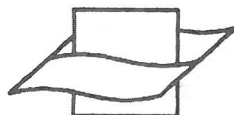


THE PROSOBRANCH MOLLUSCS OF BRITAIN AND DENMARK

PART 2 — TROCHACEA
VERA FRETTER and ALASTAIR GRAHAM
Department of Zoology, University of Reading

263391



Vlaams Instituut voor de Zee
Flanders Marine Institute

SUPPLEMENT 3
THE JOURNAL OF MOLLUSCAN STUDIES
JULY 1977

TROCHACEA

A group of diotocardians which have nearly achieved monotocardian status. The right ctenidium and osphradium are lost though the right auricle and kidney persist. The left ctenidium retains a bipectinate form at its anterior end but is monopectinate elsewhere. An epipodial fold with tentacles and sense organs on either side of the foot is continued anteriorly to form neck lobes at the level of the mouth of the mantle cavity (acting as inhalant and exhalant siphons) and on to the head to form lappets between the cephalic tentacles. All these structures bear complex multicellular sensory papillae. Posteriorly the foot carries dorsally a ridged glandular area under the hinder part of the operculum, which is polygyrous. The radula is rhipidoglossan. The sexes are separate and the gonad discharges gametes through the right kidney. The left kidney is a papillary sac of uncertain function in the mantle skirt. Fertilization is external though spawn masses may be formed from material secreted by the right hypobranchial gland or the urinogenital papilla of the female. The free-swimming larval stage is of short duration and may be suppressed.

The shell is spiral, almost always approaches a conical shape and has no slit. It is frequently umbilicate and often has a nacreous appearance. The aperture and the transverse ornamentation are markedly prosocline. The protoconch has a pointed and tilted tip, except in Skeneidae.

Trochaceans constitute an outstandingly successful group of marine prosobranchs which have undergone a wide adaptive radiation. Most are littoral or sublittoral in habitat and are primarily sweepers and scrapers of detrital fragments; the group, however, includes ciliary feeders such as *Umbonium* and carnivores like some species of *Calliostoma*. They tend to occur on hard bottoms but both *Umbonium* and *Skenea* spp. abound on and in soft ones.

In the European area dealt with four families are represented: Trochidae, Skeneidae, Turbinidae and Phasianellidae. *Circulus striatus*, the only representative in this area of the family Cyclostrematidae is here treated as a mesogastropod.

TROCHIDAE Rafinesque, 1815

The typical top-shells with all the characters of the superfamily Trochacea. The aperture has no peristome and the operculum is horny. Of the various subfamilies into which the family may be split five (if Höisaeter's revision of *Skenea* be accepted, six) are represented by the species described below.

The Margaritinae are the most primitive. The shell may be smooth but often shows spiral ornament, is umbilicate, the whorls rounded in cross section and the aperture oval. Vertical ornament is represented by occasional exaggeration of growth lines. The shell is nacreous externally and internally giving it a general pearly appearance. There are 5-6 epipodial tentacles on each side of the foot; the lips are not split mid-ventrally. Mucous spawn masses are laid on weed or stone and there is direct development.

The Gibbulinae have a bluntly conical shell in which an opaque and coloured outer layer conceals the inner nacre. The whorls, though rounded in section, tend to be flattened peripherally. The ornament is mainly spiral but some thickening of growth lines is obvious. The aperture is prosocline and rounded, the base of the shell usually umbilicate. The number of epipodial tentacles is less than in Margaritinae; the snout is notably papillose; the lips are split mid-ventrally and the edges of the split prolonged into small flaps under the snout. Eggs and sperm are broadcast and no spawn laid; there is a brief free larval stage.

The Monodontinae are to some extent intermediate between Gibbulinae and Calliostomatinae; *Monodonta* has a gibbuline shape of shell, *Cantharidus* a more conical one as in Calliostomatinae. All tend to have a tooth on the columella and to be without an umbilicus when fully grown. The ornament of *Monodonta* is as in *Gibbula*, whereas in *Cantharidus* thickening of growth lines has increased to form riblets of some prominence interacting with the spirals. The soft parts are gibbuline though the split lip is less obvious. Some broadcast gametes, others produce spawn masses.

The Calliostomatinae seem the most advanced subfamily. The shell is sharply conical, the whorls flat-sided, fitting closely at shallow sutures and showing interacting spiral and transverse ornamentation with a sharp peripheral keel. The aperture is angulated. An umbilicus may be present or not. The protoconch has a reticulate pattern of ridges on its surface. The snout is markedly papillose and a gutter-shaped or tubular extension of the mid-ventral lip runs on the right to the opening of the mantle cavity. The animals produce spawn masses and have no free larval stage.

The subfamily Solariellinae is often united with the Margaritinae but both shell and soft parts are sufficiently unlike to support separation. The group appears to derive from a margaritine stock which has adapted for a special mode of food-collecting in deeper waters. Transverse ornament in the form of ribs is conspicuous, the whorls are angulated in cross section and the umbilicus (usually present) edged with a circlet of tubercles. The epipodium is well developed. At the anterior end of the animal the front of the foot, the tentacles, snout and neck lobes are all modified for a mode of life still not known, but which may involve collection and selection of particles from the soft substratum on which the animals occur. The size of the protoconch suggests that development is direct.

MARGARITES HELICINUS (Phipps, 1774), pearly top-shell

Clio helycinus Phipps, 1774

Margarita helicina (Phipps, 1774)

Eumargarites helycinus (Phipps, 1774)

Trochus helycinus Fabricius, 1780

Helix margarita Montagu, 1808

Margarites (Gk.), a pearl; *helycinus* (Lat.), like a *Helix*.

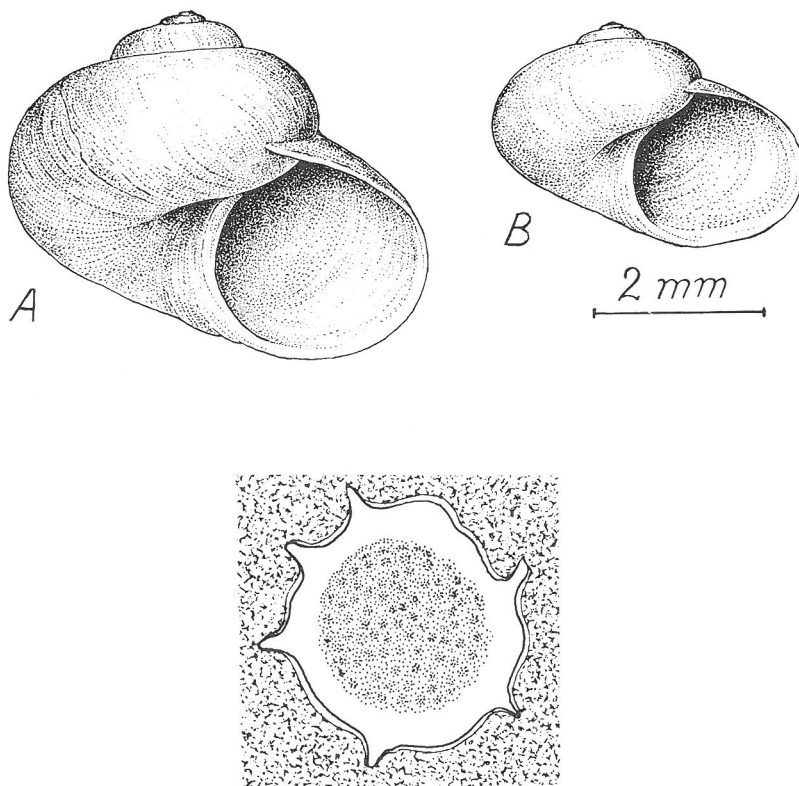


Fig. 26. *Margarites helycinus* (Fabricius). A, from Thorshavn, Faeroes; B, from Frederikshavn, Denmark. CMZ. Inset, spawn mass.

Shell. Glossy, translucent, smooth to the naked eye. In profile the general shape is a flattened, oblique oval; the spire is a depressed cone with apical angle $85-122^\circ$, commonly $105-110^\circ$. There are 4-5 whorls which are gently convex and dip noticeably to sharp sutures which lie at the periphery of older whorls. The shell is marked by very shallow growth lines which are prosocline; irregularity in their development (forming incipient ribs) causes the adapical edge of each whorl to be slightly sinuous and near the tip of the spire the minute ribs so formed may extend across the whorl abapically. Spiral ornament is absent except on the basal part of the body whorl where there are 15-20 low ridges and grooves; these extend into the conspicuous umbilicus, the mouth of which is slightly oval and partly occluded by the inner lip. The protoconch is smooth, of just over 1 whorl, with a pointed tip and measures about $160\mu\text{m}$ across.

Aperture. Oval, its long axis inclined abapically outwards at an angle about 120° from the axis of the shell. It is prosocline, its plane cutting the vertical axis at an angle of 40° . The outer lip is thin

adapically, tapering to the edge, but thickening abapically where it joins the columella. It meets the body whorl nearly at right angles. The columella is straight and the inner lip curves to meet the parietal region tangentially. The growth lines are visible internally.

Colour. Horn-coloured to orange-red, with green or purple refringency. The apex is paler and the colour of live shells may be affected by viscera showing through. Many shells have a more or less distinct brown band on the body whorl (and sometimes the preceding one) placed about one-third of the distance between suture and periphery. Internally the same colour as externally with greater refringency.

Size. *M. helycinus* has been found in Greenland 9mm high x 11mm broad, but it has rarely more than half these dimensions at the southern limits of its range. Body whorl = 90% of shell height, aperture = 45% of shell height.

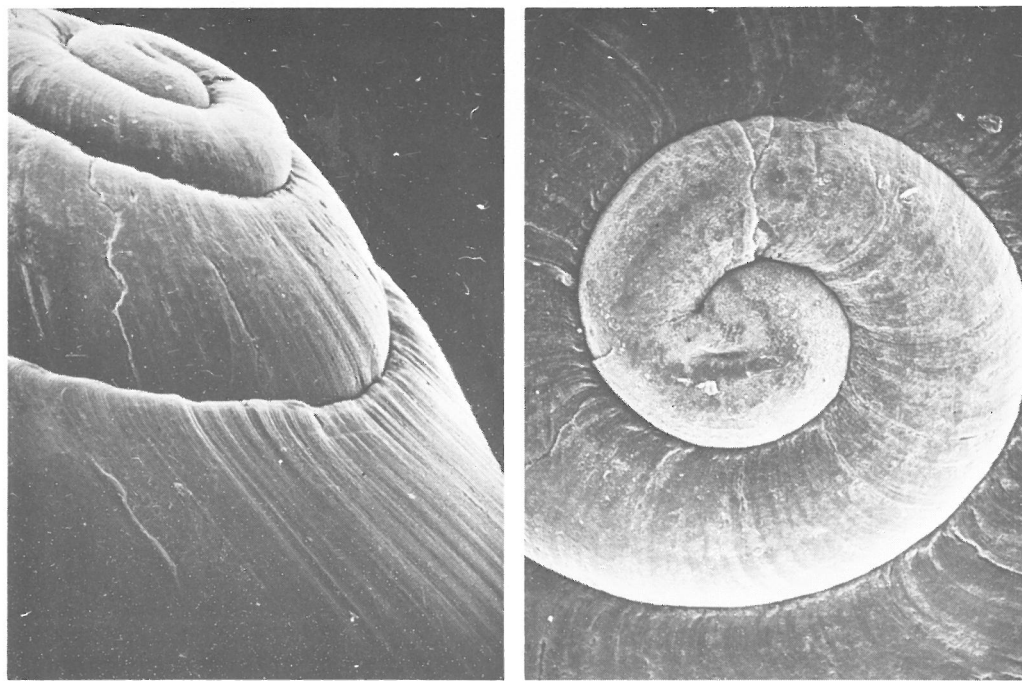


Fig. 27. *Margarites helycinus* (Fabricius). A, upper part of spire from the side, X 160; B, apical region from above, X 250. SEM photographs. Oban, RUZ.

Animal. The head carries a stout, down-turned snout, slightly expanded and lobed at the tip, the lateral margins being extended a little posteriorly to form lobes like those of *Lepeta* or *Acmaea virginea* though smaller. These extend backwards as low ridges on the sides of the snout. The dorsal surface of the snout bears many complex, multicellular papillae with apical processes, presumably sensory. The mouth lies on the truncated apex of the snout, vertically elongated when closed, surrounded by radially folded lips lacking cilia and sensory papillae. The cephalic tentacles are long and edged (medially and laterally) by papillae like those on the snout, which give them a setose appearance. An eye stalk on the outer side of each tentacle carries a black eye and on the inner side lies a small, smooth-edged cephalic lappet. On each side of the neck is a laminar lobe with a smooth edge without sensory papillae. The mantle edge is double, without lobes.

Foot narrow, elongated, rather truncated anteriorly (where it has a double edge) and posteriorly. The cleft at the front marks the anterior pedal gland whose duct extends inwards to a length about one quarter that of the sole. The sides of the foot are irregularly ridged and carry epipodial tentacles with the same papillate structure anteriorly and posteriorly as the cephalic ones and, in addition, a pigmented sense organ below the base. There are usually 6 tentacles on each side, but one may be absent; they arise from slight sheaths below a longitudinal epipodial ridge along the side of

the foot dorsally. One or more extra sense organs, without tentacles, may lie under each neck lobe. The operculum, carried on the smooth dorsal surface of the hinder part of the foot is circular, multispiral (10-12 turns) and slightly concave.

Colour. Yellow to orange, with purplish lines on the sides of the foot; dorsal surface of snout, neck lobes and cephalic lappets often dusky purple.

Geographical distribution. *M. helycinus* is a circumboreal species which extends S. into all oceans. In Europe it reaches to the W. coast of Sweden (Bohuslän); to the Yorkshire coast on the E. of Britain, the Isle of Man and N. Wales on the W.; to Dublin on the E. coast of Ireland but appears to be absent from the W. It does not occur in Denmark. In the W. Atlantic the species reaches S. to Massachusetts and in the Pacific to Vancouver Island and the northern parts of Japan.

Habitat. This top-shell occurs commonly in the lower parts of rocky shores and extends to depths of a few metres off Britain, though further north (Greenland, Barents Sea) it may live as deep as 350-400m. It is found crawling on *Fucus* and *Laminaria* fronds and amongst *Delesseria* and similar algae, but is more plentiful on the stones on which the smaller weeds grow. Intertidal animals not in rock pools hide under stones at low water and are then often in groups. When crawling the cephalic tentacles are used as a blind man uses a stick and the epipodial tentacles are very active as in trochids generally.

Food. The gut contains much detrital material—diatom cases, sponge spicules, sand grains — and algal remains. Faeces rod-shaped, about 0.3mm in diameter; a liver string is set along a groove whilst the rest of the rod shows a series of sinuous grooves and ridges.

Breeding and growth. The animals breed in spring, laying eggs in mucous masses attached to *Laminaria*, *Fucus* or the under surface of stones. Each egg measures 140 μ m across, is colourless, and is enclosed within a membrane round which is a further protective coat, the total diameter being 200-220 μ m. These coats are elaborated in the ovary. Fertilization is external. About 100 eggs are fastened together in mucus from the greatly enlarged urinogenital papilla of the female. The spawn is attached to the substratum by anchoring threads drawn from the main mass of mucus by the foot. There is no free larval stage and the young hatch as miniature snails (Fretter, 1955).

There are no studies on the growth of *M. helycinus*.

MARGARITES GROENLANDICUS (Gmelin, 1790)

Trochus groenlandicus Gmelin, 1790

Margarita groenlandica (Gmelin, 1790)

Margarita undulata Sowerby, 1838

Groenlandicus (Lat.), from Greenland.

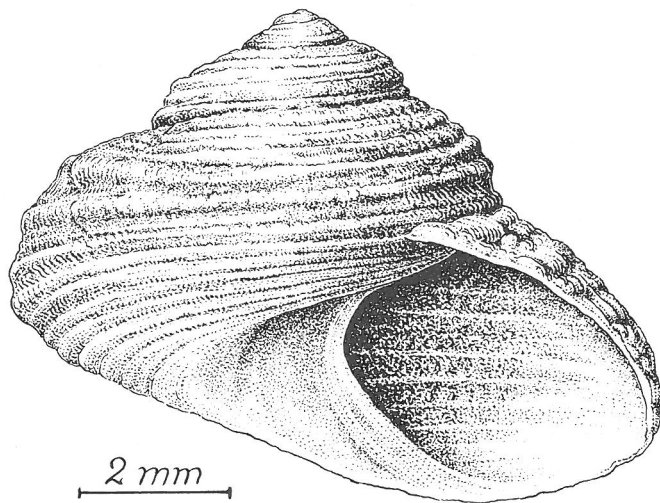


Fig. 28. *Margarites groenlandicus* (Gmelin). Nolsø, Faeroes, CMZ.

Shell. With the same general shape as that of *M. helacinus* but considerably larger when full grown, this differs in having a more elevated spire (apical angle about $105 \pm 5^\circ$) and a more complex ornamentation, though the species is notably variable in the last respect. The growth lines are sometimes elevated in groups at intervals below the sutures, representing incipient ribs. Most shells bear spiral ridges separated by furrows within which the growth lines are clearest. There are 9 or 10 ridges in full-sized specimens between the suture and the periphery of the body whorl, moderately raised and narrower than the furrows; occasionally they may be more or less regularly larger and smaller. On the base of the whorl between the periphery and the umbilicus the ridges are flat, strap-shaped areas separated by narrow, incised grooves. There are 12-15 of each in large shells; the most abapical ridge occasionally forms a distinct edge to the umbilicus which is wider than in *helacinus* and allows the whole inside of the spire to be seen. The penultimate whorl carries 5-7 ridges and the previous one 4-5. In some shells the number of ridges is reduced, those in the subsutural parts of the whorls disappearing first and leaving only a group of 5-6 at the periphery. A few shells are smooth or have only 1 or 2 furrows at the periphery and the same number of finely incised lines near the umbilicus. Where spirals are prominent the body whorl may appear angulated at the periphery. There are in all 5-6 whorls, about as tumid as those of *helacinus*, which plunge abapically more or less vertically into the sutures. The nucleus is smooth, has an uptilted tip and measures $210 \mu\text{m}$ across its $1\frac{1}{4}$ whorls.

Aperture. Prosocline. In general outline it has an oblique quadrilateral shape, its axis making an angle of about 135° with the vertical axis of the shell. The outer lip is thin but thickened at the ends of the spiral ridges, slightly flattened in its adapical half and again below the periphery. The inner lip and columella run obliquely abapically but curve rather sharply to the parietal area above. The inner lip occludes part of the umbilicus.

Colour. Cream, pale tan or pale orange, often with a tinge of pink, without the refulgence of *helacinus*. Apex pale. Internally it shows a blue-green refringence.



Fig. 29. *Margarites groenlandicus* (Gmelin). Apex of shell, X 64. SEM photograph. BMNH.

Size. 7mm high x 8 broad. Body whorl = 85% total shell height; aperture = 55% total shell height.

Animal. The snout ends in a broad disk with a deeply lobed margin drawn out into lateral points. The mouth is a vertical slit when closed and is surrounded by radially folded lips. The cephalic tentacles are long and thin, each with a rather short eye stalk on its lateral side and a plain-edged, semicircular cephalic lappet medially. The eye stalk connects with a ridge running forwards on the side of the snout to its lateral angle. Behind each tentacle a neck lobe, smooth-edged, forms the beginning of an epipodial fold. Mantle edge smooth and simple.

The foot is broad anteriorly where it has a double edge and tapers to a slightly truncated posterior margin. Its flanks are rather smooth. On each side 7 tentacles arise from short sheaths under the epipodial fold; ventral to each is a lamellar sense organ, that associated with the most anterior close to the neck lobe. Of the tentacles 4 lie alongside the operculum. Each resembles a cephalic tentacle. The operculum is polygyrous (10-12 turns) and is distinctly concave.

Colour. Cream or white with a few dark streaks on the sides of the foot, tentacles and mantle skirt. The epipodial sense organs and eyes are black.

Geographical distribution. This species occurs in Arctic waters and extends S. into the Atlantic Ocean, reaching the W. coast of Norway and the N.W. coasts of the British Isles as far S. as the N. Channel. It does not enter the Skagerrak, Kattegat or N. Sea. In W. Atlantic waters it reaches S. to Massachusetts Bay.

Habitat. As for *M. helicinus* — under stones, on weeds, in *Laminaria* holdfasts at ELWS and sublittorally to 70-75m. It is rare on British coasts, as might be expected at its extreme southern limits. Thorson (1944) described it as 'by far the most common shallow water prosobranch occurring in East Greenland', where it is always sublittoral, mainly at depths of 10-30m. In the Kola Gulf it abounds on *Lithothamnium* at similar depths (Derjugin, 1915).

Food. Presumably as for *helicinus*. Faecal rods like those of that species.

Breeding and growth. There are no observations on breeding in Britain. Thorson (1935) investigated breeding in East Greenland and found that spawn masses were probably attached to algae and that there was no free larval stage.

Notes. The common type of shell in European and American waters has numerous spiral ridges; in Greenland the usual form has a smooth shell.

MARGARITES ARGENTATUS (Gould, 1841)

Margarita olivacea Brown, 1827 (fossil)

Margarita argentata Gould, 1841

Margarita glauca Möller, 1842

Margarita harrisoni Hancock, 1846

Argentatus (Lat.), silvery.

Shell. Rather delicate, semitransparent, glossy. In general shape it is globose with a conical spire (apical angle 80-90°) of 4 convex whorls which meet at deep sutures at a level slightly below the periphery of the upper whorl (sutural angle 115-120°). Nucleus smooth, of 1¼ whorls, about 500µm in diameter. The whorls are marked by many very fine growth lines, sometimes bunched and raised below the sutures to make ribs. More obvious is a series of slight spiral ridges, narrower than or equal to the intervening spaces, most clear on older whorls and the base, less obvious at the periphery of the body whorl. There are about 100 on the body whorl, 30 on the penultimate, 12 and 8 on the preceding two. They enter the umbilicus, which is large. In some shells they are alternately larger and smaller.

Aperture. Proscloine, making an angle of 120° with the axis of the helicocone. The outer lip arises nearly at right angles just below the periphery of the body whorl and sweeps in a smooth curve, almost circular, to where the inner lip ends as a glaze on the body whorl. The aperture has a thin edge everywhere. The inner lip partly blocks the umbilicus.

Colour. Olive, grey, cream or white with a green or purple refringence best seen on wet shells.

Size. Up to about 8 x 8 mm but those collected off Scotland were only about 3 x 4 mm.

Animal. Much like that of *M. groenlandicus*. The tip of the snout is not so extended laterally and the ridges along the sides of the snout are almost absent. The eye stalks are short; they separate from the tentacle only at the level of the eye. There are only 5 epipodial tentacles on each side of the foot.



Fig. 30. *Margarites argentatus* (Gould). Apex of shell, X 120. SEM photograph. BMNH.

Colour. Cream, with a few dark speckles and a dark band along the edge of the mantle skirt.

Geographical distribution. Like other species of this genus, *argentatus* occurs primarily in Arctic seas and extends S., but less successfully than either *helicinus* or *groenlandicus* since it is both rarer and smaller in Britain, Norway and America. It reaches S. in Europe to W. Norwegian and Scottish coasts and in America to Massachusetts. It is not found in the Skagerrak, Kattegat or N. Sea.

Habitat. Sublittoral throughout its range; probably with the same mode of life as *groenlandicus*.

Food, breeding and growth. Unknown, but likely to be similar to the other species. Faeces form a rod similar to that of other species full of detrital material.

Notes. Though common in Arctic Seas this species has been dredged on only a few occasions off the W. coast of Scotland (Greenock, Skye, Outer Hebrides). Recent records are lacking.

REFERENCES

- DERJUGIN, K. M. 1915. Fauna of the Kola Gulf and its environmental conditions. *Zapiski Imperatorskoi akademii nauk*, **34**, 1.
- FRETTER, V. 1955. Some observations on *Tricolia pullus* (L.) and *Margarites helicinus* (Fabricius). *Proceedings of the Malacological Society of London*, **31**, 159-62.
- THORSON, G. 1935. Studies on the egg capsules and development of arctic marine prosobranchs. *Meddelelser om Grønland*, **100**, no. 5 1-71.
- THORSON, G. 1944. The Zoology of East Greenland. Marine Gastropoda Prosobranchiata. *Meddelelser om Grønland*, **121**, no. 13, 1-181.

SOLARIELLA AMABILIS (Jeffreys, 1865)
Trochus amabilis Jeffreys, 1865
Machaeroplax amabilis (Jeffreys, 1865)
Trochus cinctus Philippi, 1836 (fossil)
Solariella maculata Wood, 1842

Solariella (Lat.), a little sundial; *amabilis* (Lat.), lovely.

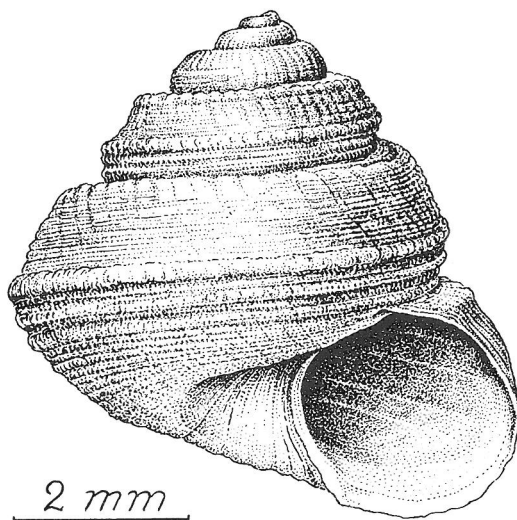


Fig. 31. *Solariella amabilis* (Jeffreys). Shetlands. (?)CZM.

Shell. Solid, glossy, pearly with a slight translucency. The spire has a stepped conical profile and an apical angle about 80° . There are 5-6 whorls, meeting at sharp sutures at an angle just over 90° , each bearing spiral ridges and ribs. The body whorl has four major spirals: (1) close to suture, (2) and (3) at the periphery, (4) on its base, round the umbilicus, (1) and (4) more elevated than the others. The whorls of the spire show only spirals (1) - (3). Numerous lesser ridges lie between the main ones of which one between (2) and (3) is best marked. They are least developed between the suture and the spiral (1); there and between (1) and (2) and (2) and (3) each whorl is flat or slightly concave whereas the base is gently convex. The ribs are less obvious in the oldest and youngest part of the shell than intermediately and on the body whorl may hardly extend abapical of spiral (2), though they affect (3) and (4) by giving them a beaded appearance. Their course is prosocline though they run at right angles to the suture until across spiral (1). They are low and broader than the intervening furrows where minor spirals often disappear. The shell is also marked with numerous growth lines which extend, parallel to the ribs, across the whole breadth of the whorls; they are best developed on the body whorl and extend into the umbilicus which is wide and deep. The sutures lie at the level of spiral (3). In the variety *affinis* ribs and spirals are of about equal development and the shell is squarely reticulated. The protoconch is prominent and swollen, of $1\frac{1}{4}$ whorls, about $280-300\mu\text{m}$ in diameter and shows a number of delicate longitudinal and transverse markings. The tilted tip found in trochids is small and squashed against the first whorl.

