Tonicella marmorea (O. Fabricius, 1780)

Images: 1 to 54 *T. marmorea*; 60 to 72 similar species. (No images 55 to 58)

Authors: Ian F. Smith (text), Paula Lightfoot and Simon Taylor.

Meaning of scientific name: *marmorea* (Latin) = resembling marble
Synonyms: *Chiton marmoreus* O. Fabricius, 1780; *Chiton ruber (non* Linnaeus, 1767) Spengler, 1797; *Chiton laevigatus* Fleming, 1813; *Chiton latus* Lowe, 1825.
Vernacular: Mottled red chiton; Marbled mail-shell; Lleuen fraith y graig (Welsh); Chiton rouge marbré (French); Marmorierte Käferschnecke (German); Marmorleddsnegl (Norwegian); Marmoreret skallus (Danish).

GLOSSARY, BELOW, uses the standardised terminology for chitons proposed by Schwabe (2010). Some of Jones & Baxter (1987) alternatives are indicated in the glossary as a.k.a.

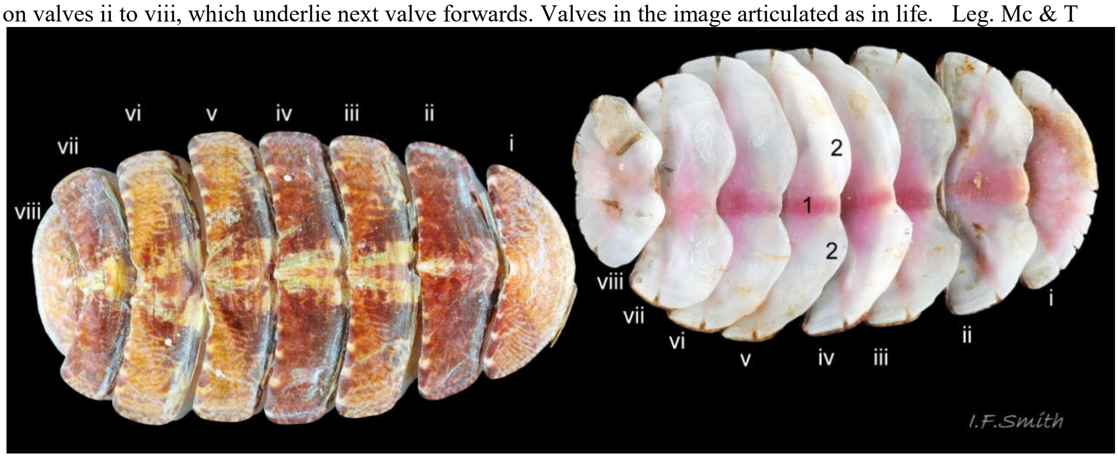
Shell Description

Low form in N.E. Atlantic up to 45 mm long and 27 mm wide (fig. 1). High form in N.W. Atlantic up to 37 mm long and 20mm wide (Kaas & Belle, 1985). In dorsal view, outline elliptical, larger specimens generally more strongly curved than smaller ones; width about 60% of length. Narrow **girdle** (total of two sides) occupies between 12% and 35% of animal width, specimens over 20 mm length generally having the proportionally wider girdles (Baxter & Jones, 1986).

figure 1 https://flic.kr/p/2gz9Ndp Girdle and valves seem smooth, except near-rectangular growth lines.

Leg. Mc & T.

figure 2 https://flic.kr/p/2gzajx3 Girdle and body removed except transverse muscles which connect the valves. i = head valve, viii = tail valve. **Left:** upper layer, tegmentum, made of coloured aragonite. **Right:** lower layer, articulamentum, made of white aragonite with pink jugal tract (**1**) and anterior curved extensions, apophyses, (**2**) on valves ii to viii, which underlie next valve forwards. Valves in the image articulated as in life. Leg. Mc & T



Eight overlapping **valves** (fig. 2) have an upper coloured layer, **tegmentum**, of aragonite, and a lower layer, **articulamentum**, of white (fig. 3) or, sometimes on jugal tract, pink (figs. 2 & 4) or yellow (fig. 5) aragonite. There are also an uppermost layer, **properiostracum**, and a discontinuous lowermost layer, **myostracum**, which are so thin and transparent as to be unnoticeable.

figure 3 https://flic.kr/p/2gzaj8q Lower layer, articulamentum, of white aragonite projects forwards on valves ii – viii as a pair of curved, wide, short (front to rear) apophyses (**1**) separated by a narrow jugal sinus (gap, **2**) that is less than 25% width of an apophysis. At ends of valves, lateral muscles, one on each side of the slit, connect to the foot, leaving an opaque scar when removed (**3**). On valves ii – viii, muscles attached to jugal sinus connect obliquely to body wall under preceding valve on which they leave comma shaped scars (**4**). Leg. Mc & T.

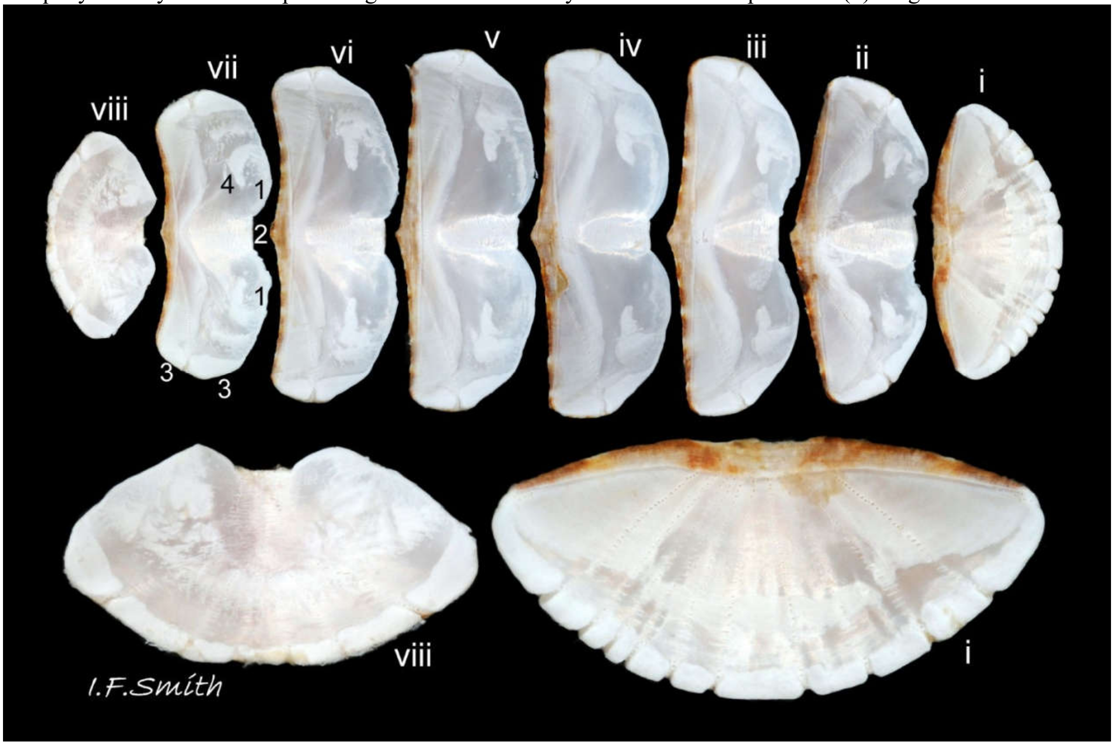


figure 4 https://flic.kr/p/2gzaiL8 Pink jugal tract (**1**). Tegmentum on valves ii –vii has slightly rounded ends (**2**), and nearly straight, parallel anterior and posterior margins, except anterior of valve ii which projects more at its jugum (**3**). Apophyses on valve ii more angular (**4**); smaller and more angular on valve viii (**5**). Leg. Mc & T.

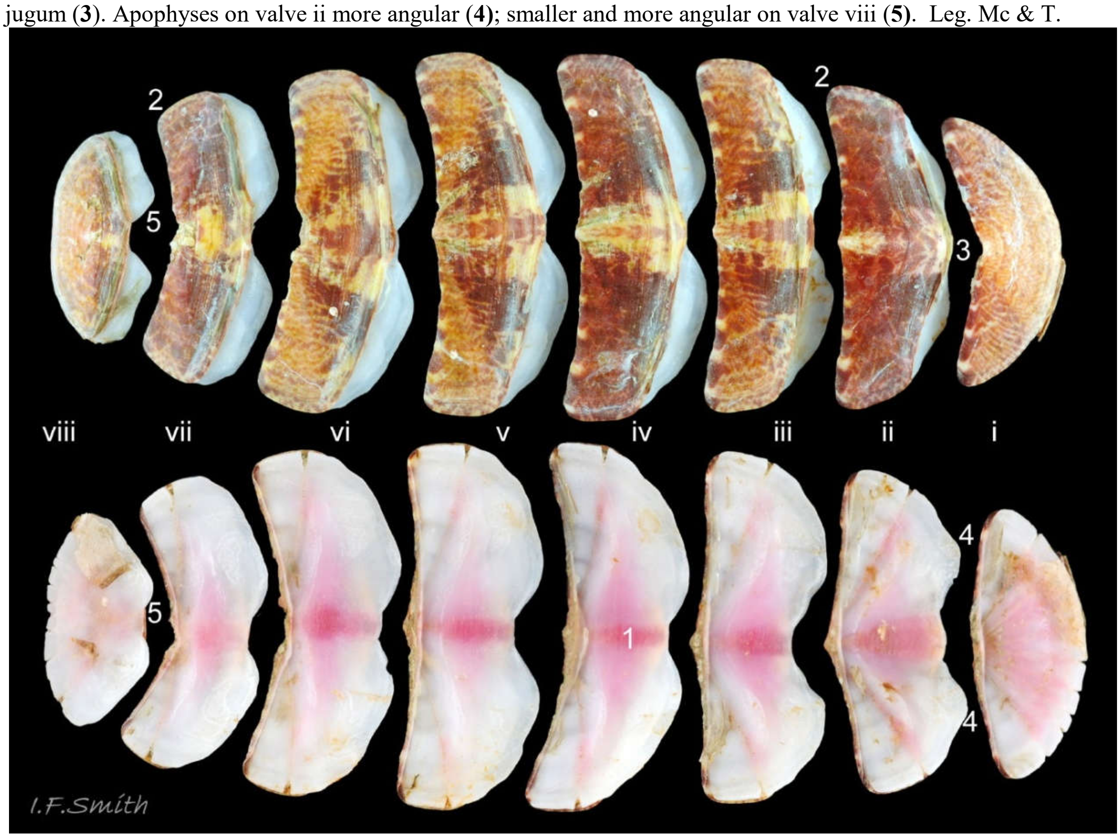
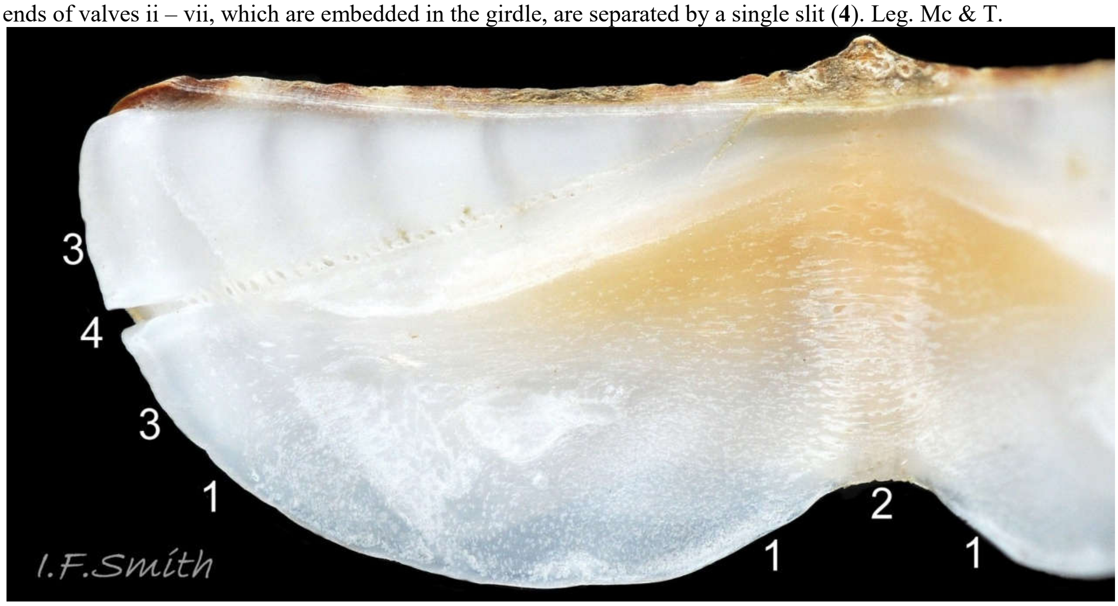


figure 5 https://flic.kr/p/2gzaipX White articulamentum with yellow jugal tract. Wide curved apophyses (**1**) are separated by a narrow jugal sinus (gap, **2**) that is less than 25% width of an apophysis. Insertion plates (**3**) on the ends of valves ii – vii, which are embedded in the girdle, are separated by a single slit (**4**). Leg. Mc & T.



