THE PROSOBRANCH MOLLUSCS OF BRITAIN AND DENMARK

PART 6 — CERITHIACEA, STROMBACEA, HIPPONICACEA, CALYPTRAEACEA, LAMELLARIACEA, CYPRAEACEA, NATICACEA, TONNACEA, HETEROPODA

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CERITHIACEA

The Cerithiacea form one of the largest groups of mesogastropods and, in the light of their early appearance in the fossil record, probably one of the most primitive. A majority of the 11 families comprises marine animals but cerithiaceans have also invaded brackish and freshwater habitats and there are almost as many freshwater genera as there are marine. The snails are predominantly tropical and warm temperate in distribution; a few genera occur in Europe and N. America, but only some turritellids live in high latitudes. In north-western Europe the superfamily is represented only by the genera *Turritella* and *Bittium* though 2—3 cerithiid species and 1 diastomid are found in Biscay, the Mediterranean and Black Seas, and some freshwater species occur in Austria and Balkan countries. Many cerithiaceans are extremely abundant (for example, *Turritella, Vermetus, Melanopsis* and *Cerithium*) and dominate the habitat in which they occur.

The cerithiacean shell is usually high-spired and slender, with many whorls. In the most primitive families, like Turritellidae, Vermetidae and Planaxidae, the ornament is predominantly spiral; in more advanced families some transverse ornament occurs, giving tuberculated or slightly ribbed shells in which varices may be common (Thiaridae, Cerithiidae). The aperture is usually small, often somewhat angulated; whilst the peristome is entire in the more primitive families in many others it shows a notch or short canal basally, and, in some genera, an anal sinus as well.

The body differs from that of most mesogastropods in three main ways: most are style-bearing, all males are aphallic and, in both sexes, the pallial section of the genital duct is open. In the absence of a penis sperm transfer seems to depend upon approximation of the mantle cavities of two animals with the respiratory current as the agent moving the sperm. Spermatophores have been described in vermetids, some thiarids, modulids and cerithiids. The mantle edge is often fringed with tentacles and this may be, at least sometimes, associated with life on softer substrata and a dependence on ciliary currents for food as well as for ventilation of the ctenidium *(Turritella).* Vermetids also feed similarly but live on hard bottoms; they may combine ciliary feeding with a mucous net or rely on that alone. Most cerithiaceans use the radula in feeding, gathering up detritus, decaying or fresh vegetation. None is carnivorous. Spawn is usually a tangled ribbon of jelly with embedded egg capsules, or an irregular pile of capsules, though some freshwater species are viviparous.

As treated here, Cerithiacea are taken to contain 11 families. Of those traditionally placed in the superfamily we have excluded (1) the Caecidae, now regarded as rissoaceans; (2) the Mathildidae, Architectonicidae Cerithiopsidae and Triforidae (= Triphoridae), on the ground that in many features they show links with Epitonacea; (3) the Abyssochrysidae which Houbrick (1979) thinks are relict Loxonematacea. Of the 11 families the marine Turritellidae and Vermetidae show a marked trend towards a sedentary and gregarious way of life dependent on ciliary-mucous feeding. Both families contain genera which have become immobilized by attachment to the substratum and some of which show uncoiling of the shell. There are 4 other marine families, Planaxidae, Cerithiidae, Modulidae and Diastomidae (= Finellidae), but the last is not well known. Planaxids and cerithiids are amongst the most abundant of inter- and subtidal prosobranchs of warm seas.

The remaining families, Syrnolopsidae, Thiaridae (often known as melaniids), Melanopsidae, Pleuroceridae and Potamididae, are inhabitants of brackish or fresh water, where they are often extremely common. Some have importance as vectors of platyhelminth parasites. The syrnolopsids and a group of thiarids constitute a collection of animals confined to Lake Tanganyika, where they have undergone a marked adaptive radiation whilst remaining within the dietary limitations imposed by the style-bearing and herbivorous habit of cerithiaceans.

HOUBRICK, R.S. 1979. Classification and systematic relationships of the Abyssochrysidae, a relict family of bathyal snails (Prosobranchia: Gastropoda). *Smithsonian Contributions to Zoology,* no. 290, 1-21.

TURRITELLIDAE Woodward, 1851

TURRITELLA COMMUNIS Risso, 1826, auger or screw shell

Turritella terebra (Pennant, 1777), non Linnaeus, 1758

Turritella tricarinata (Brocchi, 1864) forma *communis*

Turritella (Lat.), a little tower, referring to the shape of the shell; *communis* (Lat.), common (in its occurrence).

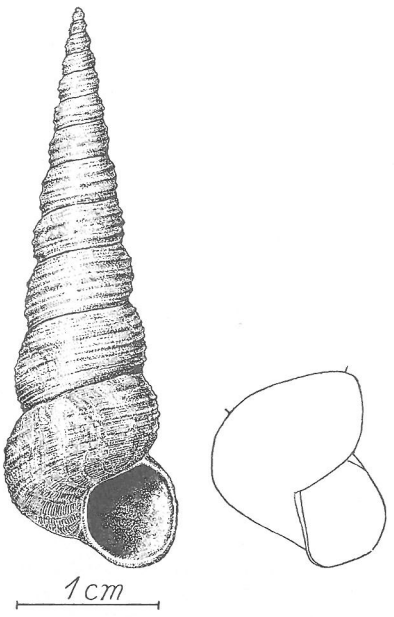

Fig. 215. *Turritella communis* Risso. Aalbaekbugt. CMZ. The shell drawn is rather more weakly sculptured than most, and the aperture is usually less rounded basally as is shown inset.

Shell. Tall, narrow and sharply conical, with a flat base; moderately thin and glossy but not transparent, older whorls often losing their polish. The spire, superficially straight-sided (neglecting the curvature of the whorls), is divisible into a basal part with more nearly parallel sides and an upper part where they are more convergent. The two parts meet 10-12 mm below the apex. This gives the shell a gently cyrtoconoid outline. The apical angle of young shells is 20-25°, of grown ones 10-15°. In some shells the upper part is slightly coeloconoid and even a little skew. There are 16-20 whorls in large shells; to this number should be added at least 2, since the protoconch is always lost. The whorls enlarge slowly, are tumid and meet at sutures well below the periphery of the upper whorl; the sutures are shallow towards the apex, deeper towards the base. The shell bears growth lines and spiral ridges and grooves, the latter the more conspicuous. The spiral ridges are numerous and of varying size: in most shells each whorl of the spire has 3 prominent ones, 1 at the periphery, 1 above and 1 below, but the number is variable and there may be twice as many. Each is narrow, with slightly flattened top; between them lie grooves, U-shaped in section and broader than the ridges. At least in younger shells some papillae, roughly aligned in spiral rows, lie on the flanks of the major ridges. In addition the whole surface of each whorl carries innumerable small ridges; some are larger, especially 1 lying in the middle of the groove between the major ridges. On the body whorl a fourth ridge forms an angle at the margin of the base and there may be another prominent one in its subsutural area. The base bears a series of equal ridges. Towards the aperture all ridges become less pronounced. The growth lines are prosocline at the suture, become opisthocline at the periphery and repeat this pattern on the base. Where they cross the spiral ridges they impart a slightly beaded appearance to them.

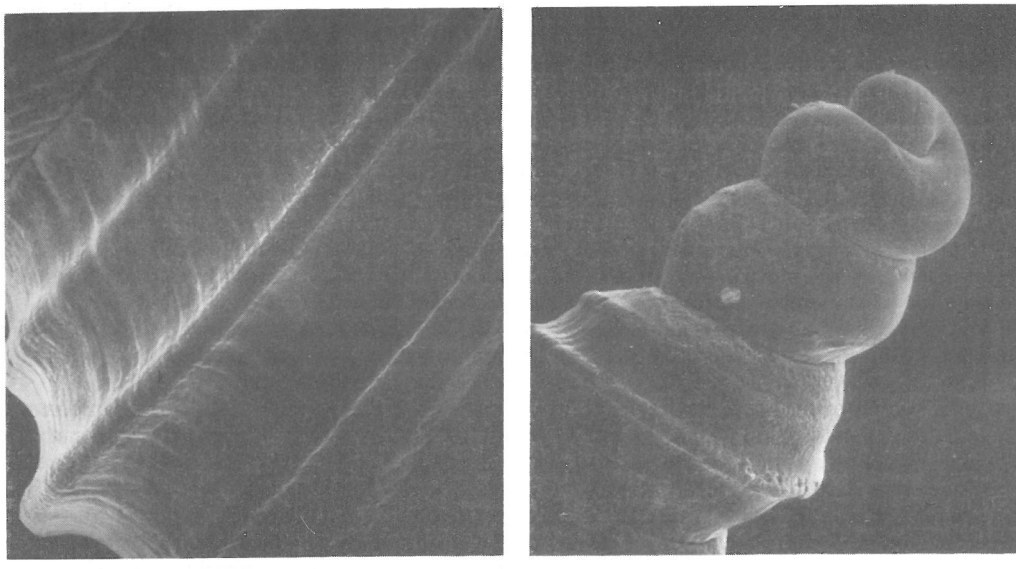

Fig. 216. *Turrritella communis.* Right: apical region × 150; left: detail of shell pattern × 270. SEM photographs. RUZ.

The protoconch has 2—2.5 rather swollen whorls which are smooth. Its diameter is *c.* 250 μm and it is not distinct from the teloconch.

Aperture. This is small, squarish and lacks a peristome; it lies in a gently prosocline plane. Except in aged specimens it has a thin edge which is almost always broken. The outer lip arises either at the angle of the body whorl or on the base below this, tangential to the base. It runs outwards and curves abapically. Its peripheral part (if complete) is sinuous following the curve of the growth lines and in profile continues the outline of the spire. It is crenulated by the edge of the main spiral ridges and turns through nearly 90° at the angle of the body whorl. The base is nearly straight and joins the pillar almost at right angles. The columella is a very little curved and leans to the left. The inner lip everts over a minute umbilical groove and forms a glaze over the body whorl. There is no umbilicus.

Colour. Brownish yellow to white. The subsutural parts of each whorl are often darker and occasional darker markings cross them. There is often a lilac tinge on the base and near the aperture. The larger spiral ridges are pale. Weathering often destroys or obscures the colour and the shell then looks white.

Size. Shells up to 55 × 16 mm have been found, but 30 × 10 is the largest likely to be collected.

Animal. The head has a broad, gently tapering snout slightly embayed at the tip, under which the mouth lies, a longitudinal slit with a bulging lip on each side. The tentacles are filiform, rather short, with an eye on a lateral bulge near the base, a little to the underside. Right of and underneath the right tentacle lies the end of a groove with high walls which crosses the floor of the mantle cavity from the left. Its left wall expands to a disk-like structure below the tentacle; the right wall forms a scroll acting as exhalant siphon. The mantle skirt carries a series of marginal tentacles: those on the right are small, often bifid or trifid, those on the left similar but also connected to a series of pinnately branched extensions lying across the mouth of the mantle cavity. The cavity, osphradium and ctenidium are all long and narrow. The anus lies far forward and between the rectum and the right wall of the cavity lies part of the genital apparatus. In males this forms a glandular tract and there is no penis; in females a ciliated oviducal tract is flanked by an open fertilization pouch and albumen gland on the right and an open receptaculum on the left.

The foot is small, with a straight double edge anteriorly and rounded behind. The operculum is small, circular, polygyrous, with sunken, central nucleus and is edged with numerous pinnate bristles. These are arranged in radial rows over the whole surface in young animals but are worn away in older ones (Ankel, 1971).

Colour. Buff, with darker and lighter spots and streaks. White predominates on the cephalic and pallial tentacles, the exhalant siphon and on the sides of the foot; black marks characterize the snout, the dorsal and posterior parts of the foot. The operculum has a reddish tint.

Geographical distribution. Along the W. coast of Europe from the Lofoten Islands S. to the Mediterranean and N. Africa. It extends into Scandinavian waters as far as the Sound but does not enter the Baltic. Less common (or perhaps absent) in S. North Sea and E. Channel.

Habitat. T. communis inhabits soft bottoms between 10 and 200 m. It occurs on soft, recently-deposited muds, on firm ones and on sandy or muddy gravel. Where found it is usually very abundant. On softer muds (Pérès & Picard, 1964; Sneli, 1975) it is often almost the sole inhabitant but in other places occurs with other molluscs, with *Pennatula* and polychaetes, but is less abundant when these occur. It is more numerous in inshore than offshore localities and it favours areas where precipitation of suspended matter occurs as a result of eddy currents.

Food. The animals are suspension feeders, straining the pallial water current with the ctenidium (Graham, 1938). Food thus collected travels to the mouth in the groove on the floor of the mantle cavity and is gathered by the radula. The faeces are egg-shaped pellets about 500×350 μm.

Breeding and growth. See Lebour (1933), Thorson (1946), Franc (1948, 1949), Thiriot-Quiévreux (1969), Fretter & Pilkington (1970), Fretter & Manly (1979). The sexes are separate but cannot be told apart except by opening the mantle cavity or by the pink colour of the ripe ovary. At Plymouth breeding occurs April—July, in the Kattegat in August, in the Mediterranean March—July. The eggs are pink, about 100 μm in diameter; 6—20 or so are enclosed in a globular capsule 640—1120 μm across, coloured pinkish-yellow by its contents. Each capsule has an apical opening plugged with a mucous cap and tapers to a thread about 1 mm long the end of which is fastened to the shell or the substratum, entwined with those of other capsules to form a group like a bunch of balloons. Each female may lay several hundred capsules. Eggs hatched (in the Plymouth Laboratory) after 6—10 days as free-swimming veligers with a shell of 1 + whorl, 160 μm across. Later they develop up to 2.5 whorls, very swollen and each only slightly larger than the preceding one. Spiral ridges gradually appear on the later whorls. The velum is bilobed and small (the larvae are not strong swimmers), colourless, the rest of the body greyish. From the small size of the velum and the rarity of larvae larger than this it has been concluded that veligers do not stay long in the plankton but settle when the shell has grown to about 250 μm. It is difficult to deduce time of metamorphosis from examination of shells, however, as there is no clear boundary between protoconch and teloconch. At a rather variable time after settling, when there are 5—10 ridged whorls, an internal calcareous septum is formed apically and the protoconch is ultimately broken off, presumably accidentally. The growth of these animals, the age to which they live and the structure of their populations are not known.

Notes. T. communis is gregarious and usually abundant throughout the year. It burrows slightly into the substratum (Yonge, 1946), lying with the axis of the shell sloping downwards at an angle of about 15°, the outer lip upwards. This may perhaps explain the frequency with which this part of the shell is damaged, either by attempted predation or by mechanical damage. The position of buried shells is marked by a small hump over the body whorl. The entrance to the mantle cavity is cleared by the foot pushing mud to one side and consolidating it with mucus from the pedal gland. Although newly-settled snails seem to feed with the radula they soon become dependent on ciliary feeding and are extremely sluggish, rarely moving once established in the substratum and hardly extending further from the shell than is necessary to maintain a pallial current. Large particles are strained from the current before it enters the mantle cavity first by the bristles on the operculum and then by the curtain of pallial tentacles; in such an environment, where the water must, on occasion, be markedly turbid, this may prevent damage to the gill. There is a crystalline style in the stomach. Fretter (1946) explained the lack of a penis as a consequence of the narrowness of the mantle cavity in such a tightly-coiled shell, though Johansson (1946) regarded it as a persistent primitive arrangement. Since copulation cannot occur, sperm must enter the mantle cavity in the feeding-respiratory current and be attracted to and collected in the open female genital tract. The gregarious habit of the species presumably helps to ensure fertilization, as would production of gamones to ensure synchronous spawning of males. The animals can retract far up the spire: then the marginal bristles of the operculum lie against the shell, being flexible, and still permit a respiratory water current to pass (Ankel, 1971).

T. communis acts as intermediate host for many species of trematode (Rothschild, 1935; Hutton, 1955; Wright, 1956). The relationship between host and one of these, *Cercaria doricha,* has been examined by Negus (1968) who showed that the cercariae were dependent on the gonad. *T. communis* is also parasitized by *Odostomia eulimoides* and *Capulus ungaricus* (Thorson, 1965).

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CERITHIIDAE Fleming, 1822
BITTIUM RETICULATUM (da Costa, 1778), needle whelk
Strombiformis reticulatus da Costa, 1778
Cerithium reticulatum (da Costa, 1778)

Bittium, perhaps a Latinized form of the Greek βίττιον, a woman's name referred to by Greek poets.
Reticulatum (Lat.), reticulated, referring to the ornament on the shell.

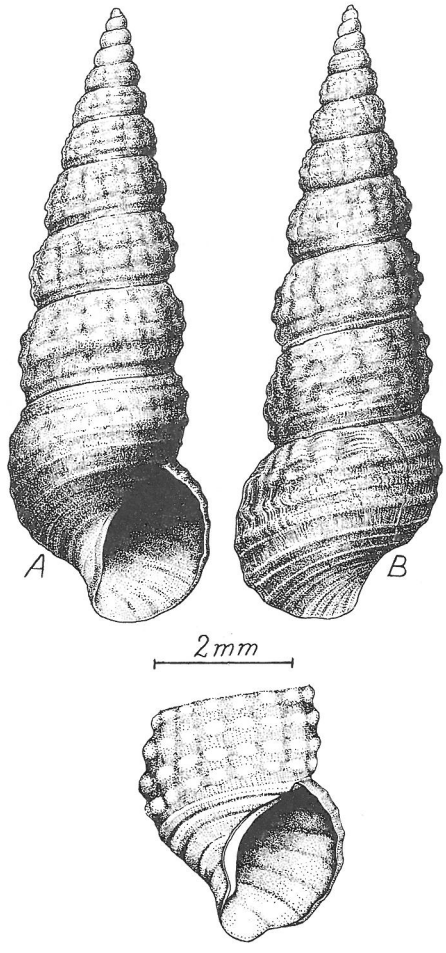

Fig. 217. *Bittium reticulatum* (da Costa). Nibe Bredning, Limfjord. CMZ. The ornament is often more obvious than the figure suggests and the siphonal notch more marked, as is shown inset.

Shell. The shell is a tall, narrow cone with a pointed apex solid, opaque, a little glossy. There may be 15 whorls, but usually 10-12 are present. They are moderately tumid and meet at sutures placed below the periphery of the upper whorl. The sutures seem deep because they coincide with a furrow between spiral ridges, and usually lie just below a thread which is the adapical part of a ridge. The spire is superficially straight-sided, but most shells are cyrtoconoid with a change in the apical angle from 25° to 15° about one third of the shell height below the apex. The ornament comprises spiral ridges and grooves, ribs and microscopic growth lines and spiral lines. The spiral ridges are about equal in breadth to the intervening furrows from which they are rather sharply delimited,

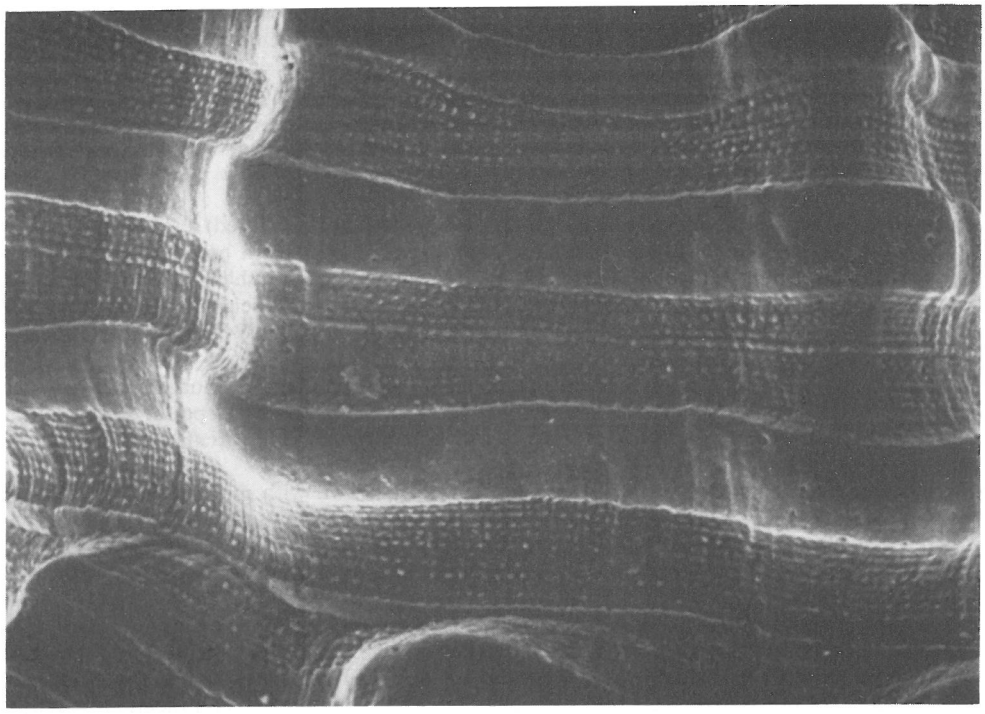

Fig. 218. *Bittium reticulatum.* Microstructure × 150. SEM photograph. Plymouth. RUZ.

particularly on their adapical side, which often forms a step lying almost at right angles to the axis of the spire. The ridges tend to increase in height where they cross the ribs. There are 9—10 on the body whorl, usually 4 on each of the next 4 whorls, 3 on the next 3, 2 on the next 2 and the protoconch has none. The ribs are slightly prosocline, often a little flexuous, and those on one whorl tend to lie below those on the previous so that the spire shows a series of slanting ridges from apex to base. They are wavelike in section, broader than the spaces between. On the whorls of the spire they extend from suture to suture but die out at the periphery of the body whorl; close to the aperture they become lower but also more frequent over a given length than elsewhere on the shell. Where spiral ridges and ribs cross both thicken to produce tubercles: these normally occur on the 4 most adapical spirals of each whorl but in some shells only on 3. The most abapical ridge on each whorl of the spire (half exposed at the suture) and all those on the base of the body whorl are not tuberculate. There are 12—20 ribs on the body whorl, 9—16 on the penult, 12—15 on the antepenult and 10—12 on such other whorls as show them; commonly whorls in the spire have 11—12 ribs and the topmost 2 whorls of the teloconch have none, only spiral ridges. The furrows between the ribs and spirals, and often the surface of these, are covered by a microreticulation of growth lines and fine spirals, usually eroded on the tubercles. On many whorls one rib is broadened and heightened to form a varix and one may lie close to the aperture.

The protoconch, of 2.5—3 tumid whorls, has a diameter of *c.* 300 μm. It is usually devoid of sculpture.

Aperture. Oval, lemon-shaped, its long axis at 20—25° to that of the spire, in some shells more quadrilateral in outline. It is surrounded by a peristome lying approximately in the axial plane. The outer lip arises normal to the surface of the body whorl level with spiral ridge 5, the most apical of those without tubercles. It curves to the periphery, continuing the profile of the spire and there turns towards the columella. Level with spiral ridge 6 it bends more abruptly, sometimes sharply enough to make the aperture a little angulated. Near the columella it forms a short recessed sinus pointing to the left. The outer lip also shows a gentle sinus between its origin and the periphery. Throughout its

course it is thin and crenulated by the ends of the spiral ridges and grooves. The columella is short and nearly straight and the lip here broadens outwards so that there is no umbilicus. Over the body whorl the inner lip forms a glaze. The throat is fluted by grooves and is very glossy.

Colour. Fawn to light chestnut-brown. The apex is pale, even white, as are the tubercles, the columella and sometimes other parts of the base of the shell.

Size. Recorded up to 15 × 6 mm, but commonly *c.* 8 × 3. Body whorl = 42% of shell height (range 36—48); aperture = 25% of shell height (range 22—34); breadth = 36% of total height (range 27—45).

Animal. The head has an elongated snout bifid distally, the mouth (closed) a subterminal ventral slit. The tentacles are long and slender, each with an eye on a prominent basal bulge. The mantle edge is broadly lobed. In the mantle cavity is a long, narrow osphradium; the anus opens far forward and to its right lies, in the male, an open prostate, in the female an open oviduct flanked by the openings of bursa copulatrix and receptaculum seminis (see Johansson, 1947, 1948, 1956). There is no penis in the male.

The foot is rather long and narrow double-edged anteriorly where the anterior pedal gland opens. It is nearly straight here, only slightly embayed; posteriorly it tapers to a blunt point. The operculum is oval with subcentral nucleus; from underneath its posterior edge the opercular lobe extends as a tongue over the dorsal surface of the foot.

Colour. The background colour is pale yellow, fawn or brown with much mottling of opaque white and black or purple-brown spots and streaks. The tip of the snout, the tentacles and the most anterior and ventral parts of the foot are pale. The red of the buccal mass shows through the head and there may be lines of orange or pink on the tentacles. The osphradium and hypobranchial gland are dark.

Geographical distribution. This is a widespread species extending from the Black Sea throughout the Mediterranean and from the Canary Islands north to Lofoten Islands. It is found through the Skagerrak and Kattegat to Kiel Bay in the Baltic and in the northern parts of the N. Sea. It occurs in Limfjord but is not present (perhaps from lack of suitable substrata) on the continental coasts of the N. Sea. It is found in the western but not the eastern Channel basin.

Habitat. B. reticulatum is common on slightly soft bottoms in association with *Zostera, Posidonia, Cystoseira* and other weeds. It also occurs (not commonly) on rock surfaces and in crevices. It does not come higher up the shore than about LWST and is common in shallow sublittoral water; recorded to 250 m. The animals may be very abundant in appropriate places. They tolerate some reduction in salinity.

Food. According to Starmühlner (1956) *B. reticulatum* is a diatom-eater, but its stomach contents suggest a more general diet since sponge spicules, foraminiferans and small molluscs are common. The faecal pellets are elongate ovoids, often with a projecting tail of sponge spicules, measuring 500 × 250 μm.

Breeding and growth. The most important references are: Lo Bianco (1909); Lebour (1936); Thorson (1956); Franc (1948); Vinogradova (1950); Chukhchin (1960); Vives (1966); Thiriot-Quiévreux (1969); Fretter & Pilkington (1970); Rasmussen (1973).

The sexes are separate and may be told (in the absence of a penis) by the differing arrangement of the genital ducts in the mantle cavity. Breeding takes place May—Aug in the Black Sea, Mar—Jul at Naples, mid-summer at Plymouth and May—Aug (maximum Jun—July) in Isefjord. The spawn has the form of a tightly-coiled spiral gelatinous ribbon of 2—4 turns, total length about 25 mm, the diameter across the spiral up to 3 mm. Thorson said the spiral was a clockwise one, but it may coil in the opposite direction. The ribbon is circular in section and contains many eggs, each 60—70 μm in diameter, cream-white in colour and lying in albumen separated by a membrane from the jelly. The diameter of the combined egg and membrane is 95—120 μm. The eggs lie in about 6 longitudinal rows, 2—3 rows deep centrally and may total *c.* 1000. Vinogradova recorded one female as laying nearly 10,000 in 7 lots in 2 weeks. Hatching time seems unknown but may be brief as Vinogradova mentioned 2 days (in unknown conditions). Free-swimming veligers are common in plankton off Sevastopol Jun—Dec, in the western Mediterranean May—Jul, off Plymouth spring and summer and in the Sound late Jul — early Nov. In Limfjord, according to Thorson, they are the dominant element in summer plankton.

The shell of the newly-hatched veliger varies from 170 μm in diameter (the Sound) to 200—230 μm (Black Sea). It is pale horn-colour with a prominent peripheral beak. The first whorl is smooth but later ones bear an irregular scattering of dark tubercles and all are tumid. The velum and the whole

body are unpigmented. By metamorphosis the shell has 2.5—3.0 whorls, a diameter of 300—330 μm and is easily recognized by a square tongue-shaped beak at the periphery of the outer lip, on to which run 2—3 spiral ridges that have appeared on the younger whorls of the shell. The larval mesopodium ends anteriorly in a lobe narrower than the propodium. Rasmussen gave the following figures for growth of the young animals: in Oct, newly-settled snails have a shell height of 2.0—2.5 mm and remain so over winter; the following Apr—May they are 4—5 mm high. They then spawn (which stops growth) but by Aug are 5—6 mm high, in Oct (age 1 yr) 6—7 and in their second spring 7—8. After a second spawning most die.

Notes. B. reticulatum may still be found not infrequently but was badly affected by *Zostera* disease earlier this century and perhaps by other factors as well, as it certainly seems to have once been much more common than it now is. In places such as the Helford River, Cornwall, great numbers of dead shells may be found but only the rare live animal. The animal belongs to one of the group of aphallic species characterized by a tall, narrow shell in which, according to Fretter (1953) the presence of a penis would interfere with respiration. Unlike *Cerithiopsis, Bittium* does not produce spermatozeugmata so how fertilzation is effected is not known. Thorson (in an unpublished note) recorded seeing many animals at Las Palmas, Canary Islands, pairing, but gave no other details beyond noting that males were fewer than females. It may be that simple approximation of mantle cavity to mantle cavity allows passage of sperm.

The shells are very variable and several varieties have been described. It may be that this is an aggregate species of which the next might be part.

BITTIUM SIMPLEX (Jeffreys, 1867)
Cerithium simplex Jeffreys, 1867

Simplex (Lat.), simple, referring to the lack of varices in the ornament.

Shell. As in *reticulatum* but lacks varices, has perhaps less prosocline ribs and is thinner.

Colour of body. Salmon pink (Bouchet, Danrigal & Huyghens, 1979).

