

ASPECTS OF THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF *TIMOCLEA OVATA* (BIVALVIA: VENEROIDEA: VENERINAE) IN THE AÇORES, PORTUGAL, AND A COMPARISON WITH *CHIONE ELEVATA* (CHIONINAE)

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ABSTRACT

Timoclea ovata occurs in the Açorean offshore seabed down to ~200 metres depth. Here, however, it only grows to half (10 mm) the shell length of conspecifics in European continental waters. In the Açores also, *T. ovata* is drilled by a naticid predator - probably *Natica prietoi*. This is the first report of naticid drilling predation upon *T. ovata*.

The shell and the organs of the mantle cavity and visceral mass, and their ciliary currents, are described (for the first time) and compared specifically with representatives of the Chioninae (within which it was traditionally placed), including the Western Pacific *Bassina calophylla* and the Western Atlantic *Chione elevata* (also illustrated herein). Anatomically all three species are similar to each other, reflecting the inherent conservatism of the venerid *bauplan*. An interesting aspect of the complex surface architectures of the shells of *T. ovata*, *B. calophylla* and *C. elevata* is that they are not successful in protecting individuals from, in particular, naticid predation even though one supposes that this is what they are for. That is, in the predator-prey "arms race", naticids are clearly winning. Notwithstanding, the complex shell architecture may also fulfill other functions such as stabilizing these shallow burrowers in soft sediments.

In other bivalve lineages, "success" has been achieved through reproductive and/or anatomical specializations. However, the two most widely distributed and, possibly, most "successful" modern bivalve lineages are the Mytiloidea and heterodont Veneroidea that are generally but not exclusively dominant on rocky and soft marine habitats, respectively. This success has been achieved by reproductive and anatomical conservatism. Thus, one can take virtually any mytilid or any venerid and they will be, as this study demonstrates for *Timoclea ovata*, generally similar to other representatives of their respective families.

RESUMO

Timoclea ovata ocorre nos fundos costeiros dos mares dos Açores até uma profundidade de ~200 metros. Aqui, porém, cresce apenas até metade (10 mm) do comprimento de concha dos seus conspécíficos em águas continentais Europeias. Também nos Açores *T. ovata* é perfurada por um predador naticídeo - provavelmente *Natica prietoi*. Este é o primeiro registo de predação por perfuração de um naticídeo em *T. ovata*.

Descrevem-se (pela primeira vez) a concha e os órgãos da cavidade palial e massa visceral, e as suas correntes ciliares, e comparam-se especificamente com outros representantes dos Chioninae, incluindo *Bassina calophylla* do Pacífico Oeste e *Chione elevata* do Atlântico Oeste (também ilustrada aqui). Anatomicamente as três chioninas são muito semelhantes entre si, reflectindo o conservantismo inerente do *bauplan* venerídeo. Um aspecto interessante da complexa arquitectura da superfície da concha chionina, incluindo *T. ovata*, é não ser muito bem sucedida em proteger os seus representantes de, em particular, predação por naticídeos embora se pense ser esta a sua função. Isto é, na "corrida às armas" de predador-presa, os naticídeos estão claramente a ganhar. Não

obstante, a arquitectura da concha chionina pode também exercer outras funções tais como estabilizar estes escavadores superficiais nos sedimentos finos.

Noutras linhagens de bivalves, o “sucesso” foi conseguido mediante especializações reprodutivas e/ou anatómicas. No entanto, as duas linhagens de bivalves modernos mais largamente distribuídas e, possivelmente, melhor sucedidas são os Mytiloidea e os heterodontes Veneroidea que são geralmente mas não exclusivamente dominantes em habitats marinhos rochoso e mole, respectivamente. Tal sucesso foi conseguido mediante conservantismo reprodutivo e anatómico. Assim, pode tomar-se virtualmente qualquer mitilídeo ou qualquer venerídeo e eles serão, como este estudo demonstra para os Chioninae, respectivamente muito semelhantes aos seus outros representantes.

INTRODUCTION

Timoclea ovata (Pennant, 1777) was classified by Keen (1969) as a member of the Chioninae Frizzell, 1936 (Veneroidea, Veneridae), representatives of which have been studied anatomically by Ansell (1961), Jones (1979), Morton (1985) and Morton & Knapp (2004). Morton (1985) compared *Bassina calophylla* (Philippi, 1836) (Chioninae) with *Irus irus* (Linnaeus, 1758) (Tapetinae Adams & Adams, 1852). Subsequently, however, Coan *et al.* (1997) synonymized the Chioninae with the Venerinae Rafinesque, 1815. Kappner & Bieler (2006) have, most recently, and on the basis of a much broader gene sequencing study, argued, however, that the Chioninae, with *Chione cancellata* (Linnaeus, 1767) as its type species, is a distinct entity from the Venerinae as proposed by Canapa *et al.* (2003). Kappner & Bieler (2006), however, have also demonstrated that *Timoclea* Brown, 1827 should be placed within the Venerinae and not within the Chioninae.