Dorsal surface (tegmentum) of valves appears smooth to naked eye apart from near-rectangular, distinct, growth lines (figs. 1 & 6)

figure 6 https://flic.kr/p/2gzaifJ Apart from near-rectangular, distinct growth lines, dorsal surface of valves seems smooth to naked eye, but at over X3 numerous small granules visible on cleaned, dry valve (see fig. 18). Steep slope (**2**) behind mucro (**1**) on valve viii is straight in lateral profile. Insertion plates at the ends of the valves are embedded into the peripheral girdle. The cuticle on the dorsal surface of the girdle appears leathery-smooth to the naked eye, but strong magnification shows a covering of very small spicules (see figs. 40 & 41). Leg. Mc & T.

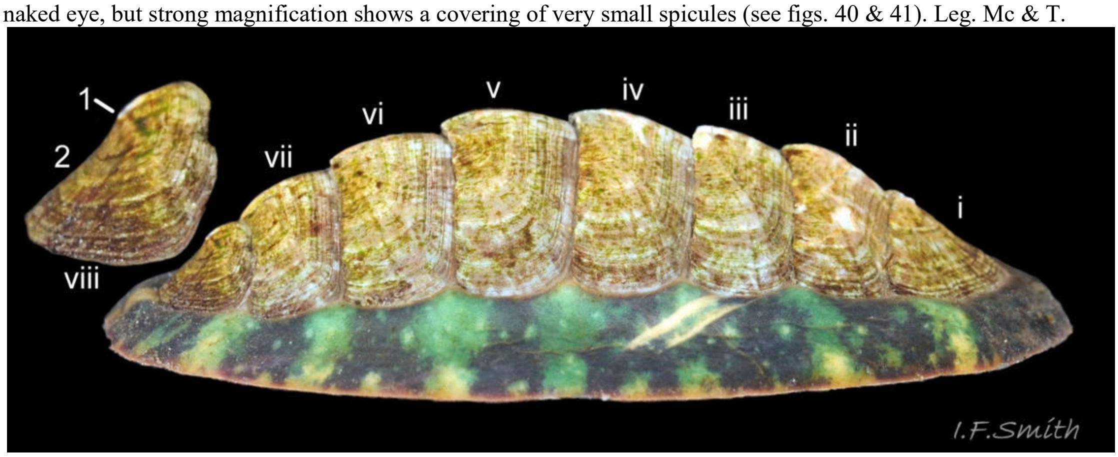


figure 7 (left) https://flic.kr/p/2gz9KP1 Valves have various colours arranged in blotches or zig-zags. Valves ii to vii have posterior beaks. Head valve (**i**) almost semicircular, with a shallow V posterior edge. Dorsally, girdle is yellowish with purplish band at ends of valves ii to vii, and several bands by valves i and viii. Girdle is overcast with distinctive verdigris-green. Leg. D. M. McKay & S. Taylor.

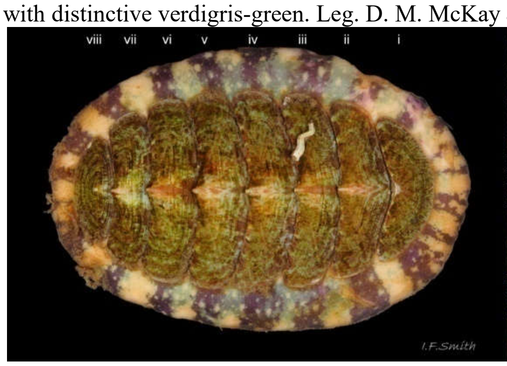


Figure 8 (right) https://flic.kr/p/2gz9Khz Beaks eroded on this one. Approximately triangular patches of lighter colours on the jugal areas. Valves ii and iv often, and vii sometimes, are darker than other valves. © P. Lightfoot.

Colour of valves variable; white, cream, brown (fig. 7), red (fig. 8) and ochre arranged in blotches or intricate zig-zags (fig. 9). Rarely, entirely marmorated. Frequently, approximately triangular patches on the jugal areas have lighter colours (fig. 8). Valves ii, iv and, less consistently, vii often have more dark colour than the other valves (figs. 8, 9, 10 & 11)

figure 9 https://flic.kr/p/2gzahiD Valve colour arranged in blotches and intricate zig-zags. Keeled, pale jugum and posterior beaks well developed. Valves ii, iv and vii are darker than other valves. © C. Rickard.

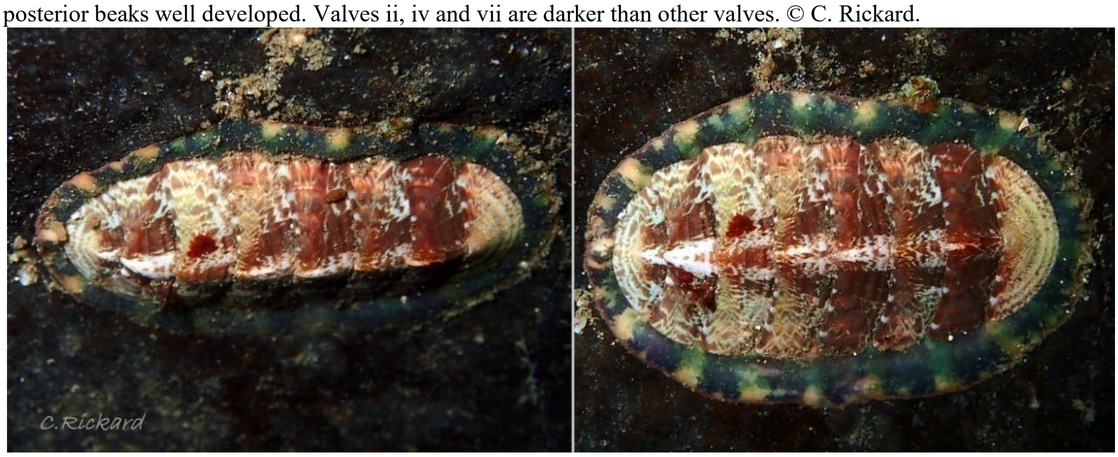
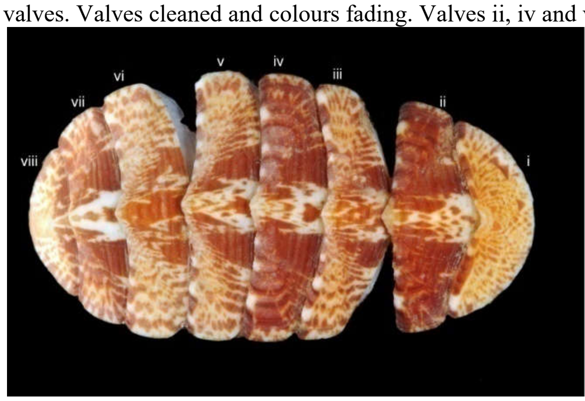


figure 10 (left) https://flic.kr/p/2gz9Jnt Girdle and body removed, apart from transverse muscles articulating valves. Valves cleaned and colours fading. Valves ii, iv and vii darker than others. Leg. P. Lightfoot.



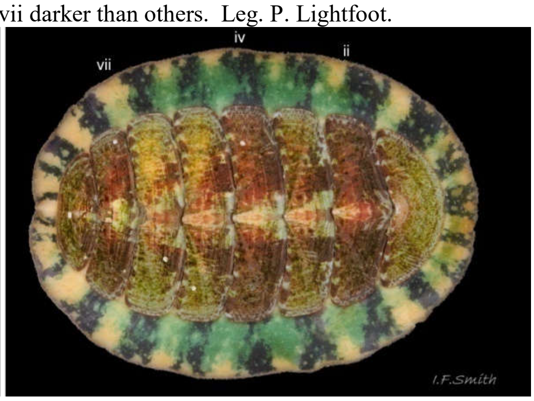


figure 11 (right) https://flic.kr/p/2gzagd2 Valves ii, iv and vii darker than others. Leg. D. M. McKay & S. Taylor.

Colour partly derives from pigment in properiostracum; brightest on live specimens in good condition and fades rapidly on specimens that are in poor condition or dead (fig. 12).

figure 12 (left) https://flic.kr/p/2gzafNQ Colours all faded to brown after 45 years in dry storage.

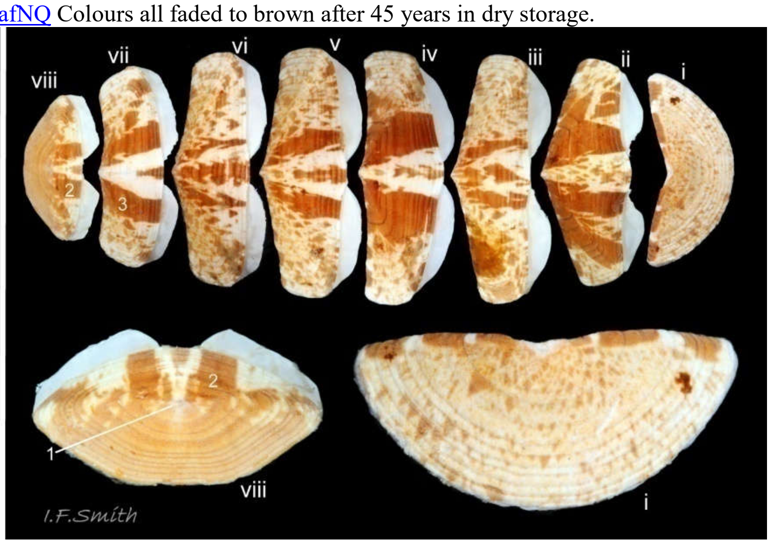


figure 13 (right). https://flic.kr/p/2gz9HfJ Inset valves viii and i (tilted) enlarged. Head valve semicircular with shallow V posterior edge when in live position. Valve viii c. 2X as wide as its antero-posterior length. Mucro (**1**) at centre of concentric growth lines. Antemucronal area (**2**) resembles jugal area (**3**) of valves ii-vii. Leg. P. Lightfoot.

The **head valve**, i, is almost semicircular (fig. 13) with a shallow V posterior edge when viewed in situ on living specimen (fig. 7). The tegmentum on **intermediate valves**, ii – vii, has slightly rounded end margins, and nearly straight and parallel anterior and posterior margins (fig. 4) apart from the anterior of valve ii which projects more at its centre. Valves ii to vii have a keeled jugum (fig. 14) with a small posterior beak (fig. 15). Beaks are often eroded away (fig. 8).

figure 14 (left) https://flic.kr/p/2gzaf1c. Valves ii to vii have a keeled jugum (**1**). Articulamentum insertion plates deeply embedded into the girdle. Coloured tegmentum (**2**) slightly overlaps the girdle. Stretched, pink, transverse muscle (**3**) that holds the valves together visible between valves when chiton rolls into a ball. Leg. Mc & T.

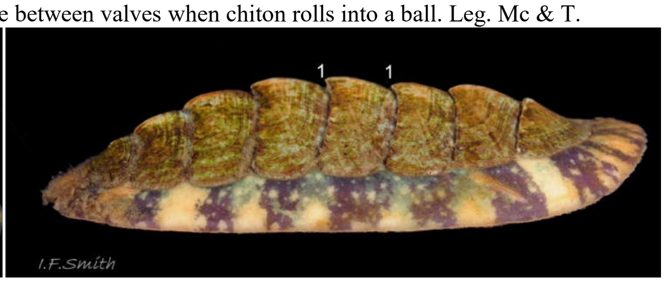


figure 15 (right) https://flic.kr/p/2gzaeRK . Valves ii to vii have a keeled jugum with a small posterior beak (**1**). Anterior of girdle raised to admit respiratory inhalent current of water. Leg. D. M. McKay & S. Taylor.

Valves vary in elevation (H/W%) from 20% to 37% or more in NE Atlantic (fig. 17), and usually more in NW Atlantic, c. 44% (Kaas & Belle, 1985). The side slopes of valves ii to vii are straight (fig. 16) or slightly convex, or a combination of straight and convex when viewed from the anterior or posterior (fig. 17).

figure 16 (left) https://flic.kr/p/2gz9Gyy Anterior view. Side slopes of valve straight (**1 to 1**). Height of arch 33.5% of its width. Barents Sea, Arctic. SEM image © B. Sirenko.

