

# THE CHARACTERS AND DISTRIBUTION OF THE SUBSPECIES AND VARIETIES OF *LITTORINA SAXATILIS* (OLIVI, 1792) IN BRITAIN.

by

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## Résumé

Ce travail comprend :

- a) un exposé sur la distribution, les caractères du test et l'autonomie des six sous-espèces et des douze variétés de *Littorina saxatilis* (Olivi) de Grande-Bretagne ;
- b) une étude des relations entre les caractères de la coquille et le degré d'agitation de l'eau ;
- c) une discussion sur la taxinomie et l'évolution de ces sous-espèces et variétés.

## Introduction

The considerable variation in form exhibited by *Littorina saxatilis* is demonstrated in the work of such authors as Dautzenberg and Fischer (1912), Thorson (1941), Seshappa (1947), Deyglun (1955), Berry (1961), Fischer-Piette and Gaillard (1960, 1961), Fischer-Piette, Gaillard and Jouin (1961), Fischer-Piette, Gaillard and James (1963, 1964), James (1963, 1964 a, b, 1968 a) and Gaillard (1965).

These animals were first considered to consist of at least twenty separate species. Later, Dautzenberg and Fischer (1912) showed that they constitute a single species with six subspecies, each with several varieties. Most subsequent authors have accepted their scheme of classification but recently Deyglun (1955) has suggested that one subspecies should be regarded as a separate species. He based this conclusion on the study of populations on a single shore at Roscoff, Finistère. The examination of the shell characters, anatomy and ecology of some populations on single shores in Britain, described in this paper and by Fischer-Piette, Gaillard and James (1964), suggests that the other subspecies and most of the varieties should also be considered as distinct species. However, as will be shown later, the examination of many populations of each subspecies and variety over a wide geographical range indicates that the concept of a single variable species should be retained.

## Material and methods

*Littorina saxatilis* was collected over a period of ten years from 1958 to 1967, from 178 shores around the coast of Britain, in the areas shown in the map (Fig. 1). Most of these were rocky shores but some muddy estuarine stations and salt marshes were visited. Specimens were also examined for comparison from Venice, Spain, France, Norway, Canada and U.S.A.

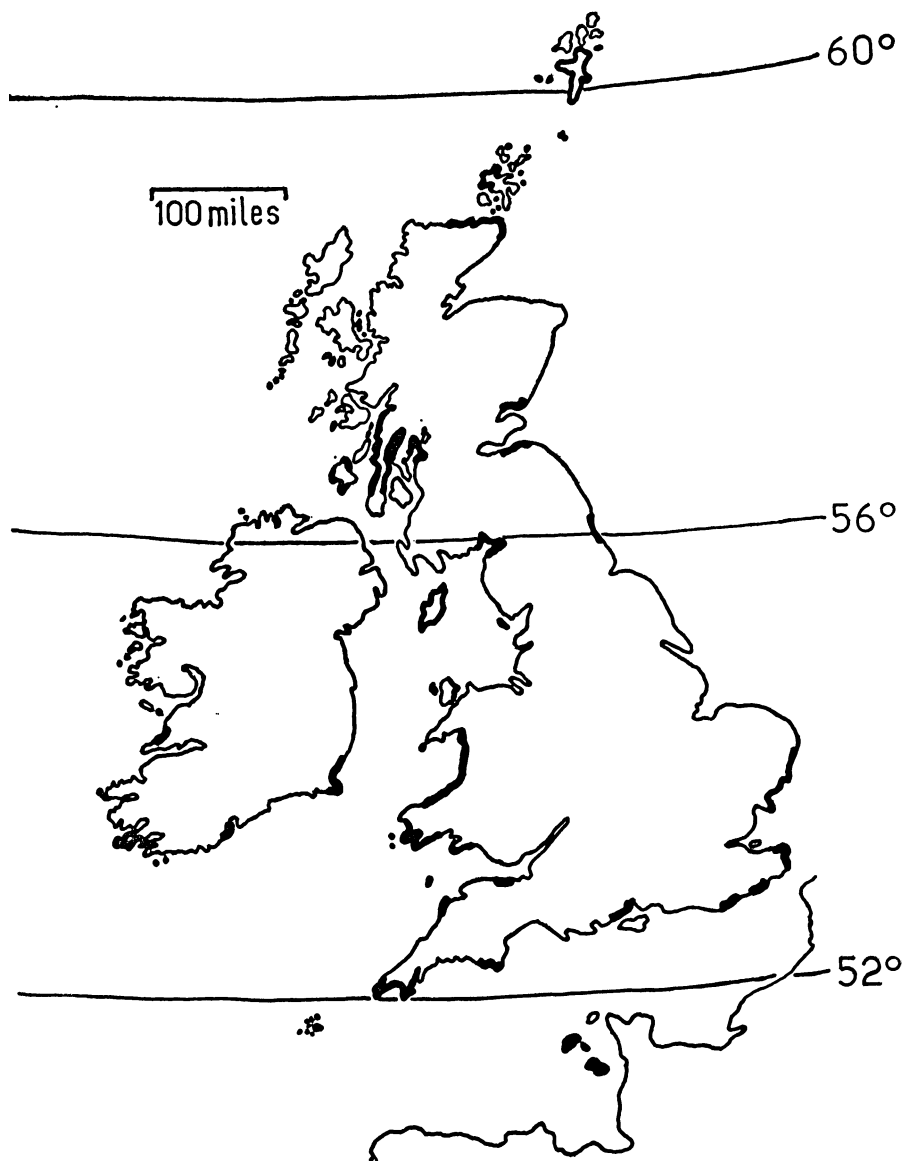


FIG. 1.

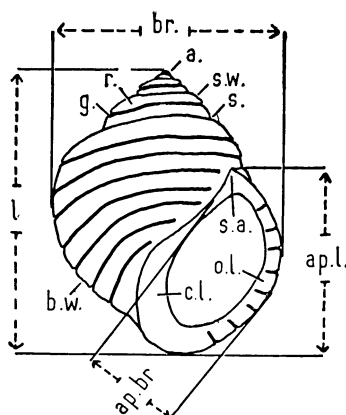
British Isles showing the coastal areas, marked by a heavy line, where *Littorina saxatilis* was collected for this survey.

The degree of exposure to wave action of each rocky shore in Britain was estimated by considering both physical and biological features as described by Ballantine (1961). His exposure scale (1-8) (Fig. 17) is used throughout this paper. A further number (9) is used in the graphs (Figs. 17-23) to denote extremely sheltered muddy estuarine stations or salt marshes. This is not meant to suggest that a further exposure grade be added to Ballantine's scale for rocky shores. Each shore was divided into the biologically defined zones of Stephenson and Stephenson (1949) and, wherever possible, the relationship of the zones to height above chart datum and tide levels calculated.