Aperture. Nearly circular internally but angulated externally by the spiral ridges, especially (1) and (4); outer lip thin; the inner, which slightly occludes the umbilicus, curves to form a film on the body whorl which joins the outer. Within the aperture the shell shows slight grooves coincident with the major external spirals.

Colour. Pearly white outside and inside, with a slight pink refringence; sometimes with a few reddish spots.

Size. Up to 8mm high, 8mm broad. Body whorl = 70-75% of shell height; aperture = 40% of shell height.

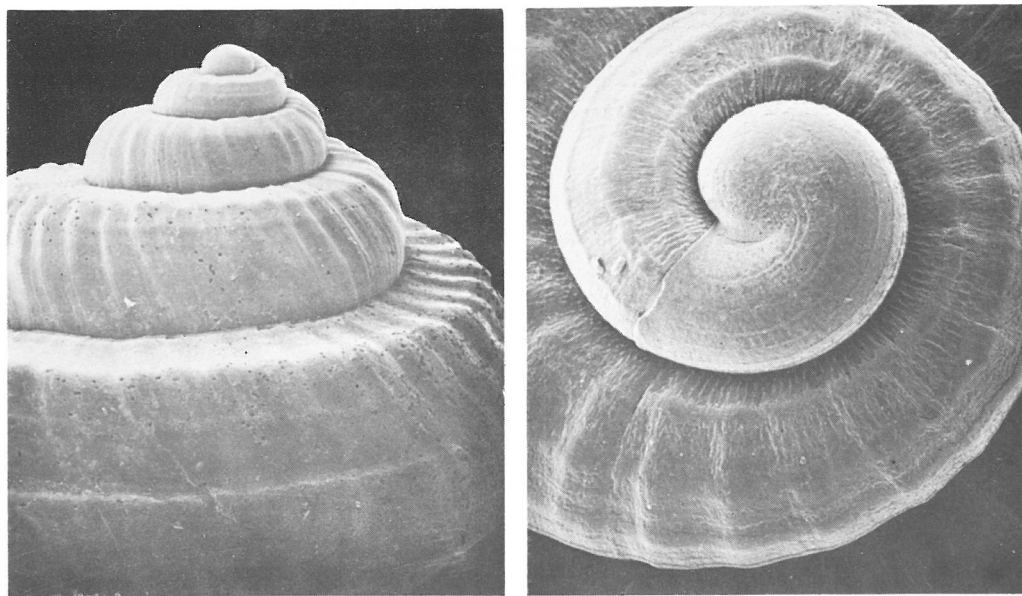


Fig. 32. *Solariella amabilis* (Jeffreys). A, spire in side view, X 40; B, apical region from above, X 165. SEM photographs. BMNH.

Animal. The snout is very depressed, its tip elongated transversely. The edges of the oral disk are drawn out into finger-shaped processes and the mouth is a transverse opening in their centre. The cephalic tentacles are very long, tapering to fine tips and not setose; at their base lies a short and rather slender eye stalk carrying a small eye. There are no cephalic lappets. The neck lobes are much reduced; that on the left forms a short tentacle, that on the right a small flap joined to the underside of the eye stalk and rolled into a tube.

The foot is large, broad anteriorly and tapering behind. Its anterolateral corners are drawn out into long, grooved processes, the grooves continuous across the front of the foot. The flanks are papillated and bear an epipodial ridge on each side from below which three stout tentacles project alongside the opercular lobe. No sense organs apparent.

Colour. Cream with some brown markings on the side of the foot.

Geographical distribution. N. Atlantic, from the Bay of Biscay north to the Shetlands; not in the Channel and N. Sea. Its western extension unknown though Nordsieck recorded it from the W. Indies. Abbott (1974) does not regard it as an American species.

Habitat. Never littoral; dredged from bottoms of sand and gravel at depths of 155 - over 1200m.

Food. Unknown, though it is said to be a predator (Nordsieck). The presence of tentaculiform extensions of the lips and foot suggests the evolution of sensory processes capable of locating food at depths where eyes are of decreasing value and where only animal food and detritus are available. The grooves on the anterior pedal extensions, ridges which occur on the right neck lobe of *S. infundibulum*, the extensions of the lips and the reduced snout indicative of a small buccal mass, are all compatible with either a ciliary food-collecting mechanism, or a sweeping of the substratum as in *Lepeta* spp. or a combination of both. This is supported by the nature of the faeces, which contain predominantly sand grains and empty foraminiferan and other protozoan shells. Their form is as in other trochids — a rod with a groove containing the liver string, the surface of the rod bearing numerous sinuous ridges. That trochids are capable of evolving a ciliary food-collecting mechanism has been demonstrated by Fretter (1975) in *Umbonium vestiarium*.

Breeding and growth. The sexes are separate. The eggs are very large — about 300µm in diameter — and surrounded by jelly; they are not numerous. There is no enlargement in the specimens which we have seen of the terminal part of the oviduct and the hypobranchial gland is not noticeably large: unless these occur at egg-laying, their lack suggests that the eggs are laid singly, though conceivably attached to the substratum by their own jelly coat. Development is almost certainly direct with suppression of free-swimming larvae as suggested by the large eggs and protoconch.

Notes. *S. amabilis* has been found only a few times off British coasts — off Unst — and that nearly a hundred years ago. How much this reflects current scarcity of the animal and how much inadequate searching is difficult to decide. In other parts of the Atlantic where dredging has been done — Celtic Sea and western coasts of France and Iberia it has been found not uncommonly as claimed by Marshall (1898). Abbott (1974) records other species (*lacunella* Dall, *lamellosa* Verrill & Smith) as common off eastern America: if they resemble *amabilis* their anatomy and biology deserve study.

REFERENCES

- ABBOTT, R. T. 1974. *American Seashells*. Van Nostrand Reinhold Co., New York.
DALL, W. H. 1890. Scientific results of explorations by the U.S. Fish Commission steamer "Albatross". VII. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887-88. *Proceedings of the United States National Museum*, 12, 219-362.
FRETTER, V. 1975. *Umbonium vestiarium*, a filter-feeding trochid. *Journal of Zoology, London*, 177, 541-52.
MARSHALL, J. T. 1898. Additions to "British Conchology". *Journal of Conchology*, 9, 61-74.
PELSENEER, P. 1888. Report on the anatomy of deep-sea Mollusca. *Challenger Reports*, 27, II, 1-42.

GIBBULA CINERARIA (Linnaeus, 1758), grey top-shell
Trochus cinerarius Linnaeus, 1758
Trochus lineatus da Costa, 1778 (not *Turbo*)
Trochus inflatus Blainville, 1826

Gibbula (Lat.), a little hump; *cineraria* (Lat.), ash-coloured.

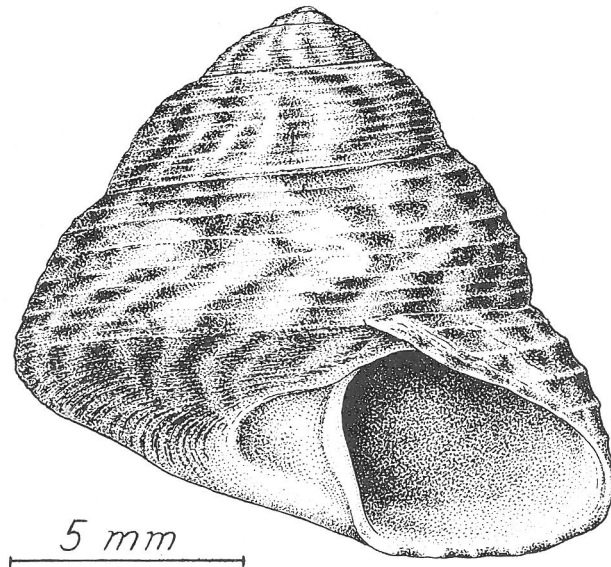


Fig. 33. *Gibbula cineraria* (L.). Limfjord. CZM.

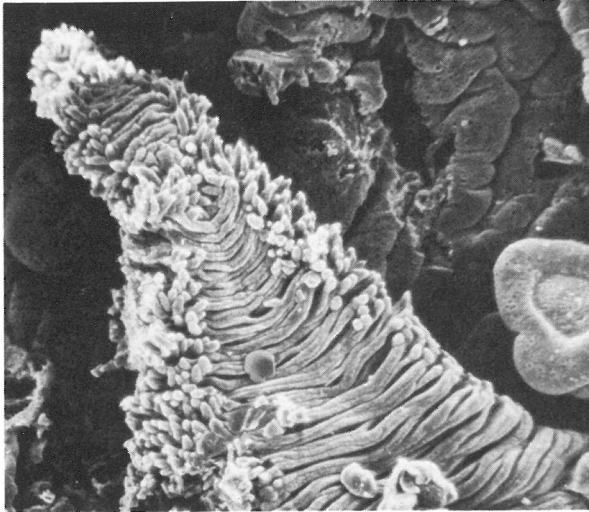
Shell. Solid, opaque; young shells and the less exposed parts of older ones slightly glossy. Generally conical in shape and almost always a little dome-shaped (cyrtocoid) though not so much as *umbilicalis*, with flat base and an angulated body whorl (80-85°). Apical angle of shell 70-100°, commonly 85-90° in mature shells but noticeably more (90-125°) in young ones; occasional older shells retain this squatter shape. There are 5-6 whorls, slightly swollen and dipping a little to sutures which are well marked on young shells and older whorls of old ones but may be indistinct elsewhere. Sutural angle approaches 180°. Below each suture the whorls may be a little flattened, giving a slightly turreted profile. The ornamentation is spiral ridges and grooves, and growth lines. The ridges are low and the furrows shallow, both variable in disposition: body whorl (above keel) — 6-15, commonly 8-10; penultimate — 7-11, commonly 8-9; antepenultimate — 7-10, fairly regularly 8-9. They are rarely of equal size or equidistant, though more nearly so on younger whorls; there is commonly a group of low, narrow ridges at the periphery of the body whorl and each whorl makes contact with the previous at this level, sometimes obscuring all, sometimes exposing a few. There are 10-17, most frequently 13-14, ridges on the base. Most spiral ridges show an alternation of elevations and depressions along their length. Growth lines are prosocline, curving back from the suture on the adapical parts of the whorls, the concavity facing up the whorl towards the apex; on the base the curvature is reversed so that each line is S-shaped. They are commonly visible only in the spiral furrows. Erosion may destroy all ornamentation and expose the underlying nacre. The umbilicus is rather small, its mouth egg-shaped, the narrow end pointing to the origin of the outer lip; in eroded shells the umbilical cavity may tunnel through the whole shell with loss of the apex. Apex depressed, of 1¼ whorls, with a pointed, reversed tip, smooth and about 140µm across.



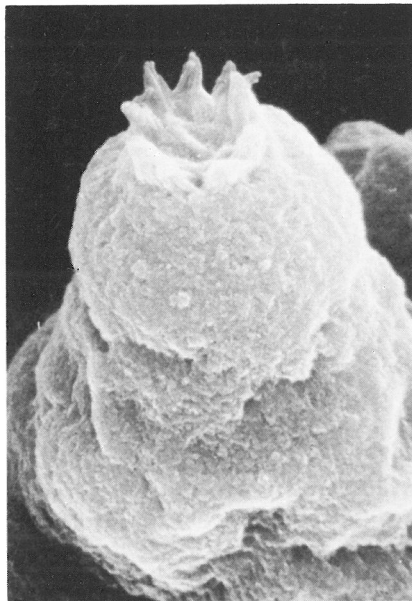
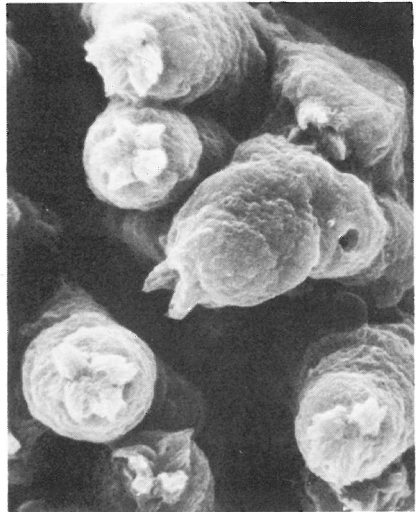
Fig. 34. *Gibbula cineraria* (L.). Apical region of shell from above, slightly oblique, X 250. SEM photograph. Plymouth RUZ.

Aperture. Prosocline, its plane at an angle of 130° to the vertical. It is a quadrilateral, somewhat rhomboid opening. The outer lip arises at or near the periphery, at right angles to the body whorl in young shells but at an acute angle in older ones. Apically rather straight, it curves sharply to run, again rather straight and slightly out-turned, to the columella which it joins almost rectangularly. The columella is nearly straight, vertical, with a slight tooth centrally. The inner lip turns outward over a groove leading to the umbilicus and spreads as a film over the body whorl to the outer lip. In basal view the basal lip is rather straighter than in *G. umbilicalis*.

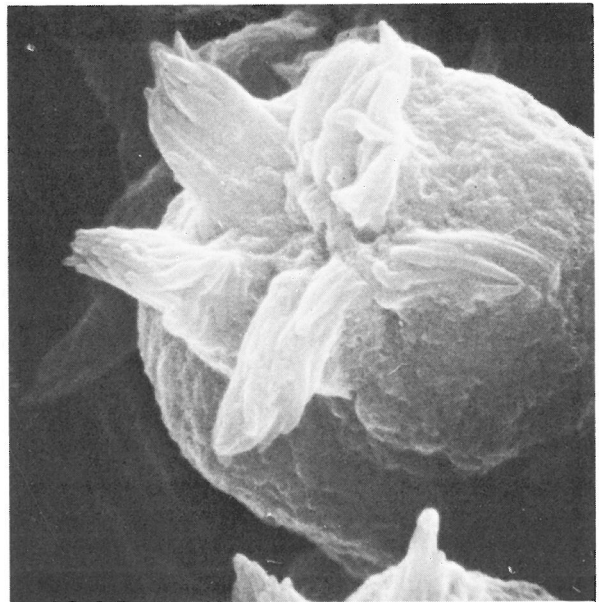
A



B



C



D

Fig. 35. *Gibbula cineraria* (L.). A, epipodial tentacle showing lateral lines of sensory papillae; sense organ on right, X 100; B, sensory papillae, X 900; C, papilla, X 2200; D, papilla, X 4000. Millport; Bedford College, University of London. (Courtesy of Dr Elizabeth Andrews.)

Colour. Externally, grey or yellowish with many fine, reddish, brown or purple lines, sometimes interrupted to give streaks or spots, less frequently branching, but so fine as to provide a general pigmented appearance to the naked eye. They are opisthocline and cross the growth lines more or less at right angles; the pigmented parts of the spiral ridges are less raised than the unpigmented ones. The umbilical area is not pigmented. Internally, the pigment bands produce a narrow row of spots on and within the outer lip bounded by a groove within which is a white area; the rest shows a blue nacre.

Size. Up to 16 mm high x 15 mm broad, occasionally much lower for the same breadth. Body whorl = 60-72% of shell height; aperture = 40-42% of shell height.

Animal. Snout of moderate size, convex dorsally, flattened ventrally, its anterior edge lobed. The tip is truncated, somewhat triangular in shape, with a central \wedge -shaped mouth surrounded by radially lobed lips. Mid-ventrally the lip is split by a groove of which the right wall is drawn out into a flap. The ventrolateral edges of the snout extend into longitudinal folds edged with papillae and others are set in an incomplete row over the dorsal surface of the snout at its tip. The cephalic tentacles are long and papillated; at their base laterally is a short, stout eye stalk with apical eye, each connected dorsal to the tentacle base to a cephalic lappet fringed with about a dozen papillae and with others on its ventral surface. A short postoptic tentacle projects from the ventral side of the right eye stalk. Posterior to each stalk (united to the right one) is a neck lobe, the right smooth-edged, the left fringed with more than one row of papillae which may branch; during life both roll to form a tubular entrance to and exit from the mantle cavity. Mantle edge smooth.

Foot oval at rest, narrower behind, with a longitudinal median furrow and numerous transverse ones which are less obvious during movement when the foot shows direct ditaxic waves. There is no anterior pedal gland. The edge of the sole and the most ventral part of the sides of the foot are papillated, the rest covered with rounded lobules. At a dorsal level on each side lies an epipodial fold with a fringed edge. Below it lie three long epipodial tentacles, the most anterior with a sensory papilla behind its base, the others with papillae below the base. They arise out of short sheaths. Extra papillae lie one under each neck lobe. Operculum polygyrous. The dorsal surface of the foot between the attachment of the operculum and the posterior lip is marked by a series of transverse ridges and grooves.

Colour. General colour of the flesh is yellow-grey with speckles or bands of purple on exposed parts — transverse lines on the snout; transverse and often a central longitudinal line on the cephalic and epipodial tentacles; longitudinal lines on the sides of the foot. Northern animals tend to be darker than southern ones.

Geographical distribution. Western European coasts from Gibraltar to N. Norway, Iceland. On all Channel and N. Sea coasts, in Limfjord, and in the Kattegat to Øresund, but not in Isefjord.

Habitat. Like all top-shells *G. cineraria* prefers rocky shores with stones, broken surfaces, crannies and pools; it is better able to tolerate sand than some others and may be frequent on rocky shores with sand. It requires some shelter and avoids the most exposed situations, preferring flatter to steeper shores unless these are well provided with crevices, preferences reflecting its relatively poor powers of adhesion (Ebling *et al.*, 1948). It occupies the lower half of the beach from about LWNT and extends to depths of about 130m. It may occur in pools, especially in the north, at levels above LWNT. It can be found on and amongst weeds (*Fucus serratus*, laminarians, *Bifurcaria bifurcata*, many small reds), under stones, under ledges and often in large numbers in pools; it dislikes too much weed cover and avoids mud. It always occurs most densely at a level lower than *G. umbilicalis* since it tolerates only up to 30% emersion but may be found relatively higher on shores from which *umbilicalis* is absent. The animals survive in salinities down to 25‰ (Arnold, 1972) and may be a little more resistant than *umbilicalis* (Nelson-Smith, 1967).

Food. Although it may be seen to rasp macrophytic algae and may ingest some of their tissue, this is primarily a scraper of fine material, its gut being filled with detrital material of all sorts. The faeces are rod-shaped with a gutter on one side in which lies a ridge covered with mucus — the liver string. The remainder forms the stomach string. Coarse particles lie in the walls of the groove whereas the outer surface is fine and sculptured with well-marked sinusoidal ridges and grooves. Rods measure up to 1.0 mm in diameter, 3-4 mm long.

Breeding and growth. See Gersch (1936) and Underwood (1972). The sexes are separate and can be told apart only by examining the colour of the ripening gonad — cream in ♂♂, green in ♀♀. There is no clear annual cycle and mature gametes may be found all the year round, but records suggest that the animals spawn in spring. The eggs, when shed, are 120-140µm across but are

enveloped in a jelly coat produced within the ovary which increases the total diameter to 160-180 μ m. The larval life is brief and settlement occurs widely over the shore, though only those at low levels survive. The growth of this species is less well known than that of *umbilicalis* and *Monodonta lineata* but may well follow the same pattern.

Notes. This is the only top-shell to be found between tide-marks on all British and Irish shores and on the continental coasts of the Atlantic and N. Sea. It is particularly common, where conditions are appropriate, on N. Sea shores and is normally larger in the north. In many places it abounds (densities up to 25m⁻²) and must be regarded as an eminently successful species.

In most shells from British shores the bands of pigment are narrower and more numerous than they are represented in the drawing and the spiral ridges are slightly broader and more nodose.

GIBBULA UMBILICALIS (da Costa, 1778), flat top-shell

Trochus umbilicalis da Costa, 1778

Trochus obliquatus Gmelin, 1790

Trochus umbilicatus Montagu, 1803

Trochus cinerarius Blainville, 1826

Trochus agathensis Récluz, 1843

Gibbula (Lat.), a little hump; *umbilicalis* (Lat.), with an umbilicus; to emphasize its conspicuousness compared with that of *cineraria*.

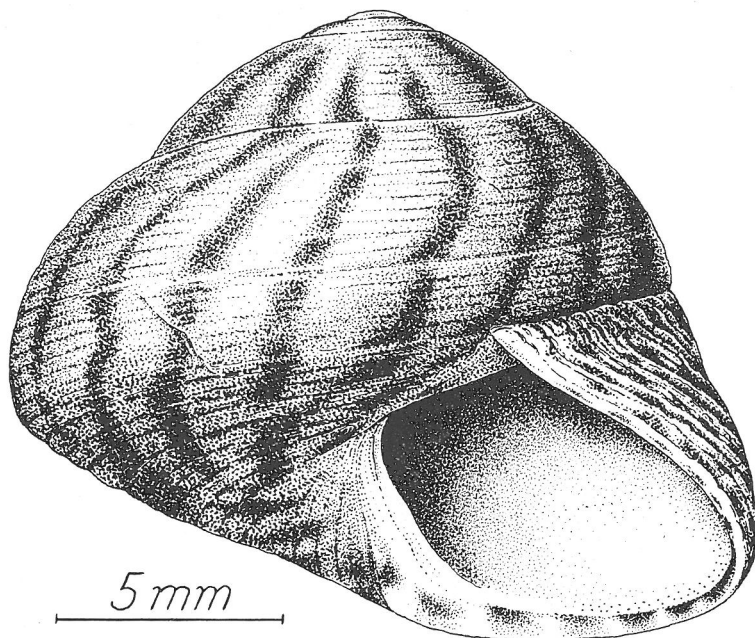


Fig. 36. *Gibbula umbilicalis* (da Costa). Falmouth. BMNH.

Shell. In general like that of *cineraria* but easily distinguishable by having fewer, broader and brighter bands of colour and a larger, more circular umbilicus. The shell is also more dome-shaped, almost paraboloid, never conical as sometimes in *cineraria*, the body whorl more sharply angulated (70-80°), especially in young shells, and occupying a greater proportion of the total height. The ornamentation is as in *cineraria* though usually even more completely obscured by wear, but the number of ridges and grooves on the base of the body whorl is less (8-11) and the groove closest to the periphery is often much excavated, especially in young shells; the ridges do not show beaded elevations as in *cineraria*. Growth lines are often indcipherable and always less well marked.

Aperture like that of *cineraria* save that the outer lip and columella meet at a more obtuse angle because of the less vertical direction of the latter. The inner lip curves more over the groove leading to the umbilicus. The basal lip in basal view is more curved near the columella than in *cineraria*.

Colour. The basic shell colour is cream often with a green tinge especially marked in young shells, crossed by opisthocline bands of colour, broader, further apart and redder than those of *cineraria* so that the shell is clearly banded to the naked eye. They often branch towards the base of the whorl where they run to the very edge of the umbilicus rather than stopping short of it as in *cineraria*. Internally the row of coloured spots within the outer lip is broad and conspicuous and is usually red at the lip and green within.

Size. Up to 16 mm high x 22 mm broad — so broader than tall. Body whorl = 80% of shell height; aperture = 50% of shell height.

Animal. The differences between this species and *cineraria* are slight and relate mainly to colour and degree of papillation: the fringes on the snout are less well developed; the ventral labial flap is smaller; the cephalic lappets have a simple lobed margin as does also the left neck lobe. On the other hand the papillae around the edge of the sole are better developed and the sheath round the base of each epipodial tentacle is more obvious and lobed. The sole of the foot is less grooved. There are two epipodial sense organs ventral to the right neck lobe.

Colour. Yellowish, sometimes with a pink tinge, and marked with dark lines of purplish black. These run transversely on the snout and on the cephalic and epipodial tentacles (on which there may also be a longitudinal central line) and they mottle the sides of the foot, accentuating the grooves between the lobules, except near the edge of the sole which is left pale. The grooves of the dorsal subopercular area are also pigmented.

Geographical distribution. A more southern form than *cineraria*, *umbilicalis* extends N. along the Atlantic coast of France and W. coast of Britain to Orkney (Rendell, 1956) though uncommon and sublittoral north of Anglesey. It reaches along the Channel to the W. part of the Isle of Wight on the English side but as far as Calais on the French. It is found on most Irish coasts, but neither in the N. Sea nor in Scandinavia.

Habitat. This species is found on the same kind of shore, and often the same shore, as *G. cineraria*, but is perhaps more tolerant of exposure. It invariably occurs at a higher level, from about MLWS to MHWN, higher in pools and in a narrower belt in the north, tolerating up to 75% emersion. It survives in brackish water at salinities greater than 20-25‰. At low water it may be found in pools, under stones and ledges or amongst weed, for no special kind of which does it exhibit preference. Smaller animals live at a lower level than larger ones. See Colman (1933), Moore (1940), Evans (1947), Southward & Crisp (1954), Southward & Orton (1954), Bakker (1959), Moyses & Nelson-Smith (1963), Williams (1965), Nelson-Smith (1967), Arnold (1972).

Food. As for *cineraria*; it is particularly common rasping rock surfaces. The faeces are similar.

Breeding and growth. Sexes separate, distinguishable only by colour of gonad, which is cream-pink in males, green in females. Accounts of the annual cycle vary, though Williams (1965) and Underwood (1972) agree that the eggs, which are like those of *cineraria*, are spawned singly. According to Williams, working on a population in Cardigan Bay, this occurs in May-June and settlement of the spat in September. In their first year the animals grow to a shell width of 6.5 mm, double that at the end of the second year and then slowly reach a maximum of 16-17 mm. They become sexually mature at 8-9 mm in their second year; the maturation of gametes starts in the November before spawning and all animals are spent by October when a resting phase precedes the start of the next cycle. Underwood studied animals from Plymouth Sound in which he found maturation starting January — February with spawning in summer and early autumn. The free-swimming stage is brief and settlement is in early autumn; young animals may be found at most levels of the beach, though younger ones tend to be lower than older ones. Bakker (1959) showed that they exhibited a marked negative geotaxis and this may be responsible for an upward migration to their final level in the zone dominated by the fucoids *Fucus vesiculosus* and *F. spiralis*.

GIBBULA PENNANTI (Philippi, 1836)

Trochus obliquatus Gmelin, 1790 (in part)

Trochus lineatus Blainville, 1826

Trochus pennanti Philippi, 1836

Gibbula umbilicalis var. *agathensis* Récluz, 1843

Gibbula umbilicalis var. *imperfurata* Dautzenberg & Fischer, 1925

Pennanti (Lat.), Pennant's, named after Thomas Pennant (1726-98), author of *British Zoology*.

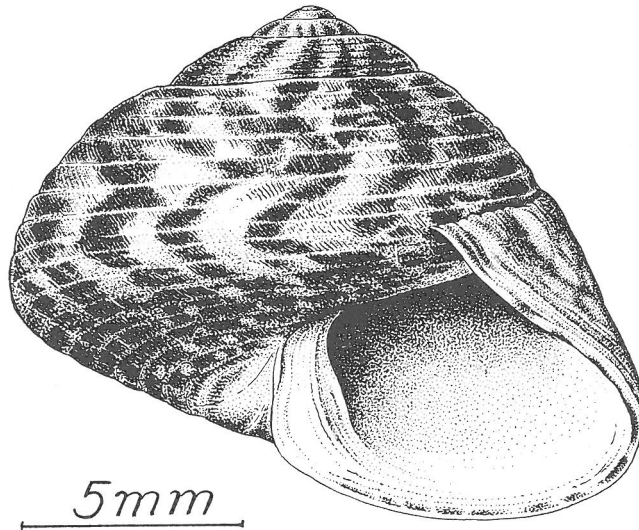


Fig. 37. *Gibbula pennanti* (Philippi). Guernsey. BMNH.