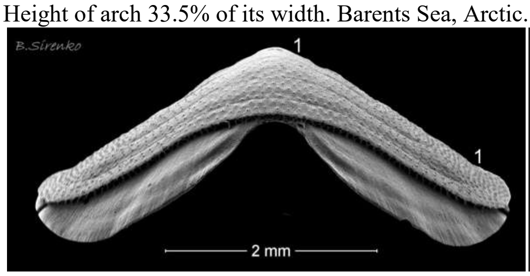
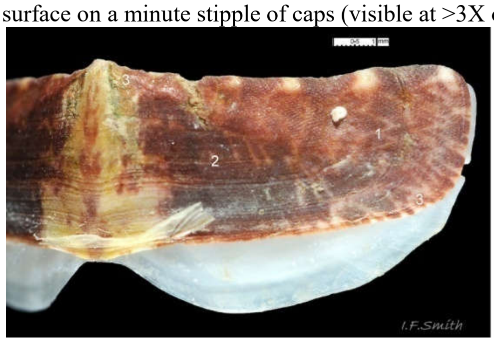


figure 17 (right) https://flic.kr/p/2gzaeBw. Posterior views, valve v. Comparison of three species. Intraspecific variation in Height/Width %, and interspecific overlap. *T. marmorea* (1, 2, 3, 4) H/W 20% to 33%. Side slopes are straight (**7**) or slightly convex (**8**). *Boreochiton ruber* (5) H/W 23%. *Lepidochitona cinerea* (6) H/W 32%.

The lateral areas of the valves are very slightly raised and separated from the central area by a shallow, unobtrusive, diagonal depression (figs. 18, 19 & 20).

figure 18 (left) https://flic.kr/p/2gzaeov Valve v. Lateral area (**1**) slightly raised and separated from the central area (**2**) by an unobtrusive, diagonal depression (**3 to 3**). Canals permeate the tegmentum and terminate on its dorsal surface on a minute stipple of caps (visible at >3X on cleaned valve). Leg. D. M. McKay & S.Taylor.



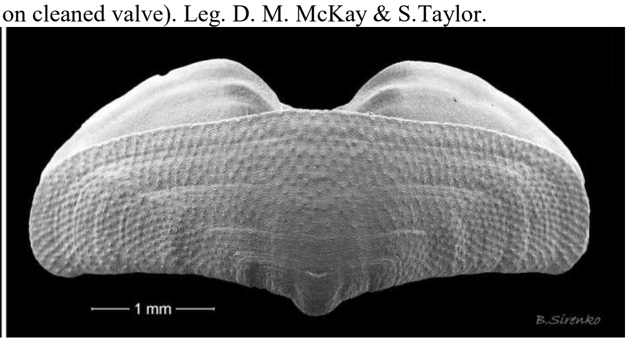
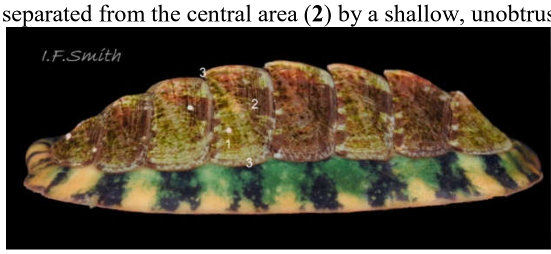


figure 19 (right) https://flic.kr/p/2gzaed5 . SEM image. Aesthete caps arranged in offset grid pattern. Growth lines turn 90° at diagonal junction line of lateral area and central area © B. Sirenko.

The **tail valve (viii)** is small and about twice as wide as its antero-posterior length. The unobtrusive, antemedian mucro is encircled by the concentric growth lines (fig. 13 & 21).

The steep postmucronal slope is straight in lateral profile (fig. 6). The colour of the antemucronal area resembles that of the jugal area of intermediate valves (fig. 13).

figure 20 (left) https://flic.kr/p/2gzadZ4 The lateral area (**1**) on each intermediate valve is slightly raised and separated from the central area (**2**) by a shallow, unobtrusive, diagonal depression (**3 to 3**). Leg. Mc & T.



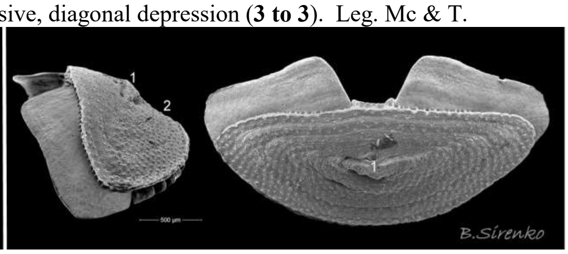
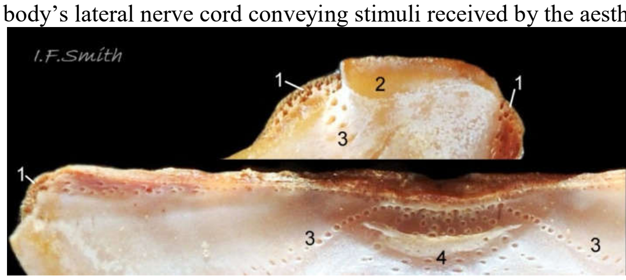


figure 21 (right) https://flic.kr/p/2gz9FQz Tail valve viii. The unobtrusive, antemedian mucro (**1**) is encircled by concentric growth lines. The steep postmucronal slope is straight in lateral profile (**2**). SEM image © B. Sirenko.

Canals permeate the tegmentum (figs. 22 & 23) and terminate on its **dorsal surface** as a minute stipple of caps; surface seems smooth to naked eye, at least 3X magnification and cleaned valve needed to discern (fig. 18). Caps are arranged in a hexagonal lattice (fig. 24). Some canals penetrate the articulamentum to form holes on its ventral surface, especially in the slit rays and jugal tract (figs. 23, 25 & 26).

figure 22 (left) https://flic.kr/p/2gzadNh Top**:** broken end of intermediate valve. Bottom**:** posterior edge of head valve i. Edge of tegmentum (**1**) with exposed aesthete canals. Edge of articulamentum lacks canals (**2**). Canals vertically penetrate the articulamentum locally in the slit rays (**3**) and jugal tract (**4**), as conduits for branches of the body's lateral nerve cord conveying stimuli received by the aesthetes on the surface of the tegmentum.



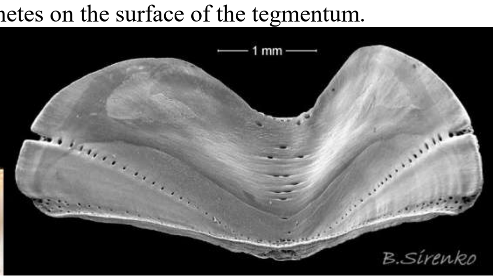
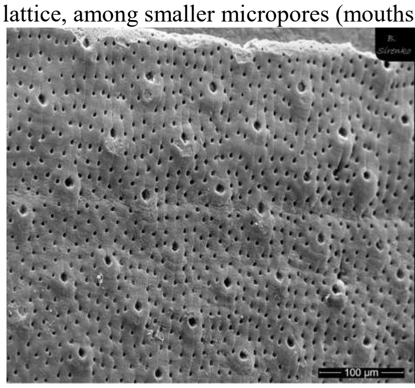


figure 23 (right) https://flic.kr/p/2gzadLi Canals penetrate the articulamentum in the jugal tract and slit rays. Two insertion plates on each end of valve are separated by a single slit at end of slit ray. SEM image © B. Sirenko.

figure 24 (left) https://flic.kr/p/2gz9FCA Macropores (mouths of aesthete canals) on raised caps in a hexagonal lattice, among smaller micropores (mouths of offshoots of main canal). SEM image 0.5mm wide © B. Sirenko.



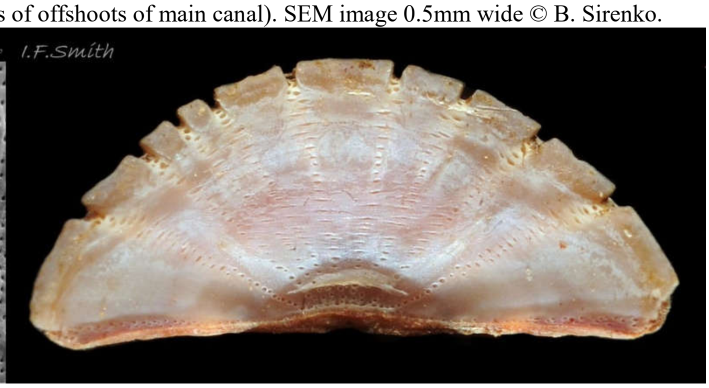
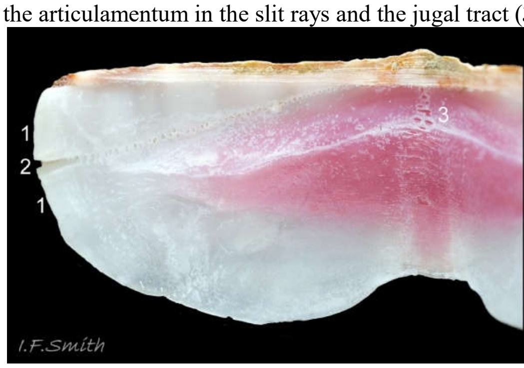


figure 25 (right) https://flic.kr/p/2gz9Foc Insertion plates on anterior edge of head valve with 10 slits separating them. A diagonal slit ray with aesthete macropores runs from each slit. Head valve lacks apophyses.

Insertion plates on ends of valves ii – vii embedded in the girdle are separated by a single slit (figs. 5 & 23); head valve i has 7 to 13 slits (fig. 25) and tail valve viii has 5 to 11 slits (fig. 27). On the ventral articulatum a diagonal **slit ray** runs from each slit to the posterior edge of valves i – vii (figs. 25 & 26) and from the slits to the mucro position where they meet the open canal ends in the jugum on valve viii (fig. 27).

The articulatum on valves ii – viii (fig. 3) projects forwards as a pair of curved, wide, short (front to rear) **apophyses** separated by a narrow jugal sinus (gap) that is less than 25% width of an apophysis (fig. 28). The apophyses on valve ii are more angular, and those on valve viii

figure 26 (left) https://flic.kr/p/2gz9Fkw Insertion plates (**1**) of articulatum on ends of intermediate valve separated by a single slit (**2**). Diagonal slit ray runs from slit to the posterior edge of each valve. Aesthete canals penetrate the articulamentum in the slit rays and the jugal tract (**3**). Leg. D. M. McKay & S. Taylor.



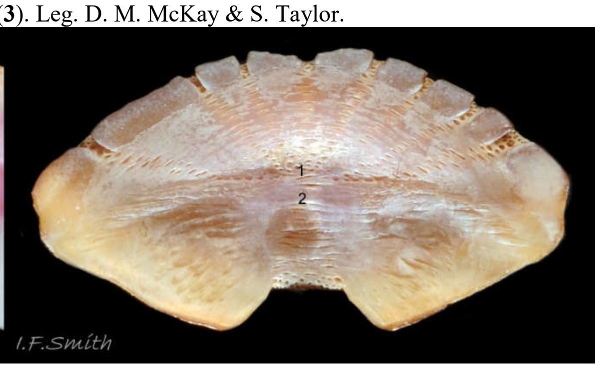


figure 27 (right) https://flic.kr/p/2gz9FcF Insertion plates of articulatum on tail valve separated by 8 slits. A slit ray runs from each slit to the mucro (located on dorsal face) position (**1**). Macropores in the jugum (**2**).

are smaller and more angular (fig. 4). Apophyses extend under the next valve forwards (fig. 2) and leave a scar of similar shape on it when the connecting muscle is removed (fig. 29). The head valve (i) is the only one that lacks apophyses as there is no valve to its anterior to be attached to (fig. 25). [It is difficult to cut away the muscle without breaking the apophyses on freshly dead chitons. They can be disarticulated without damage to the valves by standing them to girdle depth in shallow 10% NaOH overnight. CAUTION; extremely caustic].

figure 28 (left) https://flic.kr/p/2gzad9b Articulatum projects forwards as pair of curved, wide, short (front to rear) apophyses (**1**) separated by a jugal sinus (**2**) that is less than 25% width of apophysis. Leg. P. Lightfoot.

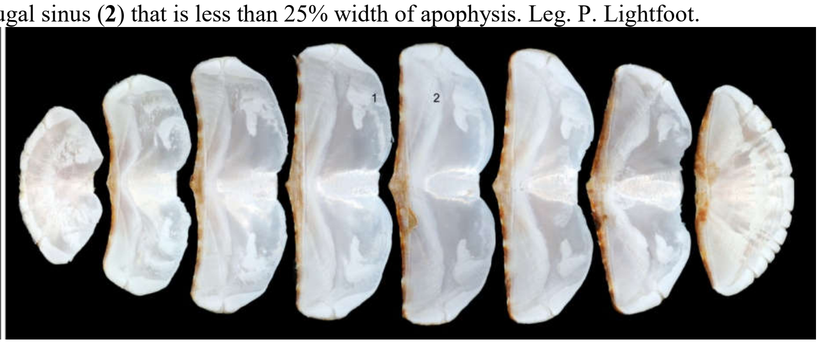


figure 29 (right) https://flic.kr/p/2gzad5Z Apophyses (**1**) extend under the next valve forwards and leave a scar of similar shape on it (**2**) when the connecting muscle is removed. Leg. P. Lightfoot.