Ansell (1961) compared the anatomy of the British species of Veneracea (Veneroidea) but, surprisingly, had little to say about *Timoclea* (as *Venus*) *ovata* noting only that, in common with *Gaffarium minimum* (Montagu, 1803), the inner apertures of the siphons possessed membranes that, in the case of the inhalant, directed the incoming water dorsally

(Figure 5B). Jones (1979) compared the anatomy of *Chione cancellata* (Linnaeus, 1767) with those of other chionines. Morton & Knapp (2004) re-examined some aspects of the anatomy of the Atlantic *C. elevata* and compared it with the Pacific *Bassina calophylla*, specifically with regard to how the shell architecture, in particular, protects (or rather does not) the contained animal from drilling predators of the Naticidae.

Timoclea ovata has a wide distribution from northern Norway and Iceland south to Angola (West Africa). It is also recorded from the Canary Islands, the Açores and the Mediterranean and Black Sea. Despite this wide distribution there is, as noted above, little known about the anatomy of *T. ovata* and little also about its basic biology. Labrune *et al.* (2007) described changes in the species composition of the macrofauna of the Bay of Banyuls-sur-Mer in the Mediterranean between 1967 and 2003 noting that the greatest changes were in the *T.* (as *Venus*) *ovata* community between 1967-1968 and 1994. The size frequency distribution of a population of *T. ovata* from the Pliocene of Volpedo, Italy, was described by Benigni & Corselli (1981) and Dauvin (1985) undertook a study of the population dynamics of a Recent population of the same species from the Bay of Moraix in the Mediterranean noting there to be pluri-annual variations in recruitment, growth and production, thereby explain-

ing the observations of Labruno *et al.* (2007). Anfossi & Brambilla (1981) noted that *T. ovata* has been a member of the Mediterranean's detrital biocenosis since at least the Pleistocene. In terms of predation, only Mienis (2003) has noted that the starfish *Astropecten aranciacus* (Linnaeus, 1758) preys upon *T. ovata*.

This study was the first to be undertaken on *Timoclea ovata* in the Açores, a species initially recorded from there by Morton (1967). The study's aims were three fold: (i), to obtain support for (or not) the proposal of Kappner & Bieler (2006) that *T. ovata* should be placed in the Venerinae; (ii), to document information on the biology of this species in the remote mid-Atlantic Açores and (iii), to provide a picture of its anatomy that might explain facets of its biology and give clues to the success of the venerid *bauplan*.

MATERIALS AND METHODS

Biology

For ten days from 17-26 July 2006, the sea bed off the southern coast of the island of São Miguel, Açores, was sampled using a benthic box dredge at six stations to the east and west of Ilhéu de Vila Franca do Campo. Station details are described by Martins *et al.* (2009). Station depths ranged from -50 to -250 metres C.D.. All living and empty shells of *Timoclea ovata* (plus any living naticids) were sorted from the samples. These were analyzed in the following manner.

Living individuals of *Timoclea ovata* were measured along their greatest lengths using vernier calipers to the nearest 0.5 mm. Empty shell valves were identified and both left and right ones were measured in the same manner. Empty valves were also examined for drill holes. Where these were encountered, the following records were made

of: (i), which valve and (ii), the location of each drill hole was plotted on master illustrations of the left and right valves.

Statistical analyses

The dataset comprising the numbers of living, empty and drilled shell valves of *Timoclea ovata* among the six stations was tested for normality and homogeneity of variances using the Shapiro-Wilk test and Levene statistic, respectively, both at the $p = 0.05$ level of significance before ANOVA. One-way ANOVA's were performed on the dataset to test the null hypothesis that there were no significant differences in these variables among locations. Where differences were detected, Student's Newman-Keuls (SNK) tests were carried out to identify where the differences lay. The shell lengths of living *T. ovata* and empty and drilled valves were also compared using a one-way ANOVA and the Student's Newman-Keuls (SNK) test.

Anatomy

Living individuals of *Timoclea ovata* were observed alive in aquaria. Other living animals were dissected and drawings made of the anatomy, notably the organs of the mantle cavity. The ciliary currents in the mantle cavity were detected using a suspension of carmine in seawater. Living individuals of *Chione elevata* from Florida were also examined in the same way.

RESULTS

Biology

Living individuals of *Timoclea ovata* were collected from all six stations and there was no significant difference in the numbers collected between them. Figure 1 illustrates length frequency histograms for A, living individuals, B and C, empty left right shell valves, respectively, and D

and E, drilled left and right shell valves, again respectively. Living shells ranged in shell length from 1.5 mm to 9.0 mm, as did, approximately, the empty and drilled valves. One empty right valve was 10 mm in length.

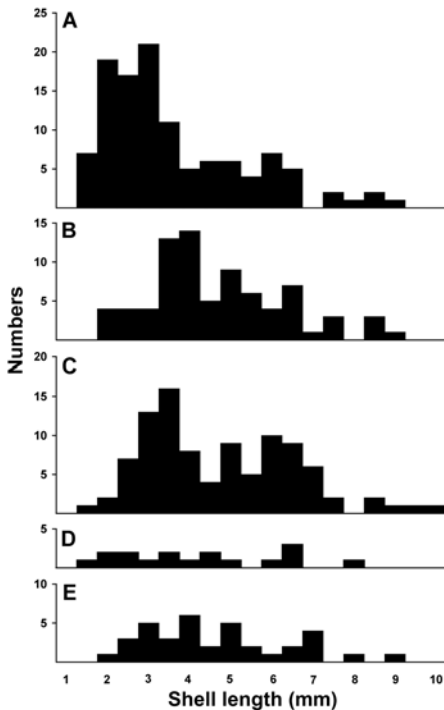


FIGURE 1. *Timoclea ovata*. Five histograms showing the size distributions of A, living individuals; B, empty left and C, right shell valves; C, and D, drilled left and right shell valves, respectively.

