot and lying inside the shell. The body was not consumed by the *Conus*.

(2) An individual of shell length 93 mm attacked an *Oliva amethystina* Röding, 1798 (shell length 32.0 mm) at approximately 08.00 h. It was swallowed at around 14.00 h. On dissection 5 h later, the *Oliva* body was in the stomach. The prey was enveloped in mucus, partially digested, with the visceral mass and mantle absent, while the foot was mostly intact. No *Conus* teeth were found in the prey body having probably been dislodged during ingestion. Dimensions of the prey were 16 × 9 × 5 mm. Weight of the body of the predator was 12.9 g, compared with that of the prey 0.45 g (3.5%). The lower (anterior) part of the U-shaped stomach, which usually has diameter of about 2–3 mm, was extremely distended, with a diameter of about 11 mm (Fig. 1E, F).

Feeding episodes of Conus textile

(1) An individual with shell length 39.5 mm extended from the shell and swallowed the body of *O. amethystina* (shell length 28.0 mm) in about 2 h. The *Conus* was dissected after 24 h and the prey found to occupy the entire foregut and anterior part of the stomach. It was covered with mucus, but poorly digested. Prey dimensions were 16 × 9 × 8 mm. The predator body weighed 1.38 g, and that of the prey 0.37 g (27%).

(2) An individual with shell length 73.5 mm was observed at 21.00 h sitting on the aperture of *C. magus* Linnaeus, 1758 (shell length 63.5 mm) (Fig. 2B). Observations were not made overnight, but before 07.00 h next morning feeding was finished. At 13.15 h the body was dissected and preserved. During fixation the *Conus* partially regurgitated the prey, so that part of the visceral mass was protruding through the proboscis and rhynchostome. The proboscis was greatly contracted, forming a series of telescopic folds, while the buccal tube was very expanded with a diameter of about 9 mm (Fig. 2F). The body of the prey was strongly distorted with a roughly cylindrical shape (Fig. 2C, E), and it occupied all the length of the foregut and the anterior part of the extremely swollen stomach. It was consumed entire, including the operculum which, nevertheless, was only loosely attached to the foot. The prey was partially digested, with the mantle mostly absent and the body wall also partially dissolved, exposing the venom gland and the radular sac. The predator body weighed 6.7 g, and that of the prey weighed 3.3 g (49%). Dimensions of the prey were 42 × 12 × 10 mm.

(3) A specimen of shell length 48.5 mm, after two weeks in the aquarium, stabbed an *O. amethystina* (SL 27.0 mm) several times 10 min after the latter was put into the aquarium. Five minutes later, the *Conus* positioned itself on the aperture of the prey and 40 min later moved away, leaving an empty *Oliva* shell. The specimen was dissected after 18 h. The prey body was still in the mid-oesophagus, highly digested and represented only by the visceral mass, with the head-foot absent.

(4) During one hunting episode of *C. textile* feeding on *Turbo* sp. (University of Utah), when the predator was still sitting on the prey's aperture, the latter was taken from the *Conus*. The body fell loose from the shell and was examined under a stereomicroscope. No signs of digestion, nor deterioration, of the columellar muscle were observed.

Feeding episode of Conus omaria

Conus omaria of shell length 68 mm was observed at 7.00 h consuming *Strombus gibberulus gibbosus* (Röding, 1798) (shell length 51 mm). The time of completion of feeding was not recorded. The next day after 28 h it was dissected. The anterior foregut and stomach were empty. I cannot positively state that the prey was totally digested; it is possible that the *Conus* may have regurgitated or rejected the prey, which might then have been ingested by other specimens of *Conus* in the same aquarium.

DISCUSSION

Although, as mentioned above, the feeding behaviour of molluscivorous *Conus* species has already been described in the literature, some questions have never been addressed, such as the size of the prey that can be swallowed, and where digestion takes place.

How is the body of the prey removed from the shell?

The mechanism of the attachment of the columellar muscle to the shell is still unclear. It is difficult to detach the muscle in a live snail, and even the body of a dead gastropod remains firmly attached to the columella until the decay begins. Nevertheless, there is no scar on the shell at the site of the muscle attachment (Price, 2003), suggesting that muscle fibres do not penetrate into the shell.

During the unsuccessful feeding episode of *C. bandanus* preying on *T. rubeta* and in the fourth episode of feeding of *C. textile*, the bodies of the prey came out of the shell complete. Examination under a stereomicroscope did not reveal any signs of deterioration of the columellar muscle. These observations suggest that the columellar muscle simply tightly embraces the columella and that conotoxins cause its complete relaxation. The prey is forced out of the shell by strong, steady, pulling action applied by the rostrum of the *Conus* that is attached to the prey's body.

How is the body of the prey engulfed after extraction from the shell?

The body of the *Turbo*, completely removed from the shell in the previously described fourth observation was given back to *C. textile*. The *Conus* engulfed it quickly, in a matter of seconds, with a speed similar to that at which piscivorous *Conus* engulf fish. Dissection of the predator's body proved that the prey did not remain in the rostrum, but passed through the proboscis to the oesophagus.

