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Oliva Shells

The genus Oliva and the Species problem

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external anatomy

CHAPTER 6

the Oliva animal

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FOR A FIRST GENERAL VIEW of molluscan anatomy see BRUSCA & BRUSCA (1990). For more detail, see FRETTER & GRAHAM (1962). Drawings of live *Oliva* specimens are already present in the old literature. For instance, in DUCLOS (1835-40) one finds good representations of *Oliva elegans* (Pl. 32, figs. 1, 2), *O. flammulata* (Pl. 30, figs. 3, 4), *O. miniacea* (Pl. 31, fig. 7), *O. oliva* (Pl. 7, figs. 2, 14), ?*O. ponderosa* (Pl. 31, fig. 8), *O. reticulata* (Pl. 33, figs. 3, 4), *O. scripta* (Pl. 30, figs. 5, 6), *O. sericea* (Pl. 32, figs. 5, 6) and *O. vidua* (Pl. 32, figs. 3, 4).

The anatomy of only a few species of *Oliva* have been studied in detail. These are *O. peruviana* by KÜTTLER (1913), *O. fulgurator* f. *circinata* by MARCUS & MARCUS (1959a), *O. bulbosa* and *O. sayana* by KANTOR (1991), *O. oliva* and *O. ouini* by KANTOR & TURSCH (1998). Although the organs of all these species differ only in detail, some anatomical criteria effective at the specific level have been found. Future work will most probably reveal more.

6.1. external anatomy

THE GENERAL ASPECT of the *Oliva* animal, removed from its shell, is shown in Figure 6.01. This drawing is purposely very incomplete and shows only a few of the organs. The **proboscis** (the entry point of the digestive system) is a retractable organ, and is mostly everted only for feeding activities. It is clearly seen only on specimens anaesthetised and relaxed prior to fixation. The radula is located at its tip.

The foot of *Oliva* species is quite large, but does not entirely cover the shell, as it does in *Cypraea*. It can entirely retract into the shell, in contrast to *Harpa*. The muscular foot is not only used for locomotion. The foot (see Figures 6.02, 6.03) is clearly separated by a distinct dorsal furrow and a less clear ventral furrow into two parts, anterior (the **propodium**) and posterior (the **metapodium**). On the ventral side, the **propodial furrow** is formed by straight edges joining at a nearly right angle in the middle part of the sole. The propodium is crescent-shaped, divided by a deep longitudinal cleft (see Figure 6.04). This feature allows the animal to use the propodium as pincers for seizing and manipulating objects. The propodium is an important sensory organ and contains the highest nerve density in an *Oliva*.

The metapodium has large, paired lateral lobes, the **parapodia** (also called the *pedal lobes, metapodial flaps* or *metapodial lobes*). The parapodia are very mobile and cover the sides of the shell when the animal is crawling. We have observed specimens of different *Oliva* species swimming, waving their parapodia like wings.

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The foot also contains many glands and can secrete copious quantities of mucus. The foot is not as smooth as it appears to be at first glance. Its microstructure is shown in Figure 6.02.

The sole of the foot has a most peculiar feature: the animal can fold its posterior part to form a **ventral pouch** (see Figure 6.03). If one observes through the glass wall an *Oliva* crawling in an aquarium, one can see that the sole of the foot is completely flat but presents a somewhat darker spot in its posterior part. This spot indicates the position of the pouch, which is formed when the mollusc captures prey. In preserved specimens, the foot is (in most cases) folded in such a way that a more or less deep depression appears at the location of the pouch. In other cases, only the posteriormost part of the foot is folded. This probably indicates that the pouch is formed by involuntary contraction of the muscles of the foot.

This pouch serves to store the food prior to actual ingestion. The food is pre-digested in the pouch: the epithelium of the pouch displays a **proteolytic activity** not found in other parts of the foot (for more details see Section 6.3).



Figure 6.02. The foot of *Oliva xenos* and the fine structure of the sole. The head is at right. Specimen from Hansa Bay, Papua New Guinea.



below, showing ventral pouch and ventral pedal gland.

