

ANATOMY AND BIOLOGY OF *MITRA CORNEA* LAMARCK, 1811 (MOLLUSCA, CAENO-GASTROPODA, MITRIDAE) FROM THE AZORES

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ABSTRACT

Mitra cornea Lamarck, 1811, a member of the taxonomically complex group of small brown miters, is described anatomically, including observations on shell ultrastructure and diet. Morphological features confirm its taxonomic placement within the genus *Mitra*, and indicate a closer relationship with the western African *Mitra nigra* than with the Mediterranean *Mitra cornicula*. *Mitra cornea* shares the morphological adaptations of the anterior alimentary system that have evolved in conjunction with a specialized sipunculan diet, and that appear to be fairly uniform within the Mitrinae. Studies on the composition and pharmacological effects of the secretions of the salivary glands and hypobranchial gland are needed to better interpret the origin and evolutionary pathways that gave rise to the extreme trophic specialization of the Mitridae.

RESUMO

Descreve-se anatomicamente *Mitra cornea* Lamarck, 1811, um membro do grupo taxonomicamente complexo de pequenas mitras castanhas, incluindo-se observações sobre a estrutura da concha e sobre a dieta. As características morfológicas confirmam a sua localização taxonômica no gênero *Mitra* e indicam um relacionamento mais chegado com *Mitra nigra*, da África ocidental, do que com a mediterrânea *Mitra cornicula*. *Mitra cornea* possui as adaptações morfológicas da porção anterior do sistema alimentar que evoluíram juntamente com uma dieta especializada de sipúnculos, e que parece ser bastante uniforme dentro dos Mitrinae. São necessários estudos sobre a composição e efeitos farmacológicos das secreções das glândulas salivares e da glândula hipobranquial para melhor se interpretar a origem e os percursos evolutivos que fizeram aparecer a especialização trófica extrema dos Mitridae.

INTRODUCTION

The Mitridae comprise a diverse and cosmopolitan family of predatory neogastropods that are common in the tropics, but are also present in temperate seas. Mitrids usually occur at intertidal to subtidal depths, but extend into the bathyal zone (Cernohorsky, 1976; Ponder, 1998). Taylor (1993) noted that Mitridae are perhaps the most trophically specialized family of Neogastropoda, as all species studied to date have been found to feed exclusively on Sipuncula (e.g., Kohn, 1970; Fukuyama &

Nybakken, 1983; Loch, 1987; Taylor, 1989; 1993).

The mitrid fauna of the Azores is not diverse, with the family represented by two Recent species. *Mitra zonata* Marryat, 1818, is easily distinguished by its large size and two-toned periostracum that is lighter in color along the apical portion of the shell above the suture. Cernohorsky (1976:367) regarded this Recent taxon to be a subspecies of the Pliocene *Mitra* (*Mitra*) *fusiformis* (Brocchi, 1814). He reported it to be limited to the western Mediterranean and northwestern Africa, but it has since been documented to occur

in the Azores by Burnay & Martins (1988). Martins (2004:94) noted that this species lives on offshore, sandy bottoms.

A smaller species that inhabits the intertidal and subtidal rocky substrates of the Azores has a long and complicated taxonomic history. Multiple names have been applied to various phenotypes of small, smooth, dark brown mitrids that inhabit the Mediterranean and eastern Atlantic. Rolán *et al.* (1997) reviewed the systematics of the "dark brown Mitridae", concluded that three morphologically similar species are involved, and apportioned the multiple available names among them. According to these authors, *Mitra cornicula* (Linnaeus, 1758) is endemic to the Mediterranean Sea, *Mitra nigra* (Gmelin, 1791) ranges from the Cape Verde Islands to Angola, while the broad ranging *Mitra cornea* Lamarck, 1811, overlaps the range of the other two, occurring in the western Mediterranean Sea, the Macaronesian Archipelagos (Azores, Canaries, and Cape Verde Islands) and along the west coast of Africa as far south as Angola. The Mediterranean *M. cornicula* can be easily distinguished by its smaller shell size (to 25 mm), brown shell and brown periostracum, larger protoconch (320 µm) with fewer whorls (1¼), an animal that is entirely white, and a distinctive radula with lateral teeth that retain prominent dentition along their entire width (Rolan *et al.*, 1997:fig. 16D). *Mitra nigra* and *M. cornea* are more similar in protoconch size, radular morphology, and periostracal color. *Mitra nigra* reaches a larger shell size (to 70 mm, compared to 40 mm for *M. cornea*) and has a black shell and brown to reddish-violet animal, while *M. cornea* has a light brown to pale grey shell and a distinctive white animal with yellow stripes along the tentacles and lateral margins of the foot (see Martins, 2004:65, fig. M). It should be noted, however, that this distinctive col-

oration is evident in living animals, but alcohol preserved specimens are brownish, becoming stained as the hypobranchial gland exudate oxidizes to a purplish brown.

Thus, the small brown mitrids of the Azores are *Mitra cornea* Lamarck, 1811. Earlier literature (e.g. Dautzenberg, 1889) may refer to this species as *Mitra fusca* Reeve, 1844, which, however, is a junior synonym of *M. cornea* and is preoccupied by *Mitra fusca* Swainson, 1831, an Indo-Pacific species. Cernohorsky (1969:972, fig. 28) designated as lectotype for *Mitra cornea* Lamarck, 1811, a specimen from the west coast of Africa, thus fixing its type locality. He regarded this taxon to be a synonym of *M. cornicula*, a species that is endemic to the Mediterranean and readily distinguished from *M. cornea* on the basis of shell and radular morphology. *Mitra aquitanica* Locard, 1892, is an unnecessary replacement name for *Mitra fusca* Reeve, 1844 non Swainson, 1831.

Azorean records of *Mitra cornea* were, until recently, reported as *Mitra nigra* (e.g., Cernohorsky, 1976:371; Knudsen, 1995:152; Morton *et al.*, 1998:57, 65, 76).

The present study documents the anatomy, shell morphology and biology of *Mitra cornea* from São Miguel, Azores, in order to provide a basis for more comprehensive studies of the systematics and relationships of the three small, smooth mitrids of the eastern Atlantic and Mediterranean Sea.

