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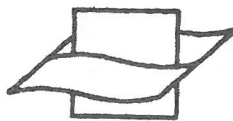
THE PROSOBRANCH MOLLUSCS OF BRITAIN AND DENMARK

PART 4 — MARINE RISSOACEA

by

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RISSEOCEA

The Rissoacea are a large group of prosobranchs characterized by small size: a few species may have a shell 10 mm high but most are smaller, or very much smaller. The group is rich in species — perhaps 1500 in all — but it is right to caution that many are very incompletely known, especially anatomically. There has always been a tendency to use the Rissoacea as a dump for animals with small, featureless shells lacking clear signs of other affinities. The animals are variable, responding to environmental factors, and seem still to be in the active speciation which has characterized the superfamily since Tertiary times.

Rissoacean shells have normally a short conical spire and an entire peristome. The ornament is varied: many are smooth but spiral ridges, transverse ribs or both may occur. The protoconch is equally variable. The body of the animal has a moderately long snout, markedly bifid at the tip, and a foot which may often be transversely folded into anterior and posterior halves; it is narrow and often has a median groove into the posterior part of which opens the pore of a mucous gland. There are metapodial and pallial tentacles in most; the operculum is spiral and horny. The animals have a crystalline style, a simple oesophagus and a short intestine. The sexes are commonly separate, males having a long thin penis. The eggs are usually laid in lens-shaped capsules.

Rissoaceans are predominantly marine, frequenting shallow seas, but they have successfully invaded brackish and fresh water and a few are terrestrial. They abound on weeds and on hard and soft bottoms: they are mainly detritus and bacterial feeders, obtaining their food from the surface of the weeds or the grains of the substratum on which they live. They are agile and athletic movers, crawling rapidly and clambering about their habitat on mucous threads. In pools they may creep on the surface film. Most are annuals with perhaps more than one breeding period, often very numerous in summer and scarce in winter. Their small size enables them to exploit habitats and foods barred to larger animals.

It is difficult to say how many families the Rissoacea contains — between 14 and 20 depending on the authority consulted. Representatives of most occur in N.W. Europe.

The families Hydrobiidae, Bithyniidae, Truncatellidae and Assimineidae have been associated by Nordsieck in a group Hydrobioidea. They are all similar in shell and anatomical organization and are generally more primitive than other rissoaceans — the foot less modified, the nervous system less concentrated, the shell without marked sculpture, the protoconch almost featureless. Some hydrobiids have still a predominantly marine habitat; others, and bithyniids, favour brackish or fresh water: few, therefore, retain a free larval stage. The families Truncatellidae and Assimineidae stand a little apart, both inclining to a terrestrial mode of life, the former distinct because of its decollated shell, the latter specialized in several ways.

Most species fall into the family Rissoidae which is almost exclusively marine. The external appearance of the soft parts hardly varies from species to species, but the genera show characteristic shell ornament — predominantly smooth in *Cingula*, spiral ridges with incipient ribs in *Onoba*, usually with distinct ribs and small spirals giving a pitted surface in *Rissoa*, and with a relatively coarse reticulation in *Alvania*. The protoconchs are equally characteristic — simple in *Cingula*, with some spiral lines in *Rissoa*, and most elaborately patterned in *Onoba* and *Alvania*. In the last genus the microstructure of the shell surface seems to have diagnostic value. The family Barleeidae is close to Rissoidae but the shell is nearly smooth, the protoconch pitted and the operculum has an internal process. Most species in this group have free veliger larvae but they are occasionally suppressed.

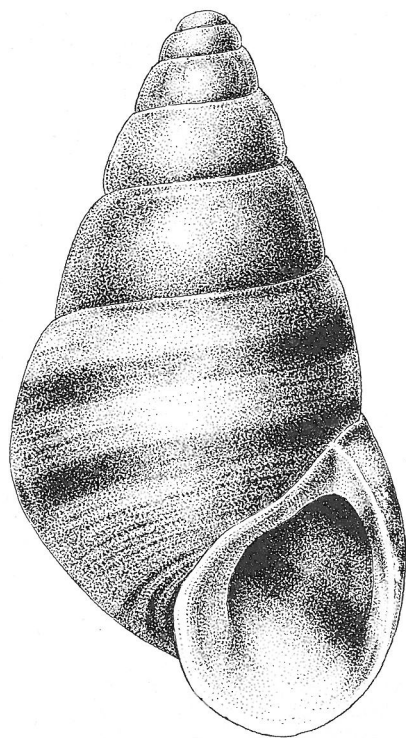
The remaining families can hardly be regarded as more than an assortment of prosobranchs sharing only the character of small size. Some of their features may simply reflect this; their anatomy is sometimes so unusual as to make it uncertain whether they are rissoaceans — or even prosobranchs. The families here are Vitrinellidae, Caecidae, Tornidae (= Adeorbidae), Cingulopsidae, Rissoellidae, Skeneopsidae and Omalogyridae.

Of this collection the Vitrinellidae and Caecidae — though unusual in their shells — have soft parts which suggest that they are genuine rissoaceans. Tornids may be joined with them, especially as it now appears that they possess a penis. Cingulopsids have no penis, no crystalline style and a double female duct: these points separate them from most rissoaceans though there is a rissoacean appearance to their shell. The remaining families must be acknowledged as in the Rissoacea for no better reason than that they are small: much of their anatomy argues against this being their proper systematic position.

We have been conservative in our use of names, partly because our attention has been limited to a few species only, partly because the anatomy of so many remains unknown.

RISSOIDAE Gray, 1847
CINGULA CINGILLUS (Montagu, 1803)
Turbo cingillus Montagu, 1803
Rissoa cingillus (Montagu, 1803)
Rissoa trifasciata (Adams, 1800)

Cingula (Lat.), a small girdle; *cingillus* (Lat.), again with the meaning of a small girdle, both referring to the bands of colour on the shell.



1 mm

Fig. 131. *Cingula cingillus* (Montagu). Norway. BMNH 1911.10.26 23631-23650.

Shell. Solid and opaque, somewhat glossy, the spire a moderately elongated cone with nearly straight sides (slightly cyrtocooid) and a rather blunt tip (apical angle *c.* 52°). There are 6-7 whorls which are only slightly swollen; they meet at clear though shallow sutures which are slightly channelled and lie just below the periphery of the upper whorl. Each whorl is marked by growth lines which follow a gently curved course, concave towards the aperture and so prosocline at the suture. On the 3rd and 4th whorls they may be so raised as to suggest incipient ribs and make the lower edge of the suture sinuous. The body whorl also shows spiral ridges and grooves, the former low and flat-topped. They vary from 12-20: when few, restricted to the base of the shell (where they are always most marked), when numerous, over the whole surface of the whorl. One or two ridges may occur above the suture of whorls in the spire. The protoconch consists of 2 whorls marked by fine spiral lines and clearly separated from the teloconch. Its diameter is 450-600 μ m, that of the initial swelling 200-250 μ m.

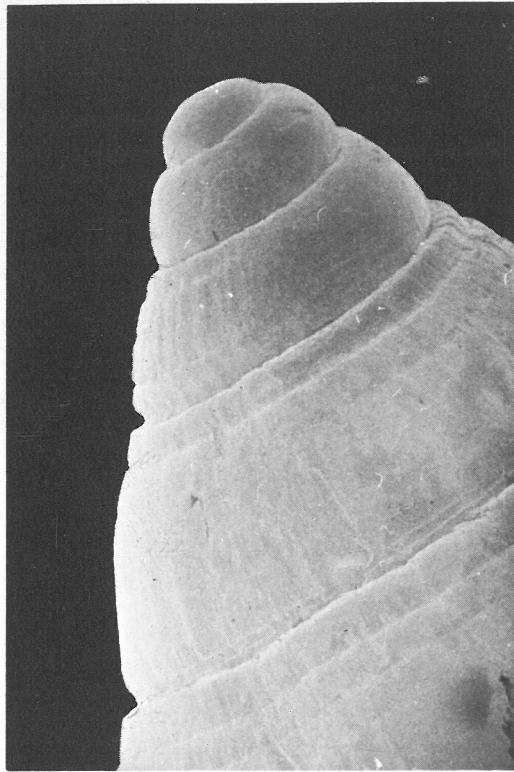


Fig. 132. *Cingula cingillus*. Apical part of shell $\times 96$. SEM photograph. Plymouth. RZ.

Aperture. Relatively small, round and broad abapically but drawn up adapically to a narrow point; bounded by a rather thick peristome. It lies in the axial plane and shows a shallow anal sinus a little below the origin of the outer lip. This arises nearly tangentially from the body whorl at the level of the peripheral pigment band and runs straight, continuing the outline of the spire; basally it turns out to form a broad spout. The columella is short. The inner lip turns out and broadens in some shells but may be quite narrow; it is rather thick over the body whorl. There is a small umbilical groove but no umbilicus as it is blocked by the inner lip. Where inner and outer lips meet adapically the two are pressed together rather than fully fused, leaving a small cleft.

Colour. Yellow-brown or orange, the apex usually paler because of wear of the periostracum. There are 3 dark brown bands on the body whorl: (1) a little below the suture; (2) at or just below the periphery; (3) in the region of the umbilical groove. Band (1) is usually the narrowest though it may broaden to reach the suture; bands (2) and (3) sometimes nearly fuse. On the whorls of the spire band (1) and a little of (2) are usually visible. The peristome is usually pale except at the ends of the bands which may be seen by transparency in the throat where there is often an orange-brown band parallel to the peristome. The variety *rupestris* shows no coloured bands and is usually cream or white. Some shells may be a uniform dark purple or black.

Size. 4×2 mm; body whorl = 60% of total shell height; aperture = 40% of total height.

Animal. The head bears a rather broad, slightly depressed snout the sides of which are wrinkled especially near the tip. This is bifid, the mouth subterminally placed on the ventral side between rounded lateral lips. The tentacles are rather long, slightly tapering to blunt tips, the eyes on slight basal bulges. The mantle edge is simple with a very short tentacle on the right. The ctenidium is short, with about 15 filaments. Males have a large penis attached to the dorsal surface of the head behind the right tentacle. It curves back to the left side of the mantle cavity and tapers to a fine point.

The foot is rather narrow though broad and truncated in front where the edge is double and a voluminous anterior pedal gland opens by a long duct. It then narrows in the middle of its length and broadens again before tapering to a point behind. The sole has a longitudinal median groove to which opens the duct of a posterior pedal gland. A short triangular metapodial tentacle projects from under the whole rear edge of the ear-shaped operculum. It does not reach the end of the foot.

Colour. Cream to white. The snout shows yellow jaws by transparency and an orange-red tint from the buccal mass. There is an opaque white spot behind each eye. At the front end of the foot the anterior pedal gland shows as a V-shaped internal white mass.

Geographical distribution. The species extends N. from the Bay of Biscay to the W. coast of Norway. It occurs in the Channel and on British coasts of the N. Sea though not the continental ones. It is apparently absent from the Skagerrak and Kattegat though empty shells have been found at Bohuslan.

Habitat. This is a common gregarious animal on all rocky shores and it may be dredged from similar bottoms to 20 m. It may be found amongst algae at low-tide level, under stones (especially where there is muddy material underneath) from above mid-tide level downwards, but it is most characteristically a member of the crevice fauna, extending nearly to the top of the *Chthamalus* zone (90% emersion). It also occurs in silt at the bottom of rock pools in the upper half of the beach, especially where they are shaded from bright light as the snails are strongly negatively phototactic. The variety *rupestris* is confined to crevices and does not appear to occur mixed with individuals with pigmented shells. The animals withstand some reduction in salinity. In favourable circumstances, they may be as abundant as $30 \times 10^3 \text{ m}^{-2}$.

Food. *C. cingillus* is a microphage, gathering detrital material from its surroundings. The faeces are brown ovoid pellets 200 μm long 100 μm broad, full of diatoms, sponge spicules and similar detrital fragments.

Breeding and growth. The sexes are separate, males recognizable by the penis. Breeding (at Plymouth) occurs March — June. The eggs are whitish, about 160 μm in diameter, and are laid, most frequently 1—2 (but occasionally up to 4) in a lens-shaped horny capsule, diameter 640—720 μm , which is attached to the walls of cracks or crevices in the rocks amongst which the snails live. The capsules may be exposed at low tides and have markedly thick and tough walls. The veliger stage is passed within the capsule and young snails hatch with a brownish shell of 2.5 whorls, about 500 μm in diameter. There are no records of growth.

Notes. The distribution of *C. cingillus* in crevices has been well described by Glynne-Williams & Hobart (1952) in Anglesey and by Morton (1954) at Plymouth. The snails abound in the middle regions of crevices from MHWN to about the *Fucus serratus* zone. These are situations where the deposition of detrital material, on which they depend for food, is maximal. The front edge of the foot and the lobes of the snout are used to plough up the substratum from which particles are taken up by the radula.

The relationship between the variety *rupestris* and typical snails is not understood, nor why mixed communities seem not to occur. The distribution of *rupestris* may be related to exposure since it completely replaces the usual form at Whitsand Bay, near Plymouth, though it is not immediately obvious how exposure would affect a crevice dweller.

CINGULA ALDERI (Jeffreys, 1858)
Rissoa soluta var. *alderi* Jeffreys, 1858
Putilla alderi (Jeffreys, 1858)

Alderi, Alder's; named for Joshua Alder (1792-1867), best known as co-author with Albany Hancock of *A Monograph of the British Nudibranchiate Mollusca* (1845-55). He was a provision merchant of Newcastle upon Tyne and an amateur malacologist, author of more than 50 papers mainly on animals of N.E. England.

Shell. Small semitransparent and glossy; globose-conical in shape. The spire is cyrtocoid with a blunt tip; apical angle $54 \pm 4^\circ$. There are 4—5 noticeably tumid whorls which meet at deep sutures placed just below the periphery of the upper whorl and deeply incised; each whorl is often a little flattened below the suture. The ornament is of delicate growth lines and fine spiral ridges, neither visible except with considerable magnification. The growth lines are slightly prosocline, in some shells elevated to small ribs which are broader than the intervening spaces and run right to the suture to make it wavy. The spiral ridges equal the intervening grooves in

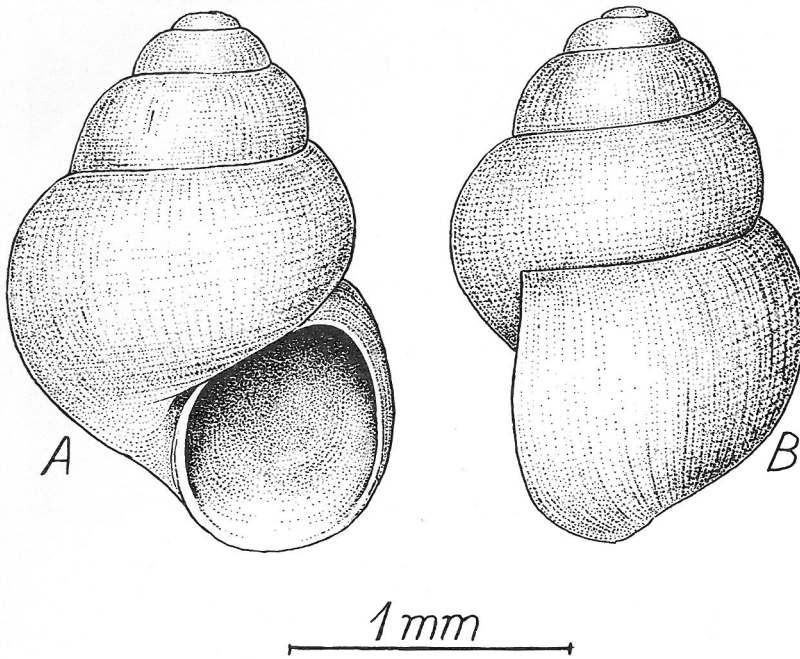


Fig. 133. *Cingula alderi* (Jeffreys). Isle of Skye. CMZ.

breadth; there are *c.* 30 on the body whorl, 18–20 on the penultimate, 10 on the next. They tend to be few or absent on the subsutural shelf. Ridges and growth lines intersect to produce a very shallow square reticulation. There is a distinct umbilical groove on the base of the shell leading to an oblique umbilicus. The protoconch has 2+ whorls decorated with a few delicate spiral lines. Its initial swelling is 80–100 μm across, its total diameter *c.* 300 μm .

Aperture. Very slightly prosocline with a peristome, not quite plane, the outer lip having an adapical anal sinus and a slight peripheral extension. It is a rounded oval in general outline, angulated adapically and again where body whorl and columella join. The outer lip meets the body whorl at right angles below the periphery and at first runs straight; at its most abaxial point it may be a little angulated and basally it is out-turned. Its edge is thin. The columella is nearly straight. The inner lip turns out over the umbilical groove and umbilicus.

Colour. Uniform pale horn colour or cream.

Size. 2 \times 1.4 mm. Body whorl = 70% of total height; aperture = 40% of total height.

Animal. Like that of *C. cingillus* in general organization. The tentacles are delicate and setose; the eyes rarely are seen beyond the edge of the shell; there is only one pallial tentacle, on the right.

Colour. Cream, with numerous minute white points.

Geographical distribution. This species extends along the whole western coast of Europe from Iberia to Norway. It does not occur, however, on the eastern shores of the N. Sea nor in the Baltic.

Habitat. *C. alderi* is a sublittoral species which has been dredged amongst algae and on sandy or gravelly bottoms at depths of 10–50 or 60 m. It is local and not uncommon where it does occur.

Food. A collector of detritus. Faecal pellets ovoid.

Breeding and growth. As in all rissoids the sexes are separate with the male recognizable by the penis. The reproduction is unknown though Rodriguez Babio & Thiriot-Quiévreux (1974) deduced a free-swimming veliger stage from the appearance of the protoconch.

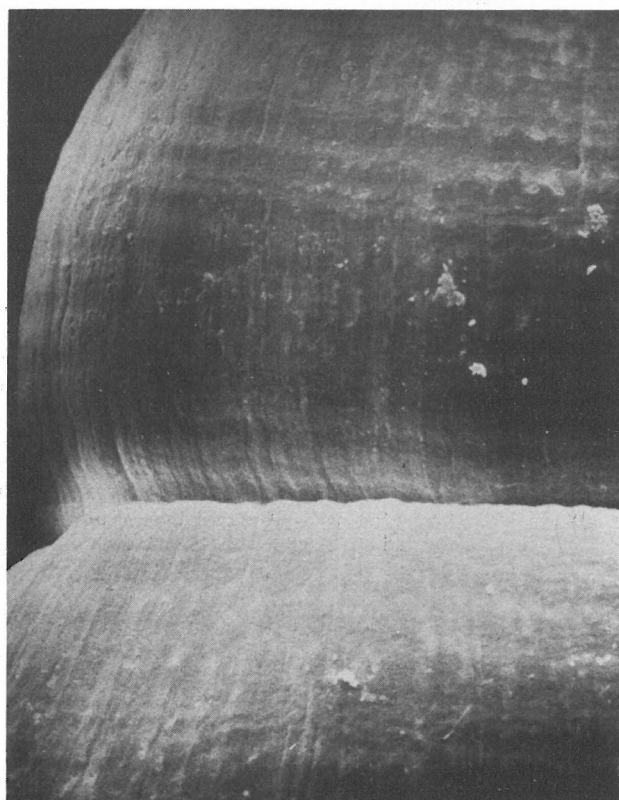
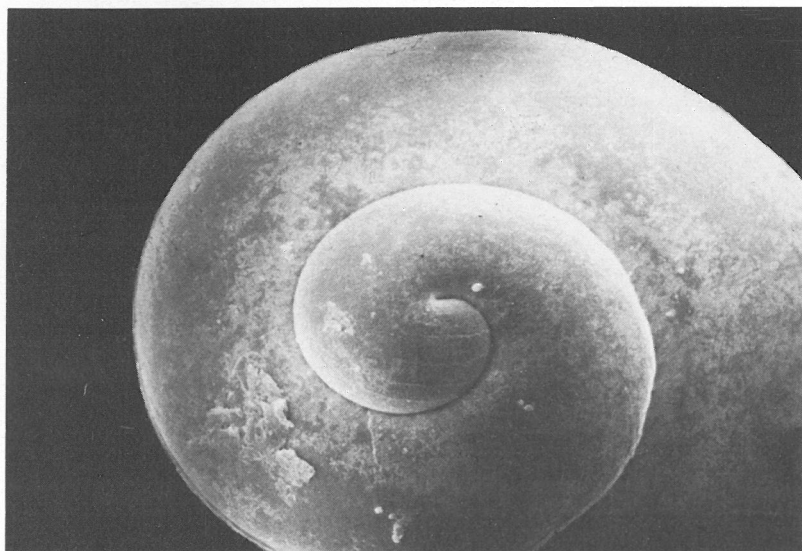
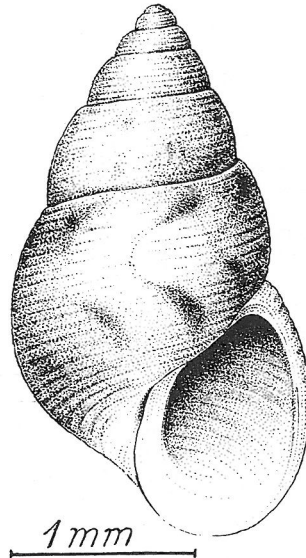


Fig. 134. *Cingula alderi*. Above, apex of spire $\times 290$; below, detail of shell surface $\times 250$. SEM photographs. Oban. RZ.

CINGULA SEMISTRIATA (Montagu, 1808)*Turbo semistriatus* Montagu, 1808*Rissoa semistriata* (Montagu, 1808)*Setia semistriata* (Montagu, 1808)*Setia marmorata* (Cantraine, 1842)*Setia subsulcata* (Philippi, 1844)*Semistriata* (Lat.), partly striated, referring to the spirals on the shell.Fig. 135. *Cingula semistriata* (Montagu). Weymouth. CMZ.

Shell. Solid, opaque, not glossy when the periostracum is intact but moderately so when that is lost. Oval-conic in general shape with a rather straight-sided spire, cyrtconoid near the pointed apex. The apical angle is 35–45°, 65° in young shells. There are 5–6 whorls, slightly tumid, meeting at slight sutures placed below the periphery of the upper whorl. Occasionally the subsutural part of the whorls appears swollen making them a little angulated and some shells show a slight keel at the periphery of the body whorl. The ornament consists of growth lines and spiral ridges and grooves. The growth lines are slight, prosocline and close-set, but rather irregular. There are no ribs, even at the aperture. The spirals are very slight; there are about 24 on the body whorl but only those near the suture and on the base (only the former in the spire) are readily visible. There is no umbilicus, but a groove is present. The protoconch has 2.25 whorls, 250–350 μ m in diameter, decorated with delicate spiral lines and papillae.

Aperture. Oval, angulated adapically and surrounded by a peristome. This lies in a slightly prosocline plane and shows gentle projections at the periphery and again where the inner lip spreads over the umbilical area. The edge of the peristome is rather thick. The outer lip arises nearly tangential to the body whorl and its adapical part is nearly straight, continuing the profile of the spire; basally it is a little out-turned. The columella is rather short and shows a slight swelling in some shells. The inner lip everts over the umbilical groove and spreads appreciably over the body whorl.

Colour. Yellowish white to pale or medium brown when the periostracum is present, practically white in its absence. There are 2 rows of reddish brown marks on the body whorl, one below the suture and one at the periphery, the latter sometimes split into two; on the spire only the upper and part of the lower row are visible. The individual marks are rather broad and comma-shaped, opisthocline in the subsutural row and prosocline in the peripheral one.

Size. 3×1.6 mm; body whorl = 65 — 70% of total shell height; aperture = 40—45% of total shell height.

Animal. In general like *cingillus*. The snout is rather short, the tentacles a little flattened. There is a short pallial tentacle on the left and a rather larger one on the right.

The foot is figure-of-eight shaped, slightly angulated anterolaterally. A three-pointed metapodial tentacle projects shortly from under the rear edge of the ear-shaped operculum. The rather small pore of the posterior pedal gland opens to the sole at the broadest posterior part of the foot.

Colour. Cream. There is a yellow blotch behind each eye and further yellow markings on the opercular lobes.

Geographical distribution. *C. semistriata* is found throughout the Mediterranean and northwards to Norwegian coasts becoming generally rarer in the north. It extends into the Kattegat but is absent from the eastern shores of the southern N. Sea.

Habitat. The snails are confined to rocky shores where they are found on the lower half of the beach (50% emersion or less) and sublittorally to 100 m. They are gregarious and groups occur under stones and at the base of weeds, hydroid or bryozoan colonies. They are particularly fond of silty places and are common in the muddier parts of rock pools. They become abundant in summer in the south of their range.

Food. The snails eat the detritus amongst which they live, using the anterior edge of the foot to stir it up and collecting particles from the dorsal surface of the foot. The faeces are ovoid pellets $200 \times 100 \mu\text{m}$.

Breeding and growth. See Lebour (1934) and Fretter & Pilkington (1970). The sexes are separate, the male recognizable by the penis. Breeding occurs March — August at Plymouth. The eggs are cream, measure c. $80 \mu\text{m}$ across and are laid in groups of 12—22 in capsules fastened to weeds in the places where the adults live. The capsules are hemispherical, attached by the flat side, are about $600 \mu\text{m}$ in diameter and $250 \mu\text{m}$ high, and are clear and colourless. On hatching the veliger larva has a shell of 1.25 whorls, $100\text{--}120 \mu\text{m}$ in diameter, marked with a peripheral apertural beak; it grows to 2.5 whorls, $250\text{--}350 \mu\text{m}$ across, at metamorphosis. The larva has a large, bilobed velum edged, in older larvae, with a thin red line; it has further red markings on the sole of the foot. There are no observations on the growth. The animals, however, like most of their relations, are likely to be annuals.

CINGULA PULCHERRIMA (Jeffreys, 1848)

Rissoa pulcherrima Jeffreys, 1848

Setia pulcherrima (Jeffreys, 1848)

Pulcherrima (Lat.), most beautiful.

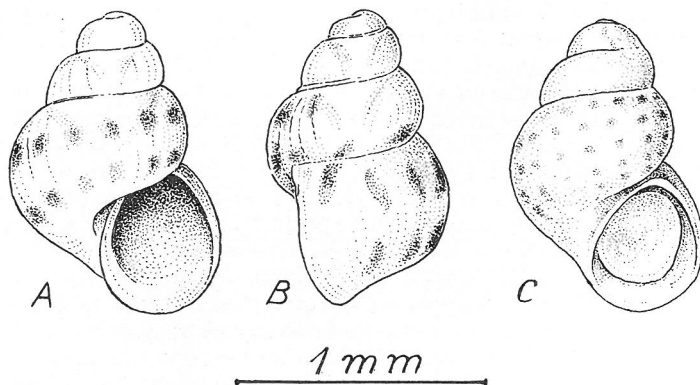


Fig. 136. *Cingula pulcherrima* (Jeffreys). A, B, no locality given; C, Puerto de la Cruz, Canary Islands.

Shell. Conical glossy and semitransparent, with a short spire ending in a blunt, rather bulbous apex (apical angle $52-65^\circ$, usually $56-58^\circ$). There are 4–4.5 whorls, tumid and meeting at deep sutures far below the periphery of the upper whorl. The whorls are nearly smooth, marked only by a few minute spiral striae and a few equally minute, distinctly prosocline growth lines. There is no labial rib. The umbilicus is well marked. The protoconch has 1.25 smooth whorls usually distinctly separated from the teloconch. The initial swelling has a diameter of $150-200\ \mu\text{m}$, the whole larval shell of $350-400\ \mu\text{m}$.

Aperture. A rounded oval, narrower adapically and surrounded by a thin peristome. The outer lip arises at right angles to the body whorl, just below the periphery; the first part is gently curved to follow the profile of the spire while the base has a smaller radius of curvature and may be a little flattened. The columellar region is nearly vertical, rather short, the lip everted over the umbilical groove. The peristome may be a little detached from the surface of the body whorl and here be sigmoid, straight or gently concave.

Colour. Colourless to pale horn colour, the apex slightly darker and occasionally with a pale lilac tint. There are often brown streaks, orthocline or prosocline, on the subsutural part of the body whorl along with 2 rows of brown spots or short streaks at the periphery and a third below it; these tend to form incomplete V-shaped markings, the wide end towards the aperture. In some shells the subsutural lines break, to give 4 rows of spots in all.

Size. $1.25 \pm 0.8\ \text{mm}$. Body whorl = c. 75% of total height; aperture = 45–50% of total height.

Animal. As in other species. There are no pallial tentacles; the metapodial one is long. The ctenidium is vestigial.

Colour. White, spotted with yellow; opercular lobes dark.

Geographical distribution. This species is found from the Azores N. to the Channel Islands. The animals have not been recorded from the British Isles or north thereof, except, perhaps, for specimens from the Clyde (see below).

Habitat. On rocky shores, among fine weeds at LWST.

Food. Detritus and perhaps the weeds amongst which they live. Faeces ovoid pellets $50 \times 25\ \mu\text{m}$.

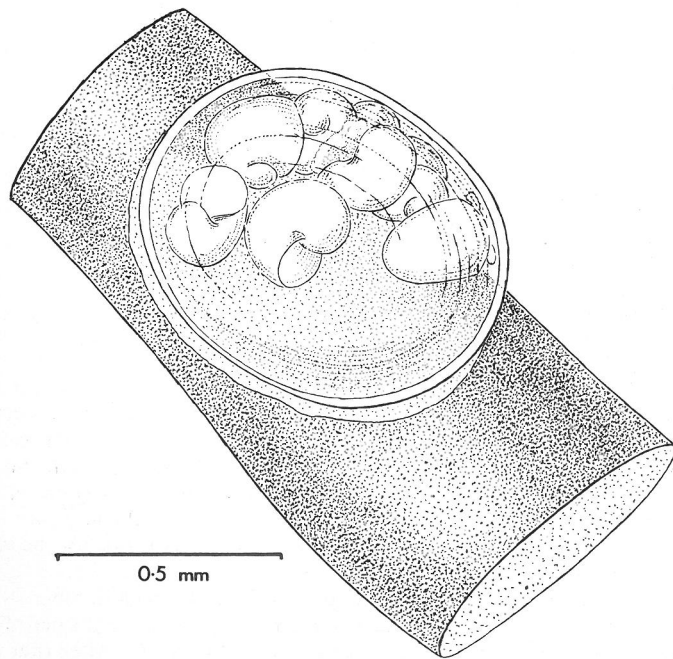


Fig. 137. *Cingula pulcherrima*. Spawn on alga. Canary Islands. Unpublished drawing by G. Thorson.

Breeding and growth. Thorson (unpublished notes) found egg capsules on brown weeds at low levels on the rocky shore at Puerto de la Cruz, Canary Islands. They have the usual lentiform rissoid shape, measuring $800 \times 600 \mu\text{m}$, with an attachment base but neither suture nor plug. Each contains 3-9 embryos which never have any trace of velum and hatch as juveniles. There are no details of growth rates in this species.

Notes. Fretter & Patil (1961) described (under the name *Setia inflata* Monterosato, 1884) a small rissoid of which a few specimens had been found at Kames Bay, Isle of Cumbrae. Although there are a few points of difference between it and typical *pulcherrima* (the shell is a uniform greenish brown, blunter apically) it is probable that this is only a variety of that species.

CINGULA TURGIDA (Jeffreys, 1870)

Rissoa turgida Jeffreys, 1870

Pseudosetia turgida (Jeffreys, 1870)

Putilla turgida (Jeffreys, 1870)

Turgida (Lat.), swollen, referring to the whorls, especially the body whorl, of the shell.

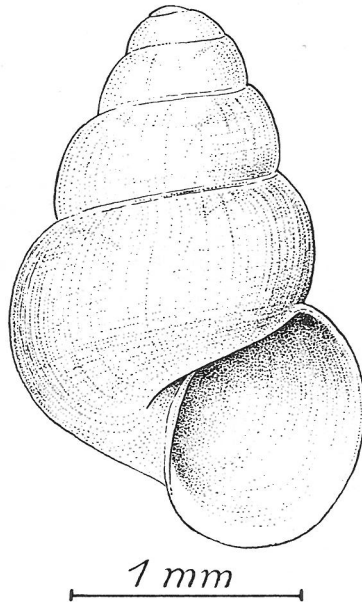


Fig. 138. *Cingula turgida* (Jeffreys). Thor sta.273, Skagerrak, 38.6 km NW of Hirtshals. CMZ. The drawing shows a shell with only an indication of the spiral ridge often present on the body whorls.

Shell. Ovoid-conical, semitransparent, rather glossy. The spire has a blunt point, but is nearly straight-sided (neglecting the curvature of each whorl); apical angle $45-50^\circ$. There are 5 whorls, distinctly swollen, especially the body whorl, which meet at deep sutures each just abapical of the periphery of the upper whorl. The general appearance of the shell is smooth, but there are faint growth lines and spirals; in many shells one spiral is elevated into a small keel which encircles the body whorl near (usually just below) the periphery. There is no labial rib. There is a well-marked umbilicus. The protoconch of 1 + whorls is flattened, a feature responsible for the blunt tip, and has a diameter of $300-330 \mu\text{m}$.

Aperture. Nearly circular, a little constricted adapically, bounded by a thin peristome. It lies more or less in the axial plane and exhibits a slight anal sinus and an equally slight peripheral protrusion. The outer lip arises at right angles to the body whorl, level with the keel when that is apparent, and curves to the columella, slightly out-turned at the base. The columella is thin, a little oblique, the lip here hardly everting over the umbilical groove. Over the body whorl the peristome is thin.

Colour. Whitish or pale horn-colour.

Size. 2—2.5 × 1.25—1.5 mm. Body whorl = 66—70% of total shell height, aperture = 46—48% of total height.

Animal. As in *C. cingillus*.

Geographical distribution. A northern species extending from the Arctic S. on Scandinavian coasts to the Kattegat. Not recorded from the British Isles.

Habitat. On muddy bottoms down to c. 1000 m.

Food. Foraminiferans.

Breeding and growth. Unknown. The free-swimming larval stage is probably suppressed, the animals hatching as juveniles.

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ONOBA SEMICOSTATA (Montagu, 1803)
Turbo semicostatus Montagu, 1803
Turbo striatus J. Adams, 1797 (preoccupied)
Rissoa striata (J. Adams, 1797)
Onoba candida (Brown, 1844)

Onoba, the name of a city in the Roman province Hispania Baetica (= modern Andalusia); *semicostata* (L.), partly ribbed referring to the ornament on the shell.

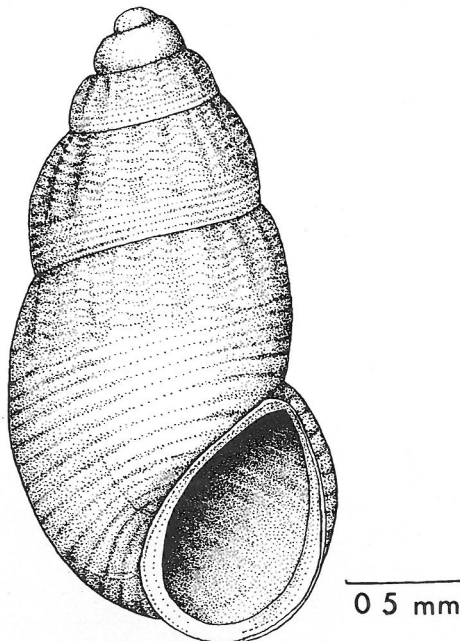


Fig. 139. *Onoba semicostata* (Montagu). Oban. RZ.

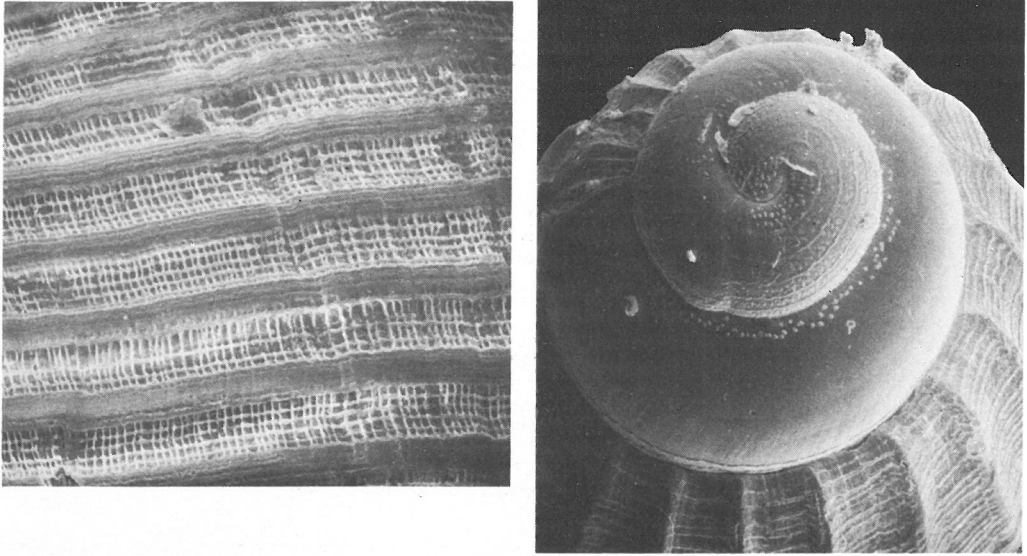


Fig. 140. *Onoba semicostata*. Right, apex of shell $\times 185$; left, detail of shell surface $\times 350$. SEM photographs. Plymouth, RZ.