The population density of each subspecies and variety present in each zone was recorded and a sample collected. On returning to the laboratory, the length, breadth, aperture length, aperture breadth (Fig. 2) and the density of the shell and contained animal

FIG. 2

*Littorina saxatilis*, diagram showing how shell measurements were made. a. apex, ap.br. aperture breadth, ap.l. aperture length, b.w. body whorl, br. breadth, c.l. columellar lip, g. groove, l. length, o.l. outer lip, r. ridge, s. suture, s.a. shell angle (angle between outer lip and body whorl), s.w. spire whorl.



was measured for each specimen in the sample. These were used to measure shell size and age (length), shell shape (length/breadth), spire height (length/aperture length), aperture shape (aperture length/aperture breadth) and shell thickness (density of shell and contained animal). The nature of the sculpturing and other shell characters were also noted. The animal was then removed from the shell and a record made of the number of penial glands on the penis, the extent of development of the pigmentation on the head and tentacles and the length of the radula. Each specimen was also examined for larval Digenea. The morphology, life cycles and the specificity of the twelve species of larval Digenea found in the subspecies and varieties of *L. saxatilis* are described elsewhere (James, 1964 *b, c*, 1965, 1968 *a, b, c, d*). A total of 55,318 specimens of *L. saxatilis* were examined in this way.

In addition, monthly records were made of the population density, migration and reproductive cycle of four subspecies on selected shores at Aberystwyth. The techniques used and results, mentioned briefly in this paper, have been published in more detail elsewhere (James, 1968 *b, c, d*).

### The definition of some terms used to describe the shell of *Littorina saxatilis*

It is necessary, in order to compare the shells of the subspecies and varieties, to use comparative terms, such as broad, fairly broad, tall and very tall, which will mean little to a reader unless he has specimens of most of the subspecies and varieties in hand. Since this is unlikely, photographs (Pl. 1 and 2) and definitions, based on shell measurements, are provided to clarify the meaning of the comparative terms.

#### a) shell thickness

	density of shell and contained animal in gm./cm <sup>3</sup>
very thick	more than 1.75
thick	1.75 - 1.60
thin	1.60 - 1.45
very thin	1.45 - 1.30
extremely thin	less than 1.30

#### b) shell shape

	shell length/shell breadth
broader than long	less than 1.0
very broad	1.0 - 1.10
broad	1.10 - 1.20
fairly broad	1.20 - 1.30
narrow	1.30 - 1.40
very narrow	more than 1.40

#### c) spire height

	shell length/aperture length
very short	less than 1.35
short	1.35 - 1.50
medium	1.50 - 1.65
tall	1.65 - 1.80
very tall	more than 1.80

#### d) aperture width

	aperture length/aperture breadth
very wide	less than 1.30
wide	1.30 - 1.40
fairly wide	1.40 - 1.50
narrow	1.50 - 1.60
very narrow	more than 1.60

### THE CHARACTERISTIC FEATURES OF THE SUBSPECIES AND VARIETIES OF *LITTORINA SAXATILIS* IN BRITAIN

The six subspecies found during this survey, namely subsp. *saxatilis* (Olivi, 1792), *rudis* (Maton, 1797), *jugosa* (Montagu, 1803), *tenebrosa* (Montagu, 1803), *groenlandica* (Menke, 1830) and *neglecta* (Bean, 1844), are described in turn below.

Subspecies *saxatilis* (Olivi, 1792) (= *Turbo saxatilis* Olivi, 1792; *Littorina saxatilis* (Olivi) *forma typica* Dautzenberg and Fischer, 1912)

(Pl. 1, 1, a-f) measures 0.43—0.47 mm long on leaving the brood pouch of the adult and grows to a maximum of only 7.0 mm long. The shell is very thin to extremely thin, usually broad to fairly broad, the spire medium and the aperture relatively large and narrow to wide. The range (and mean) of the shell density, the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in adults are 1.23—1.40 (1.34), 1.09—1.30 (1.23), 1.50—1.65 (1.58) and 1.30—1.56 (1.45) respectively. The spire apex is sharply to bluntly pointed, the sutures deep, grooves and ridges may be absent or a few widely separated weakly developed humped ridges may be present on the body whorl. The outer lip meets the body whorl nearer to the suture between the body whorl and the first spire whorl than in subsp. *neglecta* (Pl. 1, 6, e,f). The angle between the outer lip and the body whorl (the shell angle) is, as in all other subspecies except some forms of subsp. *rudis* (Pl. 1, 8, c), almost a right angle. The columellar lip is thin.

The shell colour of my specimens is pale grey or grey and white but within the aperture a uniform dark brown. The most frequent colour patterns are *hieroglyphica* Fischer-Piette, Gaillard and Jouin, 1961 (Pl. 1, 1, a,c) and *tessellata* Dautzenberg, 1893 (Pl. 1, 1, b,d,e).

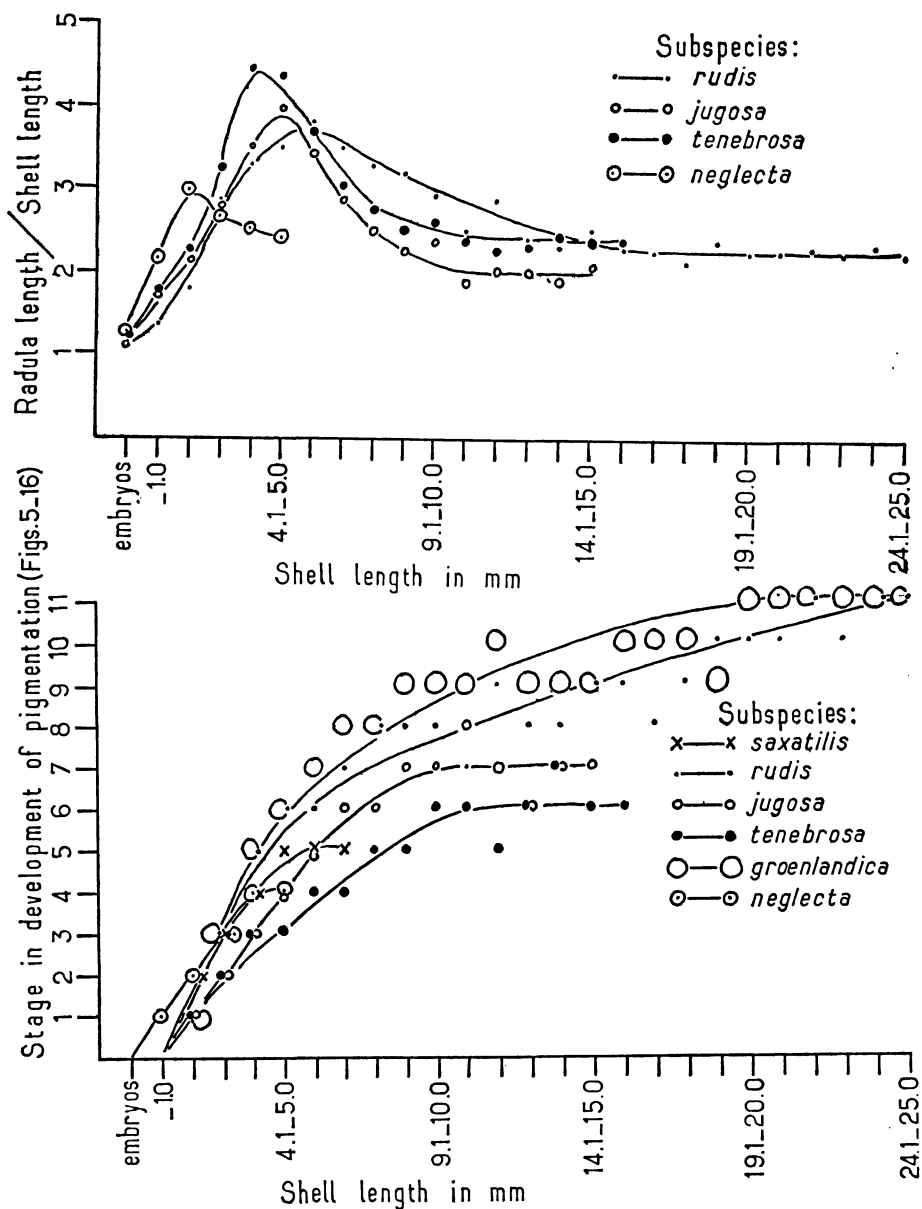
The pigmentation on the head and tentacles (Fig. 4) increases with age as in all the other subspecies. The range of pigmentation in adult specimens is from stage 3 (Fig. 8) to stage 7 (Fig. 12) and 4—9 (6) penial glands occur in a single row on the penis.

