Bernard TURSCH
and
Dietmar GREIFENEDER

Oliva Shells

The genus *Oliva* and the Species problem

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11.7. feeding

Yuri KANTOR (°) and Bernard TURSCH

are the authors of Section 11.7.

ALL *OLIVA* SPECIES ARE CARNIVOROUS, feeding on live or dead prey. Data on very few species have been published and some appear contradictory, suggesting that species could differ in details of behaviour.

11.7.1. the *Oliva* menu

Graham (1955) qualified *Oliva* species as scavengers. Olsson (1956: 164) reported that, in Ecuador, *Oliva undatella* feeds upon *Olivella semistriata*. Marcus & Marcus (1959a) found small crustaceans and “juice” in the stomach contents of their “*O. sayana*” (now known to be *O. fulgurator* forma *circinata*). Petuch & Sargent (1986: 13) reported that *Oliva* species “prefer live food” and that “small, smooth-shelled bivalve prey” could be their general preference. Vermeij (1993: 100) said that Olives have a specialised molluscan diet.

Below we list all published records we know of, together with original observations.

A. *observations in aquarium*

Olsson & Crovo (1968) reported that *O. sayana* readily eats pieces of fish, shrimp or steak but is “especially partial” to live Bivalves of the genera *Donax* and *Laevicardium*. *Chione cancellata* (a Bivalve with a rough surface) was consistently rejected. Two good photographs of *Oliva* capturing prey are given.

Fotteringham (1976) raised the problem of what could be the alternative food of *O. sayana* in the winter, when its usual prey (*Donax*) is not available. Therefore, he observed in aquarium the reaction of *O. sayana* (already fed with raw shrimp) to a variety of live additional foods (seven of the most common macro-invertebrates, other than *Donax*, *Laevicardium* and *Nassarius*, sharing the habitat of *O. sayana*). Only *Lepidopa websteri* and *Emerita portoricensis* (Decapod Crustaceans) and small specimens of *Polinices duplicatus* (Gastropod) were consumed. Some species (large *Polinices duplicatus*) not consumed when alive were eaten when dead. *Onuphis eremita* (Polychaete, the most abundant macro-invertebrate syntopic with *O. sayana* in the winter) was never eaten. On considerations of potential prey abundance, the author concluded that “the hypothesis that *O. sayana* switches to alternate prey during the winter is not supported by these data. It seems more reasonable that *Oliva* depends upon scavenging or upon a reduced rate of consumption to survive the winter months”.

Zeigler & Porreca (1969: 11-14) devoted a special section to the feeding habits of *Oliva sayana*, including many further interesting comments and a series of excellent photographs by Ms. Crovo, completing her previous publication (Olsson & Crovo, 1968). It is reported, amongst others, that food attracts the *Oliva* day or night. Other smooth-shelled bivalves (*Mulinia, Tellina*) are added to the food preferences. One more bivalve with a rough shell (*Pecten irradians*) is consistently rejected when alive but eaten when dead. At times several Olives would line up to feed “*like little pigs at a through*” from a dead *Pecten*. The feeding process is described in much detail.

(°) A. N. Severtzov Institute for Problems of Evolution, Academy of Sciences, Lenin Avenue 33, Moscow 117071, Russia.

Casual observations on feeding were made at Laing Island Biological Station, in aquaria without a sediment layer. This allows easier inspection but could possibly affect the feeding behaviour. The density of *Oliva* in our aquaria was abnormally high; so the frequency of observed *Oliva-Oliva* interactions is probably much higher than under natural conditions.

Olives, after fasting for some time, are attracted by a large variety of foods. *O. concavospira* was observed eating a small holothurian. An 18 mm specimen of *O. elegans* consumed a 12.5 mm *Nassarius margaritiferus*, completely cleaning the shell in less than 1 hour (this was checked by cracking the empty shell). When *O. sericea, O. oliva, O. reticulata* and *O. carneola* were offered pieces of fresh Spanish mackerel (*Scomberomorus commersoni*), they quickly detected the presence of prey and eventually found it. If a piece of fish was too big, the *Oliva* still tried to engulf part of it in the pouch.

If there was only one Olive species and if an excess of food was present in the aquarium, we have never observed (in well over one hundred observations) any agonistic behaviour or attempts at stealing stored food from conspecifics. This is in total agreement with the observations of Mrs. Crovo on *O. sayana*.