Shell. A rather elongated, narrow, oval-conic to cylindrical shell with a blunt apex (apical angle $25\text{--}35^\circ$). In abapertural view it is usually slightly banana-shaped because of the greater breadth of the body whorl + outer lip compared with the spire. It is solid and opaque, not glossy to the naked eye but clearly so under a stereomicroscope. There are 5–6 whorls, tumid, rather flattened peripherally and sometimes also below the suture. The sutures are deep and lie below the periphery of the more apical whorl. The ornament consists of spiral grooves and ridges and of ribs. The spiral ridges are of two sizes, major and minor, the latter visible only with considerable magnification. The major spirals are about equal in breadth to the intervening furrows, not very high, but a conspicuous element of the ornament. They are not obvious on the subsutural area of the whorls of the spire and may also be lacking on the very base of the body whorl. There are 18–26 on the body whorl, 10–15 on the penultimate, 6–12 on the previous, about 5 on the next and only 1–2 on the basal part of the next. Minor spirals occur on the surface of the major spirals, in the furrows between them and in the subsutural areas; they are numerous and lie at varying distances from one another. The subsutural region occupied by these is greatest in older whorls, least on the body whorl. In most shells ribs occur on the adapical parts of the whorls; they run from the suture about halfway across the whorls of the spire, a short distance across the body whorl; they tend to disappear on the youngest part where there is only a not very conspicuous labial rib crossed by the major spirals. There are 18–21 on the body whorl, 17–20 on the penultimate, 16–18 on the next, though they are variable in development and are small or absent on some shells (var. *ecostata*). Each rib is flexuous (concavity adapertural), fairly sharp-edged, with gently sloping sides. Between ribs growth lines give rise to a squarish, very shallow network with the micro-spirals. The protoconch has 2.25 whorls in all, divisible into 2 parts, an initial whorl decorated with *c.* 9 delicate spiral ridges with irregular papillae between, and a further part of 1.25 whorls, mainly smooth but with scattered papillae adapically and 1–2 spirals abapically. This changes abruptly to the teloconch. The diameter of the first whorl is $190\text{--}200\ \mu\text{m}$, of the whole *c.* $250\text{--}340\ \mu\text{m}$.

Aperture. Rather small, oval, narrower above than below, the long axis at 30° to that of the spire. There is a peristome, thick-edged and with a distinct anal notch. The outer lip arises tangentially from the body whorl, well below the periphery, so rises a little before curving downwards. It is out-turned basally where it joins the inner lip. The columella is short and oblique and the inner lip turned

out over an umbilical groove; except in young shells there is no umbilicus. The parietal part of the peristome is thick. In young shells the outer lip is denticulated by the ends of the spirals. The throat is slightly constricted a little way within the outer lip.

Colour. Black, brown, orange, fawn or white. The colour is in the periostracum; as this usually wears away at the apex and on ribs and ridges the colour may be limited to grooves. There may be 2 brown bands in the underlying shelly material on the body whorl about the periphery. White shells are less opaque than pigmented ones and the spirals may then be seen through the throat. The peristome is pale but a belt of orange-yellow lies internally parallel to the outer lip.

Size. Up to 4×1.75 mm, more commonly 2×1 mm. Body whorl = 60–65% of total height; aperture = 36–40% of total height.

Animal. The head has a rather broad, slightly depressed snout, wrinkled laterally, bifid distally with the mouth (closed) a longitudinal slit under the tip. The tentacles are long and hardly taper, setose, with an eye at the base. The mantle edge is smooth with a tentacle on the left and, in many animals, on the right as well. In males a long, slender penis lies within the mantle cavity attached anteriorly to the right of the mid line behind the tentacles and curving dorsally to end at the left inner end of the cavity.

Foot rather narrow, axe-shaped anteriorly where a flap dorsal to the centre of the anterior edge marks the opening of the anterior pedal gland. It narrows in its middle and tapers posteriorly. There is a single metapodial tentacle, flattened and narrowly triangular which projects from under the operculum, sometimes to the tip of the foot. The operculum is delicate and spiral.

Colour. White, cream, pale yellow with darker colour on the snout and dorsal surface of the foot. There is an opaque white patch behind each eye. The anterior pedal gland shows white through the foot.

Geographical distribution. Norway S. to the Mediterranean. It is absent from Danish and German N. Sea coasts but extends, becoming less common, through the Kattegat, the Sound, Great and Little Belts into the most saline parts of the Baltic.

Habitat. The animals tend to avoid more open areas of sea and to be distributed close to shores. They are common, sometimes abundant, on all rocky and stony shores from near low water mark to 100 m, becoming sublittoral to 1100 m in the northern part of their range. They are gregarious under stones, amongst weeds and corallines, among mussels and tunicates, in shelly gravel, *Lima* nests, crevices, but always where there are considerable quantities of silt.

Food. The detrital material among which it lives. This is disturbed by the foot, gathered on its dorsal surface and licked in by the radula. Faeces ovoid pellets $175\text{--}200 \times 75\text{--}100 \mu\text{m}$.

Breeding and growth. The sexes are separate and recognizable by the penis of the male. The largest animals seem to be female. Breeding occurs at Plymouth from December to June. Eggs, whitish in colour and $200\text{--}240 \mu\text{m}$ in diameter, are laid, usually singly, in capsules which are fastened to sand grains or weed. Each capsule is more or less egg-shaped and has a diameter of $480\text{--}640 \mu\text{m}$, mean $560 \mu\text{m}$ (Plymouth). The capsule is thick and tough, without any mucous plug and is fastened by the centre of one side. The veliger stage is passed within the capsule and a juvenile escapes with a shell of 1.7 whorls measuring $320\text{--}340 \mu\text{m}$ in diameter (Warén, 1974). Figures for Plymouth animals based on the size of the protoconch of adult shells ($200\text{--}250 \mu\text{m}$) differ from these but agree with measurements made on the protoconch of a shell from Roscoff (Thiriou-Quévieux & Rodriguez Babio, 1975, fig. E, pl. 1) which has a diameter of $250 \mu\text{m}$. These figures suggest differences in the reproduction of this animal between north and south.

The description of this species apparently given by Rasmussen (1951, 1973) has been shown by Warén (1974) to apply to *O. aculeus* (see below). The same is probably true of the description given by Thorson (1946) of a capsule from Iceland.

Notes. The correct name of this abundant animal is problematic, and we give only that in common use.

Turbo semicostatus Montagu, 1803 was probably based on immature shells and not this species. *T. striatus* Adams, 1797 (another name in frequent use) is preoccupied by *T. striatus* Da Costa, 1778 (= *Pomatias elegans* Müller, 1774). Warén (in litt.) has suggested to us that *T. shepeianus* J. Adams, 1798 might be appropriate. Rather than wait for the solution of this problem we use a name by which the animal will be well known.

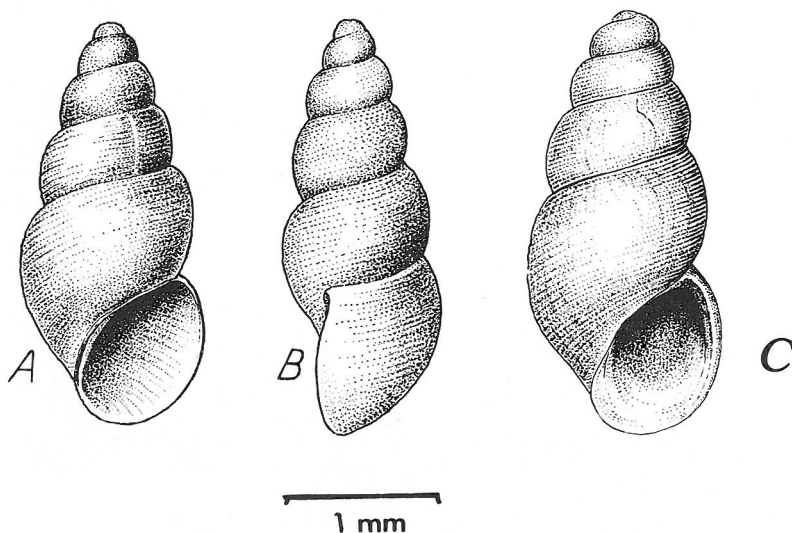
ONOBA ACULEUS (Gould, 1841)*Cingula aculeus* Gould, 1841*Onoba saxatilis* (Müller, 1842)*Onoba arctica* (Lovén, 1846)*Aculeus* (Lat.), a small needle or sting, referring to the shape of the shell.

Fig. 141. *Onoba aculeus* (Gould). A,B, Nibe Broad, E, Limfjord; C, Iceland. CMZ.

Shell. Very similar to that of *O. semicostata* and that of *O. proxima* in shape, size and ornament. The differences from *semicostata* are: (1) the restriction of ribs to 1–2 of the upper whorls; (2) their lesser conspicuousness; (3) a less clear microreticulation of the shell surface; (4) the larger protoconch 330–575 μm in diameter though with the same ornament as in *semicostata*. The differences from *proxima* relate to the spiral ridging which is coarse in *aculeus* (20–28 on the body whorl) but fine in *proxima* (c. 40 on the body whorl).

Colour. Like *semicostata*s though brown bands are usually absent.

Size. Up to 3×1.25 mm; body whorl = 57–77% of total height of shell, commonly c. 65% in grown shells; aperture = 33–48% of total height, usually about 40%.

Animal. As in *semicostata*.

Geographical distribution. A panarctic species which extends S. to the Sound in Denmark. There are a few Hebridean occurrences mentioned by Marshall (1898); we have found them off Oban and in material from Orkney. Dr S. Smith has recorded them from a number of Scottish and Irish localities (*in litt.*). They reach Iceland, Greenland and to New Jersey in the Western Atlantic.

Habitat. Found to about 200 m on algae, avoiding the siltier conditions which attract *O. semicostata*; it tolerates brackish water more readily than *semicostata*. Common only in the far north.

Food. As for *semicostata*.

Breeding and growth. A very full account has been given by Rasmussen (1951, 1973) though he believed he was dealing with *O. semicostata*. Thorson (1946) described egg capsules which probably belong to this species. Breeding occurs in Denmark (Roskildefjord) from November to March. Eggs, whitish in colour and 200 μm in diameter are laid usually singly in capsules fastened to sand grains, weed or shells of other animals. Each capsule is approximately hemispherical and has a diameter of 550 μm (Iceland, Thorson), 600–850 μm , mode 650–700 μm (Roskildefjord). The capsule is thick and tough, its walls marked with striae encircling a centre located to one side of the wall and without any mucous plug, the young perhaps escaping through the centre of the concentric striae. It is

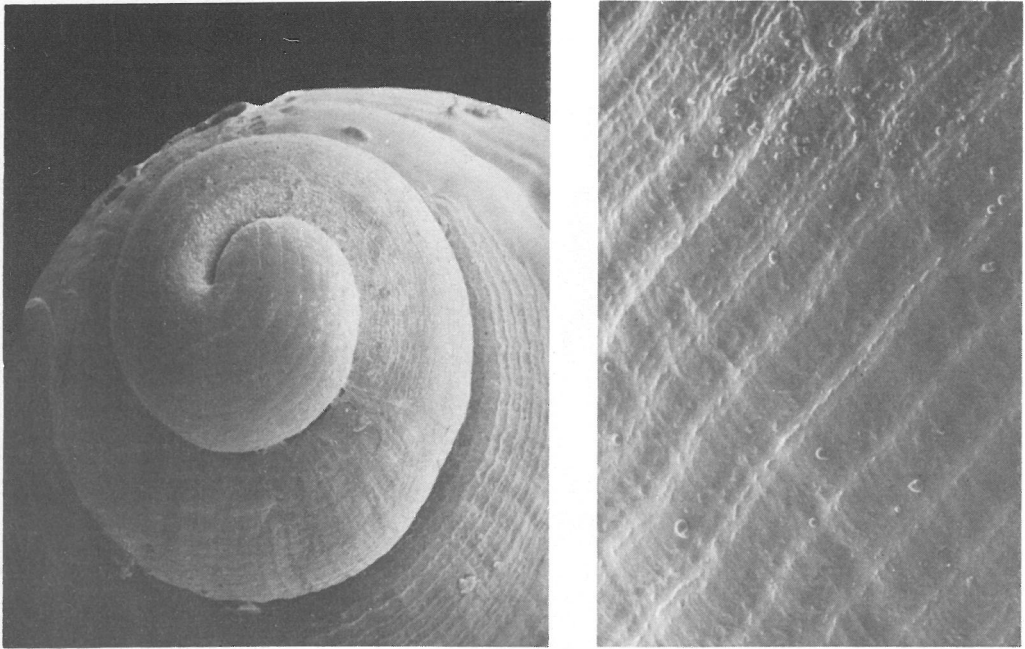


Fig. 142. *Onoba aculeus*. Left, apex of shell $\times 180$; right, detail of shell surface $\times 520$. Rannefjord, Norway. SEM photographs. RZ.

fastened by its base. The veliger stage is passed through within the capsule and young snails escape after 3–4 months (in laboratory), at temperatures between -2° and 8°C , average 5° . The diameter of the shell on hatching was $330\text{--}560\ \mu\text{m}$ (Warén, 1974) and it had 1.3 whorls. The unhatched embryo from Iceland available to Thorson measured $420\ \mu\text{m}$ across the shell.

ONOBA PROXIMA (Forbes & Hanley, 1850)

Rissoa proxima Forbes & Hanley, 1850

Ceratia proxima (Forbes & Hanley, 1850)

Hyalia proxima (Forbes & Hanley, 1850)

Proxima (Lat.), nearest, emphasizing the great similarity of the shell to that of *Onoba* (then *Rissoa*) *semicostata*.

Shell. Tall, columnar, semitransparent, glossy under a well-developed periostracum. The spire is cyrtocoiled, most of the curvature being just below the blunt tip, the rest with nearly parallel sides; the apical angle is *c.* 25° , of the juvenile *c.* 50° . There are 6 whorls meeting at deep sutures, set very obliquely, well below the periphery of the upper whorl. The ornament consists of growth lines and spiral ridges. The former are orthocline or very slightly prosocline and irregular. In some shells they may be bunched in 1–2 upper whorls so as to suggest the beginning of small ribs below the suture. There is no labial rib. The spiral ridges and grooves are about equal in breadth, fine and numerous — 20–40 on the body whorl, 16–18 on the penultimate, 15 on the next, 10 on the next, the rest smooth. In some shells they are not precisely parallel to the sutures and may arise out of them and they disappear close to the peristome. As in *semicostata* and *aculeus* a series of microspirals lies along the major ones and in the grooves between; they are crossed by the growth lines to give a reticulation. The protoconch has 1.5 whorls (diameter $450\ \mu\text{m}$) and bears some fine spiral lines.

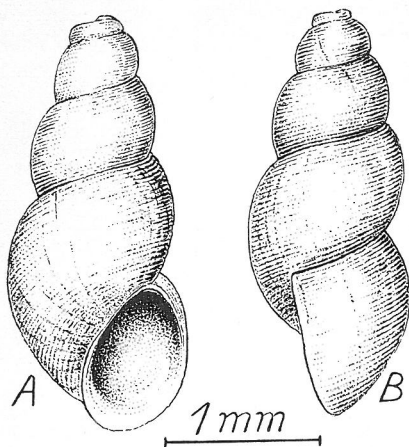


Fig. 143. *Onoba proxima* (Forbes & Hanley). No locality known. BMNH 1907.12.30 546-548.

Aperture. Oval-gibbous, angulated adapically and usually with a distinct sinus at the adapical end of the outer lip. There is a peristome, plane except for the sinus, lying axially; it has a rather thick periostracal edge but the shelly part is thin. The outer lip arises below the periphery of the body whorl and has a nearly semicircular course to the inner lip, distinctly out-turned at its base. The spiral ridges do not crenulate it. The columella is short and curved and the lip alongside everts over a slight umbilical groove. Parietal lip nearly straight, forming a thick glaze over the body whorl.

Colour. Periostracum yellow, pale tan or pale orange over a white shell.

Size. 3×1.25 mm; body whorl = 66% of total height; aperture = 36% of total height.

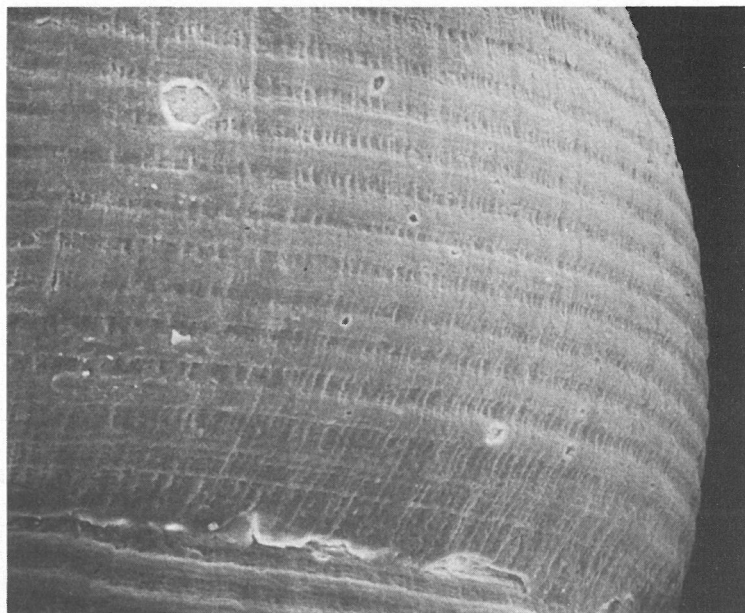


Fig. 144. *Onoba proxima*. Microstructure of shell surface $\times 160$. SEM photograph. Carna, Co. Galway, Ireland. RZ.

Animal. Generally as in *O. semicostata* but differing in the lack of pallial and metapodial tentacles and in having the posterior part of the foot deeply cleft in the mid-line. This character is visible through the operculum when the animal is retracted. The anterior end of the foot is also divided and produced anterolaterally to a greater extent than in that species.

Colour. White with chalk-white spots; snout tinged apically and laterally with red.

Geographical distribution. This species occurs off the W. coast of Europe from the Mediterranean to Britain, where it is limited to western coasts. Previous records from further north have been shown to be wrong (Warén, 1974).

Habitat. Dredged from 10—170 m (usually 35—45 m in British waters) on bottoms of muddy sand. Not common.

Food. A detritus feeder. Faeces oval pellets $150 \times 75 \mu\text{m}$.

Breeding and growth. Unknown.

ONOPA VITREA (Montagu, 1803)

Turbo vitreus Montagu, 1803

Rissoa vitrea (Montagu, 1803)

Hyala vitrea (Montagu, 1803)

Cingula vitrea (Montagu, 1803)

Vitrea (Lat.), glassy, referring to the shell.

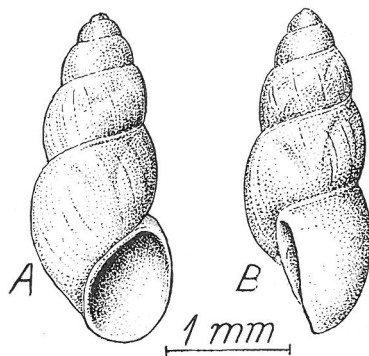


Fig. 145. *Onoba vitrea* (Montagu). Frederikshavn.

Shell. In general shape like that of other *Onoba* spp., tall columnar, semi-transparent, not glossy. The spire has very nearly parallel sides towards the base but tapers rather rapidly to a blunt tip though this is more pointed than in *O. proxima*; the apical angle of grown shells is c. 15° , of young ones c. 55° . There are 5—6 moderately tumid whorls meeting at deep sutures; that between the body and penultimate whorls (above the outer lip in apertural view) is so deep as to indent the profile to the same level as, or more than that between penultimate and antepenultimate whorls. The sutures lie very obliquely across the spire. Growth lines and spiral grooves are usually present, the former rather markedly prosocline and irregular, the latter very weak and not always visible. There is no umbilicus and hardly any groove. The protoconch has 2.5 whorls: no shell which we have seen showed any pattern on it, but this may be due to wear. The diameter is c. $330 \mu\text{m}$.

Aperture. An elongated oval narrowed adapically. There is a peristome lying nearly in a prosocline plane with a very slight anal sinus and peripheral bulge. The outer lip arises much below the periphery of the body whorl, curving in and downwards to its surface. It is thin, noticeably

flattened basally where it is a little everted. The columella is very short and slightly curved; the inner lip is hardly out-turned and has a rather straight course over the body whorl.

Colour. Yellowish, but white under the periostracum. There is no pattern. Darker apically and sometimes greenish when viscera show by transparency.

Size. 3×1.5 mm. Body whorl = 60% of total shell height; aperture = 35% of total shell height.

Animal. In general like that of other *Onoba* spp. It resembles *proxima* in particular in lacking pallial and metapodial tentacles and in having the posterior end of the foot bifid.

Geographical distribution. Found from the Mediterranean north to Norway. It extends through the Skagerrak and Kattegat to the Sound, is found on the British but not the continental shores of the N. sea and is absent from the eastern Channel Basin.

Habitat. Muddy bottoms at depths of 10–50 m in the northern parts of its range, but extending to 120 m in the south. Always uncommon.

Food. Presumably a detritus feeder.

Breeding and growth. The only records are those of Thorson (1946) who found larvae in the Sound between May and November, more frequently in the autumn. The larval shell is smooth and colourless; the aperture has a prominent peripheral beak; the larva is colourless apart from the brown digestive gland, two dark spots alongside it and the black eyes.

Notes on Onoba species. All four are generally alike so far as the shell is concerned: it is slender and tall with predominantly spiral ornament, though *vitrea* is distinct in the very slight degree to which this is developed. The aperture is small compared with that of other genera in the Rissoidae. In the soft parts *proxima* and *vitrea* are unlike the others in having the posterior end of the foot split into right and left halves: this is a considerable difference in rissoid terms and may therefore indicate that they should be placed in the genus *Ceratia* H. & A. Adams, 1852. It seems unnecessary to separate *proxima* in *Ceratia* and *vitrea* in *Hyala* H. & A. Adams, 1852 because of the reduced ornament of the latter.

It is tempting to regard *semicostata* as the southern, more truly marine form of a species of which *aculeus* is a northern form, more tolerant of brackish conditions. This idea would find support in the great variability of the two — in *aculeus* the ratio body whorl: total shell length ranges from 0.47–0.75, the ratio aperture height: total shell length from 0.29–0.41 and the ratio breadth: height from 0.34–0.47, whilst in *semicostata* the corresponding figures are 0.37–0.78, 0.32–0.50 and 0.37–0.64; the degree of development of ribs in *semicostata* is equally variable and they may, in extreme cases, be absent. The protoconchs are alike in pattern in the two species, though in rissoids this is by no means an accurate indicator of relationships — for example, *Alvania punctura*, *A. zetlandica*, *Onoba semicostata* and *O. aculeus* have identical patterns. On the other hand the size of the protoconch is different in *semicostata* and *aculeus*, the micropattern on the shells, though similar, is different and they prefer different habitats. They appear good species though closely related.

Species of *Onoba* tend to live in muddy places, often so muddy that one wonders how the animals keep the mantle cavity clear. *O. proxima* and *vitrea* are uncommon; *O. semicostata* is the commonest of the four and the most likely one to be found in Britain; *aculeus* is limited to northern localities. *O. semicostata* is particularly common in silty places, *O. aculeus* much more frequent on weeds on harder bottoms (Smith, personal communication).

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ALVANIA CRASSA (Kanmacher, 1798)

Turbo crassus Kanmacher, 1798

Rissoa crassa (Kanmacher, 1798)

Manzonina crassa (Kanmacher, 1798)

Rissoa costata (J. Adams, 1796)

Alvania. We have not succeeded in finding the origin of this name; *crassa* (Lat.), coarse, thick, referring to the shell.

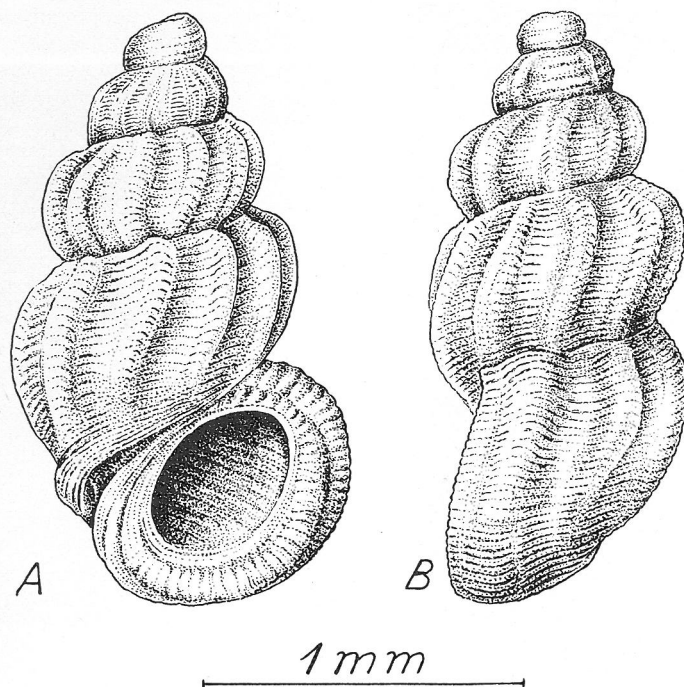


Fig. 146. *Alvania crassa* (Kanmacher). Madeira. BMNH 1911.10.26 22993-23007.

Shell. A tall, rather narrow shell (apical angle *c.* 45°), semitransparent, glossy and glass-like. There are 6 tumid whorls meeting at deep sutures placed well below the periphery of the upper whorl and slightly sinuous because of ribs. Below each suture the whorls are flat so that the outline of the spire is nearly saw-toothed. The ornament comprises ribs and spiral grooves, the former the more conspicuous, well-developed and slightly sinuous. On the whorls of the spire they arise orthoclinally at the suture but become opisthocline below; on the body whorl they are opisthocline and fade below the periphery, above the spiral keels. Each rib is much narrower than the intervening spaces. There are 10 on each whorl but they are slight on the third whorl and absent above that. Round the aperture is a strong labial rib, crossed (like the others) by spiral ridges and grooves though in worn shells these may disappear on the summits. The spiral ridges are narrow, strap-like bands separated by narrower grooves; at high magnification each groove is seen to contain 2–3 fine ridges and the intervening bands to be marked with spiral rows of pits. Two groups, each of 2–4 spiral ridges, form powerful, semicylindrical keels on the base of the shell; the upper runs from the adapical end of the aperture to the labial rib at the base of the outer lip, the lower from the level of the columellar lip to the base of the inner lip; the space between the keels contains 7–8 small spiral ridges. There are 16–18 spiral bands on the body whorl above the keels, 14–15 on the penultimate, 13 on the antepenultimate, 5–6 on the third and none above. The protoconch has 2 whorls, total diameter *c.* $200\ \mu\text{m}$, the first marked with a delicate upraised reticulate pattern, the second smooth. The first (= embryonic shell) is distinctly separated from the second (= larval shell) and that from the teloconch.

Aperture. A rather small oval with the narrow end adapical, its long axis set at *c.* 30° to that of the shell. It has a peristome which is not plane and is opisthocline and exhibits an anal sinus. Its edge is thin, projecting a little from adapertural faces of the labial rib and spiral keel. Basally the peristome is a little expanded but the inner lip is nowhere out-turned so that an umbilical groove, though no umbilicus, is plain.

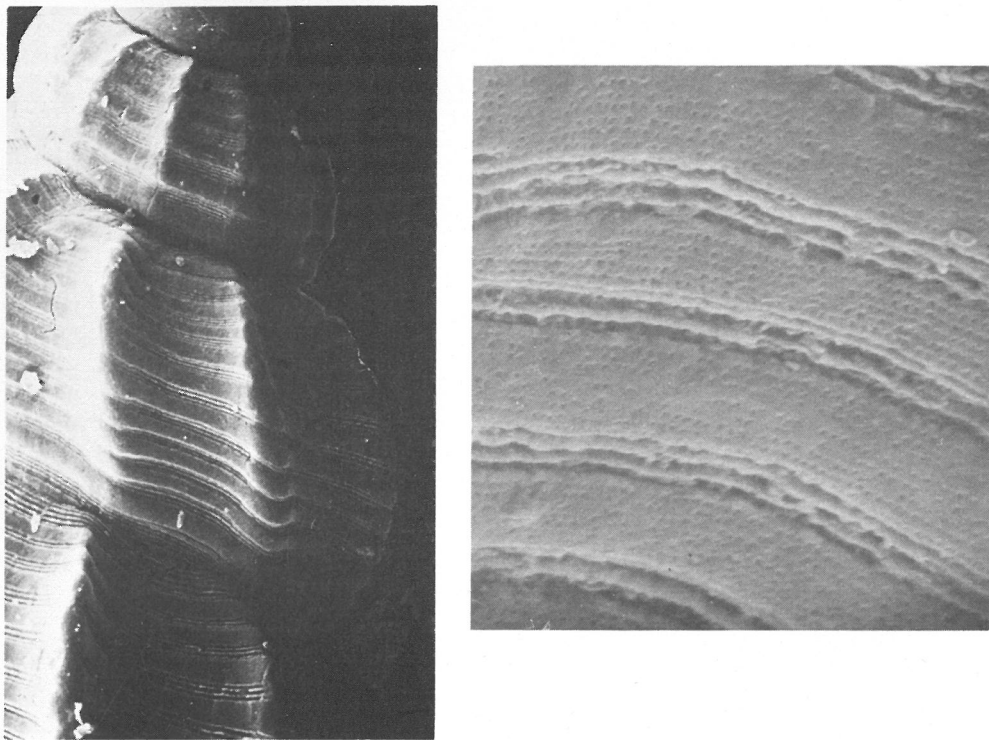


Fig. 147. *Alvania crassa*. Left, surface of shell $\times 66$; right, detail of surface $\times 750$. SEM Photographs. Plymouth. RZ.

Colour. White.

Size. 3—3.5 \times 1.5—2 mm. Body whorl = 60—65% of total shell height; aperture = 40% of total shell height.

Animal. The head has a long, rather broad snout, deeply cleft with the mouth (closed) a subterminal ventral longitudinal slit bordered by swollen right and left lips. Tentacles long, slender, a little flattened, each with an eye at the base hardly offset from the tentacle. Mantle edge plain with a pallial tentacle on both right and left sides, the latter more conspicuous. Males have a long penis arising from the dorsal surface of the head behind the right tentacle and curving to the left.

Foot figure-of-eight shaped, bluntly rounded anteriorly where the opening of the anterior pedal gland produces a double edge, tapering to a blunt posterior point. The sole has a median groove to which a posterior pedal gland opens. A well-developed metapodial tentacle projects from under the posterior edge of the operculum, sometimes reaching beyond the tip of the foot, and there is a similar projection from each metapodial lobe, making a kind of triple tentacle in all.

Colour. Pale yellow throughout.

Geographical distribution. A southern species which extends N. from the Mediterranean to the coast of Norway. It is absent from the continental shores of the N. Sea and only some dead shells have been found in the Kattegat.

Habitat. Under stones and amongst weeds, occasionally at low water mark, but more common sublittorally to depths of 50 m. It prefers sandy situations.

Food. It is said by Pelseener (1935) and Vahl (1971) to eat corallines, but this seems improbable: it is more likely that, as in other rissoids, the food is the diatoms and detrital materials on the surface of the weeds. This constitutes the bulk of the ovoid faecal pellets (150 \times 75 μ m).

Breeding and growth. The sexes are separate, the male recognizable by the penis. The breeding season and egg capsules are not known but free-swimming veligers occur (at Plymouth) in late summer and autumn. They have a large bilobed velum marked by a marginal red band, a foot with

much black pigment, a median beak at the aperture and the reticulate pattern on the first whorl of the shell described above (Fretter & Pilkington, 1970). There is no further information.

Notes. Moderately common in Western Channel dredgings, this is found alive rarely in the north, though dead shells occur. The aperture and the arrangement of ribs and spiral keels make it unlikely to be confused with other species.

ALVANIA BEANI (Thorpe, 1844), agg.

Cingula beani Thorpe, 1844

Rissoa beani (Thorpe, 1844)

Turbona beani (Thorpe, 1844)

Rissoa reticulata (Montagu, 1803), seg.

Rissoa calathus Forbes & Hanley, 1850, seg.

Beani, named in honour of W. Bean (1787-1866) of Scarborough, a well-known 19th century collector of shells.

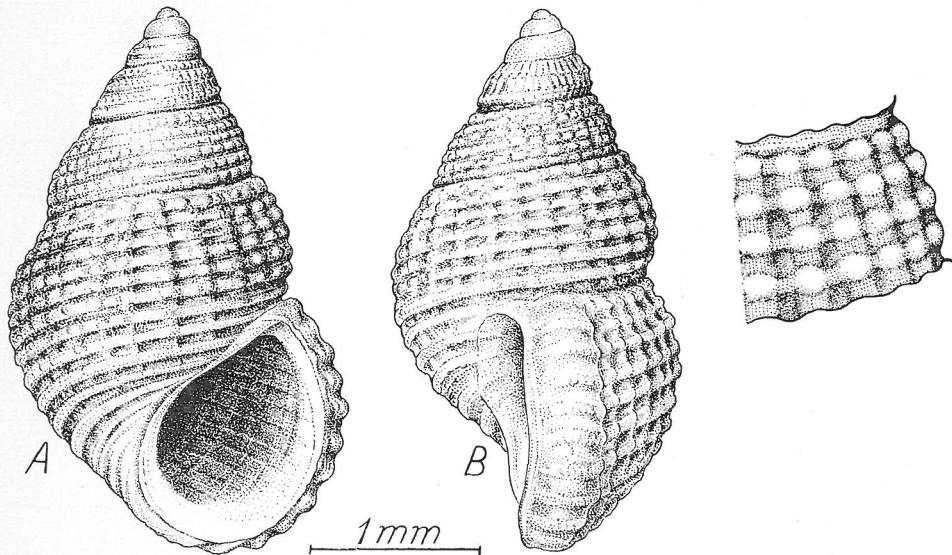


Fig. 148. *Alvania beani* (Thorpe). Gt. Britain. The main drawings show *reticulata* seg.; inset is part of the penult whorls of *calathus* seg. The drawing does not show clearly ridges on the throat within the outer lip.

Shell. Glossy, a little transparent, the spire plump, noticeably cyrtocoiled, with a sharp tip. The apical angle of young shells is about 60° , dropping to 30° at maturity. There are 7 whorls which are slightly tumid (though rather flat-sided) and meet at sutures placed below the periphery of the upper whorl. The sutures are deep and lie at the base of vee-shaped nicks in the profile of the spire. Older whorls are more tumid than younger ones. The ornament comprises spiral ridges and ribs which interact to cover all except the base of the body whorl with a reticulation, square on the spire, more oblong on the body whorl. The ribs are about half the breadth of the intervening spaces, low and slightly prosocline. They cross the whorls of the spire but do not extend (except as represented by small tubercles) below the periphery (spirals 6-8) of the body whorl. There are 35-45 on the body whorl, 40-42 on the penultimate, 36-38 on the previous 2, and the uppermost 3 have none. In some shells ribs extend to the labial rib on the body whorl, in others not so far. The labial rib is broad and crossed by 12-13 spiral ridges. These ridges are as broad as the ribs, those on the base of the shell larger and set further apart. There are 10-13 on the body whorl, 4 or 6-7 on the

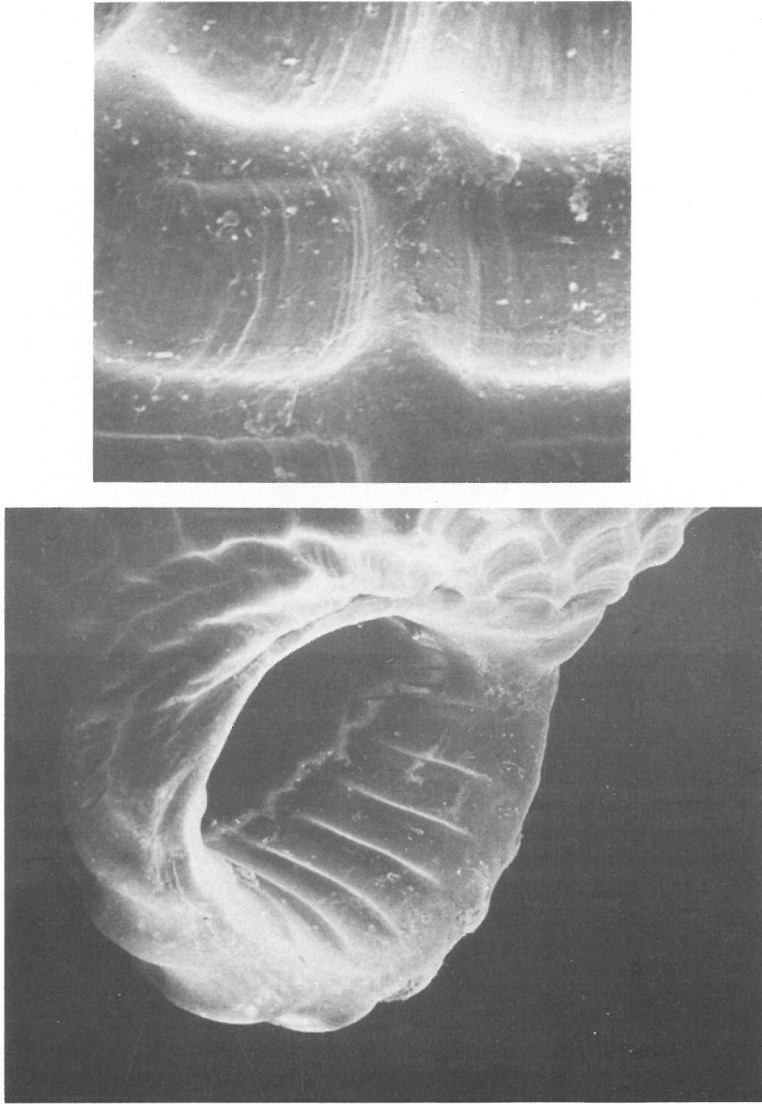


Fig. 149. *Alvania beani*. Above, detail of shell surface $\times 200$; below, teeth in throat $\times 60$. SEM photographs. Oban. RZ.

penultimate and successively one less on each older whorl. Where ribs and ridges cross the surface is raised to rounded knobs. In the spaces of the reticulation is a microstructure of growth lines crossed by minute spiral lines grouped near the edges of the spiral ridges. There is no umbilicus and hardly any groove. The protoconch shows 2.5 whorls, diameter $250\ \mu\text{m}$ (shells from Roscoff) to $350\ \mu\text{m}$ (shells from Oban); it is decorated with spiral lines and spiral rows of papillae.