Notes. In all other features of anatomy this seems identical with *B. reticulatum* and has probably not been distinguished from it in most observations. We cannot therefore say more about its biology than that it is presumably similar to that of *reticulatum.*

Whether this is a colour variety of *reticulatum,* a separate species as is now usually claimed, or a segregate of an aggregate must await fuller knowledge.

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STROMBACEA

A small group containing 4 families (or 3 if xenophorids are regarded as calyptraeacean), only one of which, Aporrhaidae, is found in European seas. The animals exhibit a marked preference for soft substrata, struthiolariids and aporrhaids living in shallow burrows within the substratum, xenophorids and strombids on the surface.

The shell is usually high-spired and in most genera shows both spiral and transverse ornament, with projections where the two cross, though a few (e.g. *Terebellum*) have smooth shells. The aperture is often narrow and elongated with an angulated peristome, and the outer lip is drawn out to form an ear-shaped expansion, sometimes with a series of finger-shaped marginal extensions. The apical part of the lip shows a tendency to wrap itself over the spire, partially hiding it from view. At the base of the aperture is a notch or canal, often extended into a spike-like rostrum.

The animal has a narrow, sometimes hook-shaped operculum and an extensible foot with which it can take a series of forward lurches, usually being incapable of normal crawling, much of the sole being lost. The strombids are browsers, xenophorids and aporrhaids particle feeders, but struthiolariids are ciliary feeders in much the same way as turritellids. All have a crystalline style and a long mantle cavity. The sexes are separate, the pallial genital duct open in males, closed in females, but there always seems to be a ciliated tract leading out from the mantle cavity. The spawn is usually a tangled mucous rope.

Strombaceans appear to have undergone a mosaic evolution. The struthiolariids are, on shell structure, the most primitive family, the aperture in *Perissodonta* being large and rounded, with practically no expansion of the outer lip, and in *Struthiolaria* showing just the beginnings of angulation of the peristome; on the other hand they must be regarded as advanced in respect of their ciliary feeding. Aporrhaids possess a shell which is more advanced in its narrow aperture and expanded outer lip but retain more primitive modes of feeding and locomotion. The xenophorids have a sedentary life like that of an aporrhaid except that they live on the surface of the substratum, where they are disguised by their habit of cementing objects to their shell as camouflage, rather than within it. The strombids show in shell (especially *Pterocera*) and locomotion the greatest departure from the primitive type, but seem to retain a primitive mode of feeding by browsing on weeds.

In many respects strombaceans show a general resemblance to cerithiaceans, but the way in which growth of the outer lip tends to elongate and narrow the aperture and partially cover the spire links them with Lamellariacea and Cypraeacea.

APORRHAIDAE Gray, 1850

APORRHAIS PESPELECANI (Linnaeus, 1758), pelican's foot

Strombus pespelecani Linnaeus, 1758

Chenopus pespelecani (Linnaeus, 1758)

Aporrhais quadrifidus (da Costa, 1778)

Aporrhais (Gk.), said to be derived from ἀπὸ, asunder, and ῥαίω I break; *pespelecani* (Lat.), pelican's foot; both terms refer to the shape of the outer lip.

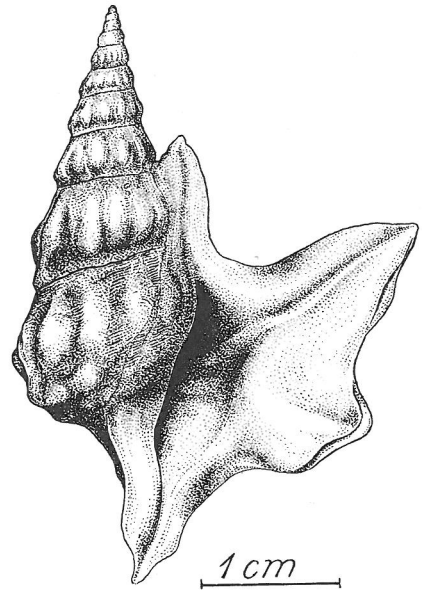

Fig. 219. *Aporrhais pespelecani* (Linnaeus). The Sound. CMZ.

Shell. The mature shell is readily distinguished by the projecting outer lip, but this is absent in juveniles. Solid, opaque, very slightly glossy in the younger parts. The spire is tall, with an elongated base, a little coeloconoid; the apical angle of a mature shell is *c.* 40°, of a young one *c.* 26°. There are 8—10 whorls depending on what number have been lost from the apex; this always seems to happen and the opening is sealed with a convex plate. Each whorl is swollen and dips to a marked, wavy suture placed well below the periphery of the upper whorl. The youngest whorl (at all ages) has an angulated periphery. The body whorl of the mature shell expands in diameter so that in abapertural view the suture between it and the penult is not parallel to the others. The ornament consists of growth lines, ribs, and spiral ridges and grooves. The growth lines are not obvious on older whorls but may be clear on young ones: they are flexuous, very prosocline at the suture, but change direction as they approach the periphery, becoming opisthocline, so that they have a reversed C shape. Ribs on older whorls follow a similar course and are thin, with a rounded crest, less broad than the intervening furrows. From about the antepenult whorl they develop a tubercular peripheral elevation and the other parts of the rib disappear. On the body whorl 2 other rows or tubercles lie abapical of the periphery; traces of the upper row may be seen above the suture on the whorls of the spire. The number of visible ribs on the body whorl is 10—13, on the penult 10—11, on the previous 13—14, rising a little on the upper ones. In young shells, where ribs are not obscured by lips, these numbers rise by 3—4. The number of subperipheral tubercles is slightly more than double the number of ribs and that of basal tubercles still greater. In some shells the tubercles of the last row join to form a ridge as do both other rows towards the aperture. The whole shell is also covered with

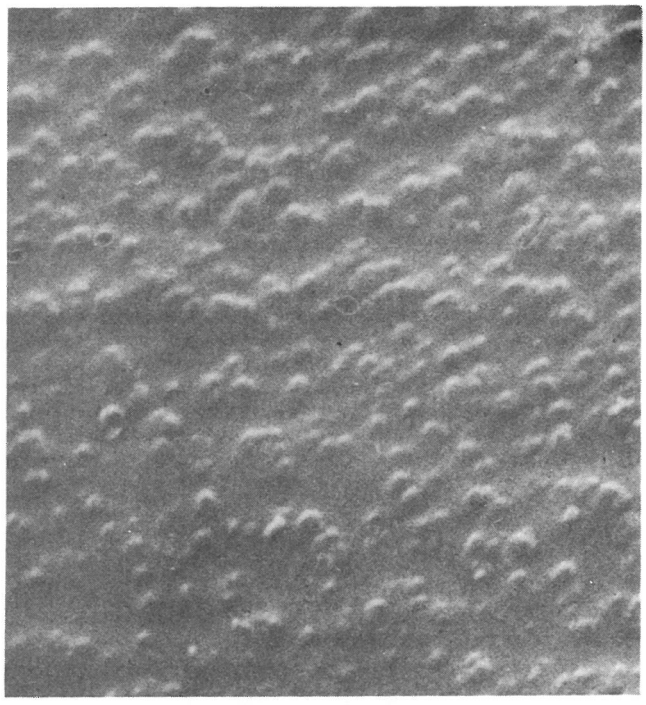

Fig. 220. *Aporrhais pespelecani.* Microstructure of columellar lip × 176. SEM photograph. Off Dunstaffnage, Argyll. RUZ.

spiral ridges and grooves except for the youngest part near the outer lip, though they are usually worn away on the ribs. Each ridge is strap-shaped, 3—4 times as broad as a groove, with a finely pustular surface. There are about 40 on each whorl of the spire. The protoconch is not clearly separate from the teloconch; it is at first smooth but gradually develops spiral ridges at a diameter *c.* 1 mm. The whorls (2—3) are swollen, with deep sutures, the first two lying in almost the same plane.

Aperture. The appearance depends on the animal's age. In young shells (up to *c.* 8 whorls) it is a narrow, elongated oval, the axis at 30° to that of the shell. It is drawn out into a rostrum basally which projects along the axis of the spire. The outer lip arises at the angulation of the body whorl and follows a smooth curve, its edge crenulated by the ends of the spiral ridges and angulated at the periphery. Basally it turns to form one edge of the rostrum, the other made by the straight columella, over the base of which the inner lip is slightly out-rolled. There is no glaze on the body whorl. In older animals (8—9 whorls) the body whorl starts to widen ad- and abapically, at first slowly, then rapidly and the outer lip grows out into a moderately thin sheet of calcareous matter, glossy on the throat side and drawn out into 5 lobes. Lobe 1 extends adapically as a flat keel set edgeways to the spire and running roughly parallel to its axis; it is fused to the penult and (sometimes) antepenult whorls basally but ends in a short point projecting clear above that; a groove runs along its apertural side, notching the tip a little. Lobes 2, 3 and 4 extend to form a triple-pointed tongue in more or less the same plane as lobe 1 but extending at right angles to the axis of the spire; lobe 2 is the largest and is separated from lobe 1 by a deep sinus with recurved edge; lobe 4 is the smallest and often lacks the groove and notched tip found on 2 and 3. Lobe 5 runs basally to the columella and is grooved; its tip bends (increasingly with age) towards the aperture and its outer surface becomes worn. The peripheral tubercles of the body whorl run to the point of lobe 2 and the subperipheral rows to lobes 3 and 4. Lobe 5, and sometimes 1, have ridges unrelated to other topographical features. The inner lip at this stage is out-turned over the columella and forms a film over the body whorl. The columellar edge is lobed by tubercles under this film. Further growth is restricted to a thickening of the edge of the outer lip so that it becomes laminated and the glossy part restricted to

an elongated narrowly pentagonal shape. When the shell is viewed along the axis of the aperture the thickened edge of the outer lip and spire then form the sides of a trough; its ends are marked by the sinuses between lobes 1 and 2 and lobes 4 and 5; in older shells the curvature of lobe 5 adds a second basal opening between itself and the body whorl. The glossy parts of the lips and columella are covered with a microstructure of rows of closely-set, rounded, minute tubercles.

Colour. Cream or white with a yellow or fulvous tinge, especially on the expanded outer lip. A band of brown, sometimes with a greyish green or lilac tinge, runs parallel to the peristome on the outer part of the throat.

Size. 42 × 28 mm (breadth to tip of outer lip). Body whorl = 55% of total height; aperture (tip of lobe 1 — tip of lobe 5) = 75—80% of total height.

Animal. The head carries a rather long, rapidly tapering snout, obliquely truncated distally; the mouth, a T-shaped slit when closed, lies on the terminal disk. The tentacles are long, taper only at the tip and have each an eye at the base on a bulging lobe. Mantle edge plain or gently scalloped, extending to cover as much of the lips as is glossy. Males have a penis, a recurved, thick tentaculiform structure attached to the floor of the mantle cavity behind the right tentacle. It carries an open groove, an extension of one running from the male opening at the inner end of the mantle cavity; a prostatic gland discharges to it. In females the oviduct is closed though there is an elongated pore (Johansson, 1948) from which a ciliated tract runs to the edge of the floor.

The foot has a double edge anteriorly. It is shield-shaped, narrow, with roughly parallel sides, pointed behind. The operculum is solid, narrow, set across the foot, with a terminal nucleus.

Colour. Ground colour white on most exposed parts but carmine on the dorsal surface of the snout, on a belt along the dorsal surface of each tentacle and on patches of the foot. There are many points of white and sulphur yellow on the carmine areas, predominantly yellow on the tentacles and snout, white on the foot. In some individuals the foot may be unpigmented.

Geographical distribution. This species extends from the Mediterranean north along the coasts of Europe to N. Norway and Iceland. It is less common or absent in the Isles of Scilly, the Channel and central parts of the North Sea than elsewhere and does not occur off the W. coast of Denmark nor in its fjords. It extends through the Kattegat to the Sound but is not found in the Baltic.

Habitat. A. pespelecani is always sublittoral. It frequents mud, muddy sand and sand (especially if a little muddy) at depths to 180 m. Where it occurs it is not uncommon.

Food. This animal is a detritus feeder, selecting mainly vegetable fragments to be raked in with the radula. It has a crystalline style. The faeces are ovoid pellets *c.* 500 × 350 μm.

Breeding and growth. See Lebour (1933), Smidt (1944), Thorson (1946), Franc (1948), Thiriot-Quiévreux (1969), Fretter & Pilkington (1970).

The sexes are separate, the male recognizable by the penis though the animals are often reluctant to emerge from the shell enough to let this be seen. Breeding occurs in January at Algiers, February — July in the W. Mediterranean, March — July (Plymouth), July — September in the Sound. Egg capsules are probably passed from the female pore along the ciliated groove to the foot and attached singly or in twos or threes to grains of substratum. Each is spherical, *c.* 240 μm in diameter, slightly yellow and transparent though usually covered by detritus. There is one egg (120 μm across) per capsule. It hatches in about 14 days as a veliger larva with a smooth shell of 1.5 whorls, 200—250 μm in diameter. By metamorphosis there may be 3 whorls (diameter 1.5 mm) with the beginnings of spiral ridges and basal rostrum. The early whorls lie in almost the same plane. At hatching the larva has a velum with 2 narrow lobes elongated anteroposteriorly, each with a red blotch at each end and a red line along the ciliated groove. The red blotches are apparently not always present in larvae from Danish waters. Later the velum becomes 4- and then 6- lobed, all similarly pigmented. There is also red colour on the osphradium and black, later red, on the head. The foot is long and mobile with red pigment on the sole. Settlement takes place — as the hypertrophied velum would suggest — after a rather long stay in the plankton. There is no information on growth rates or on length of life.

Notes. A. pespelecani lives either wholly or partially buried, though it must emerge to feed (Yonge, 1937; Barnes & Bagenal, 1952) and copulate. Burrowing is done by pressing apertural lobe 5 into the substratum, the ridge on its outer side acting as ploughshare. Removal of bottom material to make the burrow is effected by movements of the snout, which is mobile and extensile. When the burrow is large enough the foot enters and by contraction of the columellar muscle the shell is pulled under. The process is repeated until the snail lies horizontally, its position marked by a small hump on the surface. The snout is then used to construct an inhalant opening, sited over the columellar region of the aperture, and an exhalant one over the sinus between lobes 1 and 2. Many shells

carry rich epizoic growths: this suggests that burrowing may be partial or that lengthy periods are spent out of the substratum feeding.

The movement of the unburied animal is both awkward and agile and is a process of stepping rather than creeping (Weber, 1925). At rest the shell rests firmly on the apertural side of the body whorl and the thickened edge of lobes 2—4; the head and foot then occupy the trough between these parts. A step begins when the foot is released from the substratum extended forwards and re-attached; contraction of the columellar muscle then pulls the shell forward in one movement to a new resting point and the process repeated.

APORRHAIS SERRESIANUS (Michaud, 1828)

Rostellaria serresiana Michaud, 1828
Aporrhais macandreae Jeffreys, 1867
Aporrhais pes-carbonis Brongniart, 1823

Serresianus, called after the French naturalist P.M.T. de Serres (1782 or 3 — 1862), who was professor of Geology and Natural History at the University of Montpellier from 1820.

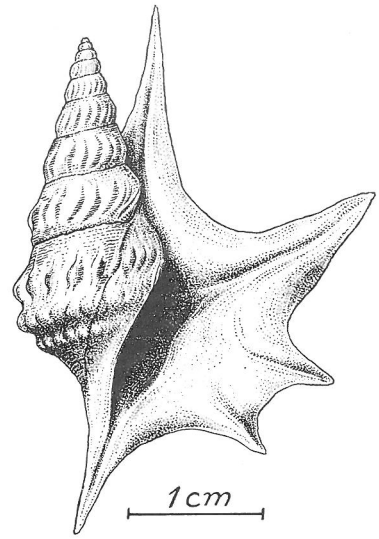

Fig. 221. *Aporrhais serresianus* (Michaud). 112 km E. of Yell, Shetland, 150 m deep. CMZ.

Shell. In general shape like that of *A. pespelecani* but differing in a number of details: it is smaller, thinner, more delicate and glossier within; there are only 7-8 persistent whorls, the most apical always being lost and the hole sealed; the growth lines are clearer and interact with the spiral ridges to form a fine reticulation, most obvious on older whorls; ribs and tubercles are more numerous by 3-4 on each whorl and tend to have sharper summits; the spiral ridges are fewer, more prominent, and frequently larger and smaller alternately. On the base of the body whorl they become narrow. The first 1-2 (persistent) whorls are smooth, the next shows spirals and the next a reticulation the transverse elements of which gradually rise into ribs. The protoconch is largely lost but comprises 2-3 smooth whorls with diameter of 1.2—1.6 mm.

Aperture. Differs from that of *pespelecani* in that the expansion of the outer lip is thinner and less arched, its lobes finer, longer and separated by deeper bays. The trough between lip and body whorl is narrower. Lobe 1 is greatly elongated, its apex overtopping the spire and leaving only about 4

whorls free. Lobes 3 and 4 are clearly separated by a bay. Lobe 5 is longer, not expanded and not curving towards the aperture. The glossy parts bear a less dense series of spiky tubercles.

Colour. White.

Size. 38 × 24 mm. Body whorl = 50% of total height; aperture = total height. (Measurements made as in *pespelecani.*)

Animal. As in *pespelecani.* The tentacles are relatively longer.

Colour. The body is more translucent than in *pespelecani.* There is red on the upper surface of head and snout, the former a triangular patch, the latter split by a median white line into right and left halves. The tentacles lack red and have a mid-dorsal white line.

Geographical distribution. From the Mediterranean north to N. Norway and Iceland. Though common in Norwegian fjords it is absent from the Skagerrak and all Danish seas. In the British Isles it is found only off the W. coast of Ireland and off Scotland and around the northern isles. Absent from the N. Sea and English Channel.

Habitat. As for *pespelecani,* but this species lives on finer muds and at greater depths, down to 1000 m, but more commonly to about half that.

Food. Presumably as in *A. pespelecani.*

Breeding and growth. The sexes are separate, males with a penis. The spawn is unknown but the veliger larva has been described by Thiriot-Quiévreux (1976). The larval shell is globular, smooth and by the time of metamorphosis has 2.5—3 whorls and a diameter of 1.2 mm. As in *pespelecani* the early whorls tend to lie in one plane and the umbilicus is large. The velum has 6 lobes each with a terminal reddish brown blotch and an edge of the same colour. There is also red on the head, oesophagus and intestine. It is distinguishable from the larva of *pespelecani* by the greater length of the velar lobes and larger pigment patches; by the absence of spiral ridges until after metamorphosis; by a more circular umbilicus and less elongated siphonal process.

Notes. This is a little-known animal largely because of its restriction to deep muds and muddy sands. On the evidence of Yonge (1937) and Reyss (1971) there are few reasons for supposing its mode of life to be fundamentally different from that of *pespelecani.* The greater development of the outer lip may prevent sinking on the softer bottoms it favours. Northern forms are usually placed in the subspecies *macandreae* Jeffreys, 1867.Typical Mediterranean *serresianus* are bigger and coarser in appearance.

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HIPPONICACEA (= AMALTHEACEA)

We have been broadly in agreement with the accepted classification of the prosobranch superfamilies so far described. This is not true of the mesogastropods which fall into this and the next superfamily, Calyptraeacea. They present such a number of overlapping features that it is difficult to see why they have been separated and, if they deserve separation, why the dividing line falls where it has customarily been drawn. An indication of uncertainty in the mind of taxonomists about the status of families in this area is given, for example, by the placing of the Capulidae in the Calyptraeacea by Thiele (1929) and by Franc (1968), but in the Hipponicacea by Taylor & Sohl (1962) and Abbott (1974). Another is the placing of the family Xenophoridae with the Calyptraeacea by all these workers except Thiele, who put them with the Strombacea. In the following paragraphs discussion of the Xenophoridae is postponed until other points have been dealt with.

The characters which concern us are (1) shell shape and the development of periostracum; (2) an internal partition in the shell; (3) the enlargement of propodial lobes; (4) sexual biology; (5) mode of life; (6) the radula.

In primitive members of the Hipponicacea and Calyptraeacea (using, for the moment the traditional assignment of genera to these superfamilies) the adult shell has a moderately high spire as in *Fossarus* and *Trichotropis* (hipponicacean examples first, here and elsewhere), though with distinct signs of enlargement of the body whorl, whereas in more advanced genera *(Hipponix; Calyptraea)* it becomes cap-shaped or conical, though in different ways. In both superfamilies the shell may develop a hypertrophied periostracum *(Hipponix; Trichotropis, Torellia, Capulus).* Calyptraeids have a shell partially subdivided internally by a septum formed by addition to the primitive columellar region and used for attachment of the columellar muscle; a septum is also found in *Cheilea,* traditionally classified as a hipponicid (= amaltheid), though as its development is not known, its precise correspondence with that of a calyptraeid is an assumption. In both superfamilies there is a marked tendency for the propodium to expand into lobes. Sometimes these remain separate from other structures *(Vanikoro),* sometimes they fuse to the sides of the snout, forming cephalic lappets *(Calyptraea, Crepidula),* and in other genera they appear as a 'proboscis', a grooved extension of the snout, collecting food *(Fossarus, Hipponix; Trichotropis, Torellia, Capulus).* All these structures are innervated from the pedal ganglia.

The sexual biology of calyptraeids has been well studied and most are known to be protandrous hermaphrodites; the condition in Hipponicacea is less clear, but most seem to have separate sexes. All the animals traditionally classified as calyptraeacean are extremely sedentary in their mode of life after an early phase (often coincident with the period of male sexuality) during which they may move about. This habit is to be associated with life in a situation where detrital material is within easy reach of the proboscis *(Trichotropis, Torellia)* or with ciliary feeding *(Calyptraea, Crepidula),* semi-parasitism *(Capulus),* total parasitism *(Thyca).* A very similar way of life is found in *Hipponix* (Yonge, 1953, 1960) which is attached by a calcareous pedal secretion to the substratum and feeds like a trichotropid. These genera all have a crystalline style, though whether it occurs in other hipponicaceans does not seem to be known. All also have a tendency to brood their egg capsules from which veliger larvae normally hatch, though sometimes juveniles. *Capulus,* somewhat surprisingly, has an echinospira larva, though other links with Lamellariacea are not obvious. The mode of life of other hipponicaceans is not well known.

In respect of all the characters so far mentioned the two superfamilies (as traditionally constituted) overlap: a feature found in some calyptraeacean can nearly always be found in some hipponicacean. This appears not to be so true of the radula and jaws. The latter are generally present in Hipponicacea and absent in Calyptraeacea; the former, though short in both groups, has a better developed rachidian tooth in the Hipponicacea than in Calyptraeacea, where it is simpler or even absent.

What conclusions regarding classification may be drawn from these facts? In the first place we would agree with Abbott (1974) in transferring *Capulus* and *Thyca* from the Calyptraeacea to the Hipponicacea in view of their great resemblance to *Hipponix* in shell and proboscis. We would also accept the transfer of *Cheilea* from Hipponicacea to Calyptraeacea in view of its possession of an internal shell septum. However, it seems right that, wherever *Capulus* is placed, the trichotropids should also go, since they too possess a thick periostracum, a grooved proboscis and are protandrous hermaphrodites. This would imply that Hipponicacea comprises the 5 families Fossaridae, Vanikoridae, Hipponicidae, Trichotropidae and Capulidae, leaving the Calyptraeacea with only 1, Calyptraeidae. This re-arrangement places together in one superfamily, Hipponicacea, animals whose shells are without an internal partition but have a tendency to produce a thick periostracum, and which (4 families out of 5) have a propodial proboscis; it leaves in another superfamily, Calyptraeacea, animals whose shells have a septum but lack a hypertrophied periostracum, and which are also characterized by ciliary collection of food. There still remains some overlap which leaves unanswered the question whether this collection of prosobranchs is better grouped as two superfamilies or as one larger, more variable one.

The last topic to be mentioned is the position of the family Xenophoridae, traditionally assigned to the Strombacea. Morton (1958) suggested that it might be provisionally associated with the Calyptraeacea, a move accepted (with an apparent finality much greater than the original proposal implied) by Franc (1968), Taylor & Sohl (1962) and Abbott (1974). The character on which the argument fundamentally rests is the shell, because in all other respects, anatomical and biological, xenophorids are more akin to such strombaceans as the aporrhaids than they are to any calyptraeid. They are radular feeders, have a robust buccal apparatus with jaws and lack such typical calyptraeacean characters as propodial lobes. Morton pointed out that the xenophorid shell is more

like that of a calyptraeid than that of a strombacean in being depressed, with a short apical-abapical axis held in life at right angles to the substratum, and in having a peripheral flange, or series of processes, which forms a canopy over the base and under which the animal shelters. On the other hand the strombacean shell has an elongated apical-abapical axis held in life parallel to the substratum and the canopy under which the animal lives is an expansion of the outer lip.

In calyptraeids the production, at an early stage of development, of a peripheral flange on the shell which later comes to form the columellar side of the aperture is brought about by eversion of the mantle edge on the columellar side and is accompanied by formation of the internal septum and a very rapid expansion of the whorls to give an ultimate limpet shape, with the shell muscle attached to the septum. How the flange of the xenophorid shell is formed is not known but it is (in the absence of a septum and with a normal helicoid spire and columellar muscle) explained more readily as an outgrowth of the outer lip. There is a fundamental difference between the two arrangements in that in xenophorids (as in strombaceans) the roof of the shelter formed by the flange or lip is not part of the space continually occupied by the animal and lined by mantle, but merely a cover to the space into which it may temporarily emerge, whereas in calyptraeids the entire volume of the shell is continuously occupied by the mollusc.

It is wisest to suspend judgement on the final location of this family until development of its shell form has been studied. Nevertheless it seems to us that the xenophorids are more closely tied to the Strombacea than they are to the Calyptraeacea. If their calyptraeacean resemblances be thought too strong to allow their incorporation in Strombacea then they constitute a superfamily in their own right.

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TRICHOTROPIDAE Gray, 1850
TRICHOTROPIS BOREALIS Broderip & Sowerby, 1829

Trichotropis, Gk. θρίξ, τριχός, a hair, and Gk. τρόπος, a turning circle, referring to the spirals of periostracal bristles on the shell; *borealis* (Lat.), northern referring to the distribution of the species.

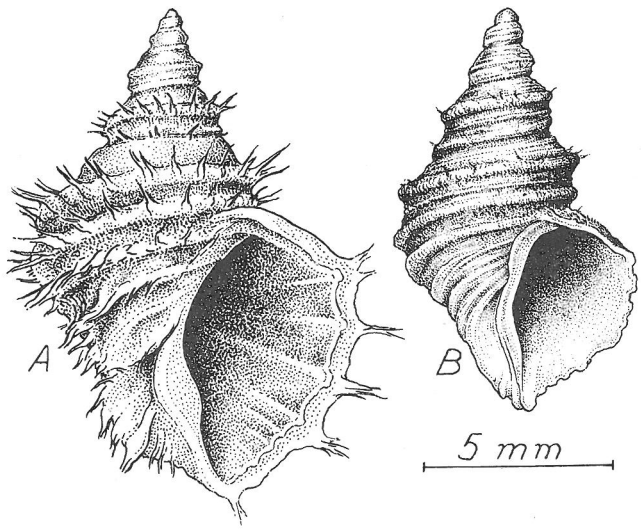

Fig. 222. *Trichotropis borealis* Broderip & Sowerby. A, from off south-east of Kuno, Faeroes; B, Skagerrak, about 72 km north-west of Roshage, 108 m, *Thor* station 1566. CMZ.

Shell. A rather fragile shell, opaque and mainly covered by a conspicuous periostracum. There is a moderately tall spire (apical angle 60-70°), turreted in profile with up to 5 tumid whorls meeting at deep sutures lying below the periphery of the upper whorl. The base of the shell is extended abapically to a rather narrow point. The ornament comprises spiral ridges and growth lines. The spiral ridges are prominent and responsible for the angular appearance of the whorls in profile. On the body whorl 4 major ridges are placed between the suture and the periphery and about 5 lesser ones circle the base. Smaller ones (usually 3) lie on the shoulder between the suture and the first major spiral and others occur in the grooves between the other prominent keels. At the base of the shell a thick, rounded, spiral ridge lies along the columellar region of the aperture. The growth lines are fine and prosocline. The periostracum along the spiral ridges is drawn out into triangular plates or single or multiple stiff bristles.

The protoconch has *c.* 2 whorls marked with first 1, then 2 spiral ridges and already bears a periostracal covering; these features are usually lost in mature shells.

Aperture. Large, pear-shaped or triangular, broad adapically and narrow below, with a peristome lying in a slightly prosocline plane. The outer lip arises more or less at right angles to the surface of the body whorl at the level of spiral 3 and follows a nearly straight, slightly S-shaped course (initially convex then concave) to spiral 1, where it bends through *c.* 90° and runs, generally straight, to the base of the aperture to meet the columellar lip. The two form a V-shaped spout but there is no recess to characterize a siphonal canal. The columellar lip runs nearly adapically, curving slightly into the aperture. It is everted a little over a narrow umbilical groove the abapertural side of which is formed by the basal, thickened spiral ridge. Over the body whorl there is only a glaze. The outer lip is thin and crenulated by the ends of the spiral ridges; in the throat their position is marked by grooves. The periostracum projects a little beyond the edge.

Colour. Most colour is due to the periostracum, the calcareous shell being white-yellow on the body whorl, often with a slight pink tinge, whiter on the spire and on the more prominent growth lines where the periostracum tends to be eroded.