Shell. Though in general like that of *G. umbilicalis*, of which it was once regarded as a variety, the shell is rather variable. It is more conical at the apex than *umbilicalis* (apical angle 100-120° (mode about 112°), in young shells; 95° in grown ones). As in *cineraria* large shells may be taller than they are broad. The upper whorls are more tumid than those of *umbilicalis* and the sutures correspondingly more marked. Many shells show a shelf-like subsutural area which gives the profile a shape more like that of *tumida* and *magus* than that of *cineraria* and *umbilicalis*. The ornament is as in *umbilicalis*. Occasionally growth lines are in slighty raised groups, increasing the resemblance to *magus* but this is never as obvious as in that species. Young shells have an open umbilicus but this normally is closed as the animal grows, though a depression and occasional chink persist. The outermost groove and ridge on the base are not different from more central ones as they usually are in *umbilicalis*.

Aperture. As in *umbilicalis*, though the columellar region and inner lip are a little more vertical and a little broader.

Colour. The species is variable in this respect though most shells present more or less the same pattern as *umbilicalis* with splashes of purple rather than red. On the base the alternating areas of colour and background normally form a reticulate pattern rather than the stripes found in *umbilicalis*. The background may be white, cream, yellow or, less frequently, green, bluish or black. Some shells show no pattern, only a homogeneous coppery red, pea-green or black, with or without spiral bands of red or white at the periphery.

Size. Up to about 16 x 15mm. Body whorl = 66-80% of total height; aperture = 50-60% of total height.

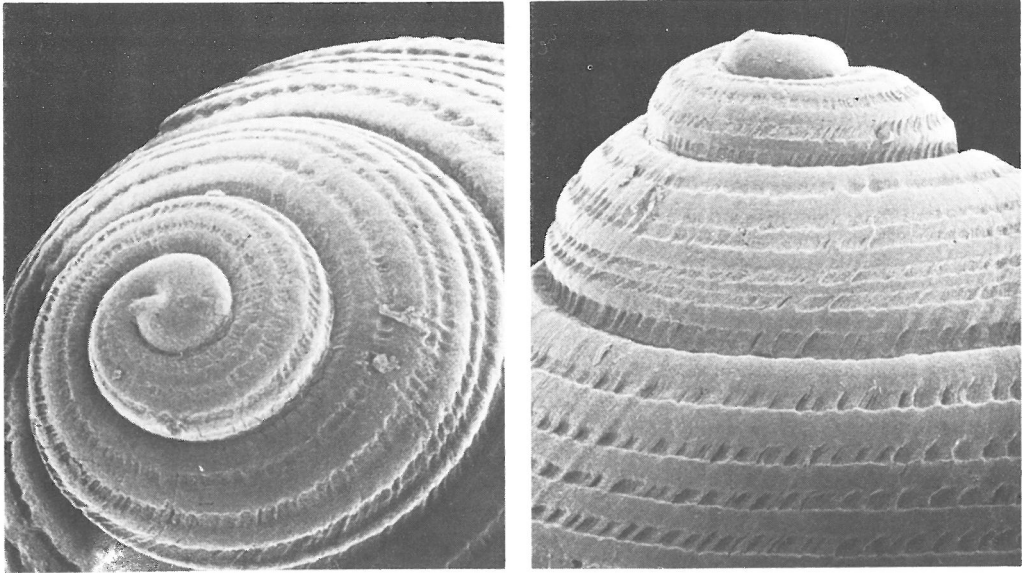


Fig. 38. *Gibbula pennanti* (Philippi). A, apical region from above, X 116; B, upper part of spire from the side, X 116. SEM photographs. BMNH.

Animal. Like that of *G. umbilicalis*.

Colour. Greyish with bands or speckles of purplish black. Sometimes yellowish but less frequently than *umbilicalis* though the neck lobes and sole of the foot are normally rather bright and rather pale yellow respectively. There are white flecks commonly on the sides of the foot.

Geographical distribution. Atlantic coasts of Spain and France, Channel Islands. It does not occur on the French Channel coast E. of Barfleur and is absent from all British shores and those further N.

Habitat. See Fischer-Piette & Gaillard (1956). This species occurs on the same type of rocky shore as *G. cineraria* and *umbilicalis* and often with them, needing a certain degree of shelter. It lives lower than *umbilicalis*, therefore at LW, but in sufficiently humid areas may extend to appreciably higher levels. It seems to be more selective of its habitat than *umbilicalis* and so is more local. It is particularly common under stones in low level pools, amongst the algae (*Bifurcaria bifurcata*, *Himanthalia elongata*, *Fucus serratus*) which cover their sides, and under submerged overhangs. It may also be found on the surrounding rocks, though not usually more than about 1m from the edge of the pool unless the rock surface is unusually wet. In such circumstances the animal may live permanently out of a pool.

Food. As for other *Gibbula* spp. The faeces are also similar.

Breeding and growth. The sexes are separate and distinguishable by the colour of the gonad, cream in males, greenish in females. In the absence of information applying to this species it may be assumed that the eggs are shed separately, fertilized externally and develop to a brief free larval stage as in related species.

Notes. Though originally regarded as a variety of *G. umbilicalis* the work of Tomlin (1921) on the shell and of Peile (1921) on the radula have made it certain that this is an independent species.

GIBBULA MAGUS (Linnaeus, 1758)*Trochus magus* Linnaeus, 1758*Trochus tuberculatus* da Costa, 1779*Gibbula maga* Risso, 1826

Magus (Persian), a wise man or magician, referring to the resemblance of the shell to the traditional turban which he wore.

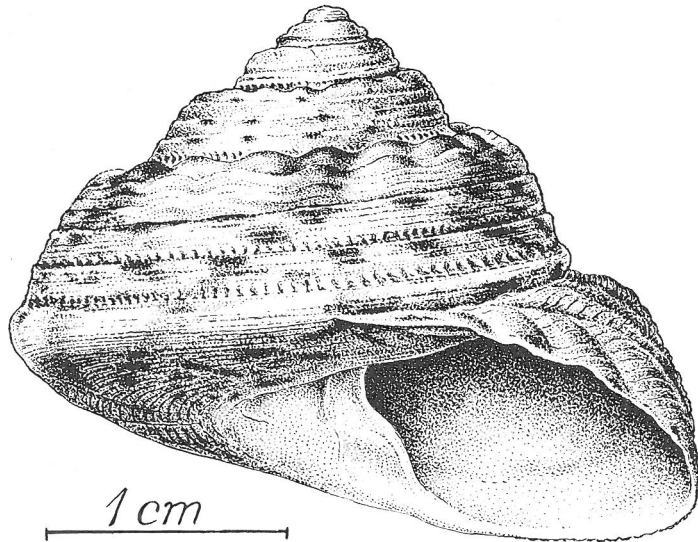


Fig. 39. *Gibbula magus* (L.). Cornwall. BMNH.

Shell. Solid and opaque, dull. Conical, sometimes elevated (apical angle about 80°), sometimes more depressed (apical angle about 100°), stepped in profile because each whorl (of which there are 7-8) is flattened below the suture, which is deep; sutural angle $105-110^\circ$. The base of the shell is rather flat and is inclined to the axis of the cone at an angle of about 75° . The ornamentation consists of growth lines, spiral ridges and grooves, and ribs. The first are markedly prosocline, making an angle of 120° with the vertical axis; they are most obvious below the sutures, on the base and in the furrows between ridges though usually also visible on these in living and unworn shells. The spiral ridges vary in size, number and arrangement, but are always absent from the area between the suture and the adapical ends of the ribs; there is always an enlarged one at the periphery of the body whorl, forming a keel. On the biggest whorl the number varies from 15-22 (commonly 17-18) between suture and keel, from 22-27 on the base; on the penultimate whorl they number 10-16 (usually 12-14), and on the preceding 6-8. The oldest whorls are often too worn to show them but 3 may be seen. Two or three of these ridges may be larger than the others and small ridges often occur in furrows. In shells from intertidal areas the ridges are smooth; in those from deeper water they may be markedly imbricated. The whorls are shouldered by the development of adapical ribs which fail to reach both suture and periphery and appear as a series of slightly opisthocline, elongated tubercles on the upper part of each whorl. There are usually 20 on the body whorl (range 16-23 in shells of 7-8 whorls), 14-18 on both penultimate and antepenultimate, and they are recognizable, though often much worn, on all the smaller ones. Each suture lies along the peripheral keel of the older whorl. The umbilicus is large and deep, its mouth edged by an enlarged spiral ridge which overlies a groove within it. It is also partly occluded by the inner lip. The nucleus is smooth, its initial part drawn out to a point, and measures about $210\mu\text{m}$ across.

Aperture. Markedly prosocline and rather quadrilateral in outline. The outer lip is thin and the columella a little flattened where the two structures join. The inner lip projects over part of the umbilicus and then extends as a pale glaze over the body whorl to the under side of the outer lip.

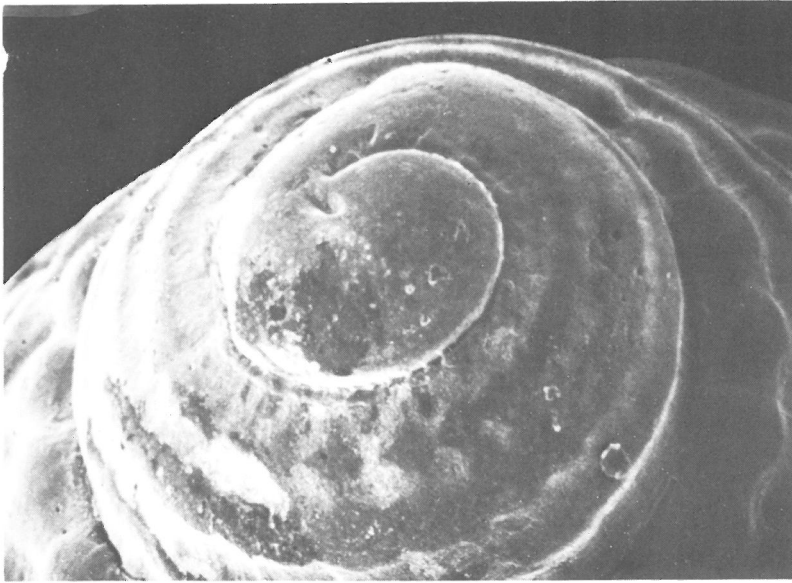


Fig. 40. *Gibbula magus* (L.). Apical region of shell from above, slightly oblique, X 130. SEM photographs. Roundstone, Co. Galway. RUZ.

Colour. White, grey or yellowish externally, marked with irregular streaks and blotches of brown, red or purple, which are often arranged in relation to every third rib adapically to give a local striped appearance, but which become irregular towards the periphery and often break into rows of spots on the base. Internally there is no coloured band within the outer lip though there is a matt area contrasting with the pale glossy refringence of the remainder.

Size. Up to 30 mm high, 35 mm broad; even in taller shells the breadth always exceeds the height. Body whorl = 70% of total height; aperture = 40% of total height.

Animal. The snout is rather long, densely papillated at its tip dorsally and laterally and has a ventrolateral fringe on each side. The mouth is dorsoventrally elongated and the lip split mid-ventrally to extend into a small flap. Each tentacle is long, slender and setose with a stout eye stalk at its base carrying a large eye. The cephalic lappets are large, with a markedly lobed margin and connected over the tentacle base to the eye stalks. The right eye stalk is fused to a smooth-edged neck lobe with a single finger-shaped projection (perhaps a postoptic tentacle or extra epipodial sense organ) on its under surface; the left is separate and its margin is scalloped. The sides of the foot carry many small papillae near the sole, but these become fewer and larger dorsally. On each side the neck lobe is continuous with an epipodial ridge below which three epipodial tentacles spring from deep sheaths with papillated edges; at the base of each tentacle is a projecting flap-like sense organ also bearing spikes, those on the right always bigger and spikier than those on the left. In many animals the most posterior one on the right is double. The foot is grooved on the sole, bluntly rounded in front and pointed behind where it has dorsally, under the posterior part of the operculum, an area marked by numerous transverse grooves. The operculum is slightly concave, with about 13-15 turns. The mantle edge is slightly lobed.

Colour. Much of the head and foot is yellowish pink or orange with purple-black blotches. These form transverse lines over the snout and at the anterior end of the foot. The tentacles have a central dark line and transverse bars. The epipodial tentacles are sulphur yellow with their sheaths and sense organs white. The papillae on the foot and snout are pale yellow or white, the neck lobes and cephalic lappets yellow.

Geographical distribution. *G. magus* extends north from the Mediterranean and Azores to the western basin of the English Channel, up the W. coast of Britain as far as Shetland, and all round Ireland. In the Channel it is commoner on French than on English coasts, dying out just E. of the Cotentin peninsula and in the Swanage-Poole area. It does not penetrate the N. Sea nor is it found in Scandinavia though empty shells have been found at Scarborough and Bohuslän.

Habitat. This species occurs on the same kind of shore as other top-shells but at a lower level, being mainly infralittoral, where it is not uncommon on muddy gravel to a depth of 70m. Occasional specimens may be found at LWST and there are localities such as southern shores of Co. Galway, Ireland, where intertidal specimens are common. They are more squat than those from deeper water which are also more frequently spiny. The animals occur on rock and weed and under stones; they require some shelter but are more tolerant of sandy situations and shingle beaches than most trochids. They do not like reduced salinity.

Food. The animal is primarily a scraper, collecting diatoms, bacteria and detritus. The faeces are grooved rods with a very tight and regular sinusoidal pattern of ridges and folds on the surface. The liver string forms a prominent ridge, triangular in section, set in the groove.

Breeding and growth. The sexes are separate. The eggs are small (120 μ m in diameter), yellow and, as in other species, surrounded by a jelly coat of ovarian origin, which swells rapidly when they are laid. They are shed singly in spring and early summer; trochophore larvae hatch after 20h and settle after a brief larval life. No further details are known.

GIBBULA TUMIDA (Montagu, 1803)

Trochus tumidus Montagu, 1803

Trochus patholatus Dillwyn, 1817

Tumida (Lat.), swollen, referring to the shape of the whorls.

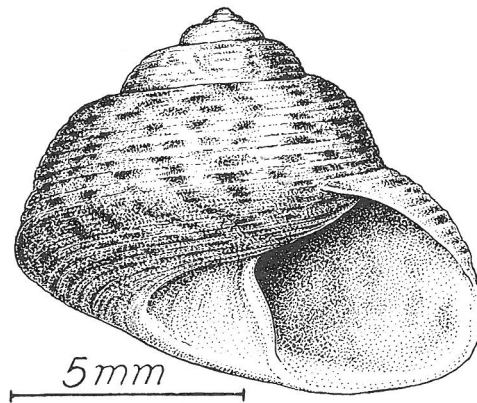


Fig. 41. *Gibbula tumida* (Montagu). Øresund. (?)CZM.

Shell. Solid, opaque, a little shiny. In general with the shape of *G. magus* — a moderately depressed cone with a rather flat base and a stepped profile. The apical angle of mature shells is 75–80°, in young ones 100–120°, a change reflected in the cyrtocoid spire. 6–7 whorls meet at well marked and rather deep sutures, the older ones convex; with growth the shape changes because of the development on each whorl of a flattened shoulder below the suture and a rather straight-sided area in the central part which ends abapically in a rounded keel. The angle between the flat area and the base is just over 90°. The ornament consists of growth lines and spiral ridges and grooves. The



Fig. 42. *Gibbula tumida* (Montagu). Apical region of shell from above, slightly oblique, X 295. SEM photograph. Roscoff. RUZ.

former are prosocline and raised at intervals of about $30\mu\text{m}$ to form small crests running over spiral ridges and furrows, though, to a casual look, apparently absent from the ridges. Each forms a small escarpment, the steep face on the adapertural side. Similarly the spiral ridges are steeper adapically. There are 14-18 on the base of the shell, the most central sometimes more prominent round the umbilical area, 16-18 on the body whorl between suture and periphery (of which 2-5 lie on the subsutural flat area), 14-16 on the penultimate whorl, 10-15 on the next and 7-10, 4-6 on the uppermost. In addition extra minor ridges may develop between these. All young shells have a deep umbilicus which is gradually closed by outgrowth of the inner lip; even in adult shells, however, it may persist as an oval opening or a small chink. The protoconch has $1\frac{1}{4}$ whorls, is smooth, has a markedly up-turned tip and the aperture drawn out to form a beak on each side; it measures $150\text{--}160\mu\text{m}$ across.

Aperture. Prosocline, lozenge-shaped and rather equal-sided. The outer lip arises at the periphery of the body whorl, runs at an angle of 45° to the axis of the shell, then nearly parallel to it, curving through 90° at the keel to run to the columella. It is thin and appears a little out-turned abapically. The columella is about vertical and bears a low swelling at its mid-point. Inner lip wrapped over the columella and everted to form a sheet partly or wholly blocking the umbilicus.

Colour. Straw-coloured, usually with a greenish-blue iridescence. Brown or chestnut spots lie in the spiral furrows, often aligned one below the other to produce bands across the whorls; these are usually opisthocline adapically, becoming vertical or prosocline abapically and produce alternating patches of light and dark on the keel. Apex always darker and base always paler, becoming white at the umbilical area. Inside the shell glossy with a violet iridescence except for a narrow band within the lip; internal to this lies a white callus.

Size. Up to 9mm high x 10mm broad. Body whorl = 75-80% of total height; aperture = 50% of height.

Animal. The animal closely resembles other *Gibbula* spp. The snout is, however, more depressed, less papillated and bears a pronounced lateral ridge on each side. The lips are split mid-ventrally but not extended to form a flange. The lateral ridge connects with the base of the corresponding eye stalk and that in turn to the cephalic lappet, dorsal to the tentacle base. The margin of the lappet bears small processes. The right eye stalk connects with the epipodial fold; that on the left is separate. The cephalic tentacles bear dense fringes of sensory papillae laterally and are slightly grooved dorsally. Mantle edge smooth.

The foot is shield-shaped, broad anteriorly (where there is a propodial groove), tapering behind. The neck lobes are not large, that on the left having a lobed margin. There are 3 epipodial tentacles on each side, each springing out of a sheath to the posterior side of which lies a bulbous sense organ. A fourth, more digitiform, lies under each neck lobe. The sides of the foot are markedly papillated. Behind the operculum lies the usual grooved area.

Colour. Cream, with puce lines and flecks on the dorsal surface of the snout and the sides of the foot; there are also numerous small white blotches, particularly on the cephalic lappets and epipodium. The sole of the foot is white, its sides brown anteriorly, yellow posteriorly.

Geographical distribution. This is a northern species extending S. from Iceland and N. Norway to Øresund, N. Sea, Channel, British, Irish, French and Iberian coasts. Its occurrence in the Mediterranean is doubtful.

Habitat. Not a littoral species. It occurs below intertidal levels where plants of *Laminaria* are attached and at greater depths (to 1200m) where there are stones on a sandy-muddy bottom.

Food. A collector of detritus like the other species. Faeces like theirs.

Breeding and growth. The breeding has been described at Heligoland by Gersch (1936). It reproduces there in March-April (Ankel, 1936). The eggs are green, measure 140 μ m in diameter and are surrounded by a jelly coat with a total diameter of 180 μ m across. The jelly is produced around the eggs within the ovary and this causes them to adhere to form spawn masses.

REFERENCES

- ARNOLD, D. C. 1972. Salinity tolerances of some common prosobranchs. *Journal of the Marine Biological Association of the U.K.* **52**, 475-86.
- BAKKER, K. 1959. Feeding habits and zonation in some intertidal snails. *Archives néerlandaises de Zoologie*, **13**, 230-57.
- COLMAN, J. S. 1933. The nature of the intertidal zonation of plants and animals. *Journal of the Marine Biological Association of the U.K.* **18**, 435-76.
- EBLING, F. J., KITCHING, J. A., PURCHON, R. D. & BASSINDALE, R. 1948. The ecology of the Lough Ine rapids with special reference to water currents. 2. The fauna of the *Saccorhiza* canopy. *Journal of Animal Ecology*, **17**, 223-44.
- EVANS, R. G. 1947. The intertidal ecology of selected localities in the Plymouth neighbourhood. *Journal of the Marine Biological Association of the U.K.*, **27**, 173-218.
- FISCHER-PIETTE, E. & GAILLARD, J. M. 1956. Sur l'écologie comparée de *Gibbula umbilicalis* da Costa et *Gibbula pennanti* Phil. *Journal de Conchyliologie*, **96**, 115-18.
- GAILLARD, J. M. 1953-54. Révision des espèces des côtes de France du genre *Gibbula* Risso. 1. *Bulletin du Muséum nationale d'Histoire naturelle*, (2), **25**, 584-93. 2. *Bulletin du Muséum nationale d'Histoire naturelle*, (2) **26**, 238-43; 3. *Bulletin du Muséum nationale d'Histoire naturelle*, (2) **26**, 370-5.
- GERSCH, M. 1936. Der Genitalapparat und die Sexualbiologie der Nordseetrochiden. *Zeitschrift für Morphologie und Ökologie der Tiere*, **31**, 106-50.
- MOORE, H. B. 1940. The biology of *Littorina littorea*. Part II. Zonation in relation to other gastropods on stony and muddy shores. *Journal of the Marine Biological Association of the U.K.*, **24**, 227-37.
- MOYSE, J. & NELSON-SMITH, A. 1963. Zonation of animals and plants on rocky shores around Dale, Pembrokeshire. *Field Studies*, **1**, 5, 1-31.
- NELSON-SMITH, A. 1967. Marine biology of Milford Haven: the distribution of littoral animals and plants. *Field Studies*, **2**, 435-77.
- PEILE, A. J. 1921. Note on *Gibbula pennanti* Philippi. *Journal of Conchology*, **16**, 253.
- RENDALL, R. 1956. Mollusca orcadensia. *Proceedings of the Royal Society of Edinburgh*, **66B**, 131-201.
- TOMLIN, J. R. le B. 1921. Note on *Trochus pennanti* Philippi. *Journal of Conchology*, **16**, 236.
- UNDERWOOD, A. J. 1972. Observations on the reproductive cycles of *Monodonta lineata*, *Gibbula umbilicalis* and *G. cineraria*. *Marine Biology*, **17**, 333-40.

MONODONTA LINEATA (Da Costa, 1778), top-shell
Turbo lineatus da Costa, 1778 (not *Trochus*)
Trochus crassus (Pulteney, 1799)
Osilinus lineatus (da Costa, 1778)
Trochocochlea lineata (da Costa, 1778)
Gibbula lineata (da Costa, 1778)
Monodonta colubrina (Gould, 1851)

Monodonta (Gk.), one tooth, referring to that on the columella; *lineata* (Lat.), marked with lines — the pigment streaks on the shell.

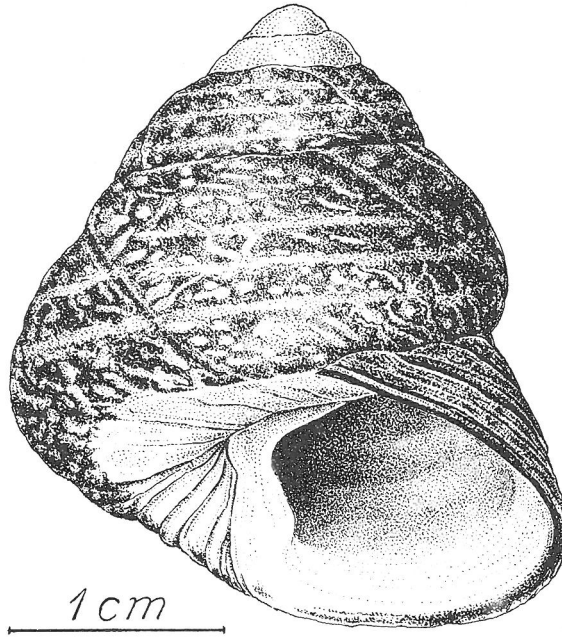


Fig. 43. *Monodonta lineata* (da Costa). Ireland. (?)CZM.

Shell. Solid, opaque and dull; rather globose in general shape, of 5-6 rapidly expanding whorls. The spire is conical with relatively straight sides in the smaller shells, but often dome-shaped (cyrtocoid) in older ones. The apical angle varies between 75-100°, the lower figure characteristic of larger shells. Whorls swollen, each meeting the previous one above its periphery so that the angle at the sutures is more than 90°. Sutures shallow. The shell is marked with numerous growth lines which are fine and prosocline; they are S-shaped, arise at the adapical suture more or less normal to it, bend back at an angle of about 30° to the vertical axis of the shell and straighten somewhat on the base of the body whorl. Occasional thickenings, mainly on younger whorls, mark disturbances of growth which are not annual. There are also spiral ridges and grooves. In older shells the ridges are flat and broader than the grooves; they are narrowest below the suture, broaden towards the periphery and are most marked on the base of the body whorl; each may appear double because marked by a secondary groove. In young shells all the ridges are sharper and narrower. With age all ornament becomes less pronounced and the apex and spire are often so eroded that it is lost and the underlying nacre exposed. Nucleus smooth with reversed tip and measuring c. 100µm across; it is normally lost in older shells.

Aperture. Rather square and lying in a plane at 30° to the axis of the shell. The outer lip is bevelled sharply to a thin edge, arises from just above the periphery of the body whorl over which it is reflected downwards a little. Its upper course is rather straight, sometimes even concave, but it

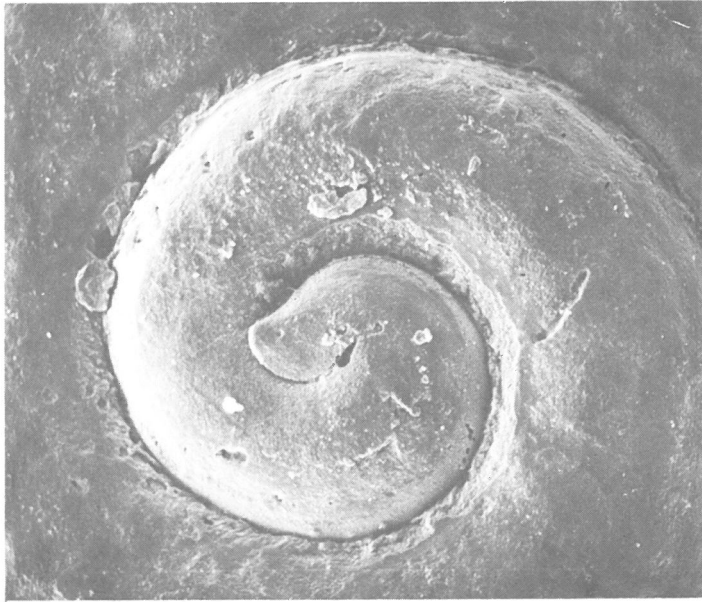


Fig. 44. *Monodonta lineata* (da Costa). Apical region from above, X 320. SEM photograph. Plymouth. RUZ.

then curves markedly, the base slightly out-turned. The columella and inner lip are thick, reflected over the umbilicus, always leaving a depression and sometimes a chink in adult shells. Young shells show a narrow opening. Near its base the columella bears an elongated and prominent bulge (tooth). The inner lip spreads over the under-side of the body whorl to reach the outer one. Internally the spiral ridges are visible through the shell.