Aperture. Drop-shaped, angulated above; it lies in the axial plane of the shell and the peristome is normally plane. The outer lip arises at right angles to the surface of the body whorl below the periphery, at the level of the 8th spiral ridge, and runs in a smooth curve to the columella. It is bevelled internally and externally to a sharp edge and is a little out-turned at the base of the columella which lies slightly obliquely. The inner lip spreads a thin film over the parietal area and

ends a little ahead of the outer. The throat of the shell is very glossy and within the outer lip (of mature shells) lie 10—12 low ridges opposite the spiral furrows on the outside of the shell.

Colour. Pale orange, cream or white. There are frequently 2 darker bands, one on the subsutural area, the other on the subperipheral part of the body whorl; the first occurs on the whorls of the spire. The periphery and base of the body whorl are pale, the latter, with the labial rib, nearly white. The subsutural spiral is likewise pale. The dark bands show in the throat of the shell and the pillar lip is pigmented.

Size. 3.5×2 mm. Body whorl = 67% of total shell height; aperture = 40—45% of total height.

Animal. Snout broad, depressed, slightly bifid terminally. Mouth as in *crassa*. Tentacles long, slender, setose and bearing a longitudinal ventral ridge; an eye lies on a distinct lateral bulge at the base of each. Pallial tentacles as in *crassa*; penis as in that species.

The foot is rather square anteriorly; the double edge, where the anterior pedal gland opens, extends some way down the lateral margin. The sole has a slight median groove but the opening of the posterior pedal gland is not obvious. The metapodial tentacle has a main lobe with a smaller one on each side.

Colour. Translucent white. Lips browner and there is a bright patch of yellow behind each eye. The anterior pedal gland shows as a conspicuous white area.

Geographical distribution. From the north of Norway to the Mediterranean, Azores, Canary Islands. It is found in the Skagerrak and off the Swedish but not Danish shores of the Kattegat. It is absent from the Danish and German shores of the N. Sea.

Habitat. Though occasionally found at low water this species is predominantly sublittoral, to depths of about 50 m, or 540 m in the Mediterranean. It lives both amongst weeds and on stony ground, even where there is a considerable amount of sediment.

Food. A detritus feeder. Faecal pellets ovoid, 150×75 μ m.

Breeding and growth. The sexes are separate, males usually smaller. Thiriot-Quévieux & Rodriguez Babio (1975) suggested, on the basis of the protoconch, that there is a free veliger larva, but there is no definite information.

Notes. We use the term *beani* as the name of an aggregate of which *reticulata* and *calathus* are segregates, perhaps also *cimex* and *c. calathiscus*. There are shells with 4 spiral ridges on the penult whorl, others with 6—7; these traditionally separate *calathus* and *reticulata*. Typical specimens of the former are also larger, with a coarser reticulation on the shell.

ALVANIA CIMICOIDES (Forbes, 1844)

Rissoa cimicoides Forbes, 1844

Turbona cimicoides (Forbes, 1844)

Rissoa sculpta (Philippi, 1844)?

Cimicoides, like the species *cimex* in its appearance.

Shell. In general shape like *beani* but the whorls are more convex, the V-shaped nicks at the sutures more marked and the reticulation on the surface coarser with more prominent tubercles at its nodes. Solid, nearly opaque, vitreous and glossy. There are 6—7 whorls, each a little flattened at its periphery and meeting at deep, excavated sutures. The apical angle is 55—58°, the spire less cyrtocooid than in *beani*. There are 9—12 spiral ridges on the body whorl, 4—6 on the penultimate, 3—4 on the next, 2 on the next, the rest being protoconch. The body whorl bears 16—20 ribs, the penultimate 15—22, the antepenultimate 16—20, the next 13; on the body whorl they die out just below the periphery. All are slightly prosocline and, like the spiral ridges, narrower than the spaces between. In fully grown, not young shells, there is a thick labial rib crossed by spirals and set not quite at the outer lip. The square depressions of the reticulate pattern are filled with a microstructure mainly of irregular tubercles set in clear spiral and less clear vertical rows. The protoconch has 3 whorls, the total diameter about 450 μ m, the initial part, not distinct from the rest, with a diameter of 150 μ m. The whole bears a reticulate pattern of interlinked zigzag spiral lines. There is an abrupt junction with the telococonch.

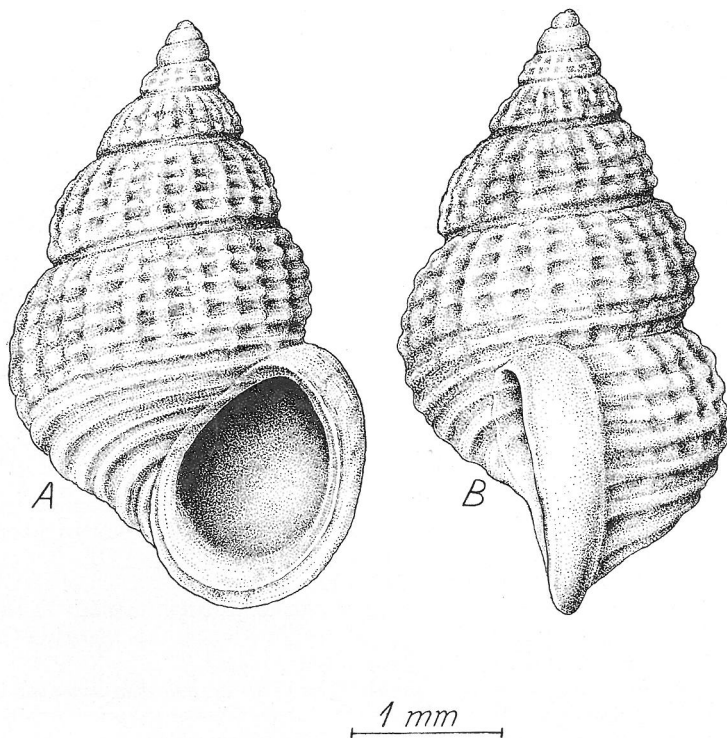


Fig. 150. *Alvania cimicoides* (Forbes). Breidifjordur, Iceland, *Ingolf* sta. 87. CMZ. The drawings do not show the ridges on the throat within the outer lip.

Aperture. Oval, angulated above, the long axis set at about 30° to that of the spire; it is bounded by a peristome with an anal sinus and projecting inner lip. The outer lip arises below the periphery of the body whorl at right angles to it. It is thickened initially by the labial rib and at its base (where it is a little out-turned) by the most basal spiral ridge. The columella is short. The inner lip is everted over the umbilical groove and obliterates the ornament in the parietal region. In the throat 9–12 short ridges lie along the outer lip; they do not occur in young shells where this lip is crenulated by the spiral ridges and in which the aperture is rather pointed at the base of the columella.

Colour. White or yellowish with pale orange protoconch. A vertical brown band lies on the abapertural side of the labial rib adapically and crosses the rib at the periphery to the outer lip. Occasionally both ends of this extend some way up the body whorl producing subsutural and peripheral bands; still less frequently traces of a subsutural brown band may be seen on the whorls of the spire. The brown on the body whorl shows through the throat of the shell.

Size. 4×2.5 mm. Body whorl = 65% of total height; aperture = 40% of total shell height.

Animal. As in *beani*.

Colour. White, dark brown on the snout.

Geographical distribution. From the Mediterranean to N. Norway, perhaps extending to Greenland. Probably absent from the Channel and N. Sea.

Habitat. Sublittoral, from the laminarian zone downwards, but mainly in deeper water, to 500 m; it is usually found on rather soft bottoms.

Food. Unknown, but presumably a detritus feeder.

Breeding and growth. Unknown; the protoconch suggests that there may be a free veliger stage.



Fig. 151. *Alvania cimicoides*. Apex of shell $\times 185$. SEM photograph. RZ.

ALVANIA CANCELLATA (da Costa, 1778)

Turbo cancellatus da Costa, 1778

Rissoa cancellata (da Costa, 1778)

Acinopsis cancellata (da Costa, 1778)

Rissoa crenulata (Michaud, 1832)

Cancellata (Lat.), latticed, referring to the surface of the shell.

Shell. Solid and opaque, slightly glossy. The spire is conical (apical angle 65°), a little cyrtocoid and distinctly stepped in profile by subsutural flat areas on the whorls, of which there are 6–7, moderately tumid, their profile masked by protuberant spiral ridges. They meet at distinct but not excavated sutures below the periphery of the upper whorl. Ribs and spiral ridges intersect to produce a deep, rather coarse lattice, the nodes marked by upstanding, slightly rounded knobs. There are 15–17 ribs on the body whorl, high, sharp and narrower than the recesses between, slightly prosocline, 15 on the penultimate, 13 on the previous ones except on the protoconch. They extend over the whole breadth of the whorls of the spire and over all the body whorl save its most basal part. There are 7 spiral ridges (like the ribs in their proportions) on the body whorl, 3–4 on the penultimate, 2 on the rest. The most adapical one on each whorl stands a little away from the suture to produce a level shoulder. The labial rib is slight in immature shells but broad, sometimes double, in grown ones, crossed by the spiral ridges. The whole shell is covered with a microstructure of regular transverse and longitudinal rows of minute tubercles each $20\text{--}25\ \mu\text{m}$ across; they are usually eroded on upstanding parts. There is no umbilicus. The protoconch has 2.25 whorls (diameter $440\ \mu\text{m}$) with an initial part $120\ \mu\text{m}$ across; it is sharply separated from the teloconch, decorated with spiral rows of tubercles which tend to fuse to lines especially in the basal parts of the whorls.

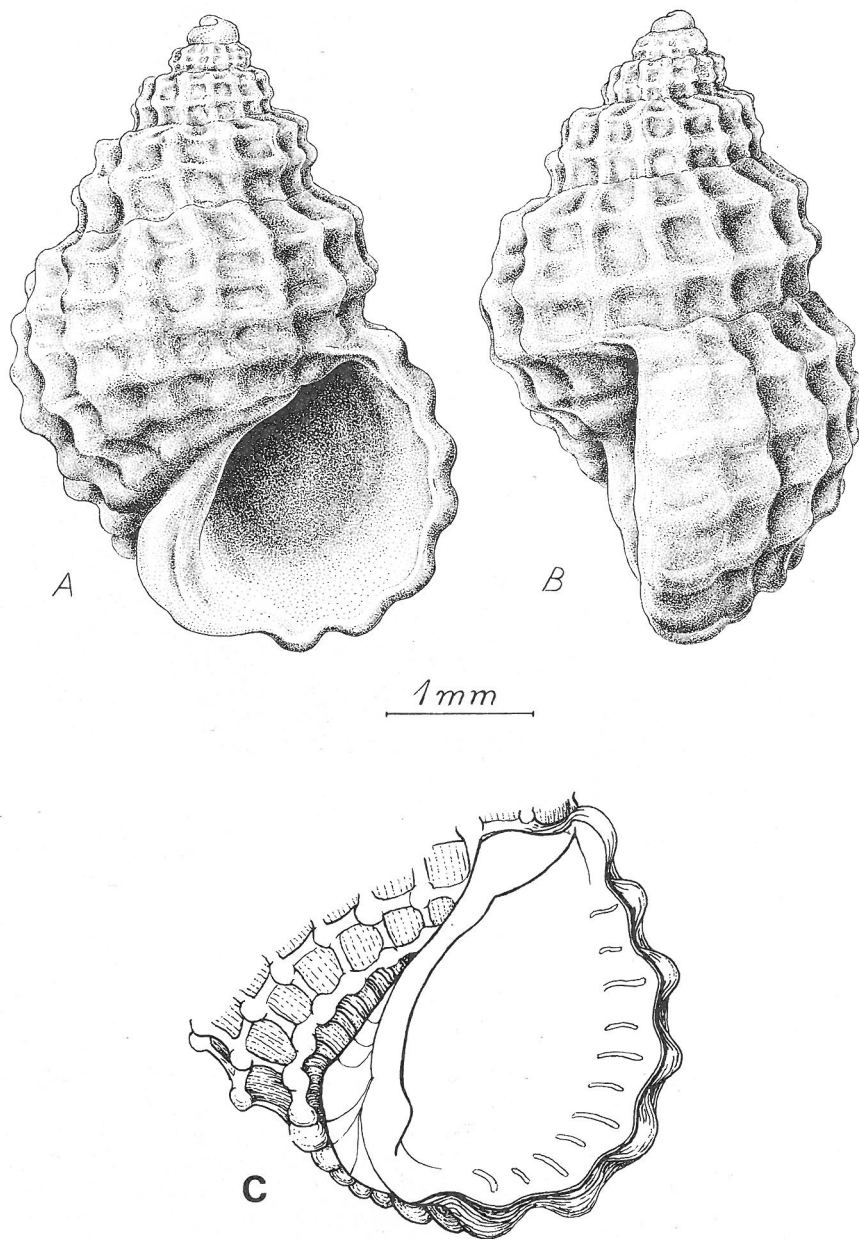


Fig. 152. *Alvania cancellata* (da Costa). A,B, young shell; C, to show columellar turbercle and ridges on throat of adult shell. Guernsey. BMNH 1911.10.26 22350-22368.

Aperture. Oval, a little angulated at the adapical end, rather large. It is set at 30° to the axis of the spire, in an axial plane, bounded by a peristome with an anal notch. The outer lip arises at spiral 4, below the periphery of the body whorl and normal to its surface. It curves smoothly (but on a slightly wavy course because of the ends of the spiral ridges) to the base and is not noticeably out-turned. The columella is not quite vertical but leans a little to the right; near its base it carries a

prominent blunt tubercle and, in some shells, there are indications of a second closer to the body whorl. The inner lip is a little everted over the most basal spiral ridge; it forms a thick glaze over the body whorl, not quite obscuring the ornament, and ends about one lattice square ahead of the outer lip. The throat of the shell carries 12—13 narrow ridge-like teeth more or less aligned along the spiral ridges; they are absent in young shells where the lip is thin and crenulated.

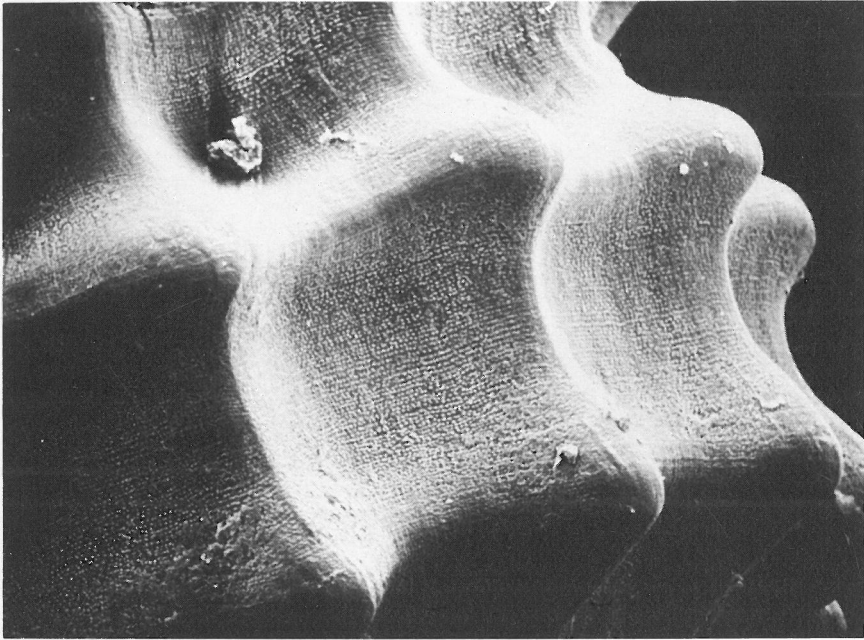
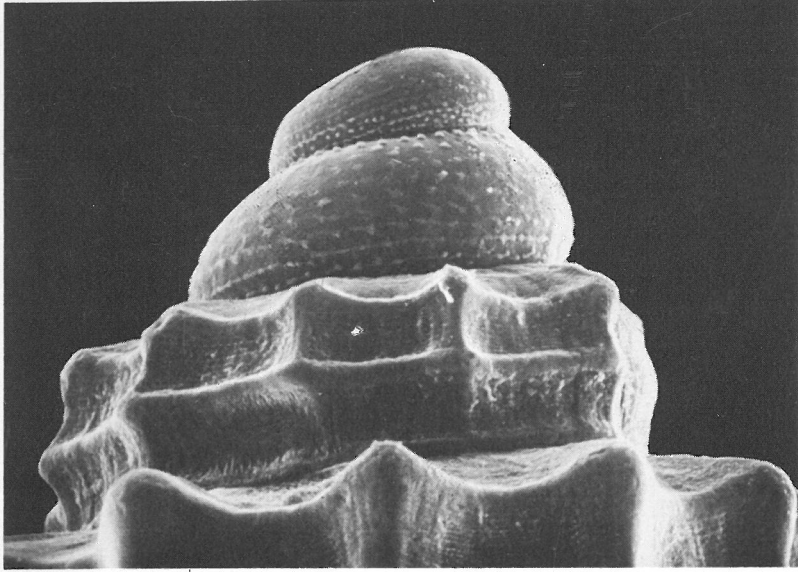


Fig. 153. *Alvania cancellata*. Above, apex of spire $\times 120$; below, detail of shell surface $\times 160$. SEM photographs. Herm. RZ.

Colour. White, cream or pale orange. Some shells show darker bands below the sutures or on the first spiral ridge, at the periphery and along the abapertural side of the labial rib. The labial rib and basal spiral are usually unpigmented and there are usually further areas of light orange in the throat, internal to the teeth, and on the parietal region.

Size. 5 × 3 mm. Body whorl = 70% of total height; aperture = 45% of total shell height.

Animal, colour. Much as in *beani*.

Geographical distribution. This is a southern species with its northern limits in the British Isles. It has been recorded as far north as the Shetlands but is rare everywhere north of the Channel.

Habitat. Under stones and in debris among rocks, very rarely at LWST, predominantly sublittoral to 90 m.

Food. Presumably a detritus feeder.

Breeding and growth. Unknown, but likely to show a free larval stage.

Notes. Through the kindness of Dr Anders Warén we have been able to examine some shells of the variety *paupercula* Jeffreys, which he regards as a species distinct from *cancellata*. There are not many points of difference between typical *cancellata* and the variety in the small number of specimens we have seen — the number of ribs, of spirals and the ratio of body whorl, aperture and breadth to shell height are identical or very close and the micro-patterning of the shell surface is the same. The columellar bulge, however, is less noticeable, the shells only about half as high, and the protoconch has only 1.5 whorls as against the 2.5 of *cancellata*. The shells were too worn to show pattern on the protoconch. On present information this could be a true species, or, as it appears not to occur N. of the Channel Islands, a southern form of *cancellata*.

ALVANIA ZETLANDICA (Montagu, 1815)

Turbo zetlandicus Montagu, 1815

Rissoa zetlandica (Montagu, 1815)

Flemellia zetlandica (Montagu, 1815)

Zetlandica, from Shetland, the locality from which the first specimens came.

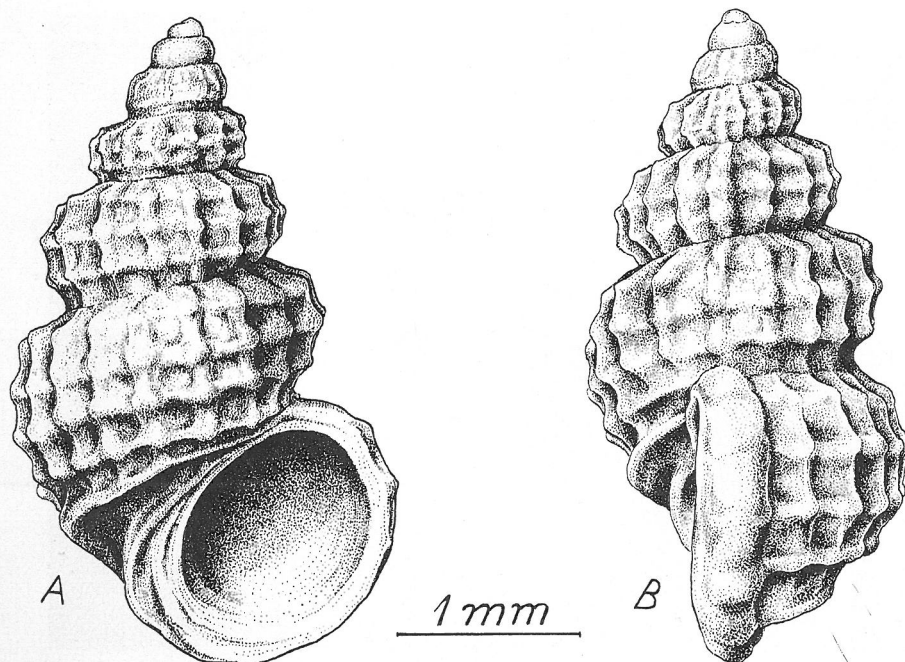


Fig. 154. *Alvania zetlandica* (Montagu). Bergen. CMZ.

Shell. Solid, slightly transparent and glossy, with a rather tall and slender spire with a blunt tip and cyrtocoid profile (apical angle $42-46^\circ$). There are 6-7 tumid whorls which meet at deep, wavy sutures placed well below the periphery of the upper whorl. The whorls bear a coarse cancellation caused by the interaction of spiral ridges and ribs with tubercles where they cross (worn away on most shells). Both are less broad than the intervening depressions which are square (oval in worn shells) though on the body whorl sometimes slightly larger between ribs than between spiral ridges. There are 13-16 ribs on the body whorl, 13-14 on the penultimate, 11-12 on the next, the uppermost with none. Each rib is a little prosocline and moderately sharp-edged. They cross the whorls of the spire but end below the periphery on the body whorl just before or at the level of the fifth spiral ridge. There is a labial rib varying in development from distinct to massive over which the spiral ridges may usually be traced. The spiral ridges are of about the same breadth as, or a little narrower than the ribs; there are 6 or 7 on the body whorl; the number decreases by one on each preceding whorl. On the body whorl the fifth spiral from the suture forms a large, smooth keel separated by a deep furrow from spiral 6 which abuts the columella and ends by disappearing into a blocked umbilicus. The furrow bears many fine ridges lying at right angles to the spirals. At high magnifications the depressions on the whorls show a regular series of minute ridges, separated by equally minute grooves, all about $20\ \mu\text{m}$ broad, which cross the hollow from spiral ridge to spiral ridge. The protoconch has 2.5 whorls, diameter *c.* $285\ \mu\text{m}$, with a distinct initial whorl, diameter *c.* $130\ \mu\text{m}$. The latter bears a pattern of raised spiral lines with rows of small tubercles between; the former bears tubercles roughly aligned in spirals.

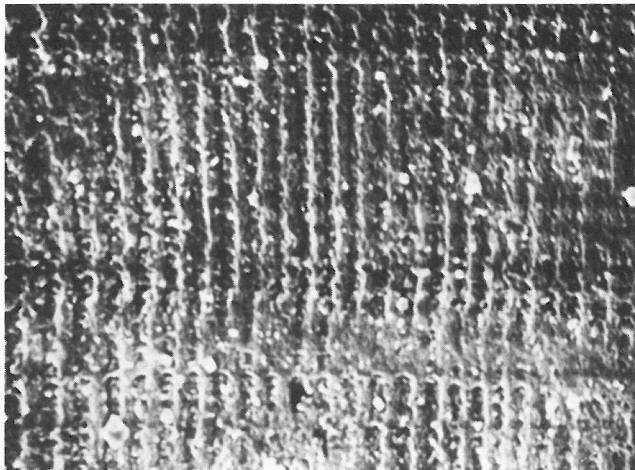


Fig. 155. *Alvania zetlandica*. Microstructure of shell surface $\times 800$. SEM photograph. RZ.

Aperture. Oval, a little pinched adapically, lying in a slightly opisthocline plane and bounded by a thick peristome; its long axis is set at *c.* 30° to that of the spire. The outer lip has no anal notch, arises between spirals 4 and 5 on the body whorl almost tangential to its subperipheral curvature and bends abruptly to follow a rather straight course to the base. Here it turns through 90° and crosses to the columella where it is a little everted. The columella is short. Between the inner lip and spiral 6 lies a very shallow groove. The throat is smooth.

Colour. Almost milk-white or cream, pale fawn, pale orange. Most shells have the 5th spiral on the body whorl pale orange and a band of this colour often lies along the abapertural side of the labial rib, though that remains pale. Other spirals may also be pigmented and may then be seen through the shell.

Shell. $4 \times 2.4\ \text{mm}$. Body whorl = 60% of total shell height; aperture = 40% of the total shell height.

Animal, colour. As in *beani*.

Geographical distribution. This species has been found from Norway south to the Mediterranean and, despite its name, appears to be a southern form.

Habitat. Never intertidal, but found from 20—350 m on sandy, gravelly or muddy bottoms. A rare animal everywhere.

Food. Unknown, but presumably a detritus feeder.

Breeding and growth. Unknown. Thiriot-Quévieux & Rodriguez Babio (1975) deduce a free veliger stage from the protoconch which seems to show initial embryonic and later larval sections.

ALVANIA JEFFREYSI (Waller, 1864)

Rissoa jeffreysi Waller, 1864

Alvinia jeffreysi (Waller, 1864)

Jeffreysi, named in honour of J. Gwyn Jeffreys (1809—85), the lawyer turned malacologist, author of *British Conchology* (1862—9).

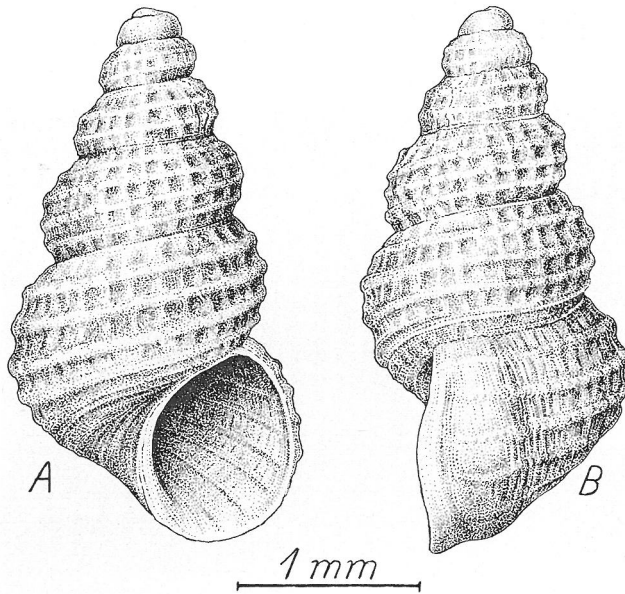


Fig. 156. *Alvania jeffreysi* (Waller). West Norway. CMZ. The drawings do not show the pattern of wavy lines on the protoconch: these are normally easily seen.

Shell. A tall, rather slender shell with a blunt tip, semitransparent and glossy. There are 5—6 whorls, tumid but a little flattened at the periphery so that their profile resembles a half hexagon. The whorls meet at deep sutures well below the periphery of the upper whorl. The apical angle is c. 45°. Spiral ridges and ribs cross to give a reticulated surface over most the spire. The spiral ridges equal about one-half of the intervening space; there are 9—10 on the body whorl, 3—4 on the penultimate, 3 on each of the others except the protoconch. The most adapical lies some distance from the suture. Below the periphery of the body whorl they are less pronounced, the most basal lying on the abapertural side of the umbilical groove, neither thickened nor buttressing the peristome as in *carinata* and *crassa*. In many shells the spirals fade away on the youngest part of the body whorl. The ribs have the same size as the spirals; there are about 45 on the body whorl, 40 on the

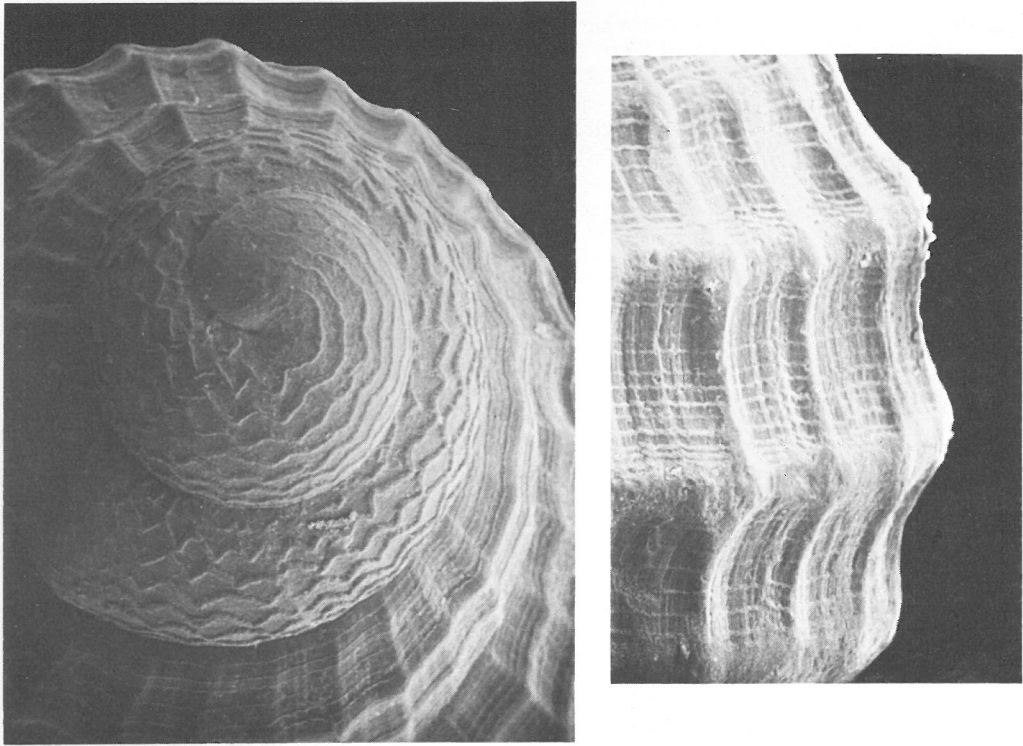


Fig. 157. *Alvania jeffreysi*. Left, shell apex $\times 145$; right, detail of shell surface $\times 230$. SEM photographs. Plymouth. RZ.

next and 28—30 on the others. They cross the whorls of the spire but are barely detectable below spiral 6 on the body whorl; they are slightly prosocline. In young shells there is no labial rib but one is developed in older ones; it varies from slight to strong and is crossed by spirals. Where ribs and spiral ridges intersect are small tubercles. In addition to the reticulation just described, high magnification reveals a microreticulation of minute spirals and growth lines in the interstices of the macroreticulation. The transverse components of this are approximately evenly spaced but the spirals are aggregated alongside the major spirals and far apart elsewhere. There is a distinct umbilical chink. The protoconch has 1.7—2 whorls; its initial part is partly smooth but 7—8 spiral lines soon appear; these are at first sinuous but become zigzag after the first half whorl. The diameter of the protoconch varies from c. $475 \mu\text{m}$ (shells from Hardangerfjord) to c. 275 (shells from Roscoff—Rodríguez Babio & Thiriot-Quévèreux, 1974). The change from larval to adult shell is abrupt.

Aperture. Rather round, a little longer than broad and angulated adapically. There is a peristome, not thickened, its plane a little prosocline and showing no (or only a very slight) anal notch. The outer lip arises at right angles to the body whorl at the level of spiral 5, well below the periphery, and follows a nearly circular course; it is a little flattened at the base and where it joins the inner lip. In young shells it is thin and crenulated by the ends of the spiral ridges. The inner lip turns out slightly over the umbilical groove and forms a film over the parietal region.

Colour. White, occasionally with a tawny tint.

Size. 3×1.5 mm. Body whorl = 55—60% of shell height, aperture = 33% of shell height.

Animal. As in *beani*. The metapodial tentacle is short, flattened and lobed.

Colour. White, eyes brown.

Geographical distribution. This species has been recorded from the Mediterranean to the Arctic in Europe and empty shells have been found in Iceland. It is found in the Skagerrak but not the N. Sea or east Channel Basin. It is a rare animal. In British waters there is only one 20th century record of

two animals dredged in 180 m on the White Strip Bank off Uist (Turk, 1972). Records from the last century refer only to deep water off Unst, Shetland. On the other hand Rodriguez Babio & Thiriot-Quiévreux (1974) found it common off Roscoff though there are only empty shells in records at Plymouth.

Habitat. Always sublittoral, from about 50–600 m in the north, deeper in the Mediterranean, on sandy bottoms.

Food. Foraminiferans.

Breeding and growth. Unknown. The protoconch suggests a free-swimming larval stage.

ALVANIA PUNCTURA (Montagu, 1803)

Turbo puncturus Montagu, 1803

Rissoa punctura (Montagu, 1803)

Alvinia punctura (Montagu, 1803)

Arsenia punctura (Montagu, 1803)

Punctura (Lat.), pricked, referring to the small hollows on the shell produced by the intersection of ribs and spiral ridges, especially when these have become so worn as not to rise above the general surface.

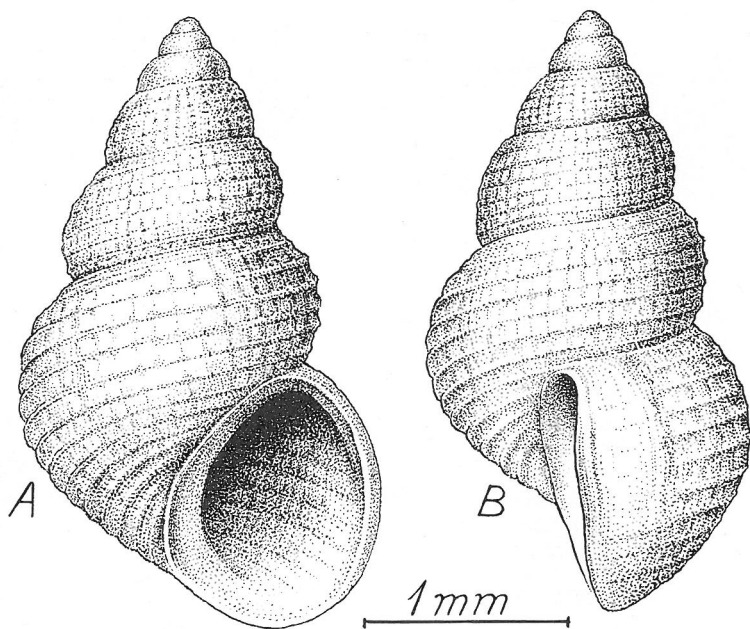


Fig. 158. *Alvania punctura* (Montagu). Hellebaek. CMZ.

Shell. Oval-conic, more or less glossy, semitransparent, a little elongated, with the profile of the spire (neglecting the tumidity of the whorls) a little cyrtocoid, especially near the apex, which is rather pointed. Apical angle $41 \pm 4^\circ$ rising to *c.* 50° in small shells. The periostracal layer is rather obvious. There are 6 tumid whorls; the sutures are deep and lie well abapical of the periphery of the upper whorl. Spiral ridges and ribs, equally developed, make a clear square reticulation on the spire, more oblong on the body whorl; on the body whorl the ribs disappear below the periphery. Both ridges and ribs may be narrower than or equal to the intervening spaces. On the spire the most abapical spiral ridge is distinct as the upper edge of the groove in which the suture lies; on the body

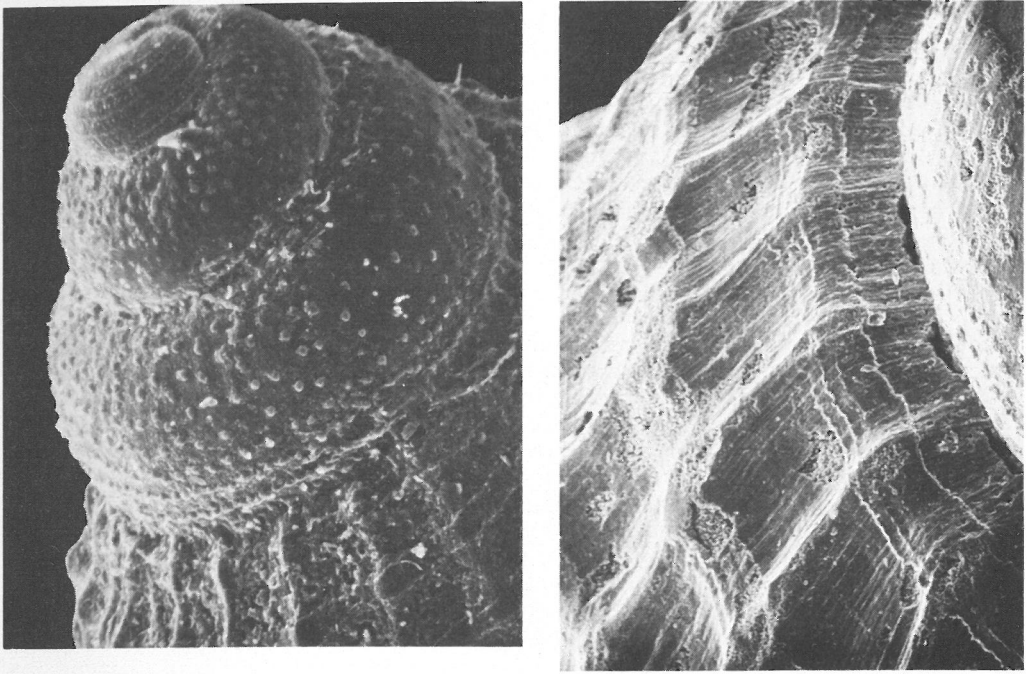


Fig. 159. *Alvania punctura*. Left, apex of shell $\times 250$; right, detail of shell surface $\times 590$. SEM photographs. Plymouth. RZ.

whorl the ridges become flatter and weaker below the periphery. There are 12—15 on the body whorl, 5—8 on the penultimate, 4—5 on the next, the next 3 apparently smooth. The ribs run orthoconchally across the whorls but curve prosoclinally to the upper suture. They cross the whorls of the spire but vanish on the body whorl about the periphery, level with the spirals 6—8. Their number is rather variable — 33—46 on the body whorl, 29—34 on the penultimate, 28—33 on the next. There is a labial rib, not massive, crossed by spiral ridges, set at or a little back from the outer lip. Where ribs and spiral ridges cross there are small, blunt spines, often eroded. High magnification shows a micropattern in the hollows of the reticulation — a few irregular spiral lines alongside the main ridges with numerous fine growth lines. The protoconch has 2.75 — 3 whorls divisible into an initial whorl (diameter 85 — 95 μm), showing 6—7 spiral lines with spots in the intervening spaces, and a second part, the larval shell (total diameter 200—250 μm) with small tubercles set in about 10 spiral rows; at the periphery they may fuse to form a ridge. The transitions from embryonic to larval shell and to teloconch are abrupt.

