

THE PROSOBRANCH MOLLUSCS OF BRITAIN AND DENMARK

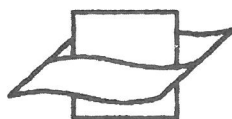
PART 5 — MARINE LITTORINACEA

by

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LITTORINACEA

A very successful superfamily of prosobranchs usually regarded as close to the base of the mesogastropod stem, but on an evolutionary line distinct from the oldest members of that group, the Cerithiacea. Their success seems to rest primarily on general physiological efficiency as few show any particular anatomical specialization.

The shell has a moderately high spire, is solidly built and is usually pigmented. When ornament is developed it is the spiral element which is usually more pronounced. In most respects the body of the animal shows a generalized monotocardian structure. Though the nervous system is advanced in the approximation of cerebral and pleural ganglia, the reproductive system remains primitive in the persistently open genital ducts of the male.

The superfamily is divisible into 4 families — Lacunidae, Littorinidae, Pomatiasidae and Aciculidae, though a fifth (Chondropomidae, of New World snails) is sometimes split from the Pomatiasidae. The characters of the Pomatiasidae and Aciculidae have been given above (p.117). The Lacunidae and Littorinidae are more primitive than the others, the lacunids more than the littorinids in that their shell is smooth, taller, and retains an open umbilicus, which is occluded by an expanded columellar lip in littorinids. Both families are predominantly littoral in distribution with a preference for rocky, weedy substrata over which they browse. Lacunids usually live sublittorally or lower on the beach than littorinids which often extend to its topmost levels. The animals may produce pelagic egg capsules, most commonly lay jelly-like spawn, and both families show a trend towards suppression of free-swimming larval stages. This may pass into ovoviviparity in several species of *Littorina*. The littorinids show considerable tolerance of estuarine conditions and of emersion: it is this which has probably led to the ability to survive in damp terrestrial or in semiaquatic situations exhibited by the littorinid genus *Cremnoconchus* in India and by the families Pomatiasidae, Chondropomidae and Aciculidae.

LACUNIDAE Gill, 1871
LACUNA VINCTA (Montagu, 1803), chink shell
Turbo vinctus Montagu, 1803
Lacuna divaricata (Fabricius, 1780)

Lacuna (Lat.), a gap, referring to the umbilicus; *vincta* (Lat.), encircled, referring to the colour bands on the shell.

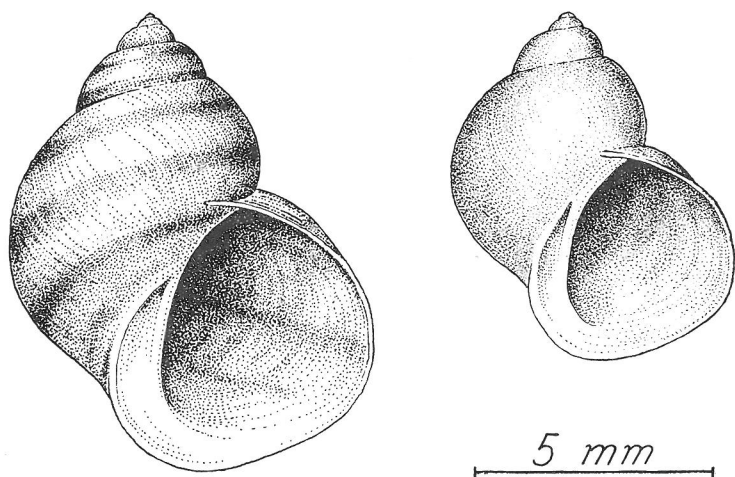


Fig. 196. *Lacuna vincta* (Montagu). Aarhus Bay. CMZ.

Shell. Rather delicate, slightly transparent, glossy under a thin periostracum. Spire well developed, the apex a little blunt, apical angle about 54° ; in profile it is a little cyrtocoid towards the apex, otherwise (neglecting the curvature of the whorls) straight-sided. There are 5–6 tumid whorls meeting at clear sutures placed well abapical of the periphery of the upper whorl and sometimes a little filled in by thickened periostracum. The whorls are a little flattened peripherally and the body whorl is occasionally a little angulated where it starts to taper to the base. The ornament consists of delicate spiral ridges and grooves, not visible to the naked eye, and extremely fine on young shells and the upper whorls of older ones. They are slightly sinuous; each ridge is about $60\text{--}100\text{ }\mu\text{m}$ broad, the intervening grooves narrower. The growth lines, markedly prosocline, are rather irregular. On most whorls they are not affected by the spirals which appear only between them; on the base of the body whorl, however, there is some interaction and they are beaded in appearance. Umbilicus rather narrow, shaped like an inverted vee. Protoconch of up to 2.5 whorls measuring $450\text{--}500\text{ }\mu\text{m}$ in diameter. It displays an initial part of 1.25–1.5 whorls (diameter $200\text{--}225\text{ }\mu\text{m}$) which is the embryonic shell, marked with 2 spiral lines and scattered spots, clearly demarcated by a line from a second part, the larval shell, smooth except for growth lines, and with a well-marked beak lying by the suture.

Aperture. Oval or ear-shaped, its long axis nearly parallel to that of the spire. The aperture is prosocline, lying in a plane making an angle of 135° with the shell axis. The outer lip arises at the periphery of the body whorl and slants abapically at an angle of about 135° ; at the broadest part of the aperture it is a little less curved and below this slightly angulated. The basal part is again straight and lies a little oblique to the axis of the spire. At the base of the columella the outer lip apparently turns apically to form the abapertural side of a groove and ends by forming the abapertural lip of the umbilicus to which the groove leads. The inner lip runs as a glaze across the body whorl from the outer lip and forms the lip on the apertural side of the umbilicus. Thereafter it runs basally as the

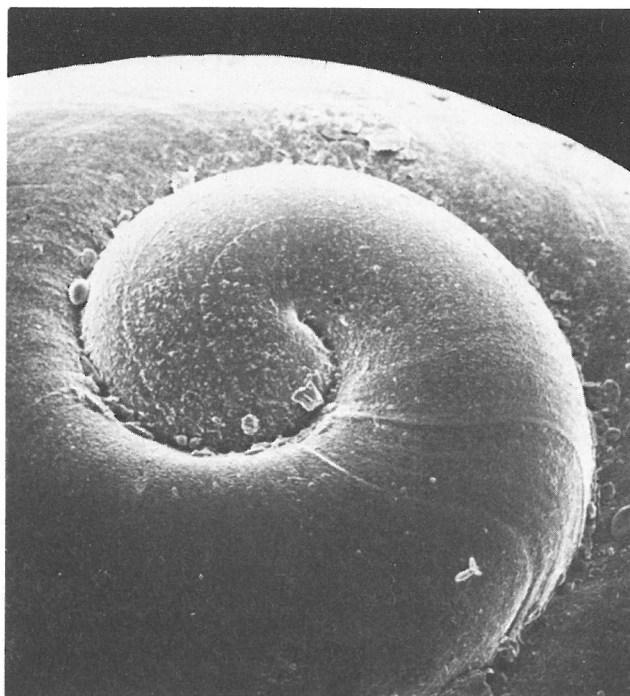


Fig. 197. *Lacuna vincta*. Shell apex $\times 280$. SEM photograph. Plymouth. RUZ.

apertural side of the umbilical groove and fades away. At the umbilicus the inner lip lies so as to overlap the apparent outer lip in most shells, so that the latter enters the umbilicus, but in some shells they lie at the same level. Umbilical groove smooth.

Colour. Shelly substance white but the overlying periostracum imparts a pale horn colour and a darker brown to the lips. Most shells have 4 orange-brown bands on the body whorl, 2 above the periphery, 2 below, the lower pair entering the aperture. In some shells 2 bands may fuse to give a total of 3, or the pairs may fuse to give 2 broader bands; in others all join giving a brown shell. The bands are variable in breadth, that nearest the periphery usually broadest. The apex of the shell is generally a homogeneous purplish brown. In some shells the pigment bands are very pale or absent.

Size. Up to 10×5 mm. Body whorl = 82–88% of total height; aperture = 55–60% of total height.

Animal. Head with long, broad and tapering snout ending in a disk with the mouth at its centre. When closed the mouth is a more or less transverse slit with mid-ventral extension. At the base of the snout are long, tapering tentacles each with an eye on a lateral bulge. Males have a penis attached to the floor of the mantle cavity below and behind the right eye and normally extending to a narrower tip at the inner end of the cavity. Mantle edge simple and smooth.

Foot elongated, the anterior end rather straight with a double edge, the sole with a median posterior furrow, the posterior end rounded. From the hinder margin of the metapodium a short, flattened tentacle projects on each side from under the operculum. Operculum horny, thin, of 2–3 turns, rapidly expanding, the nucleus on the columellar side.

Colour. Pale yellow, sometimes with a pink tinge. Sides of the foot shaded grey, its sole pale.

Geographical distribution. A northern species which extends S. from Arctic seas — in Europe as far as the Channel and Atlantic coasts of France (where it is rare); as far as Rhode Island on the American Atlantic coast, and to California in the Pacific. It occurs on all British and Irish coasts, on those of Norway, West Sweden, in the Kattegat, Limfjord, Isefjord, the Sound, the most western parts of the Baltic; at Heligoland, but it is otherwise rare on the eastern shores of the N. Sea.

Habitat. *L. vincta* is found on shores where there is sufficient growth of fucoids, red weeds or *Zostera* to sustain it and where there is considerable turbulence in the water, though it avoids the greatest degrees of exposure. It is most common on shores where weeds flourish and on softer bottoms with much *Zostera*. On the former it is most abundant on *Fucus serratus*, laminarians, *Lomentaria*, *Rhodymenia palmata*, *Gigartina stellata*, *Chondrus crispus*, *Laurencia* spp., but occurs occasionally on bare rock and in pools, disliking silt. In more sheltered areas it is found crawling on the fronds of the weeds, elsewhere it is more likely in holdfasts. Between tidemarks the animals do not go much higher than LWST (20% emersion), but they extend sublittorally to 40 m round Britain and to 60 m further north. They can withstand salinities reduced to 20‰ and may perhaps live best at about 25‰ (Fralick, Turgeon & Mathieson, 1974). They may be very dense: Rusanova (1963) recorded 1170 animals on one plant of *Rhodymenia palmata*.

Food. Mainly the weeds on which they live, both fresh and in decay, but some diatoms and detritus are always ingested; the younger animals eat only these until powerful enough to eat weeds. Faeces ovoid pellets $50 \times 20 \mu\text{m}$.

Breeding and growth. The most important recent papers are by Hagerman (1966), Fretter (1972), Smith (1973), Rasmussen (1973), Manly (1975), Grahame (1977) and Fretter & Manly (1977). Earlier observations were made by Hertling & Ankel (1927), Hertling (1928) and Lebour (1937).

The sexes are separate, males being distinguished by the penis, and the sex ratio appears to be 50♂: 50♀ at the beginning of the breeding season. Russell-Hunter & McMahon (1975) found that it changed from this near Woods Hole to 60♂: 40♀ in May and 70♂: 30♀ in June and the former figure is quoted by Warburton (1974) for May at Cullercoats. The breeding season is long in lower latitudes — January to October, low in January, February (Isefjord); March—August (the Sound); January to May (Plymouth) or June (N.E. England, Heligoland), low early, rising to a May—June maximum — but perhaps shorter in higher latitudes, March, June—July or August in the White Sea (Kuznetsov, 1963; Mileikovsky, 1960, 1970). The eggs are white or yellow, each 94–125 μm in diameter, and float singly in an albumen-filled capsule 170–180 μm in diameter. Between 1000 and 1500 capsules are deposited in a clear mass of jelly attached to weeds, mainly *Fucus serratus*, *Laminaria*, various reds and *Zostera*. Each spawn mass is a cylinder about 1.75 mm in diameter coiled in a ring or short spiral, the ends just overlapping, the whole measuring about 3 mm across. The jelly, initially firm, swells by uptake of water to a diameter of 5–6 mm, softens and in 2–3 weeks the young hatch as free-swimming veligers. During the breeding period each female lays several masses of spawn. Smith calculated, on field observations, that, on average, a female laid 13.4 masses during the last 4 weeks of her breeding, containing a total of 16 163 eggs; Grahame estimated on observations made in aquaria that the total mean number of eggs laid by a female was 53 432. According to Mileikovsky (1970) there is a lunar periodicity in the spawning of animals in the White Sea, not observed in N.E. England.

The veliger has been figured by Hertling (1931), Thorson (1946), Fretter & Pilkington (1970), Fretter (1972). At hatching the shell has 1.5 whorls lying nearly on one plane, is transparent, colourless, its surface marked with many small elevations locally arranged in spiral lines. The aperture has a median beak. The shell measures 200 μm in breadth and height. The velum is bilobed and reddish pigment develops at its margin and later in the foot. The larvae spend a long time (2–3 months) in the plankton during which the shell grows to 2.5 whorls with a diameter about 500 μm , height 2–3 mm, loses the apertural beak and is marked only by growth lines. At this stage the larvae normally settle on algae and metamorphose, but if they fail to find a suitable site they have the power of staying in the plankton and may reach a shell size of 800 μm (Fretter & Shale, 1973). Larvae are common in the plankton off Plymouth February–May; in the Sound April–July (Thorson, 1946) and in the White Sea June–September (Mileikovsky, 1970).

In N.E. England the smallest specimens found by Smith (1973) were nearly 3 mm in shell height. They added 0.83 mm to this each month, but when old enough to spawn (6 mm height, 5–6 months from settling) growth dropped to 0.11 mm per month. All had died within 12 months. As breeding occurred over an extended period this population consisted of several cohorts. In Plymouth populations, on the other hand, Manly (1975) found no evidence of cohorts. Large numbers of recently-settled animals (0.4–1.0 mm shell height) were seen in June and some settlement persisted until September. Growth was much slower than in the N. Sea at only 0.4 mm increased height per month. Rusanova (1963) suggested that the maximum span of life of White Sea animals might be 6 years. Hagerman (1966) working on a population in the Sound found 3 year classes, the first,

probably aged 2, with an average shell height of 6.5 mm, the second, 1 year old, with a shell height of 2–4 mm whilst the third was composed of newly-settled animals.

Notes. *L. vincta* is one of the commonest prosobranchs of rocky shores rich in sea-weeds. It is near its southern limit in the Channel as it becomes rare in France. Northwards, however, densities increase and Smith (1973) recorded 313 m⁻² at Whitburn (Tyne and Wear). Hagerman (1966) found them most abundant in the Sound in December when they had a frequency of 1.3 animal per g of weed, and least abundant in May at 0.34 animals per g weed. The animals are greedy vegetarians and, when abundant, may destroy weed beds: Fralick, Turgeon & Mathieson (1974) recorded the reduction of a bed of *Laminaria* to holdfasts and stipes by a population numbering 277 per plant. They ate the lamina at a rate of 0.326 cm² per snail per day. Burke & Mann (1974) have calculated that *L. vincta* produces 0.06 g m⁻² yr⁻¹ in an estuary in E. Canada. Warburton (1974) showed that at Cullercoats the colour morphs occurred throughout most of the life cycle with the frequency 4-banded > 2-banded > brown > 3-banded > unbanded cream. They did not vary significantly from one weed to another. According to McMahon & Russell-Hunter (1974) *L. vincta* does not show an oxygen debt after a period of oxygen deficiency. Heat death occurred at 35°C.

LACUNA CRASSIOR (Montagu, 1803), chink shell
Turbo crassior Montagu, 1803
Lacuna glacialis Möller, 1842

Crassior (Lat.), thicker, heavier (than other lacunids) in its shell periostracum.