As far as I am aware, this subspecies occurs only in the lagoons of Venice. The description is included in this paper because this is the type locality for the species and because, in spite of the work of Dautzenberg and Fischer (1912) and Colman (1932), doubt is still sometimes expressed about the specific identity of the mediterranean and atlantic specimens.

Subspecies *rudis* (Maton, 1797) (= *Turbo rudis* Maton, 1797; *Littorina nigrolineata* Gray, 1839; *L. rudissima* Bean, 1844; *L. rudis* (Donovan) Forbes and Hanley, 1850 *in partim*; *Turbo sulcatus* Leach, 1852; *L. rudis* var. *sulcata* (Leach) Jeffreys, 1865; *L. rudis* var. *laevis* Jeffreys, 1865; *L. rudis* var. *globosa* Jeffreys, 1865; *L. rudis* var. *compressa* Jeffreys, 1865; *L. saxatilis* subsp. *rudis* (Maton) Dautzenberg and Fischer, 1912; *L. saxatilis* subsp. *nigrolineata* (Gray) Dautzenberg and Fischer, 1912; *L. nigrolineata* (Gray) Deyglun, 1955; *L. saxatilis* subsp. *rudis* (Maton) James, 1963, 1964 a, b, 1968 a) (Pl. 1, 2 d-f; 3, c-d; 4, c-d-f; 5, a-o; 6, g-h; 7, d-f; 8, c-d—Pl. 2, 1, a-c; 2, a-h; 3, d-f; 4, a-c; 5, e-f), the most variable and widely distributed British subspecies, measures 0.58—0.69 mm long on leaving the brood pouch of the adult. The maximum size attained, which varies from population to population, is influenced by the extent of exposure to air (Fig. 17) and to wave action (Fig. 18). The largest specimens (Pl. 1, 8, c-d), measuring up to 25.0 mm long, occur at about M.H.W.N., in the *Fucus spiralis* zone, on some very sheltered (7) shores. The smallest specimens, measuring up to 6.0 mm long (Pl. 1, 5, a-o) occur at about M.L.W.N. in crevices in the barnacle zone, on some exposed (3) and semi-exposed (4) shores. Subsp. *rudis* is the only subspecies in which the maximum size attained in a population is influenced by tide level. The range in maximum shell length attained in populations collected from the same level on shores with the same degree

of exposure to wave action is considerable. This suggests that other factors such as the type of substratum and available food, may also influence the maximum size attained.

The shell is almost invariably very thick in adults (Fig. 19, e-f), the range in shell density usually being 1.75—1.96. The only excep-

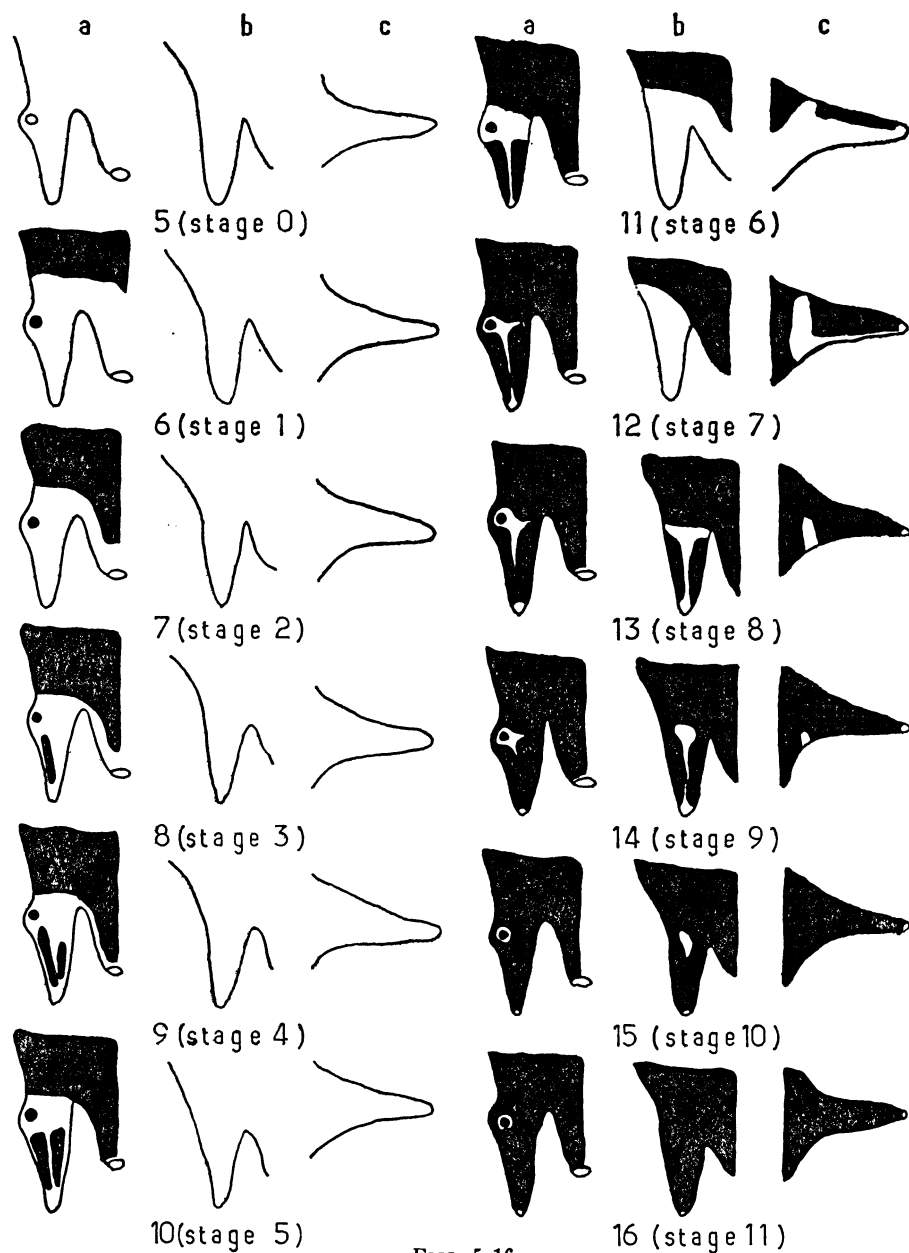


FIGS. 3, 4.