Size. 11 × 6 mm. Body whorl = 70—75% of total shell height; aperture = 60% of total height.

Animal. The head carries a very short snout, bifid at the tip, where the mouth (closed) appears as a longitudinal slit. Its ventral and lateral lips are elongated to form a short proboscis, grooved along its whole dorsal side and apparently constantly held bent to the right towards the mouth of the mantle cavity. At the base of the snout lie the tentacles, rather long and slender, and held so as to diverge markedly. Each carries an eye on a very slight bulge a short distance above the base. The mantle edge is slightly scalloped but not thickened. In smaller animals (males) a rather long, curved and slightly flattened penis arises behind the right tentacle and reaches back into the mantle cavity. An open seminal groove leads from the genital aperture along its posterior side to the tip. Larger animals are female, lack this, and have a closed duct.

The foot is squarish in front, has a slight central waist in an actively creeping snail, and a rounded hinder end. The anterior end and much of the margin of each side have a double edge. The operculum is rather triangular and appears laminated.

Colour. Colourless, with opaque white flecks on the snout, tentacles and the sides of the foot.

Geographical distribution. A circumboreal species found throughout the Arctic and extending south in Europe to Bergen, the northern parts of the North Sea, the west coast of Scotland and north coast of Ireland. In America it reaches as far as Maine on the Atlantic and British Columbia on the Pacific side.

Habitat. On stones and shells on hard bottoms, most often those which are rough and bear a certain amount of silt. It is locally common. Not intertidal; 10—270 m.

Food. A microphage. Particles strained from the pallial water current are taken to, and then along the proboscis to the mouth. The faeces are ovoid pellets.

Breeding and growth. The animals are protandrous consecutive hermaphrodites. Breeding does not appear to have been recorded except by Thorson (1935) in East Greenland where it is completed by the end of July, the starting date unknown. Females lay capsules which are slightly compressed spheres with an attachment base, usually in groups of 2—4. Each is 3—5 mm across the base. The number of eggs in a capsule ranges from 5 to 13; their size is not given. The veliger stage is passed within the capsule and the young emerge as juveniles with a shell of 1 + whorls, *c.* 1 mm in diameter, decorated with 3 spiral ridges and already covered with periostracum.

Notes. Though *T. borealis* is not an uncommon animal it is relatively little known. The size and age at which sex change occurs is not known, though it may be at a shell height of 6—7 mm. Breeding in British waters has never been described and there is no information about growth rates or life cycle. The proboscis is formed from the propodium, not, as it seems, from prolongations of the lips.

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TORELLIA VESTITA Jeffreys, 1867

Torellia, named in honour of the Swedish geologist and polar explorer Otto Torell of Lund (1828-1900); *vestita* (Lat.), clothed, referring to the thick periostracal cover of the shell.

Shell. Rather globose, thin, semitransparent and completely covered with periostracum. The spire (apical angle 120-130°) is low, though clearly raised above the body whorl, which makes up most of the shell. There are 5-6 tumid whorls which meet at deep sutures lying at or just below the periphery of the older whorl. The ornament consists of growth lines and spiral ridges which cross to produce a delicate square reticulation. The growth lines are very prosocline and fine, except at irregular intervals where they enlarge to form small steps, and are placed *c.* 100 μm apart. The spiral ridges have the same dimensions as the growth lines and are about the same distance apart. One much broader spiral forms a rounded keel running from the base of the aperture to the outer lip of the umbilicus. Except for the initial whorl of the protoconch the whole shell bears a thick periostracum. It extends into folds or ridges along growth lines and these bear bristles. There are further bristles set along the spiral ridges and those at the nodes of the reticulation are often much longer than the rest. The periostracum may be lost from the apical area.

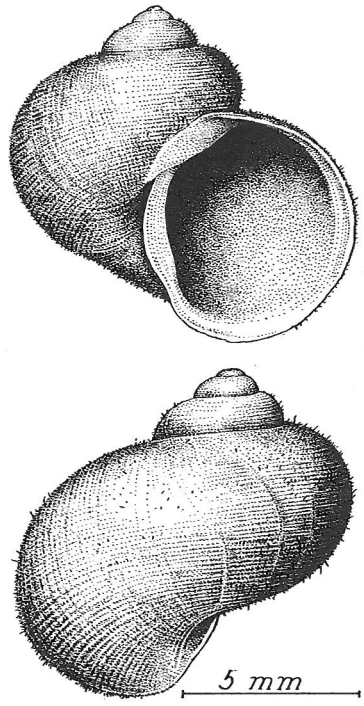

Fig. 223. *Torellia vestita* Jeffreys. About 112 km W. by S. of Lindesnes, Norway, 280 m, *Thor* station 3. CMZ.

The protoconch has 3-3.5 whorls in all. The initial whorl (embryonic) has a pitted or irregular surface, the next 1.5 whorls are smooth, whilst the last 0.5 whorl shows some distinct, well-spaced, low spiral lines and feeble growth lines. The total diameter is considerable but variable (1.5-3.5 mm). It is abruptly separated from the teloconch.

Aperture. This is large, nearly round but slightly quadrangular, with a peristome lying in a very prosocline plane. The outer lip arises nearly tangential to the body whorl just below the periphery and so curves adapically at first; it then follows a wide, almost circular course to the base of the columella where there is a suggestion of a small spout. (It is this which produces the broad spiral fold on the base of the shell.) The columella leans a little left of the shell axis and has a low, rounded bulge projecting into the throat at its lower end. Alongside it the apertural lip is everted over a groove leading to a narrow but deep umbilicus; over the body whorl it forms a rather extensive transparent layer. The edge of the peristome throughout is thin, the periostracum projecting a little beyond it as a bristly fringe. The throat is smooth, the external ornament visible by transparency.

Colour. Cream — yellowish.

Size. Up to 15 × 15 mm. Body whorl = 80-85% of total shell height; aperture = 67% of shell height.

Animal. In its general features this animal is similar to *Capulus.* There is a broad and depressed snout with the mouth at its tip, the ventral and lateral lips drawn out into a long tapering proboscis, grooved dorsally. At the base of the snout are the tentacles, rather stout, each with a large eye on a low bulge. The mantle edge has a finely scalloped outer fold and a smooth, thick inner one. The mantle cavity is broad, not particularly deep. The ctenidium has long filaments and the anterior part of its axis with the filaments which it bears, project beyond the mantle edge dorsal to the head. Males (or animals in a male phase) have a cylindrical, slightly flattened penis, bent into a J shape, with an open seminal groove, originating in the genital aperture, along its posterior edge.

The foot is broad and oval. The anterior edge has a thick propodium between which and the sole is the wide opening of a deep anterior pedal gland. The operculum is a broad oval, pointed posteriorly where the nucleus lies, but this has usually been lost by wear.

Colour. Yellowish, some darker pigment on the tentacles.

Geographical distribution. A North Atlantic species, widespread from high to low latitudes, the depth at which it lives increasing towards the south, where it may be found over 2000 m deep. Off Scandinavia, however, it is dredged at 100-150 m and at about the same depth off New England. British records are limited to the area east of the Shetlands and there are none from Denmark.

Habitat. Dredged from stony bottoms.

Food. Presumably a microphage, behaving like *Capulus* or *Trichotropis.* The faeces are irregular segments of a rod, or roughly shaped pellets about 500×250 μm; they contain only very fine detrital material.

Breeding and growth. Unknown, but may be as in other trichotropids.

Notes. This species has been largely excluded from the British fauna lists. It has, however, been recorded in surveys related to oil exploration and may be more common than supposed. It is not possible to make definite statements about its reproductive biology. All specimens at our disposal had a penis though it was smaller in the largest specimens (10 mm shell height) than in the smallest ones, a fact that suggests sex change as in *Trichotropis.* The smallest animals had a male gonad and male ducts whereas larger ones seemed to have no distinct gonadial tissue. This does not contradict the idea of sex change but emphasizes the need for further evidence.

The specimens examined all showed large protoconchs (2.5-3.5 mm across): those pictured by Bouchet (1977, pl.13, E, F) were much smaller (1.4-1.8 mm). The proboscis has been found in several positions: it is therefore more like that of *Capulus* than the immobile one of *Trichotropis.*

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CAPULIDAE Fleming, 1822

CAPULUS UNGARICUS (Linnaeus, 1758), Hungarian cap shell

Patella ungarica Linnaeus, 1758

Pileopsis hungaricus (Linnaeus, 1758)

Capulus (Lat.), literally, that which is grasped, so a holder or container; *ungaricus* (Lat.), Hungarian (cap). Both refer to the shape of the shell.

Shell. Rather fragile, slightly transparent and mainly covered with a periostracum; except for the protoconch exposed shell is not glossy. The shell could be described as cap-shaped but is more accurately involute, almost a plane coil with no elevated spire. There are 2.5-3 whorls, of which the first 1.5 are tightly coiled, whereas the last part of the body whorl expands rapidly, flares as it nears the aperture and separates from the previous whorl. The ornament consists of growth lines and of spiral ridges and grooves. The growth lines are slight, though emphasized at irregular intervals marking breaks in growth, and usually more pronounced on the older parts of the shell. The spiral ridges are steep-sided and rather flat-topped; they are numerous (60-70 near the aperture), narrower in older parts and broader in younger, where their number is increased by the appearance of new ridges in the grooves. Growth lines are visible in the grooves but not over the ridges. Except in the oldest areas, where it is worn away, a well-developed periostracum obscures this ornament. It is marked by a series of flounces roughly parallel to the edge of the aperture, each with its margin drawn out into triangular projections which correspond to the spiral grooves. The periostracum projects freely a short way beyond the peristome.

The protoconch comprises *c.* 1.75 tightly-coiled whorls marked by about 6 spiral ridges (usually worn away) and a few growth lines. It tends to be glossy, shows a wide umbilicus on its under side, and is abruptly separated from the teloconch. It may be about 1.8 mm across.

Aperture. A large oval, elongated along the plane of spiral coiling and more pointed at the outer than at the columellar side. It is surrounded by a peristome which may be plane or not, but matches the surface to which it is attached; while always approximately in the plane of the shell axis it may be

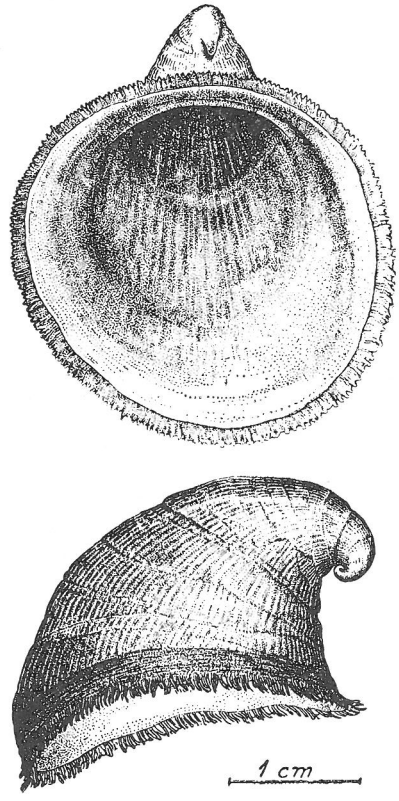

Fig. 224. *Capulus ungaricus* (Linnaeus).

slightly prosocline or slightly opisthocline. The peristomial edge is thin and toothed by the ends of the spiral ridges; just within the edge the throat is marked with small grooves lying under the spiral ridges. The throat is glossy except where marked by the horseshoe-shaped shell muscle (opening towards the periphery) and by the pallial line. Between these marks and the apertural edge it bears many minute ridges parallel to the edge.

Colour. The periostracum varies from straw colour to a reddish brown, the calcareous matter is white. Throat white but occasionally pink.

Size. Up to 40 mm long, 25 broad, 15 high (these orientations refer to an attached specimen). In the northern parts of the Kattegat a dwarf form not exceeding 11 mm in length is the common adult type (Thorson, 1965).

Animal. The head is rather broad and bears two tentacles, each with an eye some distance up from the base. Anterior to the tentacles is a short snout with the mouth at its tip; the lateral and ventral lips are drawn out to form a long proboscis, deeply grooved along its dorsal side from mouth to tip. It may be held in a variety of positions, varies in length and is much reduced or absent in the dwarf animals from the Kattegat. The mantle skirt is thick at its edge, which is smooth and double and lacks marginal glands. The osphradium and ctenidium stretch across the anterior part of the mantle cavity from the left end of the shell muscle. Small animals (usually 3-4 mm shell length) are male and have a curved penis arising behind the right tentacle and carrying an open seminal groove originating at the genital aperture in the mantle cavity. Larger animals (4+ mm) are female. In these the genital duct is closed and the penis reduced to a small papilla.

The foot has a rounded oval sole, anterior to which lies a transversely elongated, depressed and glandular area. This is bordered anteriorly by a straight, thickened edge carrying the opening of the anterior pedal gland, and posteriorly by a frilled ridge. There is no operculum.

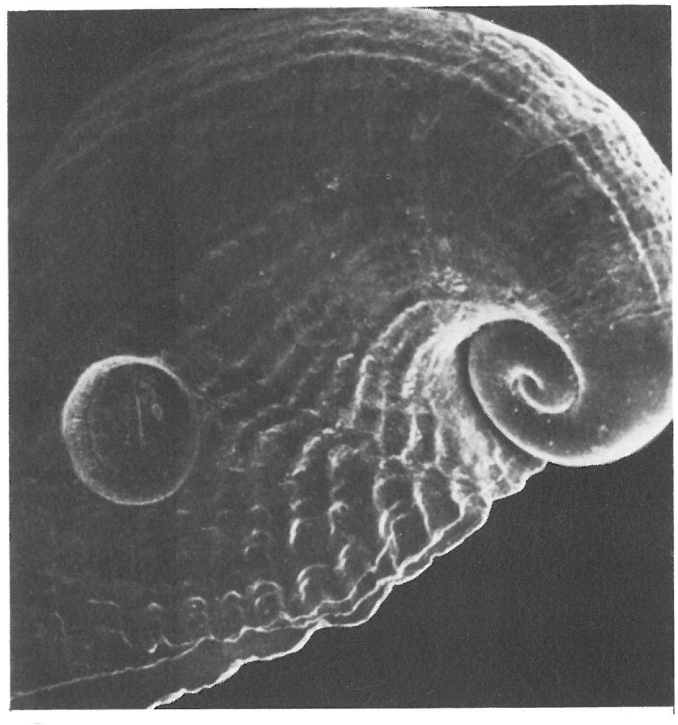

Fig. 225. *Capulus ungaricus.* Protoconch × 24. SEM photograph. Off Dunstaffnage, Argyll. RUZ.

Colour. Yellowish, often with many white flecks, especially on the mantle; sometimes pinkish.

Geographical distribution. Mediterranean; Atlantic coasts of W. Africa and Europe to N. Norway; Faeroes, Greenland and eastern American shores to Florida and Bermuda; apparently absent from Iceland. It extends into Skagerrak and Kattegat, becoming rare in the south. Not found in most parts of the North Sea, though recorded from the Moray Firth and off Berwickshire.

Habitat. C. ungaricus is not usually found between tidemarks but sublittorally to considerable depths (850 m), attached to stones and shells, particularly of living horse mussels *(Modiolus modiolus),* queens *(Chlamys opercularis)* and scallops *(Pecten maximus).* It has also been found close to the aperture of shells of *Turritella communis* while young ones may live near the opening of *Pomatoceros* tubes.

Food. This is a microphagous feeder, straining the pallial water current. This may be supplemented by what is picked up by the proboscis, especially when the animal is associated with a host. The faeces are ovoid pellets *c.* 400 × 200 μm.

Breeding and growth. The animals are protandrous consecutive hermaphrodites. Breeding appears to occur late spring — early summer at Naples (Lo Bianco, 1888, 1899) and at Plymouth. The eggs are brooded by the female in a large, yellowish, sausage-shaped egg mass wrapped in a membrane and held across the glandular propodial region of the foot anterior to the sole. It is not clear whether this is a single giant egg capsule or a pedal secretion. It may measure 10 × 5 mm when freshly produced and become slightly larger as development proceeds; it may contain up to 5000 whitish eggs, each about 200 μm in diameter. These hatch as echinospira larvae, veligers the normal shell of which (1 smooth whorl, 240 μm across) is enclosed within a second, which is soft, uncalcified and nearly spherical, about 400 μm across, decorated with many minute rounded elevations lying in more or less radial lines. The larval velum has 2 colourless lobes which later show traces of being double. The foot is rather small, but carries an operculum, lost at metamorphosis, and is drawn out to a narrow point posteriorly. Not much more is known of the larva but comparison of the size of the shell at hatching with the size of the protoconch suggests that larval life may be prolonged.

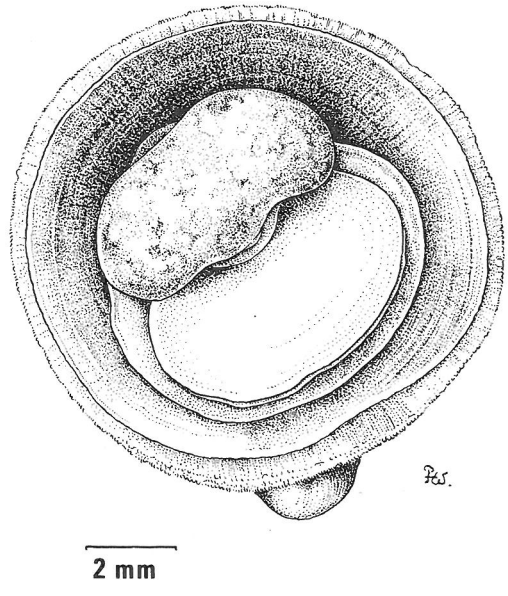

Fig. 226. *Capulus ungaricus.* Female with spawn mass.

Notes. This prosobranch can live independently, when it collects food from the water stream ventilating the mantle cavity (Yonge, 1938). The particles are carried by cilia to the dorsal surface of the front of the foot and there taken up by the proboscis which is itself, as in trichotropids, formed from the propodium. More frequently, however, it is found associated with a suspension feeding bivalve or the gastropod *Turritella,* usually at the margin of a valve in the former or at the base of the aperture in the latter, the anterior edge of its shell projecting a little over the lip of the host's shell, which is often a little broken. Here the proboscis, which is mobile, has been seen (Sharman, 1956) to intercept food collected by the host — or more probably pseudofaeces in bivalves — and this is diverted to the use of the *Capulus.* Sharman also showed that, on *Chlamys,* the *Capulus* showed a preference for the lower, slightly flatter valve and avoided the posterior area where the exhalant current emerged. The prosobranch tends to leave a round scar on the shell on which it lives.

The association between *Capulus* and bivalves is always with asiphonate forms. The limpet tends to place itself so as to lie across the path of water entering the mantle cavity of the bivalve. It seems likely, therefore, that it may benefit from a direct exploitation of the ingoing current, especially when its own ciliary equipment does not seem particularly well developed. A siphonate bivalve would not offer the same combination of a strong current plus a hard local substratum for attachment. Any use of the proboscis for uptake of pseudofaeces is therefore a bonus. This supposition would explain how the dwarf specimens examined by Thorson (1965) — which had either a reduced or no proboscis — would still find it valuable to sit astride the ingoing water current of *Turritella.* Examination of Thorson's figures shows them in exactly this situation.

The time and size at which sex change occurs appears variable. Lebour (1937) described an animal at Plymouth with an egg mass which had a shell 4 mm 'across'. Jones (1949) recorded males 5—8 mm in shell length off Port Erin associated with females 16—20 mm long. The dwarf animals found by Thorson (1965) were immature up to 4 mm shell length, male 4—6 mm and female from 7+ mm.

The discovery of an echinospira larva in *Capulus* raised the possibility that the genus should be classified as a lamellariacean. This was discussed by Graham (1954), who decided its connexions were much closer to Calyptraeacea, though, as discussed above, it now seems better to place it in the Hipponicacea.

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CALYPTRAEACEA

The characters of this superfamily are dealt with in the discussion of Hipponicacea (p. 300).

CALYPTRAEIDAE Blainville, 1824

CREPIDULA FORNICATA (Linnaeus, 1758), (American) slipper limpet

Patella fornicata Linnaeus, 1758

Crepidula (Lat.), a little slipper; *fornicata* (Lat.), arched. Both refer to the shape of the shell.

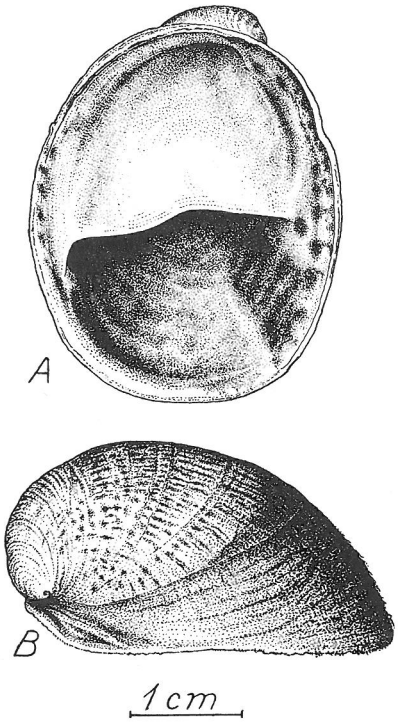

Fig. 227. *Crepidula fornicata* (Linnaeus). A, apertural view; B, from the right. Nykøbing, Mors, Limfjord. CMZ.

Shell. The orientation of the shell is such that the aperture is applied to the substratum while the spire lies at the animal's posterior end and on its right. The right slightly concave side is therefore the adapical surface of the body whorl. The abapical, convex, surface is on the animal's left. In comparing the shell with that of other prosobranchs the general shape is therefore planorboid, with the whorls coiled nearly in one plane.

Solid, opaque, rather glossy. There is hardly any spire; it is a little involute and the whorls rapidly expand. There are only two whorls, 1 belonging to the protoconch. The body whorl is oval in cross section, its long axis at right angles to that of the spire; its peripheral region is markedly curved but the ad- and abapical surfaces nearly flat, the former sometimes slightly concave. The degree of involution depends on the shape of this whorl. Ornamentation is slight and restricted to growth lines which are irregular in their development.

Aperture. Oval or slightly kidney-shaped, surrounded by a peristome which is irregularly curved to match the surface to which it is applied, but often has a peripheral sinus and slight projections above and below. In young shells the peristome lies almost in the axial plane but with increasing age it becomes very prosocline and lies finally almost at right angles to the axis of coiling. Except in very young shells the peristome makes no contact with the older parts of the shell. Its edge is thin, a little thickened near the spire. Some way within the aperture the throat is half blocked by a slightly concave partition attached to its columellar side; its edge is thin and it has a shallow median bay and small abapical sinus. The throat is very glossy, but when examined closely is seen to be marked with many low ridges. These lie at right angles to the lip just within the lip but parallel to it elsewhere. They tend to be pustular on the septum.

Colour. The background colour is white to yellow or red-brown with many reddish brown, short, spiral streaks. There is commonly a white, or paler, stripe along the periphery. The throat is chestnut brown even in pale shells, the partition milk-white, its origin from the shell usually marked by a dark red-brown area.

Size. 25 mm high, 50 mm across. Body whorl = aperture = total shell height.

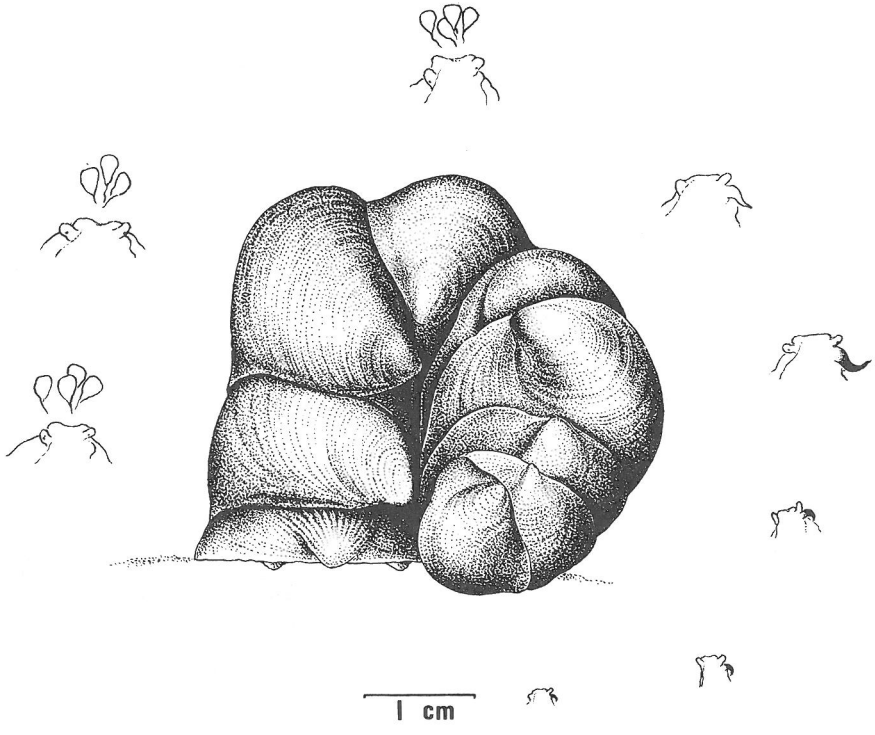

Fig. 228. *Crepidula fornicata.* Chain, showing the reproductive state of the members. Nissum Bredning, Limfjord, 6-8 m. CMZ.

Animal. The head is elongated but most markedly behind the tentacles, the snout being short, wide and depressed; it is bifid at the tip where the mouth (shut) is a vertical slit between slightly swollen lips. At the base of the snout are the tentacles, moderately long and tapering, with an eye on a basal bulge. Behind and ventral to the tentacles there is on each side a propodial fold (= cephalic lappet), a flat, semicircular flap inserted ventrolaterally and reaching back to the level of the mantle cavity. A ciliated groove runs over the base on the left lappet: anteriorly it passes dorsal to the left tentacle, posteriorly it leads to the opening of the mantle cavity where it crosses to the mantle edge and goes to a pouch embedded in the thickness of the mantle skirt directly over the head. The right lappet bears an anterior lobe which stretches ventral to the right tentacle nearly to the mouth. Posteriorly this connects with the food groove running to the inner end of the floor of the mantle cavity. The mantle skirt has a thickened, slightly lobed edge; a more prominent lobe placed a little right of the mid-line separates the food pouch on the left from the anterior tip of the ctenidium on the right. At intervals round the margin of the skirt there lie about 16 repugnatorial (?) glands. The mantle cavity narrows backwards from a wide opening and is long, reaching to the posterior tip of the visceral mass. The ctenidium extends its whole length, with many long, narrow filaments; its axis forms a glandular strip, the endostyle. In small animals, which are male, a long recurving penis arises immediately behind the right tentacle; it may be twice as long as that and carries on its posterior face an open seminal groove leading from the genital opening in the mantle cavity over the right epipodium. Larger animals are female, have lost the penis and their genital duct is closed.

The foot is a broad oval in outline with a double edge anteriorly, the propodial part often lobed. The posterior half of the foot lies external to the shell partition and has no operculum.

Colour. Yellowish with dusky colour on head and tentacles and more solid black on the mantle edge and penis.

Geographical distribution. Originally American, where it is found from Chaleur Bay, Gulf of St Lawrence, south to Texas, this species has been accidentally transported with oysters to the Pacific coast of the United States (Washington) and to parts of Europe. It was brought to England in 1887-1890 and has now extended its range on British coasts from the original site of importation (Brightlingsea, Essex) along the E and S coasts of England and into the Bristol Channel. In Ireland it has been found in Belfast Lough and Co. Kerry. Its spread in the North Sea has been documented by Polk (1962). It was introduced with oysters into Holland (1929) and has travelled thence to the German Bight (1934), Limfjord (1935) and the Norwegian and Swedish shores of the Skagerrak and Kattegat. It reached Ostend in 1911 but spread more slowly West, not reaching Calvados till 1955, but it is now found on French Channel and Atlantic coasts south to the Ile d'Oléron. It has also been recorded from Sicily and the Adriatic (Parenzan, 1979).

Habitat. Usually sublittoral to depths of *c.* 10 m, but sometimes at low water mark or thrown up after storms. The animals live in chains of up to 12 individuals sitting one above the other so that the peripheral areas of the peristome are aligned; the chain is therefore curved. The largest, oldest animals lie at the base and the smallest ones above in order of settling. The lowermost shell may be attached to a stone or an oyster, mussel or scallop shell, but it is often empty, in which case the chain is loose. A few animals, usually young, live alone.

Food. C. fornicata is a microphagous mucous feeder. Faeces ovoid or elongated pellets *c.* 400×200 μm.