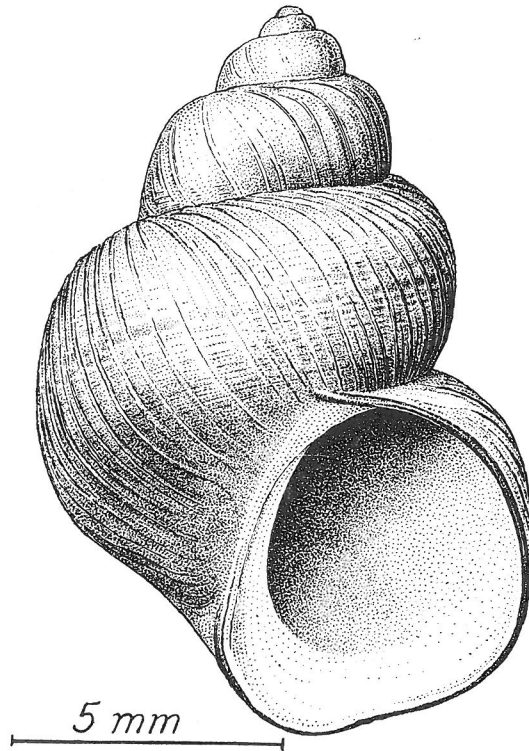


Fig. 198. *Lacuna crassior* (Montagu). Weymouth. BMNH 1911.10.26 18600–18606.

Shell. A more robust shell than *vincta* with a much thicker periostracum. There are 6–7 whorls meeting at deep sutures placed below the periphery of the upper whorls and so producing a rather

high spire. The whorls are tumid, each a little flattened subsuturally so that the profile of the spire is rather stepped. The ornamentation is as in *vincta* though the spiral ridges and grooves are often rather prominent in the peripheral region of the body whorl. The epidermis usually displays a series of prosocline ridges. Umbilicus often closed and the groove leading to it reduced, but if it is present it is as in *vincta*.

Protoconch of c. 2 whorls, up to nearly 1 mm across, mainly smooth, but showing some spiral lines.

Aperture. Rather large, prosocline, with a peristome. The outer lip arises below the periphery of the body whorl and runs at first nearly at right angles to the shell axis. It is slightly angulated at the outer end of its base; at the columellar end it is distinctly everted to form a spout rather like that of *parva*. From this point the apparent outer lip curves to the umbilical region and meets the inner lip running abapically from the origin of the outer lip.

Colour. Yellow with a brownish tint.

Size. Up to 14 × 10 mm. Body whorl = 75% of shell height; aperture = 45—50% of shell height.

Animal. As in *vincta*. Cephalic tentacles long and slender, metapodial tentacles not much flattened.

Colour. Pale yellow, darker dorsally and darkest on the dorsal surface of the snout; metapodial tentacles white.

Geographical distribution. Arctic seas, extending S. In Europe it has been described as a separate species only from British coasts, but see below. It has been recorded from Greenland and various parts of Arctic Canada and Alaska.

Habitat. Usually stated to occur on soft bottoms in which there are stones and old shells at LWST and sublittorally to 90 m.

Food. Unknown, but presumably a vegetarian or detritivore.

Breeding and growth. Unknown.

Notes. *L. crassior* is an uncommon animal and has not been recorded from most British shores. Earlier reports seemed to confine it to some areas on the east coast from Scarborough northwards but recently we have seen specimens from Dorset (courtesy of Mr D. R. Seaward) and from Milford Haven and the Celtic Sea (courtesy of Dr J. Hartley); it may therefore be widespread. The habitats ascribed to it are very different from those associated with other species of the genus, which are rarely found away from weeds, though they are commoner on softer bottoms in the sublittoral parts of their range, with which the habitat of *crassior* is more strictly comparable. Some observations made by Dr Hartley suggest an association with *Alcyonidium gelatinosum* though examination of stomach contents and faecal pellets suggests that the snails may be eating detritus on the surface rather than the bryozoan itself.

Hubendick & Warén (1976) give *L. crassior* as a synonym of *L. vincta*. The differences in size, periostracum, aperture and habitat, however, suggest to us that it is a distinct taxon.

LACUNA PARVA (da Costa, 1778), chink shell

Cochlea parva da Costa, 1778

Lacuna puteolus (Turton, 1819)

Parva (Lat.), small.

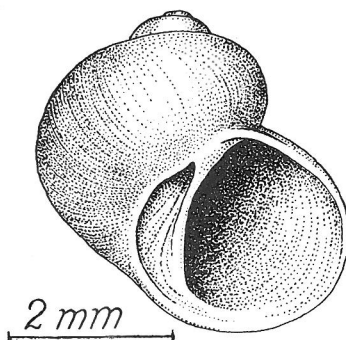


Fig. 199. *Lacuna parva* (da Costa). 5.5 km ENE of Agernæs, Funen, 23 m; Thor station 1650.

Shell. Rather delicate, glossy under the periostracum. There are 3 rapidly expanding tumid whorls meeting at deep sutures placed a little above the broadest part of the upper whorl. Spire low, with a blunt apex (apical angle $110-115^\circ$), the body whorl large. The subsutural part of each whorl forms a flat shelf and the body whorl is often angulated just below the periphery. Ornament as in *vincta*. Protoconch of 1.5 whorls usually distinctly marked off from the teloconch, its diameter $650-850\ \mu\text{m}$; the initial swelling is smooth, the rest has the same surface as the teloconch.

Aperture. The shape varies in the two sexes. In males it is rounded, about as wide as high, the outer lip not much out-turned basally; in females it is appreciably higher than broad and the basal part of the outer lip is turned out to form a spout. The outer lip leaves the peripheral region of the body whorl, runs round to the base of the columella and curves adapically forming the abapertural edge of the umbilical groove and umbilicus. The inner lip is as in *vincta* but always clearly overlies the apparent outer lip at the umbilicus. Umbilical groove broad and marked with longitudinal ridges and grooves.

Colour. Shell creamy white but the periostracum imparts a deep horn colour. Spire often with a lilac tinge. Peristome often dark at the edge. Danish specimens may be pinkish brown, matching the red weeds they live on.

Size. $4 \times 4\ \text{mm}$. Body whorl = 90% of total height; aperture = 70% of total height.

Animal. As in *vincta*.

Colour. Yellowish white in general; mantle skirt and head often slightly pink; tentacles white; sides of the foot shaded grey, sole pale with whiter edge.



Fig. 200. *Lacuna parva*. Spawn on the weeds *Delesseria* and *Phyllophora*, \times about 7. Drawing by Kai Olsen.

Geographical distribution. A more southern species than *vincta* extending, in Europe, south from the Arctic to Spain; in America to Cape Cod. On all British and Irish coasts; on those of Norway and West Sweden and in the Kattegat. Records for Danish waters are few but include Isefjord.

Habitat. As for *vincta*, but also on *Fucus vesiculosus*. Off Helsingor they are found on *Delesseria* and *Phyllophora*.

Food. As for *vincta*.

Breeding and growth. The sexes are separate and the animals may be sexed by the shell as well as by the penis of the male. Thorson (unpublished) has shown that off Helsingor the snails lay semitransparent hemispherical spawn masses on red weed, preferably *Phyllophora*. Each mass contains about ten white eggs which hatch to crawling juveniles. The mass measures c. 2×2 mm, each egg c. $200 \mu\text{m}$. It is likely that this method of reproduction is generally true since Lebour (1937) stated that spawn, similar to but different from that of *vincta* had been found at Plymouth. There are no studies on growth.

LACUNA PALLIDULA (da Costa, 1778), chink shell

Nerita pallidula da Costa, 1778

Lacuna patula Thorpe, 1844

Pallidula (Lat.), pallid, referring to the colour of the shell and animal.

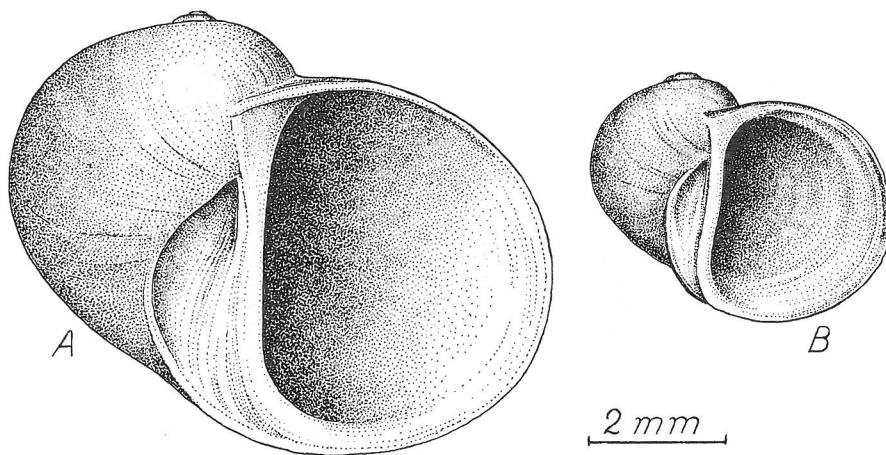


Fig. 201. *Lacuna pallidula* (da Costa). A, female; B, male. No locality given.

Shell. Delicate, glossy under a periostracum. There are 3—4 rapidly expanding whorls, the body whorl composing most of the shell; they meet at slightly excavated sutures. The spire is extremely short, with a low apex (apical angle about 150°). In some shells the peripheral region of the body whorl is a little flattened and its subsutural part a little depressed or insunk. Ornament as in *vincta* though the spiral ridges and grooves are rarely visible except on the base of the body whorl. The umbilicus is deep, showing much of the inner surface of the spire, and the umbilical groove bears numerous ridges; in the variety *patula* the umbilicus and the groove leading to it are much reduced. Protoconch of 1.5 whorls, diameter about $500 \mu\text{m}$, initially smooth and gradually developing the adult surface markings. There is usually some disturbance coinciding with hatching.

Aperture. Very large. In general as in *parva* but the umbilical groove is relatively broader and the umbilicus itself more open. In the shell of males the umbilical groove is relatively wider than in female shells.

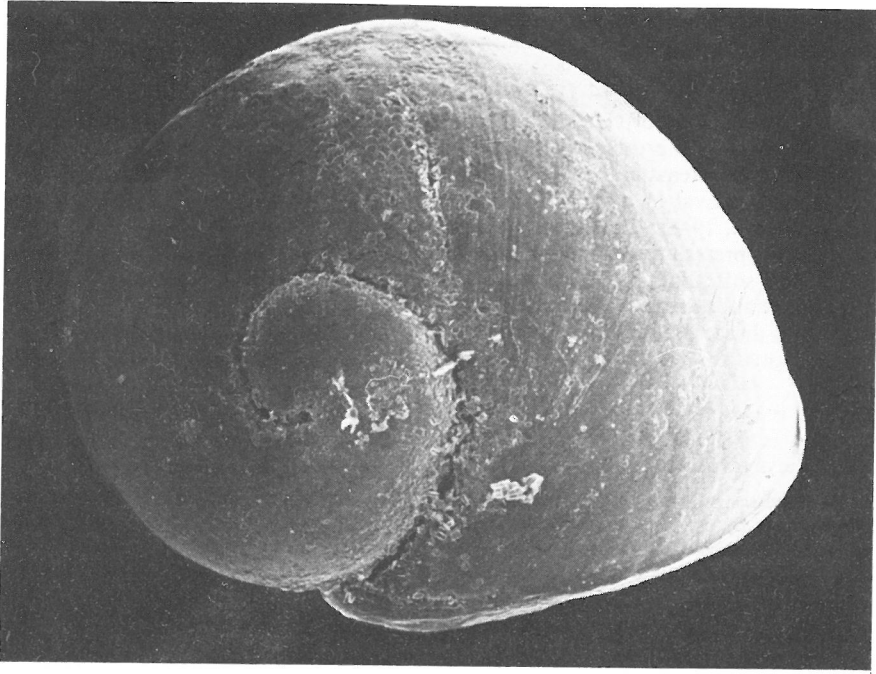


Fig. 202. *Lacuna pallidula*. Apex of shell $\times 90$. SEM photograph. Plymouth. RUZ.

Colour. Yellowish green to green; sometimes nearly white.

Size. There is a clear sexual dimorphism; females reach 12×6 mm, males 6×3 mm, though usually both are appreciably less. In both body whorl = 97% of total height; aperture = 80–88% of total height.

Animal. As in *vincta*.

Colour. Nearly white, sides of the foot shaded with grey.

Geographical distribution. A northern species extending S. from Arctic latitudes to the Atlantic coast of France in Europe; from Greenland to Connecticut in America. It is found on all British and Irish coasts, on the coast of Norway and W. Sweden, in the Kattegat, Limfjord, Isefjord and western parts of the Baltic.

Habitat. Like *vincta* this species is associated with many weeds but is most commonly found on *Fucus serratus*, less abundantly on *F. vesiculosus* and *Laminaria* and it is rare on *Zostera*. In the southern part of its range it is more abundant on red weeds. It occurs on the same type of shore and at the same levels as *vincta*, extending sublittorally to about 70 m.

Food. The weeds on which it lives. Faeces oval pellets 70×30 μ m.

Breeding and growth. The sexes are separate and show considerable difference in shell size (Gallien & Larambergue, 1936, 1938). Smith (1973) and Grahame (1977) both recorded sex ratios of 3 males to 1 female in N.E. England whereas Rasmussen (1973), working in Isefjord, found 41.2%♂ and 58.8%♀ in September, 16.4%♂ and 83.6%♀ in November and said that males were rare in January and early spring. Copulation occurs over a long period (November–April, N.E. England), males at the beginning of this time often fertilizing females that will not be mature until the following spring. Spawn is deposited January–May. In the White Sea (Kuznetsov, 1963) spawn may be found every month of the year except October.

The eggs are lemon yellow in colour, each lying in albumen in a capsule, the capsules aggregated in a slimy fluid to form a spawn mass which is attached to the weed on which the females are living. Dimensions of all these items vary from place to place — eggs: 254–276 μ m (Wimereux), 263–269 (Robin Hood's Bay), 250–297 (Whitburn), 270–300 (the Sound), 270–280 (Isefjord); capsules:

571 μm (Wimereux), 400 (Plymouth), 531—563 (Whitburn), 670 (the Sound), 900 (Isefjord); spawn mass: $3.9\text{--}5.3 \times 3.5\text{--}4.5$ mm (Heligoland), 4.5×3.5 (Whitburn), 3.9 (the Sound), 5.0 max. (Isefjord); number of capsules per spawn mass: 110—125 (Wimereux), 60—150 (Heligoland), 52—105 (Robin Hood's Bay), 15—113 (Whitburn), 35—75 (the Sound), 9—60 (Isefjord). These figures suggest the existence of clines in capsule size and number from S.W. to N.E. Smith (1973) estimated that each female produced a total of 700 eggs (= 6—46 spawn masses); Grahame (1977) suggested 1365 eggs per female.

The spawn mass is oval or circular in outline, not kidney-shaped, and rather like an inverted watch-glass (Thorson, 1946). The capsules lie in more or less concentric rings, 1 layer deep at the margin, 2 centrally, pressed together so that they have angular outlines. The jelly in the centre of the mass tends to be soft though the outermost layer is firm. There is no marginal rim of jelly. Attachment to the substratum is firm and the spawn is not easily removed from it. See also p. 261.

Development is direct and rather slow and Polyanski (1965) has shown that it continues even when the eggs are exposed to temperatures of -15°C on the Murmansk coast. Small snails hatched at Whitburn in 8.5—14 weeks with a shell about 0.7 mm in diameter. They grow at a rate of 0.9—1.0 mm per month; in males this drops to nearly zero after 5—6 months, but the females grow for nearly as long again so as to double the size of the males. Males die after copulating, females, on average, 2 months after they start to spawn. All are dead 10—12 months after hatching.