The results of the ANOVA show that there were significant differences between the collected *Timoclea ovata* shells of the various categories, that is, living, empty and drilled valves, in term of their mean shell lengths ($F = 6.96$, $p < 0.0001$). However, the results of the *post hoc* Student-Newman-Keuls (SNK) test for

shell length showed that the valves of empty and drilled individuals, irrespective of whether they were the right or left valves, did not significantly differ in terms of mean shell length ($p > 0.05$) whereas the valves of living individuals were significantly smaller than the empty valves (except for the drilled left valves, probably due to the small sample size).

Figure 2 shows outline drawings of the left and right shell valves and the numbers and the distribution pattern of naticid drill holes made in them. There were over twice as many in the right ($n=33$) as in the left ($n=15$) valves and the pattern of distribution was unusual in that they were not near the umbones (an often favoured location for drilling gastropod predators, as will be discussed). Rather, they seemed to be located mostly over the position of the pallial line, that is, where the thick, recessed, mantle edge is united to the shell internally.

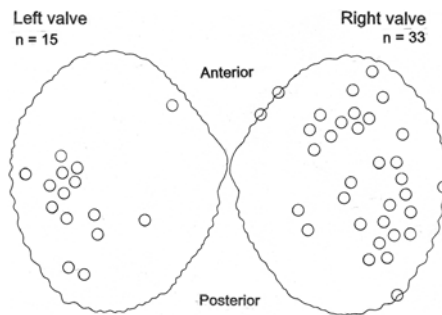


FIGURE 2. *Timoclea ovata*. The distribution pattern of naticid drill holes made in the left and right shell valves.

Anatomy

The shell

The shell of *Timoclea ovata* is illustrated in Figure 3 from various perspectives. In general terms, the shell is equivalve and approximately equilateral, and thus (also approximately) isomyarian, but pointed

posteriorly, so that the beaks are distinctly prosogyrate (Figure 3A) and result from a strong tangential pattern of growth. This gives the shell its equilateral shape that increases during ontogeny so that the juvenile is more oval, the adult more angular.

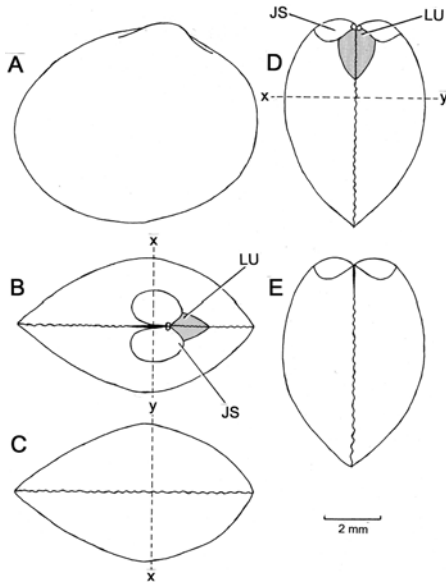


FIGURE 3. *Timoclea ovata*. Five stylized views of the shell and illustrated from A, the right side; B, dorsally; C, ventrally; D, anteriorly and E, posteriorly. (x—y is the approximate position of the greatest width to the shell.) For other abbreviations see page 119.

In dorsal view (Figure 3B), there is a small anterior, heart-shaped, lunule (LU) (as defined by Carter, 1967) each valve here also interlocking by means of marginal denticles as in *Chione elevata* (Morton & Knapp, 2004). Unlike other venerids, however, the lunule is not well defined because it is sculptured like the remainder of the shell but is defined by a light indentation and is coloured slightly differently. The more oval juvenile shell

(JS) is also illustrated. There is no distinct posterior escutcheon because the ligament is internal, although it can be seen as a thin, black, line extending posterior to the umbones about one quarter of the way towards the posterior margin. The ventral shell valve margins (Figure 3C) are interlocked virtually everywhere along the extent of the shell margin by the expanding radial ribs. The shell valves of *T. ovata* are thus very difficult to separate, again like those of *C. elevata* (Morton & Knapp, 2004). Figures 3B & C also show the approximate position of the greatest shell width (x-y). It lies just posterior to the umbones above the ligament.

The shell is illustrated in anterior view in Figure 3D and again shows the lunule (LU) and juvenile shell (JS). The greatest width to the shell when seen from this perspective (x-y) is dorsal to the mid point of the dorso-ventral height of the shell. A similar situation is seen when the shell is illustrated from the posterior perspective (Figure 3E).