On the sole of the most anterior part of the metapodium of females, there is a **ventral pedal gland**, which opens by a short, narrow longitudinal slit with thickened edges (Figure 6.03). The ventral pedal gland is used for moulding and hardening of the egg capsules.

The **siphon** is an extensible tubular organ and is really a snorkel, circulating water into the mollusc mantle cavity. It functions even when the *Oliva* is buried, as it usually protrudes above the sediment. The water current entering through the siphon has a dual pur-

pose. It is brought to the **ctenidium** (the gill) for respiration and to the **osphradium** (a special chemosensory organ) for monitoring chemical signals in the water.

The head of *Oliva* is rather peculiar (see Figure 6.04). It is small, formed of vertical flattened flaps with long tentacles, bearing small eyes. The rhynchostome has a form of narrow slit and is located under the right cephalic flap in the species we have studied. It opens into the *rhynchocoel* (or proboscis sheath), the cavity in which the **proboscis** is located, when retracted.

There are three different mantle appendages: the anterior and posterior mantle filaments (also called tentacles) and the mantle lobe. The **anterior mantle filament** normally protrudes from the anterior notch of the shell, where it is often wrapped like a collar around the base of the siphon. Its function is totally unknown. The **posterior mantle filament**, very variable in size and shape, is normally housed in a special part of the shell, the filament channel that constitutes a unique character of some of the genera in the family Olividae. The function of this organ (already described in 1834 by QUOY & GAIMARD) is still a mystery. The possibility of a sensory function was raised by KEEN (1971). BURCH (1988) also reported that it senses water currents. VERMEIJ (1993: 30), possibly referring to the posterior filament, reported that the notch or canal at the posterior end of the aperture in *Terebellum* (Seraphsidae) and Olividae is "... occupied by a sense organ that detects danger from behind while the animal is burried in the sand". But it has been shown (see MARCUS & MARCUS, 1959a) that the filament is poorly innervated, which is inconsistent with a sensory role. The hypothesis was put forward



Figure 6.04. *Oliva bulbosa*, anterior **view of the head and propodium**. Scale bar: 5 mm. After KANTOR, 1991.

that that it could serve to indicate complete burial in the sediment, but ablation of the posterior mantle filament does not significantly alter burial depth (VAN OSSELAER, *unpublished results*). Histological examination by a colleague (DANGUY, *unpublished results*) shows that the filament is a tridimensionnally striated muscle (like a tongue) endowed with many secretory glands. It is conceivable (but not at all established) that this puzzling organ serves for the production of chemical messages. ZEIGLER & PORRECA (1969: 21) suggest it could be a defensive weapon, as *O. sayana* has been observed "*flailing and lashing away with this narrow filament*" when caught.

The **mantle lobe** is a small variously shaped (usually concave) lobe, located at the base of the posterior mantle filament. MARCUS & MARCUS (1959a) supposed that its main function is the secretion of the "columellar callus". It seems probable that both the anterior and the posterior filaments are involved in carbonate deposition. Both organs are located very near thickened portions of the shell (the anterior filament is very near the *shoe* and the *anterior band* and the posterior filament touches the *spire callus* (for names of the parts of the shell, see Chapter 7). Furthermore, the anterior and the posterior filaments are very similar in aspect (translucent, with large granules) and in colour, when observed on live *Oliva* specimens. Finally, the colour marks on the spire and those on the anterior band of a given *Oliva* shell often look very similar and even their deposition seems synchronous (GREIFENEDER, *unpublished observations*).

Male specimens are easily identified by the possession of a large **penis**, located at the right side of the head.

In contrast to some other genera in the family Olividae, all the species of the genus *Oliva* are devoid of an operculum.

The **colour ornamentation** of the Oliva animal might have some use as a character at the supraspecific level. For instance, in the closely related members of the O. miniacea group (see TURSCH & GREIFENEDER, 1996), the species we had the opportunity of observing alive (O. irisans f. concinna, O. miniacea, O. sericea) share similarities in the coloration of the animal (pattern formed of large, isolated dark spots). The same pattern is reported for O. ponderosa by DUCLOS (1840, Pl. 33, fig. 8). Interpretation at the specific level is somewhat more delicate. The colour ornamentation of the Oliva animal is as **variable** as that of its shell and often matches the colour of its surroundings. In contrast, the ornamentation of the eye tentacles and of the anterior filament appears to have more diagnostic value at the species level.