Colour. Externally, a ground colour of pale buff marked extensively by irregular streaks of red, brown or green; in one and the same shell different areas may be differently coloured. The streaks often join to isolate patches of ground colour, but in general form prosocline lines, often with branches at right angles. They tend to arise at right angles to the sutures where there is often a regular alternation of light and dark blotches. Pigmentation is greater on the adapical part of the body whorl, lessens towards the base and is absent from an area around the umbilicus. As a consequence the spire is darker than the body whorl though this effect is usually lost because of erosion. Internally, there is a band of dark colour within the outer lip bounded by a groove internal to which are (1) a chalk-white band, (2) iridescent nacre. Inner lip and columella creamy white.

Size. Up to 30 mm high, 25 mm broad; most shells less. Body whorl = 75% shell height; aperture = 35-38% shell height.

Animal. Head with a well-developed snout, D-shaped in section, the flat surface ventral; ends in a series of small lobes. The truncated apex carries the mouth, \perp -shaped when closed, surrounded by lips with many radial folds. Cephalic tentacles moderately long with lobed sides; at their base, laterally, is a broad eye stalk with a black eye. That on the right has a small postoptic tentacle as in a zeugobranch. Each eye stalk is connected over the base of the tentacle to a smooth-edged cephalic lappet, semicircular in outline. A similar lappet lies on each side of the snout ventro-laterally. The base of each eye stalk is fused to the anterior end of a neck lobe, the left one with 20-25 tentacles on its outer edge, the right one plain but carrying a single process on its ventral surface. Mantle edge plain, double.

Foot more or less oval, tapering behind. The sole (at rest) has a median longitudinal furrow and numerous transverse folds but is smooth during creeping when it shows direct ditaxic waves, especially near the edge (Miller, 1974). It has no double edge anteriorly, its margins being finely papillated. The flanks of the foot are covered with small tubercles and the posterior half carries an epipodial fold dorsally. Ventral to this on each side are three epipodial tentacles each with two

sensory papillae at its base. Additional papillae may occur between tentacles and under the neck lobes, one under the left, two under the right. On the dorsal surface, under the operculum, is a glandular area marked by transverse ridges and a median longitudinal groove. Operculum multispiral, of about 15 turns, flat, chestnut brown.

Colour. Body grey-green with numerous black or purple lines. Each tentacle has often a central longitudinal streak with divergent lines. The pedal sides are dark, its sole and sensory papillae pale.

Geographical distribution. The species centres in the Biscay area, extending S. to Portugal, Morocco and Madeira, and N. to the British Isles. It extends into the Channel as far as St. Alban's Head (Hawthorne, 1965) on the English side and the Cotentin peninsula on the French (Crisp & Southward, 1958). In the Irish Sea it occurs on Welsh coasts as far as Anglesey but is absent from the Irish and Manx ones. It is found on the southern and western shores of Ireland N. to Donegal. Even within these areas its distribution is patchy and erratic.

Habitat. Important references for this and the next section are McMillan (1944), Southward & Crisp (1954), Southward & Orton (1954) Crisp & Southward (1958), Williams (1965), Desai (1966), Nelson-Smith (1967).

The species is restricted to rocky shores, especially those with considerable areas of bedrock or consolidated boulders with crannies; not usually found where boulders are movable or where there is shingle or sand. It occurs both where there are visible growths of weed (*Pelvetia canaliculata*, *Fucus spiralis*) and on what appears to be bare rock, rather high on the beach for such a large animal primarily dependent on surface scraping for food, about the upper limit of the mid shore, from MHWS-MLWN, moving higher where there is freshwater seepage and liking the neighbourhood of rock pools. It avoids exposed shores and prefers gentle to steep slopes, perhaps because it is unable to cling powerfully. Its level varies with the season: in winter it is found appreciably lower and less commonly on exposed surfaces.

Food. This is an algal browser, mainly eating microscopic forms and detritus scraped from the rock, not feeding on the large weeds with which it may occur. Manly (1975) has shown that even when rock seems bare there are enough blue-green algae and stages in the life history of weeds like *Porphyra*, *Bangia*, *Entophysalis* and *Enteromorpha* to sustain prosobranchs. The faeces are rods with a groove on one side partly filled with a keel-shaped ridge (liver string); the rest (stomach string) is paler and finer, the finest material on the outer surface, which exhibits many slightly sinuous ridges (diameter about 1.5 mm, length 3-5 mm).

Breeding and growth. See Gaillard (1965), Williams (1965), Desai (1966), Regis (1972), Underwood (1972). Sexes separate, distinguishable externally only by greater size and yellow colour of the female urinogenital (right kidney) opening in the mantle cavity. The animals mature when they measure about 18 mm across the shell. The gonadial cycle starts in October and spawning occurs the next summer (May or June-August) followed by a brief resting phase before restarting. Eggs, greenish in colour, and measuring about 150 μ m in diameter, escape from the mantle cavity in ones or twos; they are enclosed in a membrane and a jelly coat produced within the ovary and have an overall diameter of about 200 μ m at laying, rising shortly to 500 μ m from swelling of the jelly. The veliger hatches after 30h (15-20°C) and starts to settle in 4-5 days when its shell measures 1 + mm across. The smallest animals (up to 5 mm) are found low on beaches in pools, under stones and in crevices (because they shun light), rarely in the adult habitat, to which they migrate when later they become positively phototactic. Growth seems initially very rapid, the animals reaching a shell width of 7-8 mm (height 6-7 mm) by December; it is slow over winter but accelerates in spring and 1 year after settling the snails measure 10-11 mm in width (15 mm high). There is always a decrease in growth rate at spawning. The animals may live 10 years in the Channel but in warmer areas grow faster and die sooner (4 years at Socoa on the Basque coast). The spat-fall seems to fail in some years.

Notes. *Monodonta lineata* is the largest littoral top shell of the British Isles and is usually abundant where it occurs. It is susceptible to cold, being near the northern limits of its range, and many populations were destroyed by the cold weather of early 1963 (Crisp, 1964). Since its free larval life is only a matter of a few days, many of these are not yet fully re-established. The species seems to flourish only within rather narrow limits of emersion, exposure, temperature, and perhaps other factors, so that it is not yet possible to say why it does not occur in many apparently suitable sites.

The green coloration of shell, flesh and eggs is probably due to a bile pigment, perhaps derived from food (Bannister, Bannister & Micallef, 1968 a, b). According to Micallef (1966) and Micallef & Bannister (1967) this and other species of *Monodonta* are better adapted for respiration in air than under water provided that humidity and temperature are such as to prevent desiccation.

REFERENCES

- BANNISTER, W. H., BANNISTER, J. V. & MICALLEF, H. 1968a. The green pigment in the foot of *Monodonta* (Mollusca) species. *Comparative Biochemistry and Physiology*, **24**, 839-42.
- BANNISTER, W. H., BANNISTER, J. V. & MICALLEF, H. 1968b. Bile pigment in the shell of *Monodonta turbinata* (Mollusca: Gastropoda). *Comparative Biochemistry and Physiology*, **27**, 451-54.
- CRISP, D. J. (ed.) 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-210.
- CRISP, D. J. & SOUTHWARD, A. J. 1958. The distribution of intertidal organisms along the coast of the English Channel. *Journal of the marine biological Association of the U.K.*, **37**, 157-208.
- DESAI, B. N. 1966. The biology of *Monodonta lineata* (da Costa). *Proceedings of the malacological Society of London*, **37**, 1-17.
- GAILLARD, J. M. 1965. Aspects qualitatifs et quantitatifs de la croissance de la coquille de quelques espèces de Mollusques Prosobranches en fonction de la latitude et des conditions écologiques. *Mémoires du Muséum national d'Histoire naturelle*, série A, Zoologie, **38**, 1-55.
- HAWTHORNE, J. B. 1965. The eastern limit of distribution of *Monodonta lineata* (da Costa) in the English Channel. *Journal of Conchology*, **25**, 348-52.
- McMILLAN, N. F. 1944. The distribution of *Monodonta (Trochus) lineata* (da Costa) in Britain. *North-Western Naturalist*, **19**, 290-2.
- MANLY, R. 1975. *The settlement and growth of some species of prosobranch gastropods in the Plymouth area*. Ph.D. thesis, University of Reading.
- MICALLEF, H. 1966. *Ecology and behaviour of selected intertidal gastropods*. Ph.D. thesis, University of London.
- MICALLEF, H. & BANNISTER, W. H. 1967. Aerial and aquatic oxygen consumption of *Monodonta turbinata* (Mollusca: Gastropoda). *Journal of Zoology, London*, **151**, 479-82.
- MILLER, S. L. 1974. The classification, taxonomic distribution and evolution of locomotor types among prosobranch gastropods. *Proceedings of the malacological Society of London*, **41**, 233-72.
- NELSON-SMITH, A. 1967. Marine biology of Milford Haven: the distribution of littoral animals and plants. *Field Studies*, **2**, 435-77.
- REGIS, M. B. 1972. Etude comparée de la croissance des Monodontes (Gastéropodes Prosobranches) en Manche et le long des côtes Atlantiques et Méditerranéennes françaises. *Vth European marine Biology Symposium*, 259-67.
- SOUTHWARD, A. J. & CRISP, D. J. 1954. The distribution of certain intertidal animals around the Irish coast. *Proceedings of the Royal Irish Academy*, **57B**, 1-29.
- SOUTHWARD, A. J. & ORTON, J. H. 1954. The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. *Journal of the marine biological Association of the U.K.*, **33**, 1-19.
- UNDERWOOD, A. J. 1972. Observations on the reproductive cycles of *Monodonta lineata*, *Gibbula umbilicalis* and *G. cineraria*. *Marine Biology*, **17**, 333-40.
- WILLIAMS, E. E. 1965. The growth and distribution of *Monodonta lineata* (da Costa) on a rocky shore in Wales. *Field Studies*, **2**, 189-98.

CANTHARIDUS EXASPERATUS (Pennant, 1777)*Trochus exasperatus* Pennant, 1777*Jujubinus exasperatus* (Pennant, 1777)*Trochus exiguus* Pulteney, 1799*Trochus matoni* Payraudeau, 1826

Cantharidus, the meaning appears doubtful; *exasperatus* (Lat.), much roughened, referring to the coarser ornament as compared with *C. striatus*.

Shell. Opaque, solid, somewhat shiny. A straight-sided, rather sharply pointed cone with a rather flat base. The apical angle is 50-60°, that at the keel of the body whorl 70-80°. There are 6-8 whorls which meet at slight sutures, each whorl (except the 2 oldest which are a little tumid) flat in profile. The ornament consists of growth lines and of spiral ridges and furrows. The growth lines are markedly prosocline, making an angle of 140° with the axis of the helicocone. They are raised at regular intervals to form lamellar crests running across the furrows from spiral ridge to spiral ridge, each leaning towards the aperture; there are about 5 mm⁻¹, about 75µm in thickness and about 150µm apart. They interact with the spiral ridges to produce a series of raised beads upon them, most pronounced on the subsutural and peripheral ridges of each whorl. There are 6, sometimes 7, spiral ridges on the base of the shell, 5 between suture and peripheral keel on the body whorl and 5-4 on each preceding one. The peripheral ridge on the body whorl (often compound) forms a prominent keel. The apex of the shell shows 1¼ whorls, is smooth with a slightly tilted tip and

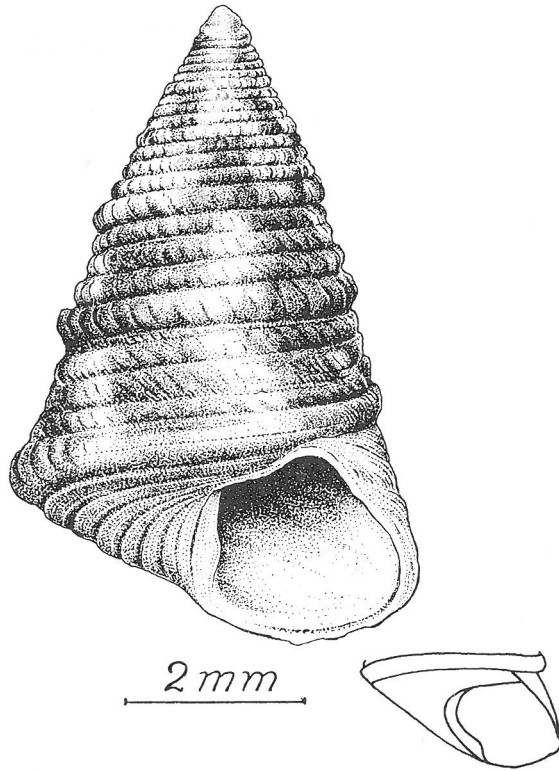


Fig. 45. *Cantharidus exasperatus* (Pennant). Madeira. BMNH. Inset, aperture of specimen from Roscoff. RUZ.

measures 125-140 μ m across; at each side the aperture of the protoconch is extended to form a small beak. Shells up to 3 whorls show a small umbilicus, closed in older ones.

Aperture. Prosocline. Rather square. The outer lip arises from the body whorl at a level just below the keel and at an angle approaching 90° so that its initial course is nearly a continuation of the profile of the spire; it is rather sharply angulated at the keel of the body whorl whence it follows a gently curving course to join the columella. This is nearly vertical and bears a low curved tooth. The inner lip is not very distinct but curves outwards over a shallow groove to block any umbilical chink. In the parietal region the ornament is partly worn away.

Colour. The background colour is pale tan, brown, carmine or greenish, with blotches of darker hue and of white on the spiral ridges. Most shells, whatever other colour they may have, are somewhere tinted with carmine or purplish red and the initial 2-3 whorls are nearly always of this shade or show streaks and spots of it on a paler base. Internally the shell is nacreous and glossy save for a narrow pigmented band just within the outer lip which is bounded internally by white callus. The external ornament is visible by transparency.

Size. 8 mm high x 7 broad. Body whorl = 44-50% of total height; aperture = 33-35% of shell height, = 50-55% of shell breadth.

Animal. The snout is D-shaped in section, flat below, and ends in an expanded tip with a lobed margin carrying some sensory papillae. The mouth is placed centrally on the apical disk of the snout, surrounded by radially folded lips split mid-ventrally, though there is no distinct ventral fold as in *Gibbula* spp. The ventrolateral edges of the lips form a ridge which runs back along the side of the snout to join the base of the eye stalks. The tentacles are long, tapering and setose along their medial and lateral borders because of the many sensory papillae which they carry. Each has an eye stalk at its base laterally and a large semicircular cephalic lappet with a scalloped edge medially, the

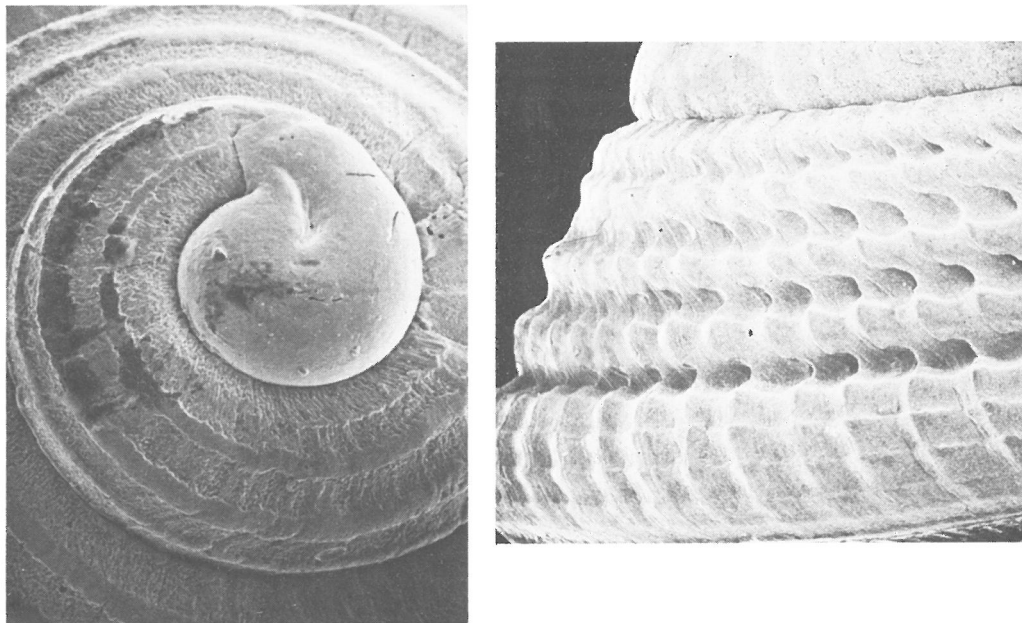


Fig. 46. *Cantharidus exasperatus* (Pennant). A, apical region from above, X 260; B, details of ornamentation of whorls, X 60. SEM photographs. Roscoff. RUZ.

two connected dorsal to the tentacle base. The right eye stalk is connected to a large smooth-edged neck lobe, the anterior end of an epipodial fold. There is a gap between left eye stalk and left neck lobe. The mantle edge is double and slightly lobed.

The foot is elongated, truncated anteriorly, where it has a double edge and slightly angulated corners, and tapering posteriorly. Its flanks are covered by rounded papillae which also edge the sole. The dorsal posterior surface, normally folded so that its edges meet, has numerous transverse grooves. The epipodial fold has a rather coarsely lobed edge from under which 3 tentacles arise on each side from short sheaths. A sense organ lies at the base of each and an extra one is placed at the base of each neck lobe.

Colour. The basic colour is cream, as shown on the sole of the foot and mantle skirt. The snout, except for the cream tip, is dark chocolate brown fading to orange and chestnut on the cephalic lappets, between the tentacles and on the neck lobes. The more dorsal parts of the sides of the foot are dark brown-black, but ventrally there is an edge of beetroot red, and the same colour is on all the tentacles. Cephalic lappets, epipodial tentacle sheaths and neck lobes have also white blotches. The papillae on the foot are in part pale, in part red or dark, the dorsal folded area madder red anteriorly, cream posteriorly.

Geographical distribution. This is a southern species occurring between the Mediterranean, Canary Islands and Azores and the British Isles, reaching N. to the W. coast of Scotland where, however, it is rare. Though common enough in Brittany and the Channel Islands it does not extend further E. except as a rarity on floating material and is absent from Scandinavia and the N. Sea.

Habitat. This occupies very nearly the same habitat as *C. striatus* and is found on weeds, particularly *Zostera*, at L.W.S.T., extending to depths of 200m. It is said to occur rather more commonly on stones than *striatus*, especially in the Mediterranean.

Food. Predominantly a collector of detrital particles but probably also able to rasp slightly the weeds over which it crawls. The faeces are rod-shaped, about 300 μ m in diameter, with a groove on one side from which projects a keel-shaped liver string; the rest of the surface is marked with sinuous ridges and grooves.

Breeding and growth. The sexes are separate. The eggs measure 160-180 μ m in diameter, increased to about 250 μ m by surrounding membranes, and are unpigmented. Fertilization is external and the eggs are laid as a zigzag string embedded in a mass of jelly which is fastened to the surface of the weeds or stones in which the snails live. The jelly is produced primarily by the enlarged urinogenital papilla of the female, perhaps augmented by hypobranchial secretion since the gland is large in this species; eggs and jelly escape from the mantle cavity along the right neck lobe curled to form a tube. The spawn mass is transparent, colourless, flattened and oval and measures 20-40mm long by 1-1.5mm broad. All larval stages are passed within the spawn mass and the young hatch as miniature snails in 5-6 days. Breeding was studied by Robert (1902); it occurs throughout the year, but is maximal in April-May at Banyuls, in August at Roscoff; no records from British waters. Growth has not been investigated.

Notes. The drawing seems to suggest that this species has a complete peristome; this is not so, the outer lip arising from the body whorl as it does in *striatus* (Fig. 47). At most a slight glaze links inner and outer lips and even this is often not visible. The nodules on the spiral ridges are often smaller and more numerous than represented here.

CANTHARIDUS STRIATUS (Linnaeus, 1758)
Trochus striatus Linnaeus, 1758
Jujubinus striatus (Linnaeus, 1758)
Zizyphinus aequistriatus de Beauchamp, 1914

Striatus (Lat.), with striae, referring to ornamentation of shell.

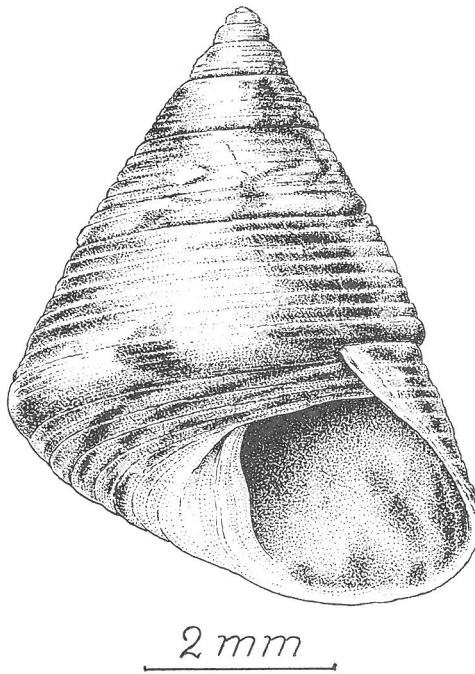


Fig. 47. *Cantharidus striatus* (da Costa). Madeira. BMNH.

Shell. In general like that of *C. exasperatus*. The spire, however, is less pointed (apical angle 55-72°, usually nearer the higher figure) so that the angle between its sides and the base is bigger (80-85°). The lamellae formed by the growth lines are finer and spaced 100-120 μ m apart and less clear on the spiral ridges, though enough to give those on the younger whorls a beaded appearance. There are 7-9 ridges on the base of the shell separated by broader furrows in which, especially peripherally, there are often smaller, secondary ridges. Interaction of growth lines and spirals is

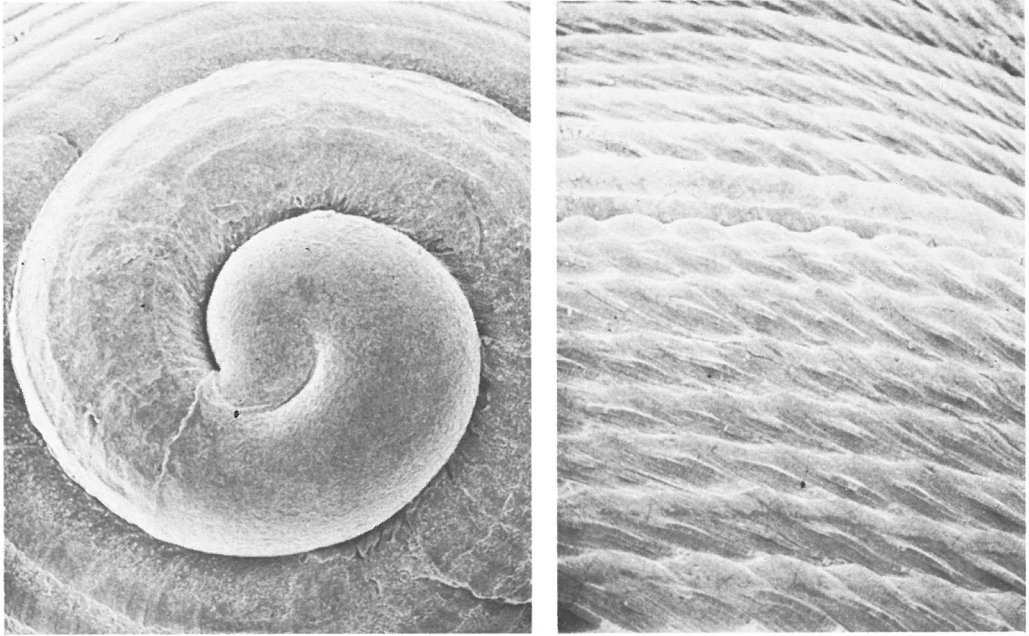


Fig. 48. *Cantharidus striatus* (da Costa). A, apical region from above, X 260; B, details of ornamentation of whorls, X 90. SEM photographs. Roscoff. RUZ.

clear here and the latter are more noticeably beaded than those of the spire. There are 8-10 ridges between suture and keel on the body whorl and 8-10 on the penultimate whorl and those above. Young shells have an open umbilicus. The apex has $1\frac{1}{4}$ whorls, a slightly reversed tip and is generally smooth with some irregular markings. Its aperture lacks the beak of *C. exasperatus*. The shell is rather variable in sculpture.

Aperture. Prosocline. Lozenge-shaped, the long axis making an angle of about 110° with the vertical axis of the shell. The outer lip, crinkled where the spiral ridges end, arises horizontally from, or makes an angle not $> 45^\circ$ with, the periphery of the body whorl and makes a rather sharp angle at the keel. Otherwise as in *C. exasperatus*.

Colour. Externally whitish, cream or greenish, with coffee- or chocolate-coloured blotches and stripes alternating rather regularly with pale ones of equal size. The apical 2-3 whorls are often pink. In some shells the pattern of blotches forms a checkerboard of light and dark which can be seen at one and the same time as prosocline and opisthocline, so regular is the arrangement. In most, however, only a few, broad, well-spaced, opisthocline bands of colour are present, often sharply edged on one side and fading into the ground colour of the shell on the other. In shells with a reticulate pattern the blotches are bigger on the peripheral keel which picks out the whorls of the spire. Internally the shell is like that of *exasperatus* save that the matt band within the outer lip is less pigmented.

Size. Up to 10mm high x 8mm broad. Body whorl = 66% of shell height; aperture = 40-45% of shell height, = 45% of shell breadth.

Animal. As in *C. exasperatus*.

Colour. Cream, with innumerable dark brown or black blotches and streaks: these are most dense on the dorsal surface of the snout and the upper parts of the foot. The tentacles have transverse black stripes; eye stalks pale. Sole of foot cream.

Geographical distribution. Like *exasperatus* a southern species found in the Mediterranean and in the Atlantic between Madeira and Azores in the S. and the S.W. coasts of the British Isles in the N. It has been recorded as far N. as the Isle of Man and as far E. as the Channel Islands.