Aperture. Oval, rather narrow, angulated above and bounded by a peristome. The outer lip arises from the body whorl at the level of spiral 7 or 8; it continues the outline of the spire, is a little flattened at its widest point and distinctly out-turned basally. The columella is straight running apically a little right of the axis. The inner lip turns out over a groove leading to a narrow, elongated umbilicus. The throat is glossy and, in young shells particularly, the reticulation of the outer surface shows through.

Colour. White to cream to brown, paler where the periostracum is worn. There are pale orange-brown rectangular marks arranged in 3 series: (1) subsutural, (2) subperipheral, (3) basal. These occasionally join to form continuous bands, especially by the aperture. The subsutural marks often curve towards the aperture at their lowest ends. The umbilical and parietal regions are stained with the same colour. There may be a transverse brown mark along the abapertural side of the labial rib.

Size. 3×1.8 mm. Body whorl = 58—65% of total shell height; aperture = 35—40% of total shell height.

Animal. Like that of other *Alvania* spp. There are right and left pallial tentacles, The opening of the posterior pedal gland is conspicuous; there is a single metapodial tentacle.

Colour. Cream, with short streaks of dark colour and some yellow speckles. There is a red patch behind each eye and similar colour on the opercular lobes.

Geographical distribution. From the Mediterranean to N. Norway. It extends to the Swedish W. coast but is absent from the Sound, the Baltic, the eastern shores of the N. Sea and the eastern basin of the Channel.

Habitat. Sublittoral to depths of c. 100 m. They are not uncommon on sandy bottoms. Manly (1975) found that they preferred sediments of particle size 150–550 μm with an organic content of 0.35–0.42%; older animals were occasionally encountered on both finer and coarser substrata.

Food. A detritus feeder. Faecal pellets ovoid, 200 \times 100 μm .

Breeding and growth. The sexes are separate, the male recognizable by the penis. Breeding (at Plymouth) occurs in summer. Eggs measure c. 60 μm in diameter are white-cream; and are laid 12–14 at a time, in hemispherical capsules, 320–480 μm across. The larvae are common in Plymouth plankton throughout summer and autumn (Lebour, 1934), were found by Thorson (1946) in late summer and autumn in the Sound (older larvae drifted thither from Bohuslän) and occur at Naples (Richter & Thorson, 1975) in spring and summer, maximally May–June. They may be identified by the horn-coloured shell with dark lips and columella, spiral rows of tubercles and prominent, blunt, peripheral beak. The velum is bilobed with one lobe often larger; though unpigmented during most of the larval life it may develop a thin red marginal line by the 2.5-whorl stage. The foot has a black stalk, the colour extending to the propodium and opercular lobes, the latter also with yellow spots. The opening of the posterior pedal gland on the sole of the foot is outlined in red. At the 3-whorl stage the left pallial tentacle is developed. Lebour stated that metamorphosis occurred when the shell had a height of 640 μm ; Manly found individuals with shells of 500 μm which had already settled. These were found only in July though others, which might have recently settled, occurred up till October. There are no figures available on the growth of this species.

ALVANIA LACTEA (Michaud, 1830)

Rissoa lactea Michaud, 1830

Turbona lactea (Michaud, 1830)

Massotia lactea (Michaud, 1830)

Lactea (Lat.), milk-white, referring to the colour of the (dead) shell.

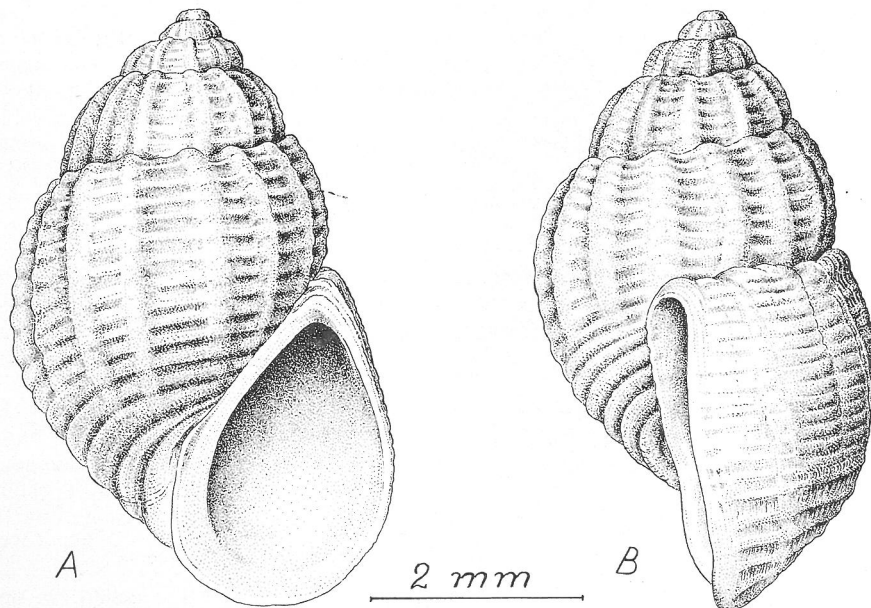


Fig. 160. *Alvania lactea* (Michaud). Jersey. BMNH 1911.10.26 22794-22801.

Shell. Oval, pointed, glossy, glassy and semitransparent; distinct from other *Alvania* spp. by the large body whorl and consequent short spire (apical angle $51 \pm 4^\circ$). There are 5–6 whorls, moderately convex in profile, slightly shouldered, which meet at sutures placed about the periphery of the older whorl. The sutures are deep and lie at the bottom of a V-shaped channel. Ribs and spiral ridges meet to produce an oblong cancellation of the surface, the recesses elongated along the whorls; this is absent on the base of the shell. The ribs are a little prosocline, rather broad (= half or less the space between ribs); they cross the whorls of the spire but end at the periphery on the body whorl. There is usually a rather weak labial rib crossed by spiral ridges, but it may be absent. The number of ribs is variable: 16–22, occasionally to 30, on the body whorl, 13–18 on the penultimate, 12–17 on the antepenultimate, 8–15 on the next, the rest being protoconch. The spiral ridges are narrower than the ribs (= space between spirals); the subsutural 1–2 and those on the base of the shell more prominent than the rest. Their number is more constant than that of the ribs: 15–17 on the body whorl, 7–9 on the penultimate, 5–6 and 2–3 on the next two. There may be tuberculated nodes where ribs cross the most adapical spirals, usually eroded elsewhere. The recesses of the cancellation exhibit a microstructure of spiral ridges and grooves with approximately vertical rows of tubercles set across them. There is no umbilicus. The protoconch has 1.5 whorls, about 300 μm in diameter, ornamented with some spiral lines and sharply delimited from the teloconch.

Aperture. A rather narrow, elongated oval, angulated above and somewhat pointed below, lying in a slightly prosocline plane, bounded by a peristome with distinct anal sinus. The outer lip arises at or just below the periphery of the body whorl, level with spirals 8–10, at right angles to the surface. Its course stands briefly away from the body whorl and then turns to run nearly straight and slightly abaxially before curving to the base where it is appreciably out-turned, pointed and often slightly crenulated by the spiral ridges. The columella is long and gently curved. The inner lip turns out over the body whorl. Throat very glossy, without teeth, showing the external spiral ridges by transparency.

Colour. Cream or milk-white, the apex often with a yellow-orange tint.

Size. 6×4 mm. Body whorl = 75% of total shell height; aperture = 50% of total height.

Animal. As in other *Alvania* spp.

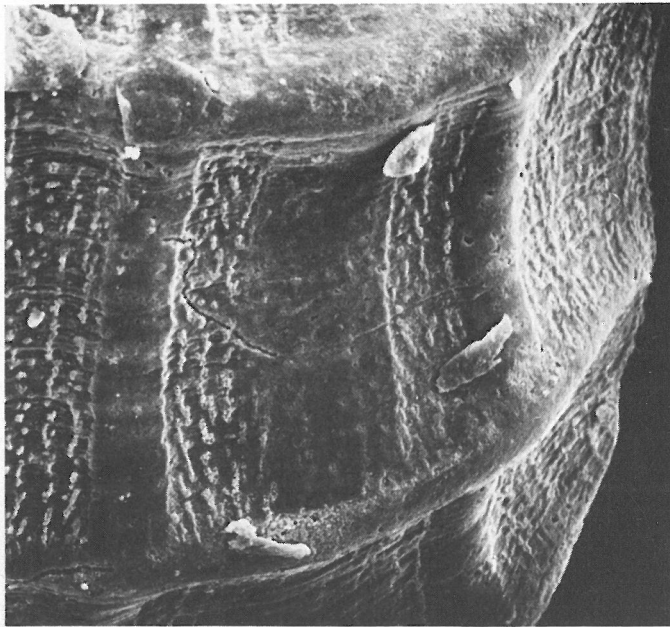


Fig. 161. *Alvania lactea*. Microstructure of shell surface $\times 390$. BMNH 1911.10.26 22794-22801.

Colour. White.

Geographical distribution. A southern species which reaches its present northern limits in the Channel Islands, though dead shells may be found as far north as the west coast of Sweden. To the south it occurs to Morocco, throughout the Mediterranean and Black Seas.

Habitat. Under stones, amongst algae, at extreme low water and sublittorally.

Food. A detritus feeder.

Breeding and growth. Unknown.

ALVANIA ABYSSICOLA (Forbes, 1850)

Rissoa abyssicola Forbes, 1850

Turbona (Actonia) abyssicola (Forbes, 1850)

Abyssicola (Lat.), living in deep water.

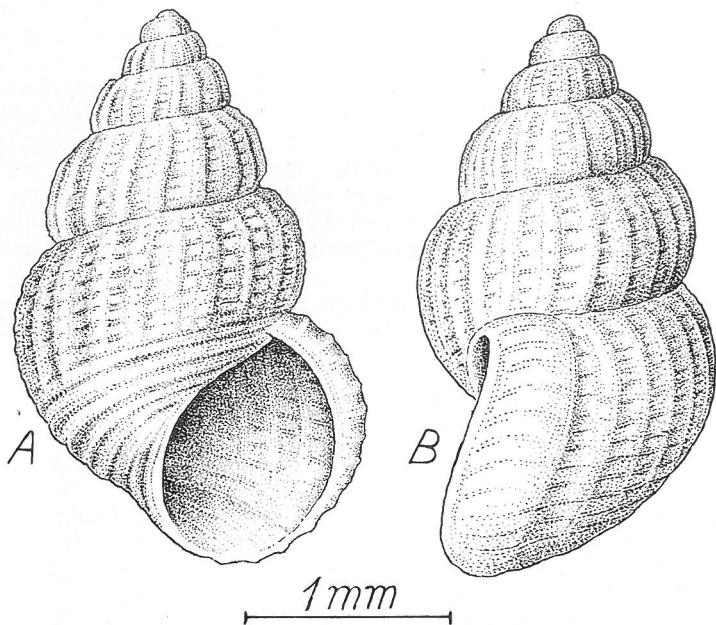


Fig. 162. *Alvania abyssicola* (Forbes). Thor sta. 302, 16 km S. of Trindelen, N.E. of Laeso, N. Kattegat. CMZ.

Shell. A glossy, solid, oval-conic shell with a blunt tip, expanded basally. The spire is rather slender (apical angle $35-40^\circ$), gently cyrtocooid; there are 5-6 whorls meeting at sutures placed well below the periphery of the upper whorl. The whorls are tumid, but show some peripheral and adapical flattening so that the sutures lie at the base of V-shaped notches as in *beani*. The shell bears ribs and spiral ridges. There are 10-15 spirals on the body whorl, 5-7 on the penultimate, 4-5 on the next, 4 on the next, the topmost being smooth. The ridges are narrower than the intervening spaces. The most adapical lies some way from the suture; on the base of the shell they enlarge and lie further apart, the most basal forming the abapertural edge of an umbilical groove and terminating on the most basal part of the aperture. There are 19-23 ribs on the body whorl, 17-20 on the penultimate, 15 and 6 respectively on the next two. In section they are V-shaped with a fairly sharp summit, the base as broad as the intervening space. They are opisthoclinal and slightly curved cross

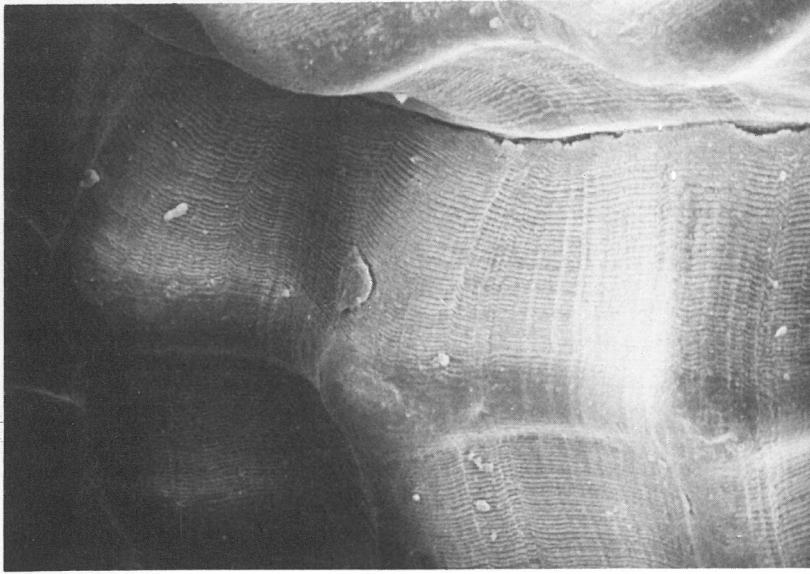


Fig. 163. *Alvania abyssicola*. Microstructure of shell surface $\times 355$. SEM photograph. West Norway. RZ.

the whorls of the spire but end on the body whorl about halfway between periphery and base. Spiral ridges and ribs interact to give a square to oblong reticulation, the spirals crossing the ribs to give nodosities; these may occur on the most basal spirals even although the ribs have disappeared. In the interstices of the reticulation numerous minute spiral bands occur, crossed by some fine growth lines. The labial rib is well developed with a rather sharp crest; it usually lies a little back from the outer lip and is a little affected by the spiral ridges. The protoconch has 2 whorls (diameter c. 350 μm); it shows a reticulate pattern on the initial whorl and is either smooth or irregularly tuberculated on the second.

Aperture. Rather large, lying in an opisthoclinal plane and surrounded by a peristome; nearly D-shaped. There is an appreciable anal sinus and the basal part of the outer lip is extended. The outer lip arises from below the periphery of the body whorl level with spiral ridge 9 and follows a more or less semicircular course to the base of the columella, which is short. The inner lip is a little out-turned over the umbilical groove leading to a very narrow V-shaped chink. There are no ridges in the throat of the shell. In juvenile shells the aperture is an elongated, rather narrow oval, drawn out basally into a small spout; the outer lip is crenulated by the ends of the spiral ridges and there is no labial rib.

Colour. White-cream, sometimes with reddish brown on the base and/or behind the labial rib, under a yellow or brown peristracum.

Size. 2.5–3 \times 1.5–1.75 mm. Body whorl = 60–66% of total shell height; aperture = 40% of total height.

Animal. As in other species. The snout is rather deeply bifid. The metapodial tentacle is rather short and single.

Colour. White with yellow and white flecks.

Geographical distribution. This species occurs from N. Norway to the Mediterranean. It extends into the Skagerrak, Kattegat and northern parts of the Sound but is not found in the N. Sea. In British waters it is more frequent off NW coasts than in the S.

Habitat. Muddy sublittoral areas at depths of 15–100 m. It is locally common.

Food. A detritus feeder.

Breeding and growth. The sole description of a possible larval stage was given by Thorson (1946); his identification of the larva rested on the exclusion of other possibilities rather than on positive evidence. The larval shell which he described as that of *abyssicola* resembles closely that of *A. crassa*

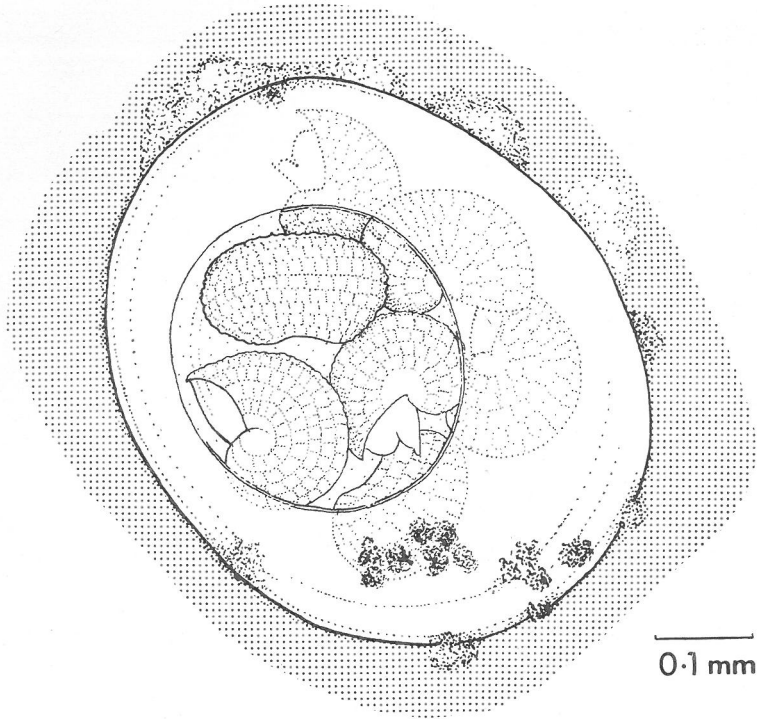


Fig. 164. *Alvania abyssicola*. Spawn. Unpublished drawing by G. Thorson.

as depicted by Fretter & Pilkington (1970). That species, however, does not occur in the Sound where Thorson collected his larvae, whereas *abyssicola* does. This similarity does not necessarily invalidate Thorson's identification since Thiriot-Quiévreux & Rodriguez Babio (1975) showed that there were only trivial differences between the protoconch of *A. punctura* and that of *A. zetlandica*. In Thorson's *abyssicola* there are 2 whorls, the first *c.* 150 μm across, with a reticulate pattern, the second (total diameter 320–330 μm) sometimes smooth, sometimes with small tubercles, but always with a peripheral keel projecting as an apertural beak. The larvae were collected in late summer and autumn. The shells of adult *abyssicola* which Thorson examined were, like all those that we have seen, worn and showed no more than a few spiral lines. His research notes show drawings of egg capsules of this species attached to a piece of shell. They are hemispherical, attached by the base about 500–600 μm in diameter and 400 μm high. They appear to have a thinner summit area about 300 μm across. Each contains 6–13 eggs. The larva is colourless and has a bilobed velum without pigment which is not well developed.

ALVANIA SUBSOLUTA (Aradas, 1847)

Rissoa subsoluta Aradas, 1847

Turbona subsoluta (Aradas, 1847)

Subsoluta (Lat.), somewhat separated, referring to the coiling of the whorls of the shell.

Shell. Oval-conical, glossy, slightly transparent, with a rather long spire (apical angle *c.* 40°). There are 4.5–5 whorls which are very tumid and meet at sutures placed well below the periphery of the upper whorl and made wavy by the upper end of the ribs. The whorls show no flattening in profile and the sutures are not channelled. There are also spiral ridges. The ribs number 19–24 on

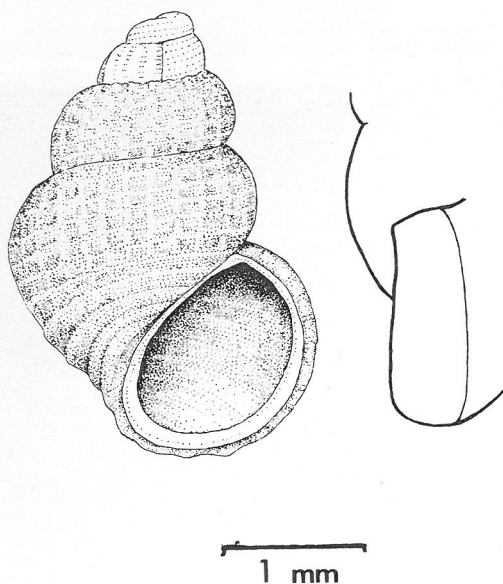


Fig. 165. *Alvania subsoluta* (Aradas). Trondheim Fjord. BMNH 1911.10.26 21967-21974. Inset, side view of apertural region.

the body whorl, 17—19, 14—15 and 6 on the next three. They are rather V-shaped in section with a sharp summit, their bases rather less than the intervening spaces. They cross the whorls of the spire but end below the periphery on the body whorl. They are slightly prosocline and their course is slightly crescentic, the concavity facing the aperture. There is a well-developed labial rib, thick and broad, with a well-defined crest, sometimes a little back from the outer lip, slightly marked by spiral ridges. These are narrower than the intervening spaces and the most adapical lies a little below the suture. They are more pronounced on the base of the shell where the most abapical arises from the base of the aperture and forms the margin of the umbilical canal. There are 11—13 on the body whorl, 5—7, 3—5 on preceding ones. Ribs and spirals intersect to give a square reticulation, the spirals over-running the ribs to cause nodosities often visible on the most basal spirals where there are no ribs. The hollows of the reticulation bear a micropattern of small spiral lines of varying size. The protoconch has $1\frac{1}{2}$ — $1\frac{3}{4}$ whorls (total diameter 450—550 μm) bearing a series (5—7) of delicate spiral lines with a few interspersed papillae.

Aperture. Oval, pointed adapically, with a peristome lying in an approximately axial plane and with a distinct anal sinus. The outer lip arises at right angles below the periphery of the body whorl; its initial part is rather straight, as is also the base. The columella is short, the inner lip a little everted over an umbilical groove leading to a small oblique umbilicus. In young shells the labial rib is absent and the base of the aperture is a little everted.

Colour. White or cream.

Size. 3.5 \times 2 mm. Body whorl = 66% of total shell height; aperture = 40% of total height.

Animal, colour. Not seen but presumably as in other *Alvania* spp.

Geographical distribution. This species has been recorded from the Mediterranean to N. Norway; though extending into the Skagerrak to Bohuslan it does not apparently enter the N. Sea. Records from British waters are extremely rare and all relate to the neighbourhood of the Scilly Islands.

Habitat. A deep-water species, reaching to nearly 200 mm on muddy bottoms.

Food. Unknown, presumably detritivorous.

Breeding and growth. Unknown.

Notes. Since this has been confused with *abyssicola*, the distribution of both species may have been muddled as a consequence.

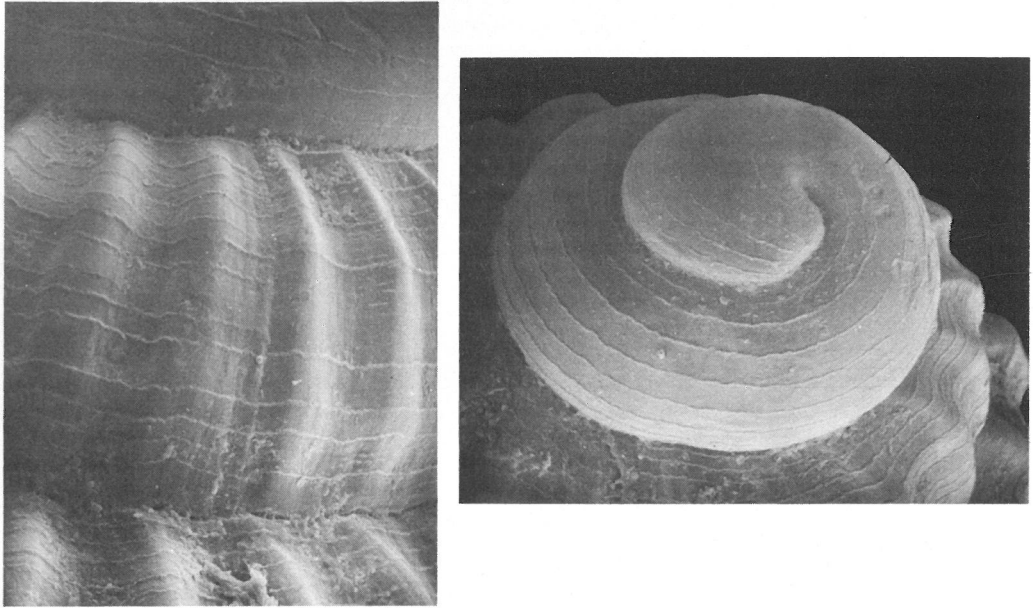


Fig. 166. *Alvania subsoluta*. Left, shell apex $\times 160$; right, detail of shell surface $\times 210$. SEM photographs. Trondheim Fjord. BMNH 1911.10.26 21967-21974.

ALVANIA CARINATA (da Costa, 1778)
Turbo carinatus da Costa, 1778
Alvinia carinata (da Costa, 1778)
Galeodina carinata (da Costa, 1778)
Rissoa striatula (Montagu, 1803)

Carinata (Lat.), keeled, referring to the prominent spiral ridges on the shell.

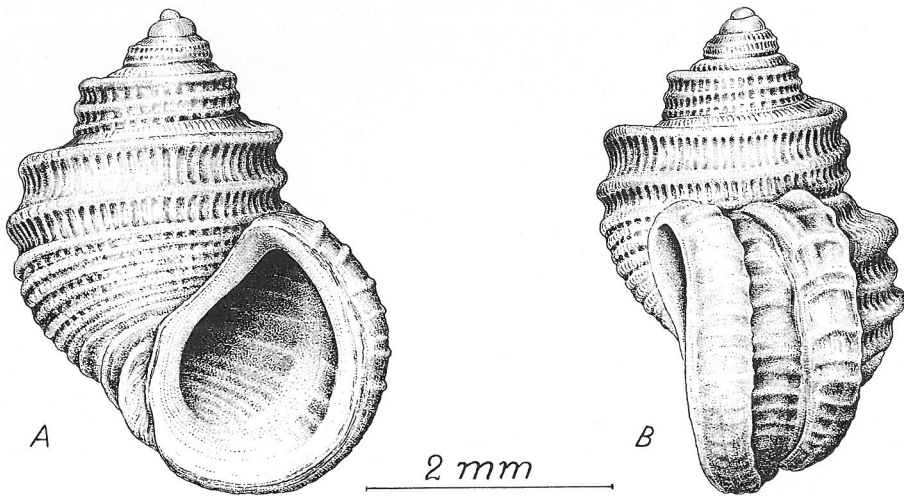


Fig. 167. *Alvania carinata* (da Costa). Guernsey. BMNH 1903.3.2730-33.

Shell. A rather swollen oval-conic shell with a stepped spire and pointed through usually blunted apex (apical angle 55–60°), glossy when alive and semitransparent, though dead shells are opaque. There are 5–6 whorls, tumid (though their profile is mostly determined by the spiral ridges they bear), and meeting at sutures lying just abapical of the periphery of the upper whorl. Sutures distinct and incised. The body whorl is large. The ornament consists of interacting ribs and spiral ridges and grooves, the latter much the more prominent. The most adapical 3 ridges on each whorl form sharp, elevated keels which lie between suture and periphery on the body whorl but are the only ridges visible on the whorls of the spire. They are well separated from one another and there is a flat area between the uppermost and the suture. On the base of the body whorl lie (1) 5–6 fairly close-set spirals lower than those above the periphery and (2) a basal group of 3 well-separated higher ones. All spiral ridges are slightly nodose where crossed by ribs. The ribs are low and numerous: 50–60 on the body whorl, 35–45 on the penultimate, 25–35 on the next. They are about equal in breadth to the intervening spaces which are marked by minute growth lines. The ribs are slightly prosocline between suture and uppermost spiral, thereafter orthocline. There is a well-developed labial rib, sometimes double, crossed by the spirals and more nodose at the intersections than other points of the shell. Protoconch of 1.5 whorls, diameter 400–500 μm , smooth and passing insensibly into the teloconch.

Aperture. This is large, lies in the axial plane of the shell and has a peristome without anal sinus; it is oval, slightly pinched above and more rounded at the base. The outer lip arises at right angles to the body whorl at the periphery, just below spiral ridge 3; it is rather thick and forms an approximate semicircle gently scalloped by the ends of the spirals. In young shells it is thin and the ends of the spirals (especially the first) appear as foldings of the edge; a trace of this may persist in older shells. The columella is short and straight, making a slight angle with the parietal part of the inner lip which turns out from the columella to meet the most basal spiral. There is neither umbilical groove nor umbilicus. The ribs and spirals may be seen through the throat of the shell.

Colour. White.

Size. 4×3 mm. Body whorl = 70–75% of total shell height; aperture = 50% of shell height.

Animal. As in all *Alvania* spp. The snout is rather long and narrow. The foot is bluntly pointed posteriorly and carries a single, rather short metapodial tentacle.

Colour. Cream. There is a red mark on the snout — the buccal mass seen by transparency.

Geographical distribution. This is a southern species living between the Mediterranean and the British Isles where it is found only on the south-west and west coasts. It is rare on the Scottish W. coast, is probably absent from the Orkneys and Shetland and certainly so far not found in Scandinavia, the N. Sea and the eastern part of the Channel. It is scarce everywhere.

Habitat. At lower water and sublittoral to 20–25 m, usually under stones which are lying on sand.

Food. Said by Pelseener (1935) to eat red algae, but probably also a detritus feeder. Faeces ovoid pellets $200 \times 100 \mu\text{m}$; sometimes green, according to Jeffreys.

Breeding and growth. Unknown. Thiriot-Quévieux & Rodriquez Babio (1975) suggest that development is direct.

Notes on *Alvania* species. We are in no position, after study of such a small fraction of the species included by some taxonomists in the single comprehensive genus *Alvania* and by others in several genera in more than one subfamily, to make very pertinent remarks on the classification of this section of Rissoidae. For this reason we have been conservative in our nomenclature. There are, however, a few points to be raised, more particularly since the micropattern on the surface of the shell seems to hold taxonomic promise.

Whatever the basis on which one attempts to group this selection of species — protoconch, shell pattern, aperture — the groups which emerge are different according to the criterion chosen, a situation which suggests mosaic evolution and perhaps the repeated appearance of the same character. Some species, nevertheless, stand apart: *crassa*, *carinata*, *lactea*, *zetlandica*, in respect of the gross and minute pattern on their shell, are both unlike one another and all other species. This supports their removal to the separate subgenera *Manzonia*, *Galeodina*, *Massotia* and *Flemellia* respectively, and suggests that these might properly be raised to generic status.

Identification of *Alvania* species dealt with here. Animals belonging to the genus *Alvania sensu lato* are usually distinguished from other rissoids by the strongly cancellated surface of the shell, though the spiral and transverse elements may not be equally developed. They also generally possess a thick peristome and labial rib. The body of the animal is like that of most rissoids and is so similar in all species as to give little help in identification. It tends to lack pigmentation, has a pallial tentacle on both right and left sides of the mantle skirt and a metapodial tentacle which is fundamentally triple except in the species *abyssicola*, *subsoluta* and *punctura* (subgenus *Actonia*) where the lateral points are reduced and it appears single.

The species fall into 3 groups on shell pattern —

- (1) *crassa*: ribs much more conspicuous than spiral ridges. Other features: small aperture with thick varix + peristome, micropattern of fine grouped spirals, protoconch with reticulate pattern on first whorl.
- (2) *carinata*: spiral ridges much more obvious than ribs. Other features: larger aperture and body whorl; protoconch smooth.
- (3) *abyssicola*, *subsoluta*, *beani* agg., *cancellata*, *cimicoides*, *jeffreysi*, *lactea*, *punctura*, *zetlandica*: ribs and spirals about equally developed.

Of group (3) three species may be separated by the presence of ridges in the throat of the shell within the outer lip — *beani* agg. *cancellata* and *cimicoides*. The other species have no such ridges. Of the three with teeth *cancellata* is distinct; it has a coarsely reticulated surface with characteristic tubercular microstructure, a large rounded aperture with a tooth on the columella and the peristome markedly out-turned where outer and inner lips meet. *A. beani* agg. and *cimicoides* are alike but may generally be separated by the large number of ribs on the body whorl of the former (35—45) and the much smaller number (16—20) in the latter. The micropatterning of the surface and the protoconchs also differ: in *beani* the micropattern is predominantly growth lines with a few minor spirals and its protoconch is smooth, the same colour as the rest of the shell; in *cimicoides* the microstructure is of tubercles and the protoconch has a complex reticulate pattern and is much yellower than the rest of the shell.

Of the remaining species *lactea* may be distinguished by the large body whorl (3/4 of the total height) combined with a tall and narrow aperture and oblong decussation. Its spire is short and its profile oval, whereas in the other 4 species the shell is narrow and the spire tall and more or less straight-sided. *A. zetlandica* has coarse ribs and spiral ridges, often prickly at their intersections, and a thick labial rib and peristome; its microstructure of vertical ridges and grooves is also characteristic. *A. jeffreysi* is easily recognized by the zigzag lines on the protoconch (which seem to defy wear and persist on most adult shells) and has a slightly coarser reticulation on the surface than either *punctura*, *abyssicola* or *subsoluta* in the last two of which the ribs are taller, broader and fewer than in *punctura*. The species *abyssicola* and *subsoluta* may be separated by the flatter whorls, more channelled suture, opisthocline ribs and aperture of the former contrasted with the more rounded whorls and orthocline ribs of the latter.

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RISSOA PARVA (da Costa, 1779)

Turbo parvus da Costa, 1779

Turboella parva (da Costa, 1779)

Turboella interrupta (Adams, 1798)

Rissoa, named for G. A. Risso (1777—1845) who lived in Nice. Initially a pharmacist he became professor of Medical Chemistry in the School of Medicine and Pharmacy there. His zoological work is concerned mainly with the systematics of Mediterranean fish. *Parva* (Lat.), small; named in relation to other species of the genus *Turbo*.

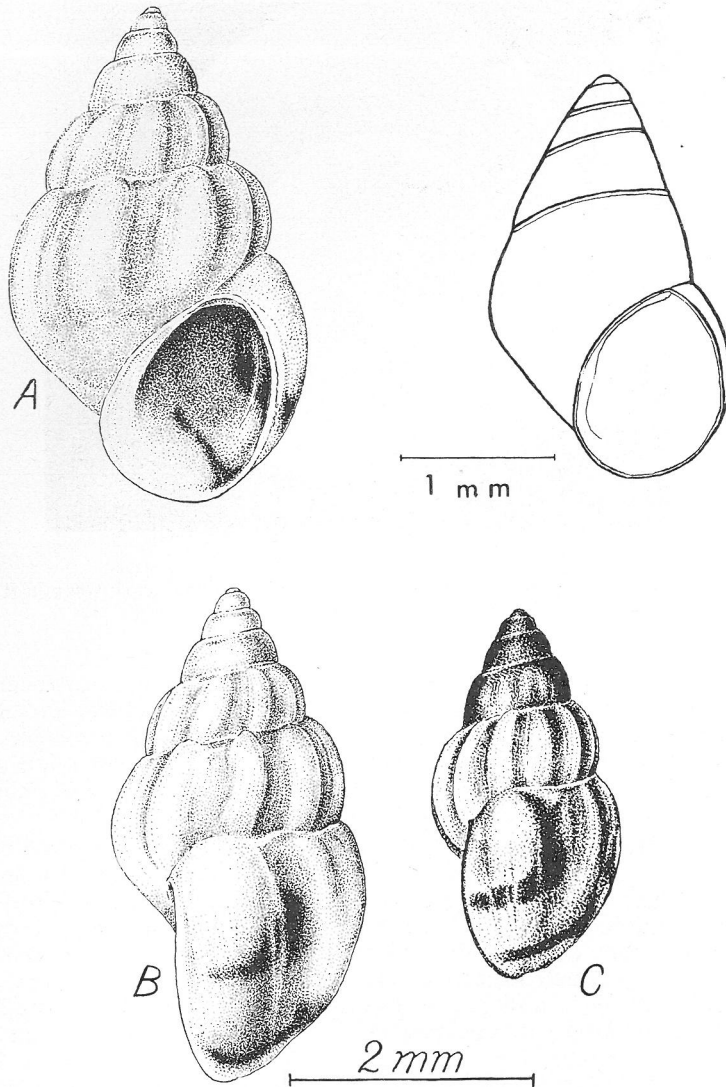


Fig. 168. *Rissoa parva* (da Costa). Guernsey. Top right, outline of var. *interrupta*. Solva, Dyfed. RZ.