Graphs showing development of the mean radula length: shell length ratio and mean pigmentation on head and tentacles, with increase in shell length (age) in the subspecies *Littorina saxatilis*. (3.) Radula length: shell length ratio. (4.) Pigmentation on head and tentacles. The stages of development (0-11) are given in Figs. 5-16.

tions (Fig. 19, g), occurring in populations of var. *nigrolineata* found in deep crevices on exposed (3) shores near St. Ann's Head, Pembroke-shire, have a range of 1.55—1.75.

The shell shape may vary with exposure to wave action (Figs. 20-22), from very narrow (Pl. 1, 2, d-f) to very broad (Pl. 2, 4, a-c),



FIGS. 5-16.

*Littorina saxatilis*, diagrams showing twelve (0-11) stages in development of pigmentation on head and tentacles. a. dorsal view of right side of head and contracted right tentacle. b. ventral view of right side of head and contracted right tentacle. c. lateral view of right tentacle.

the spire from very tall to short and the aperture from very narrow to fairly wide. The range in the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in all adult specimens are 1.08—1.55, 1.35—2.05 and 1.4—1.9 respectively. The spire apex may be bluntly to very bluntly pointed, the sutures very deep and grooves and ridges may be present or absent. When present, the ridges are humped or flattened. Specimens on exposed shores (Pl. 2, 4, a-c—Pl. 1, 5, m-o) are usually smaller (Fig. 18, f-g), broader (Fig. 20, g), more deeply grooved and have a shorter spire (Fig. 21, g) and wider aperture (Fig. 22, f) or, exceptionally, are just thinner (Fig. 19, g), smaller (Pl. 1, 5, a-l) or more distorted (Pl. 2, 3, d-f) than those on sheltered shores (Pl. 1, 2, d-f, 3, c-d, 8, c-d). However, specimens which occur in the relative shelter of crevices (Pl. 2, 1, a-c) may be similar to those on more sheltered shores.

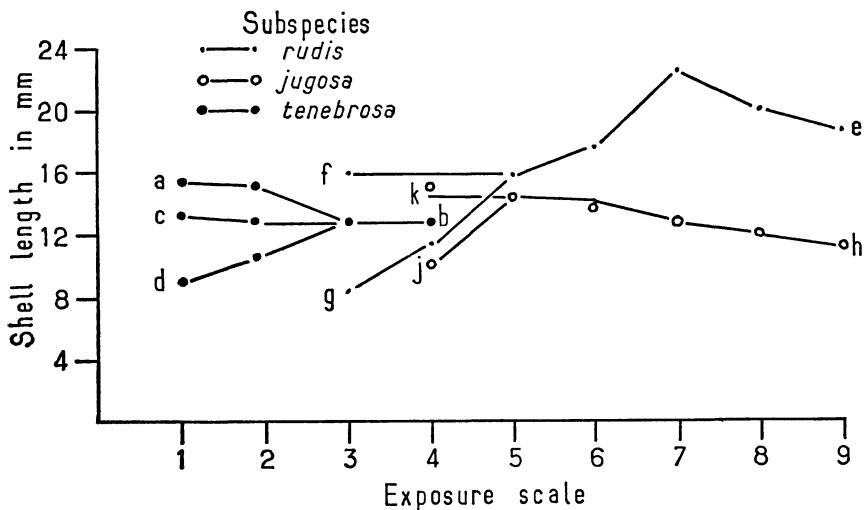
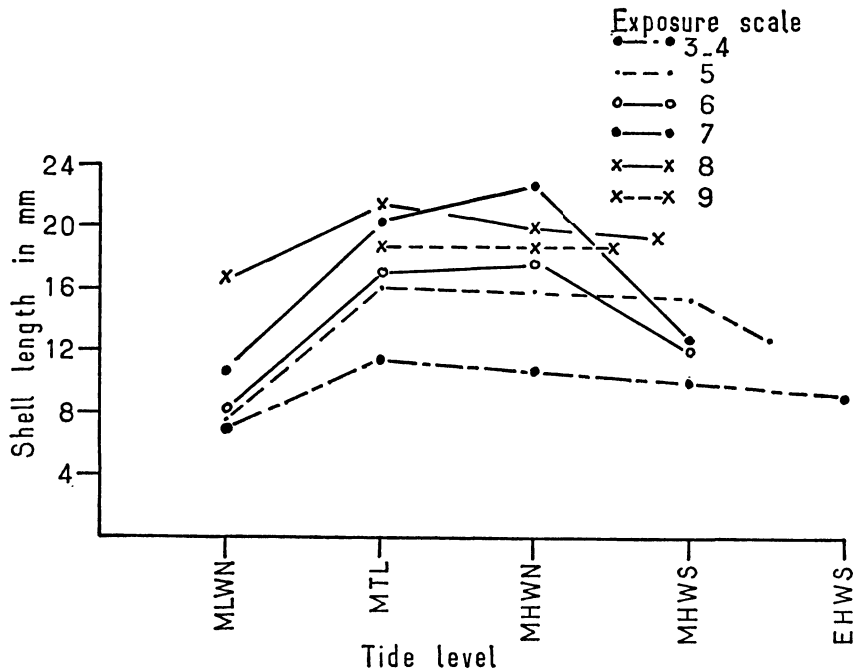
The colour forms recorded in Britain include *albida* Dautzenberg, 1887, *lutea* Dautzenberg and Durouchoux, 1900, *aurantia* Dautzenberg, 1887, *miniata* Dautzenberg and Fischer, 1912, *sanguinea* Dautzenberg and Durouchoux, 1900, *fulva* Monterosato, 1872, *fusca* Dautzenberg and Fischer, 1912, *zonaria* Bean, 1844, *fasciata* Dautzenberg, 1887, *nigrolineata* Gray, 1839 and *tessellata* Dautzenberg, 1893. The most common single coloured shells are fawn, shades of brown or grey and, more rarely, white, lemon, yellow, vermilion, carmine red, brick red or orange. Bicoloured patterns involve white, fawn, brown, grey, yellow or black but no tri- or multicoloured shells were found in this subspecies. In Britain as a whole, most populations consist mainly of dull coloured shells with rare brightly coloured individuals. Brightly coloured populations, which may consist of a single colour variety or very many colour varieties, are common, however, in the south-west, in Anglesey, Pembrokeshire, Cornwall, the Scilly Isles and the Channel Islands, all with an average minimum air temperature of over 6°C and over 4 hours of sunshine a day in winter.