Body Description

Head and foot only fractionally protrude into view naturally on live animal (fig. 30) and can usually only be seen when breeding (fig. 31) or if the animal is adhering to glass or dislodged from the substrate.

figure 30 https://flic.kr/p/2gzacGE Head (**1**) in view as girdle raised to admit inhalent water to the gills (**2**) in the mantle cavity. Girdle (**3**). Mantle fold (**4**) widens near the posterior into a mantle lappet (**5**). Leg. Mc & T.

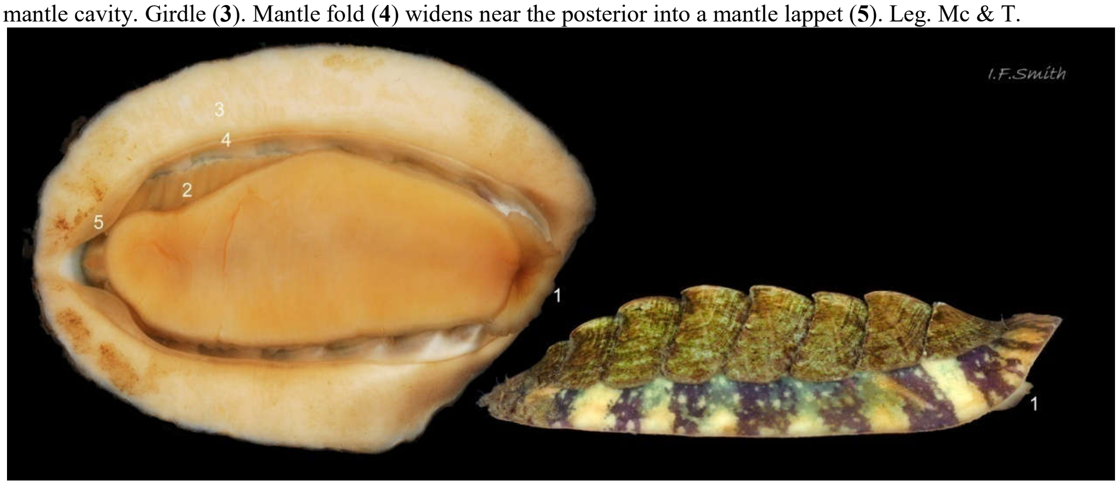


figure 31 https://flic.kr/p/2gz9EjD **Left:** male emitting sperm in gelatinous string from posterior. **Right:**female releasing individual ova. © B. Forrest.

When attached to a smooth surface, the extended **head** is anteriorly convex to fit the curve of the shell, and posteriorly concave fitting round the anterior of the foot and extending laterally as mouth lappets (fig. 32). The shape varies when the head is retracted or unattached to the substrate (fig. 33). The head lacks eyes and tentacles; its main feature is a large transverse slit-mouth with wrinkled lips. When preserved, the mouth may gape widely and its fleshy surround may distort to form a hood (fig. 32).

figure 32 (left) https://flic.kr/p/2gzabYW Live head fully extended; convex anterior fits curve of the shell, and concave posterior fits round anterior foot and extends as mouth lappets. When preserved, flesh bleaches, mouth may gape widely and its fleshy surround may contort to form a hood. Leg. Mc & T and P. Lightfoot.

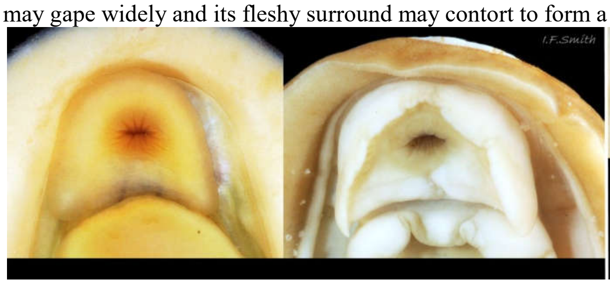
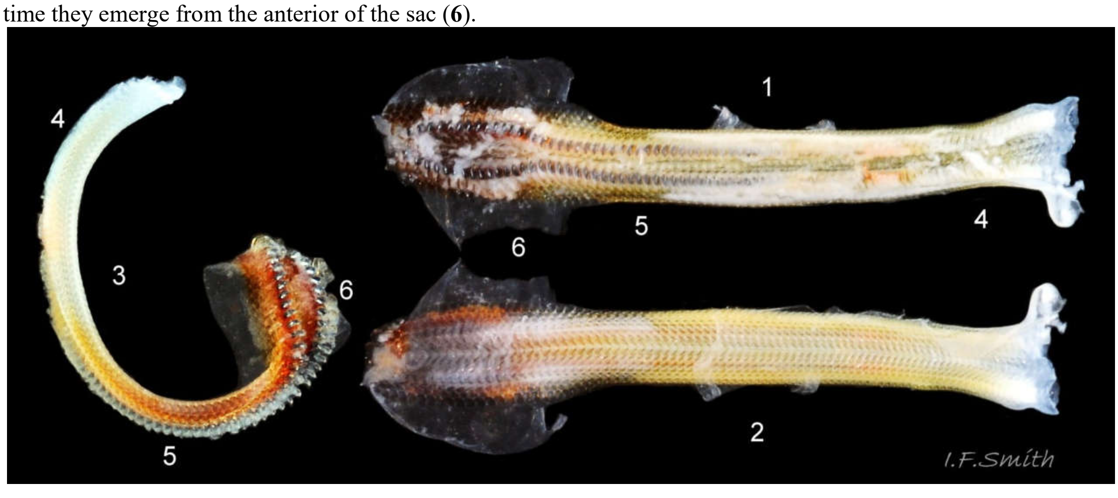


figure 33 (right) https://flic.kr/p/2gzabUC Head shape varies; has transverse slit-mouth with wrinkled lips that open and shut with sphincter action; lacks eyes and tentacles. Leg. D. M. McKay & S. Taylor.

The **radula** is a chitinous ribbon bearing teeth in rows of seventeen (fig. 34).

figure 34 https://flic.kr/p/2gz9DMm **1:** dorsal view of teeth through translucent radula sac. **2:** ventral view through radula sac. **3:** edge view; teeth colourless at rear of radula sac (**4**). Teeth darken and harden through rust-red and brown (**5**) as they move along the sac acquiring magnetite, and the principal cutting teeth are black by the time they emerge from the anterior of the sac (**6**).



In each row, the central (rhachidian) tooth is a reflexed, rectangular channel with a chisel-like terminal blade (fig. 36) [The image and text in Jones & Baxter (1987) differ from this description of the rhachidian tooth which is based on Kaas & Belle (1985) and SEM images in this account]. Next to it, the minor (first) lateral tooth is small and bladeless. The major (second) lateral tooth has a long shaft and a large tridentate head (one small, sharp denticle and two wide, rounded denticles) (fig. 35) .

figure 35 https://flic.kr/p/2gzabKK 1000µm = 1 mm. The major (second) lateral tooth has a long shaft (**1**) and a large tridentate head (**2**) with one small, sharp denticle (**3**) and two wide, rounded denticles (**4**). This is the principal, cutting tooth used to scrape micro-organisms from rock surfaces. © B. Sirenko.

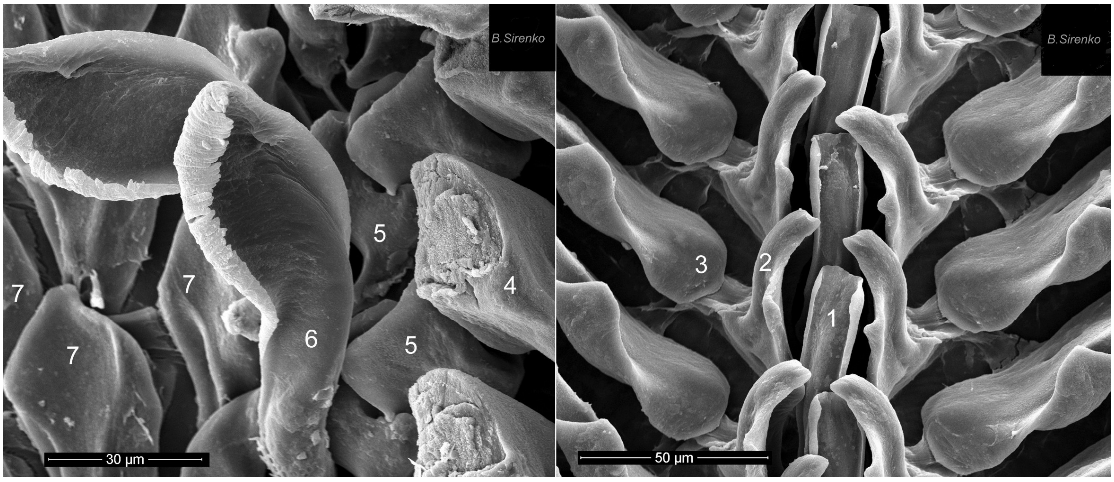
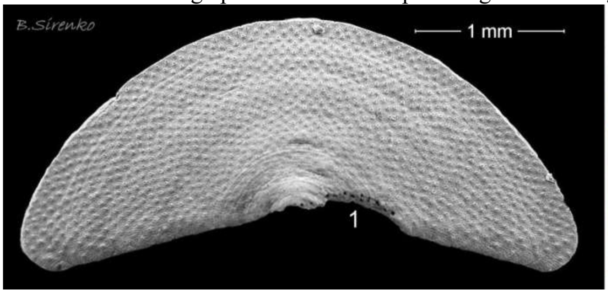


figure 36 https://flic.kr/p/2gzabrZ Left image magnified more than right one. 1000µm = 1 mm . © B. Sirenko.
Each row has 8 teeth on either side of the central tooth; total of 17.
1: central (rhachidian) tooth is a reflexed, rectangular channel with a chisel-like terminal blade.
2: minor (first) lateral tooth is small and bladeless.
3: shaft base of major (second) lateral tooth (see fig. 35). **4:** broken shaft of major (second) lateral tooth.
5: unobtrusive first and second uncinal teeth between bases of major lateral and major (third) uncinal teeth.
6: spatulate major (third) uncinal tooth; head sculptured like a feather, probably sweeps up cut food particles.
7: three low plate-like marginal ‘teeth’, at the margin of the radula.

The first and second uncinal teeth are small and unobtrusive between the bases of the major lateral and major (third) uncinal tooth which has a long shaft with head shaped and sculptured like a feather (fig. 36). At the margin of the radula in each row there are three low plates (marginal ‘teeth’). The teeth are colourless when their formation commences at the rear of the translucent radula sac. They darken and harden through rust-red and brown as they move along the sac acquiring magnetite (iron oxide), and the principal cutting teeth are black by the time they emerge from the anterior of the sac (fig. 34). Magnetite is the hardest material made by any living organism (Botelho, 2013) and causes radulae to adhere to magnets.

Aesthetes (sensory tissue) fill canals permeating the tegmentum (fig. 22 & 37). They terminate on fine stipple (at least X3 magnification needed, fig. 18) as sensory organs on the dorsal surface of valves (figs. 19, 21, 24). Canals vertically penetrate the articulamentum in the slit rays and jugal tract as conduits for branches of the body's lateral nerve cord (fig. 22).

figure 37 (left) https://flic.kr/p/2gz9CVr Broken edge (**1**) of tegmentum showing the aesthete canals which open on the surface through pores on minute caps arranged in a hexagonal lattice. Valve i, SEM image © B. Sirenko.