6.2. internal anatomy

THE INTERNAL ANATOMY of *O. oliva*, the type species of the genus, has been described by KANTOR & TURSCH (1998) and will be given as an example.

The body of a specimen with H: 15.8 mm consists of 3.75 whorls (see Figures 6.05, A,B), the mantle cavity spanning ca. 1/3 of a whorl. In alcohol-preserved specimens, the body is pale yellowish, unpigmented. The foot is thin, folding longitudinally during fixation; posteriorly it forms a pouch (Figure 6.05, A - fp). The length of the columellar muscle varies from 1 whorl (specimen H: 15.8 mm) to 1.5 whorls (specimen H: 33.4 mm).

mantle cavity.

Mantle edge even. Mantle rather thick, although the osphradium and the ctenidium are seen through it. Siphon long with smooth edges, extending substantially [33% to 44% L (lip length)] beyond the mantle edge.

Osphradium yellowish, bipectinate, becoming relatively smaller as the animal grows (compare Figures 6.05, D and 6.06, D). It varies from 83% (specimen H: 13.1 mm) to 22% (specimen H: 33.4 mm) of the width and from 84% (specimen H: 12.3 mm) to 62% (specimen H: 33.4 mm) of the length of the large, deeply hanging ctenidium. Osphradium asymmetrical: there are more lamellae on its right side than on the left; the total number of lamellae increases as the animal grows. The ctenidium occupies nearly 4/5 of the mantle length. The ctenidium becomes wider and the number of lamellae becomes relatively smaller as the mollusc grows (compare Figures 6.06, E and F). Hypobranchial gland moderately glandular, forming very low transverse folds. Anterior mantle filament flat, usually much shorter than the siphon. Posterior mantle filament not pigmented, short and measuring 15% to 25% of H. Mantle lobe small, concave.



Fig. 6.05. Anatomy of *O. oliva* (L., 1758). Specimen (male H: 15.8 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach. Scale bars: **A**, **B** - 2 mm, **C-F** - 1 mm. **A**, **B** - body removed from the shell. **C** - view of visceral mass, showing the shape of stomach. **D** - cut-out mantle. **E** - anterior part of digestive system from the right side with the proboscis everted, extended. **F** - native position of gland of Leiblein and salivary glands, from left anterior side. From KANTOR & TURSCH, 1998.

amt - anterior mantle filament	fp - pouch of foot	poe - posterior oesophagus
ao - anterior aorta	qL - gland of Leiblein	pr - proboscis
asg - accessory salivary gland	gon - gonad	prp - propodium
cm - columellar muscle	hg - hypobranchial gland	re - rectum
cme - cut mantle edge	mi - mantie lobe	s - siphon
ct - ctenidium	nr - nervous ring	sd - salivary duct
dasg - duct of accessory salivary gland	os - osphradium	sg - salivary gland
ddg - duct of digestive gland	par - parapodium	st - stomach
dg - digestive gland	pen - penis	vL - valve of Leiblein
dgL - duct of gland of Leiblein	pmt - posterior mantle	
	filament	

digestive system.

One specimen (male, H 15.8 mm) was preserved with its proboscis everted (Figures 6.05, E, F). The proboscis is not long (11% of H when contracted to 28% of H when extended), narrow (length/diameter ~ 4.3-8) and lies within the thin-walled proboscis sheath. The proboscis can be highly retracted during invertion, so that the buccal mass (Figure 6.07, E- od) and the radular sac (rs) protrude beyond its posterior end. [One should keep in mind that the relative size of proboscis is given for preserved specimens. In live Olives, the proboscis can be greatly extended; it can reach the shell length or more.]

Several thin retractor muscles are attached to the middle part of the rhynchodaeum (wall of the proboscis sheath) when the proboscis is retracted (Figure 6.07, E - prr). During evertion of the proboscis, the entire length of the rhynchodaeum becomes the proboscis walls and the point of attachment of the retractors shifts inside the proboscis.