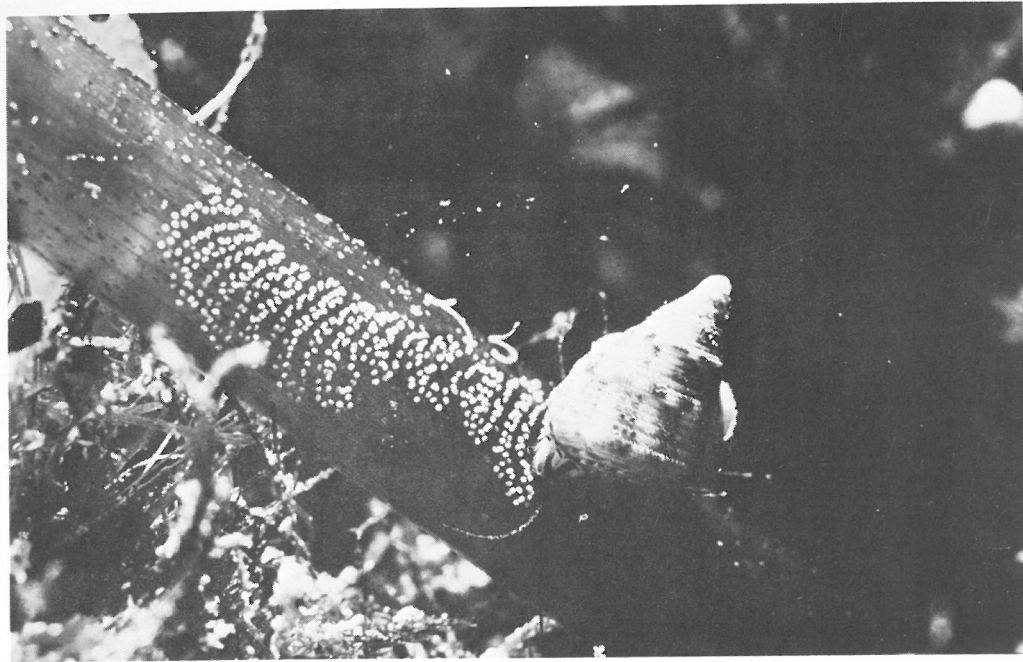


Fig. 49. *Cantharidus striatus* (da Costa). Female with spawn. (Courtesy of Dr P. Bouchet.)

Habitat. Typically on weeds, especially *Zostera*, at LWM and sublittorally to 200m. It also occurs on small stones with *Ulva* or *Codium*. It is common on Channel Island and French coasts, much less so in Britain.

Food. As for *exasperatus*.

Breeding and growth. The sexes are separate and fertilization is external. Eggs and spawn are said by Robert (1902) to be indistinguishable from those of *exasperatus* unless the parents are known. The development is similar. There are no studies on growth.

Notes. Most shells show more nodose spiral ridges than the one illustrated and the lamellae of the growth lines are also more conspicuous in the intervening furrows.

CANTHARIDUS MONTAGUI (W. Wood, 1828)

Trochus montagui Wood, 1828

Trochus montacuti Wood, 1828

Jujubinus montagui (Wood, 1828)

Montagui (Lat.), named for G. M. Montagu (1755-1815), author of *Testacea Britannica* (1803-08) in which many new species of British prosobranchs were first described.

Shell. Whilst like that of the two previous species in general this is more cyrtocoenoid than either (apical angle about 75-80° in small shells falling to 45-60° with growth); the base is less flat and the angle between it and the side of the spire is about 80°. The 6-7 whorls are all slightly tumid (the first two in particular) and dip to sutures more pronounced than those of *exasperatus* and *striatus*. The lamellae formed by the growth lines are altogether finer and more close-set than in these species (about 20mm⁻¹) and are visible over the spiral ridges only in the youngest part of the shell. The ridges form rather flat cords equalling the intervening furrows in breadth. On the base of the shell there are usually 7, on the body whorl, between suture and periphery, 6-7, as on all older whorls. The peripheral ridge is a little enlarged, subdivided by small grooves and forms a keel, both less marked and less angular than in *striatus* and *exasperatus*. A small umbilicus is present in young shells and may persist in full-grown ones, but these are usually imperforate. Apex smooth, of 1¼ whorls with a distinctly up-turned tip, measuring about 140µm across. The aperture has small lateral beaks.

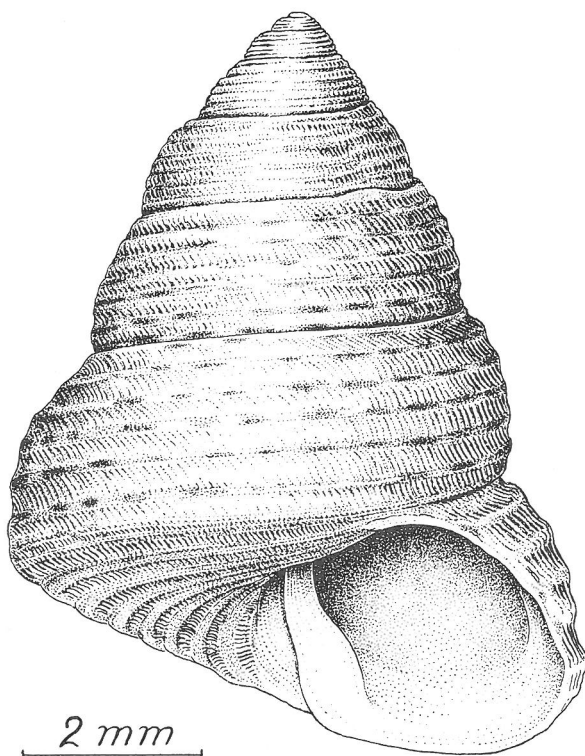


Fig. 50. *Cantharidus montagui* (Wood). Salcombe, Devon. BMNH.

Aperture. Prosocline, quadrilateral. The outer lip, thin except where thickened by the ends of spiral ridges, arises just abapical to the periphery of the body whorl, at right angles to its surface. Its initial part may be concave when the aperture becomes a little pointed adapically; it then follows a smooth, curved course, hardly marked by a keel, to the columella, which is nearly vertical and bears a low swelling about its middle. The inner lip is rolled over the columella sometimes with a visible line of separation, sometimes not. In young shells there is an umbilical opening, but it is closed in older ones. In the parietal region the spiral decoration of the body whorl comes to an abrupt end. The ornamentation is visible through the thickness of the shell.

Colour. Cream, pale brown, biscuit, darker apically. The spiral ridges are marked with blotches of reddish brown. In a few shells these are arranged to produce prosocline bands across the whorls. In young shells the ridges bear continuous lines of colour which are interrupted only from about the third whorl. Some shells show an external blue-green refringency when wet; all do internally except for a narrow band within the outer lip the inner limit of which is marked by a shallow groove.

Size. Up to 8 x 6 mm. Body whorl = 50% of total shell height; aperture = 40-50% of shell height, = 60% of shell breadth.

Animal. The differences between this species and both *exasperatus* and *striatus*, apart from colour, are trivial. The tentacles are less slender and the cephalic lappets smaller. The epipodial sense organs lie behind the corresponding tentacles.

Colour. Cream with brown and white flecks. The dorsal surface of the snout bears a brown area diverging into two arms posteriorly. The sides of the foot are blotched brown, the neck lobes and cephalic lappets have white flecks. The epipodial sense organs are dark.

Geographical distribution. *C. montagui* occurs in the Mediterranean and in the Atlantic N. to the Orkneys. It has also been collected off N.E. English coasts and from Dogger Bank. It is common in the W. Channel but absent from Scandinavia.

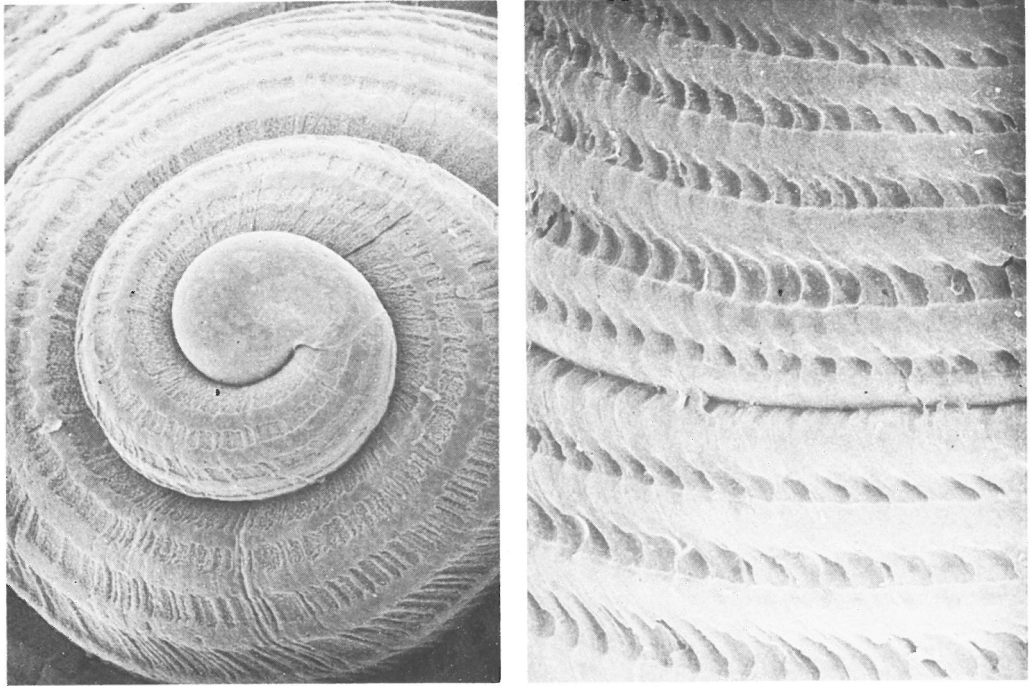


Fig. 51. *Cantharidus montagui* (Wood). A, apical region from above X 237; B, details of ornamentation of whorls, X 88. SEM photographs. Roscoff. RUZ.

Habitat, food. This is not a littoral animal and is found only in dredgings made from stony or gravelly grounds, at depths of 10-200m, so that little is known of its precise habitat or way of life. It appears to be very local in its distribution so that it may require some special environmental factors to be present for survival. It probably feeds as a detrital scraper like other *Cantharidus* spp. since the faeces (with the same characteristics) are full of detrital particles.

Breeding and growth. There appears to be nothing known of the breeding or growth of this species. However, the resemblance of the protoconch to that of *C. exasperatus* perhaps indicates that as in that species free larval stages are suppressed and that a spawn mass is laid.

CANTHARIDUS CLELANDI (W. Wood, 1828)

- Trochus clelandi* W. Wood, 1828
- Jujubinus clelandi* (W. Wood, 1828)
- Trochus miliaris* Brocchi, 1814
- Calliostoma miliare* (Brocchi, 1814)
- Trochus millegranus* Philippi, 1836
- Clelandella millegrana* (Philippi, 1836)

Clelandi, Cleland's, almost certainly referring to James Cleland who lived in Northern Ireland. He was an enthusiastic collector and supplied shells to G. B. Sowerby the First, Goodall and Wood, amongst others. In 1823 he sent specimens of 'my new nondescript Trochus, which Dr Goodall has named Trochus Interruptus' to Wood. See Matheson (1966); we are grateful to Dr and Mrs R. Clevely for bringing this paper to our attention.

Shell. Solid, nearly opaque, a little glossy. It is conical and nearly straight-sided except for a slight step at each keel and an inconspicuous swelling of each whorl, more marked in older ones. There are 7-8 whorls meeting at inconspicuous sutures. The apical angle lies between 62-70°. The shell is ornamented with growth lines and spiral ridges and grooves. The former are prosocline making an angle of about 45° with the axis of the helicocone and, except on the base, are raised at regular intervals to form upstanding ridges which cross the spirals, ridges and furrows alike. On each older whorl and on the body whorl between suture and periphery there are commonly 6 major

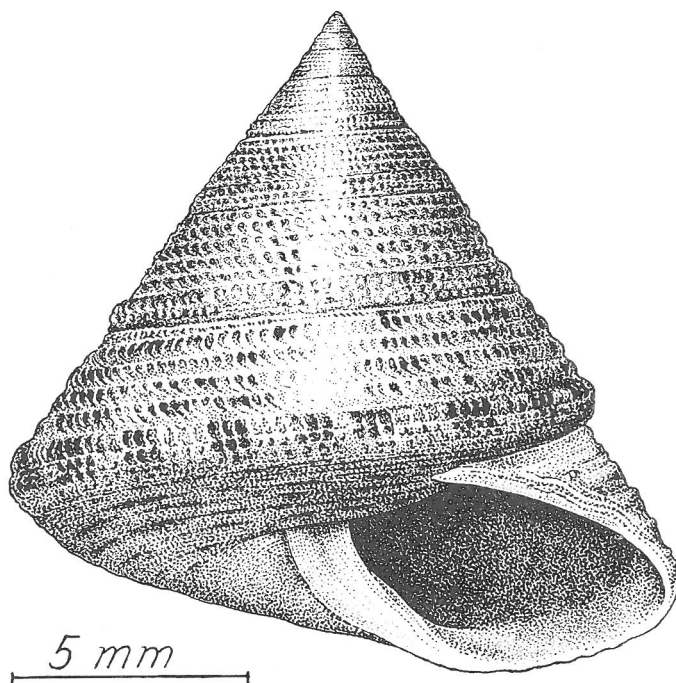


Fig. 52. *Cantharidus clelandi* (Wood). Store Middle Ground.

spiral ridges but often up to twice that number because of the presence of a minor ridge in each furrow. The peripheral ridge of the body whorl is compounded of a group of 4-5 close-set ridges of which the adapical pair are larger than the others and form a prominent keel. Ridges and growth lines together subdivide the shell surface into regular lozenge-shaped areas. Where they intersect they form tubercles, not usually visible to the naked eye on the first two whorls. The tubercles lie in slightly curved prosocline rows which, at least in the upper ones, continue from whorl to whorl so that in apical view they form an array of spirals apparently radiating from the nucleus. There are 80-90 on the body whorl and about 10 less on each older one. On the base of the shell all growth lines are of the same size and the spiral ridges are only indistinctly beaded. There are 7, sometimes more because of small intermediate ones, of which the most central bounds a slight depression which, in most shells, is obliterated by an outfolding of the inner lip, but in those with 5 whorls or less leads to a narrow V-shaped umbilicus. The base is flat and makes an angle just less than 90° with the sides of the cone. The nucleus is smooth with a pointed tip and measures about $300\mu\text{m}$ across.

Aperture. Proscloine, rhombic and nearly straight-sided. The long axis makes an angle of about 110° with that of the helicocone. Except where thickened by the ends of the spiral ridges the outer lip is thin and arises just below the periphery of the body whorl. It is noticeably angulated and pointed by the keel of that whorl. The columella bears a long, low tooth where it joins the outer lip. The inner lip is everted over the umbilicus and where it runs across the body whorl to join the outer lip it brings the spiral ridges there to an abrupt end.

Colour. White, greenish or pinkish with a refringence in the spiral furrows especially when wet. The apex is pink; pink or brown spots sometimes occur, usually on the ridges and most marked on the keel. The interior is glossy and nacreous.

Size. Up to 18×18 mm, but most specimens are only about 10-12 mm high and the same broad. Body whorl = 50-55% of shell height; aperture = 28-32% of shell height.

Animal. The snout is rather small with a short scalloped fold around its tip dorsally and laterally, but is otherwise without papillae. The mouth is a vertical slit surrounded by radially folded lips without a ventral slit or flap. The tentacles are long, slender and covered with sensory papillae like

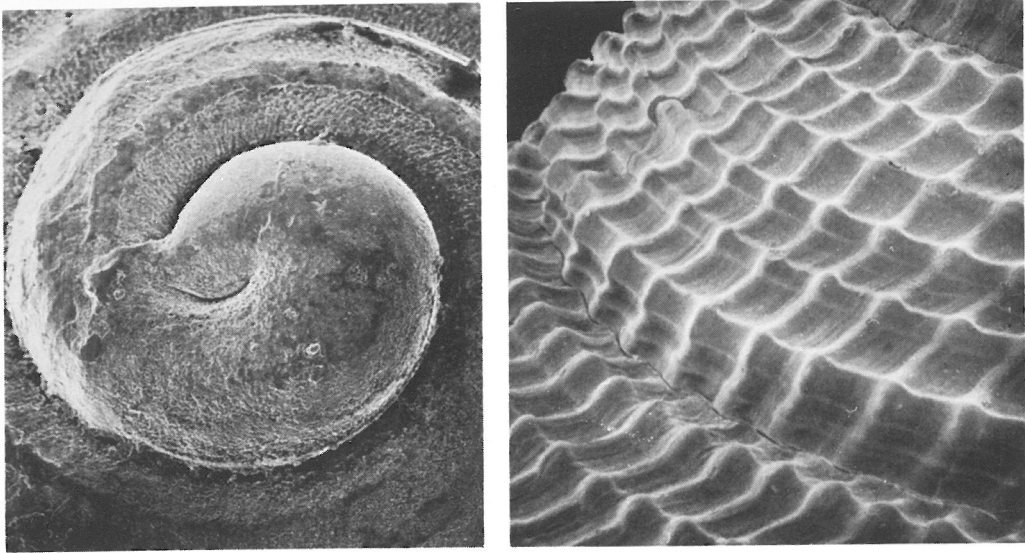


Fig. 53. *Cantharidus clelandi* (Wood). A, apical region from above, X 300; B, details of ornamentation of whorls, X 76. SEM photographs. Roscoff. RUZ.

those of *Gibbula*. At the base of each, medially, is a large cephalic lappet with a papillated edge, and laterally, a thick eye stalk with a large eye. The eye stalk on each side connects with the lappet under the tentacle base. That on the right also connects backwards with a neck lobe which has a smooth edge, is kept away from the shell to form an exhalant tube and marks the beginning of an epipodial ridge which extends to the posterior end of the foot. The corresponding ridge on the left expands anteriorly to a neck lobe with a scalloped edge which forms an inhalant siphon. The mantle edge is slightly lobed.

The foot is rather narrow, truncated anteriorly, without a propodial groove, pointed behind, its flanks covered with small papillae from the edge of the sole to the epipodial ridge. Some papillae are enlarged. On each side three epipodial tentacles spring from sheaths inserted below the ridge, each rather long, slender and papillated like the cephalic ones. The most anterior has a hemispherical sense organ behind its base, the middle one has a sense organ ventral to its base and the hindmost has a pair of sense organs, one behind and one in front of its base. In addition a single sense organ lies on each side of the foot at the level of the neck lobe. The dorsal surface under the operculum bears a few transverse folds. The operculum is pale yellow, polygyrous, with about 11-13 turns.

Colour. White or cream, with lines or spots of brown on the side of the foot. The snout is olive green dorsally with a Y-shaped mark between the tentacle bases. The tentacles have dark lines along them, one centrally and often marginally.

Geographical distribution. This species occurs in the Mediterranean and off all European coasts northwards to the Norwegian coast (south of the Lofoten Islands). It extends into the Kattegat as far as the Øresund and into the northern parts of the N. Sea, but is absent from its eastern shores (Jutland, Germany) and from the eastern basin of the English Channel.

Habitat. Never littoral; dredged from about 35 to 800m on bottoms which vary from stony to gravel and, less commonly, sand or muddy sand. It is not uncommon.

Food. The faeces form rods similar to those of other trochids. They contain much detrital material including sand grains up to about 250 μ m in diameter, foram shells, radiolarian shells and other unidentifiable matter, including some plant material. From this it may be concluded that they are detrital scrapers like related species.

Breeding and growth. Unknown. The sexes are separate. The eggs (in the ovary) measure about 150 μ m in diameter and are surrounded by a jelly coat. Robert (1902) reported that the related species *C. exasperatus* and *C. striatus* laid their eggs in jelly masses, from which it might be

expected that *C. clelandi* would too. Unless they adhere by their jelly coats there is little indication of the production of other material to effect this as in *Margarites helycinus* and *Calliostoma zizyphinum* since the lips of the genital opening are very inconspicuous. It is probable that no free larval stage occurs (Thorson, 1946).

CALLIOSTOMA ZIZYPHINUM (Linnaeus, 1758), painted top-shell

Trochus zizyphinus Linnaeus, 1758

Trochus conulus Linnaeus, 1758

Trochus conuloides Lamarck, 1822

Calliostoma, an abbreviated form of *Callisostoma* (Gk.), meaning 'with the most beautiful mouth', referring to aperture of the shell.

Zizyphinum (Gk.), the jujube tree (genus *Zizyphinum*), the fruit of which the shell resembles.

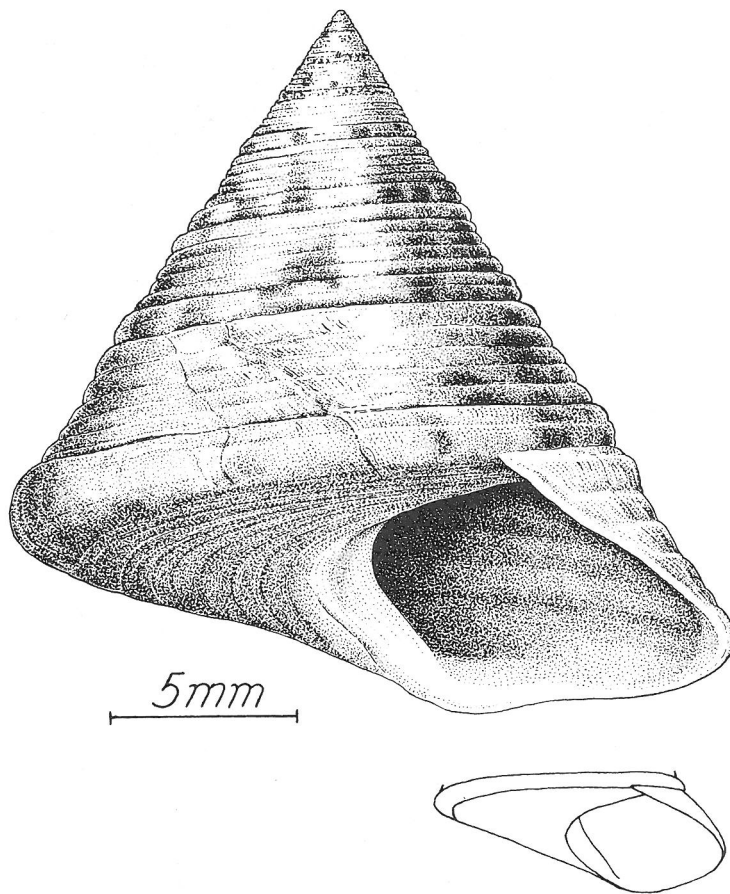


Fig. 54. *Calliostoma zizyphinum* (L.). Skagerrak off Rubjerg. CMZ. Inset, aperture of shell from Lancashire coast. RUZ.

Shell. Solid, opaque, a little glossy. Almost exactly conical with a flattish base. The apical angle ranges from 64-78° but is nearly always within 66-68°; the angle made by the base and side of the cone is commonly 72-74° but may be between 66° and 80°. In profile the spire is often straight-sided, as often slightly coeloconoid (most markedly near the apex), very rarely cyrtconoid. There

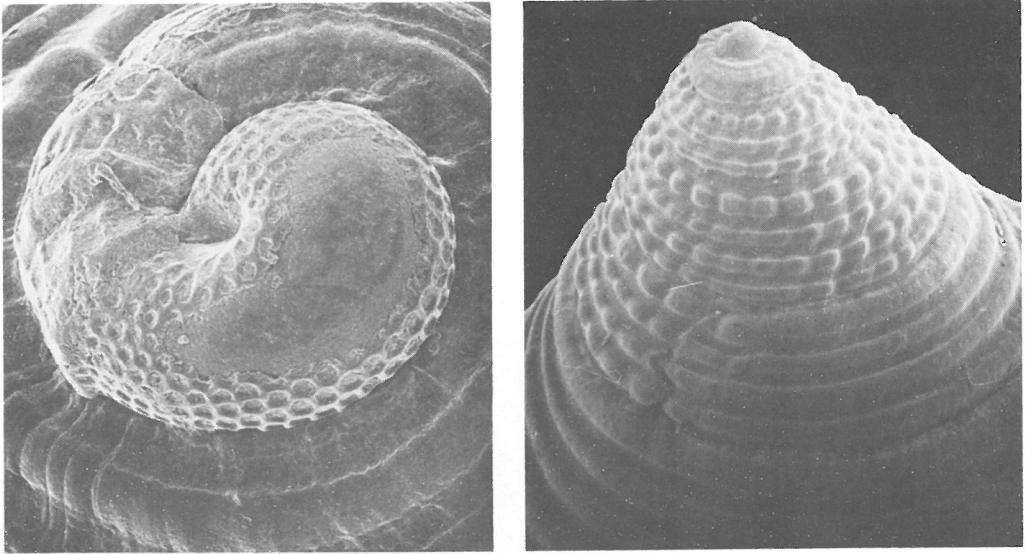


Fig. 55. *Calliostoma zizyphinum* (L.). A, apical region from above, X 240; B, upper part of spire, oblique view, X 36. SEM photographs. Plymouth. RUZ.

are ordinarily about 10 whorls but large shells may have 12-13, flat or very slightly tumid, meeting at shallow sutures, difficult to distinguish in the upper part of the spire. The shell bears growth lines and a series of spiral ridges and grooves. The growth lines are prosocline, nowhere conspicuous but more so in the furrows. The ridges are broader than the furrows, have adapical steep sides and form a series of ledges on each whorl. There are 9-10 on the upper part of the body whorl, 8-9 on the penultimate, 6-7 on the previous whorl of a full-sized shell. Many of the upper whorls show 4 ridges, decreasing to 3 and 2 in the oldest. All these numbers may vary by the development of minor ridges in the grooves, more particularly in younger whorls. In the upper whorls the ridges are all beaded by interaction with ribs. Ribs, and so beading, disappear on younger whorls, persisting longer on the subsutural ridge than on the others, but even there absent on the last two whorls of mature shells. (A few, however, in the subspecies *granulifera*, have beaded ridges on all whorls.) The ridge at the periphery of the body whorl is enlarged and broadened, forming a keel. The sutures lie at or just below the keels so that the spiral ornament on the shell appears regularly thickened. There is a small umbilicus in young shells but this is later closed. The nucleus has a pointed tip and bears a reticulate pattern liable to wear off in older shells. It measures about 300 μ m across. The first section of the teleoconch, of variable length, may exhibit only growth lines, irregularly raised.

Aperture. Prosocline, lying at an angle of about 120° to the axis of the shell. It is roughly quadrilateral, the outer half with more curved sides than the axial. The outer lip is thin, slightly thickened by the ends of the spiral ridges, and arises at the peripheral keel of the previous whorl. It curves gently to the keel of the body whorl where it bends sharply to run, nearly at right angles to the axis of the helicocone, to meet the columella almost normally. The columella is straight and has no tooth. The inner lip turns out to cover part of a shallow umbilical groove which ends blindly; it rarely can be seen extending over the parietal region.

Colour. Variable. Most shells are yellowish or pale pink with irregular blotches or streaks of brown, reddish brown, red or purple. These tend to an opisthoclinal course on the upper parts of the whorls and to straighten abapically, where they may branch. On the keels they almost always form a regular series of blotches, twice as numerous as the streaks: this pattern emphasizes the keels on the spire. On the base the colour rapidly vanishes. The apex is often redder than the rest of the shell. Occasional specimens may be wholly white or violet.

Size. Up to 30 mm high, 30 mm broad. Body whorl = 40-45% of shell height; aperture = 33% of shell height.