Notes on Lacuna species. The genus *Lacuna* is characterized by a groove leading to the umbilicus which is described as bounded by the outer lip on the abapertural side and by the inner lip on the other; the two lips are said not to meet. The organization of this area of the shell may be clarified by examination of very young specimens. In the youngest of these it is seen that the edge of the aperture curves apically on the apertural side of the umbilicus and that a shallow groove runs from the base of the shell to that opening. In older shells a ridge

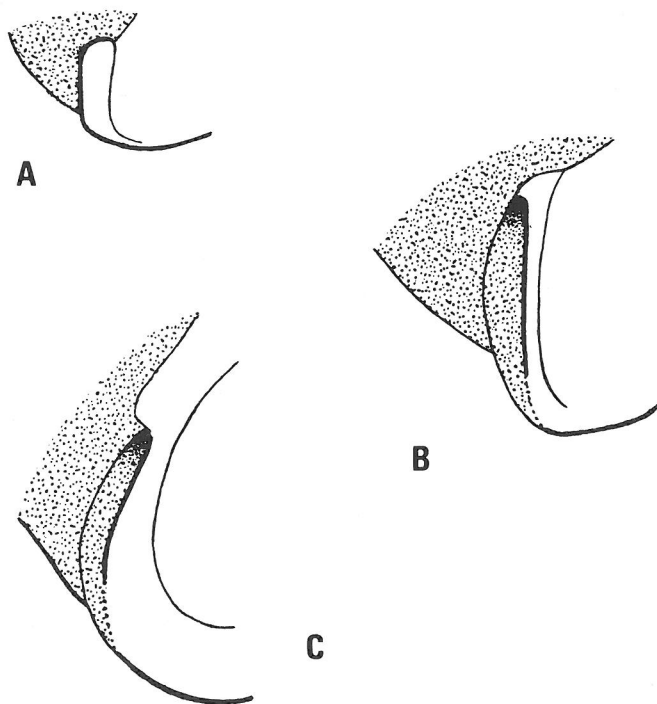


Fig. 203. Diagrams of columellar region of lacunid shell to show development of slit-like umbilicus. A, newly-settled animal, with minute umbilicus and normal columellar lip; B, older, with well-formed umbilicus and ridge from angulated base of aperture forming its abapertural edge; C, mature, with outer lip apparently confluent with this ridge and seeming to have lost its connexion with the columellar lip. The stippled area bears periostracum.

develops from an angulated point on the apertural edge where outer and inner lips meet; as the shell grows this ridge becomes more and more prominent and forms the abapertural edge of the groove leading to the umbilicus; the outer lip and this ridge appear continuous. The true edge of the aperture (the adapertural edge of the umbilical groove, formed from the inner lip) becomes less marked and ultimately seems to form a ridge within the apertural edge. The junction and continuity of inner and outer lips, however, can invariably be observed and the groove leading to the umbilicus equally clearly shown to lie morphologically external to the aperture by the fact that it is covered with periostracum and that its abapertural boundary runs into the umbilicus.

There is doubt about the N.W. European species of the genus. Most texts describe the four dealt with here. Whether these are all good species is not, however, clear. Ankel (1936) suggested that further work was necessary to show that *parva* and *pallidula* were distinct and Hubendick & Warén (1976) list *crassior* as a synonym of *vincta*. The first point may well have been cleared up by Thorson's demonstration of direct development in *parva*. The second calls for careful examination of series of *L. crassior*, though further knowledge of its mode of life and reproductive activities would also help.

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LITTORINIDAE Gray, 1840
LITTORINA LITTOREA (Linnaeus, 1758), edible wrinkle or periwinkle
Turbo littoreus Linnaeus, 1758

Littorina and *littorea* are both based on the Latin *litus*, *litoris*, a shore, and emphasize the animals' predominantly littoral habitat.

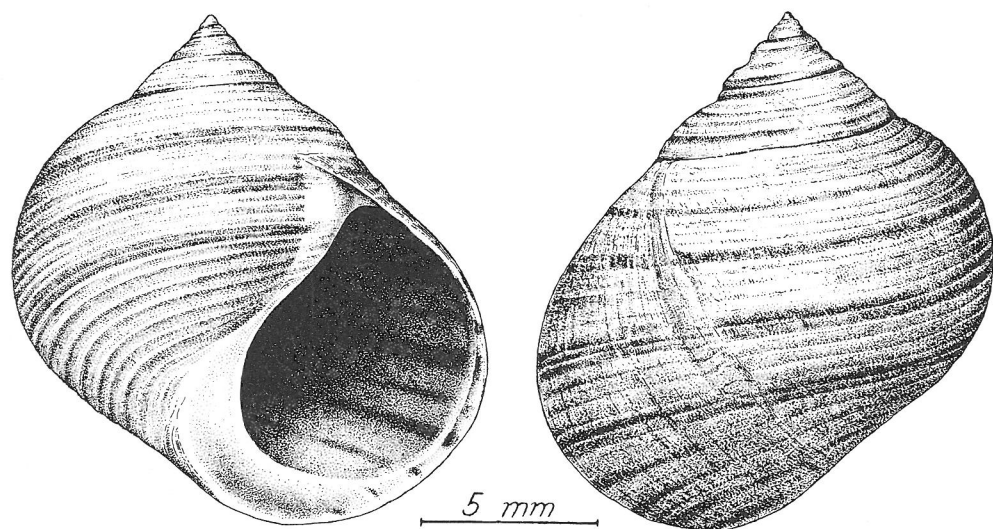


Fig. 204. *Littorina littorea* (Linnaeus). No locality given.

Shell. Solid and opaque, not glossy. The spire is rather prominent and pointed (apical angle c. 85° in young shells dropping to 65° in older), cyrtconoid in profile, occasionally coeloconoid towards the apex. There are 5—6 whorls, very slightly tumid, meeting at sutures lying about the periphery of the upper whorl. They are slight, barely excavated. The body whorl is flattened or concave below the suture, particularly near the aperture. The ornament comprises growth lines and spiral ridges and grooves. The growth lines are markedly prosocline, making an angle of about 120° with the axis of the spire; they are irregular in development, sometimes making the suture lines erratic. Spiral ridges and grooves are slight and numerous. In grown shells they are usually worn on the spire and most obvious towards the base; in young ones they are distinct on all whorls. Major and minor ridges and grooves occur. The former are strap-shaped on younger whorls, sharper on older ones and usually broader than the intervening furrows except on the base. The minor ridges lie c. $100\ \mu\text{m}$ apart and cover the whole shell, though commonly worn away on the major ridges. Growth lines and spirals together form a fine reticulation not visible to the naked eye. The protoconch consists of 2+ whorls, diameter up to $500\ \mu\text{m}$, unsculptured.

Aperture. Oval, angulated above, lying in a prosocline plane, with a peristome. The outer lip arises at the periphery of the body whorl, more or less tangentially, at an angle of $125\text{—}130^\circ$ to the axis of the spire.

Its first part is often concave, its next continues the outline of the spire to the periphery of the body whorl where it curves to the base of the columella, its edge sharp and (in young shells) crenulated by the ends of the spiral ridges and grooves. The columella is short and leans a little to the left. The inner lip turns out over this region and is thick, completely obscuring any umbilical groove. Over the body whorl it forms a glaze extending some way beyond the origin of the outer lip and separated from it by a groove. The throat of young shells is fluted by spiral ridges and grooves but in

older shells it becomes constricted by shelly material so that this is lost; a low ridge often lies within the outer lip.

Colour. Black, brown-black, brown, grey, orange, white; the older whorls of dark shells often eroded to a light fawn or ash colour. Spiral ridges are often darker than the grooves. The outer lip has an internal band of blue- or brown-black, alternately lighter and darker in shells with well-marked spiral bands of colour. Columella white; throat a diluted version of the external colour in young shells, white (sometimes with a persistent trace of brown) in old ones.

Size. To 32×25 mm. Body whorl = 80–85% of total height; aperture = 60–70% of total height.

Animal. The head bears a broad, slightly tapered snout, truncated distally, the mouth placed terminally and a little ventrally. It has, closed, the shape of an inverted U and the lip round it is split mid-ventrally where it projects inwards. The cephalic tentacles are a little flattened when contracted, each with an eye on a lateral bulge at the base. In the mantle cavity, on the left, lie a linear osphradium and a long gill; on the right, females show a closed, glandular oviduct and, on the side of the head, an ovipositor, whereas in males there is an open prostate gland and (during the breeding season) a penis. The ovipositor is a broad, glandular field, its edges slightly raised, placed behind and below the origin of the right tentacle; the penis, in a corresponding position, is sickle-shaped and tapers abruptly distally to a rather long point. Its posterior (right) edge carries a deep seminal groove arising in the prostate, its anterior face bears 16–36 glandular papillae in several rows.

The foot is elongated and shield-shaped, truncated anteriorly where it has a double edge, and with a rounded point posteriorly. The operculum has a nucleus displaced to the columellar side and shows 2–3 turns.

Colour. The ground colour is yellowish. There are numerous black streaks on the head and sides of the foot. The tentacles have a mid-dorsal black line and many transverse black stripes. The penis and ovipositor are either not, or only a little, pigmented. The operculum is chestnut.

Geographical distribution. *L. littorea* is widespread on European shores from N. Spain to the White Sea; it also occurs in Greenland and from Labrador to New Jersey — Maryland. It occurs on all British and Danish coasts and extends into the Baltic as far as Bornholm. It is rare (or absent) in the Isles of Scilly.

Habitat. Edible winkles are typically inhabitants of all rocky shores (except the most exposed) with a stable substratum. They also occur in considerable numbers on the surface of wet mud, less frequently of sand, where solid objects allow firm attachment. At low water the animals may be found exposed on rock, under weed and in pools. They also occur sublittorally to depths of c. 60 m, more especially in the north. The levels on the shore at which they live vary from place to place depending on exposure, weed cover and other factors. On most shores the population centres on MLWNT (about 30–40% emersion) but rises on exposed shores and falls on sheltered ones. On the former the upper limit may lie about HWST or, in extreme cases, as in St. Kilda (Waterston & Taylor, 1906), much higher; on the latter it may be about MLWNT. They become rare towards LWST, but in high latitudes may be found in sublittoral areas. Winkles can live in brackish water as in the western Baltic, down to $S = 9-10\text{‰}$ (Jaekel, 1952a). The animals are rather resistant to pollution.

Food and feeding. *L. littorea* is a herbivore, feeding on diatoms, algal sporelings, vegetable detritus, less commonly on larger weeds; it may also on occasion take animal detritus, but there is no basis for Jaekel's remark (1952b) that it eats barnacles, though it may rasp the shells for epiphytes. Ankel (1937) described the feeding process. Newell, Pye & Ahsanullah (1971) showed how increased rate of radular action compensated for the shorter feeding time available to animals living high on the shore. Faecal pellets are ovoid, $300 \times 100 \mu\text{m}$.

Breeding and growth. The sexes are separate, the males recognizable during the breeding season by the penis, the females by the ovipositor; the male gonad is yellow-grey, the female rose-violet. The sex ratio is usually 1:1, though there may be a slight excess of females in those with shells > 25 mm (Pelseeneer, 1926; Moore, 1936; Daguzan, 1976b). Males are said by most authors (Tattersall, 1920; Moore, 1937; Williams, 1964; Fish, 1972) to mature earlier and at a smaller size than females, but Daguzan (1976b) reported the reverse for a population on the S. coast of Brittany. Maturity occurs at 12 mths in Ireland (Tattersall, 1920); 11–12 mths in the Dovey estuary, Wales (Fish, 1972); 18 mths, second winter, at shell height 11–12 mm, in Cardigan Bay (Williams, 1964); 18 mths on the Normandy coast (Cousin, 1975); 16 mths, ♀, shell height 10.6 mm, 18 mths, ♂, shell height 11.4 mm, in southern Brittany (Daguzan, 1976b).

It seems possible for breeding to occur throughout the year as egg capsules were reported continuously in plankton off Whitstable (Smith & Newell, 1955). More commonly, however, it is interrupted by cold in the early part of the year and by exhaustion in summer—autumn. This would explain the periods given by Rasmussen (1973) for Isefjord (Dec, Feb—Jun, maximum Apr—Jun), Moore (1937) for Plymouth, Caullery & Pelseener (1910) for Wimereux, Tattersall (1920) for Ireland and Elmhirst (1923) for the Firth of Clyde (all Jan—Jun, max. Feb—May), by Grahame (1975) for Anglesey and the Menai Straits (Jan—Sep, max. Mar—Apr). More restricted periods are reported by Hayes (1929) for the Bay of Fundy (Apr—Jun), Linke (1933) for Heligoland (Mar—May), Williams (1964) and Fish (1972) for Cardigan Bay (Feb—Apr, max. Mar), Thorson (1946) for the Sound (Jun—Aug) and April—July in the White Sea (Kuznetsov, 1960; Rusanova, 1963), but most of these have a more severe climate. Unusually, Daguzan (1976b) found that winkles at Penvins (Morbihan, France) bred Oct—Apr. Fish (1972) reported that in the brackish waters of the Dovey estuary breeding had a January maximum, 1—2 mths earlier than on the open coast nearby. This would agree with Rasmussen's records from Isefjord. Breeding seems possible at temperatures of 1°C or higher.

Copulation is normally at high water at night (Tattersall, 1920; Grahame, 1975) and the female starts laying 1—2 h later, 1—5 eggs (occasionally up to 9) being laid in a lens-shaped capsule with equatorial rim. The eggs are colourless, 130—200 µm in diameter, and the capsule measures about 1.0 mm across and 0.4 mm high. Each egg lies in albumen, separated from surrounding jelly by a membrane; the jelly is in turn enclosed in a tough skin secreted by the ovipositor. Capsules are slightly denser than sea water so sink slowly, those with most eggs most rapidly, but whether this occurs in nature as distinct from an aquarium is doubtful. Each female lays about 500 capsules at a time and may have up to ten periods of laying giving a total annual output of 5000 capsules (Daguzan, 1976b). Grahame (1973b) calculated that a female, with shell 27 mm high, produced 109×10^3 eggs a year; if all are laid this would seem to require a larger number of capsules or more eggs per capsule than Daguzan's figures suggest. According to Smith & Newell (1955), Mileikovsky (1970), Fish (1979) and Alifirakis & Berry (1980) spawning has a lunar periodicity.

The capsules swell osmotically and burst after 5—6 days liberating veliger larvae which swim in the plankton for 4—5 weeks (Linke, 1933; Smith & Newell, 1955) or 6—7 weeks according to Williams (1964). At hatching the larva has a shell of 1.5 whorls, diameter about 250 µm, transparent, colourless, though becoming horn-coloured later, and unsculptured (Fretter & Pilkington, 1971). It has no apertural beak at any stage. The larva is recognizable by the semilunar areas of black-purple at the edges and anterior ends of the velar lobes and by the colourless foot. Metamorphosis occurs when the shell has 2+ whorls and a diameter approaching 500 µm. There are differing accounts as to where young winkles settle. Smith & Newell (1955), describing a population at Whitstable, found only 2 shells with a height of 2.5 mm among over 12×10^3 collected, and argued that settlement was sublittoral and that juveniles later migrated, or were rolled by waves, up the beach and Daguzan (1976b) gives support to this on the basis of a population he studied. Most accounts, however, describe settlements as intertidal, especially in cracks, amongst barnacles and in their empty shells. The timing of this is given as: April at Millport (Elmhirst, 1923); June at Plymouth (Moore, 1937); Jun—Aug in Cardigan Bay (Williams, 1964; Fish, 1972) though earlier (Feb—Mar) in the Dovey estuary; Jan—Jun in Nova Scotia (Lambert & Farley, 1968). The density of juveniles with shells < 2.5 mm high may be 4000 m^{-2} (Williams, 1964) and those up to 9 mm high (age 14 mths) always form half to three fourths of a population (Daguzan, 1976b). After settlement growth occurs at a rate of 1—2 mm per month (Cousin, 1975; Manly, 1975), varying from 0.4—1.1 mm per month in autumn—winter to 0.7—2.9 in spring. The growth rate decreases rapidly with age and its absolute rate is partly a function of the habitat. Some figures are as follows:

yr 1 8—9 mm high (Williams, 1964);	9—10 mm (Cousin, 1975);	14 mm (Moore, 1936)
yr 2 13—14	15—16	17.4
yr 3 15.5—16.5	16+	22.4
yr 4 17.5+	—	25.4

Large specimens (recorded up to 38 mm) must be many years older, the oldest known (from an aquarium) being nearly 20 years (Woodward, 1913). Exposure always increases mortality rates and the oldest winkles are invariably found on sheltered shores (Daguzan, 1976b).