The mean radula length: shell length ratio varies with age (Fig. 3). The range in adults is 1.7—4.5. The pigmentation on the head tentacles (Fig. 4) also increases with age to stage 11 (Fig. 16) in the largest specimens. The range of pigmentation in all adults including the smallest forms, is from stage 5 (Fig. 10) to stage 11 (Fig. 16). It is interesting to note that specimens parasitised by larval Digenea have less pigmentation on the head and tentacles than healthy specimens of the same size. This may be explained by the fact that larval Digenea cause gigantism in this host (James, 1965, 1968 *d*). In other words, parasitised specimens are younger than healthy specimens of the same size and, thus, have less pigmentation on the head and tentacles.

The range in the number of penial glands on the penis is 3-24, the mean number being higher in specimens on the more exposed shores (Fig. 23).

The results of marking experiments, seasonal observations of the populations density and of the breeding cycle, which have been described in detail elsewhere (James, 1968 *b, d*), show that specimens of subsp. *rudis* do not undergo extensive migrations but remain on approximately the same position on the rock, or in the pool where they were born, undergoing only limited random feeding excursions, usually of only a few centimetres but sometimes of up to several





FIGS. 17, 18.

Graphs showing variations in the mean of the maximum shell length attained in populations of *Littorina saxatilis* on different levels on the shore and on shores of various degrees of exposure to wave action. (17.) subsp. *rudis*.

E.H.W.S. extreme high water on spring tides,  
M.H.W.N. mean high water on neap tides,  
M.H.W.S. mean high water on spring tides,  
M.L.W.N. mean low water on neap tides,  
M.T.L. mean tide level.

Exposure scale for figs. 17-24. 1. extremely exposed, 2. very exposed, 3. exposed, 4. semi-exposed, 5. fairly sheltered, 6. sheltered, 7. very sheltered, 8. extremely sheltered, 9. extremely sheltered estuarine station or salt marsh. (18.) subsp. *rudis*, *jugosa* and *tenebrosa*, with exposure to wave action only. a. var. *elata*, b. var. *tenebrosa*, c. var. *similis* and *tenebrosa*, d. var. *patula*, e. var. *rudis*, f. vars. *rudissima*, *nigrolineata* and *jugosoides*, g. small forms of vars. *rudissima*, *nigrolineata* and *jugosoides*, h. var. *rudissimoides*, j. var. *tenuis*, k. var. *attenuata*.

metres, when covered by the tide. The fully formed embryos leave the brood pouch of the adult usually between January and February and, in much greater numbers, between May and September.

In Britain, the subspecies occurs, usually between M.H.W.S. and M.L.W.N., in abundance in the *Fucus spiralis* and upper *Ascophyllum* zones but extending also into the *Fucus vesiculosus* and *Pelvetia* zones, on all fairly sheltered (5) to extremely sheltered (8) rocky shores. It is also found, usually in crevices, throughout the barnacle zone and extending into the lower supralittoral fringe, on many semi-exposed (4) and some exposed (3) shores. It occurs, from M.T.L. to midway between M.H.W.N. and M.H.W.S., on some salt marshes and on mud flats in estuaries, where it may withstand a drop in salinity to 5 p. 1000 (Fischer-Piette, Gaillard and James, 1964; James, 1968 a). In these habitats, the subspecies requires a firm substratum as, unlike *Littorina littorea*, it does not occur on sand at the mouth of estuaries and only on mud when it can attach itself to the rock or stones beneath the surface. The subspecies is found throughout Europe, where it frequently forms intermediates with subspp. *jugosa* and *tenebrosa*.

Subsp. *rudis* may be subdivided, on the basis of shell characters and distribution, into four varieties namely, *rudis* (Maton, 1797), *rudissima* (Bean, 1844), *nigrolineata* (Gray, 1839) and *jugosoides* nov.

Var. *rudis* (Pl. 1, 2, d-f; 3, c-d) is devoid of sculpturing, very narrow to fairly broad and has a medium to very tall spire and usually a very narrow to narrow aperture. It occurred on all the estuarine mud flats examined, in some salt marshes and, together with vars. *rudissima* or *nigrolineata*, on most extremely sheltered (8) rocky shores, occasionally on very sheltered (7) and rarely, in crevices, on sheltered (6) and fairly sheltered (5) rocky shores. Intermediates between var. *rudis* and var. *rudissima* or var. *nigrolineata* occur on some extremely sheltered (8) to fairly sheltered (5) shores. On other neighbouring apparently topographically identical shores, the varieties may exist side by side without forming intermediates.

Var. *rudissima* (Pl. 1, 5, a-d; 8, c-d—Pl. 2, 1, a-c; 2, a-h; 3, d-f) has very shallow, wide to narrow grooves, humped ridges, a medium to short spire, a very narrow aperture and is fairly broad to very broad. It occurred on all the very sheltered (7) rocky shores examined, on most extremely sheltered (8) and sheltered (6), many fairly sheltered (5) and, occasionally in deep crevices, on semi-exposed (4) and exposed (3) rocky shores.

Var. *nigrolineata* (Pl. 1, 4, c-d, f; 5, e-l; 6, g-h; 7, d-f) is essentially similar to *rudissima* but the ridges are flat and the grooves deep and narrow. The shores on which this variety is found have the same degree of exposure to wave action as those with var. *rudissima* but only occur in the south-west. A colour form with yellow ridges and brown or black grooves occurs in Anglesey, the Channel Islands and the Scilly Isles, and a colour form with white ridges and brown, black or purple grooves, in Anglesey, Galway, Pembrokeshire and Cornwall. Intermediates between the two colour forms occur in Anglesey. Shores which have both var. *rudissima* and var. *nigrolineata* sometimes have intermediates between the two varieties but neighbouring, apparently topographically identical shores may not. All British forms of var. *nigrolineata* examined by me appear to be

viviparous and have the same vertical distribution of var. *rudissima*. In contrast, on a shore at Roscoff, Finistère, described by Deyglun (1955), *nigrolineata* has reverted to oviparity and occurs lower down on the shore than *rudissima*.

Var. *jugosoides* (Pl. 1, 5, m-o—Pl. 2, 4, a-c; 5, e-f) is broad to very broad, has a short spire, narrow to fairly wide aperture, shallow to very deep grooves and humped ridges. It occurs throughout Britain in shallow crevices on some semi-exposed (4) and exposed (3) shores and, more rarely, on fairly sheltered (5) shores. Intermediates between var. *jugosoides* and var. *rudissima* or var. *nigrolineata* may or may not occur when they are found together on fairly sheltered (5) and semi-exposed (4) rocky shores.