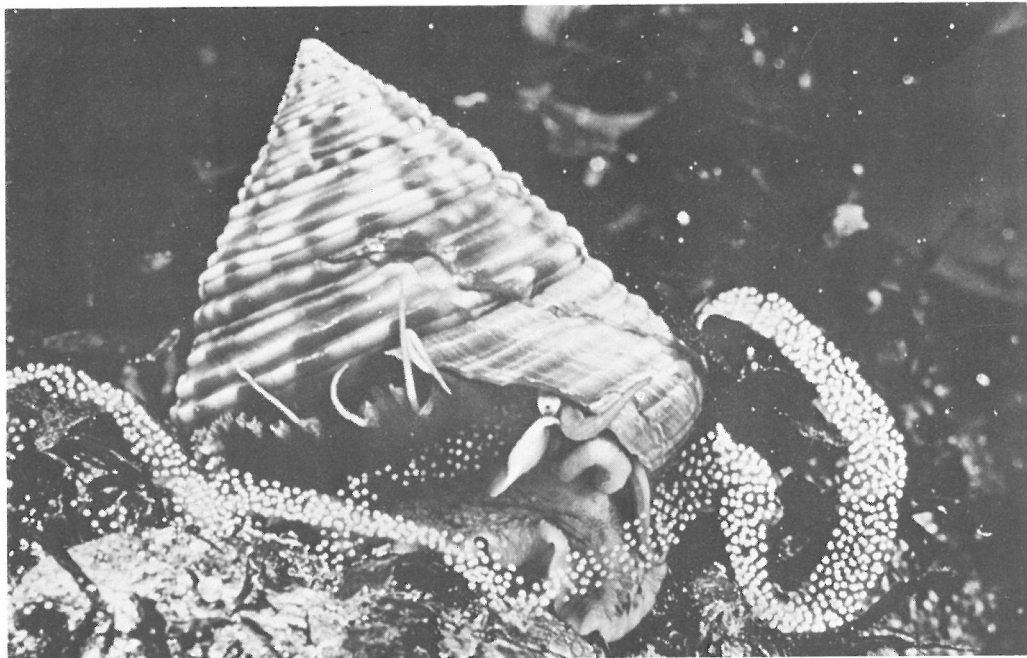


Fig. 56. *Calliostoma zizyphinum* (L.). Female with spawn. (Courtesy of Dr P. Bouchet.)

Animal. Head extended into a large snout carrying a transverse row of papillae at its tip. The mouth, closed, is T-shaped, surrounded by radially folded lips, split mid-ventrally and extended into an elongated flap which runs posteriorly to the right and is kept rolled into an incomplete tube. At the base of the snout is a pair of cephalic tentacles, long, tapering and set with fine papillae. Medial to its base each has a small cephalic lappet with a few small lobes at its edge, and laterally, a rather long, narrow eye stalk. Lappet and stalk connect dorsal to the tentacle. The eye stalks are also connected (more clearly on the left) to neck lobes with smooth margins. These in turn join epipodial ridges. The mantle edge has many minute lobes.

The foot is broad anteriorly, slightly extended at its angles, and tapers behind. The sole has transverse ridges. Immediately behind its anterior margin a deep, transverse cleft marks the anterior pedal gland. The sides of the foot are papillated and there are 3-4 larger ones set about halfway between the edge of the sole and each neck lobe. There are 4 (sometimes 5) epipodial tentacles on each side, set just ventral to the epipodium. Each springs from a short sheath but has no related sense organ. The dorsal side of the foot behind the operculum forms a flat, ridged surface, normally folded upwards so that its edges meet. The operculum is shallowly concave with about 15 turns.

Colour. Yellowish, sometimes with a red tint, blotched and streaked with brown or red; sole of the foot pale yellow or pink. The tentacles are of the same shade, or paler, and usually have a dark central line.

Geographical distribution. *C. zizyphinum* occurs in the Mediterranean and extends N. from the Canaries and Azores to Britain and the N. Sea. Animals living north of France are sometimes regarded as belonging to a subspecies *conuloide* Lamarck. It occurs on all British and Irish coasts, on those of Norway as far as the Lofoten Islands and on the Bohuslän coast of Sweden. It does not enter the Kattegat nor is it found on Dutch or Belgian coasts, perhaps because of the absence of appropriate beaches.

Habitat. Like most top-shells this species favours rocky shores with broken surfaces which are not too exposed and which bear a growth of fucoids on which it may creep. At low water it hides amongst them or under stones. It lives at a lower level than other littoral trochids — below LWNT (not more than 20% emersion) — though in the N. it may also be found in pools at a higher level. It

extends sublittorally to 300m and may be found on both hard and soft bottoms. It can withstand a reduction in salinity to 21‰. It is common.

Food. There is some doubt about what this animal eats. Like other top-shells it appears to be a scraper and both gut and faeces contain vast numbers of detrital particles — sand grains, diatom cases, sponge spicules, plant remains — and are frequently green. On the other hand there are reports (Francis, 1973; Lowry, McElroy & Pearse, 1974; Perron, 1975) that *Calliostoma* spp. are carnivorous and eat hydroids, gorgonians, anemones. These are Pacific species, but Salvini-Plawen (1972) stated that *zizyphinum* eats polyps, perhaps held by the labial tube. Both methods may be followed, though our observations suggest that scraping is the commoner mode and we have never seen nematocysts in gut or faeces. These are soft, rather shapeless rods embedded in mucus, about 0.6 mm in diameter, containing vegetable detritus and sand particles. No distinction into stomach string and liver string can be made.

Breeding and growth. The sexes are separate, the female distinguishable by enlargement of the lips of the genital opening during the breeding season. The eggs are yellowish and measure 260-300µm at laying. Each is surrounded by a membrane and jelly. The eggs are laid together and the jelly round each, with that from the genital papilla, forms a cylindrical mass 3-4 mm across and up to 35 mm long. This is attached by the foot of the female several times as it is produced so that it is tacked at intervals to stones or weeds in pools in the area in which the adults live, the rest floating. Fertilization has not been recorded and would be assumed to be external except that Lebour (1936) noted that an isolated female laid fertilized eggs. Both trochophore and veliger stages are passed within the egg mass and young snails emerge in 7-8 days with shells measuring 300-350µm across. At this stage the first part of the shell to bear spiral ridges is just being laid down and there are only 2 pairs of epipodial tentacles (Robert, 1902; Lebour, 1936).

Notes. Although this animal is one of the common prosobranchs of rocky beaches at a low tidal level little seems to be known about its feeding habits, the role of the labial tube, its life history and its general ecology.

The drawing shows a shell in which the outer lip is straighter and more acutely angled at the keel than is common: it is usually more convex and less acute as in the inset.

CALLIOSTOMA PAPILLOSUM (da Costa, 1778)

Trochus papillosus da Costa, 1778

Trochus granulatus Born, 1778

Trochus fragilis Pulteney, 1799

Papillosum (Lat.), covered with papillae, referring to the ridges on the shell.

Shell. Like that of *zizyphinum* but with a distinctly coeloconoid spire, mainly due to a bulging of the body whorl which is more tumid than the flatter-sided ones of the spire. The apical angle of larger shells may exceed 80°, but be only 60° in smaller ones. There are 7-9 whorls each bearing opisthocline growth lines and spiral ridges and grooves. There are 7-12 ridges on the upper half of the body whorl, the lowest most prominent and forming a well-marked keel. Smaller ridges often lie in the furrows between major ones. On the penultimate whorl are 7-9 ridges and a decreasing number on the preceding ones. Every major ridge bears a series of rounded tubercles which, in apical view, form prosocline spirals running from whorl to whorl. These are absent from the minor ridges and those on the subsutural ridges are double. Each ridge is a little narrower than the intervening furrows. The peripheral ridge is double or triple and the lower ones are only very slightly papillated. The sutures are shallow and inconspicuous. The growth lines (clearest in furrows) often show wave-like crests in line with the tubercles on the ridges. The base is marked by 12-14 major spiral ridges and grooves, the former broader than the latter and bearing only small granules. Minor ridges may lie in the furrows. There is a central depression but no umbilical opening, though this is present in very small shells. The protoconch bears a reticulate pattern and measures 300µm across.

Aperture. Less prosocline and less angular than in *zizyphinum*. The thin outer lip arises just below the smooth peripheral ridge of the body whorl. It may run nearly at right angles to the shell axis at first but more frequently makes an angle of 135° with it and has a rather sharp angle at the keel. Abapically it curves gently into a rather broad columella which has at most only a suggestion of a tooth. The inner lip spreads outwards over the umbilical area.

Colour. Cream, yellow or orange with brown or reddish markings which form slightly opisthocline bands on the spire and body whorl but usually not more than spots or flecks on the base. They usually occur only on the ridges.

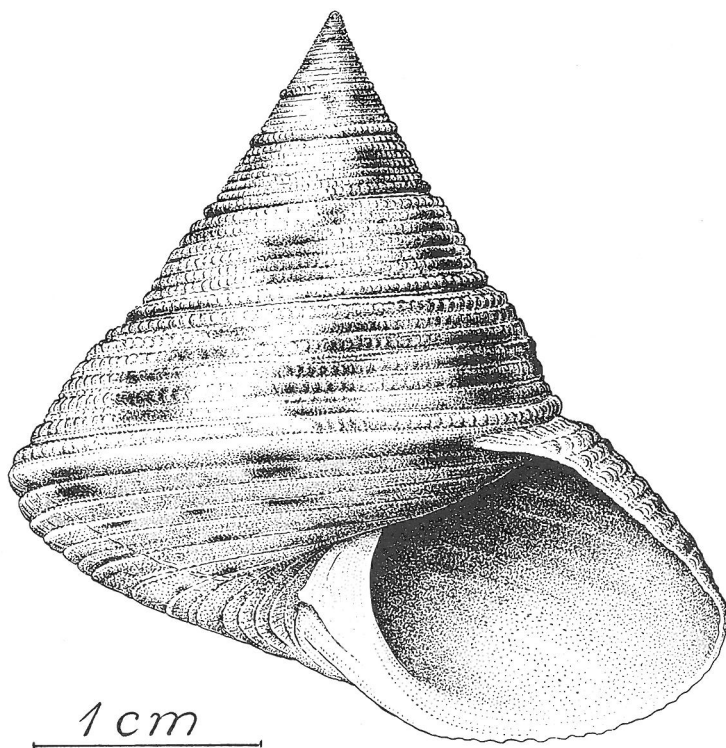


Fig. 57. *Calliostoma papillosum* (da Costa).

Size. Up to 35 x 35 mm. The body whorl = 60% of shell height; aperture = 40-50% of shell height.

Animal. In general like that of *zizyphinum*. The snout is markedly richer in papillae at its tip; these are longest at the sides where many branch. The mouth is vertical I- or Y-shaped when shut and has a labial tube as in *zizyphinum*, of which the outer surface bears some papillae; its inner is not apparently ciliated. The tentacles are noticeably setose. Under their base and that of the eye stalk a small cephalic lappet with 2-3 lobes connects with a neck lobe, that on the right smooth-edged, that on the left with a scalloped margin which is kept up-turned during life so as to expose 1-2 elongated papillae on the ventral side. The mantle skirt has many small marginal lobes.

The foot is large, truncated in front (where its corners are elongated), tapering behind, with a median longitudinal and some transverse grooves on the sole. The anterior edge is double where the anterior pedal gland opens. The sides of the foot are covered with rounded papillae and carry 3 epipodial tentacles on each side without apparent accompanying sense organs. The dorsal side of the foot, behind the operculum, bears a median dorsal cleft with wavy edges; though normally closed this may open to display a flat surface covered with many transverse ridges.

Colour. Cream, speckled with brown marks. The tentacles have a central dark line. The eyes are blue with a black centre where the vesicle opens. Eye stalks, neck lobes, epipodial tentacles and dorsal posterior part of foot white.

Geographical distribution. *C. papillosum* has a more southerly distribution than the other local species of the genus, not occurring N. of the Shetlands and being rare up to the Scottish W. coast. It does not enter the N. Sea nor reach Scandinavia and is rare in the eastern basin of the English Channel. It occurs regularly though never commonly in the western basin and S. to Madeira, the Canaries and the Mediterranean.

Habitat. Never littoral; dredged between 7 and 300m mainly on soft bottoms.

Food. Unknown, but probably as in other species. When it creeps the papillae at the tip of the snout are pressed against the substratum, though they are kept immobile: whether they are purely sensory or could act as a brush — perhaps in relation to the labial tube — is not known.

Breeding and growth. Unknown. As in other species of *Calliostoma* it is likely that there is no free larval stage.

CALLIOSTOMA OCCIDENTALE (Mighels, 1842)

Trochus occidentalis Mighels, 1842

Calliostoma alabastrum (Loven, 1846)

Calliostoma formosum (McAndrew & Forbes, 1847)

Occidentale (Lat.), western, referring to the fact that Mighels described the species from animals collected in the western Atlantic, off American coasts.

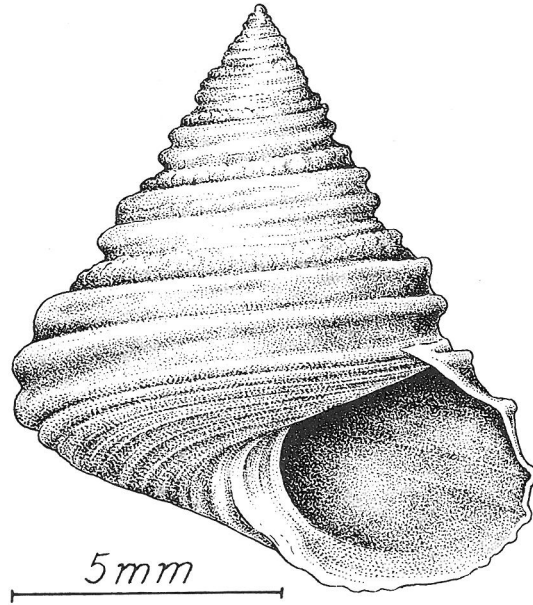


Fig. 58. *Calliostoma occidentale* (Mighels). Entrance to Skagerrak (57°24'N, 7°28'E, 108m). CZM.

Shell. Like that of *zizyphinum* in general but semi-transparent and pearly. It has about 7 slightly swollen whorls meeting at inconspicuous sutures. The apical angle has an average and modal value of 64° (range 60-72°), whilst that between the side of the spire and the base is commonly 76-78° (range 65-83°). The spiral ridges and furrows are much more prominent than in *zizyphinum* or *papillosum*. The growth lines are prosocline, all alike and slight, most easily seen in the furrows. The spiral ridges number 4-5 on the body whorl, 4 on the next two, 3 on the next two, and 2-3 on the whorls next to the protoconch. They form narrow step-like projections separated by rather flat furrows 2-3 times broader. In the oldest whorls all the ridges are beaded but in younger ones there are no beads, though they usually persist on the most adapical ridge on the body whorl. The beads arise on older whorls where slight ribs cross the ridges but ribs cannot be traced after the third whorl. The peripheral ridge on the body whorl is broader than the others, forming a prominent keel. The base shows 1-2 ridges, separated by narrow grooves, directly under the keel, and 3-5 similar ridges and grooves round an umbilical spiral groove. Between these two sets the base forms a broad, flat belt marked only by growth lines. A small umbilical chink is present. The protoconch has a large reticulate pattern and measures 250µm across.

Aperture. A rather rounded quadrilateral of which the two adapical corners are more pointed than the others. The outer lip is thin and springs at right angles from the periphery of the body whorl. It is crinkled where the spiral ridges end since they are here hollow folds rather than solid

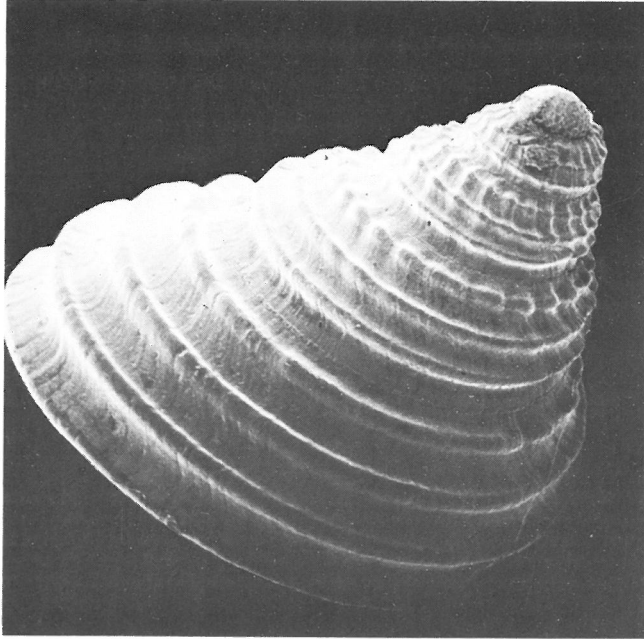


Fig. 59. *Calliostoma occidentale* (Mighels). Oblique lateral view of small shell, X 30. SEM photograph. BMNH.

ridges. Near the columella it is slightly out-turned. The columella is a rounded pillar with an indistinct basal swelling but clearly marked by its glossy, nacreous surface. The inner lip is reflected outwards over part of the umbilical groove.

Colour. Fresh shells, particularly when wet, show an opaline refulgence in the furrows, glowing with reddish colour. In most shells the spiral ridges are yellowish, in a few white. The inside is nacreous.

Size. Up to 11-12 mm high, 10-11 across. Body whorl = 55% of total height; aperture = 40% of total height.

Animal. Like *zizyphinum* except that the cephalic lappets are small or absent, the anterolateral corners of the foot more expanded and the number of epipodial tentacles is 3 (occasionally 4) on each side.

Colour. Cream or buff, speckled or striped with brown or purple.

Geographical distribution. *C. occidentale* is a boreal form found on both sides of the Atlantic. In Europe it occurs off the whole western Norwegian coast, in the northern N. Sea, off British coasts N. of the Humber on the east but not on western British or any Irish coasts. It is not found in the Skagerrak nor off Jutland. In America it has been recorded from Newfoundland S. to New Jersey. It also occurs in Iceland, but not Greenland.

Habitat. This species is never littoral. The animals are dredged on stones between 19 and 1000m. In the Kola Gulf it occurs (60-100m) with a fauna rich in tunicates and sponges.

Food. Unknown. Faecal contents suggest a mode of life like that of other species in the genus; perhaps a sponge-eater (Derjugin, 1915).

Breeding and growth. Unknown. It is likely that the larval stages are suppressed and it may be that the eggs are laid in a jelly mass.

Notes. The figure illustrates a shell with a regular series of grooves and ridges on the base: most have a plain area separating a group of peripheral ridges from a group of central ones.

Perron & Turner (1978) have just shown that this species grazes the alcyonacean *Gersemia rubiformis* and eats hydroids.

REFERENCES

- DERJUGIN, K. 1915. Fauna of the Kola Gulf and its environmental conditions. *Zapiski Imperatorskoi akademii nauk*, **34**, 1.
- FRANCIS, L. 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. *Biological Bulletin*, **144**, 73-92.
- LEBOUR, M. V. 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journal of the Marine Biological Association of the U.K.*, **20**, 547-65.
- LOWRY, L. F., McELROY, A. J. & PEARSE, J. S. 1974. The distribution of six species of gastropod molluscs in a California kelp forest. *Biological Bulletin*, **147**, 386-96.
- MATHESON, C. 1966. G. B. Sowerby the first and his correspondents. Part II. *The Journal of the Society for the Bibliography of Natural History*, **4**, 253-66.
- PERRON, F. 1975. Carnivorous *Calliostoma* (Prosobranchia: Trochidae) from the northeastern Pacific. *Veliger*, **18**, 52-4.
- PERRON, F. & TURNER R.D. 1978. The feeding behaviour and diet of *Calliostoma occidentale*, a coelenterate associated prosobranch gastropod. *Journal of Molluscan Studies* (in press).
- ROBERT, A. 1902. Recherches sur le développement des troques. *Archives de Zoologie expérimentale et générale*, (3), **10**, 269-558.
- SALVINI-PLAWEN, L. V. 1972. Cnidaria as food sources for marine invertebrates. *Cahiers de Biologie marine*, **13**, 385-400.

SKENEIDAE Clarke, 1851

This family comprises a number of species of minute snails found on both hard and soft bottoms. The shell is not nacreous, has few whorls (which are tumid), a low spire and little ornament apart from some spiral ridges. The aperture has a well-marked peristome which is prosocline and sometimes embayed. There is a wide umbilicus. The initial part of the protoconch is swollen and does not show clearly the tilted tip characteristic of all other trochaceans. The soft parts are trochacean. The reproduction is unknown but development may well be direct.

SKENEA SERPULOIDES (Montagu, 1808)

Helix serpuloides Montagu, 1808

Turbo divisa J. Adams, 1797 (?)

Skenea (Lat.), named by J. Fleming (1785-1857, parish minister of Bressay, Flisk and Clackmannan, professor of natural philosophy, University of Aberdeen and of natural science, Free Church College, Edinburgh) in honour of J. Skene (1775-1864, a friend of Sir Walter Scott and for long curator of the museum and library of the Royal Society of Edinburgh); *serpuloides* (Lat.), like the tube of the polychaete *Serpula*, like a little (coiled) snake.

Shell. Thin, nearly transparent, glossy. It is depressed (apical angle 140-145°), with the spire rising little above the body whorl. There are 3-4 tumid whorls which meet at deep sutures and which expand very rapidly so that the body whorl constitutes most of the shell. There are a few inconspicuous growth lines; apart from these the sole ornament is a series of rather sharp spiral ridges and narrow grooves confined to the area abapical of the periphery of the body whorl. There are about 30 of these on the youngest part of that whorl, round the aperture, reducing to about 10 on its oldest part. There is a broad, circular umbilicus which lets the whole lower surface of the spire be seen, but with one or two slightly raised spiral lines on it. Protoconch smooth, of 1 whorl, rather swollen initially, 180-200µm across.

Aperture. Slightly prosocline, inclined at an angle of 160-165° to the axis of the shell. The lips lie in one plane and form a peristome which is almost circular save for a small outward angulation where it abuts against the body whorl. At this point in some shells, the peristome grows a little away from the rest of the shell. The outer lip arises at the periphery of the body whorl and its initial course is at right angles to that, even rising a little adapically. There is no out-turning of the lip over the umbilicus.

Colour. Colourless or white, occasionally a little yellow from viscera showing through.

Size. 1.5 mm high x 1.2 mm broad. Body whorl = 90-95% of shell height; aperture = 70-75% of shell height.

Animal. The head is extended into a depressed snout, broad at the base and tapering to a bilobed tip. The mouth lies ventrally under the tip, I-shaped when shut. There are two tentacles, broad and flat basally, narrow and less flat distally, beset along their edges with many sensory papillae. There are no cephalic lappets. Mantle edge simple, fringed with sensory papillae. Gill reduced.

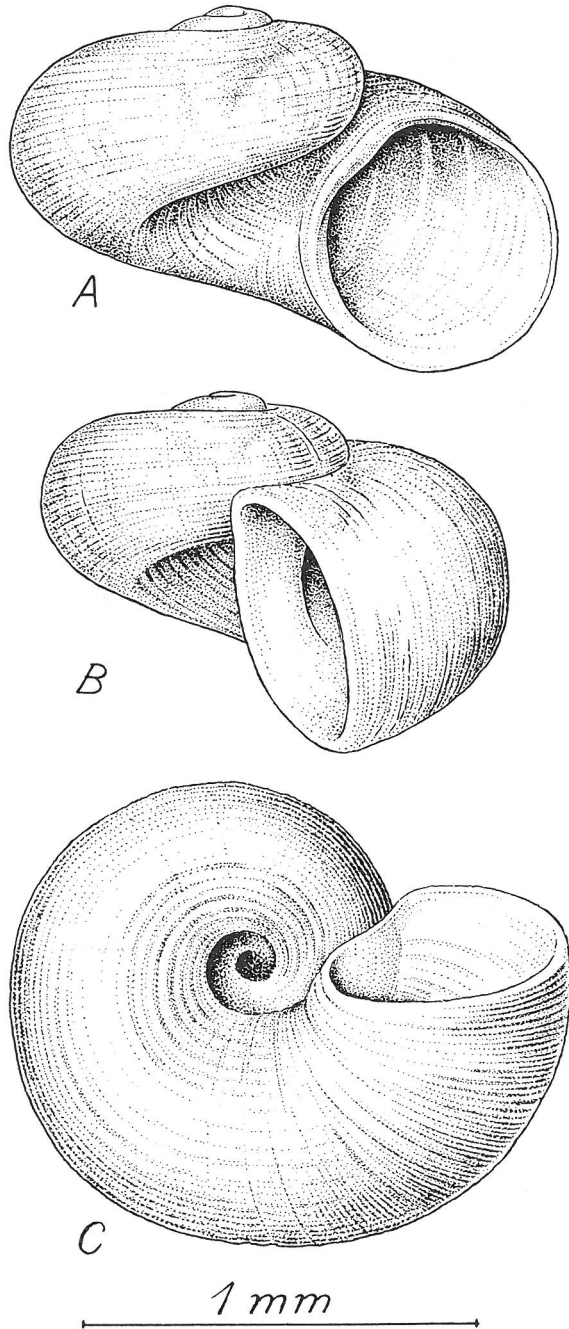


Fig. 60. *Skenea serpuloides* (Montagu). Guernsey.

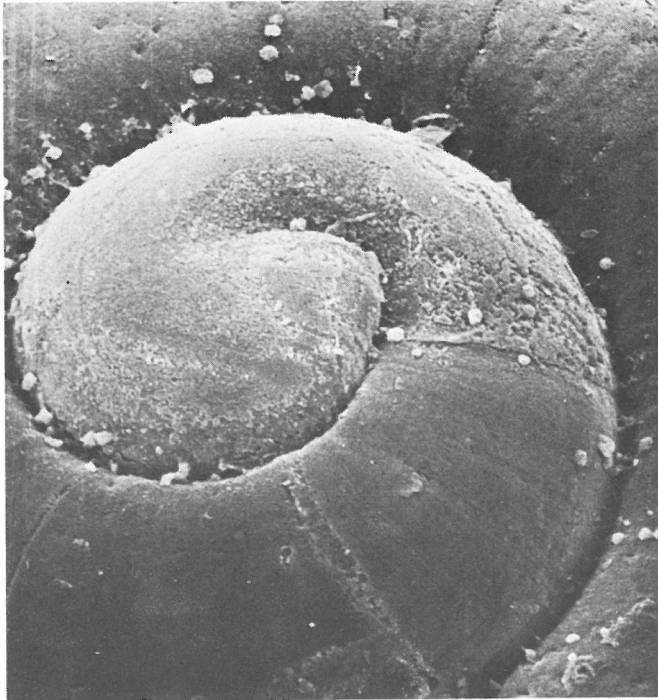


Fig. 61. *Skenea serpuloides* (Montagu). Apical region from above, X 264. SEM photograph. Roscoff. RUZ.

The foot has a broad sole, the anterior end a little embayed medianly and its lateral points elongated into tentaculiform outgrowths. There is a neck lobe, well developed on the right and with a fringed edge, smaller on the left where it has a simple edge. The right lobe is confluent with the anterior end of an epipodial fold, the left is separate. There are 3 epipodial tentacles on each side, papillated like the cephalic ones but shorter and broad; a fourth behind the right cephalic tentacle has been described as a penis. The operculum has about 6 turns round a more or less central nucleus and is glassily transparent.

Colour. White with opaque white line along each cephalic tentacle. The pale red colour referred to by Jeffreys is the buccal mass seen by transparency.

Geographical distribution. This is a southern species which finds its northern limit in the milder parts of the British Isles. It is absent from the Orkneys and Shetlands, though it has been recorded in the N. Sea as far S. as Scarborough. It is absent from all continental coasts E. and N. of Cotentin.