Shell. Ovoid conical, slightly transparent and moderately glossy. It has a rather tall, straight-sided spire of up to 8 slightly tumid whorls which meet at sutures placed some way below the periphery of each whorl. The apex is rather pointed, the apical angle between 34 and 50°, often 34—44°; occasional narrow shells (angle down to 25°) may be found. In young shells (4—5 whorls) the body whorl has often an angulated periphery and traces of this may persist in some large ones. The shell may look smooth but there are always fine spiral and growth lines. Most shells show 1—2 more obvious spiral ridges at the periphery of the body whorl which disappear before reaching the outer lip. Growth lines may also be more conspicuous and some shells show prominent ribs. These are always absent from the topmost 3—4 whorls and are otherwise erratic in occurrence — on only one, several or all remaining whorls. They are orthocline near the suture but become slightly opisthoclinal abapically, are as broad as the intervening spaces, steep-sided with rather narrow tops; 8—12 occur

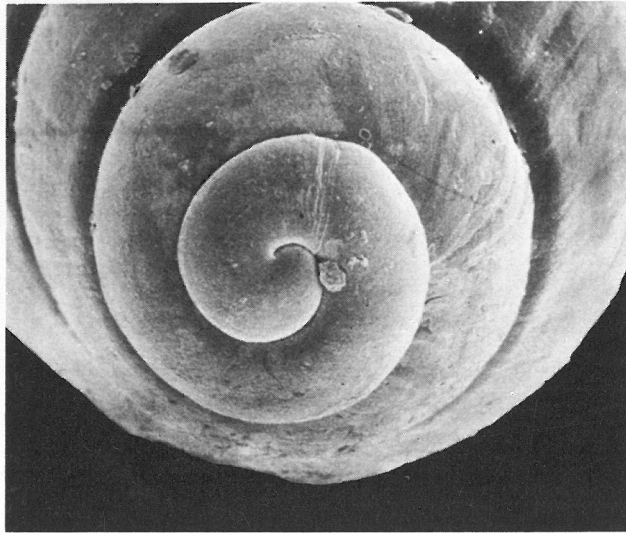


Fig. 169. *Rissoa parva*. Apex of shell $\times 135$. SEM photograph. Plymouth. RZ.

on the body whorl. They cross the upper whorls but (except for 2—3 near labial rib) end on the body whorl by joining the peripheral spiral ridge. Between ribs the spiral elements are sometimes much more marked than on ribless shells. In nearly all mature shells a labial rib occurs, whether there are other ribs or not. It may be slight or well-marked, is rather broad and lies a little away from the peristome. There is no umbilicus. The protoconch has 2.75—4 whorls: the initial embryonic one has a diameter of 100—110 μm and bears a few delicate spiral lines with small tubercles between; the larval whorls show a spiral ridge near the suture. The whole has a diameter of 250—480 μm .

Aperture. D-shaped, angulated apically where the peristome shows a small anal sinus close to the surface of the body whorl. The peristome lies in the axial plane, its edge a little thickened in older shells. The outer lip arises normal to the surface of the body whorl, just abapical of the peripheral ridge, and follows a gently curved course which continues the outline of the spire as far as the periphery; it then curves rapidly to the base and columella. In mature shells it is always a little reflected outwards and there is a slight tongue at the columellar base. The columella is short and oblique and the lip by it turns out to obscure a shallow umbilical groove. The parietal lip is thin, slightly sinuous.

Colour. Cream to horn-colour or chocolate brown, the apical region with a superficial violet tinge. The shell may be all one colour (and the topmost whorls almost invariably are) but many show orange-brown streaks on younger whorls. These are usually curved — opisthocline at the suture, becoming orthocline at the periphery so that the concavities face up the spiral. Towards the periphery of the body whorl the streaks usually disappear but sometimes they extend to a spiral band lying just abapical of the spiral ridge. In most mature shells the line nearest the outer lip is darker than the others and drawn out to form a comma-shaped mark, the tail of which may reach the edge of the outer lip or be extinguished as it crosses the labial rib. In ribbed shells the lines of colour lie between the ribs. The peristome is brown and the labial rib milky white. Within the throat of the shell the brown lines are visible by transparency; there is also brown colour on the columella.

Size. 5 \times 3 mm. Body whorl = 63—70% of shell height; aperture = 35—47% of shell height.

Animal. The head has a moderately long, rather narrow snout, deeply bifid anteriorly, the mouth a longitudinal slit within the cleft. The tentacles are long, slender, setose at the tip and have an eye on a slight swelling at the base. The mantle skirt is plain-edged with a tentacle on the right. In males a long penis is attached to the body behind the right cephalic tentacle, stretching to the inner end of the mantle cavity. It is rather swollen and tapers to a small tip where the male opening lies.

The foot is narrow, the anterior edge nearly straight, double with rectangular corners. It is constricted in the middle where there is a transverse groove along which it may fold. The posterior part of the sole tapers to a point and bears, in the mid-line, the pore of the posterior pedal gland which lies in a longitudinal groove reaching to the posterior tip. The opercular lobes are large. There is a well-developed cylindrical metapodial tentacle. The operculum is thin, horny, spirally wound with the nucleus towards the lower end of the columellar edge.

Colour. Colourless to pale yellow with prominent purple-black blotches where head and body merge, and some dark colour on the mid-line of the snout. The tentacles are pale perhaps with central white line. Behind the eye is a yellow patch. The sole of the foot is white and the opercular lobes are purple-black, showing through the operculum as two dark patches, above and below, in a retracted animal. The stomach with a green crystalline style is visible by transparency and a black line on the left marks the oosphrodirum.

Geographical distribution. The whole European coast from the Mediterranean to N. Norway, excluding the Baltic.

Habitat. Rocky shores, mainly in the infra-littoral fringe, but reaching to mid-tide level (0–5% emersion), and living sublittorally to about 15 m, though to greater depths in the south of its range. The animals are most abundant on the fronds and at the base of smaller weeds with subdivided thallus (*Lomentaria*, *Plumaria*, *Callithamnion*, *Ceramium*, *Corallina*, *Gigartina*, from which they may be obtained by washing), less commonly on those with undivided fronds (*Fucus*, *Ulva*, *Enteromorpha*, *Rhodymenia*); also common in laminarian holdfasts, in rock pools and under stones.

Food. Diatoms and detritus gathered from the substratum on which they live. Faeces ovoid pellets c. $200 \times 100 \mu\text{m}$.

Breeding and growth. See Lebour (1937), Thorson (1946), Gostan (1958, 1966), Fretter & Pilkington (1970), Thiriot-Quiévreux & Rodriguez Babio (1975), Wigham (1975a). The sexes are separate, males recognizable by the penis (visible from the 4.5 whorl stage) and their smaller size; they are less common than females (= 37% of the population according to Pelseneer, 1926). The egg capsules are lens-shaped and are laid at night on the weeds amongst which the animals live. The capsule wall is transparent. Each capsule measures about $650 \mu\text{m}$ in diameter and contains 6–50 whitish eggs, each $90\text{--}100 \mu\text{m}$ in diameter. They hatch in about 3 weeks ($12\text{--}13^\circ\text{C}$) as veliger larvae, escaping by dehiscence of the capsule along a suture line which appears in the capsule wall. Their shell is transparent, pale horn-colour, of about 1.25 whorls, $130 \mu\text{m}$ in diameter, smooth, with a few irregular spiral lines. The shell may metamorphose at any time between the 2.75 — nearly 4-whorl stage (diameter $250\text{--}480 \mu\text{m}$). It is smooth save for a peripheral spiral ridge running to an apertural beak. The larva has a large bilobed velum with marginal orange spots which may coalesce to a line; in older stages the right lobe is often bigger than the left. The stalk of the foot is pigmented though the opercular lobes are not (unlike *R. inconspicua*), while the sole may have red pigment in the mid-line with scattered yellow spots. At metamorphosis (at the 4-whorl stage) metapodial and pallial tentacles are present.

Breeding may occur throughout the year and is least in winter. The young settle, with a shell length under 0.5 mm, particularly on finely branching weeds and most abundantly in midsummer when they may constitute a quarter of the total population. Growth rates depend on the season at which settlement occurs: snails settling in summer grow about 1 mm in height per month and live 3–5 months from settlement; those which settle in autumn and overwinter to breed the following spring grow at about half that rate but live 8–9 months. Up to 6 generations may be produced in one year.

Notes. *R. parva* is one of the most abundant of all prosobranchs on rocky shores. In a given area its numbers range from about $5 \times 10^3 \text{ m}^{-2}$ in winter to $76 \times 10^3 \text{ m}^{-2}$ in summer and still higher numbers have been recorded (Petersen, 1918, for Limfjord: 10^5 m^{-2}). Most abundant in summer, when the animals may be found swarming on small, dense weeds and in rock pools. They are extremely active and clamber about the weeds or the rock pool, often moving on a mucous thread secreted from the posterior pedal gland. The foot is very mobile and can bend transversely at the middle and, in the posterior half, fold itself longitudinally to grasp its mucous thread.

The original description of da Costa makes shells with ribs typical; smooth ones were placed in the variety *interrupta* Adams, 1798. The relation between the two, especially in view of transitional forms, has been examined by Wigham (1975b). He regards shell form as the response of genetically variable animals to environmental stresses such as exposure and temperature. The proportion of ribbed shells in a given population is variable, greater in summer than winter (83.7% v. 38.3% at Wembury, S. Devon); the proportion of ribbed

shells between populations varies with exposure, greatest in sheltered and sublittoral situations (93.7% at Wembury, sheltered, v. 2.3% at Polhawn, Cornwall, exposed). Whatever the location some ribbed and some smooth shells occur in every population. These may be regarded as having respectively low or high thresholds (= nearly all or nearly none of the genes responsible) for rib formation; in animals with intermediate thresholds, shell pattern becomes dependent on local environmental factors. The forms (sometimes described as 'varieties') with both ribbed and smooth whorls in the same shell are no more than animals so genetically constituted as to respond rapidly to slight environmental changes. In these circumstances it seems improper to make a distinct species of *R. interrupta* as done by Nordsieck.

The comma-shaped mark frequently used to identify *R. parva* does not develop until the 4-whorl stage (shell 2 mm high) and may never do so. Smaller stages may often be separated from *R. albella* and *R. inconspicua* (the species most likely to cause confusion) by the angulation of the youngest whorl due to a small peripheral spiral ridge and by the violet colour of the apex: this is more diffused than in *inconspicua* where it is rather sharply limited to the embryonic and internal parts of the protoconch. In ribbed specimens the ribs end basally by joining the subperipheral spiral ridge, whereas in *albella* they fade into the general surface of the shell; in *inconspicua* the ribs are about twice as numerous as in either *parva* or *albella* and tend to form a reticulation with spiral ridges.

RISSOA INCONSPICUA Alder, 1844
Turboella inconspicua (Alder, 1844)
Rissoa maculata Brown, 1844

Inconspicua (Lat.), unremarkable, referring to what was seen as a lack of outstanding characters in the shell.

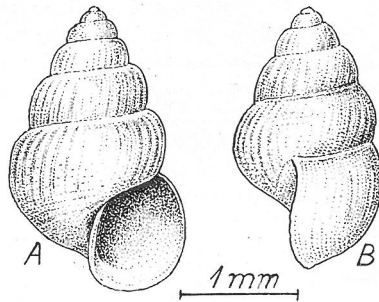


Fig. 170. *Rissoa inconspicua* Alder. Hauch sta. 489 ×, inside Rimmen, N.E. Jutland. CMZ.

Shell. Glossy and semitransparent with conical spire and rounded base. There are 5–6 whorls, each slightly tumid; the sutures are moderately deep and lie below the periphery of the whorls. The spire is sometimes appreciably cyrtocoid, the apical angle changing from about 70° in young shells to about 33° in mature, but it is often only moderately cyrtocoid and may even be flat-sided. The ornament consists of spirals along with which ribs may or may not occur. The spirals are commonly very fine, although they become more prominent towards the periphery of the body whorl where 3 or 4 often enlarge to form ridges running to the outer lip; a very few shells may have a slight keel here. Ribs never develop on the 3 topmost whorls but may be found on some or all of the remainder and may be slightly or well developed. They are slightly prosocline near the suture, slightly opisthocline at the periphery below which they are less obvious. They are about equal in breadth to the intervening spaces and are not sharp-edged. On the body whorl they tend to disappear towards the aperture though a broad labial rib usually lies a little distant from the outer lip. There are 18–30 ribs on the body whorl and the same number on the penultimate. Ribs and spirals give rise to a square reticulation usually confined to the peripheral part of the body whorl. There is no umbilicus.

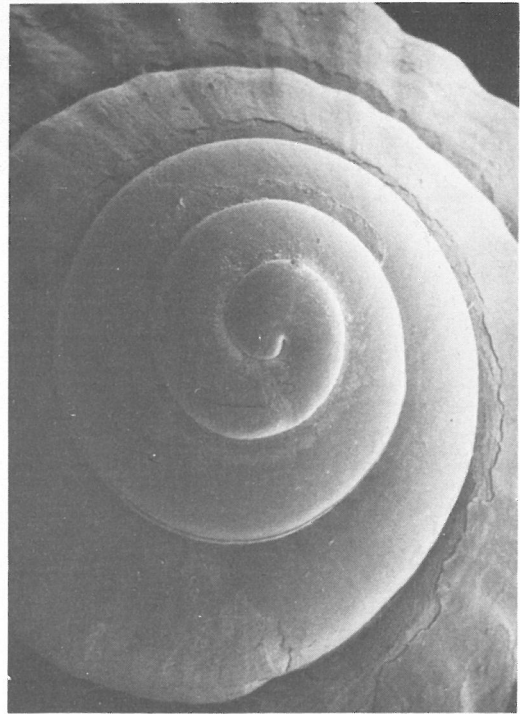
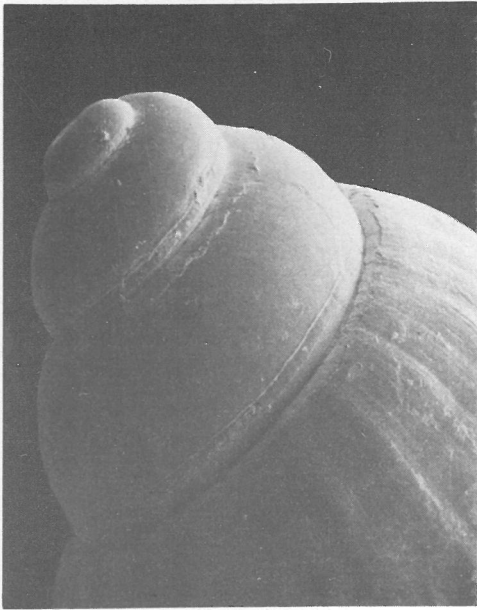


Fig. 171. *Rissoa inconspicua*. Above left, tip of spire $\times 160$; above right, shell apex $\times 185$; below, protoconch $\times 940$. SEM photographs. Plymouth. RZ.

The protoconch consists of 1 embryonic whorl, $100\ \mu\text{m}$ across, smooth, followed by 2 larval ones, the first smooth but with a spiral line close to the abapical suture, the second with 2 such lines. The total diameter of the protoconch is about $200\ \mu\text{m}$.

Aperture. Oval, surrounded by a peristome lying in the axial plane and with a thin edge even in the presence of a labial rib. It is angulated adapically and has a distinct anal sinus. The outer lip arises just below the most basal spiral ridge near the periphery of the body whorl and follows a rather straight course (continuing the profile of the spire) before curving rapidly to the base, where it is a

little everted. The columella is short and straight, occasionally bulging a little across the aperture. Behind the inner lip is a small umbilical groove. The peristome over the body whorl is delicate.

Colour. Whitish or horn-coloured, the protoconch purple and showing as a dark spot at the apex of the spire. The youngest 2—3 whorls often present a series of prosocline orange-brown bars on their subsutural parts, though these do not occur on all shells. The labial rib is white and the peristome orange-brown. Occasionally there is an orange-brown spiral band on the base of the shell.

Size. 3 × 2 mm. Body whorl = 60—70% of total shell height; aperture = 41—47% of total height.

Animal. As in *R. parva*. The metapodial tentacle is long.

Colour. Whitish or cream with yellow spots; there are two dark lines along the side of the body, one at the edge of the sole, the other in a much more dorsal position. There is a yellow spot by each eye; the opercular lobes are dark purple-black.

Geographical distribution. This species is found from the Azores and Mediterranean N. to the Arctic penetrating through the Sound as far as Lübeck Bay in the Baltic. It is absent from continental coasts between Cap Gris Nez and the R. Elbe.

Habitat. The animals may be found on weeds in low rock pools along with *R. parva* but are typically sublittoral where they live on algae and on sandy gravel among algae to depths of about 100 m. They tolerate slightly brackish conditions.

Food. Detritus from the surface of the weeds amongst which they live. Faecal pellets are ovoid, 100 × 50 μm.

Breeding and growth. See Lebour (1937), Smidt (1944), Thorson (1946), Fretter & Pilkington (1970). The sexes are separate, males recognizable by the penis and probably smaller size. The breeding season appears to be a relatively short one, August — September at Plymouth, whilst larvae are found in the Sound and Copenhagen Harbour late summer and autumn. The egg capsules are of the typical rissoid type, hemispherical, clear and colourless, 480—640 μm in diameter and 120 μm high. They are fastened to debris or the shells of other individuals. Each contains 6—9 whitish eggs about 80 μm in diameter which hatch (in the laboratory) after about 10 days as free-swimming veligers with a shell of about 1 whorl, 100 μm across, clear and colourless, though becoming brown by the swimming-crawling stage (3 whorls) and purple after metamorphosis (c. 3.75 whorls). It is smooth except for a spiral line on the periphery of whorl 2, and 2 similar on whorl 3 which lead to an apertural beak. The larva has a bilobed velum which is colourless at hatching though lines of red pigment arise later near the preoral and postoral ciliary bands. Orange spots also appear near the food groove. The foot has a long propodium which, along with the mesopodium, bears yellow spots which later fade or vanish. The opercular lobes are black except for their extreme posterior part. The metapodial tentacle is well-marked at metamorphosis though the pallial one does not grow until later. There is no information about growth or length of life in this species though the animals are probably annuals.

Notes. *R. inconspicua* is not uncommon. It is an extremely variable species in the shape, ornament and colour patterns of the shell and it has undoubtedly been frequently confused with *R. albella* to which it is close and which is also variable. Seen side by side shells of *inconspicua* are usually distinguishable from those of *albella* by having a smaller apical angle, having a greater number of finer ribs, having a less broad body whorl at the periphery of which the spiral ridges are more conspicuous and in the deep purple of the protoconch.

Marshall (1898) distinguished three main shell patterns: (1) with ribs and fine spirals, the most abundant form, predominantly southern in distribution; (2) with ribs and spiral ridges of equal height giving a delicately cancellated surface, northern (Hebridean) in occurrence; (3) smooth, lacking a labial rib, though sometimes with the top 1—2 whorls finely ribbed; said to be abundant at Guernsey and the Scillies. The ribbing of the apical whorls makes the identification of this third type as *R. inconspicua* doubtful.

RISSOA ALBELLA Lovén, 1846

Turboella albella (Lovén, 1846)

Rissoa tenuis Alder, 1844

Turboella benzi (Aradas & Maggiore, 1843) var. *albella* Lovén, 1846

Rissoa sarsi Lovén, 1846

Albella (from the Latin *albula*), whitish.

Shell. The shells which represent the typical forms of this species (form *albella*) are conical but also slightly globular (conical spire, rounded base), semitransparent and glossy. The apex is blunt

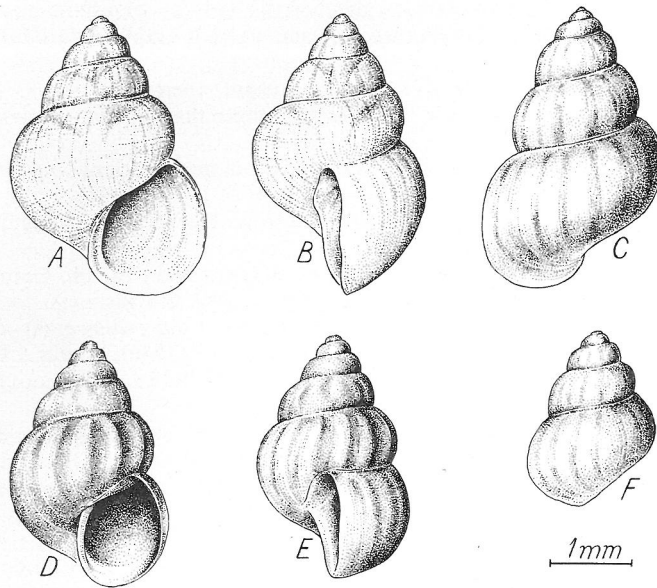


Fig. 172. *Rissoa albella* Lovén. A,B,C, *R. a. sarsi*; D,E,F, *R. a. albella*. A—C, Nibe Broad, E, Limfjord; D,E, Rudköbing; F, Taarbaek. All CMZ.

(apical angle $58-63^\circ$), the spire rather short and straight-sided, sometimes a little cyrtocoid. There are 6 whorls, tumid, sometimes a little flattened at the periphery, which meet at deep sutures; in many shells the body whorl is broad and inflated (probably females) and in some it is slightly keeled at the periphery. The ornament consists of spiral and transverse elements: the former consist of very shallow striae, not visible without magnification. All shells show irregular growth lines which are slightly flexuous — prosocline at the suture, orthocline (even opisthocline) at the periphery of the whorls, below which they are usually more marked. Spirals and growth lines together produce a very shallow reticulation of the surface. This is all the ornament on upper whorls and may be all that is found on any whorl; on some shells, however, ribs occur on whorls 4 and 5. They are usually absent from the youngest part of the body whorl though a labial rib is commonly found there. Ribs follow a similar course to growth lines, may be slight or marked but differ from those of *parva* in not being linked to a spiral ridge at their abapical ends. There are 12—17 on the youngest whorl showing them, 9—16 on the next. There is a small umbilical chink. The protoconch has 2.25 whorls, smooth on those that we have seen; the initial shell occupies 0.75 whorls and has a diameter of *c.* $90\ \mu\text{m}$, the whole protoconch has a diameter of $240\ \mu\text{m}$.

Shells of the form *sarsi* are of the same general shape, thinner, more transparent and often devoid of ribbing.

Aperture. Oval, angulated and a little drawn out adapically, its long axis set at *c.* 30° to that of the spire. It is surrounded by a thin peristome lying largely in the axial plane but showing a shallow anal sinus and equally slight peripheral advance. The outer lip arises just below the periphery normal to the body whorl; its base is rather flattened and a little everted. It joins the columella nearly at right angles and some shells exhibit a spout here. The columella is slender, straight and nearly vertical, the lip rolled outwards a little over the groove to the umbilicus. The rest of the peristome is not much more than a glaze on the body whorl.

Colour. White, cream, horn colour, the 3 apical whorls often a darker bronze colour and sometimes with a faint violet tinge. The two youngest whorls (especially in *sarsi*) often have numerous reddish brown bands which cross the penultimate whorl and run over the body whorl to the periphery. They are opisthocline adapically, becoming orthocline, and lie between the ribs if

these are present. There may be a spiral brown band on the body whorl just adapical of the umbilicus which may connect with the ends of the transverse bars. There is usually a dark brown streak on the columella, facing the outer lip.

Size. 3×2.5 mm. Body whorl = 66—73% of total height, aperture = 43—53% of total height.

Animal. As in *R. parva*. The cephalic tentacles are longer than in that species, the metapodial tentacle longer and flatter.

Colour. Cream with brown and white speckles on the head, dark markings on the stalk of the foot and on the opercular lobes.

Geographical distribution. From the Mediterranean to N. Norway, extending into the Kattegat, the Danish fjords, the Sound and the Belts.

Habitat. On rocky shores amongst weeds, especially *Zostera* and *Codium*. Occasionally between tidemarks but usually sublittoral to 15 m. It is tolerant of some brackishness.

Food. As in other species — detritus and diatoms. Faeces ovoid pellets c. 50×25 μm .

Breeding and growth. See Lebour (1935, 1936, 1937), Thorson (1946), Fretter & Pilkington (1970, 1971), Fretter & Shale (1973), Rasmussen (1973), Rodriguez Babio & Thiriôt-Quévieux (1974), Thiriôt-Quévieux & Rodriguz Babio (1975).

The sexes are separate, males recognizable by the penis and by their greater height and more slender proportions (σ breadth/height = 0.685; ρ breadth/height = 0.76). Breeding occurred in the Isefjord June — August, mainly in July; at Plymouth it has been said to breed December — May, but there is doubt as to what species has been dealt with at this locality (see below). The egg capsules described by Rasmussen (for both *albella* and *sarsi* forms) are of the usual rissoid lens shape, 700—1100 μm in diameter, with a basal rim. When laid they have a thick hollow wall, the eggs packed centrally, and no suture; later the membrane defining the inner surface of the wall disappears and the eggs fill the whole capsule, while a suture develops over the upper surface through which free-swimming veliger larvae escape. The eggs are whitish, c. 85 μm in diameter, and there are 34—70 per capsule. A single female can deposit 25 capsules in 4 weeks. There are no studies on growth.

There is considerable confusion in the literature about the characters of the veligers. Lebour (1934, 1936) described larvae of forma *sarsi* from capsules 480 μm in diameter laid on weeds in October; they had shells, 120 μm across on hatching, decorated with spiral striae with small tubercles between, though later whorls were smooth. The velum was bilobed and colourless, later acquiring a dark margin, while pigment also developed at the base of the foot. The larvae metamorphosed when the shell had 2.5—3 whorls, diameter 480 μm . Thorson (1946) found similar larvae in the Sound and assumed that they were *sarsi*. Fretter & Pilkington (1970, 1971) described (as *R. sarsi*) larvae from Plymouth plankton the first whorl of whose shell bore small tubercles arranged partly in spiral lines and partly randomly between lines. Later whorls were plain except for some transverse bands and a peripheral band of tubercles running to a beak. The body of the larva was as described by Lebour. These larvae were shown by Fretter & Shale (1973) to be common in Plymouth plankton January — May and dominant in certain periods. Rasmussen (1973) and Thiriôt-Quévieux & Rodriguez Babio (1975) found that the embryonic shells of *sarsi* were smooth or had at most a few small points; the diameter was 100—110 μm . The larval shell grew to 2.25 whorls, was smooth and had a final diameter of c. 230 μm . With our present knowledge these must be taken to be the larvae of *R. albella*.

Though the larvae from the Plymouth plankton were described as *sarsi* all authors concerned were aware that neither that variety nor typical *albella* occurs there in the numbers necessary to produce the swarms of larvae described by Fretter & Shale, and possibly not at all. The question as to what these larvae really are must be left uncertain. Rasmussen thought they might be *Littorina neritoides*, Thiriôt-Quévieux & Rodriguez Babio, *Cingula alderi*, neither of which looks appropriate when the shells are examined by SEM, neither having a peripheral strip and *C. alderi* not having been recorded adult at Plymouth.

The protoconch does not resemble that of any species of *Rissoa* so far described and is more like that of an *Onoba* or *Alvania*, though not fully like either. The only species of these genera abundant enough at Plymouth to produce larvae in such numbers are *O. semicostata* and *A. punctura*. If it were the former it would involve postulating a population with a free instead of a suppressed veliger stage; if the latter it would require the supposition that there is a double breeding period and that early and late cohorts differ in details of shell structure. Certain identification calls for the rearing of the larvae through settlement to a recognizable juvenile or adult stage.

Notes. *R. albella* and its variety *sarsi* are not common on British coasts but are abundant in many Danish waters. Though there has been a recent tendency to regard *sarsi* as a separate species there seem to be so many forms transitional between typical *albella* and *sarsi* and so much identity of body form and development as to suggest that they must be kept together.

RISSEO GUERINI Récluz, 1843
Rissoa costulata Alder, 1844
Rissoa subcostulata Schwartz, 1864

Guerini, Guérin's.

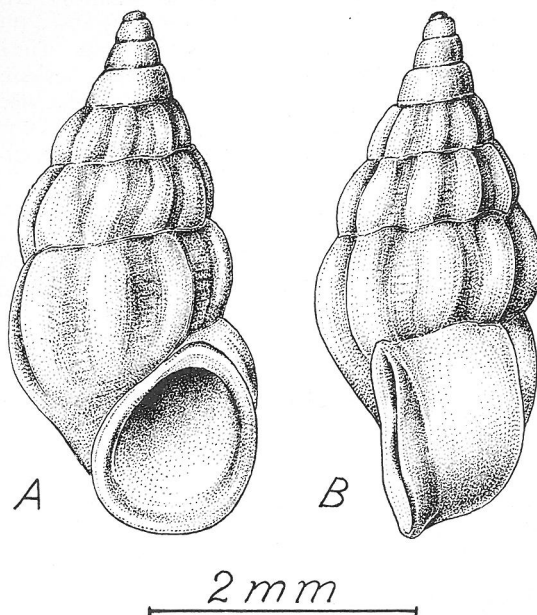


Fig. 173. *Rissoa guerini* Récluz. Weymouth. CMZ.

Shell. Ovoid-conic, the apex moderately sharp, solid and glossy. The spire is coeloconoid (apical angle $37-43^\circ$, commonly about 42°), of 8 whorls, the apical 4—5 nearly flat-sided, though the topmost 2—3 (larval) are more tumid than the next 2; the sutures lie below the periphery. The 3—4 youngest whorls are much more tumid and meet at wavy sutures below the periphery of each. The ornament consists of growth lines, ribs and spiral ridges and grooves. The ribs are confined to the youngest 3 (occasionally 4) whorls and tend to die away on the body whorl towards the aperture. Normally they are slightly opisthoclinal, though on the body whorl, especially near the aperture, they may be prosoclinal close to the suture and have as a result a slightly flexuous course. Each is about equal in breadth to an intervening furrow, with a broad summit from which spiral ridges have been eroded except on those most recently formed. On the spire the ribs on one whorl tend to lie opposite furrows on the next and to end just short of the abapical suture (though overhanging slightly in a few shells); on the body whorl they end about the periphery. There is a variable number on the body whorl (depending on their degree of development by the aperture), but the two previous have regularly 10. A short distance back from the outer lip is a well-developed labial rib equal in breadth to about two ribs and the space between on the previous whorl; it is distinctly prosoclinal, not crossed by spiral ridges but showing growth lines. These are also prosoclinal and so run obliquely over the

ribs and furrows. The whorls which bear ribs also bear spiral ridges and grooves, the former rather broader than the later, all shallow. There may be up to 30 on the body whorl, half that on the penultimate. In the grooves lie numerous growth lines which divide them into minute compartments. In young shells these spiral elements occur on apical whorls but are eroded later. The protoconch has 2.25—3.5 whorls, smooth except for a few spirals at the very apex; it measures 250—450 μm in total diameter.

Aperture. Oval or D-shaped, its long axis lying at 32—36° to that of the spire, it is bordered by a prosocline peristome which is nearly plane but usually shows shallow anal and basal sinuses and a slight projection of the inner lip. The edge is thin and bevelled internally. The outer lip arises below the periphery of the body whorl at the level at which the ribs end, more or less at right angles to the surface but sometimes curving away from the apex to meet it tangentially. Its curvature is initially slight; sometimes it is nearly straight. The columella is short and the peristome here is everted over a groove, though there is not usually an umbilicus. Over the body whorl the peristome is flattened and spread a little, but at all other points its edge turns out to form a marked though thin flange.

Colour. Cream, yellowish or brown, some colour due to periostracum. The ribs are usually white, the brown colour lying between them. There are sometime brown streaks crossing the unribbed whorls, especially near the suture. The apex is often slate-coloured or lilac when the periostracum is worn. The base of the shell is often all brown, the peristome the same colour or pale violet. The throat shows a band of brown-lilac, level with the lower border of the labial rib, and extending on to the columella.

Size. Up to 6 \times 3 mm. Body whorl = c. 55% of total shell height; aperture = 30—35% of total shell height.

Animal. Generally as in *R. parva*. The cephalic tentacles show a slight dilatation just short of their tip. The pallial tentacle is very short and apparently immobile. The metapodial tentacle has a transversely expanded base.

Colour. Yellowish, the cephalic tentacles yellower than the rest with a central yellow line. The dorsal surface of the snout, its sides and the sides of the foot are brown; there is a dense yellowish patch behind each eye. The anterior pedal gland shows white through the propodium. The metapodial tentacle is colourless or white.

Geographical distribution. *R. guerini* is a southern species found on eastern Atlantic coasts between the Canary Islands and the south-western coasts of England and Ireland.

Habitat. On weeds and *Zostera* and under stones at LWST and sublittorally. It is local and may be reasonably common.

Food. Diatoms and detritus from the substratum on which it lives. Faeces, ovoid pellets c. 100 \times 50 μm .

Breeding and growth. The sexes are separate, males recognizable by the penis. At Plymouth (Lebour, 1934, 1937) breeding occurs February—April. Egg capsules, clear, lens-shaped, are laid on the weeds on which the adults live. They are c. 960 μm across, a rim increasing the diameter up to 1400 μm , rather flatter (160 μm high) than those of other rissoids, each containing 80—100 eggs which are colourless and 90 μm in diameter. In the laboratory free veliger larvae escaped after 10 days, through an apical fissure. Their shell of about 1 whorl is initially 160 μm in diameter bearing a few spiral lines and tubercles. The shell grows to 2.25—3.5 whorls (250—450 μm diameter) before settlement and is smooth. The separation between embryonic and larval shell is clearer than that between protoconch and teloconch.

The larva is colourless at first but later acquires brown pigment between its eyes, round its mouth, on the sides of the foot and 4 prominent spots appear, 2 on each lobe of the velum. There are no studies of metamorphosis or later growth.

Notes. This may be an aggregate species with *guerini* s.s. and *subcostulata* Schwartz, as segregates occurring in Britain. They may be distinguished, according to Nordsieck, by the more slender proportions of the former. Most Channel specimens would fall into *subcostulata*.

RISSOA VIOLACEA Desmarest, 1814, agg.

Violacea (Lat.); violet, referring to the colour of parts of the shell.

This is an aggregate species which includes as segregates *violacea sensu stricto*, *lilacina* Récluz, 1843, *rufilabrum* Alder, 1844 and *porifera* Lovén, 1846. The characteristics of each have been described in detail by Smith (1970). Since there are sufficient differences in their appearance to make

the understanding of a comprehensive description difficult, it has seemed better to describe separately the three segregates which occur in north-western Europe.

R. violacea agg. is differentiated from the other species of *Rissoa* described here in having a fine reticulation of the shell surface, especially prominent in the younger half of the body whorl. The four segregates differ in geographical range, *violacea* s.s. being Mediterranean, *lilacina* living between the Mediterranean and south and west Britain and Ireland, *rufilabrum* extending from south and west Britain and Ireland to Norway, whilst *porifera* is more northerly still. Correlated with this is a tendency for the degree of calcification of the shell to decrease towards higher latitudes. Thus *violacea* s.s. and *lilacina* have solid shells, numerous ribs and nodosities constricting the throat, in *rufilabrum* these are reduced and in *porifera* they are absent and the shell altogether less heavy.

RISSOA LILACINA Récluz, 1843, seg.

Lilacina (Lat.), lilac, referring to the colour of parts of the shell.

Shell. Solid, with a glossy periostracum, oval-conic, rather broad basally (breadth on average = 52–60% of height). The spire is slightly coeloconoid apically, slightly cyrtococonoid towards its base, but may be straight-sided; apical angle ranges from 48–60°, usually 51–53°. There are 6–7 whorls, very slightly tumid, but the first two (= larval shell) noticeably more swollen than the rest; they meet at well-marked sutures which are straight on the upper whorls but made sinuous by the ends of the ribs on the lower ones. Each whorl has a minute flattened ledge just below the suture. The whole shell is marked by fine spiral ridges and growth lines which cross to make a reticulation, extremely shallow on the top 3–4 whorls (which are ribless) but becoming coarser towards the base. Where ribs occur the reticulation is normally confined by erosion to the intervening spaces but the last part of the body whorl (where ribs are again absent) displays a series of square to oblong depressions. There are here 20–30 spiral ridges, low and flat, about 100 μm broad, separated by grooves of comparable size and crossed by similar but narrower transverse ridges. The spiral ridges are least obvious below sutures and at the base of the shell. Ribs occur only on the 3 youngest whorls and are reduced or absent from the part of the body whorl by the aperture — a quarter to a half of its whole extent. When seen in apertural view ribs are normally visible on 2 whorls of a shell. Careful examination of some shells shows slight ribs even where apparently absent and a few shells (“var. *ecostata*”) show no sign either of ribs or reticulated surface. Each rib is rounded, rather broader than the intervening furrows, and often widens into a T-shaped head at the adapical suture; though arising at right angles to the suture it becomes opisthocline below. Ribs on one whorl tend to alternate with those on the next. The body whorl carries 6–9 (usually 7–8) ribs and a labial rib, the penultimate 12–15 (usually 13) and the rest 0–13 giving a total of 22–36 (usually under 30). Ribs on the spire run from suture to suture, those on the body whorl die away just abapical of the periphery. There is a well-marked wide labial rib close to, but not at, the apertural edge. The protoconch shows 1.8–2.5 tumid whorls marked by a few spiral lines; the boundary between embryonic and larval shell is clearer than that between protoconch and teloconch. Its final diameter is 250–350 μm .