Breeding and growth. The animals are protandrous consecutive hermaphrodites, the upper members of a chain male, the lower ones female and a central zone occupied by those changing sex. In a natural chain 55% of the animals are male, 6% transitional and 39% female (Wilczynski, 1959). Because of the approximation of the outer lips of the shells the penis is long enough to allow copulation and is longer in the smaller males at the end of the chain. Breeding occurs through spring and summer (Feb—Oct, maximum May—June when 80-90% of females brood), most females appearing to spawn twice, mainly after neap tides. Up to 70 stalked egg capsules are brooded under the foot of a female, attached either to the foot or the underlying shell. Each capsule is a slightly inflated triangular or heart-shaped bag with a delicate wall, cream, yellow or orange in colour, 2—4 mm across, and contains 250—300 eggs, 160—180 μm in diameter, floating in a common pool of albumen. The young hatch as veliger larvae through a slit across the top of the capsule after 3—4 weeks at 10—13°C, after 17 days at summer temperatures. They have smooth, transparent, colourless shells of 0.75 whorls, about 300 μm in diameter. They grow to 1+ whorls during a planktonic life of *c.* 5 weeks and become opaque and horn-coloured at metamorphosis when they

measure up to 700 μm. By this time the aperture has begun to dilate and a ridge has been formed on the body whorl by secretion from the edge of a posteriorly directed tongue of mantle extending out of the aperture. Later the ridge fuses with the outer lip to form the oval peristome of the metamorphosed snail, whilst secretion of the shell from the adapical surface of the tongue produces the internal partition. This development hides the abapical surface of the early whorls, the original inner lip and columella. The larva has a bilobed velum and a broad, rounded foot bearing an operculum and, anteriorly, 2 propodial lobes, the later cephalic lappets. The velar margin has a red line and some yellow or black pigment spots, a dark central line on the sole and a black posterior tip. See Conklin (1898), Orton (1912), Morse (1921), Ankel (1936), Chipperfield (1951), Werner (1955), Polk (1962), Fretter & Pilkington (1970), Lubet & Le Gall (1972), Hoagland (1978).

The larvae in Essex settle mainly in June—July when the shell diameter is about 700 μm. By October they average 8 mm in shell diameter and about 10 mm in the following spring (Orton, 1912). At Ostend Polk (1962) described a double spatfall one in May a second in September. Lubet & Le Gall (1962), however, recorded an extended settlement from May to October—November. Growth stops between January and March leading to the formation of a distinct winter ring on the shell. Young animals lose the ability to move when about 2 years old, mature at a shell diameter of 4 mm and reach full size after 4—5 years. They may live about twice as long (Walne, 1956).

Notes. An extensive literature relates to *Crepidula fornicata,* partly because of its economic importance, partly because of interest in its sexual biology.

C. fornicata is a serious pest of oyster beds. The chains are often fastened to oyster shells or, if loose, accumulate over them to a considerable depth. Since they are microphagous they compete directly with the oysters while their pseudofaeces tend to smother them and create a soft substratum repellent to settling oyster spat. They may be removed by dredging, over 8 tonnes per hectare having been taken (Cole & Hancock, 1956); though the population gradually reappears, maximal numbers are not reached for a decade or so.

Slipper limpets are specialized microphagous feeders (see Werner, 1952, 1953, 1959). At the entrance to the mantle cavity the inhalant water stream is passed through a coarse mucous filter. Particles caught here are carried to the food pouch in the anterior mantle skirt and withdrawn at intervals by the radula. Water which passes this filter has then to traverse a ctenidial one. The gill filaments are long and narrow and extend obliquely across the mantle cavity from the ctenidial axis on the roof to the food groove on the floor. Mucus secreted by the endostyle is carried by cilia over the branchial surface, trapping food particles on its way, and is rolled into a rod in the food groove along which it is carried to the anterior lobe of the right cephalic lappet and ingested. The food-catching apparatus is thus a mucous trap as in tunicates rather than a ciliary trap as in bivalves. Bulnheim (1970) has shown the existence of irregular periods of slower and faster pumping in a continuous flow of water through the mantle cavity.

The status of *C. fornicata* as a protandrous consecutive hermaphrodite was established by Conklin (1898) and Orton (1909), and its sexual biology investigated by Gould (1919, 1947, 1952), Coe (1938a, b, 1942, 1944, 1948, 1953), Bacci (1951) and Hoagland (1978). Spat may settle in isolation or as the apical member of an established chain. At this stage immature male and female cells are both present in the gonad. If the spat settles by itself a brief male stage commonly follows, passing rapidly to a female one, especially if another animal settles on it to initiate chain formation. If the spat settles on a chain (to which it is undoubtedly attracted) it becomes male and stays so for an extended period — up to 6 years — apparently stimulated to do so by a pheromone secreted by the females lower in the chain. As it matures as a male sperm come to fill the genital duct, a state which promotes growth of the penis. On transforming to a female, a process which takes about 60 days at Heligoland (Pandian, 1969), the penis regresses, usually totally, the open seminal groove closes and the glands and pouches of the female duct develop. The time at which this occurs varies, depending on environmental conditions.

The production of male gametes has been shown (Lubet & Streiff, 1969) to depend on the presence of the cerebral ganglia, which may act either by nervous, neurosecretory, control or by a blood-borne hormone. Formation and maintenance of the male duct and penis, however, are due to a harmone probably produced in the cerebral ganglia but perhaps liberated by way of the right ocular or tentacular nerve. The ocular hormone, injected into a female, can also re-create a penis from the penis area. Regression of male organs and their replacement by those of female type are affected by the cessation of production of male hormone and the secretion of a female one by pleuropedal ganglia. Once present the female organs do not require maintenance since secretion of male hormone has stopped.

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CALYPTRAEA CHINENSIS (Linnaeus, 1758), Chinaman's hat.
Patella chinensis Linnaeus, 1758
Calyptraea sinensis (Linnaeus, 1767)

Calyptraea (Gk. καλύπτρα), a veil, hood or woman's cap; *chinensis* (Lat.), Chinese (mandarin's hat). Both terms refer to the shape of the shell.

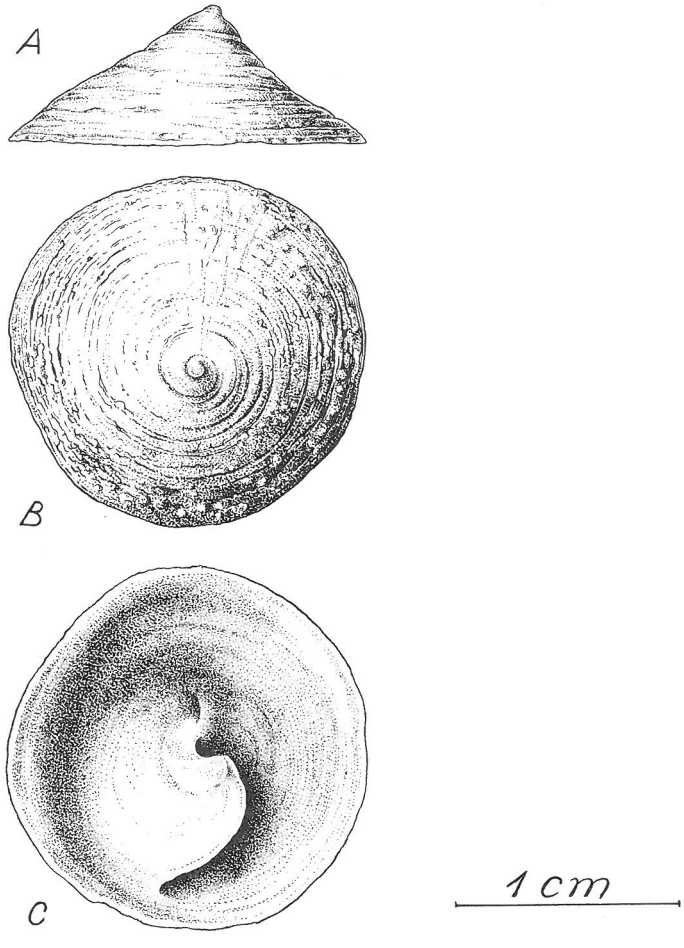

Fig. 229. *Calyptraea chinensis* (Linnaeus). A, from the right; B, apical view, anterior end below; C, apertural view, anterior end above. No locality given. CMZ.

Shell. A rather smooth patelliform shell with a sharp apex (apical angle 70—85°); it is solid (though not thick), opaque and not glossy. The apex forms a slightly upraised beak and lies a little towards the anterior end. The profile of the shell is concave anteriorly, straight on each side and straight or slightly convex posteriorly. The apex may show a spiral protoconch of 0.75 to 1 + smooth whorls, but this is often eroded. The ornament consists of slight growth lines encircling the shell. Towards the aperture these often rise adapically at regular intervals to form small, inverted V-shaped, hollow projections; these may lie in straight or spiral lines from apex to base. There is otherwise no spiral ornament.

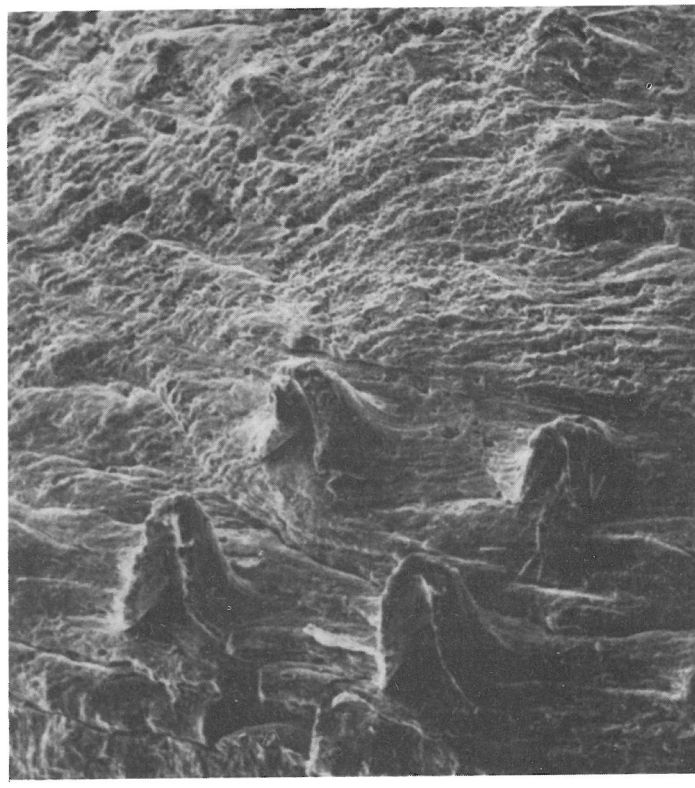

Fig. 230. *Calyptraea chinensis.* Microstructure of shell × 37. SEM photograph. Plymouth. RUZ.

The protoconch is not clearly marked off from the teloconch. Its diameter is 600-700 μm.

Aperture. Nearly circular with a thin edge bevelled internally. The peristome may lie in one plane but is often curved to match the surface to which it is applied. Internally a partition arises from the shell along a slightly curved line running from the apex to near the aperture posteriorly, a little right of the mid-line. It projects obliquely across the cavity of the shell. Close to the apex it is narrow and thick; towards the aperture it expands to a rounded tongue. The free edge of the tongue parallel to the peristome is thin; that running towards the apex is folded back on itself to enclose a small cavity. The shell is glossy internally.

Colour. White or yellowish; milk white internally.

Size. Up to 15 mm diameter, 5 mm high.

Animal. Very much as in *Crepidula,* though the visceral mass (lying above the shell septum) is smaller. The mantle skirt is thicker and more extensive laterally and posteriorly than in *Crepidula* and the number of marginal glands greater. The lobe separating food pouch from ctenidium is more obvious and is kept in contact with the dorsal surface of the head, whilst the food pouch opens to the mantle cavity rather than the edge of the mantle skirt. Most of the pedal musculature attaches to the lower side of the shell partition, but a slip enters the cavity along its central margin. The penis is relatively larger than in *Crepidula* and expands at its apex to form a bilobed knob. A vestigial penis lies above the base of the right tentacle of females.

Colour. Yellow with numerous white speckles.

Geographical distribution. C. chinensis occurs in the Black Sea (var. *polii* Scacchi, 1836), the Mediterranean, off N.W. African coasts and north along those of Europe to the British Isles where it reaches as far as the North Channel (Loch Ryan). It is not found in the eastern Channel basin nor the North Sea.

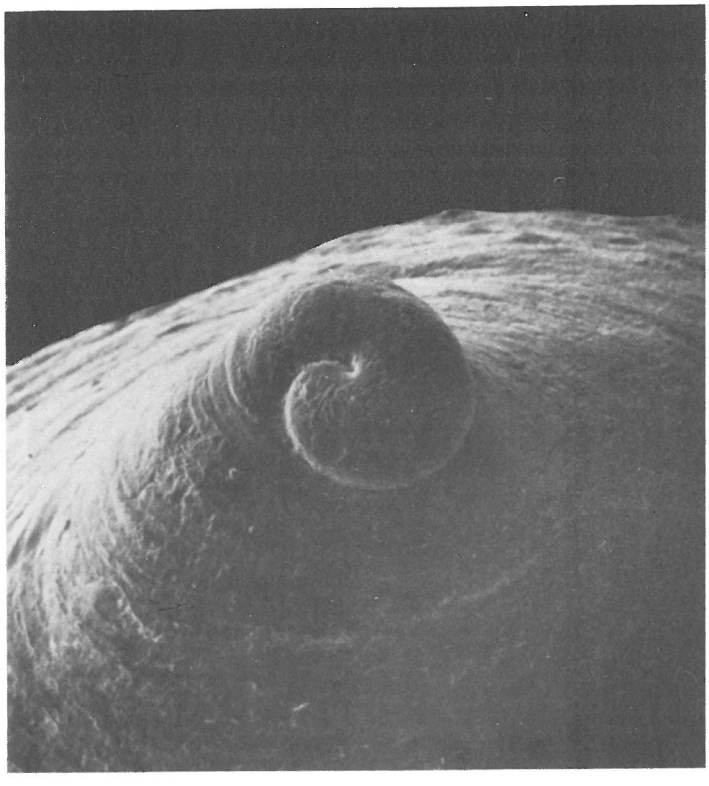

Fig. 231. *Calpyptraea chinensis.* Protoconch × 33. SEM photograph. Plymouth. RUZ.

Habitat. Predominantly sublittoral to about 20 m this animal may also be found intertidally at about LWST on sheltered shores in Devon and Cornwall. It lives on shells or under stones, usually those with smooth surfaces. It is commoner on shell gravel or softer substrata with stones than on rocky shores.

Food. A mucous feeder like *Crepidula.*

Breeding and growth. The animals are protandric consecutive hermaphrodites with a sex cycle like that of *Crepidula* except that (1) the young gonad contains no apparent female cells, and (2) the length of the male phase is constant, unaffected by association with a female, so that all animals change sex at the same age. This links with the fact that the limpets do not live in chains and come together only for breeding. The males are the mobile partners, females hardly moving. Breeding occurs April—September at Plymouth and the Black Sea, when eggs are laid in clear, colourless capsules which are oval-triangular in profile, 3 mm long by 1.5 broad and attached to a stone or shell by the narrow base. Each contains 4—25 white, yolky eggs embedded in a common mass of albumen. In the Black Sea specimens (var. *polii*) the eggs were 300 μm in diameter, at Plymouth 480 μm. The capsules are brooded by the female under the front of the shell (Wyatt, 1960). The veliger stage is passed within the capsule and the velum shed just before hatching. At this stage the shell has 1+ whorls and a diameter of 600—700 μm. The circular aperture and internal partition arise by outgrowth of a tongue of mantle tissue from the original aperture of the embryonic shell and are already present at hatching. The animals are immature until the shell diameter is *c.* 1.4 mm, male until the shell is *c.* 2 mm across, that is, during their first year, change sex and are female thereafter, probably dying at 3 years old (Bacci & Pellegrini, 1951).

Notes. The feeding mechanism of *Calyptraea* has been described by Werner (1952, 1953, 1959), the breeding by Giese (1915), Lebour (1936) and Vinogradova (1950), and the formation of the shell septum by Fretter (1972). The neurohumoral control of sex changes and development and maintenance of the gonad and genital organs (which is similar to that in *Crepidula*) is summarized by Lubet, Streiff, Silberzahn & Drosdowsky (1973).

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LAMELLARIACEA

This is one of the smaller superfamilies of Recent mesogastropods and shows characters convergent with those of Strombacea and, in particular, Cypraeacea. At most 5 families have at times been assigned to the group but of these 3 are not at all well known, contain only a single genus apiece and may, indeed, be wrongly classified. Thus only two families of undoubted lamellariaceans remain, Lamellariidae (= Velutinidae) and Eratoidae. These are very different in shell characters though similar in other ways. All are marine carnivores eating the tunicates and coelenterates on which they are usually found by means of an acrembolic proboscis. All tend to cover the shell with papillated mantle lobes. The osphradium is curved with a double row of leaflets. The foot usually possesses a large gland opening towards the posterior end of the sole and always lacks an operculum. The pedal ganglia are ovoid masses in the main nerve ring. The egg capsules are embedded in the test of the prey and the larvae which emerge are echinospiras. The surface of the uppermost whorls of the spire is smooth or, at most, very slightly marked spirally.

The family Eratoidae presents the more primitive features. The shell is robust, devoid of periostracum and its whorls do not expand rapidly. At maturity the body whorl may enclose the spire to give a convolute shell as in *Trivia.* The shell surface is often covered with a secondary deposit secreted by the enveloping mantle folds. The aperture is long and narrow and the animal can retract completely. The scaphoconch (= outer echinospira shell) has a helicoid coiling.

The lamellariids are distinguished by a shell of a few, fragile, rapidly-expanding whorls bearing little ornament. The spire is small and the aperture large, a trend reaching a climax in the patelliform *Capulacmaea* and the slug-like *Onchidiopsis,* both from Arctic seas. In *Velutina* the shell is extremely thin but has a thick periostracum and the animal can withdraw completely; in *Lamellaria* and *Onchidiopsis* the mantle lobes fuse over the shell and this is no longer possible. The scaphoconch has a nautiloid coiling.

It may be asked why, if an echinospira larva is a feature of every lamellariacean, *Capulus,* which alone outside the Lamellariacea also has one, should not be classified here. It is, unfortunately, not possible to base a coherent classification on this feature: *Capulus* has, in every other way, clear relationships with Hipponicacea. The presence of this larval type in conjunction with other points appears to suggest, at most, a general, rather remote connexion of Hipponicacea, Calyptraeacea, Lamellariacea and Cypraeacea.

LAMELLARIIDAE Orbigny, 1841
LAMELLARIA PERSPICUA (Linnaeus, 1758)
Helix perspicua Linnaeus, 1758
Lamellaria tentaculata (Montagu, 1811)
Marsenia perspicua (Linnaeus, 1758)

Lamellaria (Lat.), lamelliform, said to refer to the shape of the mantle; *perspicua* (Lat.), clear, referring to the shell.

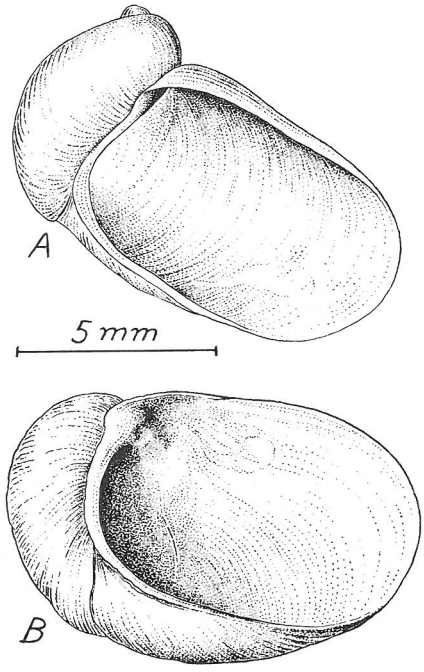

Fig. 232. *Lamellaria perspicua* (Linnaeus). A, apertural view; B, basal view. Faeroes. CMZ.

Shell. This is internal, permanently covered by fusion of right and left mantle lobes. It is clear, almost transparent when fresh, though it may become opaque white when weathered, with a very small spire and large body whorl. There are 2-3 rapidly expanding whorls meeting at deep sutures which lie below the periphery of the upper whorl. The ornament is predominantly prosocline growth lines but there may also be some slight spiral ones.

The initial whorl lies a little oblique to the axis of the rest of the shell.

Aperture. A very large rounded quadrilateral, its long diameter making an angle of 120-130° with the shell axis. It lies in a prosocline plane and is surrounded by a peristome. The outer lip is thin throughout and arises more or less at right angles to the surface of the body whorl at or below the periphery. Its first part is a little inturned so as to contract the aperture and its course is gently curved or rather straight. It then curves sharply to the basal section which is roughly parallel to the adapical edge. There is no siphonal notch. The inner lip is short, C-shaped, a little turned out, and this part is marked by slight longitudinal folds. It covers the umbilical groove and its adapical part joins the outer lip.

Colour. Varying from nearly clear and colourless when fresh to opaque white; a little iridescent.

Size. Up to 9 × 10 mm. Body whorl = 90-95% of total shell height, aperture = 80-85% of total shell height. The animal may measure up to 20 × 12 mm.

Animal. The head is flattened and not prolonged into a snout so that the tentacles arise from its anterior border. The apparent mouth (opening of a proboscis sac) is a longitudinal slit on its lower

side. The tentacles are long and slender, each with a small eye on a basal bulge. The edge of the mantle skirt is greatly thickened and flattened and is folded anteriorly to form a short upstanding siphon just left of the mid-line. The mantle is tuberculated and covers the shell. In the mantle cavity is a shield-shaped bipectinate osphradium alongside a short ctenidium. In males a large penis arises from the right side of the head some way behind the base of the right tentacle. It is laterally compressed, usually curved, and a little below the tip gives off a narrow, tapering flagellum almost as long as the thicker base. Distal to the origin of the flagellum the penis is deeply grooved. The male pore is a minute opening at the end of the flagellum.

The foot is moderately long and narrow. Its anterior end is truncated and carries a broad slit which extends a short way down each side, the opening of the anterior pedal gland. The propodium, which forms the dorsal lip of the slit, is slightly corrugated. There is neither ventral pedal gland nor operculum.

Colour. A variable animal. The mantle over the shell may be grey, grey-lilac, buff or orange. It may have no patches of other colour but often shows lines or splashes of white, yellow or black, occasionally mimicking tunicates, sponges or barnacles. The head and foot are pale and not marked. Osphradium yellow.

Geographical distribution. Mediterranean, Azores and western European coasts north to the Lofoten Islands; also in Iceland. It occurs in the Skagerrak and on Swedish (Bohuslan) but not Danish coasts.

Habitat. On rocky or stony shores from near LWST downwards to considerable depths (1200 m), especially in the more southern parts of its range. It may be found under stones, in rock pools, or under ledges, usually where there are growths of compound ascidians. It is moderately common.

Food. The compound ascidians with which it lives — *Botryllus, Leptoclinum, Polyclinum.* Faeces are ovoid pellets *c.* 300 × 200 μm.

Breeding and growth. The sexes are separate. Males may be recognized by the penis; females have no ventral pedal gland to identify them. Breeding takes place in spring and summer. Early accounts of the reproductive behaviour are given by Peach (1858) and Giard (1875), more recent ones by Pelseneer (1911), Ankel (1935), and Lebour (1935). Lebour (1935, 1937), Thiriot-Quiévreux (1969) and Fretter & Pilkington (1970) have described the larva, which is an echinospira. The eggs, each *c.* 250-300 μm across, are yellowish and laid in flask-shaped capsules with a short neck, measuring about 2-5 × 2-4 mm, which are inserted by the female into holes which she has bitten out of the test of the ascidians used as food. In the absence of a papilla in a ventral pedal gland the capsule must be inserted by general pressure until all but the mouth is embedded in the test. The capsule contains 1-3 thousand eggs lying in a layer 1 cell thick against the inner wall. Some have been said to be food eggs (Giard, Pelseneer) but this was denied by Ankel. At laboratory temperatures they hatch in about 3 weeks to give larvae with a scaphoconch 350 μm across enclosing a small shell the axis of which does not coincide with that of the scaphoconch. The scaphoconch is planispiral, glass-like and has about 2 flat-sided whorls. On each side of the shell there are 2 spiral keels, one near the periphery, the second about half way to the centre, each keel marked by numerous transverse striations (= Lebour's denticulations) 18 μm apart. By the time of metamorphosis the scaphoconch has 4-5 whorls with a diameter of 2 mm and a pronounced apertural beak. The inner shell, which is always helicoid and eccentrically placed, grows more slowly and is only about half the size of the scaphoconch. The velum of the larva is initially 2-lobed with a marginal row of yellow-brown spots; later extra spots appear scattered over the lobes and on the larval mantle and foot, especially the sole. In older stages the velum becomes 4-lobed, then 6-lobed, the middle lobe on each side smaller than the others. The larval mantle always tends to overgrow the mouth of the inner shell and by metamorphosis, when the scaphoconch has been lost, the shell is completely and permanently enveloped. Pallial tubercles do not develop until later. Some information on the internal structure of the larva at metamorphosis is given for this and the following species by Thiriot-Quiévreux (1974).

LAMELLARIA LATENS (Müller, 1776)

Bulla latens Müller, 1776
Lamellaria perspicua (Linnaeus, 1758), male
Lamellaria perspicua var. *lata* Jeffreys, 1867

Latens (Lat.), concealed. This refers to the shell and emphasizes the fact that it is completely hidden by the mantle, whereas it is at least partly visible in the other species of the genus *Bulla* to which Müller thought it belonged.

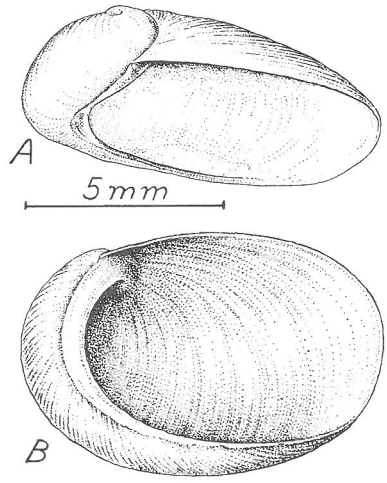

Fig. 233. *Lamellaria latens* (Müller). A, apertural view; B, basal view. Faeroes. CMZ.

Shell. Differing from that of *perspicua* in being flatter, the spire hardly rising above the body whorl, and containing no more than 2 whorls. The sutures are not so deep and the apical whorl is set less obliquely.

Aperture. Like that of *perspicua* but relatively larger. The outer lip is not inturned adapically to the same extent.

Colour. Clear and transparent when fresh, becoming white.

Size. Up to 4-5 × 9-9.5 mm. Body whorl = 96% of total shell height; aperture = 65% of total shell height. The animal may be 10 × 6 mm.

Animal. As in *perspicua,* the mantle, however, smoother.

Colour. Generally buff with speckles of dark brown or black; paler than *perspicua.* Not lilac.

Geographical distribution. From the Mediterranean north to Norway. Doubtfully absent from Skagerrak and Kattegat. This still requires investigation as the 2 species have not always been separated.

Habitat. As for *perspicua.*

Food. Presumably compound ascidians as for *perspicua.* Lebour (1935) recorded it on "*Alcyonium* and sessile animals" but it seems unlikely that it eats coelenterates.

Breeding and growth. The sexes are separate, males distinguished by the penis. The eggs have not been knowingly found but may well be laid in capsules in ascidians as described for *perspicua* and confused with them. The larva is an echinospira and one found and described by Lebour (1935) is assumed to belong to this species. It is much like that of *perspicua* but may be recognized by the coarser striation of the keels of the scaphoconch (striae 40 μm apart). The central velar lobe on each side is relatively larger than in *perspicua* and at metamorphosis the scaphoconch is 3 mm in diameter. The body of the veliger is always paler.

Notes on Lamellaria *species.* The belief that two species of this genus occur in British waters was confirmed by the work of Lebour (1935) and McMillan (1939). Separation of the two by examination of the shell is relatively

easy, the spire of *perspicua* being markedly taller than that of *latens.* To make a certain identification of the living animal is not so straightforward, the colour differences cited by McMillan (1939) not being so definite as her paper suggested, though they are helpful. An animal with a grey-purplish colour frosted with white spots is a specimen of *perspicua:* it will have a rather high, dome-shaped dorsal surface marked with tubercles and may well be over 15 mm long. Specimens of *perspicua* may also be yellow or orange in colour and have blotches of other colour, though this was originally denied by McMillan. This shade, however, is more general in *L. latens* which is further characterized by its lower shape, smoother mantle, commonly with dark speckling, and smaller size.

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VELUTINA PLICATILIS (Müller, 1776), velvet shell

Bulla plicatilis Müller, 1776

Velutina flexilis (Montagu, 1808)

Velutina, velvety, from Late Latin *velvettum,* French *velours,* velvet, referring to the texture of the shell surface; *plicatilis* (Lat.), pliable, referring to the shell.

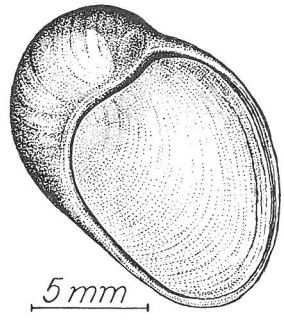

Fig. 234. *Velutina plicatilis* (Müller). Hellebaek. CMZ.

Shell. This is fragile, nearly transparent, so weakly calcified in its younger parts as to be flexible. It is covered by a periostracal layer so thick as to hide the whorls and sutures of the spire and smooth the whole surface. The periostracum bears small prickles. The calcareous shell has up to 2.5 tumid whorls, rapidly expanding, the body whorl making up nearly the whole shell. The suture between it and the penult is deep and exposes much of the surface of the latter. The apical angle of the

calcareous shell approaches 180°, but that of the periostracal cover varies from 100-120°. The ornament consists of prosocline growth lines, rather irregularly developed and sometimes standing out at intervals like incipient riblets, especially near the suture. There may also be indistinct spiral lines giving a shallow reticulation of the surface. Sometimes the transverse ornament is coarse enough to affect the surface of the periostracum.