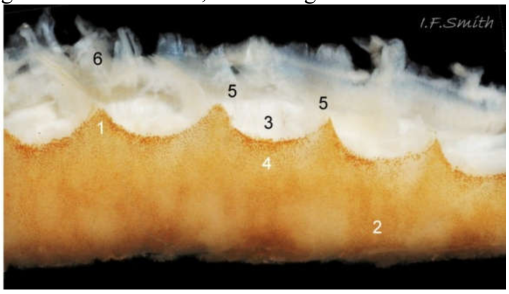
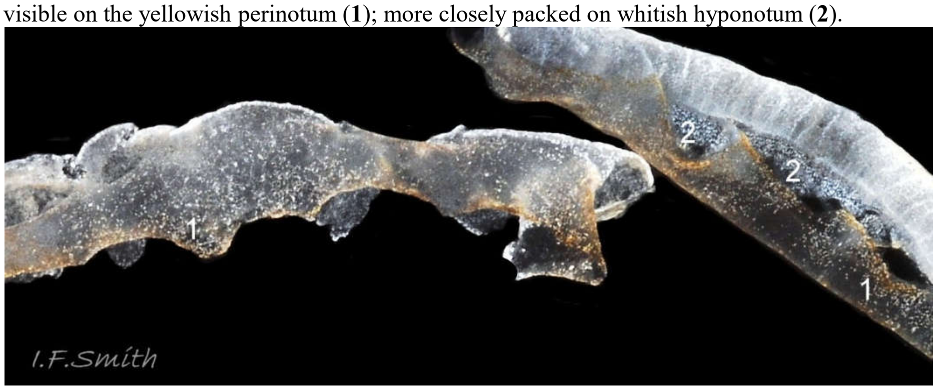


figure 38 (right) https://flic.kr/p/2gzaaV8 **1:** scalloped edge where valves removed. **2:** coloured bands faded as preserved in alcohol. **3:** white mantle tissue forming thick girdle covered by coloured perinotum (dorsal cuticle). **4:** perinotum with widely spaced, tiny spicules visible as fine grains at this magnification of a cleaned surface. **5:** strong, lateral, longitudinal muscle encircles the entire body passing under the outer margins of the valves (see fig. 50). **6:** lateral muscles connect the foot to the ends of the valves.

Immediately below the valves, the **mantle** is a thin, translucent epidermis, but it is greatly thickened where reflected around the periphery of the shell to form a fleshy **girdle** (fig. 6) into which the articulamentum insertion plates at the ends of the valves are deeply embedded (fig. 14 & 38). The girdle has cream or yellowish-white flesh with a tough transparent yellowish cuticle that survives when flesh is removed with NaOH (fig. 39).

figure 39 https://flic.kr/p/2gzaaSC Girdle with flesh removed. Minute, widely spaced spicules visible on the yellowish perinotum (**1**); more closely packed on whitish hyponotum (**2**).



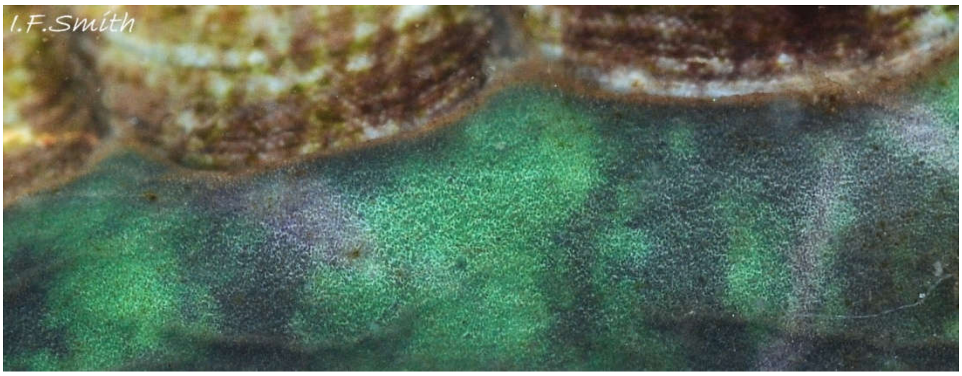


figure 40 https://flic.kr/p/2gz9CKB The dorsal cuticle of the girdle appears smooth to the naked eye, but shows very small spicules resembling the grain of leather at this magnification. This girdle is suffused with verdigris-green which partially obscures the band pattern.

The cuticle of the girdle appears leathery-smooth to the naked eye (fig. 6), but strong magnification shows a covering of very small spicules (figs. 40 & 41). Scanning electron microscope images (fig. 42) show that the spicules on the dorsal surface are small, c. 27µ long, widely spaced cones with sharp apices, and that spicules on the ventral surface are longer, c. 35µ , more closely packed ovoids with longitudinal ribs.

figure 41 https://flic.kr/p/2gz9CEG **left:** dorsal surface of girdle with widely spaced fine spicules, fades in alcohol. **right:** ventral surface of the girdle with closely packed fine spicules. Leg. P. Lightfoot.

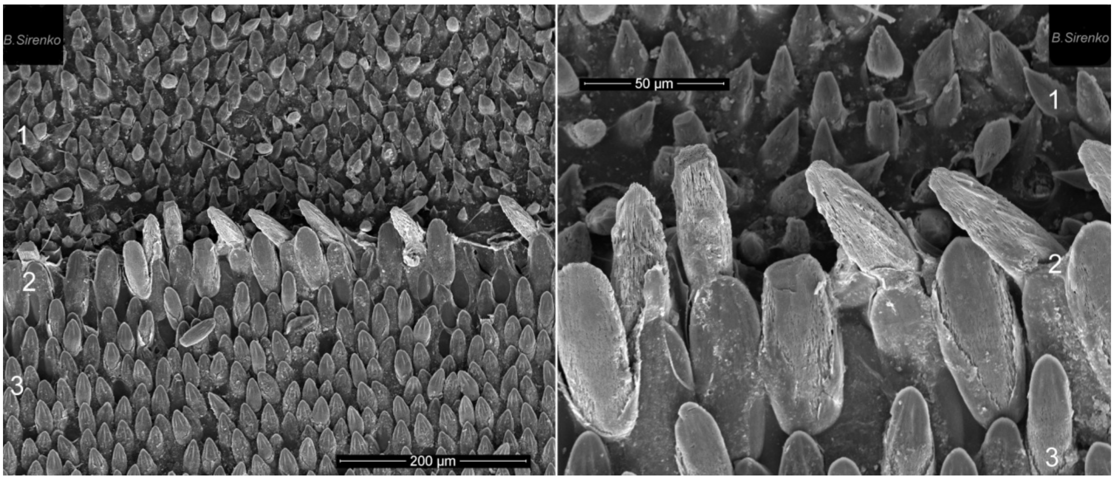


figure 42 https://flic.kr/p/2gzaaGT Two images at different magnifications showing cuticle removed from flesh of girdle and opened flat so that the dorsal spicules (**1**) are at top, separated by a line of marginal spicules with ribs (**2**) from the ventral spicules (**3**) below. The dorsal spicules are small, c. 27µ long, widely spaced cones with sharp apices. The ventral spicules are longer, c. 35µ, more closely packed ovoids with longitudinal ribs. The marginal spicules are straight, obtusely pointed and c. 48µ long. SEM image © B. Sirenko.

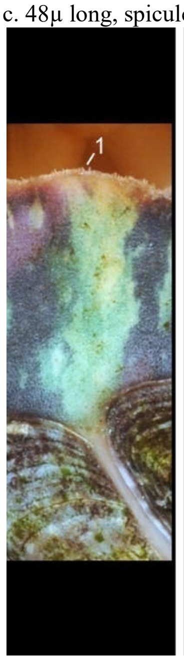
The ventral surface of the girdle is whitish, but usually extensively stained yellowish to brownish by firm contact with the substrate (figs. 43 & 44).

figure 43 (left) Stained ventral girdle. **1:**marginal fringe of spicules; slightly longer, c. 48µ, than others on the girdle, but still difficult to discern with the naked eye. Leg. Mc & T.

figure 44 (right) Leg. Mc & T. https://flic.kr/p/2gzaaj3 Muscular foot and flat ventral surface of the girdle provide a secure grip of rock surface aided by articulated shell conforming to uneven surfaces. When fully spread, foot and mantle fold conceal most of the pallial cavity.

The dorsal surface of the girdle is yellowish with, usually, a brown or purplish band at each end of valves ii to vii, and several bands associated with valves i and viii (fig. 7). The bands usually have several yellowish blotches on them. Frequently, part, or all, of the dorsal surface is suffused with verdigris-green which partially obscures the band pattern (fig. 40). The foregoing colours are usual in Britain but Kaas and Belle (1985) state that the girdle is "*of an even brownish colour, exceptionally with alternating zones of light and dark brown*". This may be the case in America, though nine images from Quebec all have banded girdles (DORIS, 2019), and dried or preserved specimens often lose the pattern (figs. 12 & fig. 38). The edge of the girdle has a marginal fringe of straight, obtusely pointed, c. 48µ long, spicules that are very difficult to discern with the naked eye (fig. 42, 43 & 45). The girdle can be flexed upwardly outwards at the anterior (fig. 30) to admit inhalent water to the peripheral mantle cavity, and at the posterior to form a channel for the release of exhalent water, faecal pellets and ova or sperm (fig. 31).

figure 45 (left) https://flic.kr/p/2gz9BP8 The edge of the girdle has a marginal fringe of straight, obtusely pointed, c. 48µ long, spicules (**1**) that are very difficult to discern with the naked eye. Leg. D. M. McKay & S. Taylor.



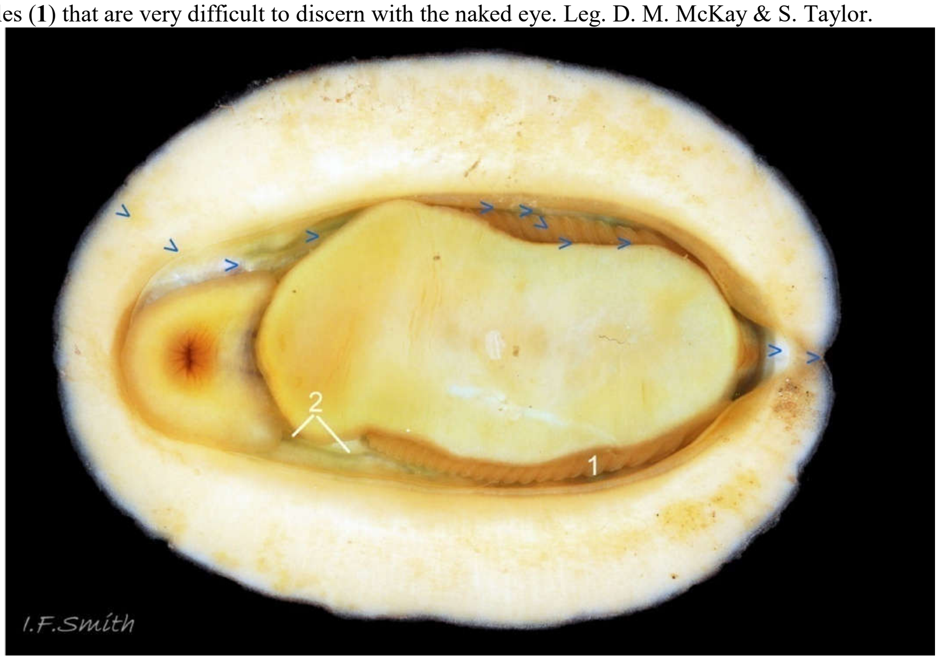


figure 46 (right) https://flic.kr/p/2gza9Xr Narrow mantle cavity around whole animal, with 15 to 26 small gills on each side (**1**), for nearly whole length of foot. Inhalent water current passes under raised anterior of the mantle, along the cavity, through the gills and then between foot and gills as an exhalent current to the posterior where it exits via a channel through the girdle. Haemolymph circulates from the head sinus through longitudinal sinuses (**2**) to the mantle, foot, and viscera, then through the gills for aeration before passing into the adjacent heart in the pericardium below valves vii & viii. Leg. D. M. McKay & S. Taylor.

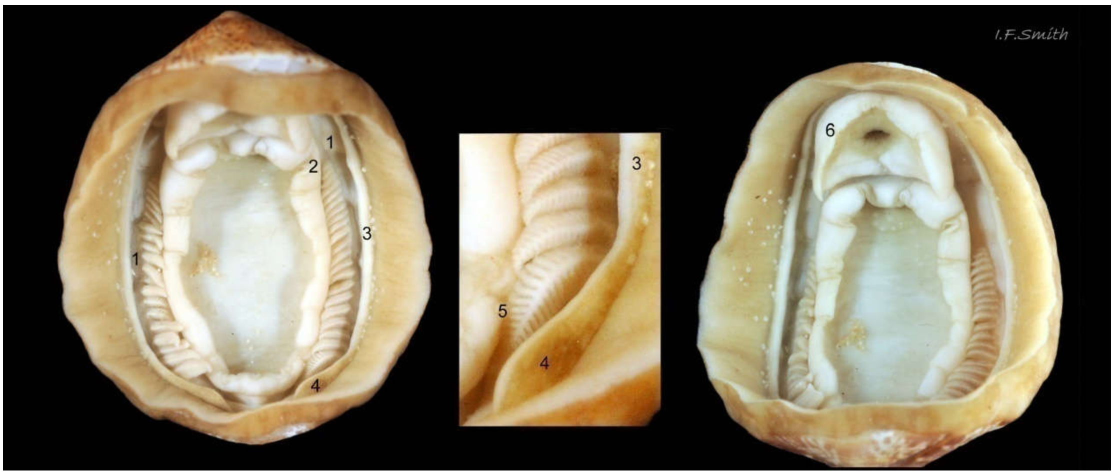


figure 47 https://flic.kr/p/2gza9KN (in alcohol) 1**:** mantle cavity. **2:** gills almost reach anterior of foot. **3:** mantle fold. **4:** mantle lappet. **5:** lamellae of pinnate gill. **6:** surround of mouth contorted into hood. Leg. P. Lightfoot.