Aperture. Oval, its long axis 30° to that of the spire, rather narrow adapically, broad and somewhat square abapically. It is surrounded by a peristome lying slightly prosoclinally, with an anal sinus and a slight projection alongside the columella. The outer lip is thin and a little out-turned everywhere. It arises from the body whorl at the level where the ribs die away, its initial half rather straight and continuing the outline of the spire, the base curved and forming a slight spout. Columella short, nearly vertical, and often swollen to produce a blunt projection into the throat. The lip here is everted over an umbilical groove though the shell is imperforate. The columella makes a moderate angle with the parietal lip which spreads extensively over the body whorl, often with a larger lobe level with the umbilicus. The throat is constricted by an expansion opposite the labial rib which frequently bears a low tubercle at its adapical end and another abapically. Rib and thickenings are not present in immature shells.

Colour. Yellowish-white with orange-brown colour between the ribs, most noticeable above and below the sutures. These bands of colour also occur on unribbed whorls where they may be very prosocline in direction. The labial rib is white. A band of bright orange-brown on its adapertural side often shows in the throat and (in some shells) is continued into a spiral band running over the

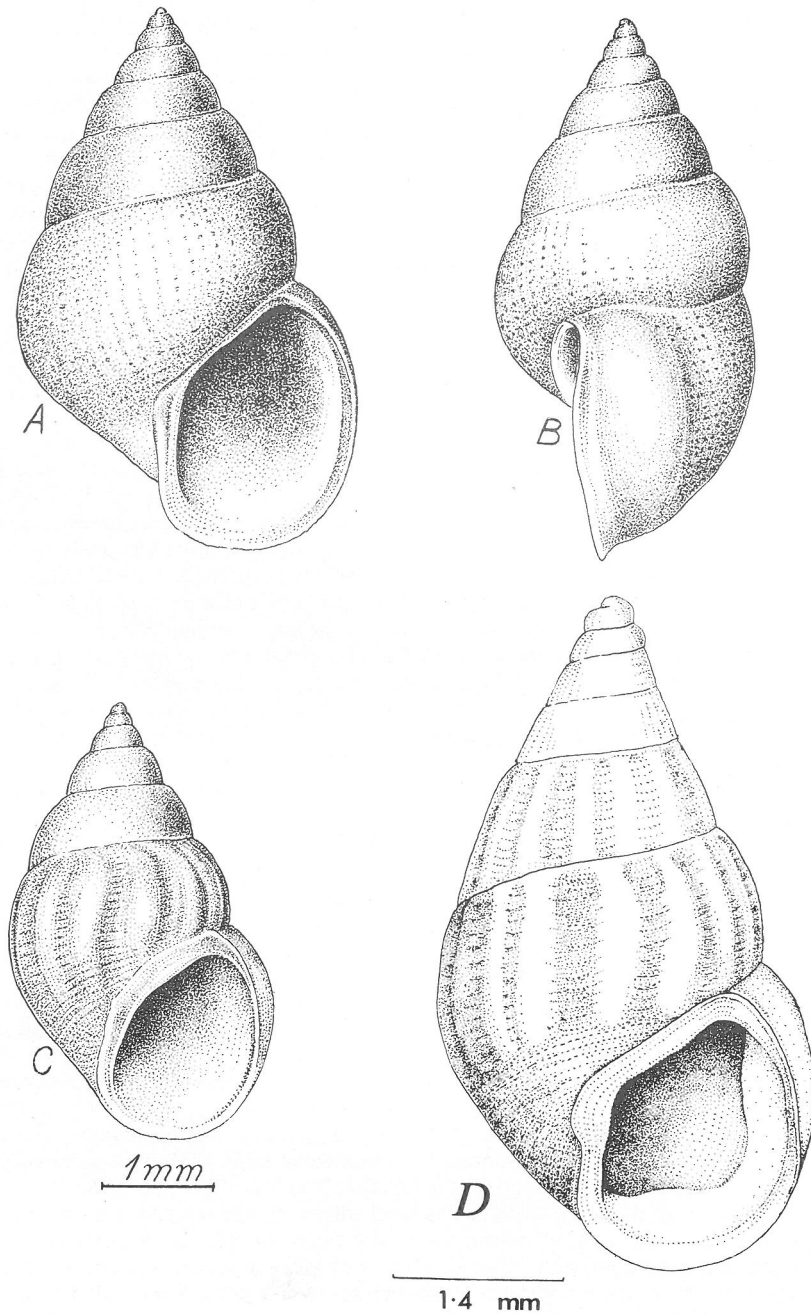


Fig. 174. *Rissoa violacea* Desmarest. A,B, *R. porifera* seg.; C, *R. rufilabrum* seg.; D, *R. lilacina* seg. A,B, Hauch sta. 504, Kattegat; C, Hauch sta. 103, Nordre Rønner, N. of Laeso, N. Kattegat; D, Carna, Ireland. A—C, CMZ; D, RZ.

body whorl from the base of the labial rib to the parietal lip. There may be a paler area of brown on the abapertural side of the rib and the whole base of the shell may be suffused with brown or lilac. The peristome is deep lilac and the protoconch a pale lilac.

Size. 5×2.75 mm. Body whorl = 60% of total shell height; aperture = 33–45% of shell height.

Animal. As in *parva*. The metapodial tentacle is long, filiform.

Colour. Yellowish. The tentacles are marked by a central bright yellow line; the dorsal surface of the snout and the sides of the foot are brown. The operculum is transparent, nearly colourless, with a yellow band along its greatest diameter.

Geographical distribution. A southern form which extends along western European coasts to the British Isles. It occurs in the Western Channel basin as far E. as the Isle of Wight and N. in the Irish Sea to N. Wales and again on the W. coast of Scotland. It is found on southern and western coasts of Ireland, but not on the eastern.

Habitat. On weeds and amongst sandy gravel from LWST to about 50 m. Not uncommon locally.

Food. Detritus and diatoms from its habitat. Faeces, brown ovoid pellets c. 100×50 μ m.

Breeding and growth. The sexes are separate, males known by their penis and generally smaller size. One egg capsule has been seen, hemispherical and transparent, with a narrow marginal brim (40 μ m wide), attached to the shell. The diameter was 760 μ m and there was no obvious plug. The capsule contained 28 cream-coloured embryos. From the appearance of the protoconch (as noted by Thiriou-Quiévreux & Rodriguez Babio, 1975) there would appear to be a free-swimming veliger. This is apparently unknown as are all other aspects of development and life history.

RISSOA RUFILABRUM Alder, 1844, seg.

Rufilabrum (Lat.), with a reddish lip, referring to the colour of the peristome.

Shell. Generally similar in shape and appearance to that of *lilacina* but differing in the following points: slightly broader (breadth = 54–64% of height); sometimes more translucent; apical angle ranging from 51–62° (commonly 55–57°); when seen in apertural view ribs normally appear only on the body whorl; they occur on only 0.5–1.5 whorls; there are 11–24 in all, 7–9 on the body whorl, the rest on the penultimate; labial rib less conspicuous; ribs on body whorl rarely extend below periphery and may disappear before reaching it. In vars *paucicostata*, *ecostata* ribs are reduced or absent.

Aperture. As in *lilacina* but the base of the outer lip makes a less marked angle with the columella and that, in turn, with the body whorl, so that the aperture appears rounded rather than square. The parietal lip does not spread so markedly over the body whorl and the nodosities in the throat may be reduced.

Colour. Much as in *lilacina*.

Size. 5×2.75 mm. Body whorl = 63–70% of total shell height; aperture = 42–48% of total shell height.

Animal. As in *parva*.

Colour. Generally as in *lilacina*, but darker.

Geographical distribution. This is found from the Channel Islands to Norway, less common than *lilacina* in the S., more common in the N.

Habitat, food. As for *lilacina*.

Breeding and growth. Nothing recorded about reproduction; presumably as in *lilacina*.

RISSOA PORIFERA Lovén, 1746, seg.

Porifera (Lat.), bearing pores, referring to the pore-like pits on the surface of the shell.

Shell. In general like that of *rufilabrum* but more delicate, and recognizable by the absence of ribs; the sole ornament is the series of squarish depressions due to crossing of spiral ridges and growth lines and visible on most whorls. There is a labial rib, though it is less well-formed than in either *rufilabrum* or *lilacina*.

Aperture. As in *rufilabrum*, though the peristome hardly spreads over the body whorl. There is some thickening of the throat opposite the labial rib, but it lacks tubercles.

Colour. Horn-coloured, white on the labial rib. Apex with a brown or reddish-lilac tinge. The same colour appears again on the outer lip, the rest of the peristome being pale.

Size. 5 × 2.75 mm. Body whorl = 65—70% of total shell height; aperture = 40% of shell height.

Animal. As in *parva*.

Colour. As in *rufilabrum*.

Geographical distribution. The most northerly of this group, ranging from W. Ireland to W. Scotland, the Shetlands, Norway and the Kattegat.

Habitat, food. As for *lilacina*.

Breeding and growth. Nothing known, presumably as in *lilacina*.

RISSOA MEMBRANACEA (J. Adams, 1800), agg.?

Turbo membranaceus J. Adams, 1800

Rissoa labiosa (Montagu, 1803)

Rissoa octona (Nilsson, 1822)

Rissoa cornea (Lovén, 1846)

Rissostomia membranacea (J. Adams, 1800)

Zippora membranacea (J. Adams, 1800)

Membranacea (Lat.), like a membrane, referring to the shell of those forms found in brackish water.

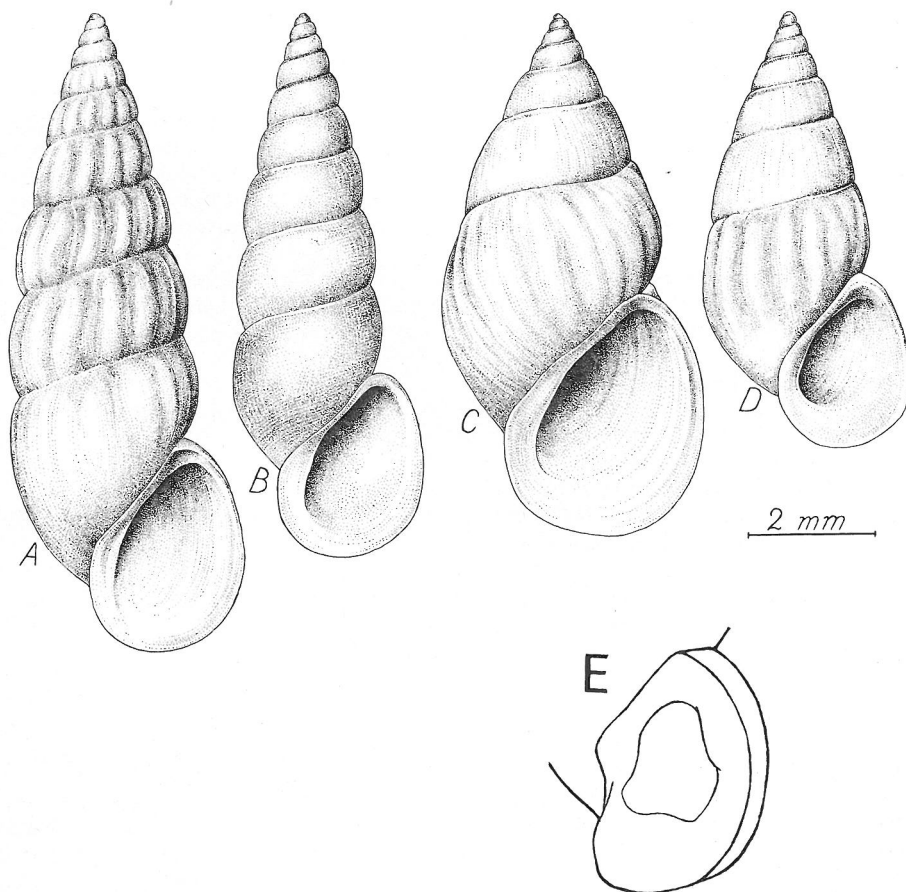


Fig. 175. *Rissoa membranacea* (J. Adams). A, B, var. *octona*; C, var. *membranacea*; D, var. *labiosa*. A, Ballen Flak, Samsø; B, Boels Reef, Mariager Fjord, E. Jutland; C, Horsens Fjord, E. Jutland; D, Nissum Broad; E, tubercles in throat of shell. All CMZ, except E, which is from the Fleet, Dorset.

Shell. Variable in many respects — sometimes thin and semitransparent, sometimes solid, well calcified, opaque; sometimes slender and elongate, sometimes squatter and more club-shaped. The former tend to occur in brackish habitats and will be described first.

Brackish forms. Shells with an elongated conical spire flat-sided, occasionally slightly cyrtocoid, thin even semitransparent, glossy. The apex is sharp, the apical angle *c.* 37—47°. There are usually 8—9 whorls but in some (forma *octona*) there may be up to 12; they are only slightly tumid and meet at well-marked sutures placed below the periphery of the whorls. The ornament consists of spirals and, sometimes, ribs. The spirals are always microscopic, usually better developed at the periphery of the body whorl, where they may even impart a slightly keeled appearance. Ribs, if present, lie on the body and some older whorls, but the most apical are smooth; there may be 10 on the body whorl. They are wave-like with gently sloping sides and rounded summits, mainly orthocline, occasionally a little prosocline adapically. Those on the spire run from suture to suture; those on the body whorl end about the periphery. The shell also exhibits growth lines which are markedly prosocline and so cross ribs and furrows obliquely. A labial rib may be present, usually a little away from the aperture. An umbilical groove or chink may be present or absent.

Marine forms. In these the spire is relatively shorter and the shell thick, solid and opaque. The apex is pointed, but the apical angle is 45—55°. There are 5—7 whorls, the body whorl larger than in brackish water shells, and the sutures deeper and a little incised. The ornament is as described above but when ribs occur they tend to be more numerous — up to 18 on the body whorl, to 15 on the next and a variable number on the next depending on what proportion of its surface is rubbed. The labial rib is well-marked, equal in breadth to about 3 others.

Protoconch of about 3 whorls, smooth, not clearly demarcated from teloconch, its total diameter 300—350 μm .

Aperture. Oval, often somewhat triangular, surrounded by a peristome which lies prosoclinally and is often not plane but concave. The outer lip arises from the body whorl below the periphery and follows a curving (often nearly straight) course before turning to the base; here it is sharply curved, in some shells nearly pointed, and forms a large flare. The inner lip shows an everted tongue over an umbilical groove, a reduced, retracted part over the umbilicus and a slight thickening over the body whorl. The edge of the outer lip is thin even when a labial rib occurs. In shells from marine environments the columella has a distinct tooth-like elevation about the level of the umbilicus and the throat is constricted by a thickening running from the base of the columella to the adapical end of the outer lip (more or less at the level of the labial rib) where it may show a nodulous swelling. In immature shells the peristome is thin and not everted. Shells from brackish water habitats tend to have more oval and less triangular apertures, a thinner peristome and reduced columellar and other thickenings.

Colour. Solid shells may be white, yellowish or greenish; semitransparent ones may be similar or pale horn-colour. All may have longitudinal yellow-brown markings which tend to occur in the spaces between ribs when these are present; they may cross upper whorls or disappear at the periphery, may branch or fuse. In some shells an indistinct band of the same colour lies on the base of the body whorl. The labial rib is always pale, but a band of yellow-brown may lie along its adapical side and/or along the outer lip as well as on the columellar region. The shell apex may have a pale violet tint.

Size. Up to 9×3 mm. In the slender forms the body whorls = 40—45% of shell height, the aperture 30—35% of total shell height; in shorter forms the corresponding figures are 60—67% and 50%.

Animal. Much as in *parva*. The tentacles are slightly bulbous apically, the penis sabre-shaped.

Colour. Variable, light or dark; animals from brackish habitats are usually paler than those from marine ones. In the latter the body is mainly purplish black save for white or yellow areas on the sole of the foot, round the mouth, behind the eyes, along the tentacles, on the penis and for white or yellow streaks running backwards from the eyes. In pale animals white appears dorsolaterally on the snout and on the front and sides of the foot. In all animals there are dark areas mid-dorsally and laterally on the snout, at the base of the penis, on the side of the foot and on the opercular lobes. The metapodial tentacle is pale.

Geographical distribution. The species is widely spread from Norway to the Canary Islands. It extends into the Kattegat and through the Sound and Belts into the Baltic Sea as far as Rügen Island.

Habitat. *R. membranacea* is normally associated with *Zostera*. It may be found, at LWST and

sublittorally to about 15 m, on *Zostera* or on weeds with body form like that of *Zostera*. It extends into brackish water to salinities of c. 7‰.

Food. Diatoms and detritus encrusting the plants on which it lives. Faeces in the form of ovoid pellets, $100 \times 50 \mu\text{m}$.

Breeding and growth. See Lebour (1934, 1937), Smidt (1944), Rasmussen (1956, 1973), Rehfeldt (1968), Fretter & Pilkington (1970). Sexes separate, males recognizable by the penis. In the south (France, Plymouth) breeding may occur throughout the year; in the north (Isefjord, the Sound) in April—August. The egg capsules are of typical rissoid pattern, clear, lenticular, with a flattened basal margin and show a transverse suture with an oval plug at the apex; their diameter is 0.7—2 mm, perhaps most commonly c. 1.5 mm. Those from fully marine localities are more thin-walled, those from brackish places thicker. They are laid on weeds, primarily *Zostera*, also *Fucus*, *Ruppia*, *Chaetomorpha* and *Ulva*. The number of eggs per capsule varies: 150—400 (Isefjord), 250—300 (Dyrnaes, Roskildefjord), 100 (Arcachon, Copenhagen harbour); 40—60 (Plymouth). Their diameter is variable (90—130 μm), their colour white or yellowish. Two modes of development have been described: in some capsules all eggs develop to embryos and free-swimming veligers escape, in others some embryos are used as food by others and a small number of juveniles hatch. In the former, according to Rehfeldt, the nucleus of the embryonic shell is c. 90 μm across, in the latter c. 125 μm . According to Lebour the shell of hatching veligers has 1.5 whorls, measuring 320 μm across, and is smooth. Fretter & Pilkington noted that it had a depressed spire and slight apertural beak, the only ornament a spiral ridge not developed until the 3-whorl stage. There is a marked umbilicus. The larva has an unpigmented bilobed velum and a foot with an elongated propodium.

Notes. When *Zostera* was abundant *R. membranacea* was a common rissoid, but it was badly affected by the *Zostera* disease of the 1930's and has become uncommon or rare.

The animals can live and breed in waters of salinity from 35—6 to 7‰ and exhibit great variability of shell form in relation to this (Mars, 1956). In addition there appears to be a tendency for northern forms to have longer, narrower and more transparent shells and for southern ones to have shorter, plumper and more solid ones. The degree of ribbing is also variable and may be subject to the same factors as influence it in *R. parva*. The interaction of these effects results in unusually high variability in the appearance of the shell, as a result of which numerous varieties have been described and some, indeed, elevated into species. The taxonomic situation is not made easier by Rasmussen's demonstration (amplified by Rehfeldt) of two different reproductive modes.

The characteristics of the main forms described are:

1. *membranacea* J. Adams, 1800: spire long, 8—9 whorls, rather flat; shell thin, usually with some ribbing; body whorl is c. 60% of total height, aperture c. 40%; fold on columella slight or absent and throat not thickened elsewhere; a northern form preferring salinities of 20—15‰.
2. *labiosa* Montagu, 1803; spire short, 7 whorls, rather flat; shell solid; 15—18 ribs on body whorl which is 66—70% of total height, aperture 50%; fold on columella and internal thickening of throat well marked; umbilicus shut; a southern form in salinities of 35—20‰.
3. *octona* Nilsson, 1822: spire long, 10—12 whorls, more tumid than in *membranacea* and *labiosa*; shell thin with 10 ribs (sometimes none) on body whorl which occupies 40% of total height, aperture 33%; fold on columella not well marked and throat unthickened; a northern form preferring salinities of 16—12‰.
4. *cornea* Lovén, 1846: a small shell of 5—6 whorls, moderately swollen; shell thin with only slight indication of ribs; body whorl about 60% of total height, aperture about 40%; fold on columella clear, throat thickened; occurring in the most brackish situations to 6—7‰ S.

Var. 1 is Jeffreys's *elata*, 2, his *venusta*, 4, his *minor*.

Parallel to this series from western European coasts is a second from the Mediterranean and Black Seas (*ventricosa* Desmarest, 1814; *grossa* Michaud, 1832; *fragilis* Michaud, 1832; *venusta* Philippi, 1844) with comparable salinity preferences. It seems, therefore, that we are dealing with one (perhaps two) aggregate species of which these are segregates. In the present state of knowledge we keep the name *membranacea* for those from Atlantic coasts.

Notes on the species of Rissoa. These are sometimes difficult to identify, partly because of a general uniformity in shell features and partly because these vary with the nature of the environment. The shell may be thick in one situation and thin in another, in one place ribbed and in another — or worse, the same place — quite smooth. The appearance of the body of the animal, on the other hand, is much more constant, apparently little affected by its surroundings and so similar from species to species as to give little help in identification. The patterning of the protoconch gives equally little aid being usually limited to a few spiral threads, sometimes with spots, in all species.

Of species described here two are easy to identify. *R. parva* is far and away the commonest and is usually instantly recognizable by the comma-shaped mark on the body whorl near the aperture. Young specimens (and a

few adults) lack it, but may often be distinguished from the young of other species by a slight angulation (due to a spiral ridge) at the periphery. This is also characteristic of the body whorl of smooth adult shells and links the abapical ends of the ribs in ribbed ones. There is often a violet apex to the shell, but this colour is diffused superficially, not located internally in the protoconch as in *R. inconspicua*. *R. membranacea* is the biggest local rissoid; those from marine habitats are readily recognized by the marked eversion of the peristome and by bulges on the columella and within the outer lip; in animals from brackish water these features are not prominent and the shell is more translucent, but the height and aperture usually differentiate it from other species present.

R. guerini is distinguished by the slightly coeloconoid outline of the spire, its ribs, the lack of a pattern of pits on the body whorl and the fact that the inner lip does not spread on to the body whorl. It is not found north of the south-western parts of England and Ireland.

R. violacea agg. is differentiated from all other local species by the pitted surface of the body whorl. Its segregates may be identified by (1) the number of ribs — these are visible on 2 whorls when the shell of *lilacina* is seen in apertural view, on only 1 whorl in *rufilabrum* and are absent in *porifera*; (2) the degree of extension of the inner lip over the body whorl — considerable in *lilacina*, moderate in *rufilabrum* and very little in *porifera*; (3) the degree of occlusion of the throat by tuberosities — maximal in *lilacina* and *rufilabrum*, less in *porifera*.

Greater difficulty may be experienced in separating *R. inconspicua* and *R. albella* with the forms *albella* and *sarsi*. Both species are extremely variable and some shells of one may be very similar to some shells of the other. On the whole, however, shells of *inconspicua* are more slender than those of *albella* and those that are ribbed have more delicate and more numerous ribs than are found in *albella*. The spiral ridges on the body whorl are also more clear and the apex is commonly purple. *R. albella* forma *sarsi* is more transparent and much less often ribbed than the type, as well as showing brighter pigment bands.

Smooth shells of *inconspicua* and smooth shells of *albella* are the most difficult to separate. The most reliable character is the colour of the apex, purple in *inconspicua*, bronze in *albella*. In shells which do not show this clearly, one can only put together hints from some other features of which the most helpful are the swelling of the whorls (more pronounced in *albella*) and the umbilicus (more conspicuous in *albella*). Where live animals are available identification is relatively simple because the metapodial tentacle of *inconspicua* is finger-shaped and that of *albella* leaflike.

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BARLEEIDAE Gray, 1857

BARLEEIA UNIFASCIATA (Montagu, 1803)

Turbo unifasciatus Montagu, 1803

Barleeia rubra (J. Adams, 1797) (probably *Rissoa parva*)

Barleeia, a genus named by Clark, 1855, in honour of George Barlee (1794?—1861), son of W. Barlee, Rector of Wrentham and Bedingfield, Suffolk. He was a solicitor in Yoxford, Suffolk, but retired early and was companion to J. G. Jeffreys on many collecting trips. *Unifasciata*, with one (coloured) band (on the whorls of the spire).

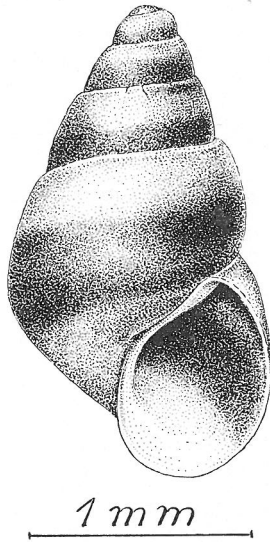


Fig. 176. *Barleeia unifasciata* (Montagu). Guernsey. BMNH 1911.10.26 24756-24775.

Shell. A rather solid, opaque, oval-conic shell, somewhat glossy and rather squat. The apical angle is c. 45°. There are 5 whorls each just tumid, meeting at shallow sutures placed a little below the periphery of the upper whorl. In many shells the body whorl is slightly keeled peripherally, the parts above and below being nearly straight in profile. The shell is generally without ornament except for irregular prosocline growth lines. There is no umbilicus though one is present in very young shells. The protoconch has a large globular, initial part, 165 μ m in diameter, and has 1½ whorls in all (total diameter 300—450 μ m); its surface bears innumerable fine spiral ridges, the grooves between them split into minute pits by cross connexions between the ridges.

Aperture. Oval, with a peristome but no labial rib. It lies in a prosocline plane making an angle of 30° with the axis of the spire. The outer lip arises normal to the surface of the body whorl and below the periphery, curving smoothly to the base of the columella, its initial part straighter than its basal part; occasionally a little out-turned at the base of the columella where a small spout may develop. Columella short and nearly straight. The inner lip is a little everted over a crack-like umbilical groove, but there is no umbilicus. The parietal part forms a thick glaze.

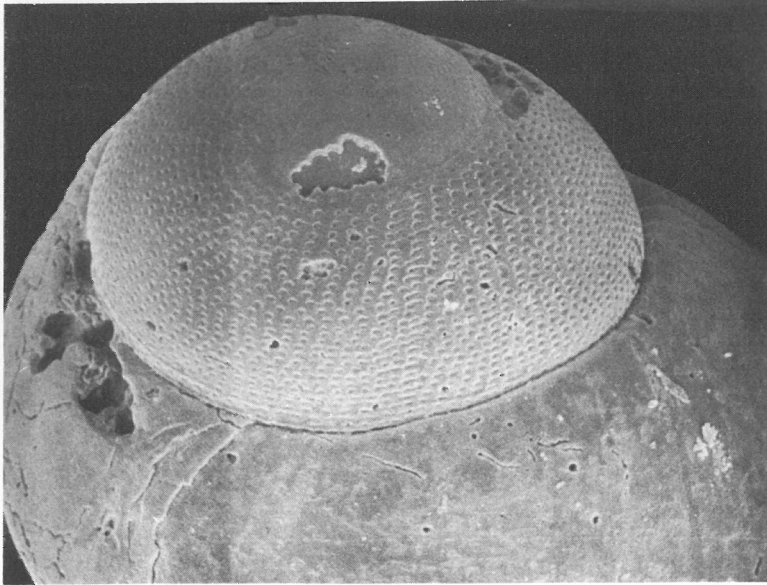


Fig. 177. *Barleeia unifasciata*. Shell apex $\times 180$. SEM photograph. Plymouth. RZ.

Colour. The shell may be uniform in colour, usually a brownish red, but may range from white to crimson. More commonly it is striped. On the spire the first 2—3 whorls are usually red; the rest have the adapical half white, the lower half red. On the body whorl the subsutural area is white, the peripheral red, the base again white with further colour in the umbilical region. The peripheral red band may be single, have a paler central area or be double; the subperipheral white band may be absent. The coloured areas usually fade before reaching the outer lip which is white, like the rest of the peristome. Within it, however, the columella and parietal region are both dark red. The peripheral red band shows clearly through the throat of the shell.

Size. 2×1.5 mm. Body whorl = 70% of total height; aperture = 40% of total height.

Animal. The head has a moderately long snout, bifid distally, with the mouth, a longitudinal slit with swollen lips, under the tip. The tentacles are rather short and tapering, not noticeably setose, each with an eye on a basal bulge. The simple mantle edge has no tentacles. Males have a long, glandular penis which arises dorsolaterally behind the right eye.

The foot is broadly oval, slightly narrowed at the middle of its length. The anterior edge is axe-shaped and double, the posterior end bluntly rounded with a median bay which marks the end of a longitudinal groove from the mouth of a posterior pedal gland. The opercular lobes are well developed; there is no metapodial tentacle. The operculum is D-shaped, also rather saddle-shaped. It has a ridge across the middle of its inner face and a tooth-like peg projects into the foot near the left end of its posterior border which is embayed at this point. The nucleus is near by; the growth lines are nearly concentric.

Colour. Yellowish with dark lines. The snout often shows the red of the buccal mass by transparency; the tentacles have a dark longitudinal line along their dorsal surface and there is a blotch of bright yellow by each eye. The opercular lobes are nearly black and the operculum is crimson with a silvery refulgence.

Geographical distribution. A southern species reaching its northern limit in the British Isles. Once thought not to occur north of the Bristol Channel it has recently been found in Shetland (Smith, 1975); this may lend credence to earlier references to its occurrence in the N. Sea.

Habitat. On algae, mainly fucoids and small red weeds, and in rock pools near low water mark on rocky shores.

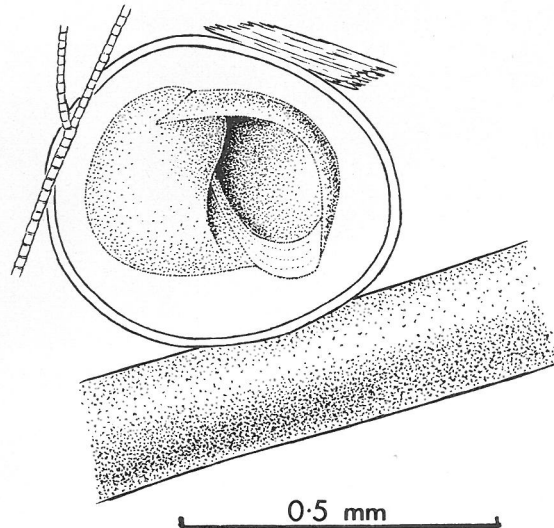


Fig. 178. *Barleeia unifasciata*. Spawn on red alga. Puerto de la Cruz, Canary Islands. Unpublished drawing by G. Thorson.

Food. A detritus feeder, ingesting diatoms from the weeds on which it lives. Faeces ovoid pellets, $100 \times 75 \mu\text{m}$.

Breeding and growth. The sexes are separate, males usually smaller than females and recognizable by the penis. Breeding (at Plymouth) occurs March — August when colourless egg capsules may be found secured to weed (mainly coralline algae) by a very narrow attachment. Each is more or less spherical, $500\text{--}600 \mu\text{m}$ in diameter, thick-walled, and contains a single colourless egg, $250\text{--}320 \mu\text{m}$ across, embedded in albumen. The veliger stage is intracapsular and the young animal emerges as a juvenile with a dark brown shell $400\text{--}480 \mu\text{m}$ in diameter. These figures rest on findings of Lebour and Thorson: the shell figured by Thiriote-Quievreux & Rodriguez Babio (1975) from Roscoff has an abrupt change from embryonic to adult sculpture at a diameter of about $300 \mu\text{m}$, suggesting rather faster development. There are no details of later growth, but the animals may well be annuals.

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CINGULOPSIDAE Fretter & Patil, 1958
CINGULOPSIS FULGIDA (J. Adams, 1797)
Helix fulgidus J. Adams, 1797
Rissoa fulgida (J. Adams, 1797)
Cingula fulgida (J. Adams, 1797)
Pseudosetia fulgida (J. Adams, 1797)
Coriandria fulgida (J. Adams, 1797)

Cingulopsis, with the appearance of a *Cingula*; *fulgida* (Lat.), shining, referring to the shell.

Shell. Rather thin and semitransparent, glossy. In general shape a squat cone, the spire flat-sided though cyrtconoid apically where it curves to a blunt tip; apical angle of mature shells $48 \pm 6^\circ$, of young ones $75\text{--}100^\circ$. There are 3—4 whorls of which the body whorl is the largest, meeting at well-marked and slightly excavated sutures placed just below the periphery of the upper whorl. There are

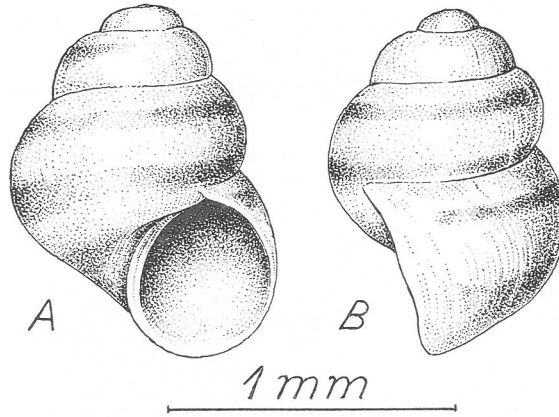


Fig. 179. *Cingulopsis fulgida* (J. Adams). Torquay. CMZ.

many fine prosocline growth lines, occasional ones larger than the others. No spiral ornament is visible except at high magnification when a few lines are obvious. The protoconch has 1.5 whorls measuring $300\ \mu\text{m}$ in diameter. It is generally smooth but has a few transverse and spiral lines near where it passes, just perceptibly, into the teloconch.

Aperture. A rather large rounded oval slightly angulated adapically and bounded by a peristome lying in a prosocline plane. The outer lip arises level with the base of the peripheral pigment band on the body whorl; it is rather thick and curves downward more or less in a semicircle to the base of the columella where, in some shells, there is a slight out-turning. The inner is almost straight, bent outwards over an umbilical groove and continues over the body whorl to complete the peristome. There is a well-marked umbilicus in many shells, whereas it appears closed in others.

Colour. White, cream or light reddish brown with red-brown spiral bands. There are usually 3: (1) below the suture of the body whorl; (2) at its periphery; (3) round the columella and umbilicus. The penultimate whorl shows only (1) and (2), the next only (1). In some shells (var. *pallida*) band (2), and sometimes also (1), may be faint or absent. The bands often disappear before reaching the outer lip which is then completely white. Young snails usually have totally brown shells.

Shells. $1 \times 0.8\ \text{mm}$. Body whorl = 66–70% of total shell height; aperture = 40% of total height.

Animal. The snout is broad, bifid at the tip, with the mouth a longitudinal slit underneath. The head bears two moderately short, setose tentacles each with an eye at the base, over rather than to the side of the tentacle. The mantle edge is simple and has no pallial tentacle. There is no penis in the male, the vas deferens opening near the mouth of the mantle cavity.

The foot is a long oval, its anterior margin straight, its sides nearly parallel, the posterior end bluntly rounded. The opening of the anterior pedal gland lies in a depression above and behind the front margin; that of the posterior pedal gland in a median groove in the posterior half of the foot. A broad triangular metapodial tentacle projects from under the hinder margin of the spiral operculum, not reaching the posterior end of the foot.

Colour. Cream with white points; white areas within the foot (triangular anteriorly, oval posteriorly) indicate the pedal glands. Operculum yellow.

Geographical distribution. From the W. coast of Scotland to the Mediterranean. The animals occur in the western Channel but are absent from the eastern Channel, N. Sea and all Scandinavian waters. Commoner in the S.

Habitat. Mainly between tidemarks, in the lower half of rocky shores and also, though less commonly, in dredgings. In spring and summer the snails are common or abundant in rock pools, especially on the bottom, though in quiet conditions they may crawl on the surface film or clamber about on mucous threads. They are also found on the small weeds of coralline pools.

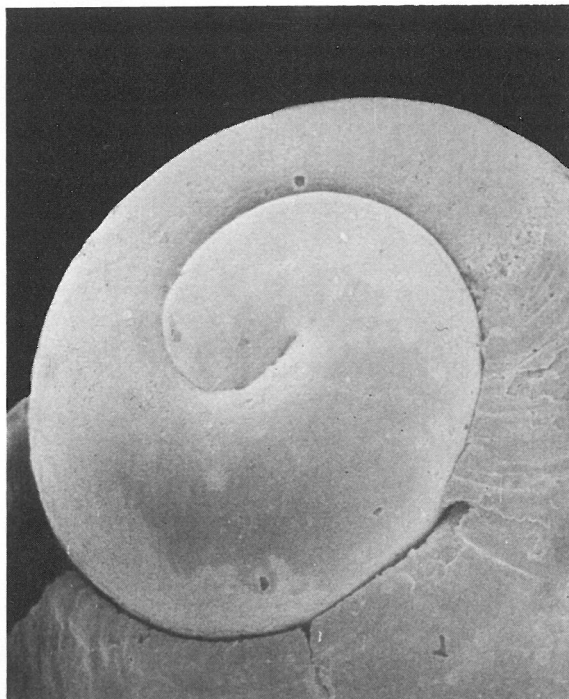


Fig. 180. *Cingulopsis fulgida*. Shell apex $\times 140$. SEM photograph. Plymouth. RZ.

Food. A microphagous animal eating detritus. Faecal pellets are ovoid, about $80 \times 40 \mu\text{m}$.

Breeding and growth. The sexes are separate though not easily recognizable, since the male has no penis. How copulation is achieved is not known. Breeding (at Plymouth) occurs in spring and summer. The eggs are colourless, few and large ($150 \mu\text{m}$ across) for such a small snail. Each egg is enclosed within a lens-shaped capsule, diameter $320 \mu\text{m}$, which is attached to coralline algae. The young hatch as small snails. Their growth has not been studied but it is probable that they are annuals, hatching in one year and dying the next after breeding.