MATERIALS AND METHODS

Numerous specimens were collected from algae covered intertidal rocks along the SW wall of the fishing pier in Vila Franca do Campo, São Miguel, Azores [N37° 42' 49.75", W25 25' 52.10"] (USNM 1114338). Additional specimens were collected on shallow (< 1 m) subtidal rocky ledges along the southern rim of the

crater of Ilhéu de Vila Franca, São Miguel, Azores [N37° 42' 18.75", W25° 26' 35.33"] (USNM 1114340).

Specimens were maintained and observed in seawater. The shells of a subset of specimens were cracked in a vice, and the animals irritated with forceps until they everted their proboscis. These animals were then preserved in 70% ethanol and transferred to 95% ethanol for storage.

Animals were dissected, portions critical point dried and examined with a scanning electron microscope.

SYSTEMATICS

Class GASTROPODA

Order Neogastropoda Wenz, 1943

Family Mitridae Swainson, 1831

Genus *Mitra* Lamarck, 1798

Mitra cornea Lamarck, 1811

Synonymy

Mitra cornea Lamarck, 1811

Mitra fusca Reeve, 1844 non *Mitra fusca* Swainson, 1831

Mitra aquitanica Locard, 1892

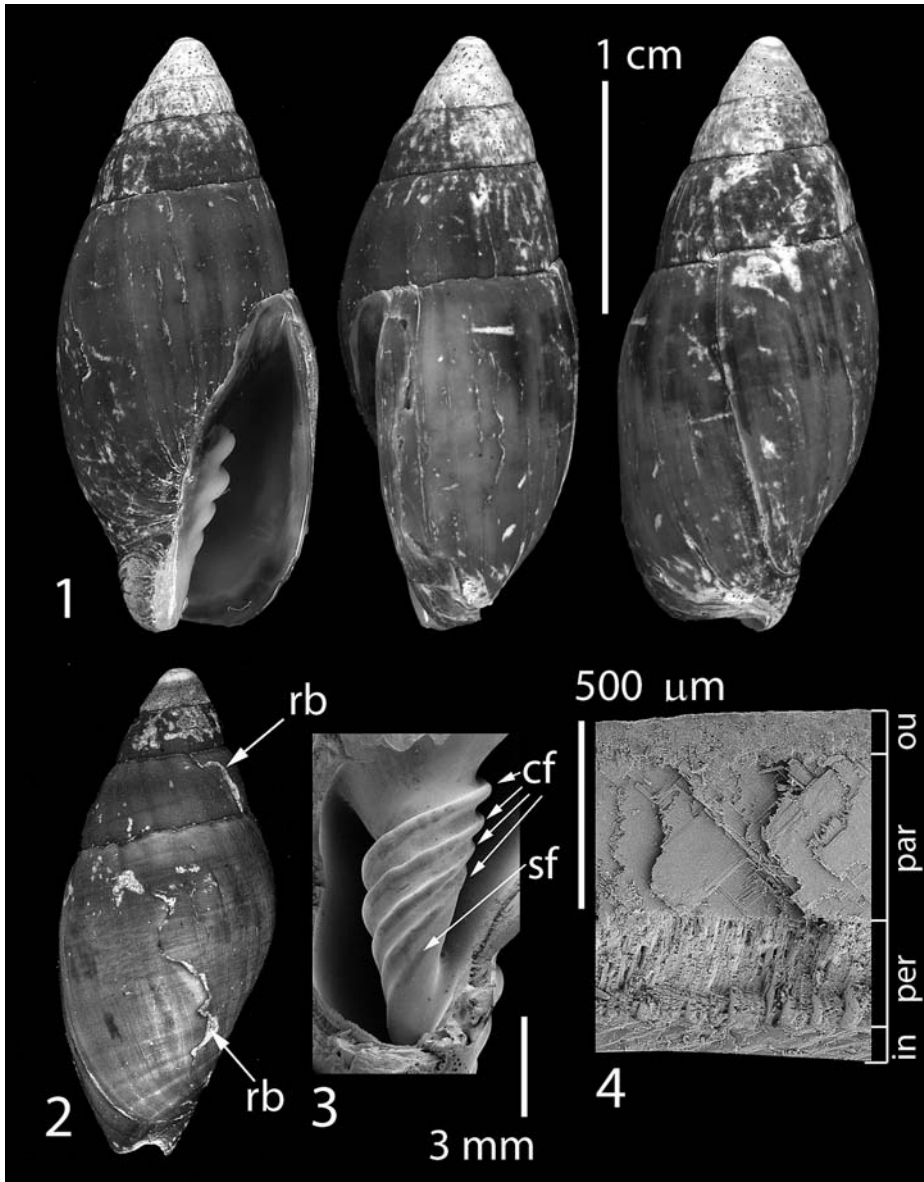
Description

Shell morphology: Shell (Figures 1, 2) small for genus (to 34 mm), thick, biconic, fusiform, with elongate aperture and 4 heavy columellar folds. Protoconch increasing from $\approx 110 \mu\text{m}$ to $\approx 1.2 \text{ mm}$ in $4 \frac{1}{4}$ evenly rounded, conical whorls, badly eroded or missing on most specimens. Transition to teleoconch indistinct, marked by change in surface from glossy to matte, and onset of spiral sculpture consisting of narrow, pitted furrows separating adjacent broad, low, spiral cords. Teleoconch of up to 7+ smooth, evenly convex whorls. Suture adpressed, irregular, showing evidence of axial lamellae. Spiral sculpture of low, abutting spiral cords separated by a series of closely spaced pits in early whorls, that become sharply incised fur-