When no excess food is present (OUIN & TURSCH, unpublished) cannibalism is observed in certain especially aggressive species (such as *O. reticulata* and *O. sericea*), the winner nearly always being the largest animal. Why compete for a small morsel when you can eat the competitor? No big difference in size is required: *Oliva* can "engulf" (place into the foot pouch) prey of nearly their own size (as already noted by Crovo cited by ZEIGLER & PORRECA, 1969).

When several *Oliva* species are kept in the same aquarium, without excess food, then attacking specimens of other *Oliva* species is preferred to cannibalism of conspecifics. There seems to be a "pecking order", some rather large species (such as *O. reticulata* and *O. sericea*) regularly winning over all the others. In contrast, *O. amethystina* is the underdog, being usually the first victim. It was repeatedly observed that if a specimen of *O. amethystina*, still very much alive, is forcibly extracted from the pouch of an *O. reticulata* then placed at some distance, the same predator will soon recognise its former victim amongst all the other *O. amethystina* present and will repeat its attack. The victim is possibly marked with some chemical "personal tag" (linked to pre-digestion?). Ms. Crovo (cited by ZEIGLER & PORRECA 1969) has removed bivalves from the pouch of *O. sayana* and noted "*Other olives do not find such a slime-covered shell attractive*". It could also be simply weakened (possibly asphyxiated), as reported by OLSSON (1956: 164): "Some Olivellas which were freed shortly after having been swallowed [by *Oliva undatella*], would appear dazed or stunned for a while but in many cases, would recover rapidly after being placed in a pan of salt water".

B. *observations* in situ

In Hansa Bay, we have observed that, at the moment of being captured, some *Oliva* specimens occasionally release from their foot pouch a freshly caught prey. Such findings are very occasional. Small bivalves and polychaetes were most frequently found but these observations are not conclusive because other small prey would most possibly have gone unnoticed. As examples, an 18.5 mm specimen of *O. carneola* was found carrying the shell of an unidentified Cardiid bivalve (8.7 mm). Three specimens of *O. carneola* were found with Polychaetes (Sigalionidae, identified by Dr. Alan Kohn) in their pouch. One specimen was found with a large shell of *Solen roseomaculatus*. One was found lying on its back, using its parapodia to transfer a polychaete to the pouch. One 36.5 mm specimen of *O. elegans* was found carrying a small Venerid (*Callista* sp., 6.5 mm). A 38 mm specimen of *O. vidua* was seen carrying an unidentified Polychaete. Another *O. vidua* was observed eating a dead crab.

Extensive observations *in situ* on the feeding of intertidal *O. tigridella* were made by Taylor and Glover, in Queensland, Australia (*personal communication*). The most commonly recorded preys were the small Umbonine gastropod *Isanda coronata* and the tellinoidean bivalve *Cadella semen*. Other prey included other small bivalves, echinoid, a small holothurian and an echiuroid.

C. *stomach content*

We examined the gut content of 149 specimens belonging to 16 species of *Oliva*, collected in Hansa Bay. For analysis, the samples were boiled soon after collection (to stop the digestion) and then fixed in 80% ethanol. Samples varied from 2 to 33 specimens per species. The results are reported in Table 11.2.

The stomach was quite often empty, sometimes in nearly all studied specimens of certain species (e.g. *O. amethystina* and *O. concavospira*). Nearly all stomachs studied were filled with mucus, which became jellied when boiled. We attributed specimens to the category "*empty*" when there were no remains besides the mucus.

Sand grains or sediment particles (including shells of diatoms) were often present in the gut content, in most cases co-occurring with polychaete spicules or crustacean remains. It is obvious that, even in the absence of any recognisable food remains, sand got into the digestive system together with captured prey (because Olives eat from the foot pouch). When no identified remains were found besides sediment particles, we included these specimens in the category "*diatoms, sand grains, sediment particles*".

The category "*chitinous remains*" most probably represent crustaceans but, in the absence of limbs or articulated remains, we were not able to identify prey positively.

Examination of the stomach content (together with aquarium and *in situ* observations) points to the fact that *Oliva* species are not specialised feeders. On the contrary, their diet is quite varied. They feed on polychaetes (both sedentary and errant), crustaceans, other Gastropods (several families, including *Oliva* itself), bivalves, and echinoderms. One should keep in mind that not all the remains of the gut content could be positively identified. For example, it is impossible to identify the remains of soft-bodied prey devoid of structural elements, like bivalves (which are known to be part of the regular diet of Olives) or other invertebrates. Thus, the natural diet is definitely more varied than we can infer from stomach content analysis.