The proboscis of *Conus* is a remarkably flexible structure. In the extended position it is thin and long (Fig. 1A) and by means of a sphincter is able to hold a single tooth, a fraction of a millimetre in diameter, At the same time, it can expand up

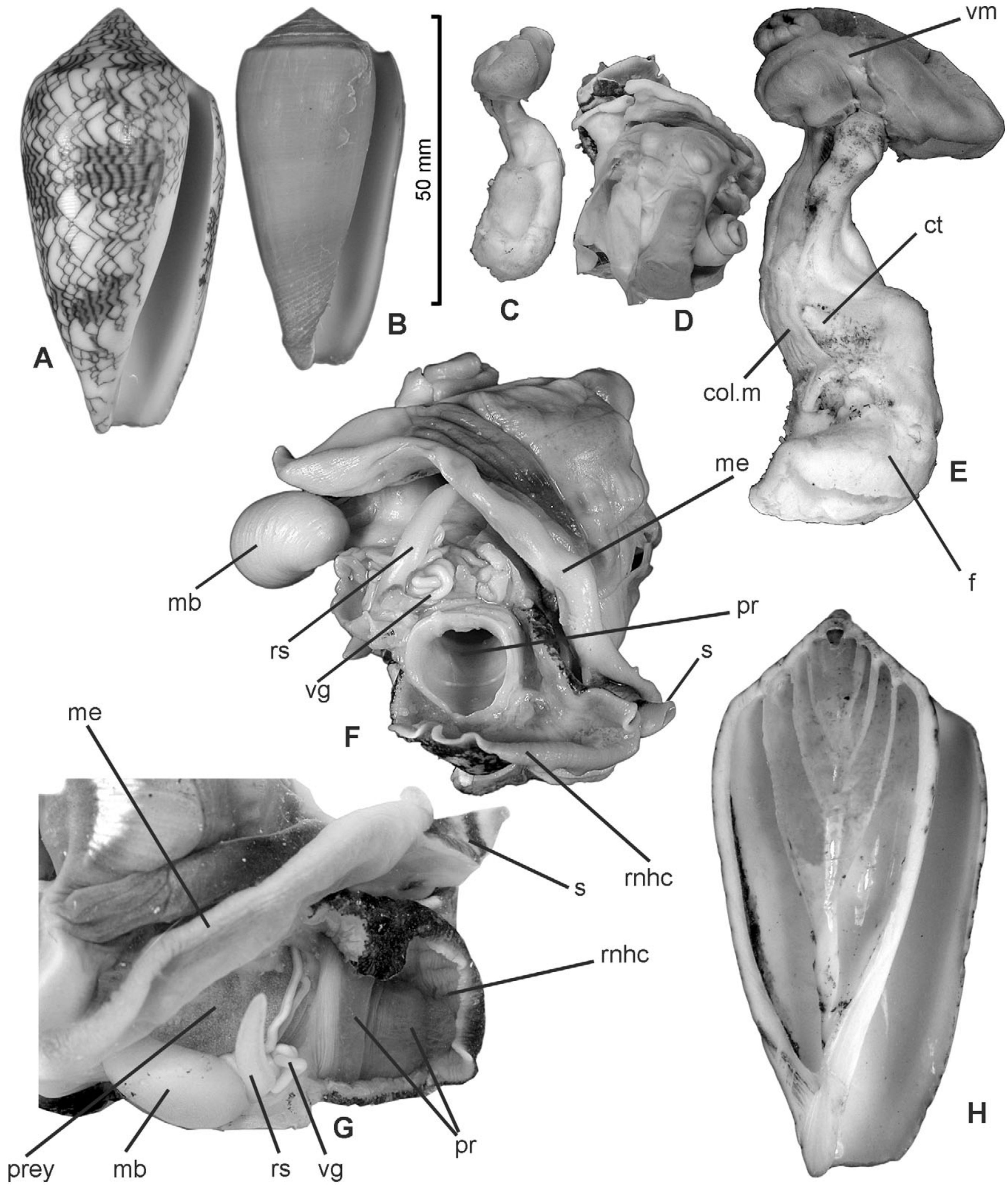

Figure 2. A. *Conus textile* (shell length 73.5 mm). **B.** *Conus magus* (shell length 63.5 mm), swallowed by *C. textile*. Bodies of corresponding *C. magus* (**C**) and *C. textile* (**D**). Body of the former extracted from the digestive tract of *C. textile*. **E.** Body of *C. magus*. **F.** Anterior view of body of *C. textile* showing widely opened buccal tube and contracted proboscis, rhynchodaeum opened along dorsal side (shell in **A**). **G.** *Conus textile* (shell length 39.5 mm), swallowing *Oliva amethystina*, rhynchodaeum opened along dorsal side. **H.** Shell of *C. textile*, cut open (shell in **A**). Abbreviations: col.m, columellar muscle; ct, cephalic tentacle; f, foot; mb, muscular bulb of venom gland; me, mantle edge; pr, contracted proboscis, forming the telescopic folds; prey, swallowed prey in the anterior oesophagus seen through its walls; rnhc, opened rhynchocoel; rs, radular sac; s, siphon; vg, venom gland; vm, visceral mass.