Habitat. *S. serpuloides* may be found on rocky shores at LWST and sublittorally to about 50m. Between tidemarks it occurs on weeds and stones; sublittorally it is dredged from shelly and gravelly sand. On the French Channel coast it occurs in the special habitat known locally as maërl — depressions containing detrital material which has been colonized by calcareous algae. Like other *Skenea* spp. it is probably often overlooked because of its small size.

Food. The animals must eat finely particulate detritus and bacteria. The faeces are in the form of smooth cylinders mainly composed of fine detrital particles.

Breeding, growth. There are no recent observations. Jeffreys stated that the spawn was attached to "the finer and membranous seaweeds". Each spawn mass contained many eggs. In view of this and the large size of the protoconch it seems likely that there is no free-swimming larval stage in the life history.

Notes. The drawing shows a shell in which the peristome separates rather clearly from the previous whorl: whilst this occurs in some shells it is by no means universal. The spiral ridges are properly drawn as most marked around the umbilicus; they are also indicated over the whole extent of the body whorl, an arrangement not true of most shells.

SKENEA NITENS (Philippi, 1844)

Delphinula nitens Philippi, 1844

Margarita pusilla Jeffreys, 1848

Nitens (Lat.), shining, referring to the glossy shell.

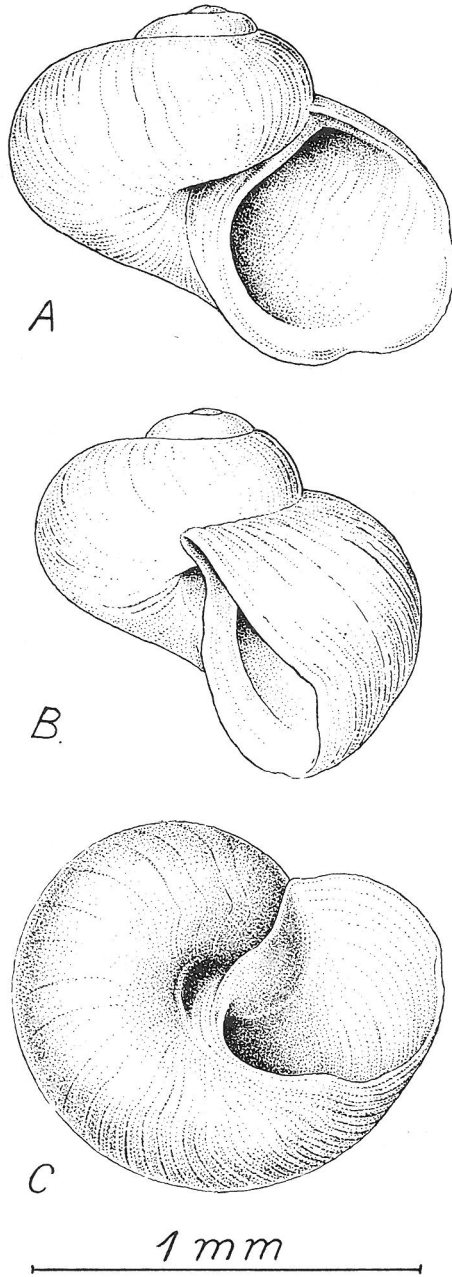


Fig. 62. *Skenea nitens* (Philippi). No locality given.

Shell. In general like that of *S. serpuloides* but the spire is slightly taller, though not relatively so tall as in *S. cutleriana*. The apical angle is 110-115°. Four tumid whorls meet at distinct sutures which lie at, or a little on the apical side of, the periphery of the older whorl. This has the smoothest shell of all the species of *Skenea* with a distinctly glossy surface, the ornamentation being restricted to a few irregular growth lines and, near the umbilicus, a few spiral grooves and ridges. The growth lines bend adapically up the spiral, reflecting the presence of sinuses on the peristome, one placed peripherally, the other basally. The latter marks the end of a small keel running on the base of the body whorl. The umbilicus has an oval mouth and on its abapertural side there runs a spiral rib-like thickening derived from the out-turning of the inner lip. The protoconch is smooth, of about 1 whorl, its initial part plump in relation to its mouth and it measures 150-170 μm across.

Aperture. Slightly prosocline, with a peristome which is somewhat ear-shaped and not plane. The outer lip arises at or below the periphery of the body whorl and curves outwards. At its periphery, and again at its most abapical point it shows two sinuses. The inner lip and columella run more or less vertically, the former a very little out-turned so as partially to block the umbilicus.

Colour. White or pale horn colour.

Size. 1 x 1 mm. Body whorl = 90-95% of total shell height; aperture = 70% of shell height.

Animal. As in *serpuloides* but without a right postoptic tentacle. Anterolateral angles of the foot shorter than in *serpuloides*.

Colour. White.

Geographical distribution. This species extends from Norway (Höisaeter, 1968a) to the Mediterranean. Except for the Norwegian record it is not known from continental N. Sea coasts through it is recorded from British ones from Scarborough northwards. It is also unknown in the eastern Channel and though recorded from the British shores of the western Channel appears to be much more abundant on the French side.

Habitat. Amongst weeds at LWST, on rocky shores, especially where there are small pools. Amongst detritus, on rocks and in maërl sublittorally to about 100m.

Food. A detritus feeder. Faeces as in other species of *Skenea*.

Breeding, growth. Unknown, but presumably as in other species.

Notes. The keel on the base of the body whorl produced by the out-turned peristome is usually more marked than is shown in Fig. 62C.

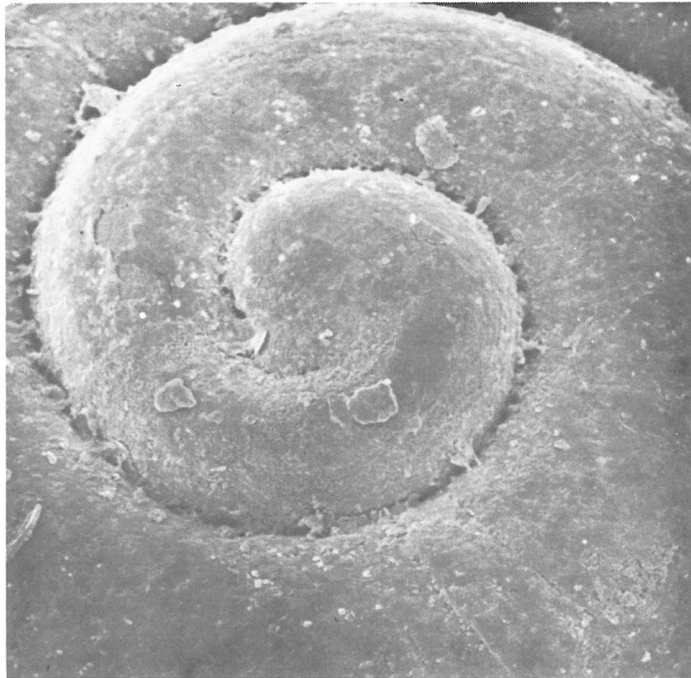
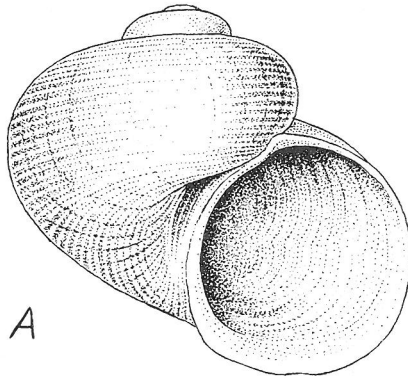


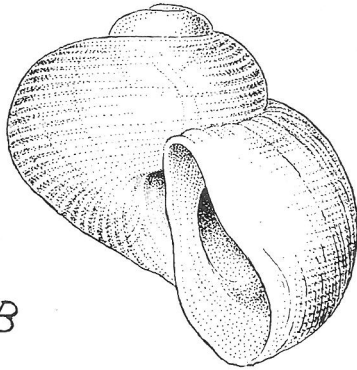
Fig. 63. *Skenea nitens* (philippi). Apical region from above, X 330. SEM photograph. Roscoff. RUZ.

SKENEA CUTLERIANA Clark, 1849

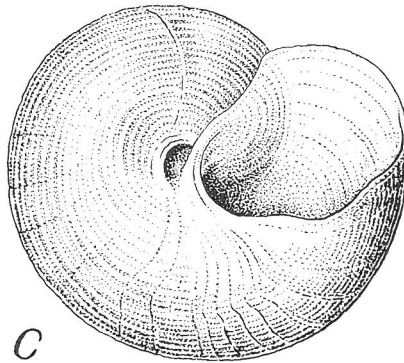
Cutleriana, named for a 'Miss Cutler, a lady of scientific taste and acquirements' (Jeffreys, 1865). We have been unable to learn more about her.



A



B



C

1 mm

Fig. 64. *Skenea cutleriana* (Clark). No locality given.

Shell. Thin, transparent and glossy. In general like that of *serpuloides* but with a taller spire (apical angle close to 100°) and more ornamentation. There are 3 swollen whorls meeting at deep sutures which lie just perceptibly below the periphery of the older whorl. As in *serpuloides* inconspicuous growth lines occur; each bends adapically at 3 points corresponding to 3 sinuses in the peristome. Spiral ridges are numerous and cover the whole surface of each whorl; there are about 30 on the body whorl and 10 on the penultimate. The umbilicus is narrow, partly obscured by a slight out-turning of the inner lip, and reveals little of the underside of the spire; a fold runs into it from the base of the aperture. Protoconch rather globular, its initial part swollen, smooth, of about 1 whorl, measuring about $170\mu\text{m}$ across.

Aperture. Prosocline like that of *serpuloides* but the peristome is not plane. The outer lip arises below the periphery of the body whorl, at right angles to it and so is directed a little basally. It is marked by three embayments, one at the level of the periphery, a second at the most abapical point, between which it is gently curved, and a third smaller sinus lying where the outer lip joins the columella. The aperture is a little pointed where inner and outer lips join.

Colour. White or colourless.

Size. 1×1 mm. Body whorl = 95% of total height; aperture = 60-65% of shell height.

Animal. As in *serpuloides*, but lacking a postoptic tentacle. The anterolateral corners of the foot are broader and shorter than in that species though better developed than in *nitens*.

Colour. White.

Geographical distribution. On the coasts of the southern parts of western Europe. In Britain it is limited to the coasts of Dorset, Devon and Cornwall and the W. coast as far north as the Isle of Man. It does not occur in the N. Sea nor in Scandinavia.

Habitat. Much the same kind of habitat as *S. nitens*, in pools and amongst algae at LWST and amongst detrital material at sublittoral levels. Its peak of abundance lies at a lower level than that of *nitens*.

Food. As for the other species.

Breeding, growth. Unknown; presumably as in other species.

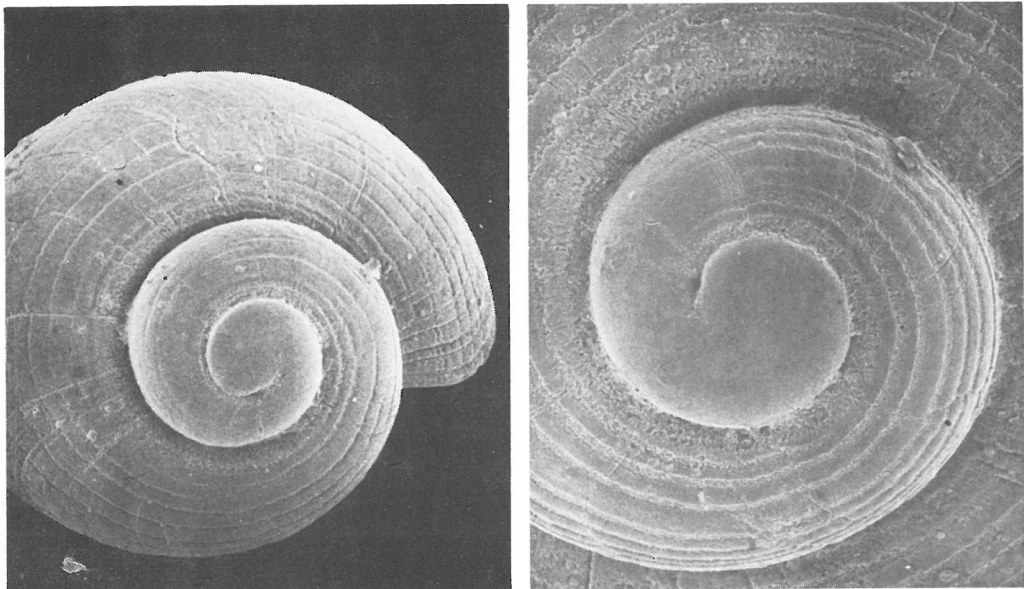


Fig. 65. *Skenea cutleriana* (Clark). A, shell from above, X 140; B, apical region from above, X 280. SEM photographs. Roscoff. RUZ.

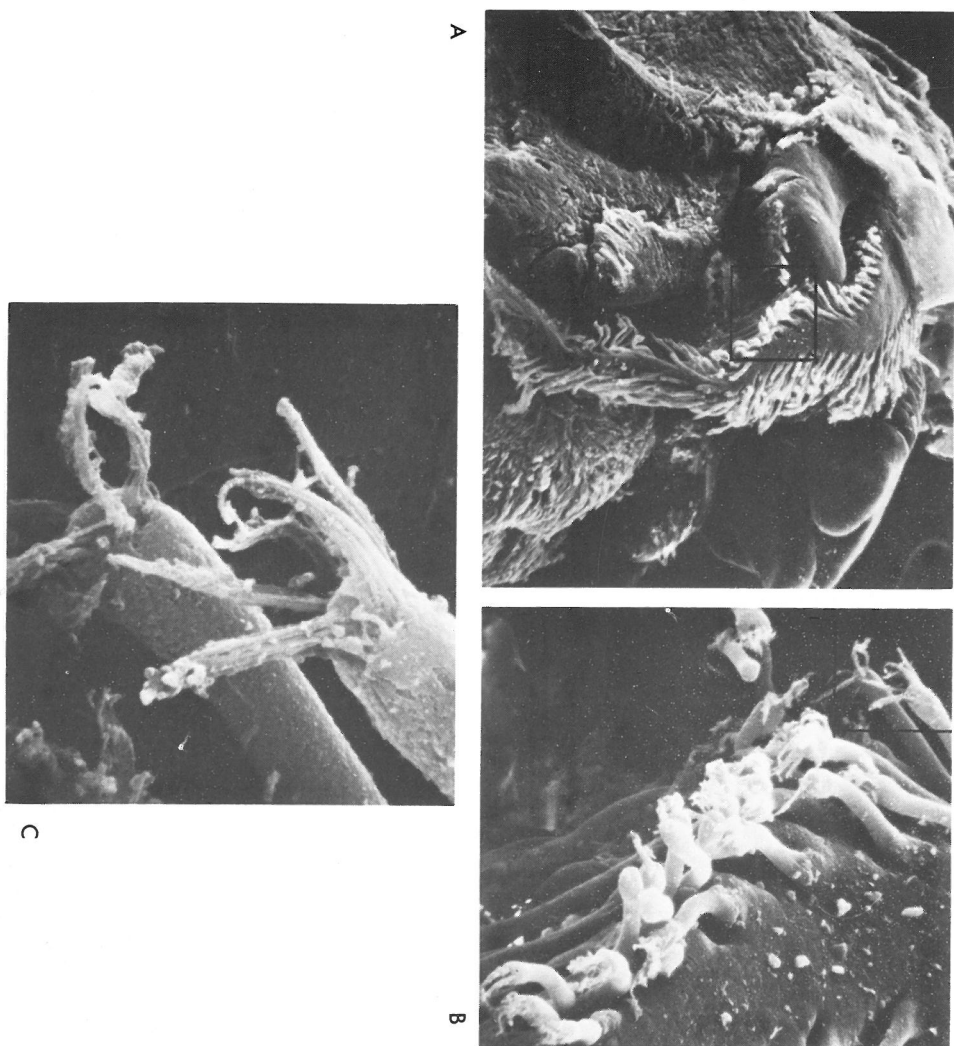


Fig. 66. *Skenea cuthertiana* (Clark), A, anterior end-snout on right, cephalic tentacle centre, eye stalk left centre, mantle edge left, X 210; B, sensory papillae from area marked in A, X 1050; C, sensory papillae enlarged from area marked in B, X 5500. SEM photographs. Roscoff. (Courtesy of Dr Elizabeth Andrews.)

SKENEA PETERSENI (Friele, 1876)
Cyclostrema peterseni Friele, 1876
Cyclostrema trochoide Jeffreys, 1875 (part)

Peterseni, Petersen's.

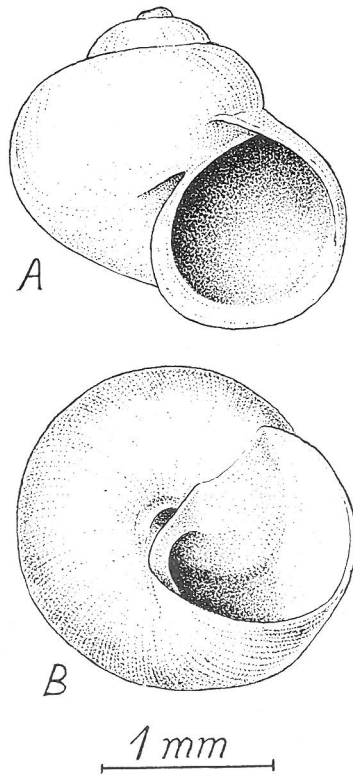


Fig. 67. *Skenea peterseni* (Friele). Patreksfjord, Iceland. 246m. CZM.

Shell. Opaque or nearly so, glossy. There are 3-4 tumid whorls with deep sutures which lie abapical of the periphery of the older whorl. The upper part of each whorl is a little flattened, giving a somewhat turreted profile to the spire, which is moderately raised (apical angle about 105°). The ornament consists of inconspicuous growth lines which are smoothly curved, concave adapically. On some shells, mainly immature ones, there are a few well-spaced and very shallow spiral ridges around the umbilicus into which runs a low ridge originating at the lowest point of the peristome. The umbilicus is a rather narrow chink, half obscured by the out-turned inner lip. Protoconch rounded, swollen initially, of $1\frac{1}{4}$ whorls, which are smooth and measure about $200\mu\text{m}$ across.

Aperture. Slightly prosocline and lying nearly in one plane. The lips form a peristome, nearly circular, but pointed where the outer lip joins the body whorl and slightly angled where it joins the columella. The outer lip arises below the periphery of the body whorl and retreats a little adapically at the periphery to form a slight sinus. It is noticeably out-turned where it joins the columella and it is from this point that the umbilical ridge arises. In the columellar region — less noticeably elsewhere — a groove lies parallel and internal to the edge of the aperture. This, as described by Høisaeter (1968b) is used as a stop for the edge of the operculum.

Colour. White.

Size. 2 x 2 mm. Body whorl = 80-85% of shell height; aperture = 60-65% of shell height.

Animal. As in *serpuloides*.

Geographical distribution. This species is found from Greenland and Norway to the Bay of Biscay and N. Atlantic generally in moderately deep to deep water. There are offshore records from Norway, but none from the British Isles. It is not recorded from the N. Sea or Danish coasts.

Habitat. According to Höisaeter (1968b) this species prefers soft bottoms, but of coarser materials than those favoured by *basistriatum*. It occurs at 60-80 m in the outer parts of some Norwegian fiords, but at 300 m in more open waters and to depths of nearly 2000 m further south. Thorson found it in similar situations off the E. Greenland coast.

Food. The animal must eat detrital particles. Faecal strings are cylinders of sandy particles as in the other species.

Breeding, growth. Unknown, but perhaps there is direct development.

Notes. As Fig. 67 B shows, there is a peristome in this species: The appearance of Fig. 67 A misleads in suggesting its absence. The ridge from the basal point of the peristome to the umbilicus is often more prominent than drawn. In *S. trochoides* s.s. the umbilicus is shut and the spiral ridges absent.

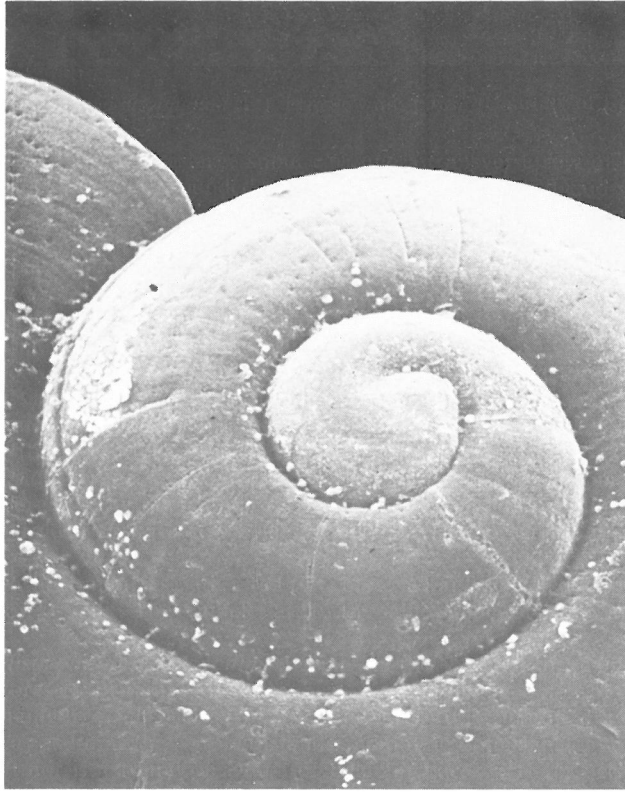


Fig. 68. *Skenea peterseni* (Friele). Apical region from above, slightly oblique, X 145. SEM photograph. Trondhjem fjord, 450m. BMNH.

SKENEA BASISTRIATA (Jeffreys, 1877)
Cyclostrema basistriatum Jeffreys, 1877

Basistriata (Lat.), with a striated base, referring to the spiral ridges found on that part of the shell.

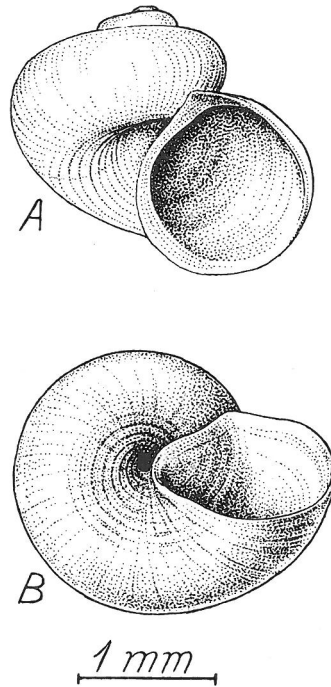


Fig. 69. *Skenea basistriata* (Jeffreys). *Thor*, sta. 213, 475m. CZM.

Shell. Opaque, somewhat glossy externally, very glossy internally. There are 3-4 tumid whorls meeting at deep sutures placed, often markedly, below the periphery of the upper whorl, the degree of this increasing towards the aperture. The adapical part of the body whorl near the aperture tends to form a flattened shelf so that the spire, which is moderately high (apical angle 105-110°), may have a slightly turreted outline. The ornament consists of growth lines and spiral ridges. The former are prosocline, often very inconspicuous, and in general form smoothly curved lines, though sometimes they show a slight adapical sinus peripherally. The spiral ridges are always visible within and around the mouth of the umbilicus but may extend over the whole base of the shell and occasionally over the whole of the whorls, though least visible at the periphery. They are narrow, less broad than the furrows between, and coarsest in the neighbourhood of the umbilicus, which is rather large and deep but without the buttress of *peterseni*. Protoconch large, of 1¼ whorls, the initial part swollen, smooth, with a few slightly raised spiral lines, about 350µm across.

Aperture. Prosocline, with a nearly circular peristome. It is nearly plane but has slight projections above and below the periphery. The peristome is angulated where the outer lip arises from the body whorl distinctly abapical of the periphery. The outer lip is rather thin and not out-turned; the inner lip turns out a little over the umbilicus and often is slightly separated from the parietal region as it runs to join the outer lip. As in *peterseni* there is a groove within its columellar region which acts as an opercular stop.

Colour. White, often with a slight yellowish tint.

Size. 2 x 2.2 mm. Body whorl = 95% of shell height, aperture = 70% shell height.

Animal. As in *serpuloides*.

Geographical distribution. Occurs off the Atlantic coasts of Norway, Britain, France and Iberia, not in Baltic, N. Sea, Irish Sea or Channel. It requires rather deep water — 90-2400 m.

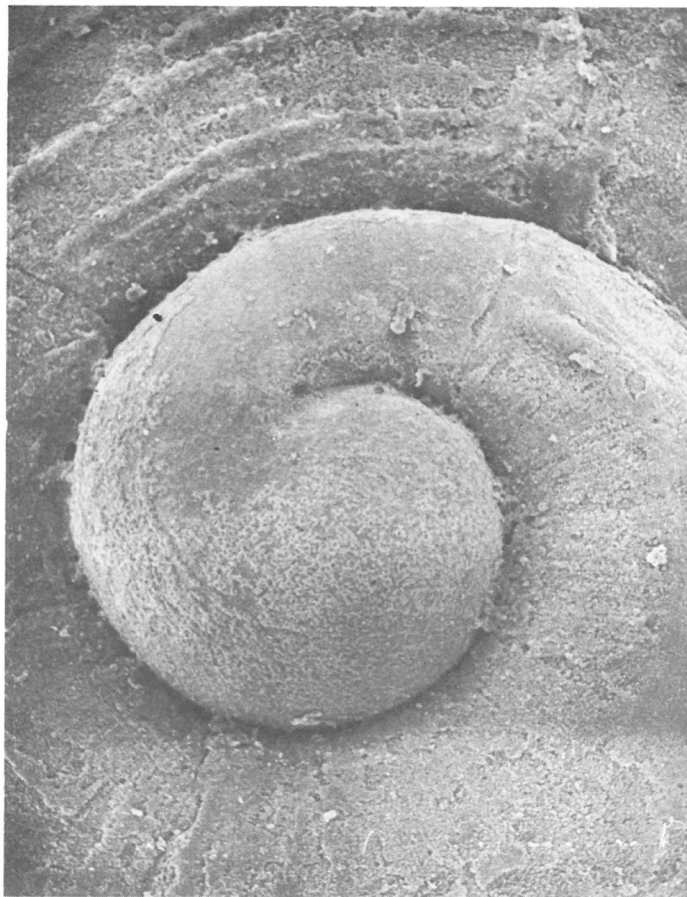


Fig. 70. *Skeneia basistriata* (Jeffreys). Apical region from above, X 210. SEM photograph. Trondhjem fjord, 450m. BMNH.

Habitat. Found on soft bottoms. Never in shallow water or littoral.

Food. Detritus. The faeces are in the form of cylindrical, smooth rods largely composed of fine detrital particles.

Breeding, growth. Nothing known, but likely to be as in the other species of the genus.