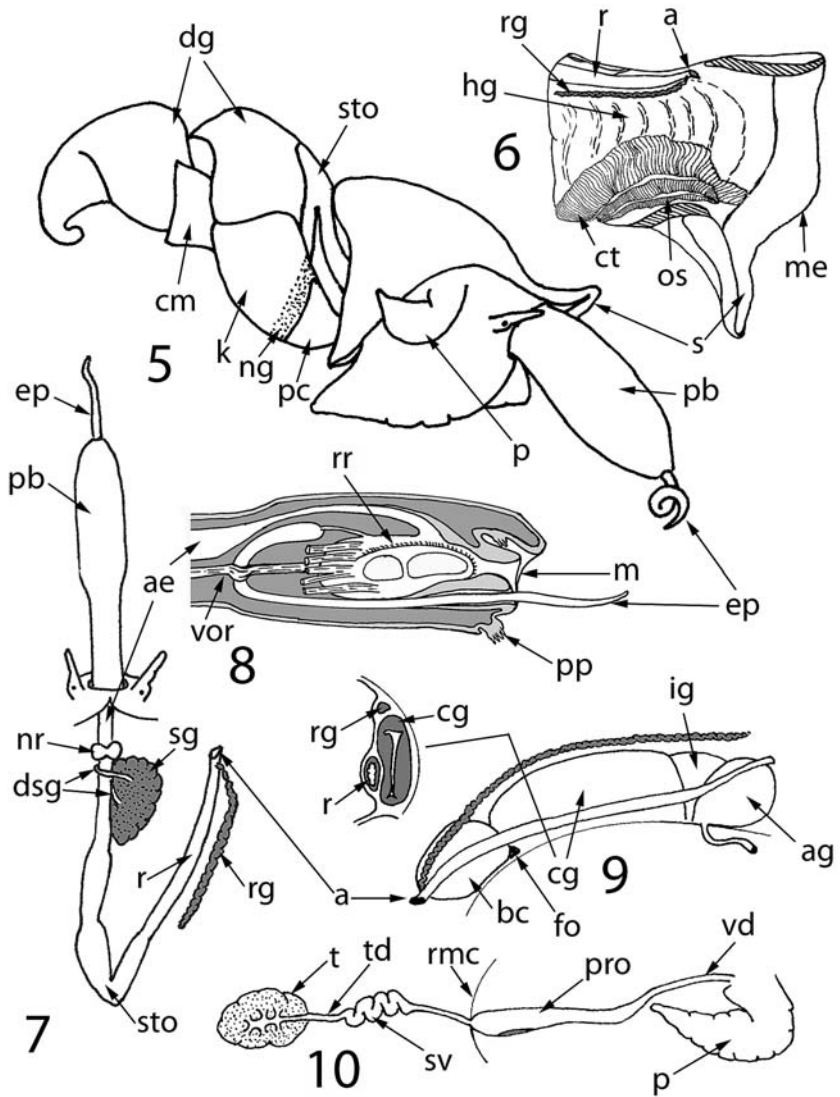
rows in later whorls, and largely obscure except along the anterior third of the final whorl. Axial sculpture consists of low, nearly obscure lamellae that are most evident at the suture of smaller specimens (Figure 2) from which the periostracum has been removed. Pitting, periostracum, and repaired breaks (Figure 2, rb) obscure the sculpture of larger specimens. Aperture elongated, tapering posteriorly beneath suture to form anal sulcus. Outer lip smooth, thickened, nearly straight along middle portion, rounded and dorsally reflected anteriorly to form siphonal notch. Inner lip with narrow, glazed inductura, four broad columellar folds (Figure 3, cf), decreasing in prominence from posterior to anterior, and a siphonal fold (Figure 3, sf). Siphonal notch broad, siphonal fasciole usually absent, but may be weak and short in larger specimens. External shell color ranges from dark chestnut brown to purplish gray and may be solid or banded. Aperture is white, especially the columellar folds, but brown color is visible through the white glaze near the anterior and posterior margins of the aperture. Periostracum thin, chestnut brown. Operculum absent.

Shell ultrastructure: (Figure 4) Shell composed of four distinct crystal layers. The innermost layer (Figure 4, in) ($\approx 90 \mu\text{m}$) comprising the glaze is whitish, while the remaining layers are golden brown. The crystal faces of the next layer (Figure 4, per) ($\approx 275 \mu\text{m}$) are crossed-lamellar, and oriented perpendicular to the growing edge of the shell. They are also perpendicular to the crystal faces of the adjacent crossed lamellar layer (Figure 4, par) ($\approx 435 \mu\text{m}$), which are parallel to the growing edge. A prismatic layer (Figure 4, ou) ($\approx 120 \mu\text{m}$) is outermost.

External anatomy: (Figure 5) The soft tissues comprise $2\frac{1}{2}$ whorls, of which the



FIGURES 1-4. *Mitra cornea* Lamarck, 1811. 1. USNM 1114338, intertidal rocks along the SW wall of the fishing pier in Vila Franca do Campo, São Miguel, Azores. 2. USNM 1114340, subtidal (< 1 m) rocky ledges along the southern rim of the crater of Ilhéu de Vila Franca, São Miguel, Azores. 3. Shell fractured to reveal columella. 4. shell ultrastructure. Surface parallel to growing edge of shell, $\frac{1}{4}$ whorl behind the lip. **cf**, columellar fold; **in**, innermost shell layer; **ou**, outer, prismatic shell layer; **par**, crossed-lamellar aragonite, crystal faces parallel to growing edge; **per**, crossed-lamellar aragonite, crystal faces perpendicular to growing edge; **rb**, repaired break; **sf**, siphonal fold.



FIGURES 5-10. Anatomical features of *Mitra cornea* Lamarck, 1811. 5. Male specimen, lateral view. 6. Roof of mantle cavity. 7. Alimentary system, semi-diagrammatic. 8. Lateral view of anterior proboscis, opened from right side. 9. Female reproductive system. 10. Male reproductive system. a, anus; ag, albumen gland; ae, anterior esophagus; bc, bursa copulatrix; cg, capsule gland; cm, columellar muscle; ct, ctenidium; dg, digestive gland; dsg, duct of salivary gland; ep, epiproboscis; fo, female opening; hg, hypobranchial gland; ig, ingesting gland; k, kidney; m, mouth; me, mantle edge; ng, nephridial gland; nr, nerve ring; os, osphradium; p, penis; pb, proboscis; pc, pericardium; pp, peristomal papillae; pro, prostate gland; r, rectum; rg, rectal gland; rmc, rear of mantle cavity; rr, radular ribbon; s, siphon; sg, salivary gland; sto, stomach; sv, seminal vesicle; t, testis; td, testicular duct; vd, vas deferens; vor, ventral odontophoral retractor muscle.

mantle cavity spans $\frac{3}{4}$ whorl, the kidney $\frac{1}{4}$ whorl, and the digestive gland and gonad $1\frac{1}{2}$ whorls. The columellar muscle is long, narrow, attaching to the shell $1\frac{1}{4}$ whorl behind the mantle edge. The foot is long, narrow, rectangular ($L/W \approx 2.0$), with a deep propodial groove along the anterior edge. In living specimens, the foot is bright white with a narrow, bright yellow band along the lateral edges of the foot and outer edges of the tentacles as far as the eyes. The color is rapidly lost in alcohol preserved specimens, which become progressively darker brown over time. The siphon is long and muscular.