The shell of *Timoclea ovata* is illustrated in internal view in Figure 4A. The left valve (Figure 4A) has a hinge plate with an elongate posterior cardinal tooth and two other larger teeth more centrally placed. These are here interpreted as a central cardinal and robust anterior (but more centrally located, unlike the elongate posterior cardinal tooth) cardinal tooth, all arising from the umbo (U). There are no lateral teeth. The ligament (L) is internal and opisthodontic. Also well defined are anterior (AA) and a larger posterior (PA) adductor muscle scars. These are connected by a thick pallial line (PL) that has a similarly thick, short, pallial sinus (PS). Both are deeply inset from the valve margin and this is characterized by a scalloped edge internal to which, extending virtually all the way round are marginal denticles (MD) that interlock with those of the other valve. The interi-

or of the shell is polished and is typically white although in those individuals with an external coloration, the interior reflects this as an orange-lilac stain. The hinge plate of the right valve similarly also has three (a central cardinal, elongate posterior or lateral and more central and robust anterior lateral) teeth (Figure 4B).

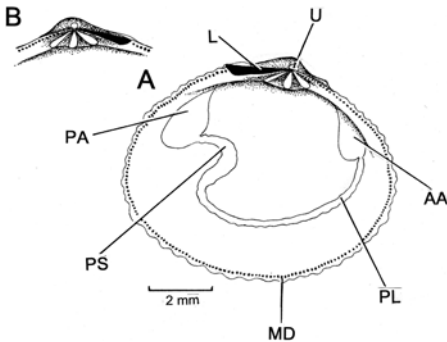


FIGURE 4. *Timoclea ovata*. A, An interior view of the left shell valve and B, an interior view of the right hinge plate. For abbreviations see page 119.

The external appearance of the shell is illustrated from the right side in Figure 5. Each valve has a stout sculpture of ~50 ribs that radiate from the umbones and because each valve has strong commarginal lamellae too, there are nodes on the ribs giving the shell a rough, file like, feel to the touch. As noted above the shell is often uniformly coloured light brown although those of most individuals are patterned with streaks and blotches of pink, red or brown. And some individuals have two radiating (antero- and postero-ventrally) bands of pigmentation, as illustrated in Figure 5.

Tebble (1966) records that *Timoclea ovata* has a maximum shell length of 19 mm while Dauvin (1985) identified a figure of 15.1 mm for this species in the Mediterranean. As noted above, how-

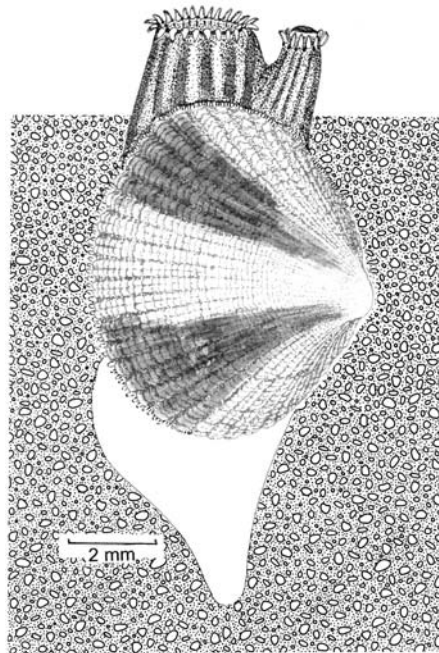


FIGURE 5. *Timoclea ovata*. An individual illustrated in its life position in the sediment.

ever, the largest Açorean individual collected had a shell length of but 10 mm.

The siphons

A living individual of *Timoclea ovata* is illustrated in Figure 5 from the right side.

Anteriorly, there is a large digging foot. Posteriorly, there is a pair of separated siphons. The exhalant siphon is conical and a ring of 12 short tentacles sub-apically surrounds its transparent cone-shaped aperture. About 12 yellow-brown stripes arise from between each tentacle and extend inwards. The inhalant siphon is much larger in diameter and is fringed apically by a cirlet of ~24 long siphonal tentacles. As with the exhalant about 24 yellow-brown stripes extend inwards. Where each stripe unites with the tentacular rings, there is a darker brown spot.

Mid-ventrally, the mantle possesses a line of papillae and pallial fusions, where they occur, are of the inner folds only, that is, type A (Yonge, 1982). The siphons are illustrated in greater detail in Figure 6.

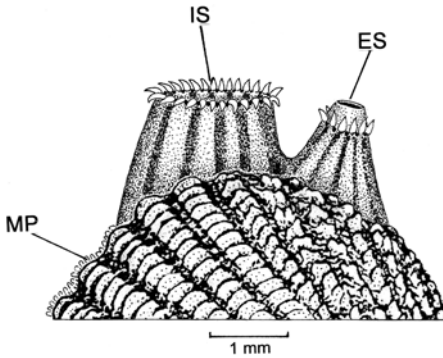


FIGURE 6. *Timoclea ovata*. A detail of the siphons.

The ciliary currents of the organs of the mantle cavity

The ciliary currents of the left mantle lobe of *Timoclea ovata* are illustrated in Figure 7. The pallial currents sweep particles of material in a clockwise direction towards the antero-dorsal regions of the mantle cavity and then downwards, so that particles end up in a ventral marginal rejection tract that transports such unwanted material towards the base of the inhalant siphon (IS) where it accumulates as balls of pseudofaecal matter (PM). These little balls are periodically ejected from the mantle cavity, via the inhalant siphon, by sharp contractions of the adductor muscles that create the pallial pressure necessary to do so.