After the proboscis, the oesophagus is rather narrow and forms a long loop when the proboscis is inverted. During evertion, the loop is completely straightened.

Valve of Leiblein small and poorly delimited from the oesophagus (Figures 6.05, E - vL; 6.07, E), which becomes very narrow to pass through the nerve ring. The nerve ring is large, massive and without visible borders of ganglia (Figures 6.05, E - nr; 6.07, E).

After the opening of the duct of the gland of Leiblein, the posterior oesophagus widens markedly towards the stomach (Figures 6.05, E; 6.07, E - poe).

Gland of Leiblein medium-sized, tubular, coiled, very light brownish, opens into the oesophagus by a constricted duct which is close to the nerve ring (Figure 6.07, E - dgL) or lies separately on the right side of the foregut (Figure 6.05, E).

Salivary glands medium-sized, ramified-tubular, rounded or elongated. Salivary ducts rather thick, shortly after leaving the glands (anteriorly to the valve of Leiblein) they enter the oesophagus walls and pass inside them.

The unpaired, small accessory salivary gland is partially embedded in the right salivary gland (Figures 6.05, E; 6.07, E - asg), with a thick duct (dasg) which passes at the right side of the oesophagus.

The radula will be discussed in Section 6.4.

Stomach small; its size and shape differ greatly among individuals and probably depend on physiological conditions. The stomach has a rather long caecum and receives the ducts of a digestive gland, opening just at the entrance of the oesophagus (Figures 6.06, C; 6.07, F) (the entrance of the oesophagus is not clearly seen on Figure 6.06, C). The stomach has a small posterior sorting area and well-pronounced typhlosoles. Anterior sorting area not defined. Anal gland is very small and tubular. In contrast to many other Neogastropoda, its epithelium does not contain granules of pigment and the gland is hardly visible on dissection. (In some species, such as *O. amethystina*, the gland is brownish and is clearly seen through the mantle.)

More details on the stomach, including remarks on its functioning, are given below in Section 6.3.1.

reproductive system.

The **gonad**, together with the digestive gland, occupies the upper whorls of the visceral mass, starting at the level of the nephridium. The gonad is usually overlaid by the digestive gland and is sometimes not seen from the outside (Figures 6.07, A, D). The penis in mature males is large, simple, terminating in a more or less long **penial flagellum** (Figure 6.07, G), which is absent in immature males (Figure 6.07, H).

Accelerated growth of the penis probably occurs at a shell length of about 14 mm. A male with H: 13.1 mm still had a penis 0.08 mm long (penis length 0.6% H), while a



Fig. 6.06. Anatomy of *O. oliva* (L., 1758). A-D -Specimen (female H: 33.4 mm) from Papua New Guinea, Hansa Bay, Boro Beach. Scale bars: A, B, D - 5 mm, C - 2 mm, F - 1 mm, E - 0.5 mm. A, B - body removed from the shell. C - stomach, opened dorsally. D - cut-out mantle. E - Shape of ctenidium lamellae. Specimen (H: 13.1 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach. F - Shape of ctenidium lamellae. Specimen (H: 22.0 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach. From KANTOR & TURSCH, 1998.

amt - anterior mantle filament c - caecum of the stomach cm - columellar muscle cme - cut mantle edge ct - ctenidium ddg - duct of digestive gland dg - digestive gland gon - gonad
ht - head tentacles
ig - intestinal groove
mi - mantle lobe
oe - oesophagus
os - osphradium
pgon - pallial gonoduct

pmt - posterior mantle filament
prp - propodium
psa - posterior sorting area
re - rectum
s - siphon
st - stomach
t - typhlosoles



Fig. 6.07. Anatomy of *O. oliva* (L., 1758). Scale bars: **A**,**B** - 2 mm, **C**-**H** - 1 mm. Specimens from Papua New Guinea, Hansa Bay, Sisimangum Beach. **A**, **H** - (male H: 14.1 mm) (drawn to the same scale). **B**, **E** - (female H: 11.43 mm) (drawn to the same scale). **C**,**F**,**G** - (male H: 25.8 mm). **D** - (male H: 19.2 mm). Scale bars: 1 mm. **A-D** - views of visceral mass, showing variability of the shape of stom-ach. **E** - anterior part of digestive system from the right side, extended. **F** - stomach, opened dorsally. **G**, **H** - ontogenetic changes of the penis shape and size. From KANTOR & TURSCH, 1998.