Notes. The edible winkle is probably the commonest large intertidal monotocardian prosobranch of the area dealt with and has attracted many malacologists to work on it. Adult animals are active when the tide leaves

them exposed and continue to move and feed until the shore dries, when they shelter in pools, under stones or weed, often in large groups. Dinter & Manos (1972) thought that these resulted from the production of a pheromone, but the aggregations are most likely to be chance assemblages of snails seeking similar conditions. Juvenile winkles do not feed when exposed but seek immediate shelter. Adults attach to rock by a film of mucus on the lips of the aperture (Wilson, 1929) hanging shell apex downwards (Haseman, 1911): they can survive thus for about 3 weeks (Thamdrup, 1935). This may relate to their lower respiratory rate in water ($49.4 \mu\text{g l}^{-1}\text{h}^{-1}$) than in air ($117.4 \mu\text{g l}^{-1}\text{h}^{-1}$) (Sandison, 1966; Toulmond, 1967; Newell & Pye, 1971). They are resistant to high temperatures, more so in air than in water, showing little change in their rate of oxygen usage over a wide range of temperature (Newell & Northcroft, 1967; McMahon & Russell-Hunter, 1973). Sandison (1967) reported heat coma at 32°C in air, 31° in water, and heat death at 42° in air, 40° in water for winkles from the Firth of Forth, and Evans (1948) gave 39° and 46° for those in Cardigan Bay. Populations are presumably acclimatized to local conditions in the same way that Gowanloch & Hayes (1926), Todd (1964), Arnold (1972) and Rosenberg & Rosenberg (1973) showed that they were adapted to local salinities. This is the more necessary since they seem to have little or no osmoregulatory powers (Mayes, 1960, 1962; Avens & Sleight, 1965). When the temperature falls below 8°C most winkles become inactive and must therefore spend part of the winter without feeding. Many appear to migrate down to the shore to avoid cold (Rusanova, 1963; Gendron, 1977) or, because unable to adhere to the substratum (Gowanloch & Hayes, 1926), are carried there by retreating tides. Underwood (1973) reported that a population at Heybrook Bay, Plymouth Sound, spent the period Sep—Jan under stones in deep pools at LWST level, dispersing over the beach in early Feb. If adults are displaced from their normal level on a beach they migrate so as to return to it; this is particularly true of those transferred to a higher level. Though they may react to bright light the main response leading to homing appears to be an orientation to the source of waves (Gendron, 1977). Newell (1958a, b) showed that phototaxes were involved in the feeding excursions made by winkles after emersion; these are normally U-shaped, the snail at first creeping seawards, then parallel to the shore-line, then turning upshore to return to its starting point. He also showed (1965) that the eye of *L. littorea* in air probably allowed some degree of form discrimination, though Land (1968) indicated that its acuity must be poor.

North (1954), working with *L. planaxis* in California, found that a snail living in a rock pool filled the gut 4—8 times each day, the food passing through in 2.5—6 h. Grahame (1973a) showed that *L. littorea*, fed on *Ulva*, ingested (g dry wt weed ingested as percentage of dry body wt) 1.27 ± 0.21 ; it assimilated 191.05 ± 33.1 J per g dry body wt, an efficiency of c. 82%. Though there is a cycle of digestive gland activity it is not related to the tidal rhythm (Merdsoy & Farley, 1973).

Though breeding males are recognizable by the penis this may not be possible at other times since Grahame (1970) reported its loss by necrosis of the attachment region; it reforms later, taking 6 months to reach full size. This loss may also result from parasitism. The initial formation and maintenance of a penis are stimulated by a hormone liberated from the right eye stalk, its regression by one from the pleuropedal ganglia (Streiff & Le Breton, 1970; Lubet, Streiff, Silberzahn & Drosowsky, 1973).

Jaekel's limiting salinity ($9-10^\circ/\text{‰}$) must be regarded as referring to a local Baltic group of winkles. The figures given by Arnold (1972) for Milford Haven, the Dauceddau and E. Canada suggest that effective movement among winkles there decreases markedly below $S = \text{about } 20^\circ/\text{‰}$, and Muus (1967) recorded *L. littorea* as a rarity in Danish fjords at $S = 10^\circ/\text{‰}$. There is some evidence to suggest that the animals are adapted to the salinity in which they are reared. The principal nitrogenous excretory substance appears to be uric acid (Daguzan, 1970, 1971; Daguzan & Razet, 1971), mainly liberated when the animals are covered after low tide.

L. littorea is the intermediate host of many trematodes (see James, 1968). Rees (1936) described their effect on the tissues of the winkle.

LITTORINA OBTUSATA (Linnaeus, 1758), flat winkle

Nerita obtusata Linnaeus, 1758

Littorina littoralis (Linnaeus, 1758) (part)

Littorina palliata Say, 1822

Littorina aestuarii Jeffreys, 1869

Obtusata (Lat.), blunt, referring to the shape of the spire.

Shell. Solid, opaque and not glossy. The spire is low, the body whorl making up most of the shell; the apex is very blunt, the apical angle being $128 \pm 6^\circ$ ($114-134^\circ$). In the spire there are 4—5 nearly flat-sided whorls; very little of the surface is visible since the sutures, which are shallow and slightly insunk, lie well above the periphery of the upper whorl. The body whorl is tumid, though there is a rather flattened peripheral zone. To the naked eye the shell appears smooth, but it bears numerous curved prosocline growth lines which are slightly less prosocline at the adapical suture and remain prosocline on the base of the shell. There are also innumerable fine spiral lines so that the surface is very finely reticulated. The protoconch bears the same ornament as the teloconch and in most shells no boundary between the two can be discerned.

Aperture. Oval or slightly squarish in shape, elongated and a little angulated apically, lying in a prosocline plane inclined at 135° to the shell axis. It is surrounded by a peristome showing a small anal sinus and a broad but shallow peripheral one. In fully grown shells the outer lip arises level with the apical end of the peripheral flattening of the body whorl, making an obtuse angle of $100\text{--}120^\circ$ with the axis of the spire. Its initial part is straight or slightly convex; it then curves, the radius of curvature shortening steadily so that it follows a nearly spiral course to the base. The edge of the lip is sharp, level with the outer surface of the shell, but it is bevelled internally and thickens rapidly. In some shells the base may be a little flattened. The columella is short, rounded and broad; the lip here spreads outwards and there is neither umbilical groove nor umbilicus. The inner lip forms a glaze over the body whorl. In juvenile shells the outer lip arises close to the suture between body and penult whorls and its initial direction is nearly at right angles to the axis of the shell. There is a small V-shaped anal sinus at its origin. It is not internally thickened and at the base of the shell is drawn out to form a slight spout.

Colour. Extremely variable, with several well-marked patterns described by Dautzenberg & Fischer (1914), and recently re-examined by Smith (1976). They are: *alternata*: brown with 2 yellow spiral bands on the body whorl; *aurantia*: uniform orange to red, purple throat; *citrina*: uniform yellow to orange, white throat; *fusca*: brown-black, no reticular markings; *inversicolor*: light or yellowish green, with 2 dark spiral bands on body whorl and sometimes also with reticular markings; *olivacea*: uniform light to dark green, sometimes greyish or brownish; *reticulata*: basic colour green, brown or nearly black, but always with reticulate pattern; *rubens*: uniform vermilion; *zonata*: brown-black with 1 light band at periphery of body whorl, with some reticulate patterning. White shells may also be found, primarily the result of erosion of the colour.

Size. Up to 15×17 mm. Body whorl = $92\text{--}96\%$ of total shell height; aperture = $75\text{--}80\%$ of shell height; breadth = $100\text{--}114\%$ of shell height. The aperture tends to be relatively larger in females.

Animal. In all essentials as in *littorea*. The penis is flat, has a short tip and is rather variable in size, but once present never regresses; it has (on average) 30 (range 16–53) glandular papillae in 2–3 rows.

Colour. Cream-yellow with black streaks which may be strongly or weakly developed, usually parallel to the degree of pigmentation of the shell. Thus in *aurantia*, *citrina* and *inversicolor* the body is pale but in dark shelled *olivacea*, *reticulata* and *zonata* is dark or quite black. In *olivacea* the background colour is greenish. The tentacles have 2 longitudinal dark stripes and the ovipositor is always pigmented in British, but not Danish animals.

Geographical distribution. From the W. Mediterranean to Tromsø N. Norway (Snell & Marion, 1970), across the Atlantic to Canada and south to New Jersey. It occurs on all Channel and N. Sea coasts and extends through the Kattegat to the Baltic as far as Lübecker Bucht.

Habitat. This abundant animal is invariably associated with weeds, especially *Fucus vesiculosus* and *Ascophyllum nodosum*, though it is also found on *F. serratus*, *Zostera* and laminarians. Juveniles are common on *Chondrus* and corallines. It occurs from about MHWN (80% emersion) to about MLWS (5–10% emersion) and occasionally sublittorally to about 5 m. At low tide it is particularly common hiding in clumps of *Ascophyllum* and *F. vesiculosus* growing along the margins of rock pools. It occurs on sheltered and exposed shores unless heavily wave-beaten and can live, though not perhaps breed, in salinities down to 10‰ . The animals may be abundant; Rusanova (1963) recorded 3750 m^{-2} of *F. vesiculosus* thallus, with biomass = 487.5 g m^{-2} .

Food. The weed on which it lives, fresh or decaying, together with encrusting diatoms. Faeces ovoid pellets c. $250 \times 100\text{ }\mu\text{m}$.

Breeding and growth. See papers by Peleneer (1926), Hertling & Ankel (1927), Hertling (1931), Linke (1934), Kuznetsov (1960, 1963), Rusanova (1963), Sacchi (1967), Guiterman (1970), Rasmussen (1973), Underwood (1973), Goodwin (1975), Daguzan (1976b), Goodwin & Fish (1977), Goodwin (1978, 1979).

The sexes are separate, males recognizable by the penis, females by the ovipositor, visible from the time that the shell reaches 7–8 mm high. Females tend to be slightly larger than males and, in general, slightly more numerous, the overall sex ratio ranging from 47.8 males: 52.2 females at Plymouth to 50.2: 49.8 at Finistère. Slightly more extreme figures have been recorded for some colour morphs — *citrina*, 40: 60; *olivacea*, 46.5: 53.5; *reticulata* 43.4: 56.6

Breeding seems to occur throughout the year in most places, with a decrease in summer (Anglesey, Cardigan Bay, Plymouth, Heligoland, Isefjord); in some more northerly latitudes the season is more

restricted (Jul—Aug in Denmark in general and Mar—Apr in the White Sea). It is preceded by a period of intense feeding. The eggs are laid in jelly masses (c. 7×3 mm) attached to damp fronds of weed, mainly fucaceans, occasionally on stones. The spawn masses are flat, usually oval, sometimes round or kidney-shaped in outline, colourless or slightly yellowish; they are deposited at night, at high tide, some hours after copulation. Within the spawn the numerous egg capsules lie rather loosely, not squashed together, so that their outline remains rounded; they lie 2—3 rows deep in the centre of the mass, 1 deep towards the margin where there is always a jelly zone devoid of capsules. The jelly is firm but usually only lightly attached to the substratum from which it may be fairly easily peeled. The mass contains a variable number of capsules, frequently about 100, but varying from 65—180. In colder localities the number drops. Each capsule (diameter 500—700 μ m) contains a single cream-coloured egg (diameter 210—250 μ m) enclosed with some albumen in an egg covering. The embryo passes through an intracapsular veliger stage and bites its way out after 3—4 weeks at 13—14°C, when the velum is degenerate or lost. The newly-hatched juvenile has a pale shell about 500 μ m in diameter, not distinguishable except by size, from that of larger animals.

The youngest winkles are not normally collected as they hide in crevices, presumably feeding on diatoms, small algae and detritus. They live in the same zone as their parents and there is no migration. When the shell height is 2.5—3 mm they may be found in tufts of smaller algae; older ones (shell height 4+ mm) shelter in fucaceans, the smallest in the centre of a bunch of fronds, the larger ones in the outer parts. In Cardigan Bay they have shells 4—5 mm high by early spring of the year after hatching, having grown at a rate averaging 88 μ m per week; over the summer they grow more rapidly and by autumn have nearly reached adult size (10 mm). The winkles reproduce the following spring at the age of nearly 2 years. How much longer they live depends on local circumstances. Goodwin suggested 2—3+ years for those in Cardigan Bay, Daguzan 4 years for those in Brittany, whilst Rusanova gave a maximum of 7 years as the life span of winkles living in the cold conditions of the White Sea.

Notes. Much information is given by Sacchi (1966, 1969, 1972), Smith (1976), Daguzan (1976b), Goodwin & Fish (1977), Goodwin (1978).

Until recently all flat winkles were regarded as falling into a very variable but single species for which the names *littoralis* and *obtusata* were both in use. Strictly *littoralis* referred to a more southern form, *obtusata* to a Scandinavian and *pallidula* was often used for arctic and American animals. Colman (1932) suggested that these intergraded and that the prior name was *obtusata*. In 1966, however, Sacchi & Rastelli showed that some of the variability was explained by the fact that two taxa had been confused, and described a new species *mariae*, leaving *obtusata* as the name for the residual part. Since most papers prior to 1966 were written without realization of this distinction they may contain observations of doubtful validity if they deal with features in which the two species differ. The differences between *obtusata* s.s., described above and *mariae* are dealt with under the latter species. *L. obtusata*, though common on fucaceans in general, is particularly associated with bladder wracks, the bladders of which it resembles in shape and often in colour. Van Dongen (1956) showed that the winkles were attracted to these plants by scent.

Smith (1976) investigated some ecological relationships of the colour morphs. In Britain *olivacea* is the commonest in most places, but less markedly so in the south and west where *citrina* and *reticulata* tend to replace it. The other morphs are relatively rare (in sum less than 2% of Smith's total of nearly 18 000 shells) and he found no specimens of *rubens*. The various morphs have associations with particular weeds and so with tidal levels: *citrina* occurs on *Fucus spiralis* in particular, *olivacea* with *F. vesiculosus* and *Ascophyllum nodosum* and *reticulata* with *A. nodosum* and *F. serratus*. *F. spiralis* is also preferred by *inversicolor*, *alternata* and *fusca*. These preferences correlate to some extent with resemblances between weed and shell colours. Other factors also affect the distribution of the morphs: *olivacea* occurs more frequently at higher tidal levels and is the commonest form on sheltered shores whereas strong wave action favours *citrina* and especially *reticulata*. The figures given by Rasmussen (1973) for the distribution of morphs in the Isefjord are perhaps invalidated by failure to recognize *mariae*. Larger animals tend to live in more sheltered situations.

The spawn of *obtusata* has been frequently confused with that of *Lacuna pallidula* which is laid in similar places. The features of the spawn of *pallidula* which contrast with those of *obtusata*, described above, are: the rather high, oval-circular shape, the firm attachment (even after exposure) to the substratum, the lack of a jelly margin, and the tight packing of the capsules in the jelly so that they have angular outlines. In *L. obtusata* spawn masses are occasionally circular in outline (6.8%), most commonly a short oval (48.9%) or long oval (37.1%), rarely kidney-shaped (1.4%) or irregular (5.9%). Most are laid on *F. spiralis* and *A. nodosum* (67.9%), or *F. vesiculosus* (20.8%), fewer on *F. serratus* (8.1%) or rock (3.2%). The figures are taken from Goodwin (1975) and refer to Cardigan Bay.