So any explanation of the distribution of *Oliva* species, based on the availability of some special food, must be considered with much caution.

Some abundant *Oliva* species (like *O. oliva*) live on rather desert beaches, where prey larger than a few millimetres seems to be rare. Nonetheless, the stomach of *O. oliva* usually contained remains of food, consisting of small invertebrates (polychaetes, minute crustaceans and gastropods).

11.7.2. table manners

Petuch & Sargent (1986: 13) reported that *Oliva* species "*. . . even share 'kills' with other members of the colony*". We have not observed the sharing of actual "kills" but we have often observed in the field that many *Oliva* specimens (even from different species) can congregate around (and share) a large dead prey.

A. *observations on O. vidua*

The feeding behaviour of Singhalese specimens of *O. vidua* in aquarium has been observed by Tursch (1991), in Brussels. In this study, the animals were fed with dead prey (mostly frozen mussels) and did not actually hunt. The process of feeding involves three steps.

SPECIES	number of specimens examined	Range of shell size (mm)	Polychaeta (unidentified)	Polychaeta, Spionidae	Polychaeta, Nereidae	Polychaeta, Nephytidae	Crustaceans	Gastropoda, Olividae	Gastropoda, Nassaridae	Chitinous remains	Diatoms, sand grains, sediment particles	Unidentified remnants	Empty
O. amethystina	10	26.2-33.5	-	-	-	-	-	-	1	-	-	-	9
O. athenia	10	12.7-19.0	-	-	-	-	1	-	-	1	-	3	5
O. bulbiformis	7	13.0-20.0	-	-	-	-	1	-	-	1	-	-	5
O. caerulea	12	14.0-41.2	1	2	-	-	-	-	1	1	-	3	4
O. carneola	33	10.4-15.8	-	-	-	-	6	-	-	1	2	6	18
O. concavospira		10	21.6-29.6	-	-	-	-	1		-	-	-	-
9													
O. elegans	7	13.5-22.5	-	-	-	-	-	-	-	-	-	3	4
O. irisans	3	20.7-42.4	-	-	-	-	1	-	-	-	-	-	2
O. oliva	12	15.7-22.0	1	1	-	-	2	-	1	2	3	-	2
O. parkinsoni	5	17.5-21.2	-	-	-	-	-	-	-	1	-	-	4
O. picta	7	9.3-12.2	-	-	-	-	2	-	-	1	1	1	2
O. reticulata	6	19.69-30.0	-	-	-	-	-	-	-	1	-	1	4
O. faba f. *smithi*	10	12.7-14.8	2	-	-	-	1	1	-	1	-	1	4
O. todosina	2	15.0-15.7	-	-	-	1	-	-	-	-	-	1	-
O. vidua	5	30.6-37.0	-	-	-	-	-	-	-	1	-	-	4
O. xenos	10	15.0-20.5	2	-	1	1	-	-	-	-	-	1	6

Table 11.02. Gut content of *Oliva* species, collected in Hansa Bay, Papua New Guinea.

Detecting food. *Oliva* are very efficient at detecting the presence of food in the aquarium. Normally they spend most of their time buried under the sand. Only by paying close attention, can one see their siphons protruding above the sand "*like a garden of bean sprouts*" (the expression is from Ms. Crovo, cited in ZEIGLER & PORRECA 1969).

As soon as some morsels are deposited in the water, all specimens quite suddenly emerge from the substrate within seconds and start searching. What just looked like an empty aquarium suddenly erupts into action. The next steps are the finding, then the actual intake of food.

Finding food. In the absence of water current, recognition distance is short (a few centimetres). Orientation is not accurate: *Oliva* will often pass in close proximity to a food morsel without finding it, as already reported by ZEIGLER & PORRECA (1969). The presence of food above the level of the substrate is most probably detected by the osphradium, in the water flow coming from the siphon. However, actual location of the food does not seem to be effected by the siphon (no scanning motions or directing the siphon towards the food) but by the anterior part of the propodium. On several occasions, the siphon has been seen to actually touch the food without provoking any reaction on the part of the animal.