The right ctenidium of *Timoclea ovata* is illustrated in Figure 8A. Each ctenidium is homorhabdic, eulamellibranchiate and comprises two unequal demibranchs. The inner demibranch (ID) is large and extends anteriorly from beneath the pos-

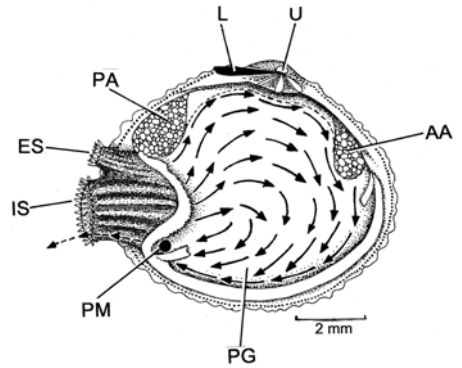


FIGURE 7. *Timoclea ovata*. The ciliary currents of the left mantle lobe after removal of the left shell valve and mantle and the body. For abbreviations see page 119.

terior adductor muscle (PA) up into the sub-umbonal cavity and ends on the postero-ventral face of the anterior adductor muscle (AA). The outer demibranch (OD) is dorso-ventrally short and, as with the inner, extends anteriorly from beneath the posterior adductor muscle to a position just posterior of the hinge plate, beneath the ligament (L). This demibranch is thus foreshortened anteriorly.

The ciliary currents of the right ctenidium are illustrated in transverse section in Figure 8B. The ciliary currents are of Type C (1) (Atkins, 1937), typical of many eulamellibranchs and, specifically, *Venus fasciata* (da Costa, 1778), *Dosinia lupinus* (Linnaeus, 1758), *Venerupis aurea* (Gmelin, 1791) and *Venerupis rhomboides* (Pennant, 1777) (Ansell, 1961). Ctenidia with a ciliation of type C (1) have oralward acceptance tracts located in the ctenidial axis and in the ventral marginal food groove of the inner demibranch (ID) only. Hence, particles filtered by the ascending lamella of the outer demibranch (OD) pass downward (although some may dorsally be carried anteriorly) (Figure 8A) and on reaching the ventral margin of this demi-

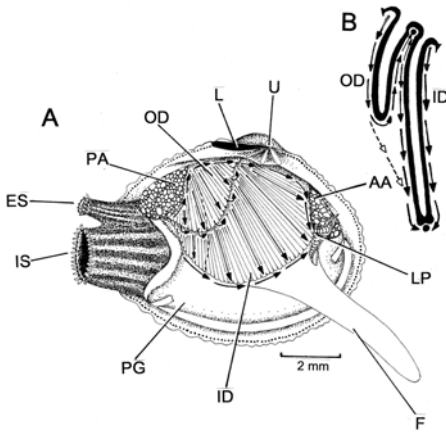


FIGURE 8. *Timoclea ovata*. A, The ciliary currents of the ctenidium as seen from the right side after removal of the right shell valve and mantle. B, A diagrammatic transverse section through the right ctenidium showing the ciliary currents. For abbreviations see page 119.

branch, turn, and pass upwards on the descending lamella towards the ctenidial axis. In the food groove of the ctenidial axis they pass anteriorly. Ciliary currents on the inner demibranch are largely downward towards the ventral margin that has an anteriorly directed food groove. Because the outer demibranch is anteriorly foreshortened, at its anterior terminus, particles arriving here in the ctenidial axis pass on to the descending lamella of the inner demibranch. Thus, particles arrive at the ctenidial labial palp junction in (i), the ventral marginal food groove of the inner demibranch and (ii), in the ctenidial axis tract, also of the inner demibranch.

The ctenidial-labial palp junction is of Category II (Stasek, 1964) and the palps (LP) are small, each possessing no more than five pleats that would, in the typical bivalve, have a sorting function, either accepting or rejecting particles of possible

food according to size. Only those particles passing directly into the oral grooves of the palps from the acceptance tracts in the ctenidial axes, an arrangement that characterizes bivalves with a ctenidial/labial palp junction of Category II (Stasek, 1964), are forwarded directly to the mouth. The reduced size and sorting ability of the labial palps may be a reflection of the low numbers and narrow size limits of particles in the Açorean waters of the mid-Atlantic. Similarly, small labial palps have been recorded for *Fragum erugatum* (Tate, 1889), an inhabitant of oligotrophic, high salinity waters in Australia (Morton, 2000). Throughout its wide geographical range, however, *T. ovata* may occur in a variety of sediment types although it seems to prefer well-sorted gravels, as in the Açores, in which case the small labial palps are an adaptation to sediments and overlying waters low in particulates.

The ciliary currents of the right side of the visceral mass of *Timoclea ovata* are illustrated in Figure 9. On the surface of the right side of the visceral mass, the ciliary currents move material in a clockwise direction, anteriorly above and posteriorly below. Eventually, all such currents become directed downwards and feed into a rejection tract that passes accumulated material posteriorly where it falls off the posterior edge of the visceral mass onto the mantle. Ciliary currents on the foot (F) also pass material into this rejection tract. Particles that fall off the visceral mass are subjected to the ciliary currents of the mantle (Figure 7).