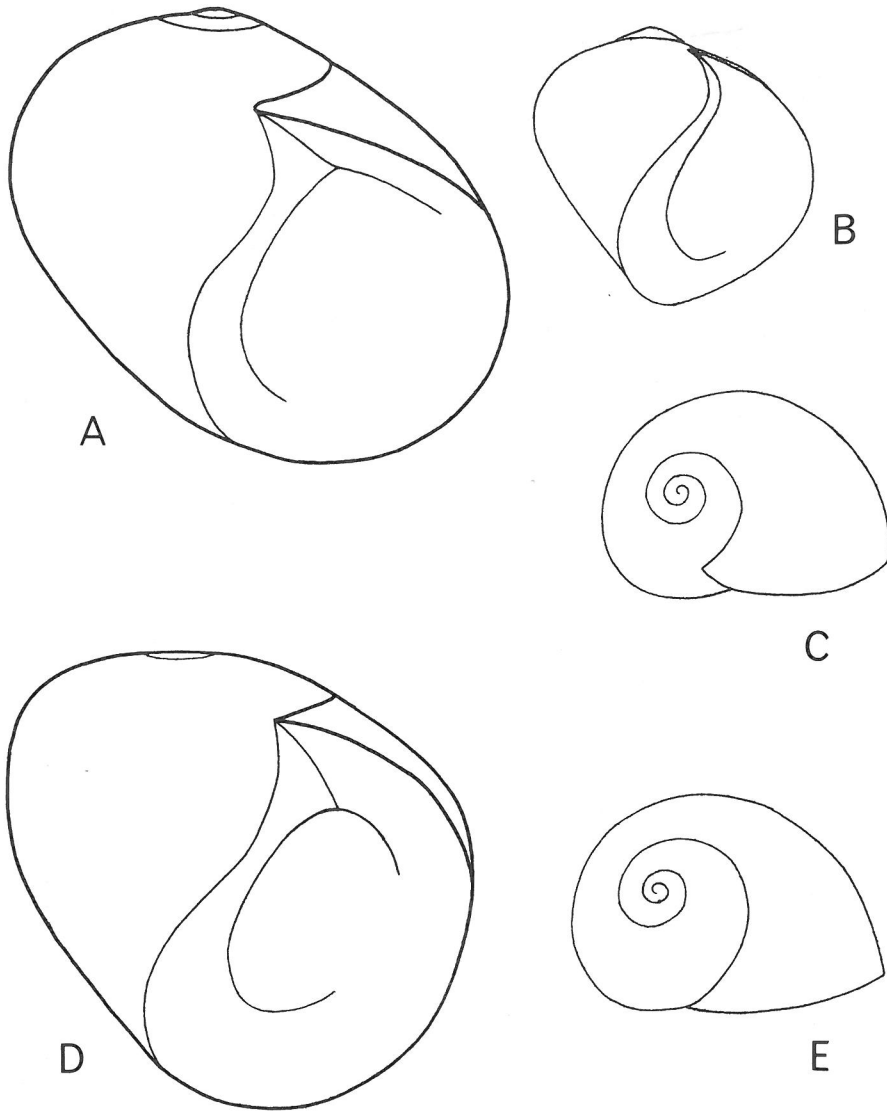


Fig. 205. A,B,C, *Littorina obtusata* Linnaeus; D,E, *Littorina mariae* Sacchi & Rastelli. A and D, apertural views of adult shells; B, apertural view of juvenile shell; C and E, apical views of juvenile shells.

LITTORINA MARIAE Sacchi & Rastelli, 1966

Mariae, Maria's. Named to honour Maria Magistretti.

Shell. Differing from that of *L. obtusata* only in details; the spire is extremely short or even non-existent, the apical angle approaching 180° ; the apical region is therefore flat and the body whorl constitutes nearly the whole of the shell.

Aperture. The outer lip arises very high up the body whorl and nearly at right angles to the axis of the shell; there is no anal sinus. The base of the aperture is rounded. The throat is constricted by

thickening so as to appear smaller than in *obtusata*. In the juvenile shell the base is rounded, lacking the spout of *obtusata*.

Colour. As in *obtusata*.

Size. Up to 11×12 mm. Body whorl = 95–100% of total shell height; aperture = 83–90% of shell height; breadth = 115–120% of height.

Animal. As in *obtusata*. In the male the penis has a long tapering tip and about 12 glands (range 5–16) in 1 row. At rest the tip is kept tucked under the glandular part.

Colour. As in *obtusata* but the ovipositor is always unpigmented.

Geographical distribution, habitat, food. Mainly as for *obtusata*. *L. mariae*, however, does not live so high up the shore, occurring from MLWS downwards, therefore mainly on *F. serratus*.

Breeding and growth. In exposed sites sexual dimorphism is as little obvious as in *obtusata* but it becomes more pronounced in sheltered localities; here all animals are reduced in size but males are affected to a greater extent than females. Differentiation of sexual organs begins in animals with shells 4+ mm high and is complete at 8 mm. The spawn resembles that of *obtusata* closely but there are minor differences: it is laid primarily on *Fucus serratus* (93.8%), since it lives where that species is dominant, rarely on *F. vesiculosus* (6.2%). It is apparently never round in outline and, though predominantly oval (65.5%), is often kidney-shaped (21.9%) or more irregular (12.7%). As might be expected from the smaller adult size the eggs are a little smaller than those of *obtusata* (195–200 μ m diameter). See Goodwin (1975) and Goodwin & Fish (1977).

Notes. The shell of this species is primarily recognizable from that of *obtusata* by the extremely flat apical region, the high and right-angled origin of the outer lip on the body whorl, the absence of an anal sinus and the constricted throat. In apical view the outer lip is tangential to the body whorl. Confirmation may be obtained from the arrangement of the penial glands and unpigmented ovipositor. The shell resembles that of juvenile *obtusata* in the flat apex; these may be recognized, however, by their thin outer lip, by the anal sinus and by the basal spout.

L. mariae is on average smaller than *obtusata*, tends to live lower on the beach and to prefer situations where water movement is more vigorous. The largest specimens are found on exposed shores. It exhibits the same colour morphs as *obtusata* but not in the same proportions, the commonest being *reticulata* (c. 80%) and *citrina* (c. 20%); the latter becomes relatively more abundant with increasing shelter. The morph *olivacea*, commonest in *obtusata*, is rare.

It is possible that a third species should be added to the *obtusata-mariae* grouping. This is *L. aestuarii*, described by Jeffreys (1869) as a variety of *obtusata* found in brackish conditions in the R. Deben near Woodbridge, Suffolk and in the Orwell-Stour estuary between Suffolk and Essex. The shell was described as smaller than the typical form but with a higher spire and with a narrower aperture without an everted lip. S. Smith (1979b) has recently reported somewhat similar animals from the Outer Hebrides to which she has given the name *L. mariae beeensis*. They live on *Fucus serratus* in situations where they are little uncovered, have a general resemblance to *mariae* but with a high spire and an even more constricted aperture. *L. aestuarii* and *L. m. beeensis* thus represent brackish-water ecomorphs of the two species of flat winkle but their strict taxonomic status has yet to be clarified.

LITTORINA NERITOIDES (Linnaeus, 1758)

Turbo neritoides Linnaeus, 1758

Turbo petraeus Montagu, 1803

Melaphe neritoides (Linnaeus, 1758)

Neritoides (Gk.), like a *Nerita*.

Shell. Solid opaque, glossy, slightly granular at high magnifications and covered with a well-developed periostracum. The surface of adult shells is almost always powdery because of erosion and algal attack. There is a prominent pointed spire in young shells, often blunted by erosion in old ones. It is straight-sided in profile, though the whole shell may be somewhat coeloconoid because of the breadth of the body whorl. The apical angle (young) is c. 70°, (old) 75°. There are 5–6 whorls, gently tumid, the sutures lying immediately below the periphery of the upper whorl. The body whorl is more tumid than the others, though near the aperture its subsutural part becomes flat or even concave. The sutures, especially that between the body and penult whorls, are rather deep, slightly excavated and irregular; they are often more or less destroyed on the spire. The ornament is made up of growth lines though on some shells a few obscure spiral ridges may be seen. The growth lines are

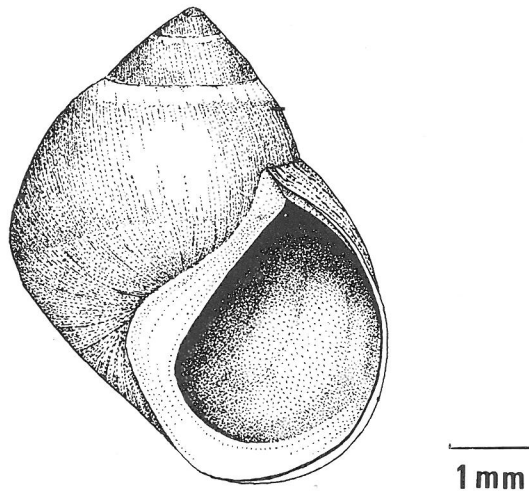


Fig. 206. *Littorina neritoides* (Linnaeus). Plymouth. RUZ.

irregularly developed, are nearly orthocline at the suture but rapidly bend to become markedly prosocline. In some shells the variation in size of the growth lines on the body whorl repeats regularly so that the whorl is transversely corrugated. There is no umbilicus. The protoconch is usually so eroded as not to be discernible, but in young shells it may be seen to have 2.5—2.75 whorls marked with spiral rows of tubercles, and a diameter of 350—450 μ m.

Aperture. Rather narrowly oval, sharply angulated adapically, with its long axis lying at 30° to that of the spire, and bounded by a peristome lying in a prosocline plane. The outer lip is thin and arises just abapical of the periphery of the body whorl. As in *L. littorea* it approaches the body whorl tangentially, the angle between it and the axis of the spire being c. 135. Its first part is slightly concave, then it curves smoothly to the base of the columella where it is everted. The columella is short and the peristome here is broadly turned out, obliterating any umbilical groove and umbilicus. Over the body whorl the inner lip is long and rather straight, forming a glaze which runs to the origin of the outer lip, a deep groove separating the two. At the base of the aperture the peristome forms a short spout angled towards the left. The inner lip and columellar region are grooved and a low ridge lies within the outer lip: these features may form an opercular stop. The periostracum projects freely beyond the outer lip, forming a flexible flap. The internal surfaces of the lips and throat are glossy.

Colour. Shells range from almost black, dark slate-colour, dark chocolate-brown to fawn or near white; worn shells become ash-coloured. Many shells show no pattern, but others have alternate darker and lighter stripes across the body whorl. There may also be spiral bands: most common is a white band on the base of the body whorl round the umbilical area, and there is often a dark peripheral spiral so placed that the outer lip arises level with its middle. There may be a second, faint, subsutural dark band or a white one. There is rarely any pattern visible on the spire. The internal surfaces of the lips and the throat are chestnut brown, the columella and inner lip usually with a slightly paler inner edge.

Size. 9 × 7 mm. Body whorl = c. 75% of total shell height; aperture = 55—60% of total shell height.

Animal. Generally as in *L. littorea*. The tentacles taper more abruptly. The penis has glands arranged in rows. The ovipositor is an oval area with raised edges placed some way behind and below the right tentacle, its posterior end connected by a ciliated groove to the female aperture. The tenidium is reduced.

The foot is relatively short and broad, truncated anteriorly and slightly pointed anterolaterally; the posterior end is rounded.



Fig. 207. *Littorina neritoides*. SEM photograph $\times 30$. Plymouth. RUZ.

Colour. The body is generally grey with dark markings. There are two dark longitudinal lines on the dorsal surface of each tentacle and some white round each eye. Sole of foot pale.

Geographical distribution. From the Black Sea through the Mediterranean and along the W. coast of Europe to W. Norway. It has not been found on the shores of the southern N. Sea nor in S. Norway. Some populations have been recorded (Lewis & Tambs-Lyche, 1962) from off Gullmarfjord, from N.W. Denmark and from Heligoland. According to Crisp & Southward (1958) it extends from the Atlantic east along the Channel as far as Calais on the French side and to Sandown, Isle of Wight, on the British.

Habitat. This is normally the highest of all *Littorina* species on exposed rocky shores, living from the *Pelvetia* level (80% emersion) to heights, largely determined by splash, at which the animals are never immersed, perhaps up to 6 m above EHWS. They are usually found in crevices but emerge to crawl over the surface of rocks when humidity is high. *L. neritoides* may also be found at lower levels, down to about MHWN (Moyle & Nelson-Smith, 1963). This may sometimes be part of a breeding migration in spring. On more sheltered shores the winkles have a narrower and lower range and are less numerous. The animals are local but may be abundant where found.

Food. This is primarily a feeder on black lichens according to Daguzan (1976a) but it also takes in microscopic plants and much vegetable "detritus". The faeces are ovoid pellets c. $50 \times 30 \mu\text{m}$.

Breeding and growth. The sexes are separate, males recognizable by the penis, females by the ovipositor. The sex ratio is $1\sigma: 2\text{q}$ but there is a preponderance (up to 60%) of males among young animals and all with shells $>5\text{mm}$ high are female. Breeding occurs winter-spring (Daguzan, 1976a), males being ripe 2 months before females. At Plymouth (Lysaght, 1941) 50–60% of the population

was ripe, males Dec—Feb, females Dec—May and both sexes were spent in midsummer. Spawning took place Sep—Apr and egg capsules occurred in the plankton Oct—Apr (Lebour, 1935). The eggs are laid in discoidal capsules 180 μm in diameter and 90 μm thick, the two circular sides both being convex, one more than the other. Each capsule contains a single egg 60—80 μm in diameter, colourless, embedded in a thin layer of albumen which is separated by a membrane from a gelatinous fluid filling the rest of the capsule. Females show a 15-day rhythm in laying, correlated with high spring tides, and lay, it is said, only when under water; to achieve this they may migrate to lower levels. Capsules may be found in high pools (Pérès & Picard, 1964) but, unless washed in to the plankton by wave action, do not develop properly. In the laboratory eggs hatch after 7—8 days (Lysaght, 1941) giving free-swimming veliger larvae that live in the plankton for about 3 weeks before settling. At hatching the veliger has a colourless shell of c. 1.5 whorls, 60 μm in diameter, with a marked umbilicus and bearing small tubercles in spiral lines; later it develops a marked apertural beak. By settlement it may have 2.5—2.75 whorls, has become horn-coloured and is 350—400 μm in diameter whilst the beak and tubercles have disappeared. The larva has a bilobed velum, initially unpigmented, later with marginal black areas anterolaterally. The foot becomes dark, like the rest of the body, though the tentacles remain uncoloured and are conspicuous for this reason (Fretter & Pilkington, 1970).

Settlement at Plymouth (Fretter & Manly, 1977) is maximal Mar-Apr and again Sep—Oct, at Penvins, Morbihan (Daguzan, 1976a) Jan—Apr. It is generally at a lower level (about MHWN) than that at which the adults live, though in exposed areas of limited vertical range larvae may settle among adults. The metamorphosing larvae settle in empty barnacle shells, in cracks amongst barnacles (Lysaght, 1941; Daguzan, 1976a) and in pits in rocks from which crystals have been lost (Fretter & Manly, 1977), probably attracted by algae growing there. They attach themselves by the secretions of special pedal glands, later lost. At settlement the shell expands radially, a change in shape which helps to wedge the animal in its crevice. The snails rapidly (24 h after settling) develop a negative geotaxis (Fraenkel, 1927; Fretter & Manly, 1977) which leads to an upward migration towards levels at which adults live and which leaves the settlement site clear for the next wave of metamorphosing veligers. Though normally the numbers settling are much less, Fretter & Manly (1977) found at periods of maximal settling densities up to 400 m^{-2} . By 2 months the juveniles have a shell 1.3 mm high, by 3 months about 2.2 mm. Year 1 animals (Daguzan, 1976a) constitute 84.3% of the population, year 2 15.3%, year 3 (all female) 0.4%.

Notes. Although *L. neritoides* is a familiar and easily recognizable snail there are still many points in its biology which are not clear. It is, for example, absent from some shores that seem appropriate for its occurrence: this suggests that the factors controlling its prosperity are not fully appreciated. This abundance has been shown by Raffaelli & Hughes (1978) to be correlated with the availability of crevices and the size range of the winkles increased as the size of crevice available grew larger. There are still questions to be answered about the extent — even about the reality — of breeding migrations. On exposed shores of considerable vertical range, where splash allows the snails to live at high levels, a downward migration of breeding females and an upward one of recently-settled juveniles would appear inevitable; where the vertical range is restricted, as on the Plymouth breakwater and in the Isles of Scilly, neither is probably needed. Fraenkel (1927) showed that in water snails crawling over a horizontal surface were negatively geo- and phototactic, whereas when they were hanging from a horizontal surface they became positively phototactic. This would lead them into and out of crevices. In air, however, the reversal of phototaxis does not occur. Colman (1933) invoked these taxes to explain the occurrence of winkles in crevices, where they can remain for long periods resistant to adverse conditions. Patané (1933) suggested they could remain dry for 5 months and Fischer (1948) showed that they could lose one third of their water content without harm. Normally, however, they emerge from crevices to feed when humidity is high, even if this be due to rain, making excursions of 10—20 cm (Daguzan, 1976a); Natale & Sacchi (1962) noted excursions up to 150 cm at Naples. Fischer, Duval & Raffy (1933) showed that after a few days in moist air snails placed in water increased their oxygen consumption by a factor of 6. Sandison (1966), finding an increased oxygen consumption from 89.6 $\mu\text{l g}^{-1} \text{h}^{-1}$ in damp air to 351.7 $\mu\text{l g}^{-1} \text{h}^{-1}$ in water, explained the change on the assumption of an accumulated oxygen debt. It may be true that snails living in air have to adjust their metabolism to levels that their respiratory system can support and that those immersed in water are capable of greater activity, but neither the work of Fischer *et al.* nor that of Sandison has investigated the respiration of this species enough to give a full explanation of the changes which they recorded.