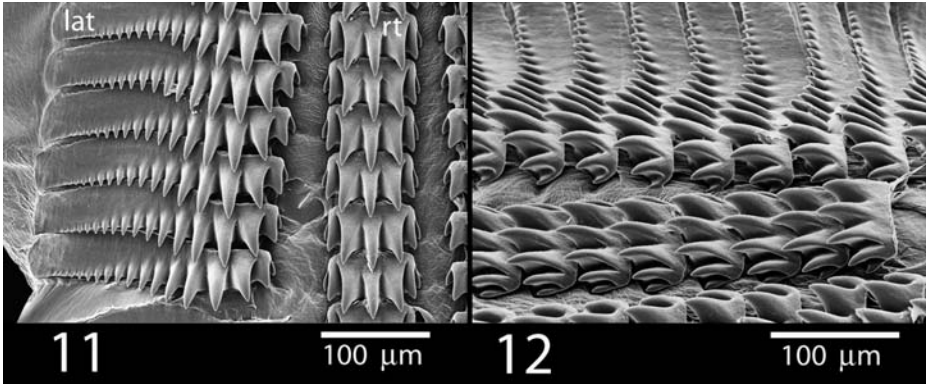
Mantle cavity: (Figure 6) The arrangement of mantle cavity organs is similar to that of most neogastropods. The mantle edge is thin and smooth, somewhat thickened at the right margin. The osphradium (Figure 6, os) is bipectinate, large, brownish, with 64-73 filaments above the ganglion and 52-60 below. The ctenidium (Figure 6, ct) is twice as broad and twice as long as the osphradium. A large renal organ (Figure 5, k), in which the primary and secondary lamellae do not interdigitate [termed *Meronephridiens* by Perrier (1889)] forms the right, rear wall of mantle cavity. The short, broad pericardium (Figure 5, pc), with a narrow nephridial gland (Figure 5, ng) lies to the left of the kidney. The hypobranchial gland (Figure 6, hg) is broad and thick, occupying much of the dorsal roof of the mantle cavity between the osphradium and gonoduct. It produces a copious viscous secretion that is clear at first, but becomes yellowish then purple, and finally dark brown. The color is alcohol soluble and stains the tissues of preserved specimens.

Alimentary system: (Figure 7) The pleuro-bolobic proboscis (Figures 5, 7 pb) is moderately long (extends to $\approx 1.5 \times$ Shell length), broad, especially distally, enclosing

a large, compact buccal mass and epiproboscis (Figures 5, 7, 8, 13-22, ep), an extensible muscular introvert unique to mitrids. When retracted, the proboscis is slightly folded within proboscis sheath and fills nearly the entire cephalic hemocoel. The buccal mass is broad, with a short, muscular, peristomal rim lined with evertable papillae surrounding the mouth. The odontophore and radular ribbon are large, with strong protractor and retractor muscles.

The radular ribbon (Figures 11, 12) is short and broad ($L/W \approx 3.8$; $L = 1.9$ mm, $W = 500$ μ m), consisting of 45-57 rows of teeth, and may be slightly asymmetrical, with left lateral teeth 5-14% wider than right in some specimens. The rachidian teeth (Figure 11, rt) have five strong, curved cusps emerging from a weakly trapezoidal basal plate that is broader at the posterior end. Each of the five cusps has a broad, thick dorsal surface continuous with the anterior end of the basal plate, and a sharply tapering, knife-like posterior-ventral edge that descends to the posterior end of the basal plate. The central cusp is longest, lateral cusps are shortest. The lateral teeth (Figure 11, lat) have a complex, semi-recurved basal plate that is broad, thin and flat along its outer edge, becoming narrower, thicker, with its anterior edge raised by up to 35° along the inner $\frac{1}{3}$ of its length. Each tooth has 14-18 cusps. The 2nd \rightarrow 4th from the inner edge are strongest, with the same knife-like structure as the cusps on the rachidian teeth. The remaining teeth become more conical and diminish in length and size toward the lateral edge, with the outermost 0.18 of the basal plate lacking discernible cusps.

The epiproboscis is a long, anteriorly tapering, muscular rod, consisting of a central core of longitudinal muscles, surrounded by circular muscles and encased in an inner and outer sheath. From its



FIGURES 11-12. Radula of *Mitra cornea* Lamarck, 1811. 11. Dorsal view of half row of radular teeth. 12. Oblique view of radular teeth. *lat*, lateral tooth; *rt*, rachidian tooth.

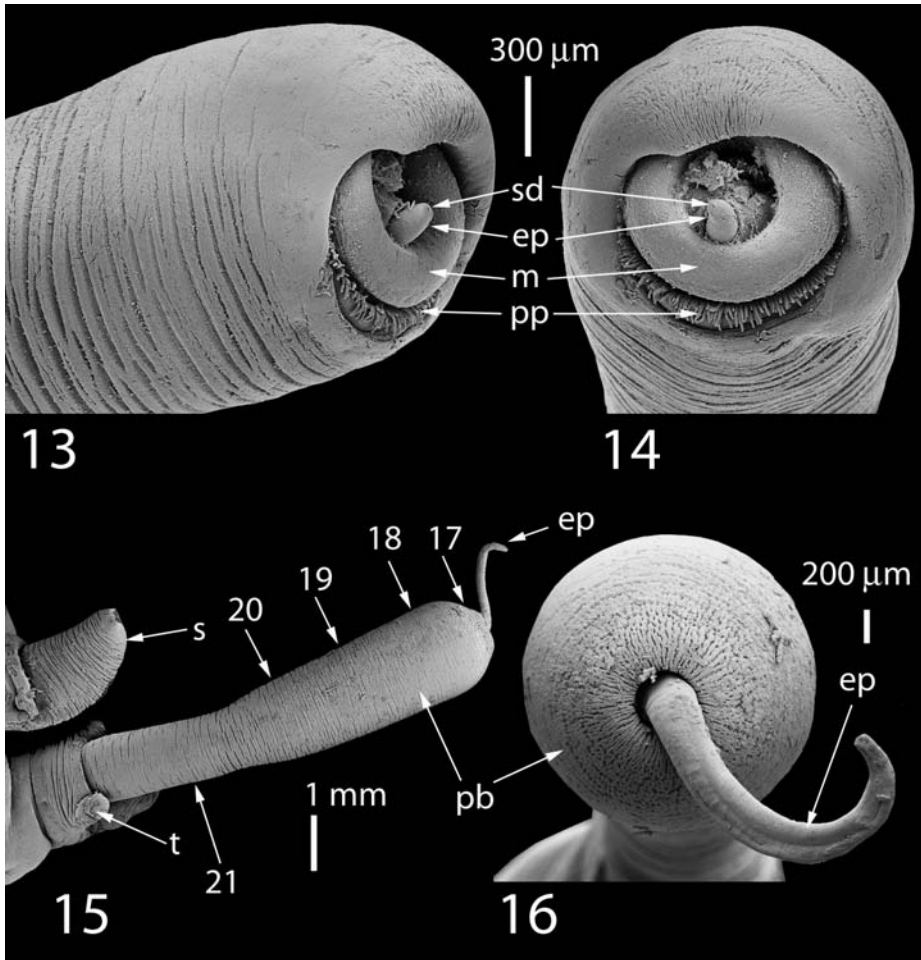
opening just below the mouth (Figures 8, 22, m), the epiproboscis runs mid-ventrally beneath the buccal mass, recurving dorsally to form a U-shaped bend behind the buccal mass to become attached to the odontophore by a short, broad retractor muscle. The large, ascinous salivary glands (Figure 7, *sg*) are situated above the nerve ring (Figure 7, *nr*) in the anterior portion of the cephalic hemocoel, generally to the right of the retracted proboscis. The ducts from these glands run anteriorly alongside the esophagus, joining the epiproboscis at the bend, running at first ventrally, then medially within the epiproboscis, merging into a single opening at its tip (Figures 13, 22, *sd*).