An open, narrow **mantle cavity** runs around whole animal; contains 15 to 26 small **gills** on each side (Baxter & Jones, 1986) often, on larger specimens, for nearly the whole length of the foot; merobranch, but nearly holobranch, arrangement (figs. 46 & 47). Number of gills increases with age. Between the mantle cavity and girdle, the **mantle fold** is unobtrusive, except where it widens near the posterior into a **mantle lappet** (fig. 30) and may partly conceal the gills. **Anus** opens at end of an anal papilla into the mantle-cavity at posterior adjacent to a channel to the exterior formed by deflection/ depression of girdle (fig. 48). The dorso-ventrally flattened pericardium containing the heart is located above the anal papilla, and is sometimes partly visible on live specimens (fig. 48). Nephridiopores and gonopores open laterally into posterior quarter of the cavity. No **penis** as external fertilization.

figure 48 (left) https://flic.kr/p/2gza9pc **1:** mantle cavity. **2:** gill. **3:** mantle lappet. **4:** mantle fold. **5:** anal papilla with anus at tip. **6:** dorso-ventrally flattened pericardium containing the heart. **7:** channel through girdle to the exterior. Exit route for exhalent water with sperm or ova from gonopores, excreta and faeces. Leg. Mc & T

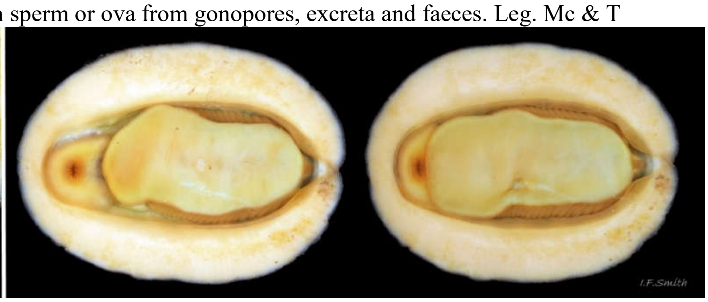
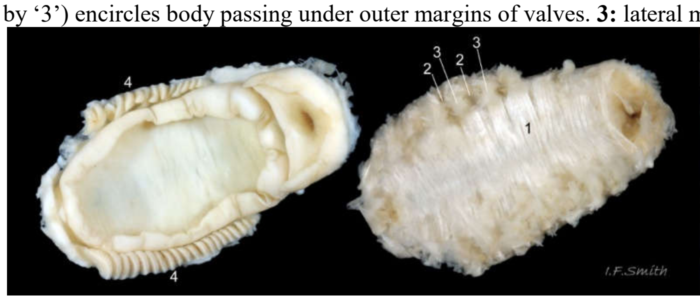


figure 49 (right) Foot is a yellow to orange, elongate ovoid. Anterior is usually wider than the posterior; curvature varies, sometimes truncate (right image). No medial line dividing the sole. Leg. D. M. McKay & S. Taylor.

Foot yellow to orange, elongate ovate, anterior wider than posterior, curvature of ends varies, sometimes truncate (fig. 49), no medial dividing line. When foot spreads widely, it and the mantle fold/lappet close and conceal much of the pallial cavity (fig. 44).

figure 50 (left) https://flic.kr/p/2gza92J **1:** transverse foot muscle. **2:** lateral longitudinal muscle (almost hidden by '3') encircles body passing under outer margins of valves. **3:** lateral muscles. **4:** gills. Leg. P. Lightfoot.



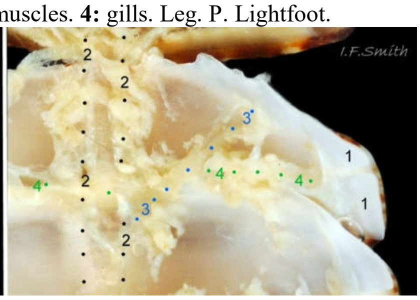


figure 51 (right) https://flic.kr/p/2gz9AHL Four sets of muscles articulate individual valves.
1: attachment points of pair of lateral muscles that connect the foot to each end of the valves (muscles removed).
2: pair of straight muscles lie along the jugum, attaching jugal sinus of valves to body wall under next valve.
3: muscle attached to the jugal sinus travels anteriorly outwards to attach to the body wall under the preceding valve on which it leaves a comma shaped scar. **4:** dorso-ventral fibres of transverse muscle connect apophyses to underside of next valve. Leg. P. Lightfoot.

The foot has many strong transverse **muscles** (fig. 50) and the body has a strong lateral longitudinal muscle (figs. 38 & 50) that encircles the entire body passing under the outer margins of the valves. The valves have four sets of muscles:
a) A pair of lateral muscles connect the foot to each end of the valves, one on each side of the slit (figs. 38 & 50), leaving an opaque scar when removed (fig. 3).
b) A pair of straight muscles (fig. 51) lie along the jugum, attaching to the anterior margin of the jugal sinus of each valve and to the body wall under the previous valve.
c) On each side of a valve an oblique muscle (fig. 51) attaches to the jugal sinus close to the straight muscle and travels anteriorly outwards. The anterior end of the muscle attaches to the body wall under the preceding valve on which it leaves a comma shaped scar (fig. 3).
d) The transverse muscle (fig. 51) consists of dorso-ventral fibres connecting the apophyses of one valve to the underside of the preceding valve where it leaves curved scars matching the

outlines of the apophyses. The muscle colour is often the same as that of the jugal tract; white, yellow (fig. 51) or pink (fig. 52).

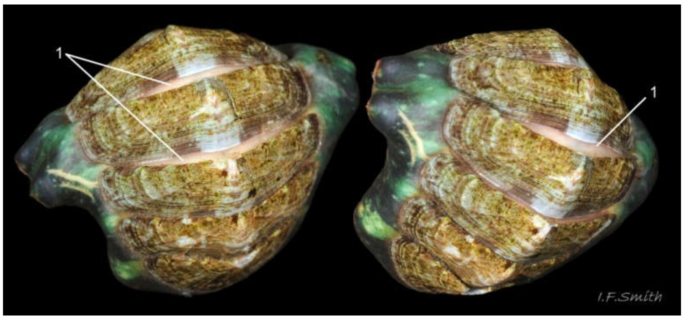


figure 52 https://flic.kr/p/2gza8R8
1: transverse muscle.
When the chiton rolls into a defensive ball, it increases protection to the foot, but exposes the stretched transverse muscle.
Leg. D. M. McKay & S. Taylor.

figure 53 https://flic.kr/p/2gz9AiY When displaced from the substrate, *T. marmorea* can use the strong, lateral longitudinal muscle to roll into a protective ball. Leg. D. M. McKay & S.Taylor.

figure 54 https://flic.kr/p/2gz9zHj Faecal pellet.
The long coiled intestine compresses faeces into oval pellets.
© B. Forrest.

Key identification features

Many features have interspecific overlap; the most reliable are valve and girdle sculpture.

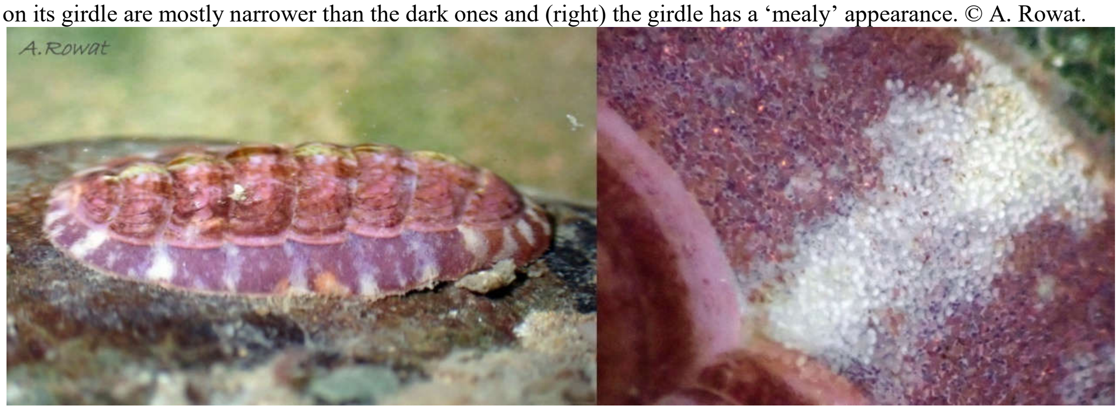
Tonicella marmorea O. Fabricius, 1780.
The following is for NE Atlantic. Those in NW Atlantic may differ.
1. Big species. Max. length in NE Atlantic is 45mm.
2. Colour variable; white, cream, various shades of brown, red, and ochre arranged in blotches or intricate zig-zag lines. Valves ii, iv and vii often have more dark colour than the other valves (fig. 9).
3. Girdle is yellowish with a brown or purplish band at each end of valves ii to vii, and several bands by valves i and viii. Usually several yellowish blotches on bands (fig. 7).
Frequently, part, or all, suffused with **verdigris-green** (fig. 40).
4. Apart from nearly rectangular growth lines, dorsal surface of **valves appears smooth** to naked eye (fig. 6), but at over X3 magnification, many distinct small granules visible (fig. 18). (Granules may not be discernible in underwater images or on specimens before deposits and properiostracum removed.)
5. Dorsal surface of girdle has widely spaced minute granules, c.27μm long (fig. 40). Usually escape notice in photographs; require strong magnification.

6. At LWS and sublittorally. **Not further south than North Wales or Northumberland**. (Many dubious records on distribution maps as often confused with *B. ruber*.)
7. 17 – 26 gills along most of each side of foot, arrangement merobranch but nearly holobranch (fig. 46).
8. White apophyses on intermediate valves are short (anterior-posterior), **wide** and gently curved (fig. 28). **Narrow jugal sinus** (gap between them) is about **quarter width** of one apophysis.

Similar species

Boreochiton ruber (Linnaeus, 1767) (Formerly *Tonicella rubra*)

figure 59 https://flic.kr/p/2iHXVNg Large (20mm) *B. ruber* sometimes resemble *T. marmorea*, but the pale bands on its girdle are mostly narrower than the dark ones and (right) the girdle has a 'mealy' appearance. © A. Rowat.



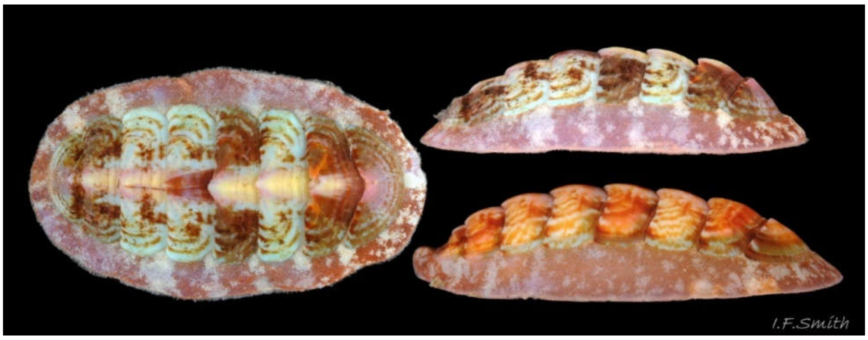


figure 60 *B. ruber* https://flic.kr/p/2gz9xMq Valves pink to brick red with cream and light brown marks. Girdle has red/pink bands alternating with thinner, paler, often fragmentary, bands which are roughly in line with shell-sutures. Leg. P. Lightfoot.