asg - accessory salivary gland c - caecum of the stomach ddg - duct of digestive gland dgL - duct of gland of Leiblein gL - gland of Leiblein gon - gonad ig - intestinal groove nr - nervous ring od - odontophore ooe - opening of oesophagus into stomach poe - posterior oesophagus pr - proboscis prr - proboscis retractors male with H: 14.1 mm already had a penis 6.25 mm long (penis length 44% of H), although not fully formed (Figure 6.07, H). Afterwards, the relative length of the penis remains more or less the same throughout life, or can even become relatively shorter (penis length 34% of H in specimen with H: 25.8 mm; 41% of H in specimen with H: 27.0 mm). The shape changes (appearance of the penial flagellum) and the seminal duct becomes well distinct and visible through the penis walls (Figure 6.07, G). Some males with H: 16.0 mm may still remain immature. The maturation of the females probably occurs at the same shell size. The smallest mature female seen by us was H: 16.2 mm. It can thus be concluded that *O. oliva* reaches sexual maturity at a shell length of at least 15 mm.

ontogenetic changes.

Besides sexual maturation, the only significant ontogenetic change noticed by us is the relative size of the osphradium and the ctenidium. In young specimens the osphradium has nearly the same size as the ctenidium; it becomes much smaller in grown-up specimens.

The use of *anatomical features as taxonomic characters* will be discussed in Section 6.5.

6.3 external digestion

6.3.1. observations on live animals

The frequent observation of extension of the proboscis into the foot pouch (see Section 11. 7.2) led us to suppose that the digestion of the prey, at least for some species, may occur in the pouch (this cannot be observed when the animal is buried and hidden in the substrate). Chemical modification of the food in the pouch was already supposed by Mrs. CROVO (cited by ZEIGLER & PORRECA 1969). She noted that "*The* Oliva *seem to use a coating of thick slime when engulfing live food; this apparently smothers the live bivalves, for once covered with this slime, they die when removed from the olive*".

External digestion has not yet been described in Gastropods, so the question deserved special attention. An easy field assay for proteolytic activity (much used by Prof. Jean BOUILLON in his work on Coelenterates) consists in depositing a drop of the mucus (or homogenate) to be tested on a black unexposed piece of photographic film. The film is then placed under the cover of a Petri dish, with a piece of humid cotton, to maintain water saturation and prevent desiccation. This is kept overnight at room temperature, then the film is rinsed with water. The presence of a transparent "window" at the location where the drop was deposited indicates that the gelatine of the film has been destroyed (hydrolysed). A blank (seawater) is always tested together with the sample to be tested.

After a specimen of *O. sericea* captured another *Oliva*, the mucus taken from inside the pouch was tested for proteolytic activity before the animal extended the proboscis into the pouch. The test was positive, indicating that proteolytic substances (probably proteases) are secreted inside the pouch and not injected through the proboscis. The test was also positive after proboscis insertion. The seawater from the aquarium tested negative, as did mucus from the anterior foot.

Positive results were also obtained for mucus collected inside the pouch of 4 more species (*O. concavospira, O. reticulata, O. oliva* and *O. carneola*), tested for proteolytic activity while feeding.

Part of the foot (region of pouch) of *O. sericea*, kept without food, was homogenised and tested for proteolytic activity. The negative result means that proteolytic activity is produced only when the prey is engulfed.

The body of the shelled prey is not swallowed whole. Cracking the shells of the "victims" (after extracting them from the pouch) allowed us to observe all intermediates between prey slightly digested and shells completely cleaned.