The anterior esophagus is broad, and flat above the buccal mass (Figure 19, *ae*), with low longitudinal ridges, but becomes narrower and more circular posterior (Figure 21, *ae*) to the bend in the epiproboscis. The esophagus passes through the nerve ring without forming a distinctive valve of Leiblein, broadens to form a crop-like structure, and runs posteriorly to join a broad, muscular stomach. Neither a gland of Leiblein nor accessory salivary glands are present. The stomach (Figure 7, *sto*) has a muscu-

lar gizzard between the esophagus and the closely spaced ducts of the digestive glands. The intestinal region has low longitudinal ridges that lead to the long intestine, which runs along the kidney and pericardium before entering the rear of the mantle cavity. The rectum (Figure 7, *r*) runs alongside the pallial gonoduct, forming the anus (Figures 7, 9, *a*) anterior to the gonoduct, but some distance from the mantle edge. A long, narrow rectal gland (Figure 7, *rg*) runs along the roof of the mantle cavity nearly its entire length, before joining the rectum near its anterior margin.

Of the 20 specimens of *Mitra cornea* dissected, 7 were found to have essentially intact sipunculans (*Golfingia* sp. = *G. margaritaceum* fide Morton *et al.* 1998:76) within their gut, usually in the crop or stomach. No other recognizable prey was found within any of the specimens.

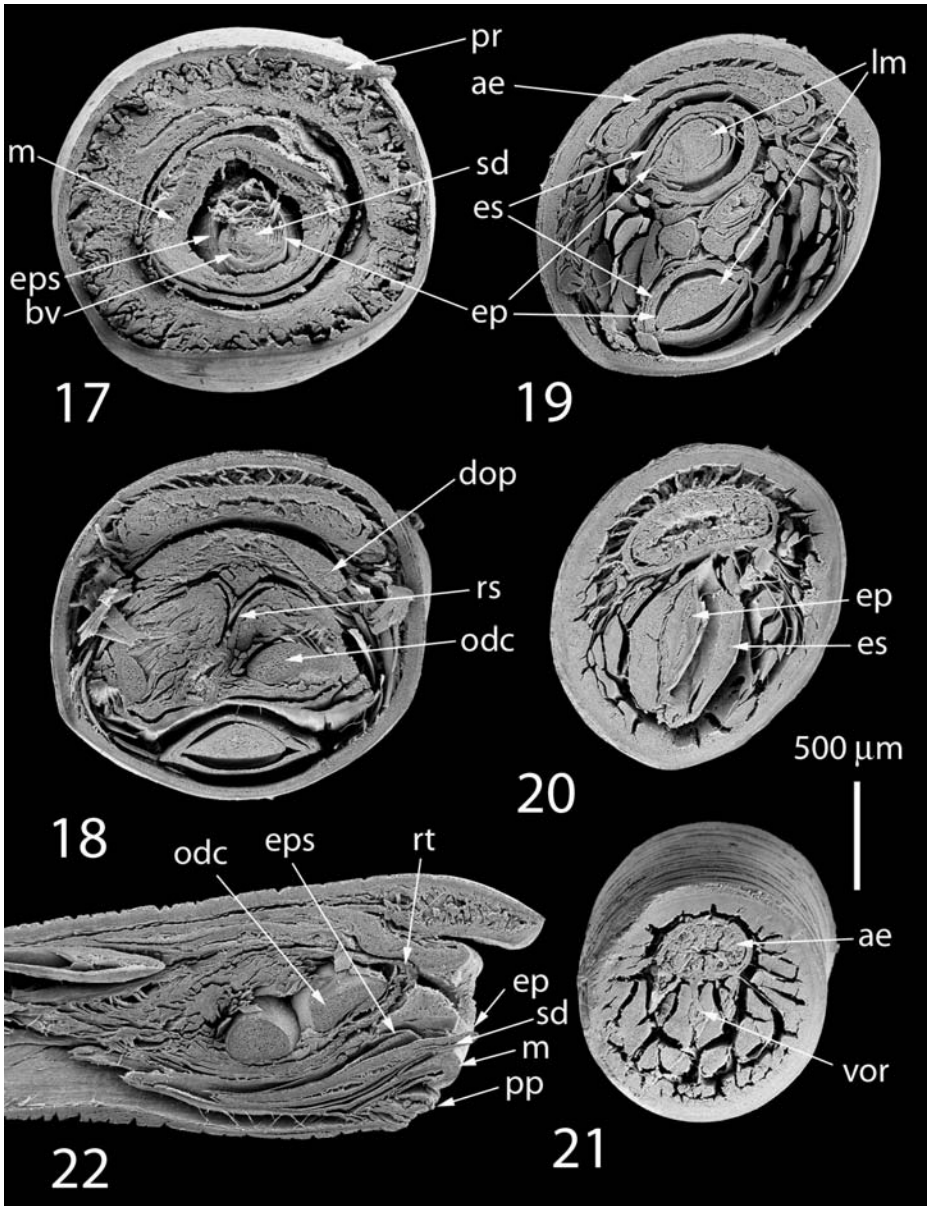
Male reproductive system: The testis (Figure 10, *t*) is yellowish, lining the right ventral side of the digestive gland. A duct leading anteriorly expands to form the broad, highly convoluted seminal vesicle (Figure 10, *sv*) near the anterior margin of the digestive gland. From