Notes. As this animal creeps the eyes rarely extend beyond the margin of the shell: this habit may perhaps be related to the lack of pigment in the pre-apertural area under which they lie. The tentacles are continually waved during creeping and, like the tip of the snout, now and again sweep over the substratum.

We have called this species *Cingulopsis fulgida*, though Winckworth (1951) placed it in the genus *Pseudosetia* Monterosato, 1884 and Nordsieck in *Coriandria* Tomlin, 1917. Since the main differences which separate *fulgida* from other superficially similar animals are in its soft parts we have felt it better to be conservative in our nomenclature until these are equally well known for species of *Pseudosetia* and *Coriandria*.

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RISSOELLIDAE Gray, 1850
RISSOELLA DIAPHANA (Alder, 1848)
Rissoa? diaphana Alder, 1848
Jeffreysia diaphana (Alder, 1848)

Rissoella, the little shell named in honour of G.A. Risso (1777—1845), who was professor of Medical Chemistry in the Medical School at Nice and contributed much to knowledge of the Mediterranean fauna; *diaphana* (Gk.), transparent, translucent, referring to the shell.

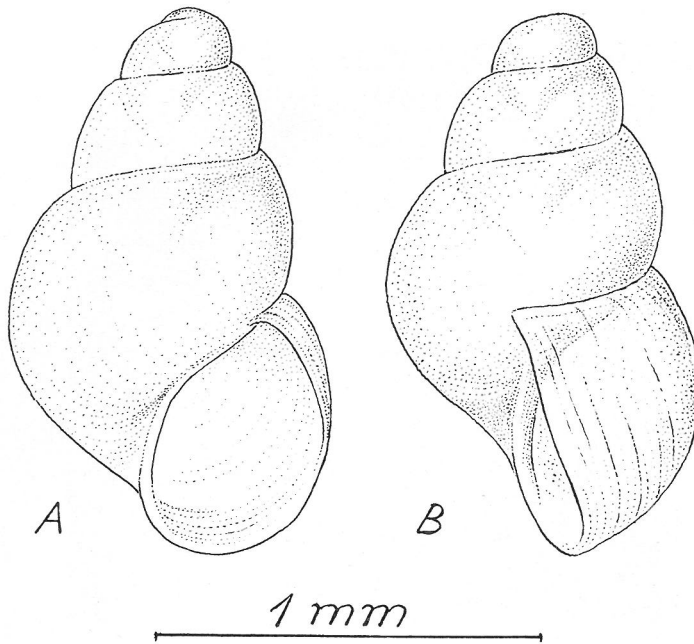


Fig. 181. *Rissoella diaphana* (Alder). Anglesey. CMZ.

Shell. Smooth, glossy, transparent and fragile. There are 4.5 tumid whorls which meet at deep sutures placed well below the periphery of the upper whorl and running obliquely to the axis of the spire. The whorls are a little flattened below each suture so that each looks a little shouldered; they expand regularly but the body whorl is relatively large, about 70% of the total height. Spire rather tall relative to its breadth (apical angle about 50°), with a blunt, rounded tip. The ornament is confined to a series of slightly prosocline growth lines, or very delicate ribs, spaced fairly evenly. The protoconch is smooth, of about 1.2 whorls and measures about $350\ \mu\text{m}$ across.

Aperture. The lips form a peristome, gibbous in outline. The outer lip is thin, arises below the periphery of the body whorl, normal to its surface and runs in a smooth curve to join the columella almost at right angles. The columella is rather straight with a rounded edge behind which lies a small umbilical chink. The parietal part of the peristome is gently concave.

Colour. Milky white; in live shells the colours of the viscera show.

Size. $1 - 1.5 \times 0.78 - 0.85$ mm. Body whorl = 60–70% of total height; aperture = 45% of shell height; breadth = 70% of shell height.

Animal. The snout is deeply bifid and each half is tentaculiform. The mouth is a longitudinal slit on the under side. The tentacles are cylindrical with blunt tips; both these and the lobes of the snout bear many motionless cilia. The eyes lie on slight bulges posterior to the base of the tentacles and never emerge from under the shell in an active animal. Along the right side of the body within the mantle cavity is a groove: a papilla at its inner end carries the female opening and a short penis extends back along it from an attachment at its anterior end. Mantle edge smooth.

The foot is rather long and narrow with a straight anterior edge embayed medially and with rounded lobes laterally. The anterior pedal gland opens on the dorsal side by a vee-shaped aperture. The foot has a slight waist and tapers posteriorly. Near the mid-point of the sole is the pore of a posterior pedal gland, connected, in crawling animals, to the posterior point of the foot by a groove. The operculum is clear, horny, with the shape of the aperture. The nucleus lies at the middle of the columellar edge opposite the umbilical chink, and is surrounded by 5–6 concentric arcs. At the nucleus there is an inwardly directed, peg-shaped process from which radiate 3 ribs, one in each direction along the columellar edge, the third crossing the operculum to the labial margin.

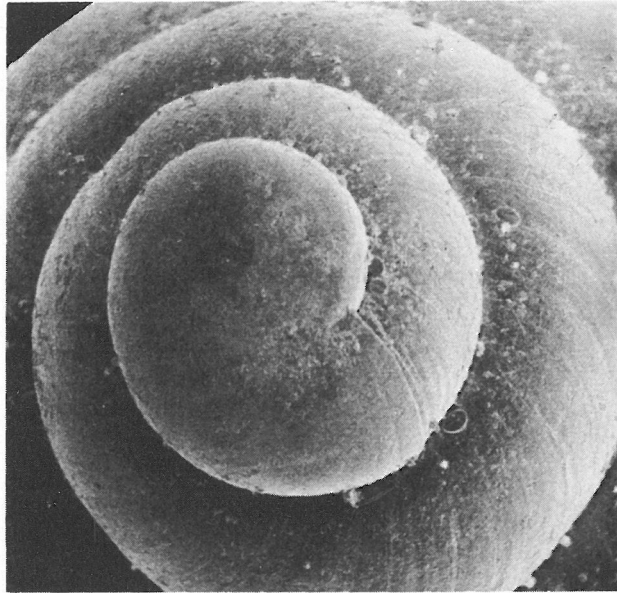


Fig. 182. *Rissoella diaphana*. Shell apex $\times 150$. SEM photograph. Isle of Lewis. RZ.

Colour. Yellowish white with patches of dark brown pigment, usually restricted in area but sometimes confluent so as to make the whole animal dark. Normally pigment occurs on the opercular lobes, on each side of the foot anteriorly and on the dorsal surface of the snout, head and neck. Some streaks also occur in the mantle skirt and there is invariably a conspicuous dark brown oval mark near the anus, formed by a group of gland cells, which is visible through the shell. The digestive gland (brown) and gonad (orange) also show. Operculum colourless save for a brown streak on the columellar edge. It shows by transparency brown arcs at the ad- and abapical ends of the labial edge: these normally remain separate and do not join as in *opalina*. An apparent groove along the pedal surface seen through the operculum marks one of the ridges on its inner surface.

Geographical distribution. Mediterranean and W. European coasts N. to Norway. Absent from most of the N. Sea, and from the Skagerrak, Kattegat and Baltic.

Habitat. Amongst the finer red weeds, particularly in coralline rock pools. Absent from bare rocks and restricted to rocky beaches between mid-tide and LWST. Abundant in summer.

Food. The weeds on which it lives, their epiphytic diatoms and some detritus. Faecal pellets rather broadly ellipsoidal, about $100\ \mu\text{m}$ long.

Breeding and growth. The animals are simultaneous hermaphrodites though passing through a phase when only male organs are mature. Breeding occurs in spring and summer. Egg capsules are ellipsoidal with a flat base by which they are fastened to green or red weeds. They measure about $480 \times 250\ \mu\text{m}$ and contain 1–2 eggs ($200\ \mu\text{m}$ in diameter) each embedded in a thin layer of albumen separated from the capsular fluid by a membrane. Development is rapid; there is no free larval stage and young snails hatch in about 2 weeks. There are no details on their growth. Young and adults abound together in summer but are much reduced in numbers in winter when all snails are immature. They would therefore appear to be annuals, overwintering as immature forms and dying after spawning.

RISSOELLA OPALINA (Jeffreys, 1848)
Rissoa? opalina Jeffreys, 1848
Jeffreysia opalina (Jeffreys, 1848)

Opalina (Lat.), looking like an opal, referring to the shell.

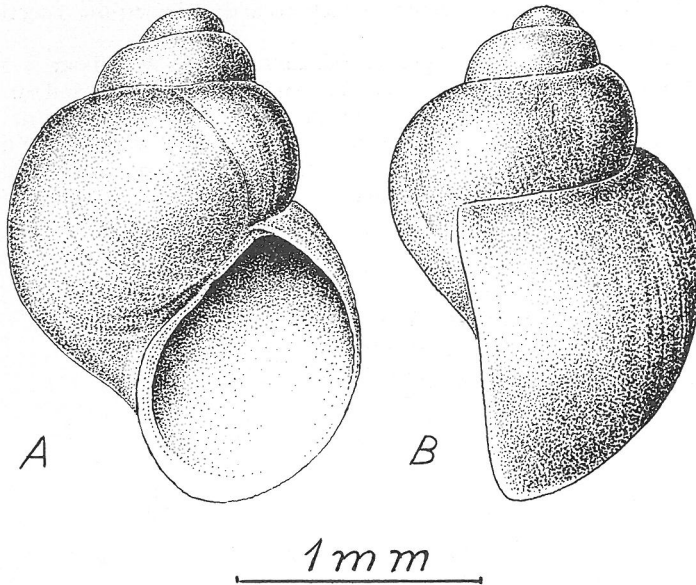


Fig. 183. *Rissoella opalina* (Jeffreys). Whalsey, Shetland. CMZ.

Shell. Smooth, glossy and nearly transparent. Globular, with a short, blunt spire (apical angle c. 75°) of 3–4 rapidly expanding and tumid whorls which meet at deep sutures distinctly abapical of the periphery of the older whorl. The ornament is confined to irregular growth lines. Protoconch smooth, of $1\frac{1}{4}$ whorls, 180–200 μm across.

Aperture. Oval to D-shaped, with a thin-edged peristome. The outer lip arises more or less at right angles to the body whorl, below the periphery, and runs in a nearly semicircular course to the columella, a little produced and out-turned basally. The columella is nearly straight, as is the parietal part of the peristome, the whole inner lip being less sinuous than in *diaphana* and the junction of outer lip and columella less angular than in that species. The columella is also thicker. A narrow umbilical chink is usually present, less clear than that of *diaphana*.

Colour. Pale yellow-brown, sometimes with a slightly darker band below the periphery, and with a refringent lustre; pale apically and on the columella. Live shells appear darker because pigmented tissues show through.

Size. 2×1.4 mm. Body whorl = 80–85% of total shell height; aperture = 55–60% of shell height; breadth = 85–90% of shell height.

Animal. Snout short, bifid, its tip slightly lobed, the mouth a longitudinal slit on the under side. The tentacles are bifid and thickly ciliated, the eyes lying behind their bases on slight bulges and never passing the edge of the shell; each is black with a pale ring round it. Penis and mantle cavity as in *diaphana*. Foot rather triangular, pointed behind. Glands and operculum as in *diaphana*.

Colour. The dorsal parts of the body are dark, mottled with purple-brown or black; the tentacles, the opening of the anterior pedal gland and the ventral parts of the foot are pale yellow. The mantle skirt has 3 dark groups of gland cells visible through the shell like the brown digestive gland; a C-shaped mark close to this is the intestine. Through the operculum may be seen a crescentic purple-

brown mark along the outer lip and a V-shaped one of the same colour is centred on the nucleus.

Geographical distribution. Not known with much certainty; the animal occurs from the Channel N. to the Shetlands and appears to be absent from the E. Channel basin, the N. and Baltic Seas and Scandinavia.

Habitat. Coralline rock pools near LWST, associated with fine weeds. Often found with *diaphana*.

Food. The weeds on which it lives, their epiphytic diatoms and some detritus. Faecal pellets as in *diaphana*.

Breeding and growth. Generally as in *diaphana*. Egg capsules ($650 \times 400 \mu\text{m} \times 500 \mu\text{m}$ high) normally contain 2 eggs ($200 \mu\text{m}$ in diameter) each embedded in a little albumen and surrounded by a membrane. They are laid in spring and summer on green or red weeds. In summer development to the hatching stage — a small snail $180\text{--}275 \mu\text{m}$ long — takes about 2 weeks. They live alongside their parents and double in size (to $430\text{--}680 \mu\text{m}$) in 2 weeks. Numbers reach a maximum in summer and fall markedly in winter. The animals are annuals with a life history like that of *diaphana*.

RISSOELLA GLOBULARIS (Jeffreys, 1852)

Jeffreysia globularis Jeffreys, 1852

Globularis (Lat.), globular, referring to the shape of the shell.

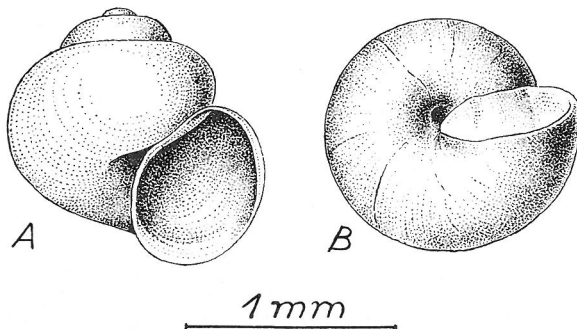


Fig. 184. *Rissoella globularis* (Jeffreys). Vadsö, N. Norway. CMZ.

Shell. Smooth, transparent, like that of *opalina* in general shape but more globose, with a shorter spire and broader body whorl. There are 3—4 tumid whorls which meet at deep sutures placed at, or even above the periphery of the upper whorl. There are a few weak spiral lines, but growth lines are often distinct, especially on the body whorl. Umbilicus deep and round.

Aperture. There is a complete peristome, ear-shaped, its long axis lying at 30° to that of the shell, and with a thin edge. The outer lip arises at the periphery of the body whorl, is a little inturned adapically and a little out-turned basally. The columella is very thin and nearly vertical. The peristome often projects a little from the body whorl.

Colour. Live shells are brown from the viscera showing through; after death they are white with a little nacreous refringence.

Size. 2×2 mm. Body whorl = 80—85% of total height, aperture = 60% of total height; breadth equals or exceeds height.

Animal. Snout bifid, each half forming a short tentacle-like process, the mouth a longitudinal slit on the ventral side. The tentacles are short, single, and the eyes prominent, placed well behind the base of the tentacles. Foot short, bilobed anteriorly, rounded behind.

Colour. Whitish with patches of dark brown pigment. Some animals are very light, others very dark, but the apex of the visceral hump always seems pale; the black spots conspicuous in the other species are not clear in this. Pigment shows along the labial edge of the operculum in retracted animals.

Geographical distribution. The Atlantic coasts of Europe from France to N. Norway but absent from the N. Sea, Denmark, Sweden and the Baltic. British records are confined to Whalsey, Shetland, and a few localities in N.W. Scotland (personal communication from Dr Shelagh Smith and Dr Graham Oliver).

Habitat. As for *diaphana* and *opalina* with which it has been found.

Food. Presumably as for the other species.

Breeding and growth. Nothing known, but probably as in *opalina*.

Notes on Rissoella species. On present information *R. globularis* is the rarest of the species, but is recognizable by the large umbilicus and great breadth. The two other species are local, but where they do occur are often very abundant in summer though numbers fall markedly in winter. Their transparent white or brownish shells, with the dark spots formed by pallial glands showing through, separate them readily from all other genera as also does the structure of the operculum. The peg on the operculum catches on the columella and acts as a hinge. The two species *diaphana* and *opalina* may be distinguished readily on shell colour, shape, snout and tentacles, pigment pattern of foot as seen through the operculum.

OMALOGYRIDAE Sars, 1878
OMALOGYRA ATOMUS (Philippi, 1841)
Truncatella atomus Philippi, 1841
Homalogyra atomus (Philippi, 1841)
Skenea nitidissima (Adams, 1800)

Omalogyra (Gk.), an even ring or circle, referring to the shape of the shell; *atomus* (Gk.), strictly what cannot be cut, but transferred to anything very small, referring to the size of the shell.

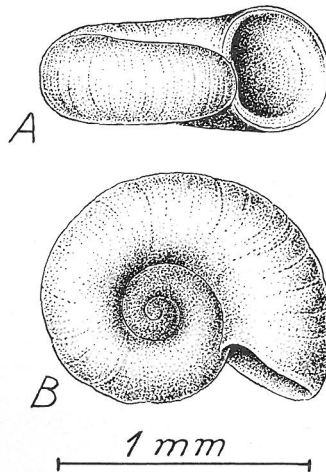


Fig. 185. *Omalogyra atomus* (Philippi). Taarbaek. CMZ.

Shell. Smooth, glossy and rather transparent. There are 2.5–3 whorls nearly in one plane so that the shell forms a plane spiral or biconcave disk; all whorls are visible both from above and below. Each is swollen, nearly circular in section but a little flattened where it rests on the preceding one. The sutures are deep and the whorls expand rapidly. The sculpture consists of orthocone growth lines sometimes irregular or thickened; some shells show a few low spiral ridges. Protoconch smooth, of about 1 whorl, and 160 μ m in diameter.

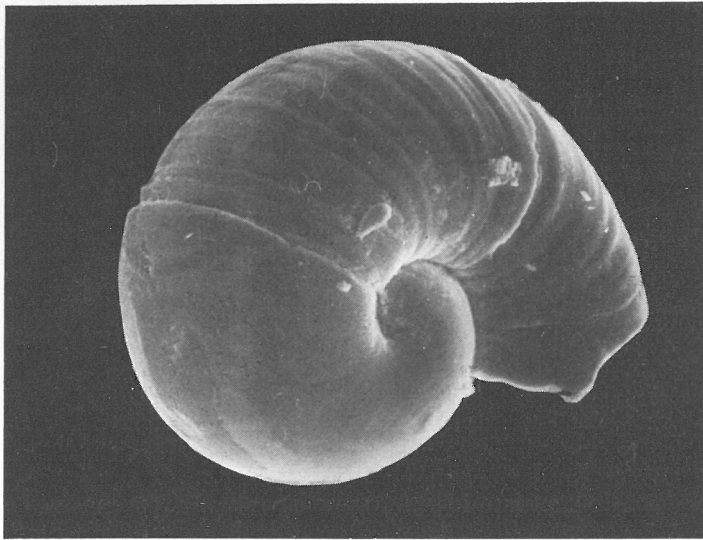


Fig. 186. *Omalogyra atomus*. Apical view $\times 260$. SEM photograph. Plymouth. RZ.

Aperture. There is a peristome, nearly circular in outline placed so that its centre lies a little above the periphery of the body whorl. In shells with spiral ridges it is a little angulated. The side in contact with the previous whorl is always flattened and may be concave. Lips sharp and very slightly everted.

Colour. Reddish brown, sometimes yellow or cream.

Size. 0.4 mm high \times 1 mm across — the smallest prosobranch to be dealt with here.

Animal. The snout is broad, depressed and deeply bifid, forming a pair of rounded, ciliated, lobes between which lies a thin membrane. The lobes functionally replace the cephalic tentacles, which are absent. The mouth is a small longitudinal slit below the connecting membrane. An eye lies flush with the general body surface at the base of each lobe; it is rarely extended beyond the edge of the shell. The mantle edge is simple; the ctenidium is absent and there is no penis visible as it is retractile into a pouch.

The foot is short and rather oblong, its anterior end a little bilobed, its posterior end rounded. The anterior pedal gland opens on the dorsal side of the foot below the mouth and the pore of a posterior gland lies in the mid-line of the sole, one third of its length anterior to the hind end. A ciliated epipodial organ lies on each side of the foot at the level of the eye. Operculum clear and horny with a central nucleus and few turns.

Colour. A nearly uniform cream, slightly darker dorsally than ventrally.

Geographical distribution. The species extends northwards from the Mediterranean and Azores to Norway. Absent from the eastern shores of the N. Sea and from the Baltic. It is also recorded from Iceland, Greenland and New England.

Habitat. On fine weeds on rocks and especially in the rock pools of the lower part of the shore and extending to 20 m depth. It is particularly common on *Ulva*, *Conferva* and *Enteromorpha*. It may also creep on the surface film and clamber about rock pools on mucous threads.

Food. The animals appear to eat mainly *Ulva* and *Enteromorpha* but may take other delicate weeds. They rasp the surface with the radula and ingest cell debris, adhering diatoms and some detritus. Faecal pellets rod-shaped, about 30 μm long.

Breeding and growth. The animals are hermaphrodite. Breeding takes place at Plymouth in spring, summer and early autumn. Egg capsules, more or less spherical, with a wrinkled surface drawn out into a little point like a nightcap (Franc, 1948), are fastened to *Ulva* or *Enteromorpha* by a slightly flattened base. A capsule is about 200–300 μm in diameter and contains 1, occasionally 2, eggs, each surrounded by albumen and a membrane. The eggs are yellowish, measure about 125 μm in diameter, develop to a veliger stage within the capsule and hatch (in about 10 days at 15–18.5°C)

as miniature snails with shells $160\ \mu\text{m}$ across. They feed eagerly and grow rapidly, reaching 0.5 mm in about 17 days and becoming sexually mature in about 7 weeks. The animals abound in summer but are scarce in winter. Those found then are immature, 0.5–0.6 mm across, presumably the progeny of late spawners, but grow to 0.7–0.8 mm by March. The snails therefore seem to be annuals, only a few autumn-bred animals surviving the winter. The reproductive system passes first through a male phase, then becomes female, copulation occurring between functional males. Animals hatching in summer, though still hermaphrodite and producing sperm, appear anatomically incapable of copulation: self-fertilization may then occur.

Notes. These snails appear to feed by holding pieces of weed between cuticular thickenings on the wall of the oral tube while rasping it with the radula.

AMMONICERA ROTA (Forbes & Hanley, 1850)

Skenea rota Forbes & Hanley, 1850

Homalogyra rota (Forbes & Hanley, 1850)

Ammonicera fischeriana (Monterosato, 1869)

Ammonicera tricarinata (Webster, 1856)

Ammonicera densecostata (Jeffreys, 1884) (?)

Ammonicera (Gk.), horn of the Egyptian ram-headed god Amun, a ram's horn; *rota* (Lat.), a wheel. Both names refer to the shape of the shell.

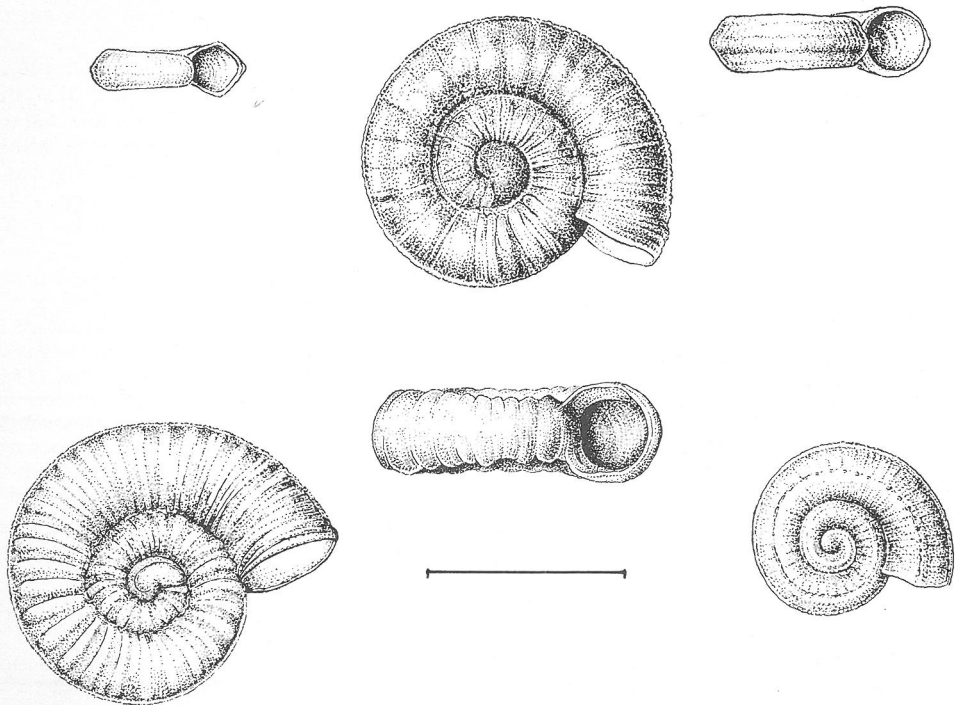


Fig. 187. *Ammonicera rota* (Forbes & Hanley). Central pair of shells, no locality given; top and bottom right, Madeira; bottom left, Carna, Co. Galway, Ireland. Line, 1 mm.

Shell. A planorbiform shell, biconcave, exposing all whorls on both sides, slightly transparent, glossy. There are 3–4 whorls, almost circular in transverse section and meeting peripherally so that about one quarter of the surface touches the next whorl. The body whorl comprises most of the shell. The ornament consists of transverse ribs; there is no spiral component so that furrows between

ribs are smooth. The ribs are numerous (30—35 on the body whorl), prosocline, low, as broad as the furrows between, and completely encircle the whorls. They are a little irregular in development and sometimes a little tuberculated at 3 points — one above, one at, one below the periphery of each whorl. When these tubercles are well marked the shell may have 3 keels. The protoconch, of *c.* 1 whorl, is rather bulbous, about 100 μm across, and smooth except for a deep spiral groove on each side.

Aperture. Oval, a little flattened where it abuts the body whorl. There is a slightly prosocline peristome which is thin-lipped, especially over the body whorl. In shells with pronounced keels the aperture may be angulated by their ends.

Colour. Reddish brown or golden yellow, the position of the tubercles often marked by a band contrasting with the rest of the shell. The throat is iridescent.

Size. Up to 1 \times 0.5 mm, more commonly 0.5 mm across by 0.25 mm high. Body whorl = aperture = total shell height.

Animal. Hardly known, but like *Omalogyra atomus*, the tentacles lobe-like with sessile eyes.

Colour. Semitransparent with a brownish tinge.

Geographical distribution. *A. rota* has been recorded from Norway (Höisaeter, 1968) to the Mediterranean. It is absent from the Danish shores of the Kattegat and from the continental coasts of the N. Sea. If *A. fischeriana* and *densecostata* are synonymous this range must be extended to cover much of the N. Atlantic.

Habitat. Amongst weeds (*Fucus*, *Laminaria*, *Cladophora*, *Corallina*, *Ulva*) and in rock pools at LWST; also on sandy bottoms to 25 m. Never apparently common in the north of its range but Franc (1948) stated that the animals were not rare at Algiers where they lived on stones half buried in sand along with *Omalogyra atomus* and *Skeneopsis planorbis*.

Food. The animals pierce algal cells using the sharp-pointed radular teeth, then suck out the contents.

Breeding and growth. The snails are probably hermaphrodite. The reproduction (of *A. fischeriana*) has been described by Franc (1948). Egg capsules were deposited at the base of strands of *Cladophora*, each more or less lemon-shaped, fixed by a small base, with the apex drawn out to a short recurved tip. It is 220—250 μm high, 150—160 μm in diameter, and contains a single whitish egg 90 μm across. The embryos studied by Franc (bred in a laboratory in Algiers) bit their way out of the capsule after 10 days, when the shell had about 0.25 whorls and a diameter of 200 μm . A few days later brown lines had appeared on it. There is no information about the life history but it may well parallel that of *O. atomus*.

Notes. Though the appearance of *A. rota* is such that it cannot easily be mistaken for any other species it is so minute a creature that it has almost certainly been frequently overlooked. It is therefore likely that both its distribution and its abundance have been underestimated. As one consequence its anatomy and way of life are almost unknown, though they may well be comparable to those of *O. atomus*: these are, however, so unusual that it is desirable that those of *A. rota* should be investigated. The rarity of the animal also means that we have barely enough information to come to conclusions about the possible specific distinctness of *rota* and *fischeriana*. We incline to Höisaeters conclusion (1968) that they are the same and we have assumed that *tricarinata* Webster, 1856 is merely a tuberculate form of this species. *A. densecostata* (Jeffreys, 1884), however, has a pattern of ribbing so distinct from that of *rota* (and *fischeriana*) that it may well be a true species.

There is considerable difference between the measurements of the protoconch given by Franc (1948) and by Rodríguez Babio & Thiriot-Quiévreux (1974) and as seen by us: these are not, however, incompatible with specimens from Algiers on the one hand and the Celtic Sea on the other.

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SKENEOPSISIDAE Iredale, 1915
 SKENEOPSIS PLANORBIS (Fabricius, 1780)
Turbo planorbis Fabricius, 1780
Skenea planorbis (Fabricius, 1780)

Skeneopsis, with the appearance of a *Skenea*; *planorbis* (Lat.), a flat ring or coil, referring to the shape of the shell.

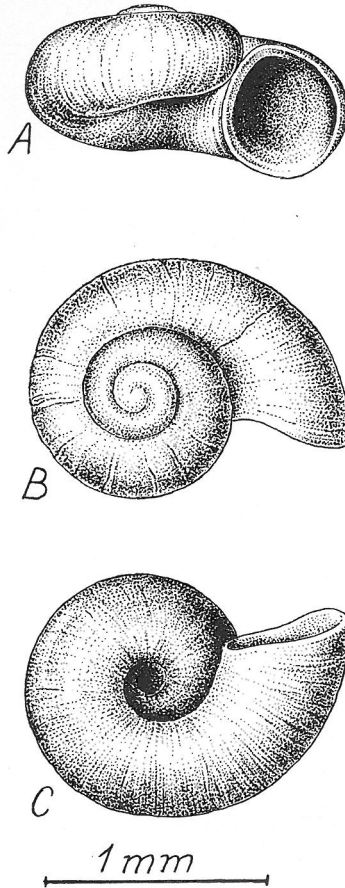


Fig. 188. *Skeneopsis planorbis* (Fabricius). Faeroes. CMZ.

Shell. Glossy, rather transparent. There are 4 whorls, tumid and nearly circular in section, rapidly expanding and meeting at deeply excavated sutures placed about the periphery of the upper whorl. The spire is extremely depressed (apical angle about $150-160^\circ$) and the base is concave and has a wide funnel-shaped umbilicus exposing all the older whorls. Sculpture mainly or exclusively growth lines, rather irregularly developed; they are sinuous, arising prosoclinally at the suture, curving towards the aperture peripherally and retreating basally. Occasionally they bunch a little to suggest incipient ribs. A few shells show slight spiral lines adapically on the body whorl. The protoconch measures about $160-170\ \mu\text{m}$ in diameter, is smooth with some spiral lines of small projections, has 1.25 whorls and is sharply delimited from the teloconch by a straight edge; here the shell may be a little pinched.

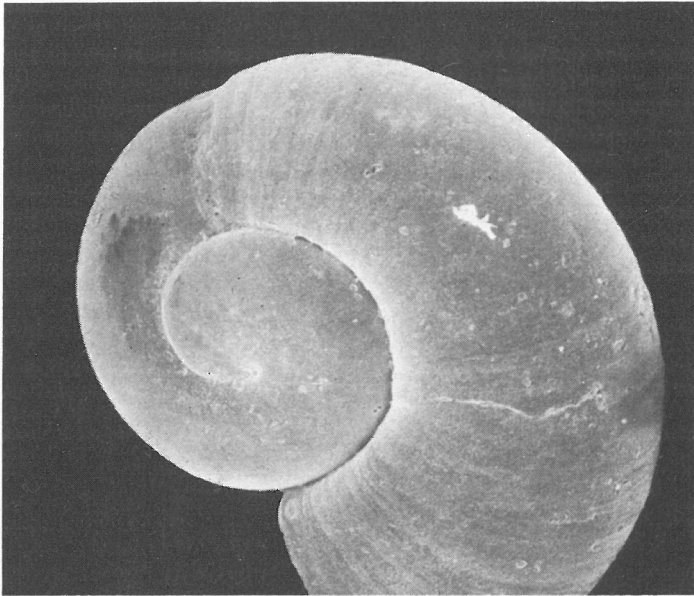


Fig. 189. *Skeneopsis planorbis*. Apical view $\times 140$. SEM photograph. Solva, Dyfed. RZ.

Aperture. The lips form a peristome, nearly circular, with a thin lip often (especially in young shells) with an uncalcified periostracal edge. It is not plane but shows ad- and abapical emarginations which cause the sinuosity of the growth lines. The outer lip arises at the periphery of the body whorl and at first runs steeply adapically; it then follows a slightly flattened course to the periphery whence it sweeps in a smooth curve to the underside of the body whorl whose curvature it follows to complete the peristome.

Colour. Chestnut brown, darkest at the apex and palest at the aperture which may be only a dark biscuit colour. Older shells are often apparently darker because of epiphytic growths.

Size. 0.75 mm high \times 1.5 broad. Body whorl = 95% of total height; aperture = 70–75% of total height.

Animal. The snout is short, bifid at its tip, the mouth lying as a longitudinal slit ventrally and subterminally. The tentacles are long, cylindrical and beset with motionless cilia, especially at the tip; they diverge widely. An eye lies on a swelling at the lateral base of each tentacle. The mantle skirt is smooth. In males a penis arises from the dorsal surface of the head behind the tentacles; it is laterally flattened and reaches to the inner end of the mantle cavity. The gill is reduced to 9 filaments.

Foot rather short, square anteriorly where it has a double edge, tapering behind. In the mid-line of the sole, about $\frac{2}{3}$ of its length back from the front lies the opening of a posterior pedal mucous gland. Operculum horny, clear, with a few turns around a central nucleus.

Colour. Grey, with occasional yellow spots. Larger areas of yellow lie between the tentacles, behind their bases and under the operculum. The floor of the mantle cavity and the metapodial lobes are dark. The front end of the foot is light because of the anterior pedal gland cells showing through.

Geographical distribution. This species occurs from the Azores N. to the Arctic on European coasts. It stretches W. through Iceland and Greenland to Arctic Canada and S. to Florida. It also occurs in the Mediterranean. Largely because of the lack of suitable habitats it is absent from E. coasts of the N. Sea nor does it occur in the Baltic.

Habitat. Amongst weeds in coralline rock pools, in gullies and on rocks at mid-tide level and down to 70 m depth. It is rarely found away from weeds and is common — in summer abundant — on the finer sorts. In pools it frequently crawls on the surface film and may descend from there on a mucous strand from the posterior pedal gland.

Food. The weeds amongst which it lives, their epiphytic diatoms and detritus. Faeces form pellets or short rods about 75—100 μm in length.

Breeding and growth. The sexes are separate, males recognizable by the penis. Breeding was said by Lebour (1937) to occur throughout the year but this is a potentiality dependent on weather conditions. It is maximal in spring and rare or absent in the normal winter, especially in the northern part of its range. Egg capsules, spherical or ovoid (up to $480 \times 350 \mu\text{m}$), with a shallow attachment disk basally, are laid on algal filaments especially *Cladophora*. Each contains 1—2 yolky eggs about 250 μm in diameter. These develop to miniature adults (3—4 weeks at 12—15°C; 2—5 weeks at 15—17.5°) and escape by rasping the capsule wall with the radula. Young animals are extremely numerous late spring — early summer, measuring 480 μm across the shell. They grow to 850 μm by January and to adult size the following spring when they breed. Most die soon after, aged about 1 year.

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VITRINELLIDAE Bush, 1897
CIRCULUS STRIATUS (Philippi, 1836)
Valvata? striata (Philippi, 1836)
Adeorbis striatus (Philippi, 1836)
Trochus duminyi Requieren, 1848

Circulus (Lat.), a little circle, referring to the outline of the shell; *striatus* (Lat.), striated, referring to its ornament.

Shell. A flattened, semitransparent, rather glossy shell with a humped, disk-like shape. There are 4—5 whorls, tumid, rounded in section, which meet at sutures lying in furrows adapical of the periphery of the whorls. The apical angle is c. 150°, the spire very depressed with the inner surface visible through a large umbilicus. The ornament consists of growth lines and spiral ridges. The growth lines are numerous and minute; they arise at right angles to the adapical suture but become markedly prosocline at the level of the first spiral ridge. Occasional lines, especially on the base are irregularly thicker. There are up to 12, commonly 9—10, spiral ridges on the body whorl, 5—6 on the penultimate, 4—5 on the antepenultimate, the rest being smooth. Each is rather steep-sided with a narrow summit, the intervening spaces about twice as broad as the summit. The ridges lie between the suture and the peripheral region of the body whorl, the most abapical a little below the periphery and often more prominent than the others. The base has otherwise no ridges though within the umbilicus each visible whorl may present 4—5 further ridges, rather puckered and tuberculated. The protoconch has 2.5 smooth whorls about 750 μm in diameter, the initial swelling only 80 μm across.

Aperture. Oval, slightly pinched adapically and flattened basally (its long axis marking an angle of c. 160° with that of the shell) but seeming nearly circular when viewed with the shell upright. There is a very prosocline peristome, not plane but showing a small peripheral sinus and subperipheral extension. The outer lip arises level with spiral ridge 6, 7 or 8 on the body whorl, normal to the surface; it has a thin edge, bevelled internally and denticulated by the ends of the spiral ridges. Basally it is a little thickened but not turned out. The inner lip is thicker and everted slightly just below the body whorl. It is not denticulated by the spiral ridges (if present); it forms a thin layer over the body whorl.

Colour. White.

Size. 1.25 \times 2.75 mm. Body whorl = 80—85% of total shell height; aperture = 70—75% of shell height.

