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The Feeding Process in *Conus imperialis*

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The neogastropod *Conus imperialis* Linnaeus, 1758, has long been known to prey, evidently exclusively, on the polychaete *Eurythoe complanata* Pallas, 1766 (Family Amphinomidae), in nature (Kohn, 1959). Its prey-capturing apparatus, the radular tooth, was the first in the genus to be subjected to a detailed functional morphological analysis (Kohn et al., 1972), and congeners with morphologically similar radulae are also known or predicted to eat amphinomids (Nybakken, 1970). However, to our knowledge the actual feeding process in *C. imperialis* has never been observed. Here we describe and illustrate a case of prey capture and feeding by *C. imperialis* in the laboratory. We attempted to record similarities and differences between this and other species of *Conus*, and to observe whether feeding involves any special behavior that would make the predator less vulnerable to the unusually stiff, sharp, and urticating setae of amphinomids, commonly called “fireworms” because of their ability to penetrate human skin and cause a painful burning sensation (Eckert, 1985).

Observations

Two specimens of *Conus imperialis* (48.5 and 58.5 mm in shell length), collected by Mr. John Earle off Makua, Oahu, Hawaii in 12 m on 18 December 1999, were observed and presented with prey organisms. Only the smaller individual fed, in a tank at the Waikiki Aquarium, Honolulu, Hawaii, on 29 December 1999. The observations were made at night, when most *Conus* species are active, but under a bright fluorescent lamp to facilitate observation and video recording. The *C. imperialis* was positioned on coarse sand in the field of a digital camcorder. A specimen of *Eurythoe complanata* was placed on the sand about 2 cm in front of the shell. It began to burrow rapidly and move away from the *Conus*, but whether or not this is an escape response remains to be determined. The worm’s activity moved it away from the smaller *Conus*, but toward the larger specimen, which was in another area of the same tank.

The times given below (min:sec) begin when the siphon of the smaller *Conus imperialis* was first observed to extend beyond the anterior margin of the shell. Because of the worm’s burrowing and crawling behavior, we repeatedly excavated it and returned it to a position near the *Conus*.

The siphon gradually extended farther anteriad, parallel to the substrate or oriented at a downward angle (Figure 1A). It eventually (at 0:50) physically contacted the *Eurythoe*, and continued to probe. Then the proboscis sheath extended toward the worm (Figure 1B). Although in the video the proboscis is visible extending from its sheath (1:12), it was not possible to capture clearly in a single frame. The moment of injection of radular tooth and venom (1:14) was clear from the recoiling response of the worm. The *Conus* evidently released the tooth immediately from the proboscis, leaving it embedded in the worm, because a cloud of venom was observed (1:15) to rise in the water from near the point of injection (Figure 1C). This was most likely due to positive pressure from muscular contraction of the proboscis after release of the proximal end of the tooth. The effect is analogous to what would occur if a hypodermic needle were detached from the syringe while the finger continued to maintain pressure on the plunger. Only one tooth was injected into the worm. After the proboscis was withdrawn, the rhynchocele, also known as the proboscis sheath or “false mouth,” expanded and began to engulf the now paralyzed worm. Although swallowing began immediately, the *C. imperialis* failed to consume the entire worm, which autotomized behind the wound caused by the radular tooth. This evidently occurred before the effect of the venom moved very far posteriad, as the posterior portion of the worm escaped by undulating through and then over the substrate.

We then removed the longer, posterior part of the worm, which at that point evidenced no ill effects of the venom but was bleeding at the position of autotomy, to a separate container until the *Conus* completed swallowing the anterior portion (7:25). About 15 minutes later, the *Conus* became active once more, lifting the body up on the foot and extending the siphon again. We thereupon returned the posterior end of the *Eurythoe* to the tank with the *Conus*, positioning it as before. The worm still undulated but now appeared incapable of directed movements. Upon contact, the *C. imperialis* expanded the proboscis sheath and proceeded to completely engulf the posterior portion of the worm (Figure 1D). We saw no evidence that a second radular tooth was injected.
Discussion and Conclusions

In observing feeding in *Conus imperialis*, for the first time to our knowledge, we attempted to detect any behavioral adaptations the predator might have to avoiding injury from the unusually long, stiff, pointed, barbed and possibly venomous setae of the amphinomid polychaete *Eurythoe complanata*.

The feeding process in *Conus imperialis* differs in one important way from that of other voracious congers, in that the radular tooth is released from the proboscis immediately after injection. In typical voracious *Conus* species, the proboscis tip retains its grip on the expanded proximal end of the tooth. The tooth and proboscis function as a harpoon and its line, with contraction of the longitudinal proboscis muscles pulling the prey into the expanded proboscis sheath (Greene & Kohn, 1989; Kohn, 1998). Release of the tooth from the proboscis after injection is typical of *Conus* species that prey on mollusks, but these typically inject two to six teeth into the same prey, and so must release each one before loading another in the proboscis (Kohn et al., 1999).

In *Conus imperialis*, immediate release of the tooth could be a means of avoiding contact of the proboscis with the setae of *Eurythoe complanata* at the moment of stinging, when the worm is thrashing about. However, our observations detected no other distinctive behavioral features that would minimize the danger of being pricked by the setae. For example, swallowing commenced immediately as is typical in *Conus*, not after the worm died and became limp. It may be that one effect of the venom is to relax the worm’s muscles sufficiently so that during swallowing (Figure 1D), the parapodia become flaccid and are deflected to a position nearly parallel to the body. This would result in the setae being swallowed from proximal to distal, that is from base to tip. Were the parapodia to be swallowed in any other orientation, their tips and forks or spurs would be more likely to penetrate and catch the skin of the predator.
The only other aspect of the feeding process in *Conus imperialis* not characteristic of other species in the genus is the presence in the venom of substantial amounts (5.1 nmol/mg dry venom) of serotonin (Mcintosh et al., 1993). Serotonin was not detected in 13 other *Conus* species tested, although it could have been present at levels two orders of magnitude lower. It is the only neurotransmitter reported to be a conotoxin component, but whether it is functionally related to predation on ammonoids remains unknown.

Nybakken (1970) showed that the characteristic radular tooth form of *Conus imperialis* is shared by several putatively closely related species. Two of these, the Indian Ocean *C. zonatus* Hwass in Bruguière, 1792 (Kohn & Nybakken, 1975) and the eastern Pacific *C. brunnescens* Wood, 1828 (Nybakken, 1979), also feed on *Erythoe complanata*. They are the only *Conus* species, and to our knowledge the only predators of any sort, known to prey on ammonomid polychaetes. Nybakken (1970) also noted that the radular tooth of the Caribbean species *C. regius* Gmelin, 1791, is also of the same form, and he predicted that it would prove to be a predator on ammonoids. To our knowledge, no one has subsequently reported on the diet of *C. regius*, but Virginia O. Maes presented the first author with a photograph of *C. regius* in the act of feeding on an ammonoid (Figure 2), thus confirming Nybakken's prediction.

We now also have independent evidence that at least some of these species are more closely related to each other than any of them is to any other congers. DNA sequence data from one mitochondrial and one nuclear gene across more than 70 species of *Conus* indicate that the three species analyzed, *C. imperialis*, *C. regius*, and *C. brunnescens*, form a distinct reasonably well supported clade (bootstrap value 70%) of predators on ammonoids (Duda & Palumbi, 1999; Duda et al., work in progress).

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**LITERATURE CITED**