FIGURES 13-16. Proboscis tip of *Mitra cornea* Lamarck, 1811, showing extension of the epiproboscis. 13. Lateral and 14. frontal views of proboscis tip in early stage of extension of epiproboscis. 15. lateral and 16. frontal views of proboscis tip with epiproboscis extended. Arrows in figure 15 indicate planes of section for figures 17-21. ep, epiproboscis; m, mouth; pb, proboscis; pp, peristomal papillae; s, siphon; sd, salivary duct opening; t, cephalic tentacle.

there, the renal vas deferens runs along the surface of the nephridium without giving rise to a gonopericardial duct, entering the pallial cavity where it expands to form the prostate gland (Figure 10, pro). The prostate gland is open to the pallial cavity along its broad posterior portion, but forms a closed

duct anteriorly that descends to the floor of the mantle cavity (Figure 10, vd) and runs to the base of the penis (Figures 5, 10, p), situated behind the right cephalic tentacle. The penis is broad basally, strongly recurved, with a flagellate pseudo-papilla, with the duct opening at its tip.



FIGURES 17-22. Proboscis tip of *Mitra cornea* Lamarck, 1811. 17-21. Transverse sections through proboscis tip shown in figure 15. 22. Saggital section through proboscis tip in figure 13. ae, anterior esophagus; bv, blood vessel; dop, dorsal odontophoral protractor muscle; ep, epiproboscis; eps, epiproboscis sheath; es, epiproboscis sheath; lm, longitudinal muscle; m, mouth; odc, odontophoral cartilage; pp, peristomal papillae; pr, peristomal rim; rs, radular sac; rt, radular teeth; sd, salivary duct; vor, ventral odontophoral retractor muscle.

Female reproductive system: The ovary lies along the right side of the digestive gland and dominates the uppermost visceral whorls. The oviduct runs anteriorly from the ovary, along the kidney and pericardium without giving rise to a gonopericardial duct, before entering the rear of the mantle cavity. The pallial gonoduct (Figure 9) consists of an albumen gland, ingesting gland, capsule gland and bursa copulatrix. The albumen gland (Figure 9, ag) is tall, narrow, and glandular, with ventral channel. The ingesting gland (Figure 9, ig) is situated between the albumen gland and long capsule gland (Figure 9, cg). The large, muscular bursa copulatrix (Figure 9, bc) is situated above the female opening (Figure 9, fo) and above and anterior to the capsule gland. A prominent ventral pedal gland is situated along the ventral mid-line of the foot, just anterior to the bursa copulatrix.

Reproductive Biology: Knudsen (1995:153, fig. 13) illustrated the egg capsule and pre-hatching larva of this species [as *Mitra nigra*], noting that development was pelagic in this species. It was not known whether the larva develops into a sinusigera larva during the pelagic phase.

DISCUSSION

As the number of mitrids species that have been studied anatomically increases, all have been found to have a highly specialized anterior alimentary system with a broad, extensible, muscular proboscis and a uniquely evolved muscular epiproboscis that is extended through the mouth (Figures 13, 14, pp), and through which pass the ducts of the salivary glands, joining into a single duct before emptying at its tip (Figures 13, 14, sd). In mitrids, the accessory salivary glands and gland of Leiblein are absent

and the valve of Leiblein is greatly reduced or absent. These anatomical structures are adaptations to a specialized diet consisting nearly exclusively of sipunculans (see Taylor, 1993 and references therein). The diet of more than 30 species of mitrids has been studied, yet there is but a single report of one individual of one species, feeding on a nemertean (Fukuyuma and Nybakken, 1983).

The earliest fossil record for family Mitridae dates to the basal Late Cretaceous [Cenomanian / Turonian] (Tracey *et al.* 1993:152), with most modern genera diverging during the Miocene (Cernohorsky, 1970:fig. 180). Yet all surviving lineages have a well developed epiproboscis, and lack accessory salivary glands and a gland of Leiblein, suggesting an early common origin of this specialized body plan, adapted for preying on sipunculans. Relatively few neogastropods prey occasionally on sipunculans [*eg.*, *Vasum*, *Drupa*, *Bursa*] and, other than Mitridae, only a few species of *Drupina* feed exclusively on them (Taylor 1989:271).

Sipuncula is a small phylum with only about 150 species worldwide (Cutler, 1994:3). Sipunculans live in a variety of habitats, burrowing in rock, sand or rubble bottoms at all depths. The diversity of Mitridae is somewhat greater, at 377 living species (Cernohorsky, 1970:Table 1).

In the tropics, mitrid diversity is high and species partition their habitat by substrate type (*eg.*, Taylor, 1989:fig. 7), although multiple species can co-occur in the same general habitat (*eg.* thick sand). In the Azores, the two mitrid species appear to partition their habitat, with *M. cornea* inhabiting intertidal to subtidal reef platforms and boulder rubble, while *M. zonata* occurs in offshore sandy substrates. Sipunculan diversity

in the Azores somewhat exceeds mitrid diversity.

Interpretation of the function of the epiproboscis has varied over the years. Several authors have proposed that the epiproboscis serves as a venomous organ (Vayssiere, 1901; Cernohorsky, 1970), is used for both offense and defense (Vayssiere, 1901), or applies the products of the salivary glands to the sipunculan prey (Risbec, 1928; Ponder, 1972, 1998). There has also been some question as to whether the salivary gland secretion weakens the prey integument, serves as a relaxant to prevent prey contraction, or acts as an adhesive substance to facilitate the removal of sipunculans from their burrows (West, 1990:774).

Several authors have reported on the feeding behavior of mitrids with varying levels of detail. Loch (1987) reported that the epiproboscis is extended during feeding and inserted into its prey, and is thought to deliver salivary secretions. Taylor (1989:262) suggested that the peristomal papillae ["circum-oral, brush like structure"] can be everted during feeding and may function to grip prey, noting that, while mitrids have a large radula with long, multicusped lateral teeth, these teeth may be used to assist with swallowing the prey, as the sipunculans are not shredded.