6.3.2. morphological modifications for external digestion

A. bistology of the foot pouch

The foot of 4 species of *Oliva* (*O. xenos, O. oliva, O. reticulata* and *O. caerulea*) was sectioned. The histology of all the species is very similar. The anterior part of the sole is lined (as in other gastropods, see VOLTZOW, 1994) with a columnar epithelium (about 45 μ m tall in *O. xenos*, Figure 6.08, section through the foot), bearing long cilia (about 10 μ m long), which are used in locomotion, for sliding. In its posterior part (in the region of the ventral pouch), this epithelium lining is abruptly replaced by another type of epithelium (about 30 μ m tall), consisting of cells with large oval vacuoles intercepted with goblet-like cells. This epithelium is obviously glandular. In three species, the epithelium of the pouch is non-ciliated, while in *O. reticulata* it bears short cilia. The border between the two types of epithelium is very sharp. (Figure 6.08). No other pronounced glandular structures were found in the sole. Therefore, proteolytic substances are secreted by the glandular epithelium of the foot pouch.

Food in the stomach is in most cases homogenised and only rarely contains more or less recognisable (although still quite small) pieces of prey flesh. This is an additional proof of external digestion.

Analysis of the shells of prey gastropods, retrieved from the pouch of Olives, revealed that the prey bodies were in different stages of consumption and, in some cases, the shells were completely empty. We cracked such shells but did not find any remains, even in the uppermost whorls, which cannot be accessed by the tip of the Olive proboscis. It is therefore very likely that the tissues in the uppermost whorls are dissolved in the pouch, while liquids are sucked through the proboscis.

B. anatomy of the stomach

In the several species we have examined, the stomach has a rather similar anatomy. The directions of ciliary currents were studied in two species, *O. miniacea* and *O. vidua* (from Nha Trang, Vietnam), on the opened stomachs of live animals, by adding carmine particles, suspended in sea water. The directions of flow were similar in both species. As an example of the Olive stomach, that of *O. miniacea* will be described below.

The stomach of *Oliva* is relatively small and narrow, especially so for a predator capable of consuming very large quantities of food (this supports the idea that food entering the stomach is pre-digested). The long axis of the stomach makes an acute angle with the shell axis (Figure 6.09, C). The stomach is rather deep and, in transverse section, is vaguely triangular, pointing down (Figure 6.09, B). The upper part of Figure 6.09, B will be called the "ceiling", the lower part the "floor". The outer shape of the stomach depends greatly on the amount of food present.





asa: anterior sorting area
dlf: dorsal longitudinal fold
ig: intestinal groove
ov: ovary
st: stomach
tgr: transversal groove.

ddg: duct of the digestive glanddg: digestive glandgrpma: ventral longitudinal groove of posterior mixing areaoes: oesophagusoeso: opening of oesophagusper: pericardiumpsa: posterior sorting areaT1: major typhlosoleT2: minor typhlosole

Functionally the stomach can be divided into 3 zones: the pouch, the style sac and the posterior mixing area (see Figure 6.09, A).

The first zone is the deep **pouch**, in which the duct of the digestive gland and the oesophagus open towards the stomach lumen. The oesophagus opens into the floor of the stomach. The opening is partly covered by an overhanging fold, continuous with the floor of the posterior mixing area (in *O. bulbosa*, adjoining the pouch there is a zone, lined with transverse parallel folds, the **anterior sorting area**, Figure 6.09, D - asa). From inside the stomach, the duct of the digestive gland looks like one single opening. Nevertheless, on examining the outer wall (adjoining the digestive gland), one can see that this opening receives two very closely spaced ducts from both lobes of the digestive gland. [In some species, like *O. caerulea*, *O. faba* forma *smithi* and *O. athenia*, the lobes are clearly separated (we can call them paired digestive glands). In other species, the border between the glands is less visible.]

A strong ciliary current (and a permanent flow of particles) runs from both the oesophagus and the opening of the digestive gland duct. In the pouch and the anterior part of the posterior mixing area, the ciliary currents are turbulent. Particles are thus kept in suspension, while moving towards the posterior mixing area.

Anteriorly, the pouch is bordered by rather deep transversal grooves (tgr) on the right and left walls of the stomach, which is lined with transversal low folds.