The protoconch has *c.* 1 whorl marked with spiral striae.

Aperture. A large and rather narrow oval, the long axis set at an angle of 150° to that of the shell, lying orthoclinally and surrounded by a peristome. The outer lip arises more or less at right angles to the surface of the shell and shows an adapical anal sinus. Its course towards the base is moderately curved but the radius of curvature then shortens markedly and the lip turns tightly towards the columella, following a nearly straight course, though also exhibiting a shallow sinus. The columella is short. The inner lip over the body whorl is also short and is flat and sinuous. There is no umbilicus. There may be a little eversion of the peristome near the base. In dried shells the whole peristome becomes distorted and may roll outwards giving a false impression of a thick-lipped aperture.

Colour. Yellowish near the aperture, mainly due to the periostracum; pinkish on the body whorl near the suture; apical area white. Some colour is due to viscera showing through the shell.

Size. 15 × 12 mm. Body whorl = total shell height;aperture = 85% of total shell height.

Animal. The head has no snout, the tentacles arising from a rather broad transverse fold with a slight median notch. The mouth (= opening of a proboscis pouch) is a slit with protuberant lips lying rather far back on the underside of the fold. The tentacles are long, with blunt tips which form distinct knobs on retraction, and have each an eye on a prominent lateral bulge at the base. The mantle skirt has a smooth edge and is thickened so as greatly to constrict the openings of the mantle cavity, leaving a small channel on the left and a larger one on the right. The osphradium, which is bipectinate, and the ctenidium are visible through the former, the anus through the latter. All animals have a penis of moderate size which arises from the floor of the mantle cavity behind the right tentacle; its base is fleshy but the distal part, which is recurved into the mantle cavity, is a narrow flagellum with the male pore at the tip. The female aperture lies within the mantle cavity.

The foot is elongated and shield-shaped, narrowing in the middle. The anterior edge is nearly straight, the lateral corners slightly recurved; it is double because of the very large and deep opening of the anterior pedal gland. The posterior end is bluntly pointed. There is neither ventral pedal gland nor operculum.

Colour. White, yellow or orange. The osphradium is brownish and the hypobranchial gland white, showing through the shell.

Geographical distribution. A circumboreal form which extends southwards to the Skagerrak, Kattegat, northern parts of the North Sea, the west coast of Scotland and of Ireland and as far as northern Spain. In the Western Atlantic it is found as far south as Nova Scotia.

Habitat. This animal is found on hard bottoms, usually in association with compound ascidians and hydroids (*Tubularia indivisa:* Ankel, 1936). It is not intertidal and has been found from 10 — *c.* 375 m deep.

Food. The ascidians with which it is found and probably also the hydroids, using the proboscis presumably as *V. velutina* does. Faeces ovoid pellets 200 × 100 μm.

Breeding and growth. The animals are simultaneous hermaphrodites. The time of breeding appears to be unknown and Lebour (1937) concluded that the larval stage had not been seen, though Pelseneer (1906) had described an echinospira from the Bay of Biscay as belonging to this species. The outer shell was nautiloid and had 1 whorl; the inner shell was excentrically placed.

VELUTINA VELUTINA (Müller, 1776)

Bulla velutina Müller, 1776
Velutina laevigata (Pennant, 1777)
Velutina haliotidea (Fabricius, 1780)

Shell. Much as in *V. plicatilis.* There are 2.5 rapidly-expanding whorls, the body whorl making up the greatest part of the shell. The whorls are tumid and meet at deep sutures, though these features, as in *plicatilis,* are obscured by a general cover of periostracum. The spire is low, in some shells the

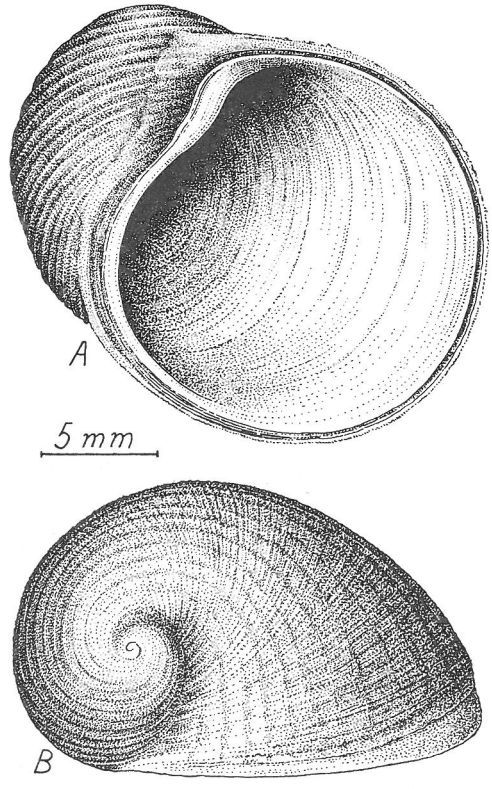

Fig. 235. *Velutina velutina* (Müller). A, apertural view; B, apical view. No locality given.

apex even being a little insunk. The ornament consists of innumerable fine, prosocline growth lines crossed by many equally fine and low spiral ridges, giving a shallow reticulated surface.

The protoconch has 1—1.5 whorls, the first part smooth, the next with numerous spiral lines; the diameter of the smooth part is about 500 μm.

Aperture. A very large, approximately circular opening indented a little towards a kidney shape by the body whorl and surrounded by a peristome lying in a prosocline plane. The outer lip arises from the body whorl adapical of its periphery, at right angles to the axis of the shell, and sweeps in a smooth, semicircular curve to the base of the columella. Its edge is thin and it has no adapical anal sinus. The inner lip forms a sigmoid curve, the concavity facing the aperture along the columella and away from it along the body whorl. The periostracum projects beyond the peristomial edge and in dried shells often contracts to form an apparently thickened lip.

Colour. Periostracum brown, darkening with age; the underlying calcareous shell is white.

Size. Up to 20 × 20 mm but commonly about half that. Body whorl = total shell height; aperture = 90—95% of total shell height.

Animal. As in *plicatilis.*

Colour. The general coloration is yellowish white, the thick mantle edge frosted with white points. The osphradium is yellow-brown, the hypobranchial gland white.

Geographical distribution. A northern species stretching round much of the Arctic seas. It extends south to the Skagerrak, Kattegat, northern parts of the North Sea, the western coasts of the British Isles to the Mediterranean. In the Western Atlantic it reaches to Cape Cod and to Monterey on the American Pacific coast. It becomes rarer and deeper in the southern parts.

Habitat. This animal is found on hard bottoms, always associated with tunicates, especially solitary forms such as *Phallusia* and (in particular) *Styela,* which it resembles in colour. It is occasionally found at LWEST but is normally sublittoral, extending to 1000 m.

Food. It bores through the siphonal region of the test of the ascidians with which it lives, using the proboscis and radula, and then ingests the flesh. Faeces ovoid pellets 200 × 100 μm.

Breeding and growth. Breeding has been described by Diehl (1956) and the larvae by Lebour (1935), Thorson (1946), Thiriot-Quiévreux (1969) and Fretter & Pilkington (1970). The animals seem to breed through most of the spring and summer. The eggs are laid in spherical capsules placed in holes bitten out of the test of ascidians, especially *Styela.* Each capsule is 3 mm in diameter and is completely buried except for the mucous plug which closes it, which lies nearly flush with the surface of the test. The capsule and the surrounding test interact to produce a swelling which may be 6 mm across. There are many eggs, each about 150 μm across, within a capsule which hatch after a long development period as echinospira larvae.

The echinospira shell is soft and gelatinous, of about 1 whorl, decorated with rows of dots radiating from its centre. The true shell lies nearly centrally within it and also has 1 whorl. The diameters of the two shells are *c.* 500 μm at hatching. The velum is then bilobed and colourless. As the larva grows the outer shell becomes more or less globular, the inner one develops spiral lines which project over the aperture as 5 denticulations, and the velar lobes become partly subdivided and bear lines of red pigment. At metamorphosis the larva may have a diameter of 2 mm, the inner shell *c.* 1.3 mm across. Velum, larval shell and operculum are lost simultaneously, the first being eaten, and the juvenile drops to the bottom. The structure of the larva is described by Thiriot-Quiévreux (1974) but there is no information on later stages.

Notes on Velutina *species.* These are not well-known animals, partly because of their northern distribution, partly because they are rarely intertidal. There is still much to be learnt about their food, feeding, growth and their sexual biology as hermaphrodites.

Separation of the two species is relatively easy: *V. velutina* is known by its dark brown colour and by the nearly circular aperture, *plicatilis* by its lighter yellow colour and by the elongated oval aperture. Though neither species has an operculum when adult they can both withdraw into the shell. The mantle skirt in *Velutina,* unlike that of some related genera, does not cover more than a small part of the outer surface of the shell alongside the aperture.

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ERATOIDAE Gill, 1871

ERATO VOLUTA (Montagu, 1803)

Cypraea voluta Montagu, 1803

Marginella laevis (Donovan, 1804)

Erato (Gk.), the lyric muse; *voluta* (Lat.), rolled, referring to the coiled shell.

Shell. Solid, nearly opaque, glossy. The spire is short, nearly flat-sided, giving the impression of being pointed though the actual apex is flattened. Most of the shell is occupied by the body whorl. The whorls of the spire are only slightly tumid and the sutures almost non-existent, each lower whorl being plastered against the surface of the upper one a little below its periphery. The ornament consists of slightly prosocline growth lines which are somewhat irregular in their degree of development. Sometimes there are a few weak spiral lines under the sutures. Nearly half the surface of the body whorl and a variable part of the spire on the apertural side have been affected by secretion from mantle lobes. This area is more translucent than the rest of the shell and its original

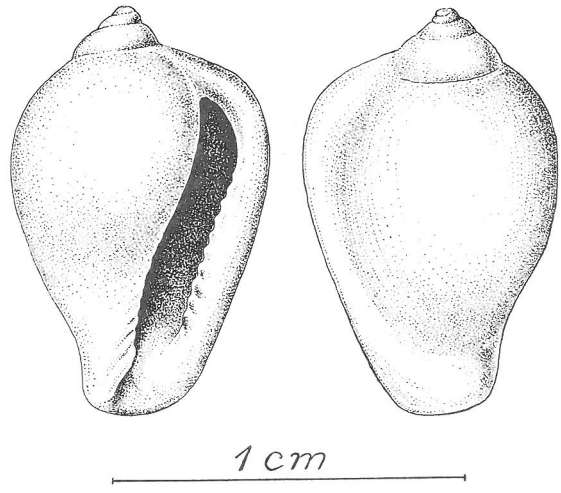

Fig. 236. *Erato voluta* (Montagu). No locality given.

ornament and sutures are obliterated. The new surface is marked with innumerable minute pustules and with fine grooves *c.* 15 μm apart running in an apical-abapical direction. The edge of this area is sometimes a little raised above the general shell surface.

The protoconch is set with its axis slightly oblique to that of the teloconch. It has *c.* 2.5 whorls, the first rather smooth, the rest with well-spaced spiral lines. It measures about 1.25 mm across.

Aperture. A long, narrow opening with parallel sides, very slightly sigmoid, the apical part curving towards the shell axis. It lies in a slightly prosocline plane. The outer lip arises from the subsutural part of the body whorl, nearly at right angles. It curves rapidly at first and then follows the curvature of the body whorl to the base. The lip is thick, with a rounded edge bearing 15-18 low, ridge-like teeth just within the throat. The lip ends by forming the edge of the siphonal canal, which is short, open and faces right. The aperture has no distinct inner lip. The columellar and parietal regions carry, the former, 3 oblique folds of which the most basal forms the columellar edge of the siphonal canal, and, the latter, a row of 12 or more tubercles which decrease in size towards the apex.

Colour. White, sometimes with a brownish tint, especially near the base; the lip may have a pink tinge.

Size. 12×7.5 mm. Body whorl = 80—85% of total shell height; aperture = 75—80% of total shell height.

Animal. The head has no snout, the apparent mouth being the entrance to a proboscis pouch. The tentacles are slender, not very long, each with an eye on a basal bulge. The mantle edge is smooth, drawn out anteriorly into a long siphon, open ventrally. Laterally the mantle expands into large lobes the outer surface of which bears a mixture of blunt and pointed tubercles. The lobes normally lie so as to cover much of the shell. The male has a penis arising from the pallial floor on the right. It is long, flattened and normally recurved. The male pore is apical and there is no open seminal groove.

The foot is long and narrow. The anterior end is rather square, slightly hollowed centrally, with a double edge: the posterior end is pointed. The sole has a median groove into the posterior part of which opens the duct of a posterior pedal gland. There is no operculum.

Colour. The basic colour of the flesh is white but this is largely obscured by a thick sprinkling of purple-brown, red, yellow and orange speckles. These are best developed on the mantle over the shell, which is often dark, with pale yellow tubercles. The tentacles have a mid-dorsal yellow line and are pale apically and round the eyes. The siphon and foot have yellow, orange and red blotches.

Geographical distribution. From the Mediterranean north to Norway, commoner in the southern parts of the range. Not found on continental shores of the North Sea, but on the Norwegian shores of the Skagerrak.

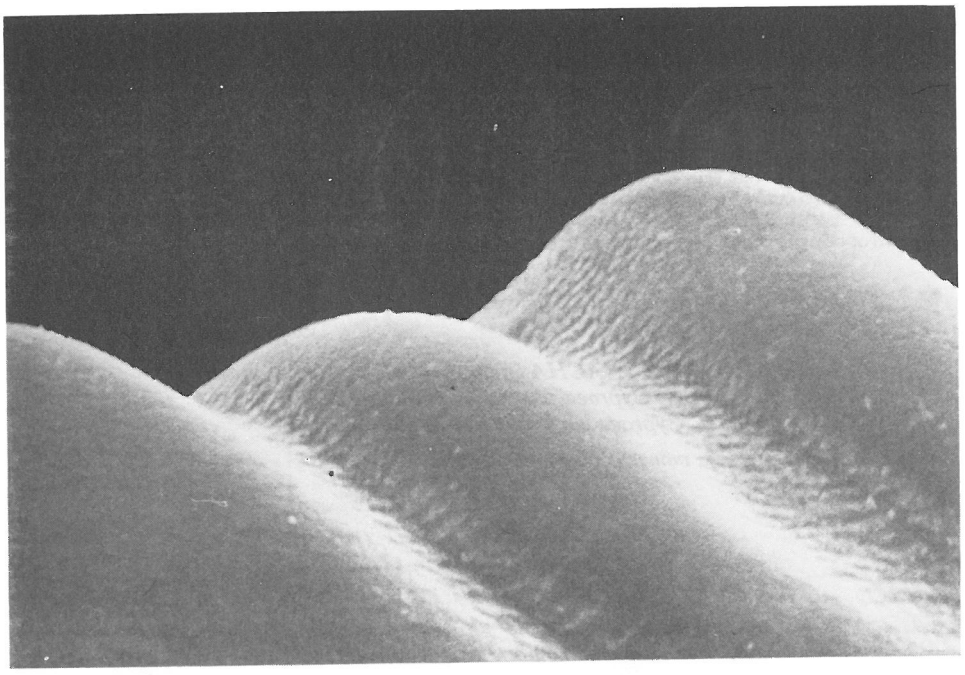

Fig. 237. *Erato voluta.* Microstructure of apertural tooth × 400. SEM photograph. Plymouth. RUZ.

Habitat. The animals are invariably sublittoral and may be found on hard bottoms in association with ascidians, at depths of 20-150 m.

Food. The natural food is not known but may well be the compound ascidians *Diplosoma, Botryllus* and *Botrylloides* which the animals readily eat in aquaria. The faeces are ovoid pellets about 300 × 200 μm.

Breeding and growth. The sexes are separate, males recognizable by the penis though this is not easy to see. Breeding has been described by Lebour (1933, 1935, 1937). It appears to take place at Plymouth in spring and summer since planktonic larvae are found Apr-Nov, maximally May-Aug. The eggs are unknown. The larvae are of the echinospira type, the true shell lying enclosed within a secondary one (the scaphoconch) which in this species is helicoid and has its axis not coincident with that of the true shell within. It has a large apertural beak. The youngest known stage has the scaphoconch 640 μm across, containing a true shell 320 μm across. The scaphoconch has a peripheral keel with a series of small beads on each side. At this stage both shells have about 1 whorl. At metamorphosis the scaphoconch has about 4 whorls (2.0 mm across) and the inner shell is half that size. The beads tend to be lost on the younger parts of the former. The youngest larvae are slightly yellow and have a 2-lobed velum with a narrow brown border. The velar lobes later become indented laterally or incipiently 4-lobed; towards metamorphosis the velum is 2 mm across. The larval foot has 3 lobes and a distinct operculum and the mantle begins to enwrap the shell and develop pigment. Metamorphosis involves two stages — first, loss of the scaphoconch (said to be cast off whole) and secondly and later, loss of the velum and operculum. Later growth and the age to which animals live are not known. The internal structure of the late larva is described by Thiriot-Quiévreux (1974).

Notes. Feeding has been described by Fretter (1951). The test of the ascidian is scanned by the siphon which is held over the mouths of zooids until one which is widely open is found. The siphon is then erected out of the way and the proboscis everted and pushed into the mouth. The tissues of the zooid are cut and rasped by the jaws and radula and then swallowed. This method avoids ingestion of indigestible test as in *Trivia.* The consumption of one zooid takes about 20 min.

With enlargement of the shell aperture the mantle cavity elongates along the right side of the body and the respiratory stream emerges a long way behind the head. The length of the penis is related to the posterior position of the female opening resulting from this movement.

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TRIVIA MONACHA (da Costa, 1778) spotted cowrie
Cypraea monacha da Costa, 1778
Cypraea europaea Montagu, 1803 (part)

Trivia (Lat.), a common thing; *monacha* (Gk.), solitary.

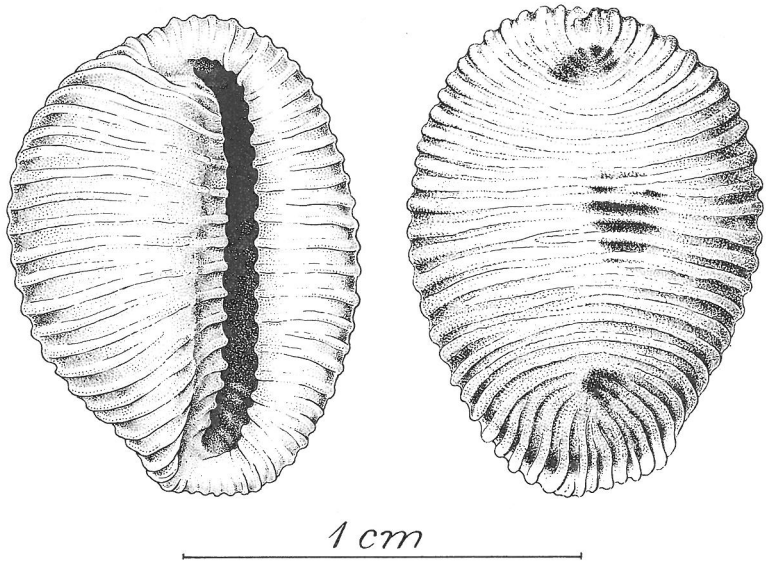

Fig. 238. *Trivia monacha* (da Costa). Roscoff, 5 m deep.

Shell. (Adult.) Solid, opaque and somewhat glossy. Egg-shaped and flattened on the apertural side. When mature the shell is convolute so that the spire is invisible, covered by an expanded body whorl, though its situation is marked in some shells by an apical pimple. If this is not clear the apical end may be told by looking at the shell in the apertural view when the broadest part of the parietal region lies towards it. The ornament consists of ridges and grooves, basically spiral in orientation, which run across the long axis of the shell. Those placed at the peripheral (= central) region run straight across, but towards the ends of the shell they are more and more curved, becoming C-shaped, the cavity facing the end of the shell. There are 20-30 such ridges, equal in breadth to the intervening grooves. The hollow of the C at each end is filled with further short ridges lying parallel to the long axis of the shell. Towards the aperture extra ridges appear in some grooves. The surface of the grooves is pustulated, the pustules most numerous and biggest near the aperture. (Young.) Up to a length of about 5 mm the shell shows a low spire, with a rather blunt point, of 3-4 rather tumid whorls meeting at clear sutures. The body whorl makes up by far the greatest part of the shell. In the

youngest stages the ornament consists of prosocline growth lines only, but in older ones some narrow spiral ridges are present.

Aperture. (Adult.) Long, running the whole length of the shell, narrow, slightly curved like a reversed C. The outer lip arises from the extreme apex of the shell and curves sharply up and then basally. It is thickened to form a labial rib and its edge is thin, though this is concealed by the way it turns inwards, blocking the abaxial part of the aperture. The spiral ridges and grooves cross the lip to give it a toothed edge. At the base the lip retreats to form the wall of a very short siphonal canal. There is no inner lip. The columella, ridged like the rest of the shell, has a concave surface. (Young). In early stages the aperture is widely open, narrowing above where the outer lip extends adapically from its origin on the body whorl. It has a thin, untoothed edge throughout and there is no distinct siphonal canal. In older stages, whilst the lip is still thin, it has grown so as to constrict the aperture considerably.

Colour. The young shell is white. In the adult the white colour persists on the parts around the aperture, on the labial rib, and there is commonly a pale or white longitudinal stripe down the mid-line of the shell opposite the aperture. The rest of this surface is brownish, reddish brown, or pinkish, sometimes with a dusky hue. The summits of the ridges are often paler than the grooves. There are 3 dark spots along the mid-line of the upper surfaces; they may be much, or only a little darker than the rest of the shell and sometimes show traces of being double.

Size. 12 × 8 mm. Body whorl = aperture = total shell height.

Animal. The head carries a short snout; the opening at its summit is that of a proboscis pouch. The tentacles are long and slender, each with a rather large eye on a bulbous base. The mantle edge is much thickened and lobulated and in an active animal extends to cover most or all of the shell. Anteriorly it is drawn out to form a long siphon. Within the mantle cavity a shield-shaped osphradium lies by the ctenidium. In males a long, slender, somewhat sickle-shaped penis arises behind and below the base of the right tentacle; the male pore lies at its tip.

The foot has a double, axe-shaped anterior edge and tapers slightly to a rounded posterior end. The sole has a median groove to the posterior part of which opens, in all animals, the duct of a posterior pedal gland. In addition, in females only, there opens, at a more anterior level, the pore of a cavity in which lies a papilla: this is the ventral pedal gland.

Colour. This is a gaudily-coloured animal. The head and tentacles are yellow, sometimes with red-brown lines with sulphur-yellow spots, or are red-brown with yellow spots. The siphon is yellow, orange or brown and the foot may be similar, though it is usually paler, especially at the edge. It may be marked with white lines and yellow spots. In young animals the mantle lobes are pale, with some black, brown, yellow or red spots; with age the spots become more numerous, enlarge and run together, giving streaks which mimic the ridges of the shell. The tubercles usually stay paler than the rest.

Geographical distribution. From the Mediterranean north to the British Isles. Perhaps not found in the North Sea and not recorded from Scandinavia.

Habitat. Not uncommon at LWST on rocky shores, under or on stones and under overhanging ledges, associated with compound ascidians.

Food. Compound ascidians, especially *Diplosoma listerianum,* but the molluscs also eat *Botryllus schlosseri, Botrylloides leachi* and *Polyclinum luteum.* The faeces are rods, or pellets, about 300 × 200 μm, often with undigested pieces of ascidian test.

Breeding and growth. Breeding has been described by Pelseneer (1926, 1932) and Lebour (1931, 1933, 1935, 1937). The sexes are separate and females may be picked out by the opening of the ventral pedal gland on the sole of the foot. At Plymouth breeding takes place in late spring and summer. The egg capsules are placed in holes bitten out of tunicate test (usually *Botryllus*) and rammed into position by the papilla of the ventral pedal gland. Each capsule is vase-shaped with a hollow neck and flared mouth, the shape being created by the papilla, when inserting the capsule. The upper part of the neck of the capsule and its mouth project above the surface of the ascidian. Each capsule is about 5 × 3 mm and contains *c.* 800 yellow-orange eggs, 160 μm in diameter, which hatch after some weeks (Pelseneer, no temperature given) as echinospira larvae. The outer shell (scaphoconch) of a newly-hatched larva is smooth, helicoid and without a keel (though its profile is made of a sequence of straight lines rather than a true curve). It measures 350 μm across its 1.5 whorls. The aperture has a marked beak. The inner shell is also helicoid, smoothly curved, without a beak, and the axes of the two shells coincide. By the time of metamorphosis the outer shell is 1.25

mm across, the inner about 0.8 mm. The velum is 2-lobed with a lateral bay suggesting an incipient 4-lobed state and has a marginal row of brown spots. The foot has an operculum and has dark brown marks on the sole and opercular lobes. At metamorphosis the scaphoconch is absorbed, not cast off, as the mantle folds envelop it. After metamorphosis the shell is white and the mantle pale, pigmentation developing gradually. The adult form is assumed about 6 months after settling when the lip thickens and the pigment spots develop.

TRIVIA ARCTICA (Pulteney, 1799), unspotted cowrie
Cypraea arctica Pulteney, 1799

Arctica (Gk. ἄρκτος, bear), relating to the Great Bear constellation and so northern, referring to its more common occurrence in the north.

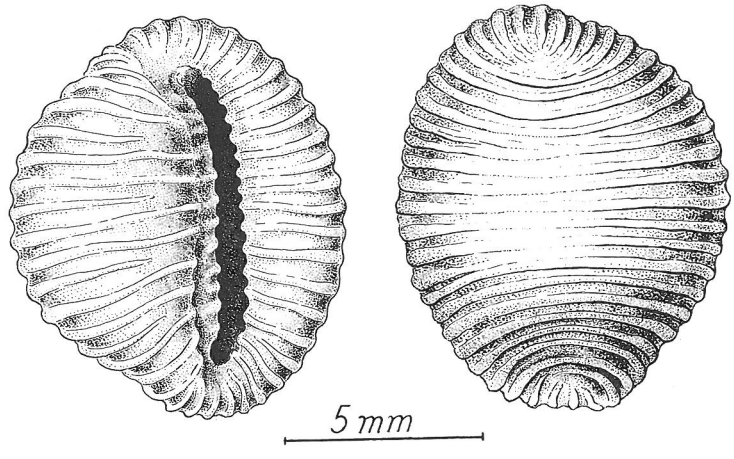

Fig. 239. *Trivia arctica* (Pulteney). About 7.5 km WNW of Lökken, 18 m deep. CMZ.

Shell. Not distinguishable from that of *monacha* except by (1) absence of pigment spots; (2) usually smaller size.

Aperture. As in *monacha.*

Colour. As in *monacha,* but lacking pigment spots.

Size. 10 × 8 mm. Body whorl = aperture = total shell height.

Animal. As in *monacha.* The penis, however, is considerably larger and leaf-like, with a ridged surface and the internal duct showing as a cord along one edge.

Colour. Like *monacha* but paler.

Geographical distribution. From the Mediterranean north to Norway, the Swedish west coast (Bohuslan) but not further south in the Kattegat. It tends to occur at greater depths in the warmer parts of its range.

Habitat. Occasionally at LWST but commonly sublittoral to about 100 m in more northerly, and about 1000 m in more southerly latitudes.

Food. Compound ascidians as for *monacha.*

Breeding and growth. The sexes are separate, females distinguished by the opening of the ventral pedal gland on the sole of the foot. The breeding has been described by Lebour (1933, 1935, 1937), though the eggs and egg capsules are still unknown and can only be presumed to be laid in ascidian tests. The larvae are echinospiras as in *monacha* but at Plymouth are found in autumn, winter and early spring. They differ from those of *monacha* in that the colour of the larva is lighter and in that

in later stages the velum becomes very large and develops 4 long lobes edged with brown. The smallest larvae seen measured 400 μm across the scaphoconch, whilst those ready to metamorphose were 1.6 mm across.

Notes on Trivia *species.* The two species *arctica* and *monacha* were formerly regarded as one, *europaea.* The work of Peile (1925), Pelseneer (1926) and Lebour (1933) has convincingly separated them. They are usually easy to distinguish by the pigment spots on the shell of *monacha;* in specimens where these are poorly shown the shape of the penis (finger-like in *monacha,* flattened in *arctica*) is decisive and there are further anatomical differences in the female ducts (Fretter, 1946). *T. monacha* is more common in the south and *T. arctica* in the north and *arctica* is less frequent than *monacha* between tidemarks. *T. monacha* is usually more brilliantly coloured than *arctica.* This is tied to its normally shallower habitat since the species are more like one another where they live side by side. The colour is derived from their food and since intertidal ascidians are more pigmented than sublittoral ones so are intertidal cowries. Interbreeding between the species is prevented not only by the shape of the penis but by the fact that *arctica* is a winter breeder and *monacha* a summer one.

When cowries feed (Fretter, 1951) the ascidian surface is tested by the siphon and the proboscis everted. The radula and jaws first bite pieces of test so as to expose the zooids. Both test and zooids are eaten, the latter ingested whole, but the test is not digestible and may be seen in the faeces. The animals are voracious and may eat up to half their volume of prey. The body of *Trivia* spp. is extremely rich in glands — the outer surface of the proboscis and the sole of the foot are covered with goblet cells and the mucus they produce is augmented by the secretion of the posterior pedal gland lying round the pedal ganglia and communicating with the pedal sole by a long duct, and by the secretion of the anterior pedal gland, though this is not mucus. Why a predator of tunicates should need this is not obvious; it may be a protection against its own enemies, though Thompson (1961) has shown that cells in the mantle lobes can produce acid.