The most detailed observations of feeding behavior were those of West (1990), who reported that *Mitra idae* located its prey with its siphon, first touching it with the siphon edge and cephalic tentacles before extending its proboscis. The peristomal rim then grasps the prey in a series of rapid eversions and contractions and the snail retracts its proboscis in attempts to pull the sipunculan from the substratum. If the prey cannot be extracted and swallowed whole, secretions from the salivary gland are applied and the radula

used to rasp a hole in the integument. The epiproboscis is then inserted into the hole, entangling the sipunculan viscera and pulling them into the mitrid buccal mass. This alternating extension and retraction of the epiproboscis is repeated multiple times. The proboscis periodically further envelopes the sipunculan and eventually frees the sipunculan from the substratum, by grasping the integument with the radula and retracting the odontophore. This behavior is characteristic of members of the subfamily Mitrinae, which includes *Mitra cornea*.

Later, West (1991:710) reported on the feeding in *Mitra catalinae*, a member of the subfamily Cyldromitrinae. As in Mitrinae, the proboscis was extended, the peristome flared to grasp the prey and the radula was used to rasp a small hole in the integument through which the epiproboscis was inserted. However, in this species, the epiproboscis was "rhythmically passed in and out of the hole" pumping sipunculan coelomic fluids and eggs into the buccal cavity and down the esophagus of the mitrid, without ingesting either viscera or the entire sipunculan. West (1991:710) noted that the sipunculans "survived the feeding session," suggesting parasitism rather than predation in this mitrid species.

Ponder (1972:335) raised the question of how the epiproboscis might have evolved. He suggested that the ducts of the salivary glands migrated ventrally, and that their openings moved from lateral positions on the buccal mass to a ventral anterior position at the edge of the mouth. The next hypothesized stage was their placement on a papilla that eventually became invaginated and elongated. Ponder noted that the salivary glands of mitrids have a second type of secretory cell not present in related families, and that these cells may produce a toxin. It is interesting to note, that

although the salivary glands are ascinous and typical of salivary glands of other neogastropods, the position of the ducts, including their becoming fused into a single duct before emerging medially at the ventral anterior edge of the buccal mass is typical of the ducts of accessory salivary glands, which are absent in Mitridae. West (1991) noted that the epiproboscis shows structural and functional affinities with other molluscan subradular organs, and hypothesized that it developed from the musculature of the buccal mass, while the sheaths were derived from the walls of the buccal cavity. According to the Ponder model, the primary function of the epiproboscis is the targeted application of salivary gland secretions. The West model is based on a primarily mechanical function of the epiproboscis. West (1991:716) commented that the ventral migration of the salivary gland ducts "to connect with the formative epiproboscis" might have changed, or enhanced its function, but that it is difficult to assess the evolutionary importance of this event without knowledge of the function of salivary gland secretions".

While the morphological adaptations of the anterior alimentary system that have evolved in conjunction with a specialized sipunculan diet are now well documented within the Mitridae, nothing is known of the chemical adaptations, including the composition and physiological effects of the secretions of the salivary glands, which are delivered to the prey through the epiproboscis. The salivary glands of related gastropods have been shown to produce neurotoxins with acetylcholine-like effects that are used to overcome prey with a paralytic secretion (West *et al.*, 1998). Still others contain proteinaceous toxins that are hemolytic and lethal (Shiomi *et al.*, 2002). Given that the Mitridae represent an adaptive radiation following an early [Upper Cretaceous]

adaptation to a highly specialized diet, the structure, specificity and toxicology of salivary gland secretions represent a fertile area for the study of chemical evolution within Mollusca, and interactions of predator and prey.

Similarly, the hypobranchial gland of mitrids is voluminous, and noted for producing substantial quantities of a secretion that oxidizes to form a purple pigment. Numerous authors since Dubois (1909) have documented that, in addition to chromogens, hypobranchial gland secretions from various neogastropods contain numerous toxic and paralytic compounds, including choline esters, serotonin and various biogenic amines (e.g., Shiomi *et al.*, 1998). The hypobranchial gland of the neogastropod *Thais haemastoma* (which co-occurs with *Mitra cornea*) contains multiple active components, including one that produces a stimulatory effect on blood pressure, and another that acts as a neuromuscular blocking agent of the depolarizing type (Hyang & Mir, 1971). Some muricids have been observed to use hypobranchial gland secretions to immobilize prey (Naegel & Alvarez, 2005:426). Other taxa, including trochids (Kelley *et al.*, 2003) and pleurotomariids (Harasewych, 2002) have been shown to use hypobranchial gland secretions to repel predators.

Despite the exceptionally thick shells, periostracum and overgrowth of calcified encrusting organisms, cleaned shells of many *Mitra cornea* show evidence of multiple repaired breaks (Figure 2, rb). This high incidence of unsuccessful predation (measured as frequency of shell repair) is an indication of high exposure to crushing predation as well as of the ability to survive such attacks by predators. Among shallow water gastropods, Vermeij (1989) reported that the incidence of unsuccessful predation was greatest in

the Indo-West Pacific and lowest in the Atlantic. Frequencies of unsuccessful predation of 0.5 breaks per individual were uncommon, and never averaged more than 1 break per individual for the most prey-resistant taxa. Repaired breaks on just the last whorl of the shell of *Mitra cornea* range from 0-5 [mean = 1.95, n = 20], suggesting both an exceptionally high rate of attack, and ability to survive attack. While this points to the possible use of hypobranchial gland secretions as a chemical defense against predators, it does not preclude the presence of other compounds or other uses for the secretory products of the hypobranchial gland.