The observation that food is not located by the siphon but probably by the anterior edge of the propodium deserves comment. MARCUS & MARCUS (1959a: 119) have already observed that this part is richly innervated and have concluded: " . . . *the much richer innervation of the propodial border suggests that also in* Oliva *this border is the most important sense organ* . . ." This would make sense as the siphon generally protrudes out of the sand in which *O. vidua* must normally find its prey. Through the siphon, the animal detects the presence (not the location) of prey at the surface. The propodium will detect (and of course locate) buried prey by direct contact.

Note that the common habit of *Oliva* species of maintaining the siphon protruding above the sediment surface is not without danger because many kinds of fish are proficient "siphon-snippers". As observed in aquarium by Ms. Crovo (cited by ZEIGLER & PORRECA 1969), when the *Oliva sayana* were exposed to frequent siphon attacks by a boxfish, they did not show their siphon anymore. When the fish was removed, the *Oliva* behaviour returned to normal.

VERMEIJ (1993: 100) stated that *Oliva* can overtake their molluscan victims below the sediment. We have not been able to verify this, as the action would be quite difficult to observe.

Intake of food. The anterior part of the foot (the propodium) is divided in two by a deep longitudinal groove. Once the food has been located, the propodium is gently slid over the prey. When steady contact is achieved, the two elements of the propodium bend downwards, acting like a pair of pincers and firmly seize the food. The food is then rapidly transferred into a pouch formed by folding the posterior part of the metapodium. This pouch of *O. vidua* can reach considerable dimensions and easily accommodates the meat of a whole mussel. The transfer of food requires some acrobatics: the mollusc has to stand nearly vertically (in sand) or to roll on its side (on a bare glass bottom). The Olive then quickly regains its normal position. The whole process generally takes place in less than 10 seconds.

Once the food is stored in the pouch, the animal nearly always moves away from the feeding place. If feeding takes place on sand, the Olive will generally bury itself rapidly. The distended pouch is trailed behind the Olive and does not appear to slow the animal down.

B. *observations on other species of* Oliva

Other *Oliva* species were observed hunting prey in aquaria, at Laing Island Biological Station. Their pattern of behaviour was generally similar to that described for *O. vidua.*

O. sericea, hunting *O. caerulea*, while testing the prey with the propodium, also touched it with its extended proboscis, which was then retracted. Sometime after transfer of the prey into the foot pouch, the proboscis is inserted into the pouch and feeding starts (as if the animal was drinking from a can with a straw). Since the proboscis is thin-walled and semi-transparent, one can clearly see the small particles of food moving along the oesophagus. The sequence of action is shown in Figure 11.18. A similar mode of feeding was recorded for other species of *Oliva* that were observed by us in aquarium.

The amount of food that can be engulfed and then consumed by an *Oliva* is quite respectable. For instance, a 64 mm specimen of *O. sericea* consumed in one night two *O. amethystina* (14.8 and 29.2 mm), one *O. caerulea* (20.6 mm) and one *O. parkinsoni* (11.5 mm). All the shells were released by the morning, mostly eaten. Eight days later, the same specimen killed and consumed at least two *O. amethystina* (22.5 and 25 mm). On the next day, (see drawings Figure 11.18), the same specimen attacked one *O. caerulea* (42 mm). The victim was released after one hour, still alive but with the propodium eaten off. The action is quite fast: *O. sericea* takes only 3-4 seconds to engulf the prey.

Another *O. sericea* (51.5 mm) was found with three specimens of *O. amethystina* (13.5, 16.3 and 16.5 mm) in the foot pouch. Two of the shells were completely empty; the third animal was only slightly digested. A juvenile *O. sericea* (13.5 mm) was seen engulfing an 11.0 mm specimen of *O. picta*. One 21.5 mm specimen of *O. concavospira* was observed engulfing a 17.2 mm specimen of *O. athenia.*

In contrast (from an unplanned experiment: an aquarium deemed to be empty still contained some snails hidden in the sand), we learned that some species can go without food for a long time (over four weeks), without apparent disability.

C. *more on external digestion*

Why two steps in feeding? The feeding of *O. vidua* and of other species completely confirms most of the earlier observations of OLSSON & CROVO (1968) on *O. sayana.* MARCUS & MARCUS (1959a) have reported that the nerve ring located around the oesophagus in *Oliva* is of small dimensions and suggested that this probably prevents the animals from swallowing anything but very small portions. However, observations on live *Olivella* (KANTOR, 1991) show that these animals, also with a narrow nerve ring, can swallow relatively large objects, indicating that the ring can greatly enlarge during the passage of food through the oesophagus. This is also coherent with the observations of OLSSON (1956: 164): "*After capture of an* Olivella *by the* Oliva *[undatella], the margin of the foot would envelope its victim completely and the smaller shell would be swallowed whole, the body of the* Oliva *swelling into a large, rounded, ball-like mass*".