As in *Erato* the current ventilating the mantle cavity enters by the siphon and leaves by an opening overhanging the posterior part of the foot.

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CYPRAEACEA

A large group containing the animals popularly known as cowries. They are predominantly inhabitants of tropical and subtropical seas where they have undergone a vast adaptive radiation; *Simnia* is the sole genus of N.W. Europe. They are closely related to, but are in several respects distinct from, Lamellariacea. The superfamily is usually regarded as containing 3 families: Ovulidae (sometimes called Amphiperatidae), Cypraeidae and Pediculariidae. Of these the Cypraeidae contains by far the most species. The shell is solid and swollen, flattened along the apertural surface. In nearly all the aperture is narrowed to a slit by ingrowth of the outer lip, and usually has apical and abapical canals, sometimes, as in some ovulids, drawn out to considerable lengths. The lips of the aperture are usually toothed or folded. The adult shell is convolute and its surface polished because of secretion from the mantle lobes by which it is covered in active animals. The spire is exposed in young animals and its whorls bear a prominent cancellate pattern.

Internally the cypraeacean body is distinguished by the possession of a triradiate osphradium and by the fact that the pedal ganglia exhibit the primitive form of cords extending the length of the foot and often with multiple cross connexions. Cypraeids seem to be rather general carnivores, as they take corals, sponges and small crustaceans; ovulids and pediculariids, on the other hand, are more selective and associate with and feed on a variety of coelenterates only. The egg capsules of ovulids are commonly laid on the surface of these coelenterates whereas those of cypraeids are attached to the general substratum. The larva which emerges is never an echinospira.

The superfamily Cypraeacea may be separated from the Lamellariacea on the ornament of the spire of the shell, the shape of the osphradium, the form of the pedal ganglia and the lack of an echinospira larva. There are sufficient other resemblances, however, to suggest that the two groups are closely related. Both superfamilies must also relate with Hipponicacea since, like all Lamellariacea, *Capulus* possesses an echinospira larva.

OVULIDAE Fleming, 1822
SIMNIA PATULA (Pennant, 1777)
Bulla patula Pennant, 1777
Ovula patula (Pennant, 1777)

Simnia. This is one of Leach's MS names and, like others of that nature, we have not been able to discover its derivation. *Patula* (Lat.) open, refers to the aperture extending the whole length of the shell.

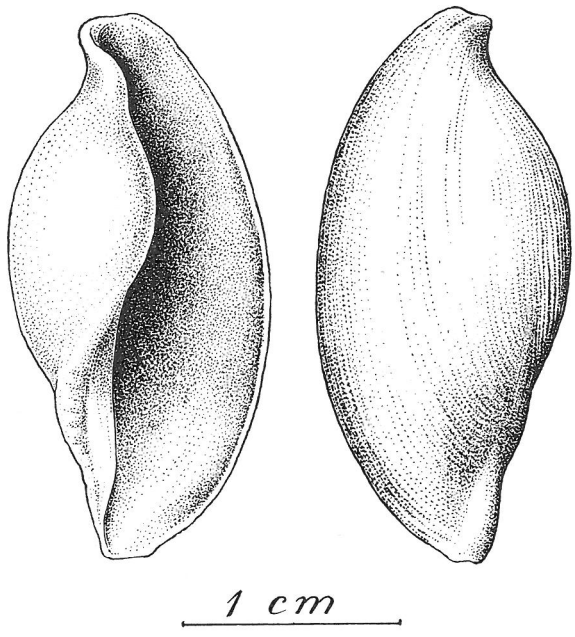

Fig. 240. *Simnia patula* (Pennant). BMNH 1911.10.26. 14268-14274.

Shell. Thin, glossy, slightly translucent. The shell is an elongated ovoid drawn out to short projections at each end, the shorter and more distinct of the two at the apical end. The broadest part of the shell lies towards it. Mature shells (length >5 mm) are convolute: no spire is visible since the body whorl has grown so as to enclose it completely. In young shells 3 tumid whorls may be seen. The ornament of the teloconch consists of many spiral ridges and grooves, the former broader than the latter, low and strap-shaped, and *c.* 80 μm broad, the distance from crest to crest *c.* 120 μm. They are crossed by innumerable very close-set growth lines only *c.* 20 μm apart. At intervals there are more marked growth lines which often disturb the alignment of the spiral ridges. In some shells the spiral ridges are less well-developed at the periphery, but they are always clear at the extremities.

Aperture. Elongated, oval to banana-shaped, ending apically and basally in canals. The apical canal is twisted to the left, short, widely open, its outer wall thin, its inner wall thickened and with its base surrounded by a smooth spiral groove. The basal, siphonal, canal is merely the terminal part of the elongated base of the shell, faces to the right and has thin lips. The outer lip of the aperture has a rather sharp edge. The columella is elongated, concave, with its abapertural edge bordered by a blunt ridge. The throat and the inner surface of the canals and columella are marked with very fine ridges.

Colour. White or yellowish, sometimes pinkish.

Size. Up to *c.* 20 × 10 mm. Body whorl = aperture = total shell height.

Animal. The head bears a short plump snout which ends in a circular cup-shaped disk, at the centre of which lies the mouth, a short longitudinal slit. The surface of the disk is divided into a

number of sectors by radial grooves. The tentacles are long and slender and each has an eye on a rather large basal expansion. The mantle skirt has a simple edge which is thickened in two places near the mid-line to form the side walls of a siphon which projects from the basal canal. The mantle is also capable of extension on each side to form a deep, thin flap, the left larger than the right. In active animals these embrace the shell so as to conceal all or most of it. In males a penis arises from the floor of the mantle cavity behind the base of the right tentacle. It is long, recurved, a little flat, and pointed; along it runs an open seminal groove originating at the male pore within the mantle cavity.

The foot is large and deep, nearly square anteriorly, with a slight central embayment and a double edge. Its upper surface, under the snout, bears a series of longitudinal folds. The sole is long, narrow, ends behind in a rounded point and has a median groove into the posterior part of which a posterior pedal gland opens. There is no operculum.

Colour. Yellow, with brown or reddish brown lines and spots, especially on the mantle lobes. The distal half of each tentacle is white, with a ring of brown behind the tip. The ridged anterior part of the foot is white with a pinkish tinge along the summits of the ridges. The siphon is white. Some animals are much darker than others.

Geographical distribution. This species occurs along the European west coast from the western end of the English Channel south to Spain. There are occasional records from west Irish and British coasts as far north as Orkney (Rendall, 1936), but it does not occur in Scandinavia.

Habitat. It is found on the coelenterates *Eunicella verrucosa, Alcyonium digitatum* and *Tubularia indivisa* dredged on hard bottoms 15-75 m deep. It is not common.

Food. The polyps of these coelenterates. Faeces are short, white rods or pellets, full of coelenterate spicules, measuring 400×300 μm.

Breeding and growth. The sexes are separate, males recognizable by the penis. Spawning (at Plymouth — Lebour, 1932) occurs April—July. The eggs are laid on *Alcyonium,* the female depositing a series of capsules side by side to form a pinkish-yellow, irregularly rounded layer *c.* 25 mm across. The constituent capsules each measure *c.* 3.5 mm in diameter and contain several hundred yellow-orange eggs 130 μm across. All develop and hatch (after 33 days in the laboratory) to free-swimming veligers. At hatching the shell has about 1.5 whorls, 140 μm across, is opaque and dark brown, marked with numerous irregular tubercles. The larval shell develops a reticulate pattern and an apertural beak. It grows to about 800 μm in length, when it has 3.5 tumid whorls. At metamorphosis the shell is nearly 1 mm across. The outer lip then rapidly expands apically and grows so as to wrap over the larval shell, a stage reached before the shell is 5 mm long. At hatching the larva has a small, colourless, bilobed velum, the rest of its body pale yellow. The velum soon becomes 4-lobed and the lobes grow very long and narrow in older larvae. They remain unpigmented. When the shell is 340 μm across, each velar lobe is nearly 500 μm long and the whole velum is nearly 1 mm across. Larval life seems to be long. Nothing further is known about the rate of growth or length of life after settlement.

Notes. The animal lies within its shell so that the head points directly to the basal canal: this relates to the median rather than left-sided situation of the siphon. The mantle cavity has rotated to the right so that the anus is placed close to the apical end of the shell. As a consequence the respiratory current now enters basally by the siphon and leaves by the apical process of the shell.

Though *Simnia* is a carnivore it has no proboscis. It feeds by placing the disk at the end of the snout over a polyp and shearing it off by means of two sharp-edged jaws lying in the buccal walls. It it not known whether it does anything to prevent retraction of the polyp (Fretter, 1951). The ridged dorsal surface of the propodium, however, is extremely glandular and its secretion, mainly mucus, may protect the mollusc against nematocysts; this may also be part of the function of the complex anterior pedal gland with a different secretion and discharging to the sole. The sides of the foot are also rich in mucous glands and the supply is further augmented by the posterior pedal gland lying around the pedal ganglia and discharging to the posterior part of the sole by a long duct.

The animals are sometimes known as poached-egg shells. This name seems appropriate enough for the related *Ovula ovum* which grows to a length of 90 mm but not for a shell usually less than an inch long.

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NATICACEA

A rather small and homogeneous group of carnivorous marine mesogastropods, all considered as belonging to the single family Naticidae. They occur in all seas and to considerable depths. Except for a number of features clearly adaptive for their mode of life they exhibit a rather generalized mesogastropod organization.

The shell in most tends to have a low spire, an enlarged body whorl, an approximately semicircular aperture, a prominent umbilicus and a smooth surface. More primitive genera, such as *Amauropsis,* have a higher spire, deeper sutures and some spiral ornament; in the most advanced (subfamily Sininae) the spire is much depressed, the body whorl greatly expanded and the aperture enlarged, with the result that the animal can no longer withdraw into the shell, though an operculum still exists. The walls of the umbilical channel are often ridged and its entrance blocked by the development of callus on the inner lip.

Naticids creep over and within soft substrata, searching for bivalve prey, though other molluscs may also be eaten. In adaptation for this the foot is enlarged, especially the propodium and opercular lobes, and it can often (? always) be distended by uptake of sea water through pores into internal spaces. When thus dilated the propodium forms a shield over the head and entrance to the mantle cavity during burrowing, as well as a shovel moving sand or mud. Feeding is usually underground, the prey being held in the foot, its shell bored by a combination of chemical and mechanical means and its flesh reached by a proboscis entering through the borehole. The tentacles are flattened and the eyes reduced or insunk. The sexes are separate and the spawn takes the very characteristic form of a collar-shaped mass of jelly strengthened with sand grains and containing many egg capsules.

NATICIDAE Gray, 1840

LUNATIA ALDERI (Forbes, 1838), moon or necklace shell

Natica alderi Forbes, 1838
Lunatia poliana (delle Chiaje, 1826) (Mediterranean)
Lunatia intermedia (Philippi, 1836)
Lunatia nitida auct. non Donovan, 1800

Lunatia, a formation from Lat. *luna,* the moon, referring to the shape of the shell; *alderi,* named for Joshua Alder (1792-1867), amateur malacologist of Newcastle upon Tyne, co-author of *A Monograph of the British Nudibranchiate Mollusca.*

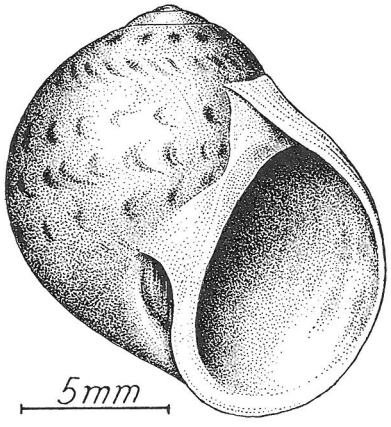

Fig. 241. *Lunatia alderi* (Forbes). NW of Anholt, Kattegat, 18-27 m, *Hauch* station 321. CMZ.

Shell. Moderately solid, opaque and glossy, rather globose, the body whorl making up most of the shell. The spire is short and blunt (apical angle 112-122°). There are 6-7 whorls which meet at rather slight sutures lying on the apical side of the periphery of the upper whorl. The lower whorl runs adapically so as to meet the upper nearly tangentially: this smoothes the profile of the spire so that it seems nearly straight. The shell appears almost without ornament to the naked eye, but is marked with numerous fine and closely-set growth lines with a very prosocline course, less marked near the suture; they are often a little coarser near the umbilicus, into which they run. There may also be some extremely ill-developed spiral lines. The shell bears a thin periostracum but this is usually worn away except within the umbilicus.

The protoconch has 3 whorls, the apical one marked by some irregular spiral lines, the rest smooth. It measures *c.* 1 mm in diameter and is sharply separated from the teloconch.

Aperture. A large semicircular to semielliptical opening lying in a prosocline plane and bounded by a peristome. The outer lip arises high on the body whorl, nearly tangential to its surface, making an angle of 120-125° with the shell axis. It follows a more or less semicircular course to the base of the columella where it is a little turned out. Throughout, its edge is rounded. The columella is nearly straight, leans a little to the right and recedes slightly from the plane of the outer lip. In mature shells the inner lip develops callus where it rests against the body whorl in the form of two pads connected by a broad bridge. The upper pad (Fig. 248A,1) is rounded and buttresses the outer lip, though separated from it by a groove; the lower pad (2) lies on the lower part of the body whorl so as partially to obscure the umbilicus, the adapical end of which becomes pointed as a result. From this pad a low ridge (3) extends up the adapertural face of the umbilical channel, a groove on its adapical side separating it from an obscure second ridge (4); this runs along the abapertural wall and is a continuation of a low keel which starts at the base of the outer lip. A third ridge (5), always slighter and often inconspicuous, starts from the narrow middle part of the columella and also runs along the umbilical wall.

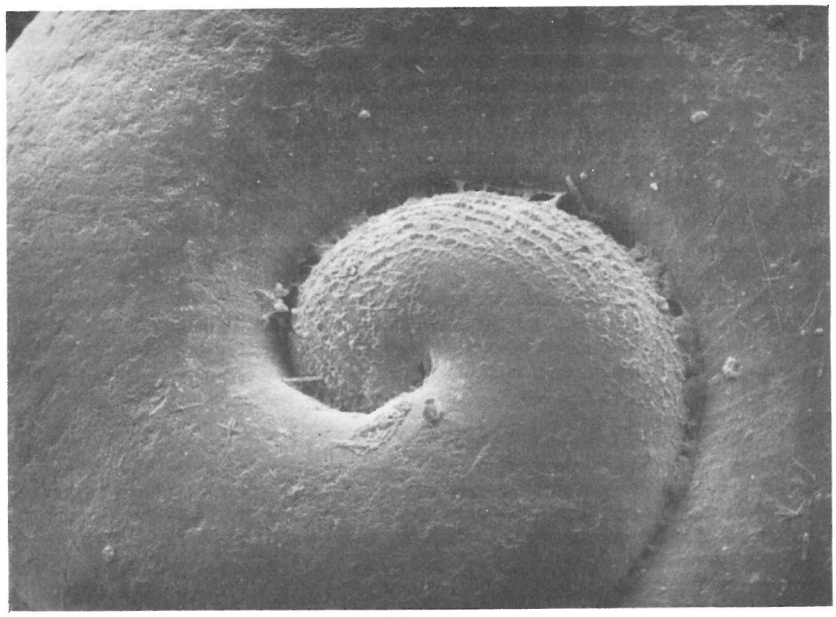

Fig. 242. *Lunatia alderi.* Protoconch × 294. SEM photograph. Plymouth. RUZ.

Colour. Buff, yellowish, usually pale on the base and columella. There are 5 spiral rows of chestnut-brown markings on the body whorl and 1 on each whorl of the spire; they are placed (1) a little below the suture; (2) halfway between suture and periphery; (3) and (4) at the periphery; (5) halfway between periphery and umbilicus. The marks are either streaks or V-shaped. The subsutural row is more orange and brighter than the others. The pads of callus on the body whorl are white, the bridge between them often brown as is also the groove running into the umbilicus from the columella.

Size. Up to 16 × 13 or 14 mm. Body whorl = 80-90% of total shell height; aperture = 75-85% of shell height.

Animal. The head bears a short, broad snout at the apex of which is the round opening of the proboscis sac. The proboscis is acrembolic. At the base of the snout are the tentacles united across the mid-line by a basal fold, and sometimes a little flattened. The eyes, though reasonably well developed, have sunk under the skin and are only poorly — if at all — visible. The mantle edge is simple. In males a large penis, terminating in a short point, arises from the floor of the mantle cavity behind the base of the right tentacle. Its posterior edge carries an open seminal groove originating at the male opening deep in the mantle cavity. In females the genital pore lies near the anus and a groove extends forward from it towards the mouth of the cavity.

The foot is complex. There is a broad, spade-shaped propodium, embayed in the mid-line; its dorsal surface ends posteriorly in a transverse fold held so as to cover all but the tip of the tentacles, the snout and the front of the shell as the animal creeps; a fold on its left acts as a siphon. Ventrally a transverse groove separates the propodium from the mesopodium, which is broad and is rounded at its hinder end. On its dorsal surface it bears the opercular lobes and operculum: the lobes are extensile and are held by the active animal so as to cover the operculum and embrace the posterior half of the shell. The right lobe reaches further forwards than the left. The operculum is semilunar in shape with a depressed nucleus at the siphonal end on the columellar side. It expands rapidly and has a flexible edge which forms an upstanding margin to the initial turns.

Colour. Cream or yellowish with reddish-brown lines and blotches. The tentacles are dark and the proboscis bright red. Operculum horn-colour.

Geographical distribution. From the Mediterranean north to Norway; throughout the Channel and N. Sea, Skagerrak and Kattegat to the Sound, but not in Danish fjords.

Habitat. An infaunal inhabitant of sandy shores, usually of clean sand, but tolerating some admixture of mud. It also occurs on gravel (Manly, 1975). Occasionally found at LWST, but more usually sublittoral between 10 and 50 m, though extending to 2000 m.

Food. N. alderi is a carnivore, eating bivalves, particularly tellinaceans (see Ansell, 1960, for list), which it pursues through the sand, and whose flesh it reaches by boring through the shell if it can find no easier entry. The first faeces produced by an animal starting to feed are isolated, rod-like, with a knob at one end, and are white because filled with shell fragments. Later faeces are ovoid pellets, dark yellow-green in colour, about 200-300 × 100 μm, and linked by mucus into chains.

Breeding and growth. See Ankel (1930), Thorson (1946), Ansell (1960), Fioroni (1966) Fretter & Pilkington (1970), Giglioli (1955), Hertling (1932), Lebour (1936, 1937), Ziegelmeier (1961). The sexes are separate and males are recognizable by the penis, but it is not usually possible to see this in a live animal. Females outnumber males 3:2. The animals breed throughout spring and summer, depositing spawn in the sand in which they live. The spawn is a ribbon-shaped structure coiled in a spiral resembling a collar, usually with rather more than 1 turn so that its ends overlap. The upper surface is gently convex, the lower gently concave. The thickness of the ribbon is 1-2.5 mm, its breadth 8-10 mm, that of the whole ring 25-30 mm, of the central hole 10 mm. The jelly of which it is composed is stiffened (but not so that it is rigid) by the inclusion of sand grains amongst which the eggs lie, each in a separate small cavity bounded by a membrane. The egg spaces are not visible externally, are arranged irregularly, but usually at only one level in the thickness of the collar and extend to the apical and basal margins of the jelly. Each measures 200 μm in diameter, and the contained egg 100-140 μm (Ziegelmeier, 1961) when fresh, figures smaller than these given by Lebour (1936) at 160 μm and 270-320 μm. The total number of eggs per ribbon varies from 2390-11760, mean 8170; the number of rings laid is not certainly known, but one female produced 19 in one complete breeding season. The eggs are said to hatch after about 3 weeks at 8.5°C (Hertling, 1932) to give free-swimming veliger larvae with a shell about 200 μm across. The embryonic whorl is marked with spiral ridges or rows of tubercles, but later ones are smooth. By metamorphosis there are 3.5 whorls with a diameter of *c.* 1 mm. At hatching the larva has a bilobed, colourless velum which soon becomes 4-lobed; later the lobes grow long and narrow and each has a prominent red-brown patch of pigment near its tip and a marginal line of the same colour. The foot develops a long narrow propodial region with a mid-ventral ciliated groove, and its opercular lobes become broad; it is grey in colour. Larval life seems to be long, since larvae with shells up to 1 mm in diameter have been met in the plankton. Growth rates are unknown. The animals may live perhaps for 5 years (Ansell, pers. comm.).

LUNATIA CATENA (da Costa, 1778)

Cochlea catena da Costa, 1778
Natica catena (da Costa, 1778)
Lunatia monilifera (Lamarck, 1822)

Catena (Lat.), a chain, supposed to describe the colour markings round the whorls.

Shell. Much as in *alderi,* with these differences: it is more globose; the spire is more sharply pointed (apical angle average 106°, range 94-111°); the whorls of the spire are tumid and meet at deep sutures, the two surfaces almost at right angles so that the profile of the spire is markedly stepped; the growth lines are more marked on the base so that the umbilical channel has furrowed walls.

The protoconch has 1.5-2 whorls which are smooth save for papillae arranged in spiral rows on the initial half whorl. It has a diameter of *c.* 600 μm.

Aperture. Much as in *alderi,* with these differences: the outer lip arises more or less at right angles to the body whorl and at a greater distance from the suture; the abapical pad of callus on the inner lip (Fig. 248C) hardly obscures the umbilicus so that this remains a wide opening, rounded at its adapical end; only 2 spiral ridges enter the umbilicus, one from the lower pad of callus on the adapertural side (Fig. 248C, 3), the other (4) from the base of the peristome on the opposite wall.

Colour. Buff, paler basally and around the umbilicus, sometimes also along the sutures. On each whorl is a subsutural row of darker, chestnut-brown streaks, usually prosocline in orientation. In

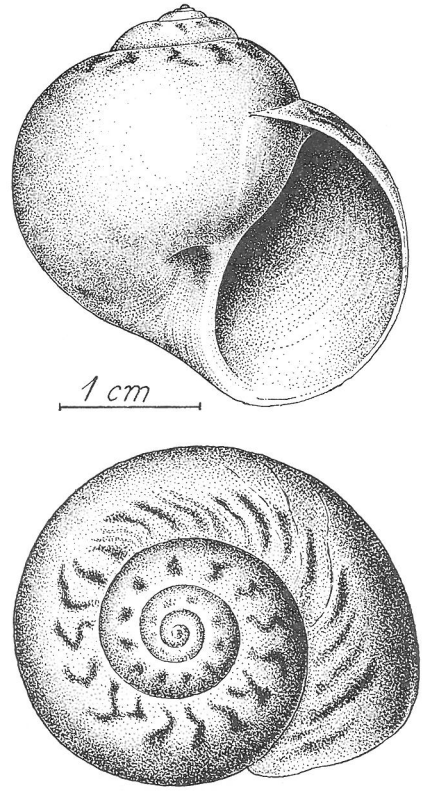

Fig. 243. *Lunatia catena* (da Costa). About 11 km NNE of Hirtshals. CMZ.

juvenile shells the body whorl may also show faint peripheral and subperipheral spiral rows of similar markings. The throat has often a pale brown tint, more marked adapically, and the callus of the inner lip has usually a brown stain where it abuts the body whorl and between the two pads.

Size. Up to 30 × 30 mm. Body whorl = 90% of total shell height; aperture = 70% of total shell height.

Animal. As in *alderi.*

Colour. Yellowish with some brown markings. Operculum a dark horn-colour.

Geographical distribution. From the Mediterranean north to the Skagerrak and N.W. Kattegat. Not found off Norwegian and Swedish coasts, nor in Danish fjords.

Habitat. Much as in *alderi,* but restricted to shallower depths, between LWST and about 125 m.

Food. As for *alderi,* tending to take larger prey.

Breeding and growth. Breeding occurs throughout spring and early summer and the spawn has the same general collar shape of that of *L. alderi.* It is, however, more rigid and the ribbon is broader (22-38 mm), thicker (1.5-2.2 mm) and longer (base = 82-170 mm); the diameter of the collar is about 75 mm. Its walls may be straight or curved. The egg capsules are arranged with some regularity in lines and are clearly visible on both sides of the ribbon, measuring 1.4-2.0 mm in diameter. They extend to both upper and lower margins of the collar. Each egg space is bounded by a membrane and contains a gelatinous fluid in which, at laying, float many eggs (mean number 86, range 50-180). All of these save about 2 (range 1-19) are, however, food eggs which soon clump to form a mass adhering to the capsule wall which is distintegrated by the velar cilia of the developing embryos and ingested. The eggs have an egg covering enclosing a small amount of albumen, the total diameter 160 μm. Most observers (Ankel, 1930; Fioroni, 1966; Thorson, 1946) have recorded the hatching after 2 months (Ankel, 1930) of juveniles which had passed the veliger stage within the capsule and emerged

with greater or lesser vestiges of the velum. Lebour (1936, 1937), however, described a free veliger larval stage from the Channel off Plymouth. It is possible therefore, that there is local variation in development though Thorson (1946) suspected that these are larvae of *L. montagui,* though this species has not been recorded at Plymouth. The shell is smooth, has about 1.5 whorls and a diameter of *c.* 350 μm, growing by the time of metamorphosis to 600-700 μm and 2.5-3 whorls. The velum is bilobed with a margin of purple-brown and there is also pigment on the opercular lobes. The growth of the young has not been studied.

LUNATIA MONTAGUI (Forbes, 1838)
Natica montagui Forbes, 1838
Natica montacuti Forbes, 1838

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

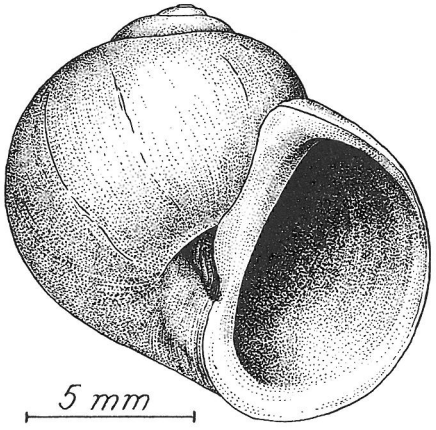

Fig. 244. *Lunatia montagui* (Forbes). Hellebaek. CMZ.

Shell. In general like that of *alderi.* The spire, however, is rather low (apical angle *c.* 115°) and is markedly stepped in profile because the whorls meet at very deep sutures channelled so as to be V-shaped in section. The shell is slightly broader than high.

The protoconch has 2.5-3 smooth whorls and is 1.1-1.4 mm in diameter.

Aperture. In general like that of *alderi.* At the origin of the outer lip from the body whorl, however, the deep channelling of the suture leaves a small nick between the lip and the whorl. The lip makes an angle of *c.* 125° with the axis of the shell. The callus of the inner lip (Fig. 248B) hardly extends over the adapical end of the umbilicus. The inner lip does, nevertheless, turn out a little by the columella and this forms the end of a prominent ridge (5) along the adapertural side of the umbilical space. On the opposite side there extends a ridge (4) beginning at the columellar base. Between these, on the adapertural side of the umbilical canal, runs a deep groove which forms a marked notch on the columella.

Colour. Fawn-buff, often with dark deposits on the upper whorls, but without colour markings. The throat shows some brown coloration and the inner lip is white.

Size. 8 × 8.5 mm. Body whorl = 80-90% of total shell height; aperture = 75-80% of shell height.

Animal. As in *alderi.*

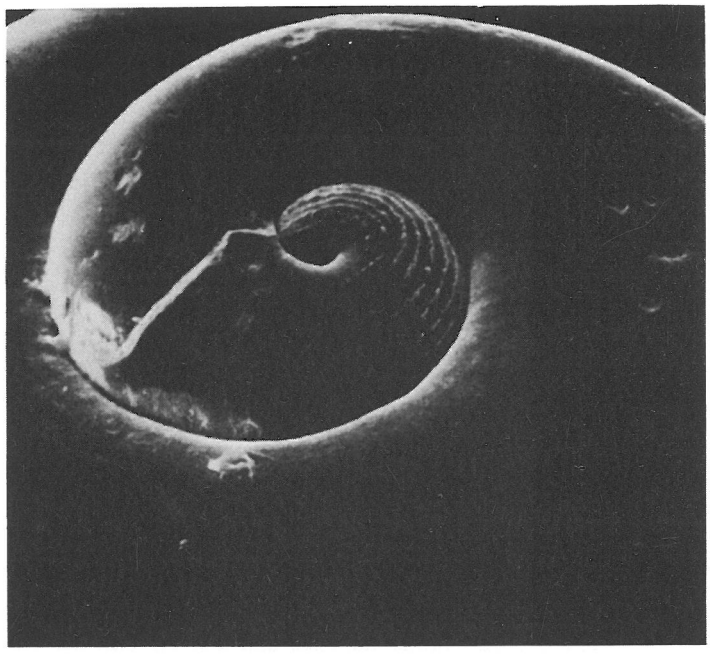

Fig. 245. *Lunatia montagui.* Protoconch × 146. SEM photograph. Plymouth. RUZ.

Colour. Cream-yellow. The tentacles are pale and the posterior propodial edge has a chestnut margin.

Geographical distribution. A northern species, but it is found on all western European coasts from the Mediterrean to the Lofoten Islands. It occurs in the Skagerrak and Kattegat, but not in Danish fjords.