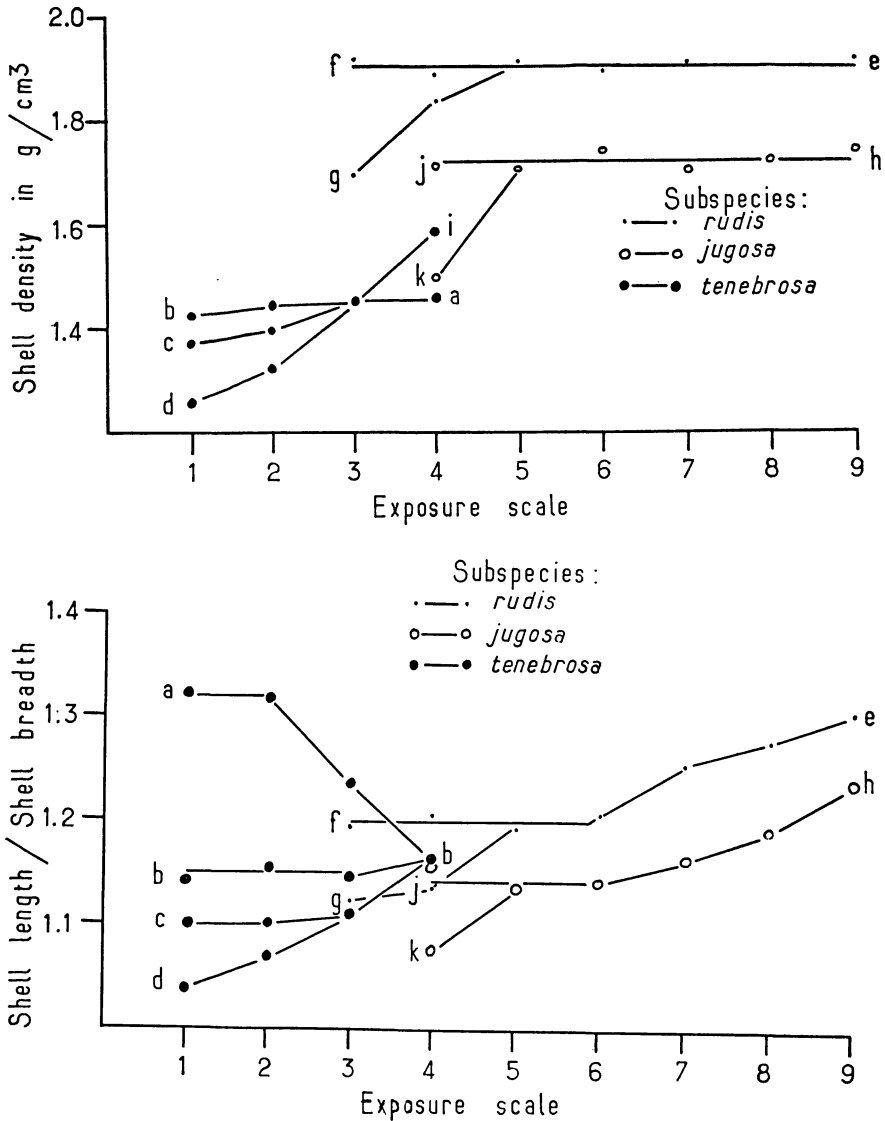
The change in form from one variety into another in this and the two following subspecies, is often correlated with changes in exposure to wave action. Thus, var. *rudis*, characteristic of estuarine stations and extremely sheltered (8) rocky shores, gives way to or gradually changes into var. *rudissima* or var. *nigrolineata* on very sheltered (7) and sheltered (6) rocky shores. These are replaced in turn by var. *jugosoides* on fairly exposed (4) and exposed (3) rocky shores. Relatively sheltered crevices on exposed shores, however, may have varieties characteristic of more sheltered shores (Pl. 2, 1, a-c).

Subspecies *jugosa* (Montagu, 1803) (= *Turbo jugosus* Montagu, 1803; *Littorina rudis* (Donovan) Forbes and Hanley, 1850 *in partim*; *L. tenebrosa* (Mont.) Forbes and Hanley, 1850 *in partim*; *L. saxatilis* subsp. *jugosa* (Mont.) Dautzenberg and Fischer, 1912; *L. saxatilis* subsp. *patula* (Thorpe) var. *attenuata* Dautzenberg and Fischer, 1912; *L. saxatilis* subsp. *jugosa* (Mont.) James, 1963, 1964 a, b, 1968 a) (Pl. 1, 2, a-c; 3, a-b; 4, a-b, e; 6, c-d; 8, a-b—Pl. 2, 5, c-d) measures 0.50—0.55 mm long on leaving the brood pouch of the adult. The maximum size attained in each population varies only slightly with exposure to wave action (Fig. 18). The largest specimens, measuring up to 15.0 mm long, occur on some sheltered (6), fairly sheltered (5) (Pl. 1, 4, a, e) and semi-exposed (4) shores (Pl. 2, 5, c-d) and the smallest up to 10.0 mm long, on some mud flats in estuaries (Pl. 1, 3, a-b) and some semi-exposed (4) shores (Pl. 1, 6, c-d). The shell is usually thick (Fig. 19, h, j) but not as thick as in the previous subspecies. The range in shell density in adults is usually 1.6—1.8. A unique population (Pl. 1, 6, c-d), on a semi-exposed (4) headland on the Dale peninsula, Pembrokeshire, however, has a thinner shell (Fig. 19, k) with a shell density range of 1.38—1.6.

The shell shape varies with exposure to wave action (Fig. 20-22) from fairly broad (Pl. 1, 2, a-c; 3, a-b) to very broad (Pl. 2, 5, c-d), the spire from medium to very short and the aperture from very narrow to very wide. The range in the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in all adult specimens are 1.0—1.3, 1.25—1.55 and 1.25—1.8 respectively. The spire apex is sharply to bluntly pointed and the sutures deep. Humped ridges are invariably present and are usually more numerous and closer together than in other subspecies. On exposed shores the shell may be smaller (Fig. 18 j), thinner (Fig. 19 k) and more deeply grooved (Pl. 1, 6, c-d) or broader (Fig. 20 k) with a shorter spire (Fig. 21 k) and a larger, wider aperture (Fig. 22 j—

Pl. 2, 5, c-d) than on more sheltered shores (Pl. 1, 2, a-c; 3, a-b; 8, a-b).

Most of the colour forms recorded for the previous subspecies have been recorded for subsp. *jugosa*. The exceptions are *zonaria*, *fasciata* and *nigrolineata*.



FIGS. 19, 20.