Also illustrated in Figure 9 are some details of the structure of the visceral mass. Below and just posterior to the hinge plate, below the ligament (L), there is a heart (H) and posterior to this the brown, paired, kidneys (K). Anterior to the hinge plate is the dark brown digestive diverticula (DD). The gut has not

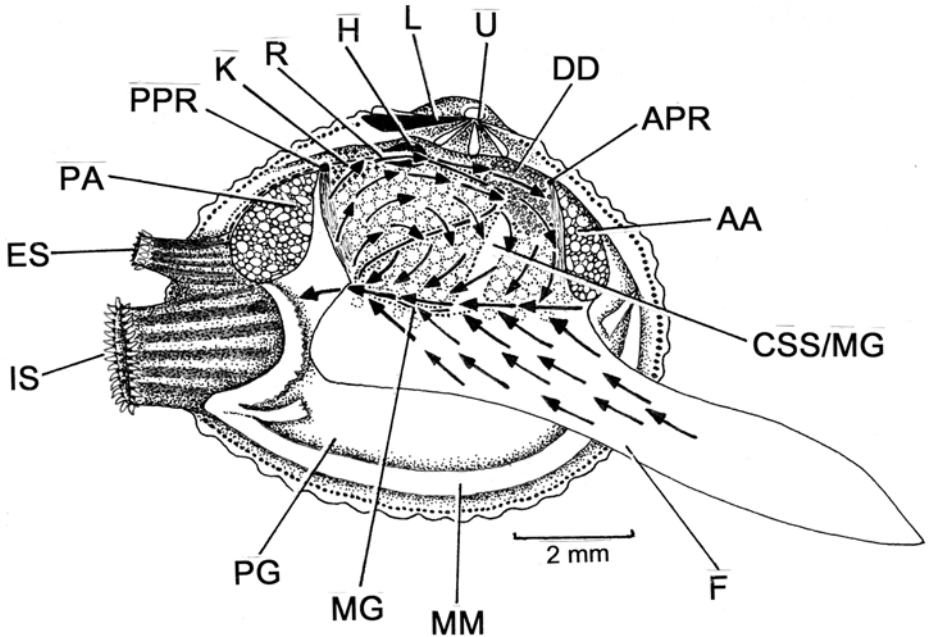


FIGURE 9. *Timoclea ovata*. The ciliary currents of the right side of the visceral mass after removal of the right shell valve, mantle and ctenidium. Also illustrated are some details of the structure of the visceral mass. For abbreviations see page 119.

been examined in detail, but a conjoined style sac and mid gut (CSS/MG) leaves the postero-ventral edge of the stomach and passes postero-ventrally into the visceral mass. Eventually, the extremely thin mid gut (MG) separates from this and makes a single, simple loop upwards back towards the stomach but then passes posteriorly, penetrating the ventricle of the heart as the rectum (R) which passes over the posterior adductor muscle (PA) to terminate on its posterior surface as an anus.

A final anatomical point is that, surprisingly, the pedal retractor muscles are minute. The posterior pedal retractor muscle (Figure 9, PPR) is located next to the antero-dorsal edge of the posterior adductor (PA) while the anterior pedal retractor muscle (APR) is even smaller

and located on the postero-dorsal edge of the anterior adductor muscle (AA). I use the word 'surprisingly' above, because, despite these tiny muscles, the foot is further surprisingly, very active. Hence, its movements must be largely related to hydrostatically induced pressure changes, as will be discussed.

Comparison with *Chione elevata*

Aspects of the anatomy and the ciliary currents of the ctenidium of *Chione elevata* are illustrated in Figure 10 and as seen from the right side after removal of the right shell valve and mantle. This drawing should be compared with the corresponding one for *Timoclea ovata* (Figure 8). In *C. elevata*, the shell has a lunule (L) beneath which are located interlocking denticles. The shell also has interlocking

valve margins and there are three hinge teeth in each valve, that is, what is here interpreted as anterior (ALT) and posterior lateral (PLT) and a large central cardinal teeth (CT). Jones (1979) also identifies three teeth in each valve of *Chione cancellata* (Linnaeus, 1767), *C. paphia* (Linnaeus, 1767) and *C. undatella* (Sowerby, 1835) but refers to them as anterior, central and posterior cardinal teeth, as described above for *Timoclea ovata*.

Internally, *Chione elevata* has anterior (AA) and posterior (PA) adductor muscles and anterior (APR) and posterior (PPR) pedal retractor muscles that are larger than those of *Timoclea ovata*. There is an extensive pedal gape (PG) as in *T.*

ovata, a large digging foot (F) and a mantle margin (MM) lined with mantle papillae (MP), all, again, as in *T. ovata*. The inhalant (IS) and exhalant (ES) siphons of *C. elevata* are very similar in structure to those of *T. ovata* and both have similarly organized ctenidia with ciliary currents of Type C (1) (Atkins, 1937). Both, therefore, have ctenidial-labial palp junction of Category II (Stasek, 1964). The labial palps of *C. elevata* are relatively larger than those of *T. ovata*, possibly because it inhabits shallow coastal waters off Florida, U.S.A..