Habitat. On sandy and muddy bottoms from 15-200 m. They prefer finer sediments than *alderi* and *catena.*

Food. As for other *Lunatia* spp.

Breeding and growth. The egg collar is in general like that of *L. alderi* (Thorson, 1946) but the ribbon is broader and stiffer. It contains numerous eggs lying each in a small space 230 μm in diameter and the spaces arranged in several planes. The eggs have a diameter of 150 μm. The larvae have been described by Thorson and by Thiriot-Quiévreux (1969). The shell is smooth and transparent with a diameter of 320-350 μm when young and growing to nearly twice that size. The velum is bilobed, becoming incipiently 4-lobed and has a margin marked with brown. The propodium is darkly pigmented and the mesopodium bears a number of yellow spots.

Notes. The drawing of the shell of this species does not show the prominent nick separating the upper end of the outer lip from the body whorl. This is produced by the deep channelling of the suture. See Fig. 248B. The notch on the columella is usually much more conspicuous than in Fig. 244.

LUNATIA FUSCA (Blainville, 1825)
Natica fusca Blainville, 1825
Lunatia sordida (Philippi, 1836)

Fusca (Lat.), dark, referring to the shell colour.

Shell. Solid, opaque, rather glossy, covered with periostracum to a greater extent than in other species. There are 6 whorls and the spire is prominent (apical angle *c.* 100°) and straight-sided. Each

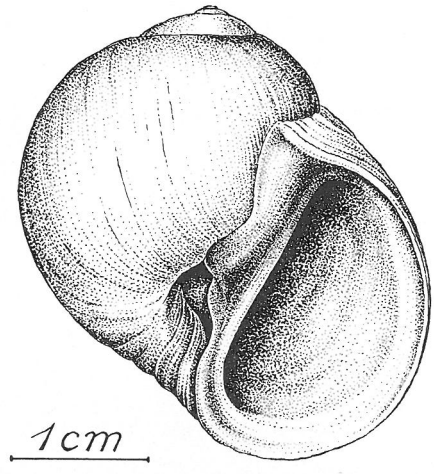

Fig. 246. *Lunatia fusca* (Blainville). Cornwall. Melvill-Tomlin collection, National Museum of Wales, Cardiff.

whorl is gently tumid, its adapical part rather flattened and shelving into the whorl above. The sutures are distinct, very slightly excavated, especially that between body and penult whorls. The ornament comprises numerous prosocline and flexuous growth lines and sometimes also a few obscure spiral grooves, more obvious on the base of the body whorl.

The apex and larval shell are normally eroded.

Aperture. Slightly prosocline, D-shaped, with a peristome. The outer lip arises at the periphery of the body whorl more or less tangentially, making an angle of 120-30° with the shell axis. Its initial part is slightly concave or rather straight but it then runs with increasing curvature to the base of the columella where it is a little thickened and angulated. The columella is straight and leans upwards to the right. The inner lip forms a bilobed callus on the body whorl: the upper lobe (Fig. 248D, 1) is separated by a small groove from the outer lip, whilst the lower (2) marks the end of a low ridge lying along the adapertural side of the umbilicus. The umbilicus is a little constricted adapically but is otherwise widely open, lined with periostracum puckered into fine ridges. A second small ridge (5) winds up the adapertural side of the umbilicus from the columellar lip level with the opercular nucleus. The lip narrows between these ridges but it not interrupted as in *L. montagui.* A third ridge (4) curves from the angulated base of the outer lip along the abapertural wall of the umbilicus.

Colour. Brownish or chestnut. The colour is mainly in the periostracum and the shell is paler where that is lost. The columellar lip and lower callus of the inner lip are always brown. The base of the outer lip and neighbouring throat region are white.

Size. 25 × 20 mm. Body whorl = 90% of total shell height, aperture = 75% of total shell height.

Animal. Much as in *alderi.* The anterior propodial edge is rounded.

Colour. Reddish brown, paler at the margins of the foot and its lobes and also on the snout and cephalic tentacles.

Geographical distribution. This is a southern species, extending from the Mediterranean to the western Channel and western coasts of Ireland and Scotland. There are some records from northern parts of the North Sea but none from Scandinavia.

Habitat. Muddy sand to 165 m; never intertidal. It is rather rare.

Food, breeding and growth. Unknown, but presumably similar to other species.

Note. Fig. 246 shows a shell with more elaborate umbilical ridging than is usual: *cf.* Fig. 248D.

LUNATIA PALLIDA (Broderip & Sowerby, 1829)
Natica pallida Broderip & Sowerby, 1829
Natica groenlandica Möller, 1842

Pallida (Lat.) pale, referring to the colour of the shell.

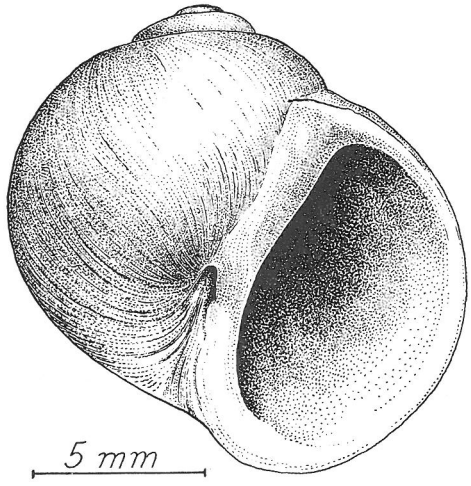

Fig. 247. *Lunatia pallida* (Broderip & Sowerby). The Sound.

Shell. Much as in other species. The sutures are only slightly channelled and lie at or just below the periphery of the upper whorl. The protoconch is normally eroded but is smooth.

Aperture. As in other species. The outer lip arises at the periphery of the body whorl curving into it at an angle of about 110° to the axis of the spire. It is convex at this part, occasionally rather straight. The base of the aperture is a little flattened and somewhat angulated at the base of the columella. The columellar lip is rolled outwards and rather thick and the inner lip develops a thick band of callus over the body whorl so that the umbilicus is reduced to a rather narrow chink. Only a few shells show any indication of a ridge entering the umbilicus; this rises from the middle of the columellar lip.

Colour. Cream. There is sometimes a brownish or orange flush especially on the body whorl, and there may be irregular brown flecks.

Size. Up to 22 × 20 mm. Body whorl = 90-95% of total shell height; aperture = 75-80% of total shell height.

Animal. As in *alderi,* but the foot is relatively smaller.

Colour. Cream with white speckles.

Geographical distribution. A circumpolar species which extends south on the west coast of Europe to the N. Sea, Skagerrak and, rarely, the Kattegat. It is found in Iceland, Greenland and extends to North Carolina on the east coast of America, to Monterey on the west. It reaches to Japan on the eastern coast of Asia.

Habitat. On clay bottoms from 10-2000 m, the greater depths in the most southerly parts of its range.

Food. Unknown, but presumably bivalves as for other species.

Breeding and growth. The spawn has been described by Thorson (1935, 1946), Lebour (1937), MacGinitie (1959). The ribbon is about 7.5-12 mm wide and the collar about 30-45 mm. It contains a rather small number of well-spaced egg spaces, each 1.5-3.0 mm in diameter which are confined to a central belt, leaving the margins unoccupied. Each space contains 1-2 large eggs up to 2.25 mm in diameter. The veliger stage is passed through within the capsule, from which a juvenile hatches after a period of several months according to Pelseneer (1926). It has a smooth shell of about 2 whorls, about 1.25 mm in diameter and a very distinct umbilicus. There is no information about its growth.

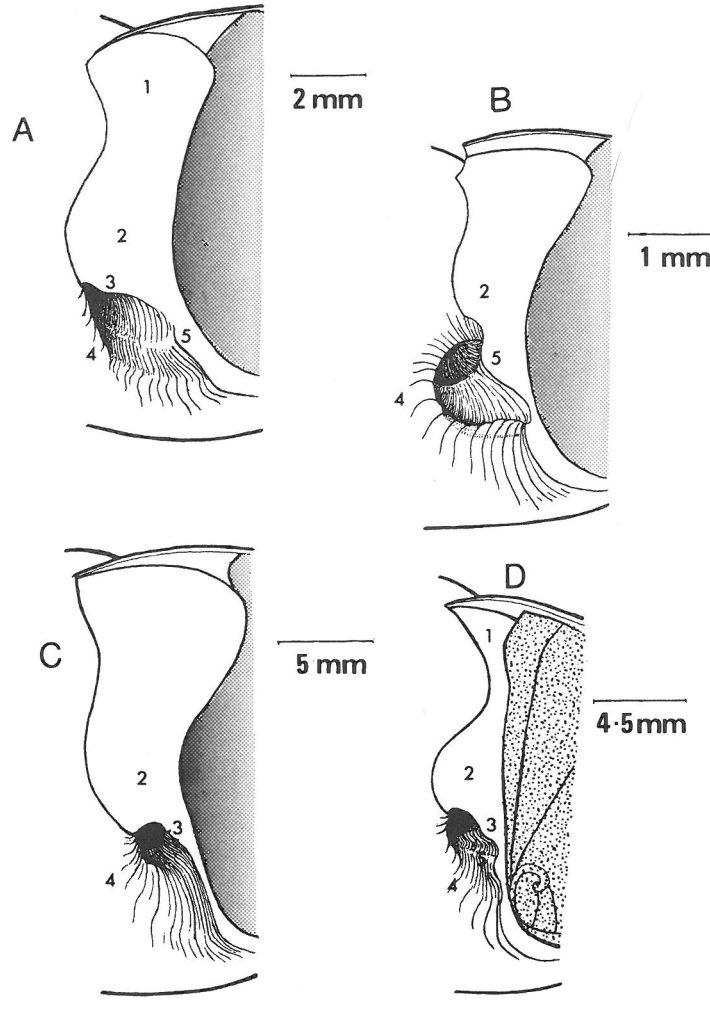

Fig. 248. Diagrams of the columellar, umbilical regions and inner lip of A, *Lunatia alderi;* B, *L. montagui;* C, *L. catena;* D, *L. fusca.*

NATICA CLAUSA Broderip & Sowerby, 1829

Natica, perhaps derived from the Latin *natare,* to swim, since the animals of this family were at one time thought to do this; *clausa* (Lat.), closed, referring to the blocked umbilicus.

Shell. In general appearance like that of any naticid. It is, however, thinner and has a more translucent look; it is glossy and covered with a thin periostracum. There are 4-5 rather tumid whorls meeting at shallow sutures which are slightly excavated and lie at or above the periphery of the upper whorl. The apical whorls often seem to coil at a slight angle to the more basal ones. The ornament is confined to delicate prosocline growth lines and obscure spiral striae.

The protoconch is small, about 500 μm across, and rather insunk. We have not been able to see ornament.

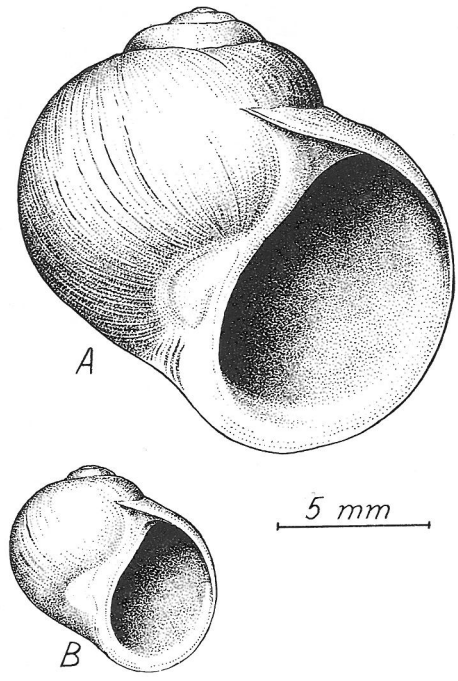

Fig. 249. *Natica clausa* Broderip & Sowerby. A, from *Thor* station 21, Skagerrak, 500-550 m; B, from Djupivogur, Berufjord, Iceland. CMZ.

Aperture. A D-shaped opening surrounded by a peristome lying in a prosocline plane. The outer lip arises about the periphery of the body whorl, more or less normal to its surface, and may be here a little concave. It is not flattened at the base and only a very slight angulation is present where it joins the columella. The columellar lip is not much thickened nor everted over the umbilical groove, but a thick pad of callus completely blocks the umbilical opening. Callus is also developed over the body whorl but not to the same extent as in species of *Lunatia.*

Colour. White, grey or yellowish; white where periostracum is lost.

Size. Up to 60 × 50 mm in the Arctic, but specimens from Scandinavia and off the west of the British Isles are not more than 12 × 10 mm. Body whorl = 88% of total shell height; aperture = 70% of total shell height.

Animal. As in *Lunatia* spp. The operculum, however, has a calcareous outer layer, is slighty concave externally, and is white and shiny. It shows a number of radiating lines on its labial half.

Colour. Cream with some darker flecks.

Geographical distribution. This is a circumpolar species which extends southwards into the Atlantic and Pacific Oceans. In Europe it is found as far south as S. Norway and, in deep water, it extends west of the British Isles to Portugal and the Mediterranean. In eastern America it reaches south to N. Carolina and, in the Pacific, to San Diego, California, and to Japan.

Habitat. On sandy, muddy and clay bottoms from about 4 m depth in high latitudes to well over 2000 m in low ones.

Food. Unknown; probably bivalves.

Breeding and growth. The egg collar of this species has been described by Thorson (1935). It has smooth margins and straight sides, has 3-4 rows of large capsules embedded in it, making its surface irregular. Each space contains only one large egg; the young hatch as crawling juveniles.

Fig. 250. *Natica clausa.* Apertural view × 22, the animal retracted into the shell. SEM photograph. Melvill-Tomlin collection, National Museum of Wales, Cardiff.

AMAUROPSIS ISLANDICA (Gmelin, 1791)
Nerita islandica Gmelin, 1791
Acrybia islandica (Gmelin, 1791)
Bulbus islandicus (Gmelin, 1791)
Natica helicoides Johnston, 1835

Amauropsis (from Gk.ἀμαυρός), as if it were blind; *islandica,* from Iceland.

Shell. Slightly transparent and thinner than that of other naticids, not glossy, covered with a thin periostracum. It is relatively more elongated than shells of *Lunatia* and *Natica* spp., with a high spire (apical angle 85-90°). The profile of the spire is noticeably stepped because of the flattening of the subsutural part of each whorl. The sutures are deep, channelled, and lie about level with, or slightly below, the periphery of the upper whorl. There are about 6 tumid whorls. The ornament consists of growth lines which are prosocline, and, occasionally, rather coarse; there are often faint spiral lines as well.

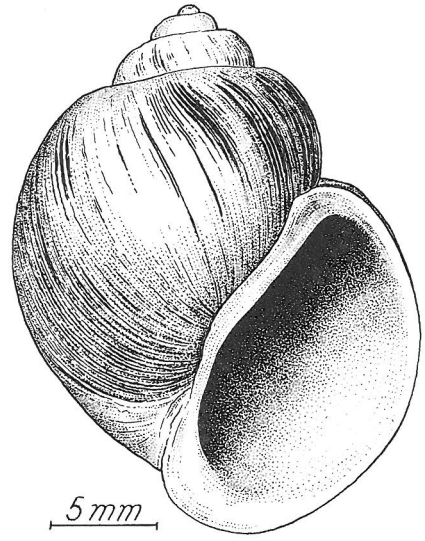

Fig. 251. *Amauropsis islandica* (Gmelin). Kattegat.

The protoconch has 2.5 smooth whorls and a diameter of *c.* 300 μm. It is sharply demarcated from the rest of the shell.

Aperture. This is large, oval and surrounded by a peristome lying in a prosocline plane. The outer lip arises nearly normal to the peripheral surface of the body whorl. Its initial part is straight, corresponding to the subsutural shelf. It then curves smoothly to the base of the columella where it is a little angulated and everted. The columella is slender and straight, sometimes a little narrowed at its mid-point by an embayment on the umbilical side. The peristome is completed by a broad inner lip spread over the body whorl; it is smooth and has no thickenings of callus as in *Lunatia* and *Natica.* There is either no umbilicus or only a very small chink.

Colour. White, though appearing yellow or brownish because of the periostracum.

Size. 25 × 18 mm. Body whorl = 85% of total shell height; aperture = 66% of total shell height.

Animal. In general like the species of *Lunatia* and *Natica.* The snout is relatively broader and the tentacles are smaller, with eyes hardly visible.

The foot is broad anteriorly where its lateral corners are reflected, narrow in the middle, and expanding posteriorly to end in a blunt point.

Colour. Cream, frosted with white speckles.

Geographical distribution. This is a circumboreal species which reaches south to the northern parts of the North Sea, the Skagerrak and Kattegat in Europe and to Virginia in eastern America.

Habitat. On sandy clay bottoms offshore, to about 80 m deep; not intertidal.

Food. Not known for certain, but likely to be as for other naticids.

Breeding and growth. The egg collar has been described by Thorson (1935) from material obtained in East Greenland. It has rigid walls 40 mm high with egg capsules arranged in several rows, to a total of 150-20. Each capsule is 1500-1750 μm in diameter and contains only one egg which is ovoid, with the major axis *c.* 1500 μm long. Development appears to be direct, with no free larval stage.

Notes. This is a little known animal occurring at the southernmost limit of its range in Scottish and Danish waters and found only rarely.

Notes on naticid species. Although at least some species appear capable of swimming (Ziegelmeier, 1958) naticids mainly burrow through the sand in which they live, usually just under the surface, in search of prey. Their path is obvious as a disturbance of the sand and their position often marked by a small hump. Burrowing is aided by the broad foot and by expansion of the propodium to form a wedge which covers the head (save for the distal parts of the tentacles) and the mouth of the mantle cavity, protecting against damage by sand grains. The burrowing habit, however, removes most of the periostracum from the shell except where it is protected

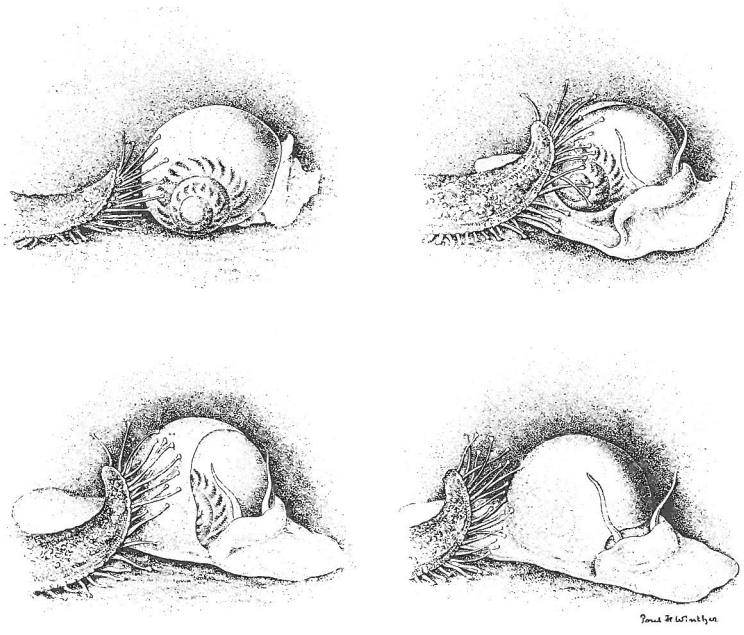

Fig. 252. *Lunatia catena.* Reaction of a retracted animal to the starfish *Asterias rubens.* Top left: the scent of the starfish stimulates the mollusc to emerge; top right: the propodium rapidly swells and a pedal fold appears behind the shell; bottom left: this is rapidly drawn forward over the shell, finally (bottom right) enveloping it completely. The mucus covering the fold allows no grip for tube-feet and the mollusc can crawl away untouched. (G. Thorson's Christmas card, 1953).

from erosion as in the umbilicus. Its persistence in *L. fusca,* a deep water inhabitant of muddier sands, may reflect less dependence on burrowing in mode of life. Russell-Hunter and Russell-Hunter (1968) have confirmed early statements by Schiemenz (1884, 1887) that naticids have a system of water channels by which the foot is inflated; Ziegelmeier (1958) and Trueman (1968) have seen water from this system ejected from pores round the propodial edge in *Polinices josephinus.* Animals of this species took up or lost 7-8 ml, equal to 2-3 times the shell volume, whilst *Natica millepunctata* (shell volume 8 ml) absorbed 6 ml. Active animals have therefore a volume greater than that of their shell and must discharge water before they can retract. They remain expanded for days or weeks and avoid littoral habitats where intertidal exposure would involve retraction. This system has not yet been demonstrated in species described here — Russell-Hunter and Russell-Hunter (1968) failed to find expulsion of water by *Lunatia alderi.* They assumed that this was because its small size made measurement difficult rather than because the system was absent. Further work is needed.

The process of feeding in naticids has been described by Ziegelmeier (1954). The prey, which can be detected at distances up to about 30 cm, is caught beneath the sand surface and is held by the propodium and mesopodium. If located above the surface it is carried on the posterior end of the foot to a place where the naticid can burrow. The anteromedian part of the propodium is retracted, forming a bay into which the proboscis is everted. It is applied to the prey in such a way that a hemispherical pad — the accessory boring organ (ABO) located ventrally at its tip — is placed in contact with the shell. Although study of its physiology has been neglected, this seems to act like the better-known ABO of *Urosalpinx* and produce secretions which soften the calcareous matter. The odontophore is then everted and the radula rasps the shell, the debris being swallowed. Boring proceeds by alternate periods of rasping and chemical action. The rasping is carried out between the centre and margin of the borehole, along different radii during each period. An incomplete borehole is therefore a rounded basin with a central upstanding knob. No such knob is formed in a hole bored by a muricid like *Urosalpinx* or *Nucella* and the completed hole may be distinguished from that made by a muricid by its more shelving sides. Boring is slow — 0.1 mm per 4 h period — and if the animal can find entry to the shell without boring it will do so. The bivalve shell is bored in places which are determined by the naticid's need for a secure grasp of its prey, mainly rather centrally in *catena,* more marginally in *alderi* (Ansell, 1960), and through one valve rather than an other if asymmetry gives a better grip on one side. There have been suggestions (Pelseneer, 1925; Verlaine, 1936) that as *L. alderi* grows it learns to bore over the gonad, but this view is not supported by Negus (1975), who showed that mechanical advantage in holding the prey was the probable determinant of the site of the borehole, especially as the whole bivalve, not just the gonad, was eaten.

The spawn is often found loose on the surface of the sand in which naticids live. It is characterized by its shape and by its reinforcement with sand grains. Its formation is difficult to study because it occurs when the animal has burrowed into the substratum and when that is covered by water. The details, however, have been given by Giglioli (1955) and Ziegelmeier (1961), the former mainly referring to *Lunatia triseriata* and *L. heros,* the latter to *L. alderi.* Although both agree that the spiral shape is achieved by a rotation of the snail as the egg-ribbon is protruded, there are important differences in their accounts relating to the direction of rotation and the forces which shape the ribbon, which suggest that the process may vary from one species to another.

Ziegelmeier described how the jelly with embedded eggs escapes from the mantle cavity on the right between propodium and mesopodium, how sand grains are incorporated into it by movements of the fold along the posterior edge of the propodium, and how the spiral is formed by a counter-clockwise rotatory creeping of the female in the sand. The arched shape of the ribbon in section is due to the sand pressing it on to the expanded surface of the right half of the mesopodium.

L. catena differs from other species in having food eggs. This kind of difference between species, however, is not uncommon and seems to have little taxonomic significance.

There is some evidence (Ansell, 1960; Fretter & Manly, 1979) that larvae settle in relation to populations of possible prey, and that older animals may migrate to such populations.

L. catena, as described by Thorson in one of his Christmas cards (Fig. 252) reacts to the touch of a starfish by covering the shell from behind by expansion of the opercular lobes of the foot. The tube feet of the starfish can obtain no grip on the mucous cover of the lobes and the naticid can escape. Presumably other species react similarly.

Identification of naticid species. The naticid species of Britain and Denmark are superficially similar to one another but may be identified without difficulty. *Lunatia catena* and *L. alderi* are the only two likely to be found alive at intertidal levels. They are normally distinguished from one another and from all other species by the colour markings on the shell (1 row in *catena,* 5 rows in *alderi*) and by the rectangular contact between outer lip and body whorl in *catena* compared with the tangential approach in *alderi.* Young specimens of *catena,* which may show more than 1 row of coloured markings are easily identified by this feature. The other naticid species have shells without markings. *L. montagui* is recognized without difficulty by the nick where the outer lip originates from the body whorl and by the notch in the columella. *L. fusca* has a somewhat similar umbilical appearance but lacks the notch and the nick on the outer lip; it is also taller, and much browner in colour because it retains more of the periostracum, and less globular. All the above species have a rather widely open umbilicus. In *L. pallida* the umbilicus is a small chink and in *Natica clausa* (not British) it is closed. The related *Amauropsis islandica* has also either no umbilicus or a very small one, but has a semitransparent shell with a much taller spire.

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TONNACEA

A moderately small group of mesogastropod snails which often reach large size. They have developed many features in common with neogastropods, more because both groups are carnivorous than because they are related. Most tonnaceans live in the warmer parts of the ocean and they are at the extreme northern limit of their range in the southernmost parts of the British Isles.

There are 5 families — Cassididae, Cymatiidae, Bursidae, Tonnidae and Ficidae — helmet shells, tritons, frog shells, tuns and fig shells respectively. They usually live offshore in shallow or moderately deep water on sandy bottoms, but bursids tend to prefer harder substrata. All have a well-developed pleurembolic proboscis, large salivary and oesophageal glands concerned with their attack on prey, which is commonly echinoderms. Bursids and cymatiids produce a strongly acid saliva for this. The foot is large for the size of the animal; in tonnids it has lost the operculum and the snails can no longer retract completely within the shell. Both body and shell are often brightly coloured, perhaps by pigments derived from the food.

The shell is varied in appearance but always has a distinct siphonal canal and tends to have an enlarged body whorl. The spire may be short (Tonnidae, Ficidae, some Cassididae) but is more frequently long. The ornament is variable, slight in most cassidids, tonnids and ficids, but marked elsewhere, with ribs, spiral ridges and varices combining to give a rough surface. The aperture is often large and the inner lip spreads extensively and often thickly over the body whorl. The peristome usually bears ridges internally and these may become so thickened *(Gyrineum, Distorsio)* that the aperture is grossly constricted. Tropical helmet shells provide much of the material from which shell cameos are carved.

In British waters 3 species of tonnacean have been found, though rarely: *Charonia lampas, Cymatium cutaceum* and *Galeodea rugosa.* Some material of a fourth, *Ranella olearium* (L.) has been recorded from off Southern Ireland, but this seems inadequate as a basis for including it in the fauna of this region.

CASSIDIDAE Latreille, 1825

GALEODEA RUGOSA (Linnaeus, 1771), helmet shell

Buccinum rugosum Linnaeus, 1771

Cassidaria rugosa (Linnaeus, 1771)

Morio rugosa (Linnaeus, 1771)

Galeodea tyrrhena (Gmelin, 1791)

Galeodea (Lat.), helmet-like; *rugosa* (Lat.), wrinkled or lined; both terms refer to the appearance of the shell.

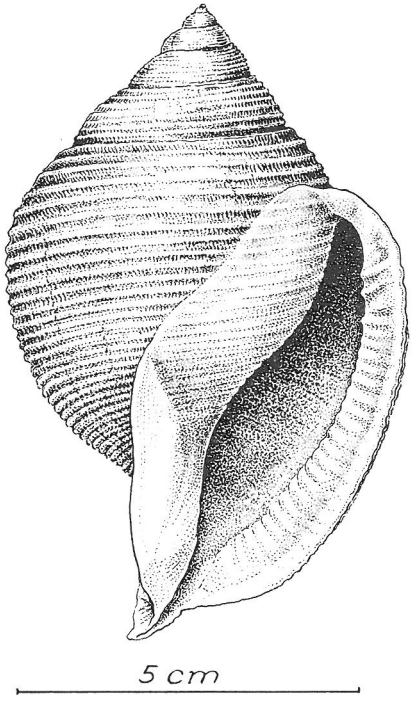

Fig. 253. *Galeodea rugosa* (Linnaeus). Off Arcachon, 128 m.

Shell. Large, solid, opaque and rather glossy. It is oval-conical in profile with a large body whorl and a rather small and sharply-pointed spire (apical angle = 82°, range 74-84°), which is slightly coeloconoid, especially towards the apex. There are 7-8 slightly tumid whorls which meet just below the periphery of the upper whorl. The sutures are deep, a little excavated and inclined to be irregular in direction. The ornament consists primarily of spiral ridges and grooves, though obscure growth lines are usually visible. The last are prosocline near the sutures but on the body whorl they follow a gently curved course (concave towards the aperture) and thus become orthocline at its base. The spiral ridges and grooves are numerous, 33-36 on the body whorl and 7-8 on each whorl of the spire. The ridges are about half as broad as the grooves on the spire and on the adapical half of the body whorl but become more tightly packed towards its base. Each tends to have a steeper adapical side. There is a thick, out-turned labial rib which rises rather abruptly from the body whorl and over which the spiral ornament is continued. Occasionally, but by no means frequently, an earlier varix is seen on the spire. The protoconch is smooth, with its tip decidedly insunk.