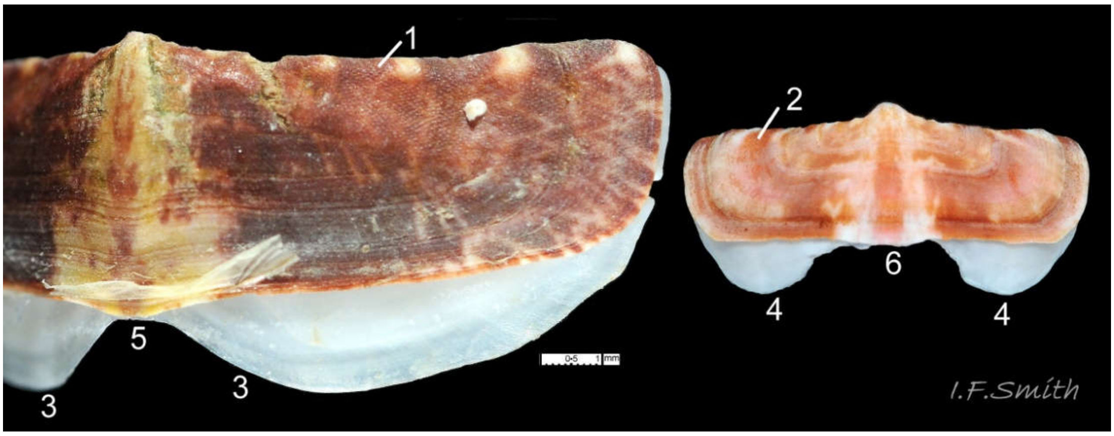
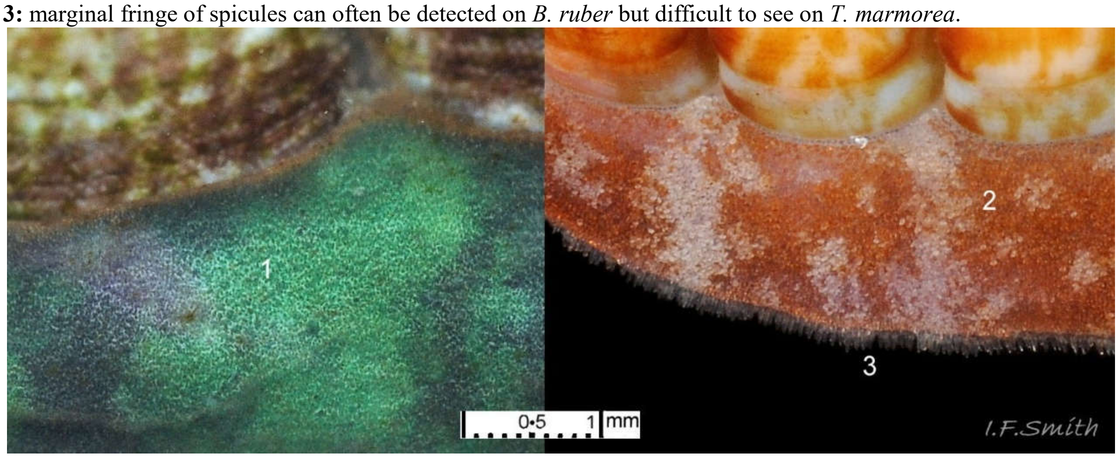


figure 61 https://flic.kr/p/2gza7Tg Comparison of valve iv, *T. marmorea* (left), *B. ruber* (right), at same scale. Leg. D. M. McKay & S. Taylor, and P. Lightfoot. Apart from growth lines, both appear to have smooth valves, but both have caps/granules that become visible at about 3X (*T. marmorea*) and X30 (*B.ruber*).
1: *T. marmorea* caps/granules visible if viewed on 50cm monitor.
2: *B. ruber* caps/granules almost or entirely invisible if viewed on 50cm monitor.
3: *T. marmorea* apophyses are, relative to valve size, short (anterior-posterior), wide and gently curved.
4: *B. ruber* apophyses are prominent and rounded, often almost semicircular.
5: *T. marmorea* jugal sinus (gap between apophyses) is about quarter width of one apophysis.
6: *B. ruber* jugal sinus (gap between apophyses) is about same width as one apophysis.

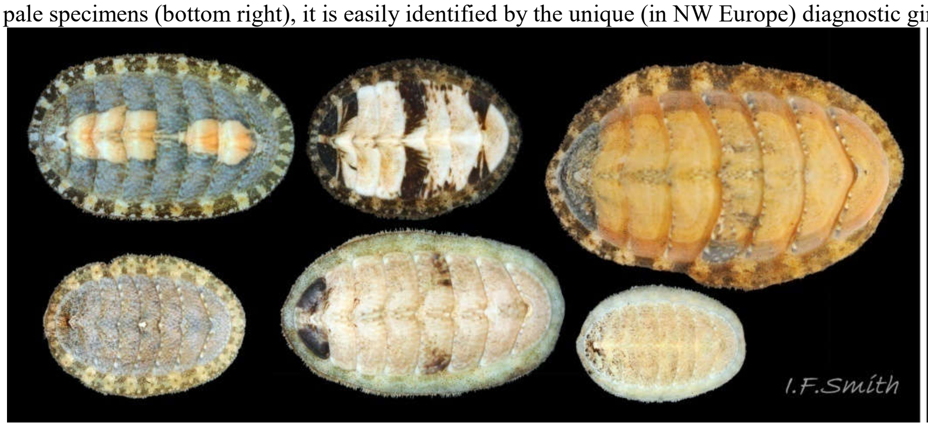
1. *B. ruber* is a medium species. Usual max. length 15mm, occasionally longer (fig. 59).
2. Valves pink to brick red with patches and streaks of cream and brown (fig. 60).
3. Girdle usually has reddish/pinkish bands alternating with **thinner**, often fragmentary, **paler bands** that are roughly in line with shell-sutures (figs. 59 & 60).
4. Apart from growth lines, dorsal surface of valves appears smooth to naked eye and needs X30 magnification for faint stippling to be visible (fig. 61).
5. Dorsal surface of **girdle** has densely-packed, elongate (50 - 60µm), club-shaped granules with packed touching heads giving a **mealy** appearance (figs. 59 & 62).
6. At LWS and sublittorally all around Britain, except NE Irish Sea and southern North Sea.
7. *B. ruber* has about 12 gills each side (range 10-15), arrangement merobranch.
8. Apophyses on intermediate valves are prominent and rounded, often **almost semicircular** (fig. 61). **Wide** jugal sinus (gap between them) is about **same width** as one apophysis.

figure 62 https://flic.kr/p/2gza7G4 *T. marmorea* (left), *B. ruber* (right), same scale. Leg. Mc & T and P. Lightfoot.
1: dorsal surface of girdle on *T. marmorea* has widely spaced, minute granules, often imperceptible in images.
2: girdle on *B. ruber* has club-shaped spicules with densely-packed, touching heads giving a mealy appearance.
3: marginal fringe of spicules can often be detected on *B. ruber* but difficult to see on *T. marmorea*.



Lepidochitona cinerea (Linnaeus, 1767).
1. Medium species. Usual max. length 12 - 16mm, exceptionally 25mm (Kaas & Belle, 1985).
2. Has diverse colour forms, some similar to that of other species (fig. 63).
3. Girdle usually has **interlocking** brown (various shades) and whitish, transverse, **lozenge-like bands** of approximately equal size. Dark bands usually have narrow waist, and light bands usually have a bulging waist (fig. 64) (or vice versa). A thin paler greyish longitudinal line often runs across the waist of dark bands. Usually a dark central spot on pale bands. Markings can be partially developed, very indistinct, or absent (fig. 63) on pale specimens.

figure 63 (left) https://flic.kr/p/2gza7Dt *L. cinerea* colour forms; some resemble other species. Except for very pale specimens (bottom right), it is easily identified by the unique (in NW Europe) diagnostic girdle pattern.



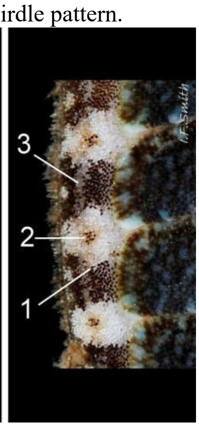
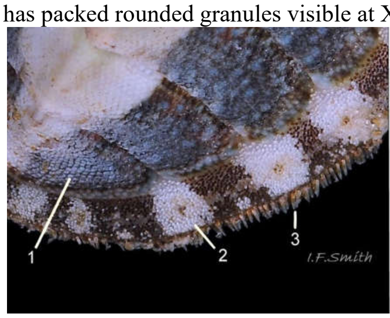


figure 64 (right) https://flic.kr/p/2gz9yX1 The girdle of *L. cinerea* has diagnostic alternating brownish and whitish, transverse, lozenge-like bands of approximately equal size. **1:** dark bands usually have narrow waist, and light bands usually have a bulging waist (or vice versa). **2:** usually a dark central spot on pale bands. **3:** thin paler greyish longitudinal line often runs across the waist of dark bands. Markings can be very faint on pale specimens.

4. Dorsal surface of valves has numerous rounded granules visible at X3 magnification, and often to naked eye. Granules tend to follow indistinct curved lines (fig. 65).
5. Dorsal surface of girdle has densely packed rounded granules (fig. 65).
6. Commonest littoral chiton all around Britain. Only common chiton species likely to be found higher than MLW on British shores.
7. Usually 16 – 19 gills each side, arrangement almost holobranch (fig. 66).
8. White apophyses on intermediate valves are gently curved. Wide jugal sinus (gap between apophyses) on intermediate valves is about same width as one apophysis (fig. 67).

figure 65 (left) https://flic.kr/p/2gza75x **1:** valves of *L. cinerea* have curved lines of rounded granules. **2:** girdle has packed rounded granules visible at X3 magnification. **3:** marginal fringe of spicules visible to naked eye.



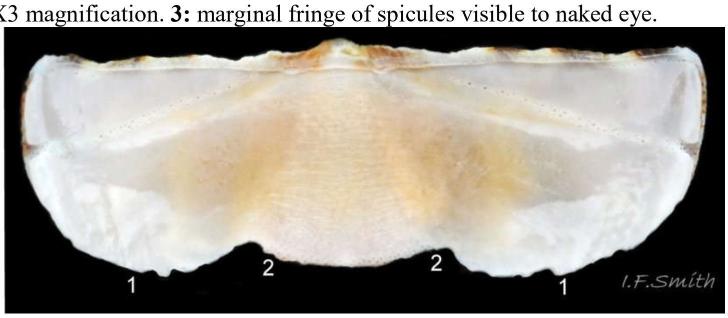


figure 67 (right) https://flic.kr/p/2gza6V9 *L. cinerea* apophyses (**1**) are gently curved, like *T. marmorea*, but *L. cinerea* jugal sinus (**2**) (gap between apophyses) is relatively much wider; about same width as one apophysis.

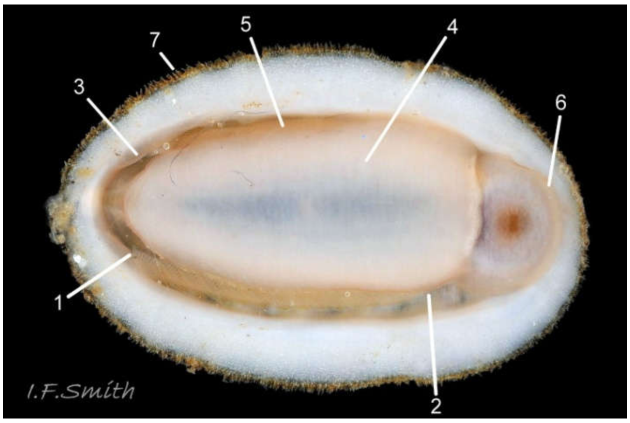


figure 66 https://flic.kr/p/2gz9yUF
L. cinerea foot and head.
1 to 2: Usually 16 – 19 gills each side, arrangement almost holobranch (almost reaching front of foot).
3: small mantle lappet.
4: sole.
5: slightly darker border around sole.
6: slightly darker border around head.
7: fringe of spicules on edge of girdle often visible to naked eye.

Callochiton septemvalvis (Montagu, 1803) (Formerly *Callochiton achatinus*).

figure 68 (left) https://flic.kr/p/2gza6TR *C. septemvalvis* valves usually some shade of red, sometimes yellow or green, with or without irregular blotches or marbling. Head and tail valves, i and viii, are often darker than the other valves. Girdle colour is usually a darker shade of the adjacent valve colour, often with a transverse cream band by sutures i/ii and vii/viii and, occasionally, by other sutures, as on this one. © R. Durrant

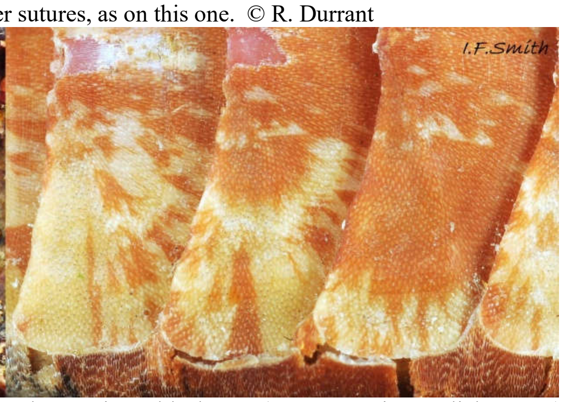


figure 69 (right) https://flic.kr/p/2gz9yHU *C. septemvalvis* has a minute black spot (X30, zoom in on Flickr to see) by each aesthete cap on valves i and viii, and on the lateral triangle of intermediate valves ii to vii. The dorsal surface of valves have numerous grooves that give a granular appearance visible at X8 magnification, but often not visible in photographs of dark specimens.