The opercular stop formed by the groove within the peristome can only be used at an initial retraction: when provoked the animal can retract much further into the shell, though during much of the retraction it uses the columella as a hinge on which the operculum rotates.

Winckworth (1932) regarded British specimens of this species as belonging to the subspecies *petraea*, the nominate subspecies being Mediterranean.

LITTORINA SAXATILIS COMPLEX

For an understanding of how we have treated the remaining species of *Littorina* it is necessary to preface the descriptions with some explanation.

Until relatively recently it was commonly accepted that four species of winkle lived on N.W. European shores: *littorea*, *littoralis*, *neritoides* and another, variously called *saxatilis* and *rudis*. In 1966, after a period of hesitation, Sacchi & Rastelli showed that one of the four, *littoralis*, was a grouping of two species, *obtusata* and *mariae*, and it is possible (S. Smith, 1979b) that *L. aestuarii* should be raised to specific rank as a third member of this group. These species have been described above and, except perhaps for *aestuarii*, have gained general acceptance as good species.

The fourth 'species' enumerated above, *saxatilis* or *rudis*, has also proved to be an aggregate but it has not yet been resolved into its component parts to the satisfaction of taxonomists, nor is there any certainty that the current analysis of the complex has reached stability. Before that stage is attained we must have (what we do not at present have) equal knowledge of the shell, soft parts and variability with environment of the suggested divisions.

L. saxatilis was described by Olivi from Mediterranean localities (Venice) in 1792, *L. rudis* five years later by Maton, from the Devon shore of the Tamar estuary. By accident these names came to be regarded as synonyms. Other species akin to *saxatilis*/*rudis* were described in the first half of the 19th century, *jugosa* and *tenebrosa* by Montagu, 1803, *nigrolineata* by Gray, 1839, *neglecta* by Bean, 1844 and *patula* by Thorpe, also in 1844. These were all treated by such later authors as Jeffreys (1865) and Winckworth (1932) as subspecies of *saxatilis*/*rudis*. The situation remained thus until Heller (1975a) suggested that on British shores the complex consisted of four species — *rudis*, *patula*, *nigrolineata* and *neglecta*. Of these four *nigrolineata* and *neglecta* have met with general approval as good species, but not the other two. In 1979 Hannaford Ellis showed (1) that Heller's *rudis* confused two species, *rudis* s.s. and *arcana*, the latter distinct by virtue of being oviparous, amongst other things, and (2) that *patula* was an artificial grouping based on a mixture of these two.

After removal of *nigrolineata*, *neglecta* and *arcana* from the original aggregate species we are left with a residue to which there still attaches uncertainty; we must await further analysis of this reduced *saxatilis* complex before we know its precise taxonomic composition. J.E. Smith (1980), however, believes that this residue contains two species, *saxatilis* s.s. and *rudis* s.s. whereas S. Smith (in litt.) regards these as members of a cline. She also (1979b) seems to suggest that *tenebrosa* should be given specific rank. There also remains the possibility that *groenlandica* may prove distinct as well.

Neglecting the last possibility, these investigations suggest the occurrence of 11 possible species of winkle in Britain: *littorea*; *obtusata*, *mariae* and *aestuarii*; *neritoides*; *nigrolineata*, *neglecta*, *arcana*, *saxatilis*, *rudis* and *tenebrosa*. Of the species proposed between 1803 and 1844 as akin to *saxatilis*/*rudis* *jugosa* alone seems to remain at subspecific level.

In the following pages we describe first, *nigrolineata* and *neglecta* as what appear to us as undoubted species. *L. arcana* seems equally valid, but since it shares many features with *saxatilis*, *rudis* and *tenebrosa* and may be externally indistinguishable from *rudis*; and since, further, much of the published information dates from a time when separation of these as species was not attempted, we have given a generalized account of them followed by notes on each. *L. saxatilis*, *rudis* and *tenebrosa* may well be good species but their standing as such, however, has yet to be unequivocally demonstrated. The first two, at present, we regard as members of a cline.

LITTORINA NIGROLINEATA Gray, 1839

Littorina rudis (Maton, 1797) var. *compressa* Jeffreys, 1866

Nigrolineata (Lat.), with black lines, referring to a common colour pattern of the shell.

Shell. Solid, opaque, not glossy. The spire is larger than in most species of the *saxatilis* group and straight-sided or very slightly coeloconoid, the apical angle ranging from about 80° to 100°, but commonly 86–87°. There are up to 6 whorls of which the last is much the most prominent, each moderately tumid, meeting at sutures placed about level with the periphery of the upper whorl. The sutures are distinct and a little excavated but less pronounced than in the other species of the *saxatilis* complex. The ornament consists of growth lines and spiral ridges and grooves. The former are

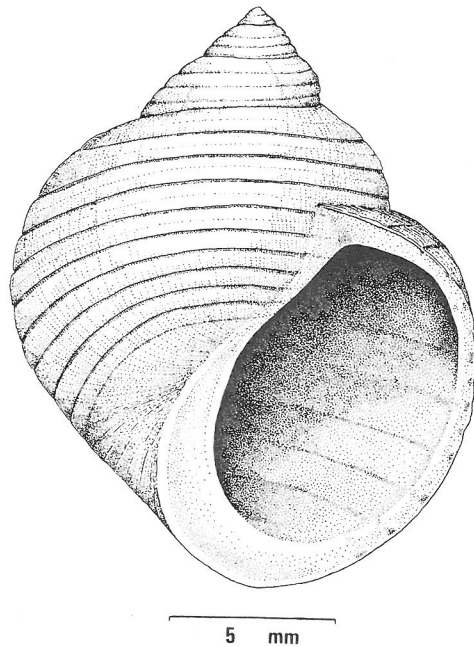


Fig. 208. *Littorina nigrolineata* Gray. Isles of Scilly. RUZ.

markedly prosocline, irregular in occurrence and sometimes so arranged as to give a slightly corrugated surface on the body whorl. The spiral ridges and grooves are well developed, though sometimes absent near the outer lip. They number 12–21 on the body whorl, 3–7 on the penult and 3–4 on the next two. They are low and straplike, 3–4 times as broad as the intervening grooves, and have a flat or slightly humped top, often with a small furrow on its centre which is most conspicuous on the abapertural side.

The protoconch has 1+ whorls, unsculptured, 500–600 μm across.

Aperture. A rounded oval, its long axis lying at 35° to that of the spire and bounded by a peristome lying in a prosocline plane which makes an angle about 130° to the shell axis. It shows a slight adapical sinus on the outer lip and a forward tongue at the periphery. The outer lip arises at the periphery of the body whorl; over its initial course it is rather straight, only gently curved, continuing the profile of the spire, but below the periphery it curves more sharply to the base of the columella. The columella is short, curved and flattened, the lip spreading out to block any umbilical groove. The peristome is completed by a glaze on the body whorl about equal to the columella in length. The edge of the outer lip is sharp and crenulated a little by the ends of the spiral ridges. It is bevelled internally and thickens rapidly to form a ridge in the throat. Thickening is greatest by the body whorl and a groove here separates inner and outer lips.

Colour. White, cream, yellow or red, the spire often duller and greyer than the body whorl. Some or nearly all of the spiral grooves on the body whorl may be coloured chestnut-, chocolate- or purple-brown; those at the periphery are the most frequently pigmented while those on the subsutural and basal areas often show no colour. There is never a tessellated pattern. Peristome white, throat chestnut-brown.

Size. Up to 30×24 –27 mm according to Heller (1975a) but most specimens do not exceed 20×16 –18 mm. Body whorl = 75–90% of total shell height; aperture = 65–75% of total shell height.

Animal. Generally like *L. littorea*. The penis, slightly flattened, has a very short tip and bears up to 12 large glands, all placed near the tip and with the most distal very close to it. The glands of the female duct are well developed and the ovipositor forms a broad, raised platform below the right eye. The ctenidium is a little less in length than in *littorea*.

Colour. The ground colour is cream with pigment developed locally to varying degrees. The dorsal surface of the head is usually very dark with a pale ring round each eye extended anteriorly along the mid-dorsal surface of each tentacle, separating medial and lateral dark lines. The lips are yellowish. The sides of the foot and dorsal surface of the opercular lobes are dark, its sole unpigmented. The penis and ovipositor are pale and this colour extends as a diagonal streak to the left over the floor of the mantle cavity. The streak and ovipositor lack a yellow tinge present elsewhere.

Geographical distribution. Not fully known in view of its recent recognition as a separate species, but probably on all British coasts except those of S.E. England. It is also found on W. Channel and Atlantic coasts of France.

Habitat. On rocky shores, amongst stones and weeds. On exposed shores it lives in the barnacle zone and extends into the *Fucus spiralis* belt (50–80% emersion); on sheltered shores it is lower and may occur with *Ascophyllum nodosum* (35–50% emersion). It tends to live at lower levels and on more sheltered shores than other species of the *saxatilis* complex.

Food. As in other *Littorina* spp. (Sacchi, Testard & Voltolina, 1977). Faeces ovoid pellets about 0.8×0.6 mm.

Breeding and growth. This species is oviparous (Deyglun, 1955; Heller, 1975a) and deposits egg masses on the underside of the stones amongst which it lives (March–April in Pembrokeshire according to Faller-Fritsch, 1975b). The spawn is jelly-like in appearance and consistency, angulated in outline and pink or cream in colour. The young hatch as juveniles with shells of 1–2 whorls measuring 500–600 μ m in diameter. Their growth has not been studied.

Notes. Much information is given by McMillan (1939, 1944) and, in particular, by Sacchi (1975).

The significance of shell colour in *nigrolineata* has been discussed by Heller (1975b). Red is associated with occurrence on red sandstone shores, particularly sheltered ones where much rock is exposed; where shelter is less the rock becomes covered with barnacles and paler shelled winkles then become abundant. Yellow shell colour is correlated with sheltered sites with thick furoid cover — when under water yellow shells, particularly when their shape appears disrupted by dark spiral grooves, are difficult to detect against the weed. Heller (1976) has also shown that the size and thickness of the shell are inversely related to the degree of exposure but directly correlated with the severity of crab predation. Both factors combine to produce large winkles with thick shells in sheltered habitats. The aperture of *L. nigrolineata* does not appear to alter in shape with degree of exposure as does that of *Nucella* (Crothers, 1973) but does become relatively larger in relation to shell height since animals from exposed shores have more globose shells than those from sheltered ones.

LITTORINA NEGLECTA Bean, 1844

Neglecta (Lat.), not collected, so overlooked (because of its small size).

Shell. Opaque and glossy; rather thin. Globular is general shape with a short, blunt spire (apical angle 90–100°). There are 3–4 tumid whorls, slightly flattened below the sutures; the body whorl occupies most of the shell. The sutures are deep, slightly excavated and placed at or just below the periphery of the upper whorl. The ornament comprises very prosocline growth lines, slightly less prosocline near the suture, and many extremely fine spiral ridges and grooves; sometimes 1 just below the suture and 1–2 at the periphery are a little more obvious. In some shells the growth lines on the body whorl enlarge so as to produce a slightly corrugated surface. There is neither umbilical groove nor umbilicus. The protoconch is smooth, has 1+ whorls and measures about 150 μ m in diameter.

Aperture. A rounded oval, nearly circular, slightly angulated adapically with a peristome lying in a prosocline plane. The outer lip arises just below the periphery of the body whorl, more or less at right angles to its surface and to the axis of the spire. Its initial part is convex, never concave as in *littorea* and *neritoides*; it then curves broadly to the base of the columella. Its edge is thin and there is no ridge within it. The columella runs adapically to the right and is longer than the part of the peristome applied to the body whorl, which forms a glaze. The columellar lip is thickened and

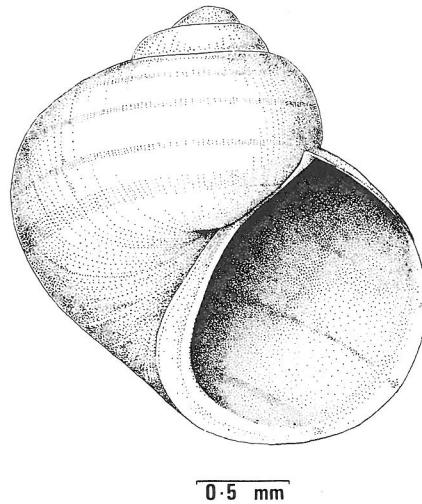


Fig. 209. *Littorina neglecta* Bean. Isles of Scilly. RUZ.

turned out a little and sinks to form a tongue blocking the umbilicus. There is no periostracal flap along the outer lip.

Colour. Variable. Many shells have a chestnut- or chocolate-brown ground colour, variegated with pale areas, others are mainly pale with dark markings. A frequent pattern on the body whorl shows a dark peripheral spiral band bordered by cream-white bands above and below; the breadth of all 3 bands is variable and the apical pale one in particular may be very narrow. The outer lip typically arises about the middle of the dark band. In many shells the brown and white of the body whorl become interrupted to form a variety of linear or tessellated patterns in which the proportions of the two colours are variable. The columellar-umbilical region is brown, the base of the aperture white; the colour of the rest of the outer lip depends on the pattern on the body whorl. The throat is a glossy brown. The operculum is pale, often with a C-shaped black mark on its columellar side.

Size. 5×4.5 mm, often smaller. Body whorl = 85–90% of shell height; aperture = 60–65% of shell height, its breadth the same; breadth of shell may equal shell height.

Animal. As in *littorea*. The penis has an elongated tip and 3–7 large glandular papillae lying in a single row. The female duct ends in a brood pouch. The ctenidium is at most a few slightly raised areas, the osphradium a curved bulge.

Colour. Dark grey with darker and lighter areas. There are two longitudinal dark lines along each tentacle and white round each eye. The dorsal surface of the snout is dark except at the tip, its underside pale. There is no light spiral band over the floor of the mantle cavity. The sides of the foot are often unpigmented.

Geographical distribution. On western British coasts, but, because of its relatively recent recognition as a separate species, likely to have a distribution wider than so far recorded. Perhaps also found in Nova Scotia; certainly at Nahant, Massachusetts.

Habitat. This species occurs on exposed to moderately exposed shores from the top two thirds of the barnacle zone downwards. The animals may be found in *Laminaria* holdfasts and on *Corallina* but are most frequent in empty barnacle shells and small crevices. They also occur, but are less common, on sheltered shores; they may be abundant in salt marshes according to James (1968).

Food. Unicellular algae. Faeces are ovoid pellets $50 \times 30 \mu$.

Breeding and growth. Most information under this head derives from Raffaelli (1976). The sexes are separate, males recognizable by the penis. The animals are ovoviviparous and the brood pouch of the female contains up to 60 embryos of various ages, especially in the early months of the year. The snails hatch with a shell diameter of c. 600μ m and mature at a shell height of 2 mm.

Notes. *L. neglecta* is primarily an inhabitant of crevices, though these usually take the form of empty barnacle shells, from which it may emerge to feed. Raffaelli (1978) has shown that within the barnacle zone the largest snails are to be found towards the top and the smallest in the middle. He interprets this as due to the interaction of several factors. Larger snails are more resistant than smaller ones to the greater desiccation in the upper part of the zone but find shelter less easily at the lower end and there is variation in the size of crevice available at the different levels (Raffaelli & Hughes, 1978). Predation by crabs probably also affects numbers and distribution, snails at lower levels being more at risk than those at higher ones.

S. Smith (1979a and in litt.) has described a small winkle from Rockall under the name *L. scotia* which she believes is an ecomorph of *L. neglecta*. The shells are only 3–4 mm high, have practically no spire and were found in irregularities of the substratum amongst algal tufts. The aperture is large allowing passage for the large foot necessary for adhesion in such an exposed habitat.