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REFERENCES

- BURNAY, L.P., & A.F. MARTINS, 1988. Acerca da presença de *Mitra zonata* Marryat, 1818 (Gastropoda: Mitridae) na costa Algarve (Portugal) e nos Açores. *Publicações Opcionais da Sociedade Portuguesa de Malacologia*, 10: 23-26.
- CERNOHORSKY, W.O., 1969. The types of the Lamarck collection in the Museum d'Histoire Naturelle in Geneva. Recent Mollusca of the genera *Mitra*, *Columbella* (in part) and *Cancellaria* (in part). *Revue Suisse de Zoologie*, 76(49): 953-994, 9 pls.
- CERNOHORSKY, W.O., 1970. Systematics of the Families Mitridae and Volutomitridae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum*, Auckland, iv+190 pp.
- CERNOHORSKY, W.O., 1976. The Mitridae of the World. Part I. The sub-family Mitrinae. *Indo-Pacific Mollusca*, 3(17): 273-528.
- CUTLER, E.B., 1994. *The Sipuncula, Their Systematics, Biology and Evolution*, 453 pp. Cornell University Press, Ithaca, NY.
- DAUTZENBERG, P., 1889. Contribution à la fauna malacologique des îles Açores. *Résultats des Campagnes Scientifique du Prince de Monaco*, 1:1-112.
- DUBOIS, R., 1909. Recherches sur la pourpre et sur quelques autres pigments animaux. *Archives de Zoologie Expérimentale et Générale*, 5(2):471-590.
- FUKUYAMA, A., & J. NYBAKKEN, 1983. Specialized feeding in mitrid gastropods: evidence from a temperate species *Mitra idae* Melvill. *The Veliger*, 26: 96-100.
- HARASEWYCH, M.G., 2002. Pleurotomarioidean Gastropods. *Advances in Marine Biology*, 42: 235-292, color plates 5, 6.
- HUANG, C.L., & G.N. MIR, 1971. Pharmacological properties of hypobranchial gland of *Thais haemastoma* (Clench). *Journal of Pharmaceutical Sciences*, 60(12): 1842-1846.
- KELLEY, W.P., A.M. WOLTERS, J.T. SACK, R.A. JOCKUSCH, J.C. JURCHEN, E.R. WILLIAMS, J.V. SWEEDLER & W.F. GILLY, 2003. Characterization of a novel gastropod toxin (6-bromo-2-mercaptotryptamine) that inhibits shaker K channel

- activity. *The Journal of Biological Chemistry*, 278(37): 34934-34942.
- KNUDSEN, J., 1995. Observations on reproductive strategy and zoogeography of some marine prosobranch gastropods (Mollusca) from the Azores. In: MARTINS, A.M.F. (ed.), *The Marine Fauna and Flora of the Azores. Proceedings of the Second International Workshop of Malacology and Marine Biology, São Miguel, Azores, 1991. Açoreana, Supplement [4]: 135-158.*
- KOHN, A.J., 1970. Food habits of the gastropod *Mitra litterata* Lamarck: relation to trophic structure of intertidal marine bench community in Hawaii. *Pacific Science*, 24: 483-486.
- LOCH, I., 1987. Peanuts for breakfast. *Australian Shell News*, 58: 6-8.
- MARTINS, A.M.F., 2004. *O Anel da Princesa*, 99 pp. Intermezzo-Audio-visuais, Lisbon.
- MORTON, B., J.C. BRITTON & A.M.F. MARTINS, 1998. *Costal Ecology of the Açores*, 249 pp. Sociedade Afonso Chaves, Ponta Delgada.
- NAEGEL, L.C.A., & J.I.M. ALVAREZ, 2005. Biological and chemical properties of the secretion from the hypobranchial gland of the purple snail *Plicopurpura pansa* (Gould, 1853). *Journal of Shellfish Research*, 24(2): 421-428.
- PERRIER, R., 1889. Recherches sur l'anatomie et l'histologie du rein des gastéropodes Prosobranches. *Annales des Sciences Naturelles (Zool.)*, 7,8: 61-315.
- PONDER, W.F., 1972. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). *Malacologia*, 11: 295-342.
- PONDER, W.F., 1998. Family Mitridae. In: BEESLEY, P.L., G.J.B. ROSS & A. WELLS (eds.), *Mollusca: The Southern Synthesis*. Fauna of Australia, Vol. 5., pp. 841-842. CSIRO Publishing: Melbourne.
- RISBEC, J., 1928. Contribution à l'étude anatomique de quelques espèces de Mitres de la presqu'île de Nouméa. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 34: 105-112, 173-180, 225-227.
- ROLÁN, E., L. DANTART & F. FERNANDES, 1997. On some dark species of *Mitra* from the Mediterranean and the Atlantic. *La Conchiglia*, 29(285): 11-23.
- SHIOMI K., M. ISHII, K. SHIMAKURA, Y. NAGASHIMA & M. CHINO, 1998. Tigloylcholine: a new choline ester toxin from the hypobranchial gland of two species of muricid gastropods (*Thais Clavigera* and *Thais Bronni*). *Toxicon*, 36(5): 795-798.
- SHIOMI, K., Y. KAWASHIMA, M. MIZUKAMI & Y. NAGASHIMA, 2002. Properties of proteinaceous toxins in the salivary gland of the marine gastropod (*Monoplex echo*). *Toxicon*, 40(5): 563-571.
- TAYLOR, J.D., 1989. The diet of coral-reef Mitridae (Gastropoda) from Guam; with a review of other species of the family. *Journal of Natural History*, 23: 261-278.
- TAYLOR, J.D., 1993. Dietary and anatomical specialization of mitrid gastropods (Mitridae) at Rottneest Island, Western Australia. In: WELLS, F.E., D.I. WALKER, H. KIRKMAN & R. LETHBRIDGE (eds.), *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottneest Island, Western Australia* pp. 583-599. Western Australian Museum, Perth.
- TRACEY, S., J.A. TODD & D.H. ERWIN, 1993. Mollusca: Gastropoda. In: BENTON, M.J. (ed.), *The Fossil Record 2*, pp. 137-167. Chapman and Hall, London.

- VAYSSIÈRE, A., 1901. Étude zoologique et anatomique de la *Mitra zonata*, Marryatt. *Journal de Conchyliologie*, 49: 77-95.
- WEST, D., E.B. ANDREWS, A.R. McVEAN, M.C. THORNDYKE & J.D. TAYLOR, 1998. Presence of a toxin in the salivary glands of the marine snail *Cymatium intermedius* that targets nicotinic acetylcholine receptors. *Toxicon*, 36(1): 25-29.
- WEST, T.L., 1990. Feeding behaviour and functional morphology of the epiproboscis of *Mitra idae* (Mollusca: Gastropoda: Mitridae). *Bulletin of Marine Science*, 46: 761-779.
- WEST, T.L., 1991. Functional morphology of the proboscis of *Mitra catalinae* Dall, 1920 (Mollusca: Gastropoda: Mitridae) and the evolution of the mitrid proboscis. *Bulletin of Marine Science*, 48: 702-718.