to 50 times (in the case of the *C. textile* swallowing *C. magus*) to allow the prey to pass into the oesophagus (Fig. 2F). The mechanism for this is the ability of the proboscis to contract strongly, with its walls forming telescopic folds (Fig. 2G) (for longitudinal section of *C. ventricosus* proboscis see Taylor, Kantor & Sysoev, 1993; for section of the proboscis of *C. catus* see Greene & Kohn, 1989). In the completely contracted position the proboscis occupies a small posterior part of the rhynchocoel. Examination of the sections of *C. textile* and other species demonstrated that both the buccal tube and oesophagus have strongly muscular walls. The prey is probably forced along the foregut by peristaltic contraction of the buccal tube and oesophagus. The strength of the contraction of the oesophagus walls is confirmed by the degree of distortion and compression of the body of the prey when it is swallowed. Thus, the body of *C. magus* swallowed by *C. textile* is roughly cylindrical, obviously compressed and compacted by the contraction of the oesophagus walls (Fig. 2C, E). Smaller prey is less compressed, as is shown by observations of Kohn (2003) on the body of a swallowed *Cantharus* from the stomach of *C. victoriae*.

How large a prey can Conus *swallow?*

My observations show that a molluscivorous *Conus* is able to swallow prey of at least half of its own weight. Nevertheless, there must be a limit determined by the internal volume and geometry of the shell of the predator. Measurement of the inner volume of the shell of *C. textile* of exactly the same size as that of the individual that consumed *C. magus*, and the inner volume of the shell of the prey, revealed that the latter (12.0 cm^3) was 64% of the former (18.8 cm^3).

The digestive system in *Conus* is rather short and in preserved specimens occupies only the last whorl, so that the prey body can potentially occupy most of the volume of this whorl, which constitutes the majority of the interior shell volume. In the mentioned case it constituted 85% (15.8 cm^3).

The volume of the consumed body of *C. magus* extracted from the digestive system of *C. textile* was only about 5 cm^3, which is less than half of the inner volume of the shell (42%). Thus the body is about 2.3 times less than the inner volume of the shell containing it. If these proportions are similar in the predator, this suggests that molluscivorous *Conus* can swallow prey with a shell having an inner volume similar to its own.

But another factor also determines the size of the swallowed prey – the shell geometry of the predator. Shells of *Conus* are characterized by a low translation rate of coiling with, therefore, strong overlapping of the whorls. In conjunction with the narrow aperture this leads to very constricted width of the lumen of the whorls (Fig. 2H). The problem is partially solved by dissolution of the inner walls. Kohn, Myers & Meenakshi (1979) considered in detail the dissolution of the inner shells walls in *C. lividus* and concluded that one of the main reasons is the provision of more space for the animal's body, since they swallow large, intact prey organisms.

In the large specimen of *C. textile* (shell length 73 mm) studied, the thickness of the inner walls was only around 0.1 mm. The inner walls were transparent and even slightly elastic. The maximal aperture width of the mentioned specimen was 10.9 mm, the maximal width of the lumen of the penultimate whorl was 7.3 mm. This means that the body of the prey (*C. magus*) was larger (10 mm in minimal dimension) than the maximal width of the lumen of the whorl through which it had to pass on the way to the stomach, not counting the part of the lumen occupied by the tissues of the predator. This is probably an artefact of the fixation of the prey's body, but it does demonstrate that prey, that is forced along the digestive system may be nearly as large as the lumen itself. Thus the size of the prey swallowed depends greatly on the shape of its body, which is limited by the narrow lumen of the strongly overlapping whorls of the predator. Obviously, the predator can swallow larger prey with narrow bodies.

Observations in aquaria demonstrated that *Conus* can kill and extract the body of prey that can be larger than its own. (See description of the hunting by *C. bandanus* of *T. rubeta*, although in this case the body was not swallowed because it was obviously larger than the permitted size.)

Finally, there remains the question of where digestion of the prey actually occurs? According to my observations, digestion starts within the anterior and mid-oesophagus. Digestion in the oesophagus suggests the forward transport of enzymes from the digestive gland ducts, as commonly occurs in piscivorous *Conus* (A.J. Kohn, personal communication). It seems that the site of digestion is not correlated with the size of the prey. Thus, in one specimen of *C. textile*, the semi-digested *O. amethystina* was still in the mid-oesophagus, although clearly it could have passed to the stomach. Digestion is a rather long process and in the mentioned case the body of the relatively small *Oliva* was only half-digested after 18 h. It probably takes several days, if not more, to digest very large prey.

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