GENERAL ACCOUNT OF
LITTORINA ARCANA Hannaford Ellis, 1978
LITTORINA RUDIS (Maton, 1797)
LITTORINA SAXATILIS (Olivier, 1792)
LITTORINA TENEBROSA (Montagu, 1803)

Shell. Solid, opaque, somewhat glossy in young snails but usually roughened by exposure. There is a moderately tall spire, pointed (apical angle 98–100°) and very slightly coeloconoid. The whorls are tumid and meet at rather deep, slightly excavated sutures placed at the periphery of the upper whorl; that between body and penult whorls seems deeper than the others. They vary from 4 to 6 according to the species. The ornament is variable and may be hardly noticeable, but usually shows growth lines and spiral ridges and grooves. The growth lines are markedly prosocline and often irregular in development; where spiral ridges are well developed the growth lines are often eroded from their summits. The ridges are low and usually broader than the intervening grooves. They may be undulate or V-shaped in section, symmetrical or skew (when they have the summit on the adapical side), or strap-shaped (Fig. 210); their shape may be different in different parts of the same shell. They are often obvious on young shells, but tend to be worn on older ones, persisting longer on the base. Even where macroscopic spiral ornament is not obvious there is present, except in badly worn shells, a series of microscopic spiral striae, 70–80 µm apart, which form a microreticulation with the finest growth lines. This may disappear from the spiral ridges but usually remains in the grooves.

The protoconch appears smooth; it shows no clear separation from the teloconch.

Aperture. Rather large and oval, not angulated much at its adapical end. It lies in a prosocline plane and is surrounded by a peristome. The outer lip arises from the periphery of the body whorl at an angle to the axis of the spire which is c. 105°, always more nearly at right angles to the axis than in *littorea*. The lip has a thin edge, buttressed under its origin by some callus, and curves to the base, continuing the profile of the spire. Where it joins the columella it is always a little broadened and everted and this feature may be pronounced. The columella is short and curved and the inner lip forms a glaze over the body whorl thick enough to mask spiral ridges, if present. There is neither umbilical groove nor umbilicus, though a depressed area on the columellar lip sometimes marks the position of the former. In young shells the outer lip is crenulated by the ends of the spiral ridges and grooves.

Colour. This is very variable and may include almost every shade between a dark brown, reddish orange, yellow and white. The shells are often uniformly coloured but spiral bands, streaks, networks and points of contrasted colour also occur, sometimes limited to the spiral grooves and so resembling those of *L. nigrolineata*. The throat may be darker than, or the same colour as the outside.

Size: Up to c. 18 × 14 mm. Body whorl = 76–83% of total shell height; aperture = 55–63% of total height; breadth = 75–90% of total height.

Animal. In essentials the organization of the body is as in *littorea*, except for differences in the glands of the mantle skirt, the female duct and the penis which are given below in relation to the different species.

Colour. Whitish, with varying development of black pigment. The cephalic tentacles have two longitudinal dark stripes along the dorsal surface, normally separated by a median white line extending from a white area around the eye. The ventral surface may be dark or light, and the snout has usually a paler tip. Pigment is present on the penis and ovipositor and usually on the floor of the mantle cavity except for a band which runs from behind the right tentacle across to the left inner end of the mantle cavity.

Geographical distribution. From the Mediterranean along all European shores to the Arctic seas; in the Western Atlantic components of the complex extend south to Delaware Bay and in the Eastern Pacific to Puget Sound. They occur on all Channel and North Sea coasts and extend through the Skagerrak, Kattegat, the Danish fjords into the Baltic, dying out at Rügen. The component species of the complex have been so recently recognized that the distribution of each is uncertain.

Habitat. Abundant on rocks, boulders and stones, in crevices and pools on all rocky shores from very exposed to sheltered, extending far up estuaries; also on tidal mud-flats, in shallow pools or wherever some object offers a solid substratum. On rocky shores they are found at the upper levels of the beach from the black lichen zone down to the top barnacles on exposed sites, to about mid-tide level on sheltered ones (100—30% emersion). The population is always concentrated in the upper part of this range, where *Pelvetia canaliculata* and *Fucus spiralis* are dominant weeds, with the youngest animals at the lower levels. The animals tolerate permanent immersion and withstand brackish water down to $S = 7-8\text{‰}$.

Food. The surface layers of the weed on which they live along with the epiphytic diatoms (Raffaelli, 1975); green filamentous algae; on bare rocks they must rely primarily on unicells and detritus (Sacchi, Testard & Voltolina, 1977). Faeces ovoid pellets $300 \times 150 \mu\text{m}$.

Breeding and growth. The sexes are separate, males recognizable by the penis which is present from a shell height of 4 mm. According to Daguzan (1976b) there was no regression of the penis in his specimens from S. Brittany but Berry (1961) recorded this in specimens from Whitstable during Jun-Aug. The sex ratio is always about 50♂: 50♀ (Daguzan; Berry) though Pelseener (1926) found 38♂: 62♀ at Wimereux. Males are said to be fewer amongst young adults (4—6 mm shell height) and during summer.

Breeding seems to take place in some areas throughout the year (Penvins — Daguzan, 1976b; Plymouth — Berry, 1961) though often with a period of reduced activity. This is sometimes in summer (Jul—Sep, Newhaven — Faller-Fritsch, 1975; Jun—Aug, Whitstable — Berry, 1961; Roscoff — Bergerard, 1971), sometimes in late summer and winter (Anglesey — Raffaelli, 1975; Isefjord — Rasmussen, 1973). The animals may be oviparous (*arcana*) or ovoviviparous (*saxatilis*, *rudis*). In the first the egg masses are like those of *L. obtusata* and *mariae* but are attached to the walls of crevices at the top of the barnacle zone and contain rose-pink eggs (Hannaford Ellis, 1979). In the two latter species gravid females may be found in all months though their number is lowest in April and maximal in September, when it rises to 75% of all females, in Brittany (Daguzan, 1976b). According to Faller-Fritsch (1975) females on exposed shores produce more, but smaller, embryos than those living in sheltered conditions. The number of embryos in the brood pouch is lowest (27—28) in young animals after their first mating (Matveeva, 1974) but rises steadily to an average of 70 (Rusanova, 1963) though it can be much higher. At any moment the embryos may be grouped into 5—6 stages of development indicating successive ovulations. Most are released June—Aug, with a mean shell height of 430—660 μm . There is evidence (Berger, 1976) that the osmotic pressure of the liquid bathing the embryos is under the control of the mother but none that any histotrophe is produced. Moreteau (1976) described the newly-born young as having an incompletely calcified shell, though calcification starts at once and is complete at a shell height of 1.4 mm.

The youngest animals which Daguzan collected had a shell of 3.3 mm high and were 3 months old. They appeared in approximately monthly waves from Oct—Jun (none in Dec, Mar, Apr) and were found in the same zone as the parent animals. The age of maturity seems variable but is mostly at about a shell height of 5—6 mm (range 3—9.8) (Rusanova, 1963; Daguzan, 1976b), perhaps earlier in exposed than in sheltered conditions (Faller-Fritsch, 1975). In temperate latitudes this is about 6 months old, but is delayed in the colder White Sea to 1 year, and in Murmansk to 3 years (Matveeva, 1974). In temperate latitudes the winkles may live 5—6 years, when they reach a maximum height of 18.5 mm. After maturity the annual mortality is 85% and only 0.3% live for more than 3 years (Moreteau, 1976). Daguzan (1976b), on the other hand, found the population at Penvins to be made up of 26.5% yr 1, 50.6% yr 2, 21.2% yr 3, 1.5% yr 4, 0.2% yr 5. Males and females seem to live for

the same length of time but females grow more so that the largest shells (> 17 mm high) are all female. In the White Sea and Murmansk the span of life is longer, up to 8 years (Rusanova, 1963). Growth is said by Moreteau (1976) to occur cyclically and its slowing with age is due to the increasing length of the resting stages. Most of the oldest animals are no longer capable of reproduction and have empty brood pouches (Inagaki, 1970).

LITTORINA ARCANA Hannaford Ellis, 1978

Arcana (Lat.), secret, referring to its late recognition as a species distinct from *rudis*.

The points which characterize this species are as follows, though those affecting the shell are not diagnostic (Hannaford Ellis, 1979). The shell is, in general, like that of *rudis* but there is a tendency for the eversion of the columellar lip to be marked and for the shell, as seen in apical view, to have a greater diameter parallel to the apertural edge than at right angles to it. The spire is relatively short.

The animals are oviparous and a check, in a mature female, for the presence of a glandular oviduct and the absence of a brood pouch is the most certain and rapid way of identifying the species. There are other differences in organization between this and the other species: (1) a ciliated field lies on the mantle skirt on the right between the genital duct and the columellar muscle, but it is not extensive nor is it red in colour; (2) in males the prostate does not extend to the level of the anus; (3) the penis is usually relatively shorter than in *rudis*, with a moderately long, tapering tip; (4) the number of penial glands is variable, 6–34; they lie in a single row, or irregularly or, rarely, in a double row, and frequently extend to or round the curved penial base; (5) in females the development of the albumen and capsule glands is marked, as would be expected in an oviparous animal.

L. arcana seems to be sympatric with *rudis* and *saxatilis*, extending from the top part of the barnacle zone to the belt of black lichens. It seems to prefer exposed shores.

This, rather than *nigrolineata*, according to Hannaford Ellis (1979), is probably the species described by Seshappa (1947, 1948) at Cullercoats as an oviparous variant of *L. rudis*. The difference between oviparity and ovoviviparity, however, with the accompanying changes in the organization of the female genital tract, seems to us to be too great to be regarded as intraspecific variation and to indicate genuine specific differentiation. The observation, commonly made, that specimens believed to be *L. rudis* are not breeding, even at the height of the breeding season, finds a more rational explanation if they are, in fact, *L. arcana*.

LITTORINA RUDIS (Maton, 1797)

Turbo rudis Maton, 1797

Rudis (Lat.), rough, referring to the outline of the shell.

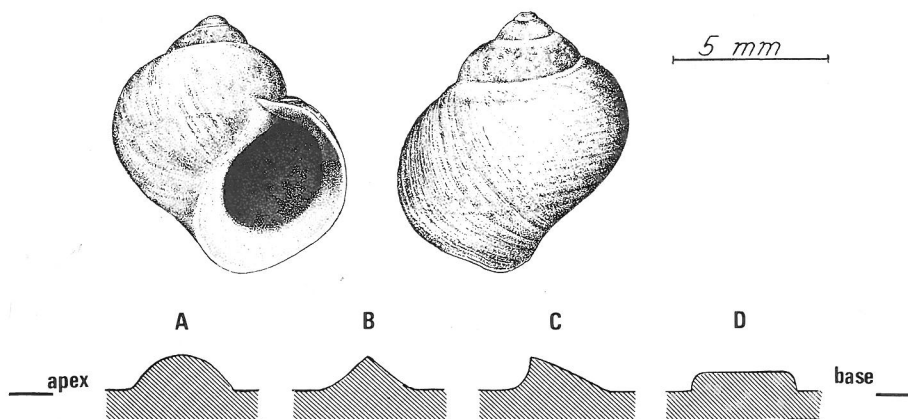


Fig. 210. *Littorina rudis* (Maton). Frederikssund, Roskildefjord. CMZ. A somewhat worn shell (cf. Fig. 211). Diagrammatic transverse sections of spiral ridges on the shell of winkles in the *saxatilis* complex. A, undulate; B, V-shaped, symmetrical; C, V-shaped, asymmetrical; D, strap-shaped. The apex of the shell lies to the left, the base to the right.

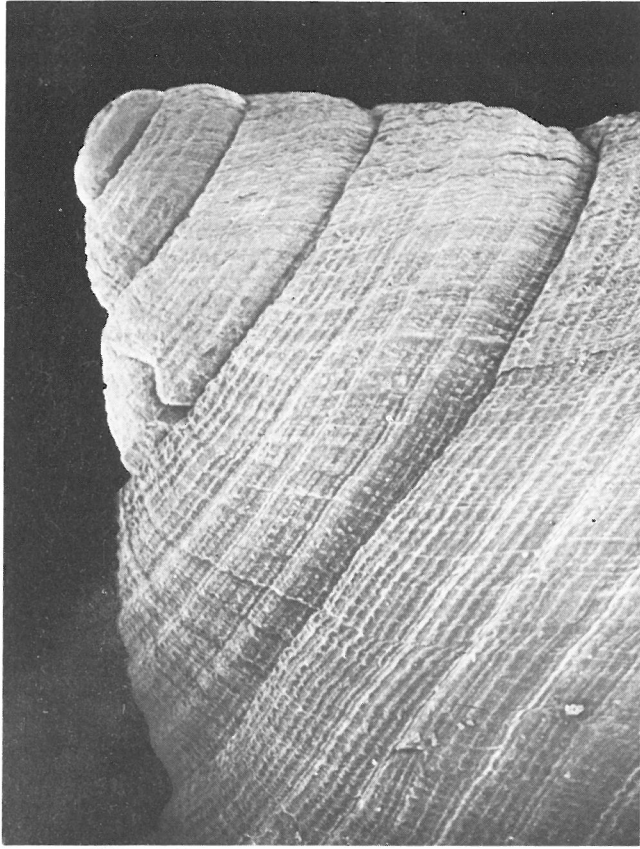
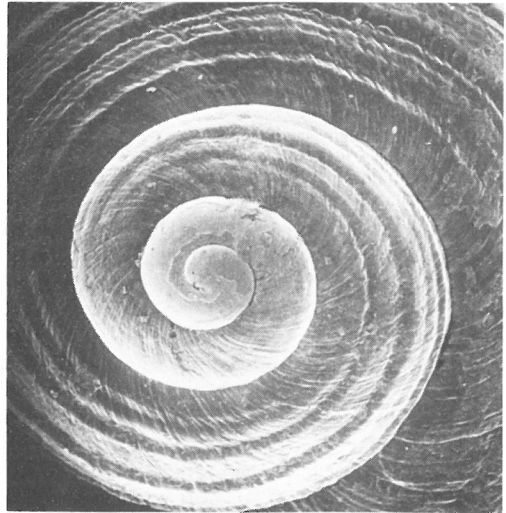
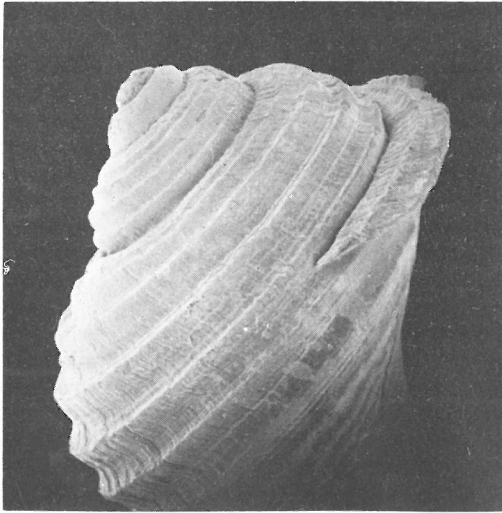


Fig. 211. *Littorina rudis*. Spire $\times 35$. SEM photograph. Chesil, Dorset. RUZ.



A
B
Fig. 212. *Littorina rudis*. A, spire of shell (body whorl broken off) $\times 20$; B, apical region $\times 40$. SEM photographs. A, from Lundy; B, from Aldeburgh, Suffolk. RUZ.

There are 5 (+ 1 embryonic) whorls at a shell height of 10 mm, 4 + 1 at 4 mm. The spiral ridges of the shell may be straplike but, if V-shaped in section, are asymmetrical with the crest displaced towards the apex of the shell. This is more marked in those on the adapical than on the basal part of the body whorl. The diameter of the shell in apical view parallel to the apertural edge and that at right angles to it are approximately equal.

The aperture has a well-developed expansion of the lip, giving rise to a spout where outer lip and columella meet. The shell commonly shows a rather uniform colouring and does not have a dark throat.

The foot of the animal is relatively small. Females are ovoviparous. By comparison with *arcana* the ciliated field between the genital duct and the right edge of the columellar muscle is extensive; in live animals it is reddish but the colour vanishes on preservation. The prostate extends anterior to the anus and the penis has a moderately long and frequently mucronate tip; the glandular papillae on it (4—26) usually lie in a single row or irregularly, though a second row sometimes occurs. The papillae are small and rarely reach the curved base of the penis.