Pre-digestion in the pouch allows very quick food consumption. Judging from casual aquarium observations we can conclude that the rate of digestion, as well as rate of ingestion, is very high. A specimen of *O. sericea*, which consumed 4 specimens of other Olives overnight, already started defecating early in the morning and finished producing faeces in several hours. Although we did not make any quantitative estimates, the amount of defecated material was extremely small compared to the amount of food consumed. This indicates a high rate of food absorption.

If digestion is external, one may wonder why the older radular teeth of *Oliva* would frequently show so much wear and tear (see Figure 6.13). In many instances, we have seen *Oliva* specimens feeding upon large dead prey that obviously could not

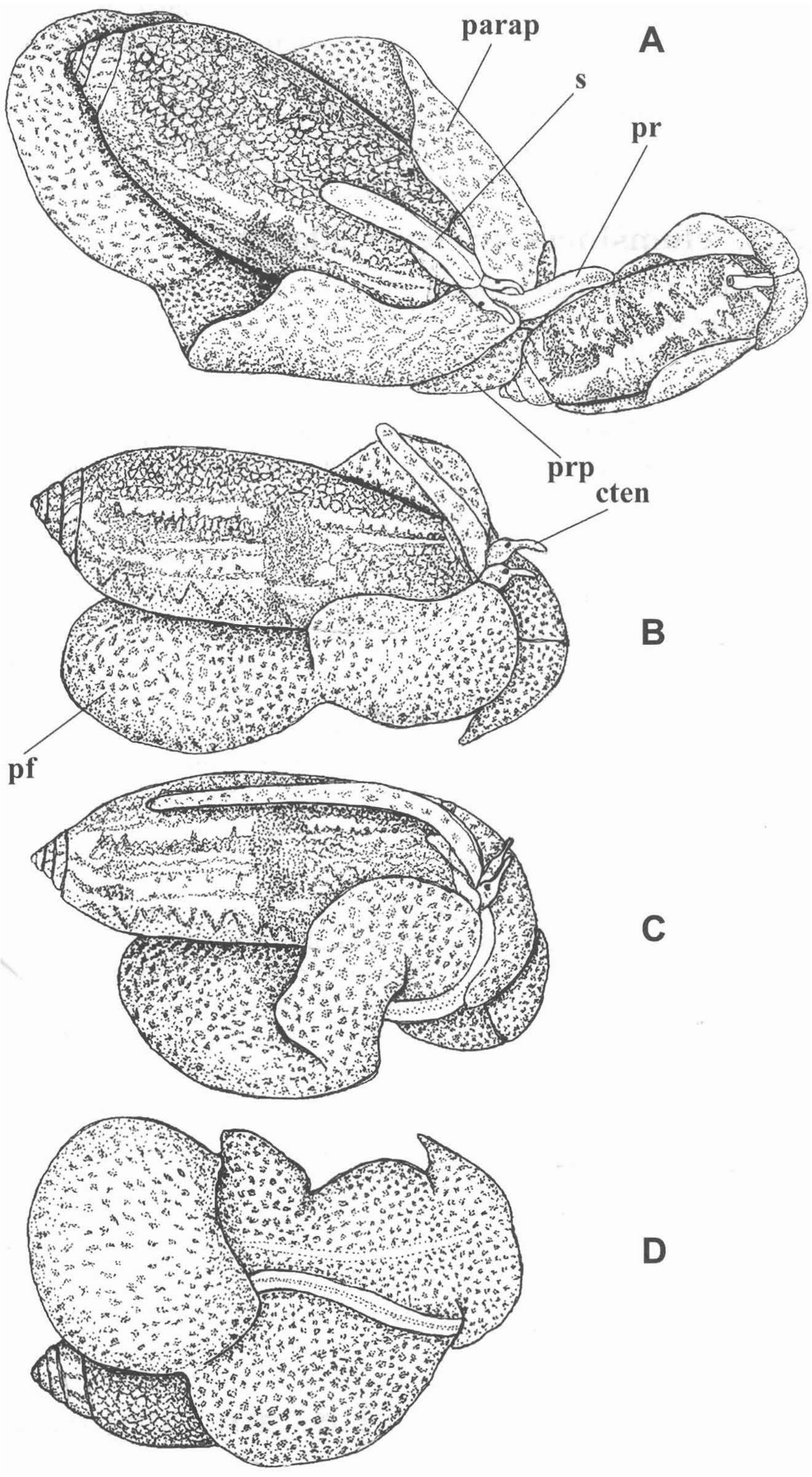

Figure 11.18. *Oliva sericea* hunting *O. caerulea*, drawn from a series of photographs.