1. *C. septemvalvis* is a big species; max. length 32 mm.
2. Dorsal surface of valves usually some shade of red, sometimes yellow or green, with or without irregular blotches or marbling. Head and tail valves, i and viii, are often darker than the other valves (fig. 68). Minute black spot (X30 to see) by each apical cap of aesthete canals on valves i and viii, and on lateral triangle of intermediate valves ii to vii (fig. 69).
3. Girdle colour is usually a darker shade of the adjacent valve colour, often with a transverse cream band by sutures i/ii and vii/viii (fig. 70), and occasionally other sutures (fig. 68).

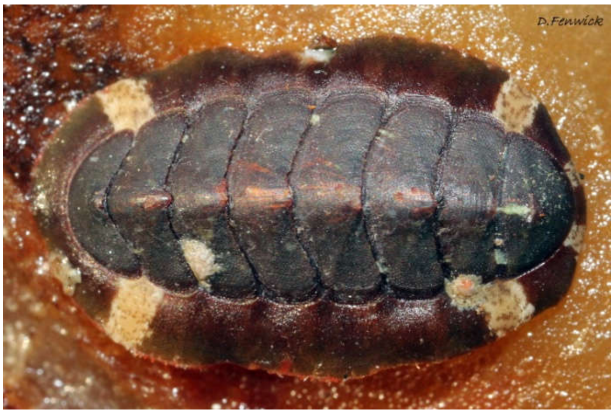


figure 70 https://flic.kr/p/2gz9yyR
On *C. septemvalvis* the head and tail valves are often darker than the intermediate valves, but this distinction is lost on specimens like this with dark intermediate valves.
Girdle colour is usually similar to that of the adjacent valve, often with a transverse cream band by sutures i/ii and vii/viii, and occasionally other sutures. On this dark ruby specimen the 'snake skin' pattern of the girdle spicules is not easily seen. © D. Fenwick, http://www.aphotomarine.com/index.html

4. Dorsal surface of valves has numerous grooves that give a granular appearance visible at X8 magnification (fig. 69), but often not visible in photographs.
5. Dorsal surface of girdle has densely packed, tessellated, 200µm long, acicular spicules that create a characteristic **snake-skin** appearance (fig. 71).
6. Rarely numerous. South, west and north coasts of Britain. Scarce on east coasts; very scarce or absent in southern North Sea and north-east Irish Sea.
7. Usually 20 to 25 gills each side, arrangement merobranch.
8. White apophyses on intermediate valves are short (anterior-posterior), **wide** and gently curved (fig. 72). They meet at the jugum with **no** jugal gap between them. This is the only British species with **two slits** and slit rays (sometimes a small third one) in the articulamentum on either side of the intermediate valves, ii to vii.

figure 71(left) https://flic.kr/p/2gz9xS5 The girdle of *C. septemvalvis* has densely packed, tessellated, 200µm long, acicular spicules that create a characteristic snake-skin pattern.

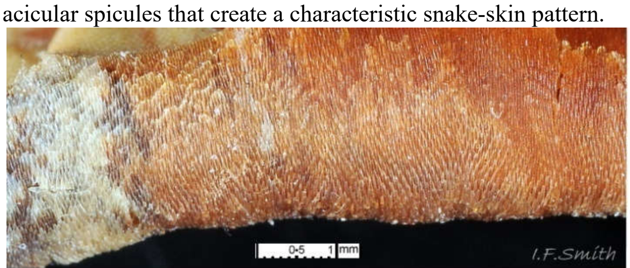


figure 72 (right) https://flic.kr/p/2gz9xtu Apophyses on *C. septemvalvis* are short (anterior-posterior), wide and gently curved. They meet at the jugum (**1**) with no gap between them. Only British species with two slits (**2**) and slit rays, sometimes a small third one (**3**), on either side of intermediate valves.

Habits and ecology

Lives on bedrock and stones at ELWS and sublittorally to about 200 metres. Four sets of muscles to individual valves (figs. 38, 50, 51, & 52) enable shell articulation to conform closely to uneven rock surface. Large muscular foot and flat ventral surface of girdle grip the rock surface firmly (fig. 44). When displaced from the substrate, it can use the strong, lateral longitudinal muscle to roll into a protective ball (fig. 53).
Respiration: cilia on gills and mantle create inhalent water-current that enters pallial cavity wherever girdle is raised at anterior (fig. 30). Adjacent gills have interlocking cilia so all work as a unit. Water current passes through gills (fig. 46) and then between foot and gills as an exhalent current to posterior where it exits via a channel through the girdle (fig. 48).

Haemolymph **circulates** from the head sinus through longitudinal sinuses (fig. 46) to the mantle, foot, and viscera, then through the gills for aeration before passing into the adjacent heart in the pericardium (fig. 48) below valves vii & viii. From the heart the blood is pumped through the medial dorsal aorta to the head sinus, giving off some channels to the gonad and valve muscles on the way. Chitons lack eyes and tactile/chemoreceptor tentacles on the head. They sense the environment through **aesthetes** exposed on the surface of the shell; only visible at high magnification (figs. 19, 21 & 24). Proposed aesthete functions include chemoreception, mechanoreception, replenishment of properiostracum materials, secretion of protective substances and photoreception, though the focusing lens and receptive retina found in aesthetes of some species are absent from *T. marmorea*. Sensory organs are also present on the girdle.

T. marmorea **feeds** by scraping microalgae and associated organisms from the rock surface using its hard, magnetite reinforced radula (figs. 34 & 35). In some Scottish sea lochs where it is common, it is an important grazer in the ecosystem (Jones & Baxter, 1987). Though it resembles early primitive molluscs in several ways, it has an elaborate digestive system with no trace of primitive rotating style in the stomach. The long coiled intestine compresses faeces into oval pellets (fig. 54). Exhalent water current in the pallial cavity carries excreta from lateral nephridiopores to posterior, where faecal pellets from anus join the flow; all expelled at posterior through channel in girdle (fig. 48).

Breeding: dioecious. Water current in pallial cavity carries sperm or ova from lateral gonopores to posterior and out through channel in raised girdle. To facilitate wide dispersal, the rear half of the body is raised from the substrate during release (fig. 31). As fertilization is external, synchronised emission of sperm and ova is needed to ensure success; trigger in many chiton species is moon-phase/state of tides. Planktonic trochophore larvae hatch and metamorphose into small adult-form young without intervening veliger stage.

Distribution and status

T. marmorea is widely distributed in the northern North Atlantic, Arctic Ocean and White Sea, from Novaya Zemlya, Spitzbergen and Baffin Island southwards to Northumbria and Wales (UK) and Cape Cod (USA). Records from further south need substantiation. Not recorded from Baltic or continental coast of North Sea. Those in north-west Atlantic have some differences from those in north-east Atlantic. There are also records of it in the Pacific southwards to the Sea of Japan (B. Sirenko, in litt.). GBIF map https://www.gbif.org/species/2306814 . It can be common in Scottish sea lochs; up to 50 /m² (Jones & Baxter, 1987). NBN UK distribution map: https://records.nbnatlas.org/occurrences/search?q=lsid:NHMSYS0021056553#tab_mapView

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Glossary

µm = 0.001 mm, 1000µm = 1 mm
acicular = slender and tapering to a point; needle-like.
aesthetes = complex of canals and cavities filled with sensory tissue that permeate tegmentum and locally penetrate articulamentum. Open as sensory pores on dorsal surface of valves; probably compensate for lack of sensory structures on head. Some sense light; other

sensory function(s) uncertain, but various authors have variously proposed chemoreception, mechanoreception, properiostracum replenishment and secretion of protective substances.
a.k.a. = also known as.
antemedian = (syn. antemedial) situated to anterior of middle.
antemucronal area = area situated to anterior of mucro.
apophysis = (pl. apophyses) anterior extension of articulamentum which underlies preceding valve; on all valves except head valve (i).
aragonite = orthorhombic crystalline mineral-form of calcium carbonate http://www.minerals.net/mineral/aragonite.aspx. Less common on land than calcite, but, currently, the more frequent mineral-form in oceans and living mollusc shells.
articulamentum = inner shell-layer of chiton valves, usually hard, white, porcelaneous aragonite and often differently coloured in central part.
calcite = trigonal crystalline mineral-form of calcium carbonate http://www.minerals.net/mineral/calcite.aspx. More common on land than aragonite, but, currently, the less frequent mineral-form in oceans and living mollusc shells.
cephalic = (adj.) of or on the head.
chemoreception = sensing of chemicals; “smell / taste”.
chitin = semitransparent flexible horny protein. Does not occur in molluscs.
chitinous = (adj.) resembling chitin.
cilia (pl.) = motile linear extensions of membrane used in locomotion, or to create water currents in feeding. (“cilium” singular).
coll. = in the collection of (named person or institution) (cf. legit).
dioecious = having separate male and female individuals.
dorso-ventrally flattened = as if pressed flat from above.
ELWS = extreme low water spring tide (usually near equinoxes).
epithelium = tissue forming outer layer of body surface, “skin”.
girdle = peripheral band of thickened, reflexed mantle that encloses ends of valves.
gonopore = genital opening through which eggs or sperm are released.
holobranch = gills in mantle cavity extend full length of foot.
hyponotum = ventral cuticle of chiton’s girdle.
insertion plate = (on most chitons) part of articulamentum on lateral margin of intermediate valves, anterior margin of head valve and posterior margin of tail valve. Inserts into, and anchors valve to, the girdle muscle block.
intermediate valve = any valve (ii – vii), except head valve (i) and tail valve (viii).
interspecific = existing or occurring between different species.
intraspecific = occurring or existing within a single species.
jugal area = summit zone of chiton valves on dorsal surface.
jugal tract = summit zone of chiton valves on ventral surface.
jugum = summit of chiton valves.
lateral area = (on intermediate valve of chiton) triangular area with its base along lateral edge of valve and its apex near the centre of the posterior edge. a.k.a. lateral triangle.
Leg. Mc&T = Leg. David M. McKay and Simon Taylor.
legit = (abbreviation; **leg.**) collected/ found by (cf. coll.)
LWS = low water spring tide, two periods of a few days each month when tide falls lowest.
mantle = sheet of tissue that secretes the shell and forms a cavity for the gills.
mantle cavity = (a.k.a. pallial groove) narrow groove around whole foot and head, roofed by mantle and containing gills, nephridiopores and gonopores.
magnetite = mineral of iron oxide, hardest material made by any living organism.
marmorated = veined or streaked like marble.
mechanoreception = sensing of touch, sound, pressure change and/or posture.
MLW = mean low water mark.
merobranch = gills in pallial cavity only in posterior two-thirds of animal.
mucro = small projection on tail valve (viii), varies in prominence and position.
myostracum = thin, inconspicuous, discontinuous, innermost layer of chiton shell.
nephridium = tubular glandular excretory/ osmoregulatory organ (a.k.a. kidney).

nephridiopore = opening of nephridium for excretion (a.k.a. renal pore).
odontophore = firm, approximately ellipsoid, structure of cartilage supporting radula, protruded like a tongue to operate radula.
pericardium = membranous sac containing heart and start of aorta.
perinotum = dorsal cuticle of chiton's girdle.
pleural area = (on intermediate valve) triangular area with its base along anterior edge of valve and its apex near the centre of the posterior edge (a.k.a. median triangle).

postmucronal = situated to posterior of mucro.
properiostracum = (on chitons) outermost layer of colour-bearing proteinaceous material, sometimes resembling collagen in texture and differing in composition from periostracum of most other mollusc groups.
plankton = animals and plants that drift in pelagic zone (main body of water).
radula = chitinous ribbon of teeth extruded on odontophore to rasp food.
SEM = scanning electron microscope.
side slope = (on chiton) shape in profile view (from posterior or anterior) of lateral areas of intermediate valves; may be straight, convex, concave or a combination of these.
sinus = 1. dilated channel or receptacle containing blood etc. 2. gap between apophyses.
slit ray = row of canal pores running diagonally from lateral slit to posterior edge on ventral surface of chiton valve (a.k.a. notch ray).
suture = line where two valves meet.
tegmentum = outer shell-layer of chiton valves, usually porous and relatively soft (covered by transparent properiostracum when live).
trochophore = spherical or pear-shaped larvae that swim with aid of girdle of cilia. Stage preceding veliger, passed within gastropod egg in most spp. but free in plankton for limpets, Trochidae and (with no veligers) chitons.
uncinate = having a hooked shape.
uncinate blades = largest two teeth in each row of seventeen on chiton radulae; principal scraping blades, often darkened more than other teeth by their high magnetite content.
veliger = shelled larva of marine gastropod or bivalve mollusc which swims by beating cilia of a velum (bilobed flap).