Animals of this species live about the level of *Pelvetia canaliculata*, lower than *saxatilis* and, unlike it, on and amongst stones rather than in crevices.

Moore (1977) described a wrinkle from Rockall which may belong to this species. It had a smooth shell about 7 mm high, with a distinct spire and large aperture. The snails were living in crevices.

LITTORINA SAXATILIS (Olivi, 1792)

Turbo saxatilis Olivi, 1792

Saxatilis (Lat.), rock-dwelling, in relation to the habitat.

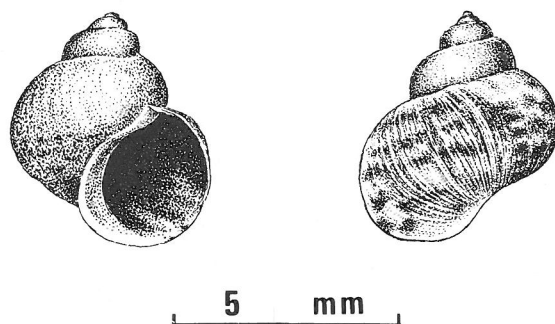


Fig. 213. *Littorina saxatilis* (Olivi). No locality given.

The shell has 4 (+ 1 embryonic) whorls at a shell height of 10 mm, 3 + 1 when less than 4 mm high. Ornament, when present, has the form of spiral ridges which are either undulate or V-shaped and symmetrical in section. The aperture is large, rounded, with a poorly-developed or no projection of the columellar lip. The shell is moderately tall and occurs in a variety of colours, often with variegated patterns of spiral lines, streaks and points. The throat is dark.

The organization of the soft parts seem to be as in *rudis*, but the animal has a relatively larger foot. The snails are ovoviparous, the embryos being larger than those of *rudis*.

This is the rough wrinkle found at the highest level of the beach, at the level of *Pelvetia canaliculata* or higher, up to the *Verrucaria* zone. Normally it is collected at low tide in crevices.

LITTORINA TENEBROSA (Montagu, 1803)
Turbo tenebrosus Montagu, 1803

Tenebrosa (Lat.), dark, referring to shell colour.

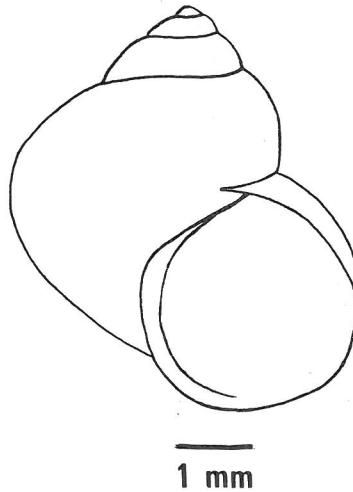


Fig. 214. *Littorina tenebrosa* (Montagu, 1803). Lettermullan, Co. Galway. Profile of shell.

In most respects this is like *rudis*, but the shell is thinner and smaller. The sutures are rather deep and there is a slight flattening subsuturally and peripherally as a result of which the profile of the spire is a little turreted. The ornament is of growth lines and some very fine spiral striae, but the general impression is of a smooth shell of 5–6 whorls.

The aperture is made slightly rectangular by the peripheral flattening of the outer lip. The columella is rather slender and at its base the lip is a little everted.

The shell is dark in colour, reddish brown to nearly black, sometimes with a subperipheral brown band on the body whorl, sometimes with a tessellated pattern. The columella and throat are brown.

The habitat is characteristic: the animals are found on weed, often permanently submerged, in sheltered situations with reduced salinity. They are ovoviviparous.

In our present state of knowledge it is not certain whether this is a true species or a brackish-water ecomorph of *L. rudis*.

Notes on L. arcana, L. rudis, L. saxatilis and L. tenebrosa. The species are not so strictly sympatric as was originally believed, though their distribution may overlap. Sexual recognition and barriers to cross-breeding seem to depend upon ecological separation, size differences, penial anatomy and behaviour since differences in breeding periods have not yet been demonstrated. The shell, being adaptive to nearly identical habitats, shows fewer signs of specific distinctness, as might be expected in early stages of speciation.

The animals are extremely successful inhabitants of the upper shore but so flexible in their mode of life as to live apparently equally well at the top of the beach or permanently immersed in brackish creeks (Howes, 1939). Intertidal animals feed when exposed so long as the air is humid enough; as they dry they retreat into crevices or under stones and continue until dried out. Under water their shells are open for ventilation of the mantle cavity but they are immobile and do not feed (Faller-Fritsch, 1975; Daguzan, 1976b), though Bogen & Farley (1974) seemed to record some underwater feeding. This cyclical feeding may be correlated with cycles of activity in the digestive gland (Bogen & Farley, 1974). Winkles living permanently submerged must have different behaviour patterns but have not been studied.

Populations of rough winkles reach considerable densities. Moore (1940) described a weedy gully at Plymouth where there were 3000 m^{-2} , a figure which seems high for most British shores. Muus (1967) obtained mean values of c. 1300 m^{-2} (biomass 23 g m^{-2}), comparable with those given by Spooner & Moore (1940) (1100 m^{-2}) for mud flats in the Tamar estuary, but considerably exceeding Faller-Fritsch's figure (1975) of 200 m^{-2} at Landshipping on the Eastern Cleddau, Dyfed. When young are present the number rises: Faller-Fritsch found

up to 2825 m⁻² (biomass 67.5 g m⁻²) in crevices and Muus nearly 250 000 m⁻². In the White Sea — Murmansk area Matveeva (1974) observed much higher concentrations of adults, up to 43 218 m⁻², with a biomass of 9800 g m⁻², although most of her figures were much lower. In all areas density of population is directly linked to density of weed cover. The availability of crevices is also an important determinant of population size at a given place. Emson & Faller-Fritsch (1976) bored artificial crevices and found a subsequent increase in the number of winkles. Raffaelli & Hughes (1978) showed that crevices were important shelters for winkles living on exposed beaches but less important on sheltered shores and salt marshes. The discovery by Emson & Faller-Fritsch that there was no slowing of growth after they had increased the number of crevices suggests that at least in some situations the winkle population is not as large as the available food supply could support.

Unlike some species of *Littorina*, young and old inhabit the same zone of the beach and there is no migration, although some movement up the beach within the zone seems to occur as the animals become larger. Even in the cold winters of northern Russia, however, where the air temperature may be down to -25°C, there is no migration to a sublittoral overwintering habitat and the animals survive in crevices (Matveeva, 1974).

The animals are preyed upon primarily by crabs and birds (Pettitt, 1972); the colour pattern of the shell may be related to the fact that these are primarily visual hunters (Pettitt, 1973). The Rev. G. Long has (*in litt.*) described the restriction of light and dark shelled animals to rock of corresponding colour on offshore reefs in Guernsey.

The effects of parasitism by larval trematodes on the digestive gland have been described by James (1965).

Notes on Littorina species. To write an account of the species of *Littorina* found in N.W. Europe is a hazardous undertaking: before one has taken the pen off the paper the text has been overtaken by events and rendered obsolete. Never before, it seems, has so much effort been put by so many people into the study of one molluscan genus as into that of *Littorina* over the last decade or so, nor have so many zoological careers started with a study of one of the many topics which its species and abundance allow. This interest is related to the fact, amongst others, that the species exhibit much polymorphism tied up with speciation. This is particularly true of forms able to exploit brackish environments since, in the north temperate areas dealt with here, these are often geologically relatively young and adaptation to them still actively proceeding.

Identification of the littorinid species of Britain and Denmark is partly easy, partly less so. *L. neritoides* is distinguished by a flexible periostracal flap along the outer lip, a narrow shell with flat-sided spire, the acute adapical angle of the aperture, a dark colour and a normally very high position on the shore. *L. littorea* has no periostracal flap but has a similar spire and acutely-angled aperture. The whorls, especially in young shells before erosion has blunted them are marked with spiral ridges and the animals are often confused with young *rudis* or *saxatilis*. They may usually be readily separated from these by the marked white colour of the columella. Alone amongst *Littorina* spp. the black lines on the cephalic tentacles are transverse, not longitudinal.

The species of the *saxatilis* complex all agree in having swollen whorls, and an aperture not acutely angled adapically because the outer lip makes nearly right-angled contact with the body whorl. Of the species involved *neglecta* is perhaps the easiest to identify: it is small, smooth-shelled, has a round aperture with no spout at the base of the columella; the shell has often a tessellated pattern and usually a brown peripheral spiral band disappearing into the aperture. The penis has up to 7–9 glands in a single row and an elongated tip. *L. nigrolineata* need not show the coloured shell pattern from which the name derives, but often does. The same pattern, however, also occurs in other species of the complex and so is not diagnostic. The spiral ridges are always low and straplike, often with a central furrow, and the aperture is rather narrow. The penis is distinctive with a short tip and up to 6 large glands; the female lays egg masses. Three other species of the complex, *saxatilis*, *rudis* and *arcana* are more difficult to separate though dissection gives valuable help. *L. arcana* is oviparous, the other two ovoviviparous; it therefore shows a greater development of oviducal glands and has no brood pouch. The male of *arcana* has a prostate which does not reach the level of the anus and which has only a small ciliated area along its right side. The male of *rudis* has a prostate extending beyond the anus and a large, reddish ciliated field. Shells of *rudis* and *arcana* are separable from those of *saxatilis* in having a spout in the region of the columellar lip, in having spiral ridges which are skew in section and in having the throat not darkly coloured. The animals live largely among stones at a lower level than *saxatilis* which lives in crevices; its shell shows less or little development of the spout, the spiral ridges are symmetrical, the throat usually dark. It should be emphasized that there is considerable overlap in these characters and it may not be possible to put a name to a single empty shell. The extent and pigmentation of the ciliated field should not be relied upon by itself as a diagnostic character in separating *arcana* from the other species. *L. tenebrosa* may be a distinct species or only an ecomorph. It may be distinguished by its thin, smooth and darkly-coloured shell and by its liking for quiet brackish water.

The species *obtusata* and *mariae* are distinct from all others of the area in the great reduction of the spire. This is more marked in *mariae* and the top of its shell may be quite flat, with the outer lip arising level with the apex; a short spire persists in *obtusata*. The throat is much narrower in *mariae* than in *obtusata*. Young shells of the two species resemble one another more than mature ones but can be separated by the presence of a small anal sinus in *obtusata*, lacking in *mariae*. In *mariae* the female has an unpigmented ovipositor, the male a penis with long tip (normally hidden under the glandular part) and about 12 glands in 1 row; in *obtusata* the ovipositor always has

some pigment (but not, apparently, in Danish specimens according to Nielsen, in press) and the penis has about 30 glands in 2—3 rows. *L. aestuarii* and *L. beeensis* may be other species in this group (p. 262).

L. groenlandica Menke, 1830 and (?) Möller, 1842 has sometimes been regarded as another variety of the *saxatilis* grouping. Wiium-Andersen (1970), however, using electrophoretic analysis of proteins and of haemoglobin from the buccal mass, was unable to separate some members of the *saxatilis* complex on this basis, but could separate *groenlandica*. It may therefore prove to be still another species in its own right.

The inter-relationships of these and other species are discussed by Rosewater (1970) and by Bandel (1974). *L. neritoides* stands apart from the others in having basal cusps on the rachidian radular teeth and so forms the sole species in the subgenus *Melaraphe*. Rosewater and Bandel differ in their placing of the others: Rosewater places them all in the subgenus *Littorina*, but Bandel separates *littorea* from the others, largely on the basis of its spawn and development and its radular structure. *L. littorea* would then fall into the subgenus *Littorina* and all the others dealt with here in *Littorivaga*.

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KEY TO LITTORINACEA DESCRIBED HERE

It is not possible to construct a key by which the species of *Littorina* may be identified using only a single character at each entry: there is too great an overlap of structure between species for this to be practicable. It is also sometimes difficult, or impossible, to be certain of identification of some species if only dead shells are available. The separation of *L. arcana* from *rudis*, in our present state of knowledge, requires an examination of pallial anatomy. Indeed, in the identification of any species (other than *littorea* and *neritoides*) it is helpful, if not nearly essential, to have the opportunity of examining penial structure and of knowing whether the animals lay eggs or not. The following key aims to help identification by including references to these points as well as to shell characteristics.

1. Shell with slit-like umbilicus and grooved columellar region leading to it; animal with 2 metapodial tentacles (*Lacunidae*) 2
 Shell with or without umbilicus but if present no groove leads to it; animal with or without metapodial tentacles 5
2. Spire high, 5-7 whorls; body whorl <90% of total shell height; umbilical groove smooth 3
 Spire low, 3-4 whorls; body whorl >90% of total shell height, umbilical groove ridged 4
3. Shell turreted, with thick periostracum, usually raised into prosocline ridges. no brown spiral bands on body whorl *Lacuna crassior* (p.247)
 Shell not turreted, periostracum thin, not ridged; usually with 4 red-brown spiral bands on body whorl *L. vincta* (p.244)
4. Spire extremely short; umbilical groove very broad; usually greenish in colour, unbanded *Lacuna pallidula* (p.250)
 Spire moderately short; umbilical groove moderately broad; usually with 3 red-brown spiral bands on body whorl *L. parva* (p.248)
5. Whorls with thick periostracum usually raised into prosocline ridges; animal with 2 metapodial tentacles *L. crassior* (p.247)
 Whorls without obvious periostracum; animal without metapodial tentacles (*Littorinidae*) 6
6. Shell with low spire; apical area flattened 7
 Shell with well-developed spire; apex pointed 8
7. Shell with distinct spire; outer lip arises below level of apex; aperture wide, throat not much constricted; ovipositor pigmented; penis with short tip and c. 30 glands in 2-3 rows *Littorina obtusata* (p.258)
 Shell with hardly any spire; outer lip arises level with apex; aperture narrow, throat constricted; ovipositor not pigmented; penis with long tip and c. 12 glands in 1 row *L. mariae* (p.261)
8. Whorls of spire rather flat, sutures shallow; outer lip arises tangential to body whorl. 9
 Whorls of spire tumid, sutures deep; outer lip arises nearly at right angles to body whorl 10
9. Adult shell large; usually with spiral ridges and grooves; columella white; no periostracal flap on outer lip; animal with transverse black stripes on tentacles *L. littorea* (p.255)
 Adult shell small, smooth; columella pigmented; a periostracal flap along outer lip; animal with longitudinal black stripes on tentacles *L. neritoides* (p.262)
10. Shell small, nearly globular, with short spire; a peripheral, spiral, brown band on body whorl entering aperture and bounded above and below by white; floor of mantle cavity dark; penis with long tip and 3-7 glands; ovoviviparous *L. neglecta* (p.268)
 Shell with well-marked spire, usually with distinct spiral ridges and grooves, but these are often eroded; no colour pattern on body whorl as above; floor of mantle cavity with diagonal white band; oviparous or ovoviviparous 11
11. Animal found on weeds in sheltered brackish situations, commonly not emerged at low tide; shell dark, usually smooth, rather thin *L. tenebrosa* (pp.270, 275)

- Animal found in upper half of beach, in rock crevices or under stones, in fully saline conditions, emerged at low tide; shell solid, usually with ridges 12
12. Shell with flat strap-like spiral ridges often with secondary central furrow; grooves often darkly pigmented; penis with very short tip and up to 12 (commonly fewer) glands; oviparous *L. nigrolineata* (p.266)
- Shell with spiral ridges which usually rise to a crest but may be strap-like; penis with moderately long tip; oviparous or ovoviviparous 13
13. Oviparous; prostate does not reach level of anus and has only a small ciliated field alongside, not red in living animals; penis with tapering tip, glands reaching to or round the curved base; found with *rudis* *L. arcana* (pp.270, 272)
- Ovoviviparous; prostate reaches beyond anus; ciliated field large, red in living animals; penis with blunt tip, glands not reaching base 14
14. Ridges on shell with crest at their adapical edge; aperture with prominent everted area at base of columella; on stones, amongst weeds, not at highest level of beach *L. rudis* (pp.270, 272)
- Ridges on shell with crest placed centrally; aperture with only small everted area; in crevices at top of beach *L. saxatilis* (pp.270, 274)