Notes on *Skeneia* species. These are little known animals, doubtless more common than records suggest because their small size leads to them being overlooked or taken for young top-shells. Their shells may be recognised without doubt by a combination of two characters — (1) the presence of a peristome and (2) the swollen initial part of the protoconch which does not show the pointed tip of other trochaceans. In very young *Margarites helacinus* something like a peristome is present — lost later — but the tip-tilted protoconch separates it clearly from skeneids.

Höisaeter (1968b), in one of the very few recent papers on this group, has suggested that the species called here *nitens* and *cutleriana* should be separated into a genus *Dikoleps* Höisaeter, 1968; this genus, he further believes, is properly classified in the Trochidae, Umboniinae. Some of the distinctions of the new genus are the sinuous course of the growth lines produced by embayments in the peristome, the relatively tall spire, the more marked spiral ornament, the rather narrow umbilicus and the lack of a 'penis' (process by the right cephalic tentacle).

Whilst it may be true that these species stand apart from the others it seems doubtful if the gap is as great as this revision suggests. Their shell structure and anatomy are not markedly different and in the nature of their protoconch they agree with other skeneids and differ from other trochids. It seems better, therefore, to regard *Dikoleps* as a subgenus of *Skeneia* rather than as a member of another family.

REFERENCES

- HÖISAETER, T. 1968a. *Skenea nitens*, *Ammonicera rota*, *Odostomia lukisi* and *Eulimella nitidissima* new to the Norwegian fauna. *Sarsia*, **31**, 25-33.
- HÖISAETER, T. 1968b. Taxonomic notes on the North European species of "Cyclostrema" sensu Jeffreys 1863 (Prosobranchia Diotocardia). *Sarsia*, **33**, 43-58.

TURBINIDAE Rafinesque, 1815

Animals in this family show the same characteristics as the trochids save that the operculum is always thickened externally by a deposit of calcareous material. As in trochids it is polygyrous. The shape of the shell and its ornament are variable but the latter is usually well marked. There is a complete peristome and an umbilicus. The soft parts are trochoid with well-developed cephalic lappets, neck lobes and epipodial folds. The lips are split mid-ventrally and often extended into a tubular elongation on the right. Reproduction using spawn masses?

MÖLLERIA COSTULATA (Möller, 1842)

Margarita costulata Möller, 1842

Mölleria, named after H.P.C. Möller (1810-45) who was Danish governor of E. Greenland and a keen malacologist; *costulata* (Lat.), with little ribs, referring to the appearance of the shell.

Shell. Rather dull, opaque. There are 3-4 rapidly expanding whorls, each more or less circular in transverse section but flat apically so as to give a stepped profile to the depressed spire (apical angle about 115°). Whorls meet at deep sutures (sutural angle about 60°) which lie below the periphery of the older whorl. The most conspicuous ornament is a series of vertical (transverse) ribs separated by hollows of about equal breadth. At first sight the ridges look imbricated but each has, in fact, approximately vertical sides and a flat top. Their course across the whorl may be straight or a little doubly sigmoid, the concavities facing up the shell above and below the periphery at which a convexity lies. Some ridges show a dichotomy mainly at or below the periphery. There are 40-50 on the body whorl. Growth lines are not obvious and spiral ornament is restricted to a few ridges on the base around the umbilicus, the outermost lying about half way between that and the periphery. Each spiral produces a small keel on the surface of each rib and their interaction gives a square cancellation of the surface. The degree of development of the spirals is variable. The umbilicus is large. The protoconch is probably smooth, has 1¼ whorls with a markedly tilted tip. The mouth of the larval shell is without projections. The protoconch is rather large — 270-280µm across.

Aperture. Only slightly prosocline. There is a complete peristome, nearly circular except where it is flattened against the body whorl. The outer lip arises abapical of the periphery of the body whorl and arches apically before curving down. It is rather thin and very slightly out-turned where it joins the columella; there is no reflection of the peristome over the umbilicus.

Colour. White, sometimes with a yellow tint.

Size. 1.5 mm high x 2 broad. Body whorl = 90% of total shell height; aperture = 65-70% of total height.

Animal. (There have been neither living nor properly preserved specimens available for our examination: the following description is based on animals extracted dry from shells and restored by soaking in dilute domestic detergent.)

The snout is broad and depressed, the closed mouth a vertical slit at its end bordered by rather fleshy lips not split or extended mid-ventrally. The tip of the snout is not bilobed but carries a slightly scalloped edge. The tentacles are setose and are flanked laterally by eye stalks each carrying a large black eye at its tip. There are no cephalic lappets.

The foot is rather straight anteriorly, its corners elongated, and tapers to a narrow posterior end. A neck lobe lies on each side, smooth-edged, unconnected to the cephalic tentacles but joined to an epipodial fold, carrying (?) 4 tentacles similar to the cephalic ones. The operculum is thick, calcified, with a central, slightly insunk nucleus and about 6 turns.

Colour. White.

Geographical distribution. This is a widespread Arctic species extending to lower latitudes at greater depths. In the East Atlantic it has been found on Norwegian coasts as far S. as Bergen. In

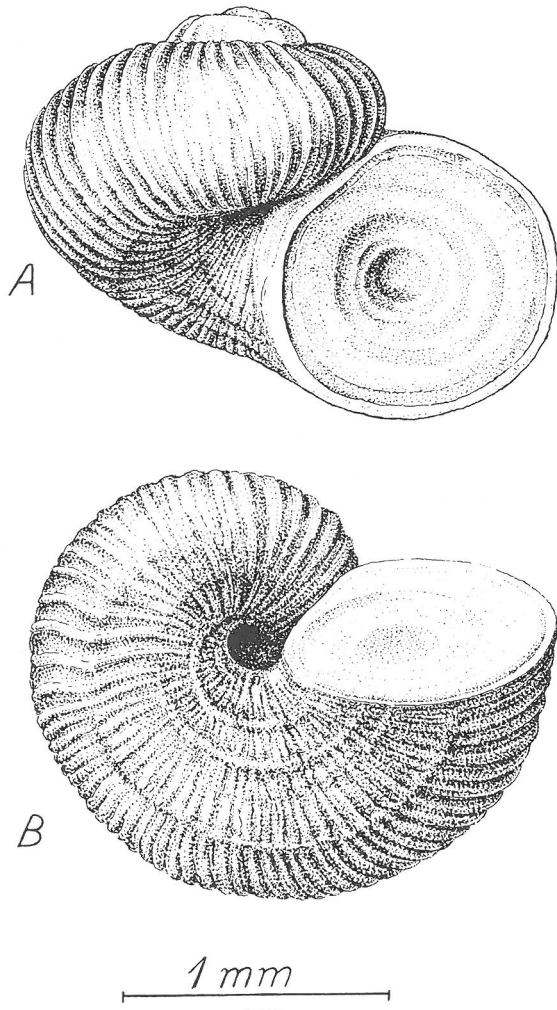


Fig. 71. *Mölleria costulata* (Moller). Insenfjord. CZM.

the British Isles it seems that such specimens as have been found are subfossil, though Jeffreys recorded it alive off Ireland. Further S. it is found in deep water in the Bay of Biscay. In the W. Atlantic it is found in shallow water S. to New England and, in deep, as far as Florida. Arctic specimens are larger, up to 2.5 mm high. It seems rare everywhere.

Habitat. Unknown in detail but generally dredged on soft bottoms with stones and shells and, if shallow enough, red algae. Found from 7-2000 m.

Food. Like other trochaceans, a detritus feeder. Faeces in the form of unformed cylinders of sandy detritus.

Breeding, growth. Unknown. The large protoconch may suggest direct development.

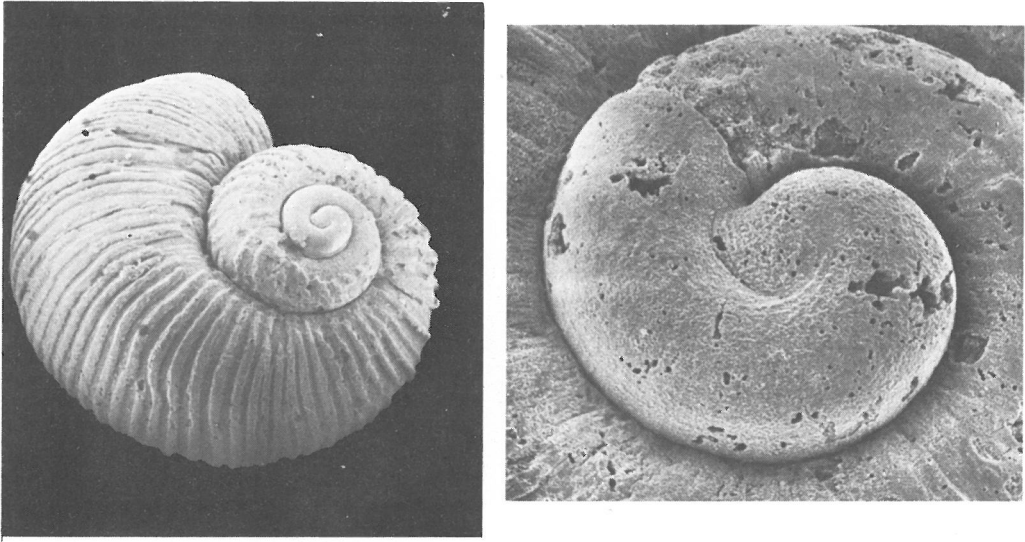


Fig. 72. *Mölleria costulata* (Möller). A, shell from above, oblique view, X 44; B. apical region from above, X 265. SEM photographs. Tromsø. BMNH.

PHASIANELLIDAE Swainson, 1840

Though occasionally united with the turbinids, phasianellids are more advanced both in shell structure and soft parts. They relate to the turbinids most closely in possessing a calcareous operculum, but it is oligogyrous. The shell is smooth, polished and porcellanous, having lost its internal naacre; it commonly exhibits bright and complex colour patterns. There is no peristome, the lip is thin and the umbilicus usually closed. The general organization of the animal is trochoid but the snout lacks papillae and the lips show no prolongation. The eggs are laid singly and there is a free-swimming larval stage of relatively brief duration.

TRICOLIA PULLUS (Linnaeus, 1758), pheasant shell

Turbo pullus Linnaeus, 1758

Phasianella pullus (Linnaeus, 1758)

Tricolia pulla (Linnaeus, 1758)

Tricolia (Lat.), perhaps indicative of three colours in the shell; *pullus* (Lat.), if the correct form is *pullus* the word is a noun in apposition to *Tricolia* with the meaning of young animal; if it is *pulla*, an adjective agreeing with *Tricolia*, it means dark in colour.

Shell, helicoid, glossy and robust. The whole shell rather oval, the spire conical in profile; when full grown with 5-6 whorls, somewhat swollen and dipping gently to incised sutures. Apical angle variable with age, being greater (80-90°) in young shells (2-4mm high) and less (55-70°) in older ones (6-9mm high). Each whorl turns up a little below the suture to approach it more vertically, and has its periphery abapical of its mid point. The shell appears smooth to the naked eye but bears fine growth lines, parallel to the edge of the mouth, and a few spiral ridges, both more obvious near sutures and the latter clearer on older whorls. The protoconch is smooth with occasional slight spiral ridges on its younger parts and others radiating from the apex of the embryonic shell. This shows the usual tilted tip of a trochacean. The aperture of the larval shell is drawn out into lateral V-shaped points. The protoconch measures 130-150µm across.

Aperture, drop-shaped. The outer lip is prosocline making an angle of 40-45° with the shell axis, smooth and rather sharp, approaching the body whorl almost at right angles (c. = 130° to vertical axis) at a level equal to about three eighths of the body whorl below the suture and below the

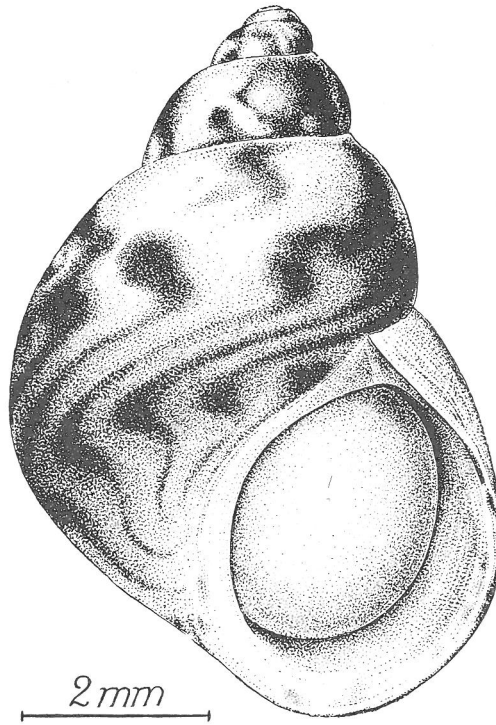


Fig. 73. *Tricolia pullus* (L.). Jersey. BMNH.

periphery; it is slightly turned out basally. The inner lip and columella form a gently curved flattened area, the former extending as a milky glaze over the body whorl to the outer lip. There is a distinct but slight umbilical groove, and in young shells a small opening.

Colour. Most shells have a cream-buff or even white ground colour and a few (< 1%) none other. The rest show an erratic pattern of reddish-brown streaks and spots. Commonly there are about 30 rows of spots on the body whorl, nearly spiral in course, running across the whorl from suture to base in rather less than one turn; their course is opisthocline and they cross growth lines more or less at right angles. The spots may become lines, branch, become thicker or thinner to give dark or light zones, change direction to produce a pattern like a chevron or conventional sign for a lightning flash. In a few shells the pattern may be regularly interrupted by white vertical bands or the lines may fuse to give a solid colour to the shell; these last patterns are commoner on older whorls, younger ones showing most frequently a simple linear array. Except just within the outer lip where the external pattern shows the inside of the shell shows the ground colour. The columella and inner lip are milk white. Operculum white.

Animal. The snout is only moderately developed. It is slightly lobed terminally and its disk-like end bears a central mouth surrounded by lips thrown into radial folds. The cephalic tentacles are long, slender and rather flattened, their narrow lateral and median edges bearing papillae of complex structure, probably sensory. The tentacles are not ciliated. An eye stalk with a black eye lies on the outer side of each. Ventral to these, on each side, lies a neck-lobe, both right and left shaped like a cock's-comb; each has 11-14 finger-like processes marginally, those on the left lobe longer than those on the right. All the processes have, at the tip, papillae like those on the tentacles. The mantle skirt has a thick, smooth edge.

Foot rather narrow, more so in front than behind, and subdivided along the mid-line of the sole by a longitudinal groove. The sole has a double edge anteriorly and laterally. The sides and dorsal

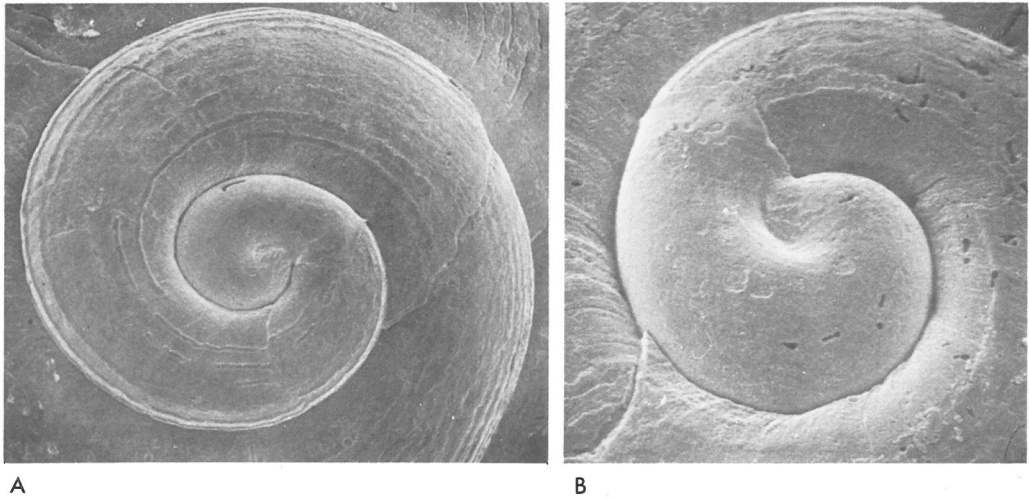


Fig. 74. *Tricolia pullus* (L.) Apical region from above, X 300. SEM photograph. Plymouth. RUZ.

surface of the foot are smooth. Three epipodial tentacles lie on each side, all with papillae as on the cephalic ones. The middle tentacle is shorter than the others. Posteriorly the dorsal surface of the foot carries a hemispherical calcareous operculum, the outer surface of which is slightly spiky.

Colour. Cream or yellow with a green cast locally and marked with reddish lines which run longitudinally on the head and sides of the foot and marginally along the cephalic tentacles. Eye stalks and mantle edge usually green.

Geographical distribution. This species extends N. from the Mediterranean to the W. Channel Basin and thence along Irish and western British coasts, becoming rare in the N. It has been recorded from N.E. Scotland but is essentially absent from the N. Sea and all Scandinavia.

Habitat. The conditions in which *T. pullus* lives have been fully described by Manly (1975). In general terms it is an inhabitant of clear water with moderate currents, though older animals are more resistant to turbidity and exposure than recently settled ones. It lives (often in rock pools) near LWST on rocky shores, extending sublittorally to 35m. Between tidemarks it is most abundant on growths of *Lomentaria* and *Laurencia*, but is common on many other red weeds (*Gigartina*, *Plumaria*, *Chondrus*, *Nitophyllum*, *Ceramium*) and is occasionally found on *Cladophora* and *Laminaria*. Its abundance on these weeds varies — up to 8 m² of weed surface (*Lomentaria*), 7 m² (*Laurencia*), 2-3 m² (*Gigartina*), 3 m² (*Corallina*), much less on others. Adults tend to distribute themselves evenly between frond and holdfast in *Lomentaria* and *Corallina*, but are commoner in the holdfast of *Laurencia*. Sublittoral specimens occur on coarse rubble substrata carrying growths of filamentous red algae. Snails of all ages avoid the most exposed areas or those where much sediment is deposited. Young animals live where currents do not exceed about 75 cm s⁻¹; older ones can survive in currents up to 156 cm s⁻¹ (about 3 knots).

Food. The snails rasp the weed over which they creep partly to ingest its substance, partly to gather diatoms and detritus from its surface. Diatom cases, sponge spicules and arenaceous particles are frequent in the faeces which form short rods, pale reddish-brown in colour, about 1 mm in length and 0.2 mm in diameter, and marked with a vee-shaped groove along one side.

Breeding. The sexes are separate and fertilization is external. Breeding occurs all the year round with larval settlement maximal in June, September and November (Manly, 1975). Eggs, orange in colour, are laid singly; each is about 150 μm in diameter and is enclosed in a coat of mucus, 5 μm thick at laying, secreted within the ovary, which swells to give a zygote 165-70 μm across. The larva hatches 10-11h after fertilization, becomes benthic after 68h and loses its velum after 4½ days by which time the larval shell has 1¼-1½ whorls; its surface is smooth. At metamorphosis, when the shell has a height of 1.1 mm the snails settle, mainly in the holdfasts of the weeds on which the adults occur. They are probably annuals.

Notes. *T. pullus* is immediately recognisable as the only British phasianellid by the white, hemispherical, calcareous operculum. It is rather rare in the northern parts of the British Isles but can be abundant in the south in summer. It creeps in a way reminiscent of *Pomatias*, shuffling one half of the foot forwards whilst gripping with the other; this movement and the median longitudinal furrow on the sole of the foot are probably interlinked. The separation (by Marshall, 1898) into males and females on the basis of apical shell angle and length of spire appears not to be valid: variation in these respects is a function of size.

REFERENCES

- FRETTER, V. 1955. Some observations on *Tricolia pullus* (L.) and *Margarites helycinus* (Fabricius). *Proceedings of the Malacological Society of London*, **31**, 159-62.
- MANLY, R. 1975. *The settlement and growth of some species of prosobranch gastropods in the Plymouth area*. University of Reading, Ph.D. thesis.
- MARSHALL, J. T. 1898. Additions to "British Conchology". *Journal of Conchology*, **9**, 61-74.
- ROBERT, A. 1908. Seconde note sur la progression des Gastéropodes. *Bulletin de la Société Zoologique de France*, **33**, 151-7.

ACKNOWLEDGMENTS

We are grateful to the Trustee of the British Museum (Natural History) for the loan of shells. The following people we thank for shells, specimens, information or all three kinds of help — Dr P. Bouchet, Muséum national d'Histoire naturelle, Paris; Dr L. Cabioch, Station Biologique, Roscoff; Dr R. Manly, Kingston Polytechnic; Mr D. Seaward, Yeovil; Dr J. A. Sneli, Biological Station, Trondheim and Dr C. Thiriot-Quévieux, Villefranche-sur-Mer. We thank the Leverhulme Trust Fund for the award of Emeritus Fellowships to help in the completion of this work. We thank Dr Elizabeth Andrews, Bedford College, University of London, for preparing the material and taking the photographs on which Figs 35 and 66 are based.

KEY TO TROCHACEANS DESCRIBED

1. Shell conical, smooth and glossy, more than 2 mm high; whorls slightly tumid; no umbilicus; aperture without complete peristome; operculum calcareous, oligogyrous, convex externally; littoral and sublittoral. *Tricolia pullus* (p. 95)
Shell not so. 2
2. Shell globular, ribbed, not glossy, less than 2 mm high; whorls tumid; umbilicus present; aperture with a complete peristome; operculum calcareous, polygyrous, flat or concave externally; not littoral, rare. *Mölleria costulata* (p. 93)
Shell not so. 3
3. Aperture with complete peristome; shells minute (2 mm high or less); protoconch without pointed tip (Skeneidae). 4
Aperture without a complete peristome; shells not minute, (> 2mm high); protoconch pointed (Trochidae). 8
4. Shell with delicate spiral striae over all or most of body whorl; peristome circular (except for slight angulation where outer lip joins body whorl). 5
Shell with spiral striae limited to area around umbilicus or absent; peristome circular or ear-shaped. 6
5. Body whorl with delicate spiral striae all over, peristome with sinuses; growth lines sinuous; umbilicus narrow; apical angle 100°. *Skenea cutleriana* (p. 86)
Body whorl without spiral striae adapically; peristome plane; growth lines smoothly curved; umbilicus large showing underside of all whorls; apical angle 140-145°. *Skenea serpuloides* (p. 81)
6. Peristome plane or nearly so and circular; opercular stop within lip; Scandinavian, not British. 7
Peristome with 2 distinct sinuses and ear-shaped; no opercular stop; shell glossy and spiral striae often inconspicuous; umbilicus rather large with ridge arising from base of aperture; Scandinavian and British. *Skenea nitens* (p. 84)
7. Peristome plane; umbilicus narrow with spiral ridge; aperture slightly angulated where columella and outer lip join. *Skenea peterseni* (p. 89)
Peristome with slight projections above and below peripheral region; umbilicus large without ridge; aperture smoothly curved where columella and outer lip join. *Skenea basistriata* (p. 91)
8. Shell conical, sharply pointed, sides of whorls flat 9
Shell conical but bluntly pointed and rather cyrtoconoid; sides of whorls not flat. 15
9. Breadth of shell approximately equal to height 10
Breadth of shell approximately equal to half height. 13
10. Spiral ridges on shell all coarsely granular, interacting with growth lines to give lozenge-shaped pattern; protoconch smooth; no tubular extension from lips of animal's mouth; sublittoral. *Cantharidus clelandi* (p. 71)
Spiral ridges not interacting in such a way; protoconch with reticulate pattern (may be eroded on larger shells); animal with tubular extension of lips running back on right from ventral side of mouth (*Calliostoma*). 11
11. Shell with 7 whorls; 4-5 elevated keel-like spiral ridges on upper part of body whorl, uppermost a little granulated; nacreous; not littoral. *Calliostoma occidentale* (p. 79)
Shell with 10-12 whorls; 7 or more low, broad spiral ridges on upper part of body whorl; coloured (occasionally white). 12

12. Spiral ridges smooth on body whorl (except perhaps the sub-sutural one), beaded on topmost whorls; spire with flat sides; columella with distinct swelling; 4-5 pairs of epipodial tentacles; often at LWST. *Calliostoma zizyphinum* (p. 74)
Spiral ridges finely granular; spire with concave sides; columella without bulge; 3 pairs of epipodial tentacles; rarely intertidal. *Calliostoma papillosum* (p. 77)
13. Whorls flat; spiral ridges broader than intervening furrows; almost always with some carmine colouring especially apically; columella nearly vertical. 14
Whorls tumid, dipping to sutures; spiral ridges narrower than intervening furrows; red coloration usually absent except for some spots on spiral ridges; columella oblique. *Cantharidus montagui* (p. 69)
14. Body whorl with 4-5 spiral ridges, all a little nodose. *Cantharidus exasperatus* (p. 64)
Body whorl with 8-9 spiral ridges, all smooth. *Cantharidus striatus* (p. 67)
15. Columella with tooth or bulge, its outline at least slightly sinuous; shell with external pigmented layer over nacre; spiral ridges present. 16
Columella without tooth, its outline a smooth simple curve; shell nacreous externally; smooth or with spiral ridges or with ribs and spiral ridges. 21
16. Upper part of each whorl tuberculated; shell profile stepped; umbilicus wide. *Gibbula magus* (p. 56)
Upper part of each whorl not tuberculated. 17
17. Umbilicus closed or almost so (often open in young shells). 18
Umbilicus open. 19
18. Umbilicus usually closed; aperture equal to or more than half shell height; coarse pattern of purple stripes; tooth on columella small; cephalic lappets fringed; Channel Islands and S. thereof. *Gibbula pennanti* (p. 54)
Umbilicus minute; aperture about one-third of shell height; fine pattern on shell; tooth on columella large; cephalic lappets smooth. *Monodonta lineata* (p. 61)
19. Shell slightly turreted; spiral ridges between suture and periphery of body whorl, 16-18, on base 14-18, umbilicus funnel-shaped, deep; mainly sublittoral. *Gibbula tumida* (p. 58)
Shell not turreted; spiral ridges less numerous; umbilicus narrow; mainly littoral. 20
20. Colour pattern on shell consisting of numerous fine lines, 13-14 spiral ridges on base, the outermost not deeper than others; umbilicus small and narrow; general shape depressed to conical. *Gibbula cineraria* (p. 48)
Colour pattern consisting of a few broad red lines; 8-11 spiral ridges on base, the outermost deeper than others; umbilicus moderately large; general shape usually depressed. *Gibbula umbilicalis* (P. 52)
21. Shell with small ribs adapically on each whorl and 2-3 prominent spiral ridges peripherally; umbilicus with beaded edge; 3 pairs of epipodial tentacles; anterior corners of foot greatly elongated; no cephalic lappets; rare. *Solariella amabilis* (p. 46)
Shell smooth or with spiral ridges but without ribs; 5-7 pairs of epipodial tentacles; foot normal; cephalic lappets present (*Margarites*). 22
22. Shell smooth, nacreous, glossy; a few spirals round umbilicus; 6 pairs of epipodial tentacles. *Margarites helycinus* (p. 40)
Shell with fine or coarse spirals on whorls; 5 or 7 pairs of epipodial tentacles. 23
23. Spiral ridges prominent; 7 pairs of epipodial tentacles. *Margarites groenlandicus* (p. 42)
Spiral ridges weakly developed; 5 pairs of tentacles. *Margarites argentatus* (p. 44)