Animal. The head has a narrow snout, a little depressed, bifid at the tip, the mouth a longitudinal slit ventrally and subterminally. Each tentacle is long, slender, setose, with an eye on a slight basal bulge. The edge of the mantle skirt is plain and carries 2 setose tentacles on the right, emerging at the adapical end of the shell aperture. Males have a small recurved penis springing from the dorsal surface of the head behind the tentacles, the male aperture at the tip. The ctenidium is large,

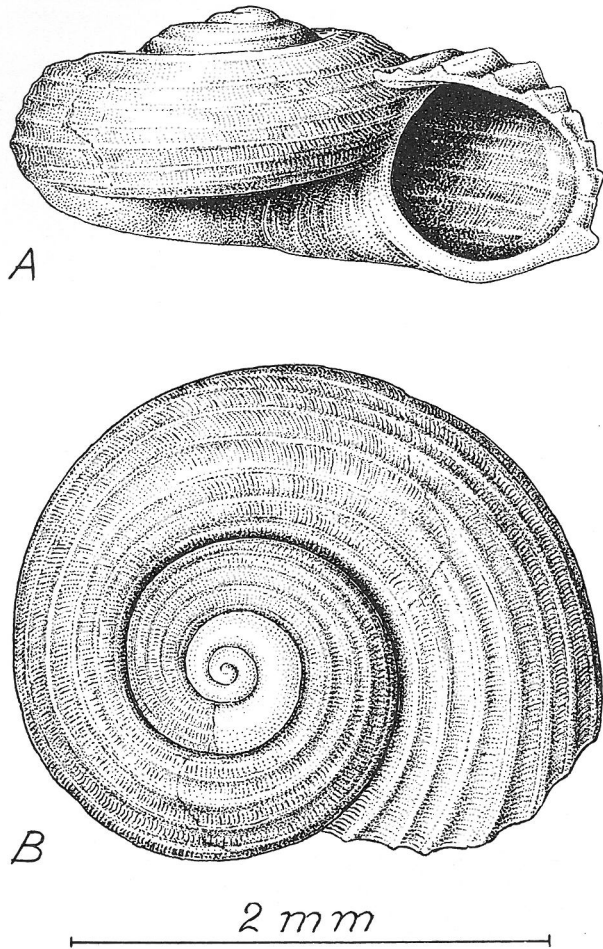


Fig. 190. *Circulus striatus* (Philippi). Bundoran, Ireland. BMNH 1911.10.26 33504-33505.

monopectinate, running from the left posteriorly to overlie the right tentacle anteriorly. A conspicuous ciliated band crosses the floor of the mantle cavity.

Foot rather narrow, notched anteriorly with recurring lateral points, expanding posteriorly where it is rounded (sometimes with median notch). Anteriorly the dorsal surface has a transverse fold at the opening of the anterior pedal gland; there is no posterior gland opening on the sole. The operculum has an approximately central nucleus and about 12 turns.

Colour. The snout is pink centrally (the buccal mass showing through), tentacles translucent with opaque white flecks. The foot is white and shows a white pedal gland by transparency. The older whorls of live shells are yellow-brown from the digestive gland showing through.

Geographical distribution. A southern species reaching N. from the Mediterranean to the coasts of Ireland.

Habitat. The only live specimens which have been seen were obtained by Fretter (1956) from the stomach of the starfish *Astropecten*. These were dredged on sandy bottoms 28–30 m deep in the Gulf of Gascony.

Food. Detritus and diatoms encrusting the sand and gravel particles among which the snails live. Faeces ovoid pellets c. $60 \times 30 \mu\text{m}$.

Breeding and growth. Unknown. Eggs in the ovary (preserved) measure 60—70 μm in diameter. The small size of the initial part of the protoconch and its final dimensions suggest early hatching and a prolonged larval life.

Notes. There has been much confusion about the systematic position of this species, largely cleared by the work of Pilsbry & McGinty (1946), Fretter (1956) and Moore (1965, 1972). It was long regarded as trochacean and many features of the shell — ornament, prosocline aperture — are compatible with such a classification, though it has not the protoconch typical of most trochaceans. The organization of the body — monopectinate ctenidium, taenioglossan radula, penis, absence of epipodium — shows unequivocally that it cannot be trochacean and allies it to rissocoans, especially the Vitrinellidae.

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TORNIDAE Sacco, 1896
TORNUS SUBCARINATUS (Montagu, 1803)
Helix subcarinata Montagu, 1803
Adeorbis subcarinatus (Montagu, 1803)

Tornus (Lat.), a turner's wheel; *subcarinatus* (Lat.), slightly keeled. The names refer, respectively, to the shape and ornament of the shell.

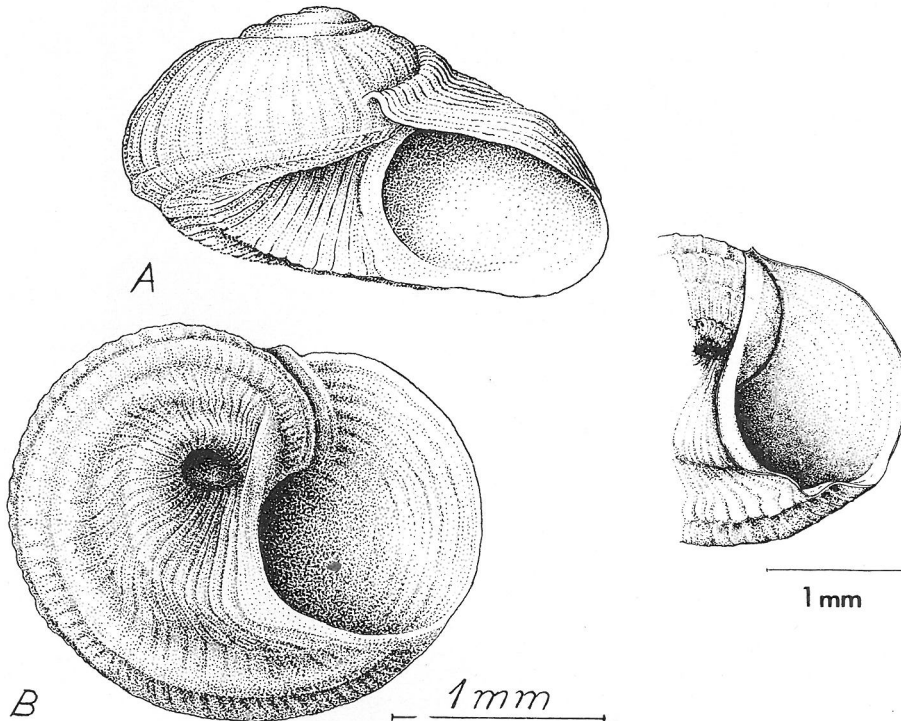


Fig. 191. *Tornus subcarinatus* (Montagu). Gt. Britain. Inset, aperture of shell with basal notch and less marked groove to anal spout (more common appearance).

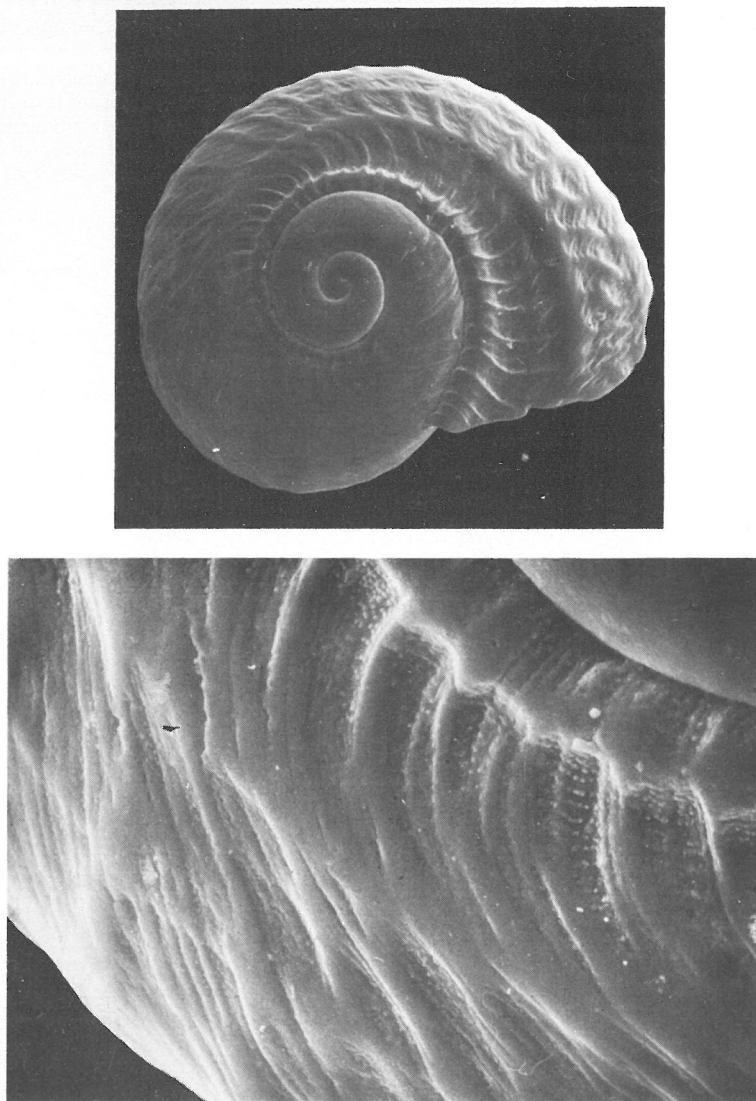


Fig. 192. *Tornus subcarinatus*. Above, shell $\times 66$; below, detail of shell surface $\times 230$. SEM photograph. Guernsey.

Shell. A little glossy, slightly transparent, nearly circular in apical view, with a very depressed spire and a wide, funnel-shaped umbilicus through which all the whorls of the spire may be seen. There are about 3.5 whorls, the last making up much the greatest part of the shell; they meet at slightly incised sutures set adapical of the periphery of the upper whorl and made sinuous by the ends of small ribs. The apical angle lies between 115° – 130° . The ornament is complex because of the interaction of growth lines, riblets, spiral keels and minute spiral ridges. The keels are conspicuous and confer some angularity on the shell. There are 6 on the body whorl: 1, immediately below the suture; 2, equidistant between suture and periphery; 3, 4, 5, above, at, and below the periphery; 6, bordering the umbilicus. The area between 1 and 2 is concave, between 2 and 3 flat, between 3 and 4 convex, between 4 and 5 flat, and between 5 and 6 concave. Only ridges 1 and 2 are visible on the spire. The riblets are equally conspicuous and cross each whorl as low ridges, narrower than the

intervening spaces. Over ridge 1 they are orthocone; between 1 and 2, markedly prosocline; between 2 and 4, slightly prosocline; between 4 and 5, orthocone and 5 into the umbilicus, distinctly prosocline. The surface of each spiral keel is folded where crossed by the ribs, most noticeably on the base of the shell as it tends to be worn away elsewhere. The pattern made by the keels and ribs is complicated by growth lines; these form small folds which run more prosoclinally than the ribs and so cross over them. Between keels 1 and 2 they appear as if branches of the ribs; elsewhere they form oblique marks between ribs. In addition all the interstices of the above pattern have an infilling of minute spirally arranged tubercles.

The protoconch has *c.* 1.5 whorls, sharply delimited from the teloconch. Its surface is smooth and its total diameter is 500—550 μm .

Aperture. Elongated oval, narrower and pinched apically. It is surrounded by a peristome lying in a very prosocline position, making an angle of 125° with the axis of the spire and with the outer lip projecting much farther than the inner. The outer lip arises at the periphery, where there is a small, upturned anal spout, and curves to the base, a little angulated, but not (in most shells) thickened, by the ends of spiral keels 2 and 3. The basal part of the lip is flattened, thickened and turned out where keels 4 and 5 end. The columella is nearly straight and the lip alongside thickened and a very little everted, especially where keel 6 ends. Over the body whorl the peristome is thin, slightly concave; it is turned out over the umbilicus and touches the body whorl only at the level of keel 5. The throat is very glossy and in some shells shows a marked groove under spiral 1, marking successive positions of the anal spout.

Colour. Worn shells are milk white; fresh ones may be white or have an orange tint.

Size. 1.5×2.5 mm. Body whorl = 80% of total shell height; aperture = 60% of total shell height.

Animal. The head has a long, narrow snout with the mouth a longitudinal, subterminal and ventral slit. The tentacles are also long. Eyes are absent or so small as not to be visible. The pallial edge is simple but carries 2 finger-like tentacles on the right; their attachment is well within the edge. At least at certain times of the year males have a penis arising behind the base of the right tentacle; it carries 5 glandular papillae along its length and tapers to a narrow tip. In active animals the gill may project from the mantle cavity; it is partly bipectinate.

The foot has a rather straight anterior edge, extended into lateral points and double because it carries the opening of the anterior pedal gland. There is no metapodial tentacle. The operculum is thin and paucispiral.

Colour. Semitransparent; pale yellow with a pink tinge.

Geographical distribution. A southern species extending N. from the Mediterranean to the British Isles. Not in the Kattegat nor in Denmark.

Habitat. The animals may be found under big boulders embedded in sand at low water and sublittorally to 3 m. The sand underneath must be well oxygenated and yellow. They have also been said to occur on algae, but are generally uncommon.

Food. Presumably detritus from the substratum on which it lives. The gut contains empty diatom cases and fine detrital particles with much mucus. The stomach contains a crystalline style, suggesting a microphagous diet.

Breeding and growth. The sexes are separate. The only male which we have seen (collected by Dr P. Bouchet at Penthièvre, Quiberon, Morbihan, France) had a penis, though this is said to be absent by Woodward (1899). The eggs (in the ovary) measure up to 180 μm across but are otherwise unknown, as are the capsules in which they are presumably laid. Planktonic veliger larvae are, however, common in summer plankton off Plymouth (Lebour, 1936; Fretter & Pilkington, 1970). The larval shell ranges in diameter from 160 μm (0.5 whorl) to 480 μm (1.25 whorls), its first whorl smooth and colourless but soon showing the first ribbing. The larva has a bilobed velum initially colourless but later dark red over its anterior half; the same colour develops over the mesopodium, though the propodium remains pale. The double tentacle is apparent on the right mantle edge by metamorphosis. There are no studies relating to growth or life history.

Brief notes are appended on two further species of *Tornus* — *imperspicuus* Monterosato, 1875 and *unisulcatus* Chaster, 1897 — treated thus because there are hardly any records of their discovery this century. It is impossible to say anything about these animals apart from their shells: it seems probable that nothing except empty shells has ever been seen. They are both minute — 1 mm or less in height — and they may therefore have been overlooked. Photographs (SEM) of the shell of *T. unisulcatus* are given by Rodriguez Babio & Thiriou-Quévieux (1974, pl. II, figs A-E).

TORNUS IMPERSPICUUS (Monterosato, 1895)

Imperspicuus (Lat.), not transparent, referring to the shell(?).

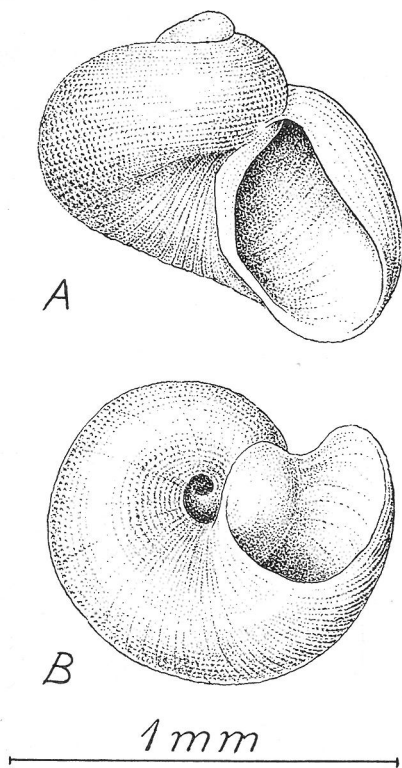


Fig. 193. *Tornus imperspicuus* Monterosato. Off Plymouth.

Shell. Rather globular, thin, hyaline, with a depressed spire. There are 2+ whorls, tumid, but flatter peripherally, below which there may be a blunt keel. The whorls are marked by minute depressions lying in spiral rows and giving an impression of spiral ridges and grooves, and by many slight, prosocline growth lines, which are absent or reduced in some shells. There is a large umbilicus. The protoconch has 1 whorl.

Aperture. Rhomboidal with a peristome lying in a prosocline plane. It shows an anal sinus, a peripheral tongue and a slight spout basally.

Colour. White.

Size. 0.8 × 1.0 mm. Body whorl = 90% of total height; aperture = 70% of total height.

TORNUS UNISULCATUS (Chaster, 1897)

Unisulcatus (Lat.), with one sulcus, referring to the deep furrow near the periphery of the shell.

Shell. In general like that of *imperspicuus* but distinguished from that (and all other species described here) by a deep infolding encircling the body whorl abapical of the periphery. A second, much shallower, groove runs on the base of the shell. The spire is more depressed than that of *imperspicuus* and the umbilicus wider, so that the whole of the underside of the spire and

protoconch are visible. The protoconch, of 1 whorl, is marked by minute depressions, irregular both in arrangement and shape. It measures c. 100 μ m across. A thick lip separates it from the teloconch.

Aperture. As in *imperspicuus* but notched by the spiral furrow.

Colour. White.

Size. 0.4 \times 0.8 mm. Body whorl = 92% of total shell height; aperture = 75% of total shell height.

Notes on Tornus species. This constitutes one of the least known of British prosobranch genera. Two of the species (*imperspicuus* and *unisulcatus*) are almost unknown and it is improbable that they will be collected; *subcarinatus* is commoner, but, even so, the habits of the animal are little known and there are some uncertainties about its structure — is, for example, the penis a seasonal organ as in *Littorina*?

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CAECIDAE Gray, 1850

CAECUM IMPERFORATUM Kanmacher, 1798)

Dentalium imperforatum Kanmacher, 1798

Caecum trachea (Montagu, 1803)

Caecum (Lat.), a blind thing, referring to the shape of the adult shell; *imperforatum* (Lat.), not perforated, directing attention to the closed upper end which was unusual for a *Dentalium*, to which genus this was supposed to belong.

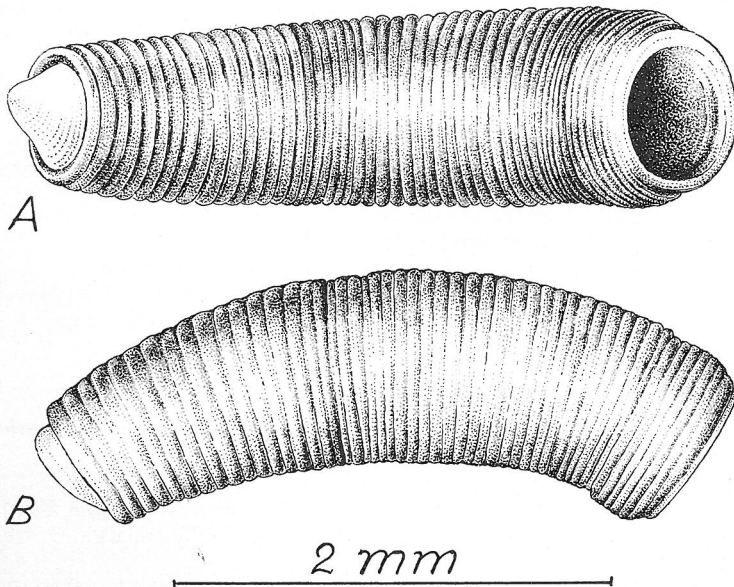


Fig. 194. *Caecum imperforatum* (Kancher). No locality given.

Shell. In the adult a slightly curved glossy tube, the radius of curvature of which varies with age. In animals up to 1.0 mm long the apex presents a spirally curved spire of 1.5—2 whorls from which the body whorl projects freely; in larger animals the spiral part is lost. The upper end is sealed by a rounded calcareous plate drawn out into a slightly eccentric point. The aperture lies at the opposite end, a trifle larger in diameter. The surface of the shell bears a series of elevated, ring-shaped, transverse thickenings, often a little irregularly arranged, of which there may be 30—50. The apical end of the tube projects minutely beyond the attachment of the seal and there is a thickening a little back from the edge of the aperture.

Aperture. Circular, its edge rather thick.

Colour. Yellowish brown, sometimes with a red tint.

Size. 4 mm long \times 0.5 mm in diameter.

Animal. The head extends into a long, flattened snout, dorsally wrinkled and rather deeply split distally. The mouth is a longitudinal slit on its underside. The tentacles are long, with setae on slightly swollen tips and eyes at the base. From each eye a fold runs back on to the floor of the mantle cavity. The mantle edge is rather thick. Although no ctenidium has been described it is likely that vestiges persist as in *C. pulchellum* and *C. nebulosum* (Moore, 1962). Males have a penis carrying several glandular papillae.

The foot has a straight anterior edge, slightly embayed in the mid-line. Its sides show a waist and the posterior end is rounded, carrying a thick, circular, nearly flat, multispiral operculum with a central nucleus.

Colour. White, with opaque white points, most abundant on the tentacles and dorsal surface of the head; operculum dark brown.

Geographical distribution. From the Black Sea and Mediterranean to the British Isles, but not N. thereof.

Habitat. Sandy and sandy-muddy bottoms to about 250 m; not intertidal.

Food. A diatom eater.

Breeding and growth. See Lebour (1936), Chukhchin (1960), Fretter & Pilkington (1970). The sexes are separate, males distinguished by the penis. The eggs and capsules are not known, but probably as in *glabrum*. Planktonic veligers are common — June to September off Sevastopol, July to January off Plymouth. They have a colourless, transparent shell of up to 2 whorls, coiled in one plane, c. 280 μ m in diameter, its surface smooth, the aperture a little flared. At a diameter of c. 300 μ m the body whorl starts to separate from the others. The larva has a bilobed velum, initially colourless but later edged with reddish purple; the rest of the body is colourless except for a dark stomach and yellow-green digestive gland. The hinder part of the foot is short, carrying a thick operculum. There are no details of metamorphosis or life history.

CAECUM GLABRUM (Montagu, 1803)

Dentalium glabrum Montagu, 1803

Brochina glabra (Montagu, 1803)

Glabrum (Lat.), smooth, contrasting the shell with the ringed one of *imperforatum*.

Shell. This differs only in details from that of *C. imperforatum*. It is smaller; the apical seal is a rounded plate not drawn into a point; the surface is marked only by slight rings.

Aperture. Circular.

Colour. White.

Size. 2.5 mm long \times 0.5 mm broad.

Animal. As in *imperforatum*; the ridges on the dorsal surface of the head are vestigial, the operculum convex.

Colour. White; operculum yellow.

Geographical distribution. From the Mediterranean to Norway and the Swedish W. coast (Bohuslan). Only dead shells have been found off the E. coast of Denmark.

Habitat, food. As for *imperforatum*.

Breeding and growth. See Götze (1938), Thorson (1946). At Heligoland breeding occurs in July — August; in the Sound larvae were common August — January. The egg capsules are transparent and spherical, about 150 μ m in diameter, with a slightly wrinkled surface, and are laid in the sand in

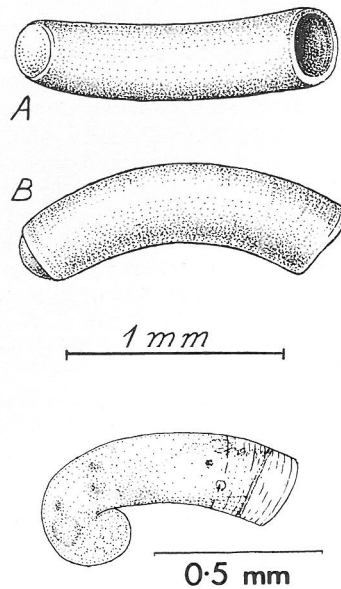


Fig. 195. *Caecum glabrum* (Montagu). Lysekil, Bohuslan. CMZ. Below, young shell with spiral protoconch still attached.

which the adults live. Each contains a colourless egg, $70\ \mu\text{m}$ across, enclosed in a membrane and lying in albumen. Free-swimming veliger larvae hatch with a plane spiral shell of 1.5 whorls, $240\ \mu\text{m}$ across, colourless, transparent and smooth. The larva has a 2-lobed velum with purple-black pigment marginally; this pigment is also present on the intestinal wall; the digestive gland is yellow-brown. When the shell measures $380\ \mu\text{m}$ across, the body whorl begins to separate from the spire. Metamorphosis occurs when the shell is about $410\ \mu\text{m}$ across and the larval shell is broken off when the whole structure has a length of about 1.0 mm.

Notes on Caecum species. These animals are unusual in the way in which the shell grows. After loss of the spiral protoconch the upper end of the body whorl is sealed with a cap of callus. This breaking and sealing may be repeated so that the shell remains a short arc subtending an angle of about 45° ; Marshall (1899), however, recorded shells without breakage which had become semicircular.

Because of some resemblance between the growth pattern of the shell of *Caecum* and that of *Vermetus*, the family Caecidae has been traditionally assigned to the Cerithiacea. Moore (1962), however, on the basis of a careful comparison of the anatomy of *Caecum* spp. and a number of small cerithiaceans, has shown that they are properly rissoaceans.

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KEY

In the following key to British and Danish rissoaceans reference is made to colour patterns on the shell: colour is sometimes in the periostracum, sometimes in the calcareous shell. Worn shells may lose the periostracum and have the rest bleached, when the colour may differ from that of the live shell described below. Vestigial colour is more easily seen in wet shells. Shells half-transparent in life may become opaque when long empty. Ornament is best seen in dry shells; ribs (especially obsolete ones) are more easily seen and counted if the shell is mounted on plasticine and viewed apically. This also allows the protoconch to be measured. Lighting is important to show shell topography.

- | | |
|--|--|
| 1. Shell a short curved tube closed by a plate at apical end (<i>Caecum</i>); shells < 1 mm may have a minute spiral coil at this end | 2 |
| Shell spirally coiled | 3 |
| 2. Surface of tube smooth; apical plate rounded | <i>C. glabrum</i> (p.234) |
| Surface of tube transversely ridged; apical plate pointed | <i>C. imperforatum</i> (p.233) |
| 3. Shell broader than high; umbilicus wide | 4 |
| Shell taller than broad; umbilicus chink-like or closed | 10 |
| 4. Shell flat, whorls in a plane spiral; no cephalic tentacles only rounded lobes with sessile eyes | 5 |
| Shell not flat but has low spire; tentacles elongate, cylindrical | 6 |
| 5. Whorls marked only by growth lines; penult whorl touches peristome abapical of mid-point of inner lip | <i>Omalogyra atomus</i> (p.221) |
| Whorls with spiral and transverse ridges of varying height; penult whorl touches peristome at mid-point of inner lip | <i>Ammonicera rota</i> (p.223) |
| 6. Shell with pronounced spiral ridges; aperture very prosocline; 2 tentacles on right of mantle skirt | 7 |
| Shell without pronounced spiral ridges | 8 |
| 7. 6 spiral ridges on body whorl; outer lip with anal spout; operculum with 3-4 turns; animal without eyes; ctenidium bipectinate | <i>Tornus subcarinatus</i> (p.229) |
| 8-10 spiral ridges on body whorl; outer lip without spout; operculum with 12 turns; eyes present; ctenidium monopectinate | <i>Circulus striatus</i> (p.227) |
| 8. Shell with 1 deep subperipheral spiral groove on body whorl; no living 20th century records in Britain, absent from Scandinavia | <i>T. unisulcatus</i> (p.232) |
| Shell without such groove | 9 |
| 9. Spire very low; whorls smooth; umbilicus very wide; aperture orthocline, nearly circular; reddish brown; common | <i>Skeneopsis planorbis</i> (p.225) |
| Spire moderately low; whorls marked with spiral lines of small pits; umbilicus narrow; aperture prosocline, elongated; no living 20th century records in Britain, absent from Scandinavia | <i>T. imperspicuus</i> (p.232) |
| 10. Shell glossy, transparent, iridescent, smooth; whorls swollen; no colour bands; operculum with nucleus at middle of columellar edge, 3 radiating ridges on its inner face; snout deeply bifid (<i>Rissoella</i>) | 11 |
| Shell and operculum not like this | 13 |

- | | |
|---|------------------------------------|
| 11. Aperture < 50% of shell height, body whorl c. 70% of shell height; umbilicus a chink; cephalic tentacles single | <i>R. diaphana</i> (p.216) |
| Aperture > 50% of shell height, body whorl > 80% of shell height | 12 |
| 12. Shell taller than broad; umbilicus small; cephalic tentacles bifid | <i>R. opalina</i> (p.219) |
| Shell as broad as, or broader than it is high; umbilicus large; tentacles single | <i>R. globularis</i> (p.220) |
| 13. Body whorl bears a reticulate series of fine pits, with or without ribs elsewhere on the shell; shell glossy (<i>Rissoa violacea</i> agg.) | 14 |
| No reticulate series of pits on body whorl though other ornament may be present | 16 |
| 14. No ribs apart from a labial rib; shell rather thin; apex and outer lip red-brown, rest of peristome and labial rib white; inner lip does not extend over body whorl; northern distribution | <i>R. porifera</i> seg. (p.207) |
| Ribs usually present; lilac colour round peristome and at apex; inner lip spreads over body whorl | 15 |
| 15. Ribs on body whorl die out at or above periphery; not > 24 ribs in all, > 15 per whorl; in apertural view ribs visible only on body whorl; expansion of inner lip over body whorl slight | <i>R. rufilabrum</i> seg. (p.207) |
| > 24 ribs in all, < 15 per whorl; in aperture view ribs visible on both body and penult whorls; expansion of inner lip over body whorl considerable | <i>R. lilacina</i> seg. (p.205) |
| 16. Ornament on shell none, or of spiral ridges, sometimes with ribs; if present ribs are confined to the subsutural parts of the whorls and do not reach the periphery; they may be on all or only a few upper whorls | 17 |
| Ornament different from this | 31 |
| 17. Breadth of shell = 50% or more of height | 18 |
| Breadth of shell < 50% of height | 27 |
| 18. Shell uniform in colour; apex blunt | 19 |
| Shell with spiral or transverse colour bands (or both) on body whorl; apex blunt or sharp | 20 |
| 19. Shell smooth but often with 1 peripheral spiral ridge on body whorl; white or yellowish; Scandinavia only | <i>Cingula turgida</i> (p.162) |
| Shell with many fine spiral ridges; globose; yellowish or white | <i>C. alderi</i> (p.156) |
| 20. Body whorl with > 1 spiral colour band and without transverse markings | 21 |
| Body whorl with numerous transverse colour markings, sometimes also with 1 spiral colour band at base | 23 |
| 21. 4 whorls; 3 spiral red-brown bands on body whorl (subsutural, peripheral, umbilical); rather opaque; growth lines distinct; outer lip thick, not everted basally; umbilicus usually clear and deep; no pallial tentacles; no penis in ♂, metapodial tentacle filiform | <i>Cingulopsis fulgida</i> (p.214) |

- Animal without this combination of characters 22
22. 6-7 whorls; usually 3 spiral red-brown bands on body whorl; spiral ridges on body whorl; peristome orthocone, angulated adapically; metapodial and pallial tentacles present; operculum yellow without internal process; usually living high on shore
Cingula cingillus (p.154)
- 5-6 whorls; usually 1 red band on body whorl; smooth; peristome prosocline, only slightly angulated adapically; no metapodial or pallial tentacles, operculum crimson with internal process; usually living low on shore
Barleeia unifasciata (p.212)
23. Shell usually with labial rib, lilac apex and dark comma-shaped mark on body whorl by labial rib; whorls a little tumid; metapodial tentacle cylindrical; opercular lobes black
Rissoa parva v. *interrupta* (p.194)
24
- Animal without this combination of characters
24. Whorls nearly flat, with 2 rows of brown transverse marks; metapodial tentacle 3-pointed; opercular lobes yellow
Cingula semistriata (p.159)
25
- Whorls tumid, sutures deep
25. 4 whorls; apex blunt; umbilicus large; columella oblique and curved; body whorl with 2-4 rows of brown spots or streaks; not N. of Channel Is.
C. pulcherrima (p.160)
- 5-6 whorls; apex sharp; umbilicus small or closed; columella nearly vertical, rather straight, transverse brown bands on penult and body whorls
26
26. *The next two species are often difficult to separate unless the body and shell are both available.*
Apex bronze; a few spiral lines on body whorl; whorls more tumid, sutures deeper and base of aperture more everted than in the next species, but these points are not obvious unless specimens are available for comparison; sometimes a spiral brown band on base of body whorl; metapodial tentacle flattened
Rissoa albella (p.200)
- Apex red-purple; sometimes indications of a fine, shallow reticulation on penult whorl; whorls less tumid and with less deep sutures; no spiral brown band on base; metapodial tentacle filiform
R. inconspicua (p.198)
27. Shell with clear spiral ridges and grooves; small ribs on some or all whorls of teloconch; sutures are very oblique
28
- Shell smooth or with obscure spirals, without ribs
29
28. Ribs on all whorls of teloconch; often 2 brown spiral bands on body whorl; larval shell rather small, up to 340 μ m across
Onoba semicostata (p.163)
- A few ribs on upper whorls of teloconch (a few shells lack these); larval shell rather large, up to 550 μ m across
O. aculeus (p.166)
29. Shell thin; spire tall (7 or more whorls); body whorl < 50% of height; a small bulge may occur on columella (Fig. 175B); peristome flared all round (the last two features may be very slight); posterior end of foot not bifid; usually from brackish habitats
Rissoa membranacea (p.208)

- Shell not thin; spire of 7 whorls at most; body whorl > 50% of height; no bulge on columella; peristome not flared though perhaps everted basally; posterior end of foot bifid 30
30. Spiral ridges distinct; shell whitish; spire rather straight-sided, apex blunt *Onoba proxima* (p.167)
- Spiral ridges very fine or absent; suture of last whorl very deep; shell thin; spire cyrtoconoid with pointed apex *O. vitrea* (p.169)
31. Ribs or transverse ridges absent from topmost whorls of teloconch but present on others, reaching at least to periphery on body whorl; metapodial tentacle single and filiform; pallial tentacle on right (*Rissoa*) 32
- Ribs or transverse ridges on all whorls of teloconch (this may not be very obvious on worn shells); metapodial tentacle triple or 3-pointed; pallial tentacles on right and left (*Alvania*) 36
32. Shell tall; aperture large, peristome flared all round; usually a bulge on columella and a thickening in throat at level of labial rib; in marine habitats *R. membranacea* (p.208)
- Shell without this combination of characters 33
33. 18-30 thin ribs on body whorl, dying out at periphery; many fine spirals; protoconch dark purple, body whorl with subsutural brown streaks, peristome brown *R. inconspicua* (p.198)
- 8-25 broad ribs on body whorl; microscopic spirals between ribs 34
34. Shell usually with dark comma-shaped mark on body whorl by labial rib; apex pink-lilac; 8-12 ribs on body whorl dying out at periphery where they join a stronger spiral *R. parva* (p.194)
- Shell without comma mark 35
35. Shell solid; spire slightly coeloconoid towards apex; whorls of protoconch rounded, ribless ones of spire nearly flat; 10 ribs per whorl; apex, peristome and throat tinged lilac; a southern species *R. guerini* (p.203)
- Shell semitransparent; spire straight-sided or cyrtoconoid; all whorls swollen; 10 ribs per whorl; apex bronze; body whorl often with brown transverse bars, brown spiral on base, dark streak on columella *R. albella* (p.200)
36. Ribs numerous, in the form of fine transverse ridges much less obvious than spiral keels; spire turreted; aperture = 50% of height *A. carinata* (p.192)
- Ribs as well developed as spirals or more so 37
37. Ribs more conspicuous than spirals which are slight except for a large basal keel; ribs opisthocline and flexuous; aperture oblique, small, with thick peristome *A. crassa* (p.170)
- Ribs and spirals about equally developed 38
38. Throat with row of ridges or teeth within outer lip 39
- No such row 42
39. A knoblike tooth on the columella; reticulation of ribs and spirals coarse; sutures deep; aperture large; 12-13 teeth in throat *A. cancellata* (p.177)
- Shell without this combination of characters 40

40. 35-45 ribs on body whorl; apex similar in colour to rest of shell (*A. beani* agg.)
16-20 ribs on body whorl; apex golden yellow
41. Reticulation of surface rather coarse; 4 spiral ridges on penult whorl
Reticulation fine; 6-7 spiral ridges on penult whorl
42. Spire noticeably cryptoconoid; body whorl = 70% of total height, interstices of reticulation oblong; aperture narrow, elongated adapically; Channel Is. only
Shell without this combination of characters
43. Apex blunt; larval shell with zigzag lines; spiral ridges on body whorl better developed than ribs; only 1 record of live animals this century in British waters
Shell without this combination of characters
44. About 14 ribs on body whorl crossed by 4-5 spiral ridges; 2 more spiral ridges lie below ribs; reticulation pointed at nodes; whorls shouldered; sutures deep; axis of aperture oblique
Many more ribs and spiral ridges on body whorl; whorls rounded; axis of aperture nearly vertical
45. 30-40 ribs on body whorl; ribs and spirals numerous and fine, the latter becoming fainter on base of shell; 6 whorls, apex pointed; protoconch of 2-5 whorls
19-24 ribs on body whorl; where ribs and spirals cross the ribs are more prominent but the spirals become more marked on the base of the shell; 4-5 whorls, apex blunt
46. Ribs and aperture opisthocline; whorls a little flattened; sutures deep; protoconch up to 400 μm across
Ribs and aperture orthocline; whorls rounded; protoconch > 400 μm across; British records all from Scilly area
- 41
A. cimicoides (p.175)
A. calathus seg. (p.173)
A. reticulata seg. (p.173)
A. lactea (p.186)
43
A. jeffreysi (p.182)
44
A. zetlandica (p.180)
45
A. punctura (p.184)
46
A. abyssicola (p.188)
A. subsoluta (p.190)