Graphs showing variations in shell thickness, as measured by the mean density of shell and contained animal, and shape, as measured by the mean shell length: shell breadth ratio, of *L. saxatilis*, with changes in exposure to wave action. (19.) shell thickness. a. var. *tenebrosa*, b. vars. *similis* and *tenebrosa*, c. var. *elata*, d. var. *patula*, e. var. *rudis*, f. vars. *rudissima*, *nigrolineata* and *jugosoides*, g. thinner form of var. *nigrolineata*, h. var. *rudissimoides*, j. vars. *jugosa* and *attenuata*, k. var. *tenuis*. (20.) shape. a. var. *elata*, b. var. *tenebrosa*, c. var. *similis*, d. var. *patula*, e. var. *rudis*, f. vars. *rudissima* and *nigrolineata*, g. var. *jugosoides*, h. var. *rudissimoides*, j. vars. *jugosa* and *tenuis*, k. var. *attenuata*.

The mean radula length: shell length ratio varies with age (Fig. 3) and is higher in young specimens but lower in older specimens than in subsp. *rudis*. The range in adult specimens is 1.5—5.5. The mean pigmentation on the head and tentacles (Fig. 4) increases with age to stage 7 (Fig. 12). The range in adults is from stage 4 (Fig. 9) to stage 9 (Fig. 14). A slight increase occurs in the mean number of penial glands on the penis with increase in exposure to wave action (Fig. 23). The range in all adult specimens is 7-25.

The migratory behaviour of this subspecies is similar to that in the previously described subspecies but the breeding cycle differs slightly in so far as the extended spatfall begins later at the end of June instead of in May.

The subspecies may form a zone above subsp. *rudis* and subsp. *neglecta* usually between M.H.W.N. and M.H.W.S., in abundance in *Pelvetia* but extending a little above and below this sea-weed, on semi-exposed (4) to extremely sheltered (8) rocky shores. On mud flats in estuaries, it extends over the same vertical range as subsp. *rudis*. Subsp. *jugosa* was found throughout Britain but only on about half of the fairly sheltered (5) to extremely sheltered (8) shores examined and on only two of the semi-exposed (4) shores (Pl. 1, 6—Pl. 2, 5). When subsp. *jugosa* is absent, the *Pelvetia* zone is occupied by subsp. *rudis*. When both subspecies occur on the same shores (Pl. 1, 2, 3, 4, 6, 8—Pl. 2, 5), they overlap in distribution but no intermediates are found in Britain.

I have also examined specimens of subsp. *jugosa* from Norway and Spain which are morphologically identical to British specimens but which share the same zone on the rocky shore as subsp. *rudis*.

This subspecies may also be subdivided into four varieties namely, *rudissimoides* nov., *jugosa* (Montagu, 1803), *attenuata* (Dautzenberg and Fischer, 1912) and *tenuis* nov.

Var. *rudissimoides* (Pl. 1, 2, a-c; 3, a-b) is fairly broad, has very shallow grooves, a medium spire and a very narrow aperture. It occurs on muddy estuarine shores but also, very rarely, on extremely sheltered (8), very sheltered (7) and, in crevices, sheltered (6) rocky shores. Intermediates may occur between var. *rudissimoides* and var. *jugosa* on rocky shores.

Var. *jugosa* (Pl. 1, 4, a-b, e; 8, a-b) is broad, has very shallow to very deep grooves, a medium to short spire and a fairly wide aperture. It occurs on fairly sheltered (5) to very sheltered (7) and, rarely, on extremely sheltered (8) rocky shores.

Var. *attenuata* (Pl. 2, 5, c-d) is very broad, has very shallow grooves, a medium to very short spire and a very large, wide to very wide aperture. I have found this variety only on semi-exposed (4) rock faces in The Wick, Skomer Island. Intermediates between *attenuata* and *jugosa* occur on neighbouring fairly sheltered (5) rock faces.

Var. *tenuis* (Pl. 1, 6, c, d) is the same shape but has a smaller and thinner shell than subsp. *jugosa*. It is always deeply grooved and occurs on some semi-exposed (4) shores on the Dale peninsula. Intermediates between var. *tenuis* and var. *jugosa* occur on some

fairly sheltered (5) shores and in crevices on the semi-exposed (4) shores in the vicinity.

Subspecies *tenebrosa* (Montagu, 1803) (= *Turbo tenebrosus* Montagu, 1803; *Turbo vestita* Say, 1821; *Turbo labiatus* Brown, 1827; *Littorina patula* (Jeffreys) Forbes and Hanley, 1850; *L. rudis* var. *jugosa* (Mont.) Jeffreys, 1865; *L. rudis* var. *similis* Jeffreys, 1865; *L. rudis* var. *tenebrosa* (Mont.) Jeffreys, 1865; *L. saxatilis* subsp. *tenebrosa* (Mont.) Dautzenberg and Fischer, 1912; *L. saxatilis* subsp. *patula* (Thorpe) Dautzenberg and Fischer, 1912 *in partim*; *L. rudis* var. *alticola* Dacie, 1917; *L. saxatilis* subsp. *tenebrosa* (Mont.) James, 1963, 1964 *a, b*, 1968 *a*) (Pl. 1, 6, a-b; 7, a-c—Pl. 2, 1, d-f; 3, a-c; 4, d-f; 5, a-b; 6, a-g; 7, a-f) measures 0.7–0.75 mm long on leaving the brood pouch of the adult. The maximum size attained (Fig. 18) in each population varies slightly with exposure to wave action. The largest specimens (Pl. 2, 7, a-c), measuring up to 16.0 mm long, occur in very deep sheltered crevices and the smallest specimens (Pl. 2, 7, d-f), up to 8.0 mm long, in shallow exposed crevices in the supralittoral fringe on some extremely exposed (1) shores.

The shell is usually thin to extremely thin and decreases in thickness with increase in exposure to wave action (Fig. 19). The range in shell density in adults of all varieties is 1.2–1.7.

#### PLATE 1

*Littorina saxatilis*, adult specimens (All the specimens in the same figure, except where stated otherwise, were collected from the same shore).

1 (a-f). Subsp. *saxatilis*, from the type locality in the lagoons of Venice. August 1960. a,c. ex.col. *hieroglyphica* (grey and white). b,d,e. ex.col. *tessellata* (grey and white). f. uniform pale grey.

2 (a-f). Specimens from a muddy estuarine station in a tidal inlet near Woodbridge. April 1962. a-c. subsp. *jugosa* var. *rudissimoides*. a. ex.col. *fulva* (fawn). b,c. ex.col. *fusca* (dark brown). d-f. subsp. *rudis* var. *rudis*, narrow form, ex.col. *fulva*.

3 (a-d). Specimens from a muddy estuarine station, Mouth of the River Leri, Ynyslas Estuary, near Aberystwyth. a-b. subsp. *jugosa* var. *rudissimoides* ex.col. *fulva*. c-d. subsp. *rudis* var. *rudis*, broad form. c. ex.col. *fulva*. d. ex.col. *fulva*.