In conclusion therefore *Chione elevata* and *Timoclea ovata* are similar anatomically, even though gene sequencing places

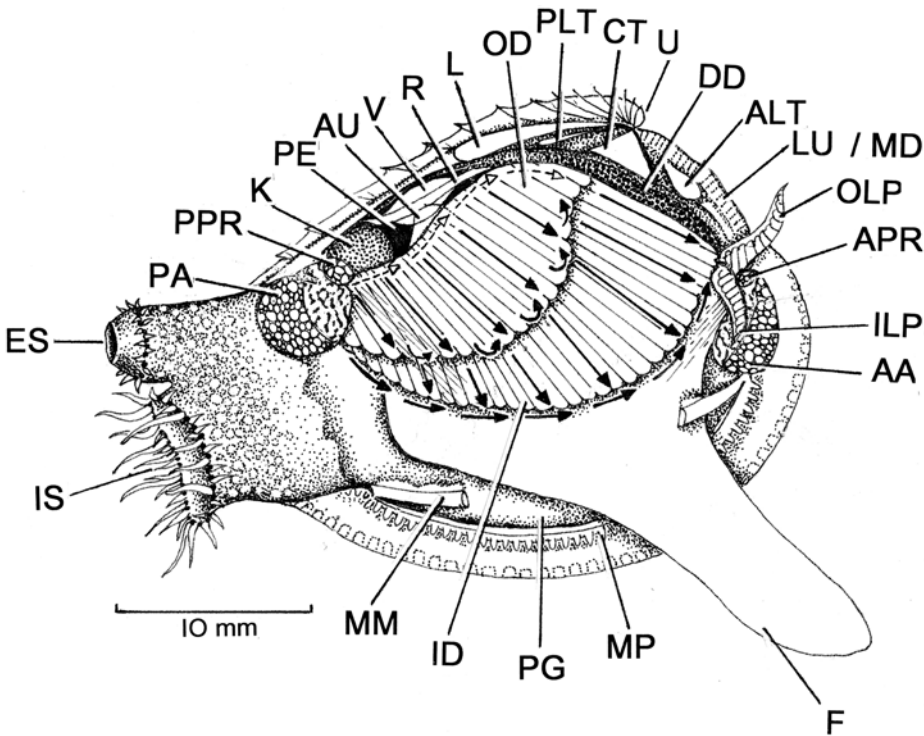


FIGURE 10. *Chione elevata*. The ciliary currents of the ctenidium as seen from the right side after removal of the right shell valve and mantle. For abbreviations see page 119.

them in two different sub-families, that is, the Chioninae and Venerinae, respectively (Kappner & Bieler, 2006). Importantly, such similarities now suggest convergence between the two thick-shelled and surface ornamented genera demonstrating the success, at least in part, of the veneroidean body plan as a whole and which seems to be based around anatomical conservatism.

DISCUSSION

Poppe & Gotto (1993) record a depth distribution of between 4 m to 200 m for *Timoclea ovata*, as does Tebble (1966), approximately. It is thus unsurprising that no differences in population numbers were recorded with depth from the Açorean dredge samples (50-200 m). Poppe & Gotto (1993) similarly note that *T. ovata* individuals from the northern part of the species' range are larger than southern conspecifics. This may explain why the *T. ovata* individuals from Açorean waters are small (half the length of northern conspecifics), but it may also be because of the low levels of nutrients available to this species in the depauperate waters of the central Atlantic.

Very little is known about the predator-prey relationships of the Açorean marine fauna (Morton *et al.*, 1998). In terms of the predatory gastropods, on rocky shores in the Açores, *Thais haemastoma* (Linnaeus, 1767) drills the intertidal mussel *Gregariella semigranata* (Reeve, 1858) at the posterior margin (Morton, 1995a). In Europe, Ansell (1960, 1982) demonstrated that *Polinices alderi* (Forbes, 1838) drilled the bivalves *Venus striatula* da Costa, 1778 and *Tellina tenuis* (da Costa, 1778) whereas in the Açores, *P. alderi* attacked the commonest shallow subtidal bivalve, *Ervilia castanea* (Montagu, 1803), by drilling in a stereotypical, posterior, position (Morton, 1990a).

Morton & Harper (2009) have studied the drill holes made in the tubes of the serpulid polychaete *Ditrupa arietina* (O.F. Müller, 1776) from depths of 50-200 metres in the Açores and concluded that the only predator present in the samples from which the tubes were collected was *Natica prietoi* Hidalgo, 1873, formerly identified as *Natica adansonii* de Blainville, 1825. Since the specimens of *Timoclea ovata* reported upon here came from the same dredge samples it seems possible (likely) that *N. prietoi* made the holes in the shell of this species too. Confirmation of this is, however, required.

Notwithstanding, Kabat (1990) has reviewed the literature on naticid predation and there are no records of *Timoclea ovata* as prey. This is thus the first record of naticid predation, possibly by *N. prietoi* on *T. ovata*, although Vermeij (1980) reports that *Timoclea marica* (Linnaeus, 1758) is drilled (laterally, as with *T. ovata*) by an unknown gastropod in Guam.