The second zone is the **posterior mixing area** (often called the caecum). It is large and long in *Oliva*, and occupies about half the total stomach length. It is lined by narrow and low, mostly longitudinal folds. On its left side, the opening of the oesophagus is bordered by a large fold that originates on the left wall of the stomach. This fold runs backward along the left wall and rises until it finally occupies a central position on the stomach "ceiling" (Figure 6.09, dlf). This fold directs the flow of some particles into the posterior mixing area. It becomes obsolete at about half the length of the posterior mixing area. On the floor of the stomach is a groove (grpma), leading from the pouch to the posterior part of the posterior mixing area. Weak ciliary currents carry the particles mostly along the right wall of the stomach, from the posterior mixing area towards the anterior part.

The third zone is the so-called **style sac**, which is anterior to the pouch. It contains major (T1) and minor (T2) typhlosoles, bordering the intestinal groove (ig). In *O. miniacea*, the typhlosoles are nearly at the "ceiling", so that the intestinal groove is very large, occupying most of the volume of the style sac. In other species, the typhlosoles are located closer to the "floor". Some species, for instance *O. oliva* (see KANTOR & TURSCH, 1998), *O. bulbosa* (see KANTOR, 1991) and *O. reticulata*, have a small posterior sorting area (Figure 6.09, D - psa), lined with narrow parallel, transverse folds. Along the intestinal groove, there is a strong ciliary current.

C. functioning of stomach

The food that was pre-digested in the foot pouch enters the stomach through the oesophagus. In the stomach pouch it is mixed with the secretions of the digestive gland, then mostly transferred to the posterior mixing area, where final digestion probably takes place.

Although one could presume that the ingested food would enter the digestive gland through the duct, the actual situation is just the opposite. There is a permanent and very strong current flowing out of the duct of the gland, never into the duct. Moreover, there is a permanent flow of very fine particles coming out of the duct.

Absorption therefore probably takes place through the stomach walls. The digestive gland very likely produces enzymes, while its duct serves for the transport of enzymes and the release of particles of yet unknown nature.



Figure 6.10. The radula of *O. ouini*, shown *in situ*. Specimen H 11.6 mm, male, Papua New Guinea, Hansa Bay.

6.4. the radula

THE RADULAE of few *Oliva* species had been examined until recently. A photograph of the radula of *O. fulgurator* f. *reticularis* is given in BANDEL (1984, Pl. 1, fig. 1). A drawing of the radula of *O. miniacea* is given in ZEIGLER & PORRECA (1969: 9), of *O. fulgurator* forma *circinata* in MARCUS & MARCUS (1959a). All these figures give little detail. The radula allows a distinction between the genus *Oliva* and related supraspecific taxa (ZEIGLER & PORRECA (1969: 21).



Figure 6.11. The radula of *O. parkinsoni*, still curled in its membraneous sheath. Specimen from Papua New Guinea, Hansa Bay.

In *Oliva*, the ribbon is narrow and long, with about 100 rows of teeth, each with 3 teeth; the rachidian (central) teeth are tricuspidate. In *Agaronia* and *Olivancillaria*, the rachidian teeth are also tricuspidate but possess small lateral denticles, not systematically present in *Oliva*. In *Ancilla*, the rachidian teeth have three

main cusps, and three to four accessory cusps on each side; the lateral teeth are strong. In *Olivella*, the ribbon is wide and short with usually less than 50 rows of teeth; the rachidian teeth are multicuspidate with small and numerous cusps and marginal plate-like teeth present.

The *Oliva* radula is comparatively small (and is easily overlooked). In its natural position, it is longitudinally curled inside a long, membranous sheath (see Figures 6.10 and 6.11) and does not at all look like the nice radular pictures one is used to seeing. These are obtained only after preparation. This entails delicately flattening (for instance with a soft small brush) the radular ribbon on a glass micro slide.

Precautions. Before jumping to taxonomic conclusions from radulae, some precautions have to be taken. The radula is best examined by electron scanning microscopy. It is of course possible to use traditional optical microscopes but the organisation of the radula being quite complex, it is sometimes difficult to know which of the transparent structures is above and which is under. This very complexity has the consequence that views of the same radula in different perspectives can look very different, a possible source of errors in interpretation (See Figure 6.12). It is wiser to compare only similar perspectives.