A: *O. sericea* (left) is testing a live *O. caerulea* with propodium and extended proboscis; buccal mass and radula are seen as the darker spot on the proboscis tip.

B: prey is transferred into the foot pouch, view from the side.

C: proboscis is inserted into the pouch and feeding starts, view from the side.

D: feeding predator, viewed through the glass bottom of the aquarium.

cten:- cephalic tentacles
parap: parapodium
pf: foot pouch
pr: proboscis
prp: propodium
s: siphon

be "engulfed" in the foot pouch. In such cases, the *Oliva* often eat "normally", by rasping the prey with their radula. Therefore, internal digestion coexists with external digestion. In the case of *O. sayana* it was reported that "*the prey is not eaten from the pouch, but it is released and fed upon*" (Ms. Crovo cited by ZEIGLER & PORRECA, 1969). PETUCH & SARGENT (1986: 13) also said that "*When dead, the food item is released from the pouch and the olive feeds by rasping bits of flesh with its radula*".

11.7.3. clumsiness or clever adaptation?

At first sight, it would seem that the inefficiency of *Oliva* at locating prey from a distance would constitute a severe handicap, when competing with the many other animals that can make a beeline for their food (and frequently outnumber the *Oliva*). But is it really a handicap?

Underwater observations (VAN OSSELAER & TURSCH, *unpublished*) have frequently shown the following scenario. When an attractive morsel of food is deposited on the bottom, in a suitably rich biotope, a number of scavenger Gastropods will emerge from the sand within a couple of minutes (in open water, detection of food takes, quite logically, longer than in an aquarium). The molluscs behave in different ways. Mitridae, Nassaridae and Naticidae, for instance, will make an accurate navigation and go straight for the prey. Their approach takes time because their locomotion is relatively slow. In contrast, the *Oliva* will generally move a lot faster, but in a rather haphazard way, keeping only a very vague general direction, and making frequent turns. This very much increases their chance of making contact with one of their slower competitors and (if it is not too big) dispatching it as a *hors d'oeuvre* before turning back to the original prey. Two servings instead of one. So, what first seemed to be utter clumsiness might in the end prove to be a very clever adaptation.

This interpretation is still pure speculation. In favour of it is the observation that *Oliva* can (and do) eat just about any smaller Gastropod. They have also been seen to take two small meals in quick succession, if given a chance. Should the *Oliva* meet a larger predatory mollusc, it could probably rely on its superior speed for escape. Against the hypothesis is the fact that the food also attracts other fast, large predators (fish). So spending time on the sediment surface increases the chances of losing the meal altogether. It also increases the exposure of the *Oliva* to attack –this is probably when a cryptic coloration of the shell (see Chapter 9) would be most useful.

Capturing and keeping prey in the foot pouch clearly is another wonderful and very efficient adaptation. It allows prolonged hunting periods without interruptions for prey consumption, thereby opening the possibility of collecting a large stock of prey whenever it is available. TAYLOR and GLOVER (*personal communication*) observed multiple prey in the foot pouch of *O. tigridella* in 28 % of cases and even found one specimen which carried 7 specimens of the gastropod *Isanda coronata*.

11.8. moving and burrowing

11.8.1. crawling

Olives spend much of their time motionless, but can progress quite rapidly when in motion. *Oliva vidua* has repeatedly been clocked at speeds above 25 cm/minute on a glass substrate (18 cm/minute has been observed for the smaller *O. oliva*). Large species move considerably faster and, in relation to their size, **Oliva *possibly have the highest speed of all Gastropods*.**

The longest linear track we have observed at Laing Island was 6.8 meters (for *O. reticulata*), parallel to the shoreline, in about one foot of water. It was possibly longer, as its beginning was already blurred by water motion. Although we have no