Aperture. This lies in a gently prosocline plane and is surrounded by a peristome. In greatest outline it is oval or pyriform, broader adapically but the throat is much narrower, especially towards the adapical end. The outer lip arises at, or a little above, the periphery of the body whorl and shows a shallow anal sinus. It curves gently towards the base, often with a flatter stretch below the periphery. Its outer edge is variable, sometimes markedly everted, sometimes very little so, sometimes thin and marked by the ends of the spiral ridges, sometimes thicker and smooth. The inner edge constricts the throat and is ridged, except over the anal sinus, the ridges placed opposite the spiral grooves on the outer surface of the shell and extending up the throat so that it bears a shallow replica of that ornament. The teeth on the outer lip are most prominent just below the anal sinus and just above the siphonal canal and are weakest at the periphery. This seems to correspond to age, as the teeth in these two positions are the first to appear in smaller shells. There are about 24 ridges in all. At the base of the shell the outer lip extends with the columellar lip to form a short siphonal canal bent more or less sharply to the left and backwards, away from the aperture; it is moderately widely open. The columella is short and straight and it bears a series of spiral ridges. The columellar lip extends into a large, thin flange (marked externally by growth lines) which forms the adapertural side of a deep umbilical cavity, the abapertural limit of which is formed by a spiral keel originating at the tip of the siphonal canal. Over the body whorl the inner lip forms an expanded shield-shaped sheet which is not usually thick enough to obscure the underlying ornament, but may do so, and carry ridges on its inner parts as well. These are so placed as to overlie the spiral grooves on the body whorl. The surface of the lips and throat is very glossy and is marked with innumerable microscopic pits.

Colour. Cream, occasionally brownish or with a reddish tint, especially towards the base.

Size. Up to 120 × 70 mm. Body whorl = *c.* 75% of total shell height; aperture = 60% of total shell height.

Animal. The head has no snout and the mouth (= opening of a proboscis pouch) is on the underside of the fold uniting the tentacle bases. Each tentacle has a lateral eye near its base. The mantle skirt has a smooth edge and is drawn out into a short siphon on the left. Males have a penis arising from the floor of the pallial cavity behind the right tentacle.

The foot is rather straight anteriorly, with a double edge, bluntly rounded behind. The operculum is an elongated oval, horny structure with a nucleus placed about the middle of its labial border.

Geographical distribution. From the Mediterranean north to the southern extremities of the British Isles where rare specimens have been dredged off S.W. Ireland, the Isles of Scilly and Pembrokeshire.

Habitat. On muddy bottoms at depths of 70-700 m.

Food. The animals are carnivorous and probably, like other cassidids eat echinoderms, molluscs and other invertebrates. The prey may be bored, crushed or attacked with an acid saliva.

Breeding and growth. Not known for certain unless the remarks made by Fioroni (1966) under the heading *Cassidaria* sp. refer to this animal. In *Galeodea* (= *Cassidaria) echinophora* and the unidentified species the eggs are laid in capsules which are dome-shaped, 4-6 mm and 4-5.5 mm across and 4.5-5.4 mm high, and aggregated into clumps. Each capsule contains 130-300 eggs according to the species, but most of these are food eggs and not more than 24 young hatch. The veliger stage is intracapsular and the young emerge as crawling juveniles with shells about 1.5 mm long.

Notes. This species is at the extreme northern limit of its range in the south of England and Ireland and less than 20 specimens in all, and none this century, have been taken.

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CYMATIIDAE Iredale, 1913
CYMATIUM CUTACEUM (Linnaeus, 1767)
Murex cutaceus Linnaeus, 1767
Triton cutaceus (Linnaeus, 1767)

Cymatium (Gk. κῦματιον, a small wave), relating to the shell form; *cutaceum* (Lat.), covered with a cuticle, the periostracum.

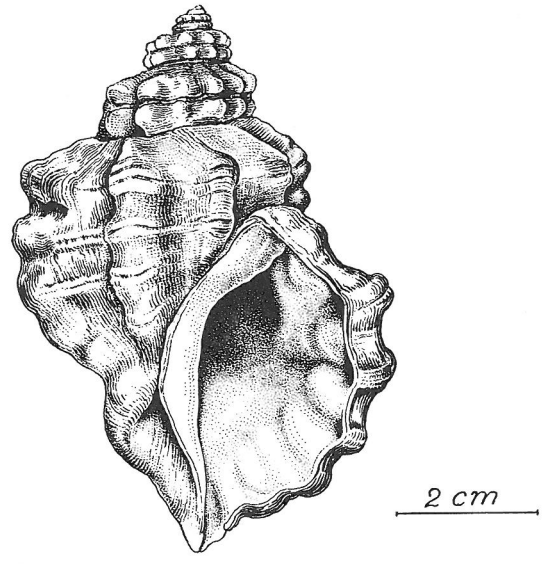

Fig. 254. *Cymatium cutaceum* (Linnaeus). Mediterranean.

Shell. Solid and opaque, glossy where the periostracum persists but dull where that is lost; oval-conic in profile with a flattened apex (apical angle = 50°). There are 6 whorls with deep, slightly excavated sutures which are often irregular because distorted by the ornament. The whorls are tumid and roughly like a half hexagon in profile; the sutures lie below the periphery of the upper whorl. The ornament comprises spiral ridges and grooves, ribs and growth lines, the ridges and ribs combining to produce a coarse cancellation on the spire. The spiral ridges are broad and strap-shaped, the intervening grooves shallow and about as broad as the ridges and both more prominent on the spire than on the body whorl. There is usually a shallow secondary groove in the middle of each ridge and a low secondary ridge in the centre of each groove. The body whorl has 8 ridges, those in the spire 4, the 2 near the upper suture less obvious than the others. The 2 peripheral ridges are responsible for the irregular profile of the spire. A rib set along the outer lip forms a thick varix tuberculated by the spiral ridges over it; another varix lies across the body whorl about 180° from the labial one, ending basally at a relict siphonal canal overhanging the umbilical groove; a third lies on the penult whorl and there may be a fourth on the antepenult. The body whorl also bears 4-5 ribs, rather low, broad elevations separated by correspondingly shallow troughs. They are weakly developed near the suture, reach their highest point level with the most adapical spiral ridge and fade level with the adapical end of the aperture. There are 7-8 ribs on the penult whorl (plus the varix), 8 on the previous ones; these cross from suture to suture. All are slightly prosocline. In addition, the whole shell surface is crossed by vast numbers of prosocline, microscopic growth lines; these are arranged in groups of about 10 in an escarpment shape, the steep edge facing the aperture, so that the surface resembles that of a fine file.

The protoconch has *c.* 1.25 smooth whorls lying almost in one plane; its sutures are very deep and it is *c.* 2 mm across.

Aperture. Oval, angulated apically and basally, the long axis set at 10° to that of the spire, surrounded by a peristome lying in a gently prosocline plane and without an anal sinus. The outer lip

arises at right angles to the surface of the body whorl below the periphery, level with major spiral 3. It is approximately semicircular, though the adapical third is straighter than the rest. Its edge is thickened and projects a little from the base of the labial varix and is made sinuous by the ends of the spiral ridges. At the base it turns out to form the edge of a short, narrowly open siphonal canal which lies in the axis of the shell and ends obliquely. The other margin of the canal is formed by an extension of the columellar lip which also forms the adapertural side of a broad umbilical groove, bounded adaperturally by a thick keel running from the mouth of the siphonal canal. The groove leads to a shallow umbilicus overhung and blocked by the end of a varix. The columella is nearly straight, the lip outspread over the umbilical region and spread over the body whorl. A few obscure folds lie on the base of the columella and others, more prominent and perhaps interrupted to form tubercles, lie on the body whorl near the adapical end of the aperture. The labial varix is hollow so that a deep groove lies just within the outer lip; its inner edge carries 6-7 prominent ridged teeth placed opposite the external spiral grooves. The throat is glossy, its surface marked with microscopic ridges parallel to the edges of the peristome.

Colour. Where periostracum occurs — light brown or dark straw colour; in its absence — dark cream, frequently with a pinkish tinge. The throat is white.

Size. Up to *c.* 60×40 mm, though larger specimens are found south of the British Isles. Body whorl = 75-80% of total shell height; aperture = *c.* 63% of total shell height.

Animal. Resembling *Charonia lampas* in general features.

Colour. Jeffreys noted that the body had dark purple spots separated by white lines and that the foot was pale violet speckled with reddish spots edged with white.

Geographical distribution. A southern species found from the Mediterranean and Canary Islands north to the Channel Islands. It is extremely rare in the last locality and it is doubtful whether it has been found alive since 1885, though rare finds of dead shells (1902, 1932) suggest that it may still survive (Crowley, 1961).

Habitat. On soft bottoms, sublittoral.

Food. Unknown, but like its relatives, the animal is carnivorous and may eat echinoderms.

Breeding and growth. Not known. If like those of other cymatiids the larvae may prove to be strong swimmers.

Notes. A little known animal and extremely rare in this area. In his description Jeffreys notes the presence of "an excavation like the top of a key-hole" at the adapical end of the aperture; this is not visible in Fig. 254, but may be seen when the shell is turned so that the aperture is viewed a little obliquely from the columellar side.

REFERENCE

CROWLEY, T.E. 1961. F.C. Lukis and the Triton. *Journal of Conchology,* **25,** 17-20.

CHARONIA LAMPAS (Linnaeus, 1758)
Murex lampas Linnaeus, 1758
Triton nodiferus Lamarck, 1822

Charonia, named for Charon who, in Greek mythology, ferried the dead across the Styx; *lampas* (Gk.), a lamp.

Shell. A large, pointed, conical shell (apical angle *c.* 60°), glossy, solid and opaque. The spire is a little coeloconoid, its profile angulated by the spiral ornament, and the body whorl swollen. There are 7-8 slightly tumid whorls which meet at shallow sutures placed below the periphery of the upper whorl. The ornament has both spiral and transverse elements — spiral ridges and grooves, growth lines and varices. The whole surface is coverd by many fine spiral ridges and grooves, the ridges low, somewhat strap-shaped and broader than the grooves. In the subsutural area they may have a sharper edge on their adapical side. From just adapical of the periphery of the body whorl to its base the ridges and grooves lie on the surface of larger spiral elements. The most adapical of these is usually separated by some distance from the suture and is nodose; the others become progressively less nodose and lower towards the base, though the most basal, which runs from the siphonal canal alongside the umbilical groove, is again thicker and higher. There are about 10 of these larger spiral ridges on the body whorl but only 2 on each whorl of the spire. The height of the nodes which they bear is very variable and nodes tend to be absent from an area along the abapertural side of each varix. All the spiral ornament is crossed by irregular and fairly close-set growth lines slightly

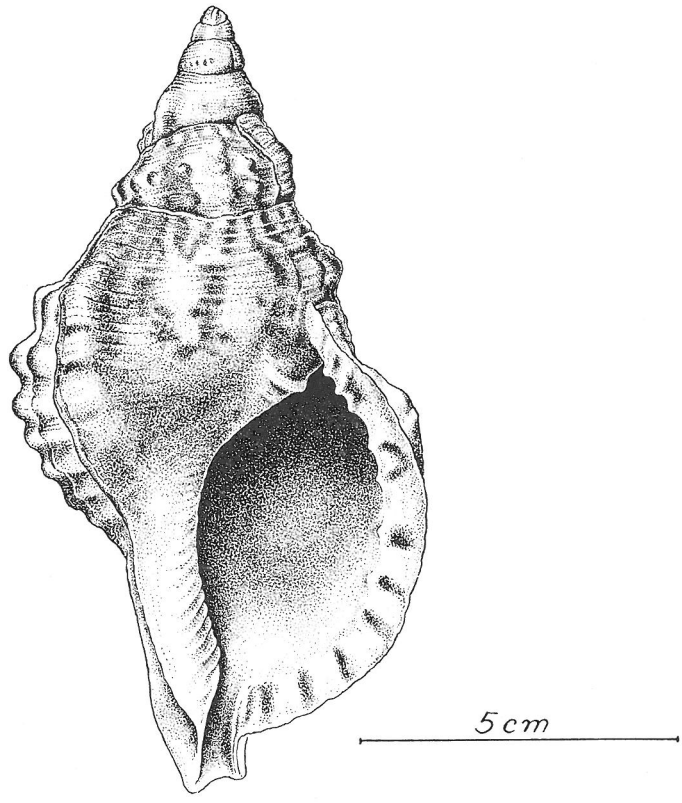

Fig. 255. *Charonia lampas* (Linnaeus). No locality given.

prosocline in direction. A labial rib marked with nodes lies along the outer lip and previous positions of the outer lip are marked by a series of varices set on the whorls of the spire at intervals of *c.* 130° (range 115-160°) from one another. When the spire is viewed apically they lie on 3 spiral curves. Each varix consists of a prominent nodose rib and a thin, out-turned flange on its adapertural face, which may be ridged. This feature is most obvious on the younger varices.

Aperture. Oval, pointed above and below, its long axis at *c.* 15° to that of the spire. The peristome lies in a very slightly prosocline plane and shows a shallow anal sinus, a peripheral bulge and a slight basal retreat. The outer lip arises at the periphery of the body whorl almost tangentially. Its first section is rather straight; it then curves to the base where there is a short canal continuing the direction of the long axis of the aperture, straight and open. The curved part of the outer lip is flared. Its whole length is marked internally by 12-15 short ridges, arranged in pairs at the adapical end but becoming single towards the base. At the margin of the lip the ridges end in small projecting points and adapically their inner ends are raised to form a fold which connects the teeth there but which becomes lower and finally disappears towards the base. The columella is gently curved and the related lip forms a thin, concave flange over the umbilical groove leaving one or two minor gaps to represent the umbilicus. The inner lip forms an extensive glaze over the body whorl. The internal half of this and most of the columellar lip are fluted by many small ridges, more or less alternately long and short. The uppermost ridge is the largest and is separated from the outer lip by a short unridged area. The throat is very glossy and is dimpled by the nodes on the body whorl and constricted by those on the penult.

Colour. White with some brown markings, the apical area (and sometimes more) of a lilac tint. The brown colour is most apparent near the sutures and varices with irregular blotches elsewhere. The teeth on the outer lip, the corresponding parts of the varices and the columellar base are also brown.

Size. Up to 330 × 180 mm. Body whorl = 65-70% of total shell height; aperture = 55% of total shell height.

Animal. The head is rather flattened with no snout, the mouth (= opening of a proboscis pouch) a small slit on its underside. Distally it carries 2 long, tapering and diverging tentacles, each with an eye on a lateral bulge near the base. The edge of the mantle skirt is slightly lobed and is extended on the left into a short siphon, which projects very little from the siphonal canal. Males have a long penis attached some distance behind the base of the right tentacle; an open seminal groove runs from the male pore in the mantle cavity to its tip.

The foot is short, its anterior end axe-shaped and with a double edge marking the opening of the anterior pedal gland; its posterior end is rounded. In females a ventral pedal gland opens to the mid-line of the sole in its anterior half.

Colour. Reddish, with scattered brownish spots of different sizes. The mantle edge is paler and the tentacles have each two black stripes along them.

Geographical distribution. From the Mediterranean and the Canary Islands north to the Channel Islands, south-west England and south-west Ireland. The northern limit of reasonably common occurrence is on the southern part of the Bay of Biscay and only sporadic finds have been reported from further north. In the British area catches have been limited to the Channel Islands (Crowley, 1961; Brehaut, 1973) where 3 or 4 were caught 1825-47, and 3 in 1972; off Co. Kerry where 4 were taken 1970-71 (O'Riordan, 1972); between Lands End and the Isles of Scilly, off Wolf Rock, 1 specimen in 1975 (Turk, 1976).

Habitat. On gravelly, sandy and muddy bottoms from a few metres to *c.* 700 m.

Food. According to Amouroux (1974) the only food taken by a specimen caught off Banyuls was the starfish *Echinaster sepositus;* others in the aquarium ate mussels and squid, though the latter seems improbable prey in natural conditions unless moribund or dead. British specimens were taken with queens and scallops which they may have been eating. Faeces orange-red pellets.

Breeding and growth. These are largely unknown. Amouroux (1974) observed a single specimen deposit spawn in an aquarium tank at Banyuls. The capsules were about 30 mm high and 5 mm broad, translucent and slightly bluish. They were attached to the substratum by a flattened base, did not narrow much above that, were nearly circular in cross section and had a markedly rounded top. Each contained 200-300 bright orange eggs. The egg capsules of the related *C. rubicunda* (Perry) and *C. capax* Finlay have been described by Laxton (1969) as cylindrical, with a rounded apex, 9-14 mm in height and 2-3 mm across, each containing albumen with many eggs 150-200 μm in diameter. There are no food eggs and the larvae are veligers. The larva of *C. parthenopeum* (von Salis) has been described by Scheltema (1966). The shell is ovoid, of several whorls covered with periostracum which obscured the sutures and from which several rows of bristles project. The larva has a powerful velum, with 4 long arms and may have a very protracted planktonic life — over 3 months — during which it may be drifted long distances ('teleplanic' larva), perhaps from one side of the Atlantic to the other.

Notes. This is a surprisingly unknown animal despite the conspicuousness conferred by large size. There is still much information needed in relation to its way of life. In most shells the pairing of teeth on the inner surface of the outer lip is more pronounced than in the one shown in Fig. 255.

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HETEROPODA (= ATLANTACEA)

A group of pelagic mesogastropods of doubtful relationships, though many suggestions have been made. All are highly modified for their mode of life. There are 3 families, Atlantidae, Carinariidae, and Pterotracheidae, of which the first is the only one containing animals whose organization instantly suggests that they are prosobranchs. The shell is light and transparent, has several whorls lying in one plane, the body whorl with a broad peripheral keel. There is a roomy mantle cavity and the animal can retract within it and close the aperture with an operculum. The head has an elongated snout and large eyes and the foot shows a well-developed propodium which acts as a swimming organ. It bears a sucker. In the Carinariidae the head-foot has expanded into an elongated cylindrical structure and the shell and mantle cavity have become smaller so that retraction is impossible. The operculum is lost. The pterotracheids have carried these trends further and have lost both shell and mantle cavity, the viscera being withdrawn into the head-foot and the gill lying naked on its surface. All the animals are carnivores, have separate sexes and are widely spread.

CARINARIIDAE Reeve, 1841
CARINARIA LAMARCKI Péron & Lesueur, 1810
Carinaria mediterranea Blainville, 1824
Carinaria atlantica Adams & Reeve, 1828

Carinaria, from the Latin *carina,* a keel or keeled vessel; *lamarcki,* Lamarck's. Named in honour of Jean Baptiste de Lamarck (1744-1829), who occupied the chair of Invertebrate Zoology at the Muséum d'Histoire naturelle, Paris, from 1793 to 1829.

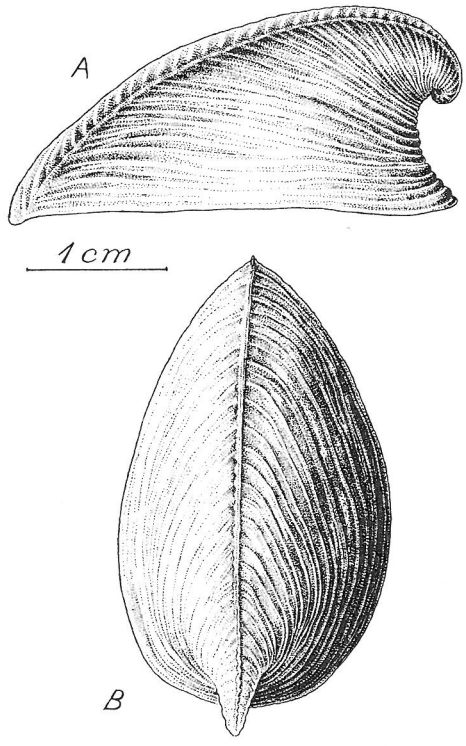

Fig. 256. *Carinaria lamarcki* Péron & Lesueur. A, from the left; B, from above. Naples.

Shell. Extremely thin and delicate, transparent and glossy. It is cap-shaped, coiled nearly in a plane spiral with only the protoconch retaining a helicoid twist. There are 5-6 whorls of which 4 belong to the protoconch, the bulk of the shell formed from a rapidly-expanding body whorl. The ornament consists of a series of growth lines which appear as transverse ridges and grooves, the former broader than the latter. The only indication of spiral ornament is a thin keel set along the mid-line of the convex anterior face (= the periphery of the body whorl) and marked into segments by extension of the growth lines into it.

The protoconch (Thiriot-Quiévreux, 1975) has up to 4 tumid whorls arranged in a helicoid spiral and separated by deep sutures; it measures *c.* 500 μm in diameter. There can be distinguished an embryonic part of about 0.75 whorls bearing raised points, and a larval part of which the first whorl is also punctate but has, in addition, 2 spiral ridges with sometimes a feebler third. The remaining whorls may have some raised points but are otherwise smooth.

Colour. Transparent and colourless.

Size. 15 mm high, 30 mm long.

Animal. An expanded head-foot forms the main part of the body, a long, more or less cylindrical structure tapering anteriorly and posteriorly, much too large to be withdrawn into the shell as it can be about 100 mm long. The head extends into a snout with a terminal mouth and bears two slender tentacles dorsally, some distance from the mouth. They are far apart because of a lateral origin; each has a conspicuous basal eye. The epidermis bears conical papillae.

The main part of the foot forms a flat keel, or fin, projecting from the body ventrally. It is more or less semicircular in outline and its posterior edge distally is excavated to form a sucker. The hinder part of the body tapers to a blunt end and bears a median dorsal and two ventrolateral fins.

The shell and visceral hump lie opposite the main fin and are connected to the body by a short stalk. They are orientated so that the protoconch and adapical surfaces of the whorls lie on the animal's right, and their basal parts on its left. The peripheral keel is mid-dorsal and forms the most anterior part of the shell. The main part of the mantle cavity, which is very shallow, lies anterior to the stalk. The mantle edge is simple. The ctenidial axis runs along the mantle edge, bearing up to 10 bipectinate filaments which tend to hang into the water outside the mantle cavity. The osphradium is a ciliated ridge along the left side of the mantle skirt. The anus opens on the right at the posterior end of the mantle cavity. By it, in females, opens the genital duct; in males an open seminal groove runs some distance down the right side of the stalk — almost to the base of the foot — to a penis. This is a cylindrical body with swollen, knob-like tip; on its ventral side it carries a spindle-shaped appendage at the tip of which opens the duct of a gland.

Colour. Colourless except for the eyes, digestive gland and kidney.

Geographical distribution. Predominantly Mediterranean but also in a variety of Atlantic areas, including the western coasts of the British Isles where it is only an occasional visitor. It has also been taken off the Pacific coast of N. America.

Habitat. A free-swimming inhabitant of open water. In British latitudes it is limited to deeper waters, 250-1000 m, but swims at more shallow depths in warmer areas.

Food. A greedy carnivore, but as it is not a powerful swimmer, mainly dependent on less rapidly moving animals such as jelly-fish, salps and worms.

Breeding and growth. The sexes are separate and the male may be easily distinguished by the penis. Animals of this species encountered in British waters are strays and are unable to breed. In the Western Mediterranean breeding occurs in spring. The larva of *C. lamarcki* has been briefly described by Pelseneer (1906) and Lo Bianco (1910); fuller accounts have been given by Franc (1949) and Thiriot-Quiévreux (1971, 1973, 1975).

Notes. Like *Janthina C. lamarcki* is not strictly a native of the waters under consideration here, but of warmer latitudes; it is brought towards the British Isles by a northward flow of water from them. It is even less likely to be found than *Janthina* since it is not gregarious, not cast ashore, more delicate and lives at depths which can only be explored with proper gear.

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KEY TO PROSOBRANCHS DESCRIBED HERE

1. Animal pelagic, shell reduced; body transparent, cylindrical, with fin opposite visceral mass	*Carinaria lamarcki* (p.359)
Animal not like this	2
2. Shell internal, mantle lobes fused over it; animal resembles a dorid but has smooth tentacles and anterior notch in mantle *(Lamellaria)*	3
Shell external, though mantle lobes may cover it temporarily in active animals	4
3. Shell with high spire; dorsal surface of animal dome-shaped, tuberculate, grey-purple frosted white, less frequently yellowish	*L. perspicua* (p.319)
Shell with low spire; dorsal surface rather flat and smooth, yellowish with dark speckles	*L. latens* (p.321)
4. Aperture a long narrow slit; shell partly or wholly covered by mantle lobes in active animals	5
Aperture rounded, oval or circular, shell exposed (partly covered by pedal lobes in active naticids)	9
5. Spire of mature shell concealed by overgrowth of body whorl	6
Spire visible	8
6. Shell smooth, aperture drawn out into canals apically and basally; white or pink, animal yellow; on coelenterates	*Simnia patula* (p.333)
Shell ridged, aperture not as long as shell; a cowrie *(Trivia)*	7
7. Shell with 2-3 dark spots on convex side; penis slender and sickle-shaped; body highly pigmented, the back end of the foot striped; usually intertidal	*T. monacha* (p.328)
Shell without dark spots; penis leaflike; body pale, the back end of the foot yellow; usually sublittoral, commoner in the north	*T. arctica* (p.330)
8. Adult animal; shell thick with pear- or harp-shaped outline, narrow basally; mantle lobes heavily pigmented	*Erato voluta* (p.325)
Juvenile; shell thin with oblong profile, broad basally; mantle lobes rather pale	*Trivia* sp.
9. Shell with internal partition visible in aperture	10
Shell without such partition	11
10. Shell conical, apex central with minute coil; partition tongue-shaped; animals solitary	*Calyptraea chinensis* (p.314)
Shell cap-shaped, apex subterminal; partition D-shaped; animals usually in chains	*Crepidula fornicata* (p.309)
11. Shell with very thick periostracum, sometimes drawn out into short processes	12
Periostracum slight or absent	16
12. Shell cap-shaped with small initial coil; periostracum fringed; animal with grooved proboscis; no operculum	*Capulus ungaricus* (p.305)
Shell not cap-shaped	13
13. Shell weakly calcified, with low spire and large aperture; animal without proboscis; no operculum *(Velutina)*	14
Shell robust, with tall spire; animal with grooved proboscis; operculum on foot	15
14 Shell with 3-4 whorls, aperture nearly circular	*V. velutina* (p.323)
Shell with 2-3 whorls, aperture oval; rather rare	*V. plicatilis* (p.322)

15. Spire tall, whorls slightly tumid with prominent spiral ridges; periostracum with coarse processes over spiral ridges; aperture pear-shaped, narrow basally	*Trichotropis borealis* (p. 302)
Spire not very tall; whorls distinctly tumid with fine spiral ridges; periostracum finely villous; aperture nearly circular, rounded basally; Scandinavian, rarely in British waters	*Torellia vestita* (p. 303)
16. Outer lip expanded into finger-shaped processes *(Aporrhais)*	17
Outer lip simple	18
17. Adapical process of outer lip not reaching level of shell apex, basal process hooked	*A. pespelecani* (p. 295)
Adapical process extends beyond level of shell apex, basal process not hooked; northern	*A. serresianus* (p. 298)
18. Spire rather tall, body whorl less than 80% of total shell height; shell not covered by pedal lobes in active animals	19
Spire rather short, body whorl 80% or more of total height; shell partly covered by pedal lobes in active animals (naticids)	24
19. Mature shell not over 40 mm high; slender (breadth about 30% of total height); aperture entire or with small basal notch	20
Mature shell over 40 mm high; broad (breadth 50-60% of total height); aperture with siphonal canal at base; animals all very rare, in extreme south only	22
20. Aperture without basal notch; ornament of spiral ridges; mantle edge with pinnate tentacles; operculum fringed	*Turritella communis* (p. 286)
Aperture with basal notch; ornament of spiral ridges and ribs; mantle edge simple; operculum not fringed *(Bittium)*	21
21. Body of animal darkly pigmented; shell with one varix on each whorl; mainly on *Zostera*	*B. reticulatum* (p. 290)
Body pale with pink markings; shell without varices; mainly on coralline and other small algae	*B. simplex* (p. 293)
22. Ornament of spiral ridges only; aperture rather narrow, columellar lip forming prominent flange over deep umbilicus	*Galeodea rugosa* (p. 352)
Ornament of spiral ridges, tubercles and varices	23
23. Spire tall, 7-8 whorls; columellar region ridged; no groove within outer lip	*Charonia lampas* (p. 355)
Spire moderate, 6 whorls; columellar region smooth; keyhole-shaped space between body whorl and origin of outer lip; deep groove within outer lip	*Cymatium cutaceum* (p. 354)
24. Shell without umbilicus or, at most, with minute chink	25
Shell with distinct umbilicus	26
25. Shell translucent; spire stepped; aperture narrowed adapically; outer lip arises normal to body whorl, initially flattened; operculum horny	*Amauropsis islandica* (p. 346)
Shell solid, spire whorls not shouldered; aperture D-shaped; outer lip arises tangential to body whorl; operculum calcified externally	*Natica clausa* (p. 344)

26. Umbilicus oval, narrow adapically; outer lip arises tangential to body whorl which has 5 spiral rows of brown marks	*Lunatia alderi* (p.336)
Shell not so	27
27. Umbilicus round, broad adapically; outer lip arises normal to body whorl which has 1 row of brown markings	*L. catena* (p.338)
Shell not so, usually without regular markings	28
28. Umbilicus small and slit-like; rare and northern	*L. pallida* (p.343)
Umbilicus dilated	29
29. Shell pale; a nick between body whorl and adapical end of outer lip; a groove along the umbilical space produces a deep notch on the columella	*L. montagui* (p.340)
Shell brown; no nick between outer lip and body whorl	*L. fusca* (p. 341)

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