Figure 6.12. Four different views of the same radula of *O. irisans* f. *concinna*. Specimen H 42.4 mm, from Papua New Guinea, Hansa Bay.



Figure 6.13. Two different views of the same radula of *O. reticulata*. Left: intact teeth, near the middle of the ribbon. Right: worn old teeth, at the tip of the ribbon. Specimen H 19.7 mm, from Papua New Guinea, Hansa Bay.

One should avoid interpreting the older teeth, near the tip of the radula. These teeth are in actual use and can show much wear and tear. In contrast, the teeth located nearer to the middle of the ribbon are in brand new condition (see Figure 6.13).

Description. As an example, the radula of *O. oliva* (see KANTOR &TURSCH, 1998) consists of 132 (specimen H: 12.3 mm) to 184 (specimen H: 23.0 mm) rows of teeth, of which 25-42 rows are not yet completely chitinized. The radula width varies from 0.73% to 1.30% of H (mean: 0.93%; s: 0.21; n=9). The basal part of the rachidian teeth has distinct borders; in dorsal view the anterior (directed towards the mouth) edge is



clearly convex, semi-elliptical. The rachidian tooth has 3 cusps, the central one being the smallest. The lateral teeth are of complex shape, typical for the genus *Oliva*: subtriangular, slightly concave plates with narrow base and curved hook-like tips (Figure 6.14, E).

In many *Oliva* species, one has the overall impression that only the lateral sides of the basal plate are embedded into the radular membrane, the remainder being unattached (See for instance Figures 6.21, A; 6.22, B).

Rate of growth. When a specimen is submitted to a "*cold shock*" (temperature decreased for a few minutes, in a freezer), the row of teeth being produced at that moment shows severe deformations, easily observed under the microscope. After a given lapse of time *t*, the specimen is killed and the number of newly produced rows is counted. This is the number of teeth produced during the lapse of time *t*.

O. carneola produced 15 rows in 7 days (2.14 rows/day), *O. oliva* produced 15 rows in 5 days (3 rows/day). Normal growth may be quicker, in undisturbed specimens.

6.5. taxonomic characters

THE ONLY COMPARATIVE ANATOMICAL STUDY published so far (KANTOR & TURSCH, 1998) concerns the discrimination of *O. oliva* (L., 1758) from the rather similar looking *O. ouini* Kantor & Tursch, 1998.

Subsequent examination of 23 additional species made it possible to identify several characters of the soft-body morphology, which can be used for species diagnosis. Among these are: the relative size of the kidney, the degree of the vertical overlap of the whorls of the visceral mass, the position and relative size of the gonad. Nevertheless, these characters are difficult to quantify and their use seems restricted to particular cases. One character, the shape of the penis, looks very promising.

6.5.1. the penis

We were able to examine the penis of 23 species of *Oliva*, mostly collected in Hansa Bay, Papua New Guinea (see Figures 6.15-6.18), with a few additional specimens from other localities.

In general, the penis is compressed laterally, with the seminal duct forming numerous loops inside the penis. In specimens preserved in alcohol, the duct is usually seen through the walls (sometimes very distinctly, sometimes only as a whitish shadow). In specimens preserved in Bouin solution, the walls of the penis become completely opaque.

The shape of penis of live specimens and the changes occurring during fixation were observed for one species: *Oliva tigridella* Duclos, 1835 (in Sihanoukville =Kompong Som, Cambodia). The lengths of the penis and the flagellum are rather variable in live males (Figure 6.17, K, L), as penis and flagellum are able to contract and elongate in a matter of seconds. The walls of the penis are very transparent and the duct is clearly seen along most of its length. In preserved specimens the shape of the penis become more uniform, with the flagellum curved ventrally, while the walls of the penis become opaque. For this species (as well as for *O. oliva*), we compared the shape of the penis of specimens collected in different parts of the area. We did not find any substantial variability, but this should be confirmed by many more observations.

We also estimated the influence of the different methods of fixation on penis shape in preserved specimens. For this, we compared specimens preserved in alcohol, boiled before preservation, frozen before preservation and preserved in Bouin solution. No significant differences were observed.