Morton & Knapp (2004) identified an almost equal distribution of drill holes (and attempts) between the two valves of *Chione elevata*. Most of the drill holes were distributed around the postero-dorsal region of the shell and there were few failed drill holes. Finally, only a very few of the drill holes were over the shell lamellae and were at inter-lamellar spaces. That is, if the lamellae have evolved as anti-predation devices, they are not very successful, in this case from the naticid *Naticarius carrena* (Linnaeus, 1758). This is not the case with the also heavily sculptured *Bassina calophylla* (Chioninae) in the Indo-West Pacific (Ansell & Morton, 1985; 1987), where the shell lamellae do protect the bivalve inhabitant, except from species of edge drilling naticids, that is, *Polinices tumidus* (Swainson, 1844) and *Polinices melanostomus* (Gmelin, 1791).

Timoclea ovata has a shell that, superfi-

cially, would appear to offer much protection against drilling predators. Protective characteristics include a relatively stout shell with tightly fitting valve margins, ventrally interlocking ribs, similarly interlocking denticles that occur all around the valve margins and large hinge teeth. Each adductor muscle is also large, facilitating sustained adduction and the pallial line is deeply inset within the shell margin. A thick shell characteristically protects bivalves from drilling predators, for example, *Corbula crassa* Hinds, 1843 in Hong Kong (Morton, 1990b), although Borzone (1988) showed that a species of *Polinices*, as demonstrated here for *N. prietoi* Hidalgo, 1873 and *T. ovata*, selectively drilled its prey, *Venus antiqua* King & Broderip, 1831, in the thickest region of the shell, that is, umbonally. *Natica catena* (da Costa, 1778) similarly bores its prey, the subtidal *Donax vittatus* (da Costa, 1778) around the umbones (Negus, 1975).

The anatomies of various representatives of the Chioninae have been described. These include *Bassina calophylla* (Morton, 1985) and *Chione elevata* (formerly identified as *C. cancellata*) (Jones, 1979; Morton & Knapp, 2004) while Ansell (1961) has described the anatomies of the representatives of the Veneridae (including a little about *Timoclea ovata*) that occur in British waters. The most obvious feature of the studied representatives of the Veneridae is their anatomical conservatism. Hence, illustrations of the ctenidia within the mantle cavity of *T. ovata* (Venerinae), and *C. elevata* (illustrated herein: Figs 8 & 10, respectively) and *B. calophylla* (Morton, 1985, fig. 10) (Chioninae) are virtually identical, differing only in labial palp size. It is well known that palp size in the Bivalvia is related to the degree of sorting necessary for the particle load in the inhalant stream. Thus, the Hong Kong continental shelf species *B. calophylla* has large palps,

the Floridian *C. elevata* has intermediate sized palps (Figure 10) while *T. ovata* has tiny palps (Figure 8). That is, because of high nutrient loading in continental shelf waters, *B. calophylla* needs big palps to reject a surfeit of unwanted particles whereas, oppositely, *T. ovata* in mid-Atlantic waters has little need to reject anything and has tiny palps. *Timoclea ovata* has also, for the same reason, a short, narrow, mid-gut.

Morton (1995b) pointed out that the two most widely distributed and, possibly, most "successful" modern bivalve lineages are the Mytiloidea and heterodont Veneroidea that are generally but not exclusively dominant on rocky and soft marine habitats, respectively. This has been achieved by reproductive (virtually all representatives being broadcast spawners) and anatomical conservatism. Thus, one can take virtually any mytilid or any venerid and they will be, as this study demonstrates for *Timoclea ovata*, similar to the other representatives of each order. In other bivalve lineages, more limited "success" has been achieved through reproductive and/or anatomical specialisms (Morton, 1995b). But the true inheritors of the bivalve *bauplan* are the modern Mytiloidea and Veneroidea.

One interesting aspect of this "success", however, is that, as discussed here, the complex surface architectures of the shell of the chionine *Chione elevata* and the venerine *Timoclea ovata* have not been successful in protecting representatives from, in particular, naticid predation even though one instinctively supposes that that is what it is for. That is, in the predator-prey "arms race", naticids are clearly winning but the chionine shell architecture may also fulfill other functions such as the stability of the shallow burrowing *Timoclea ovata*, and other chionines, in soft sediments – a habitat that their shell architectures suit them ideally to.

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ABBREVIATIONS USED IN THE FIGURES

AA	Anterior adductor muscle or scar
ALT	Anterior lateral tooth
APR	Anterior pedal retractor muscle
AU	Auricle (of heart)
CSS/MG	Conjoined style sac and mid gut
CT	Cardinal tooth
DD	Digestive diverticula
ES	Exhalant siphon
F	Foot
H	Heart
ID	Inner demibranch
ILP	Inner labial palp
IS	Inhalant siphon
JS	Juvenile shell
K	Kidney
L	Ligament
LP	Labial palp
LU	Lunule
MD	Marginal denticles
MG	Mid gut
MM	Mantle margin
MP	Mantle papillae
OD	Outer demibranch
OLP	Outer labial palp
PA	Posterior adductor muscle or scar
PG	Pedal gape
PL	Pallial line
PLT	Posterior lateral tooth
PM	Pseudofaecal mass
PPR	Posterior pedal retractor muscle
PS	Pallial sinus
R	Rectum
U	Umbo
V	Ventricle (of heart)