4 (a-d). Specimens from a fairly sheltered (5) rocky shore, near St. Martin, Channel Islands. July 1963. a,b. subsp. *jugosa* var. *jugosa*, ex.col. *albida*. c,d. subsp. *rudis* var. *nigrolineata*, yellow with dark brown lines. (e-f). from a fairly sheltered (5) shore, Gateholm Sound, Dale peninsula, Wales. December 1960. e. subsp. *jugosa* var. *jugosa*, ex.col. *miniata*. f. subsp. *rudis* var. *nigrolineata*, white with dark brown lines.

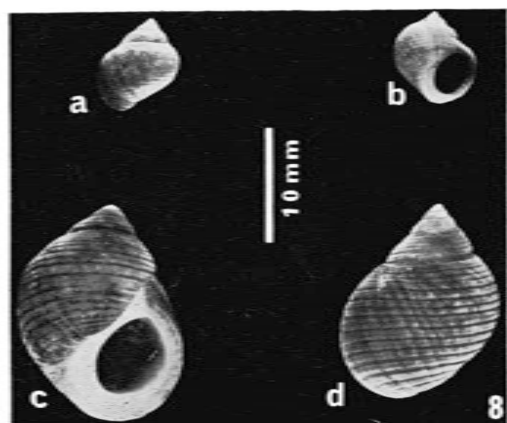
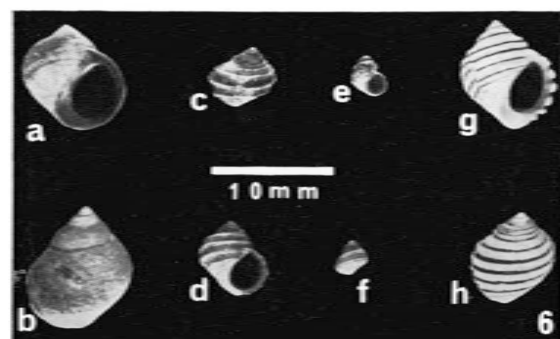
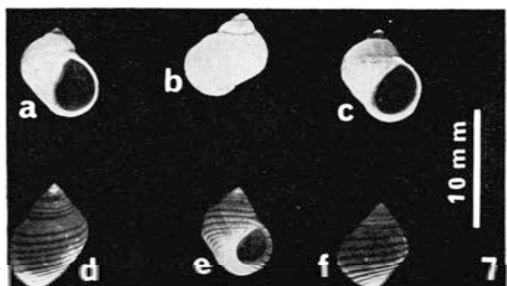
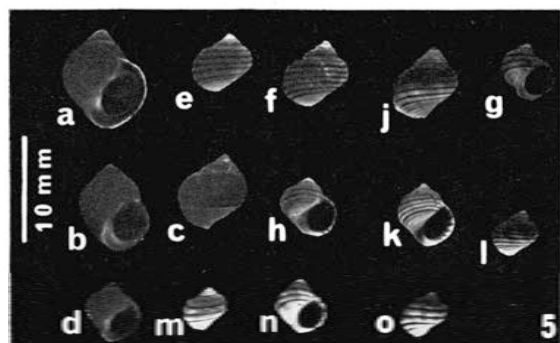
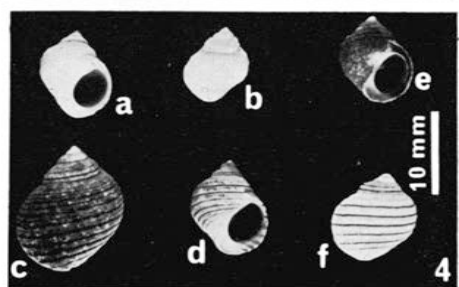
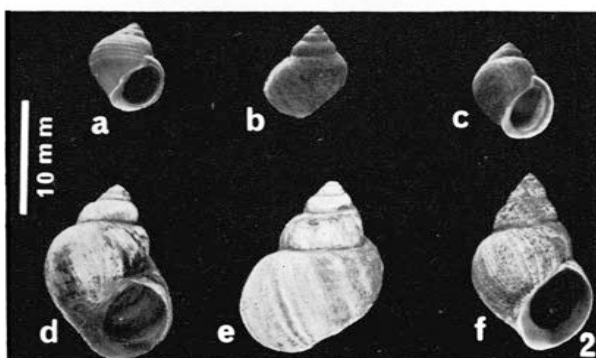
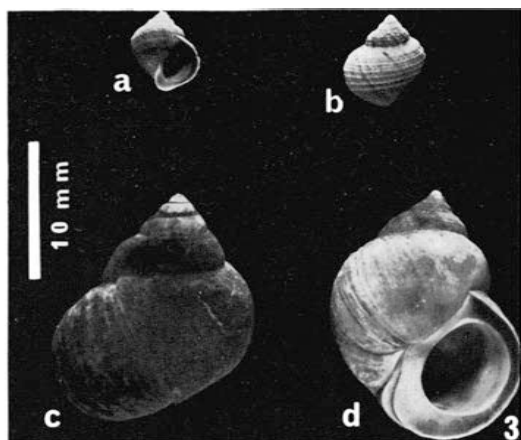
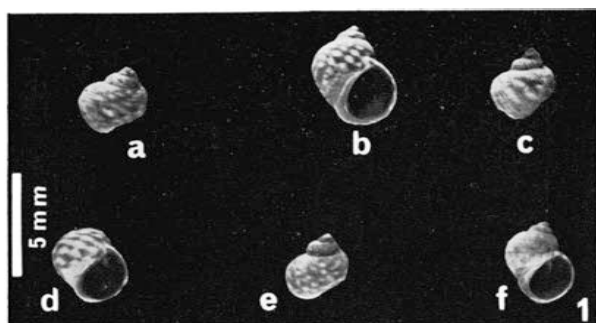
5 (a-d). Subsp. *rudis* var. *rudissima*, small form, ex.col. *fusca*, from a semi-exposed (4) rocky shore, near Hillswick, Shetland Islands. July 1963. (e-h). subsp. *rudis* var. *nigrolineata*, small form, white with dark brown lines. From an exposed (3) shore near Dale point, Dale peninsula, Pembrokeshire, Wales. December 1960. (j-l). subsp. *rudis* var. *nigrolineata*, small form, white with black lines. From an exposed (3) shore, near Lizard Point, Cornwall. July 1963. (m-o). subsp. *rudis* var. *jugosoides*, small form, yellow with dark brown grooves. From an exposed (3) shore, near St. Mary, Channel Islands. July 1963.

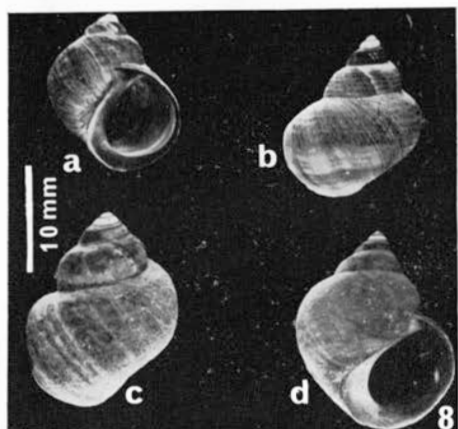
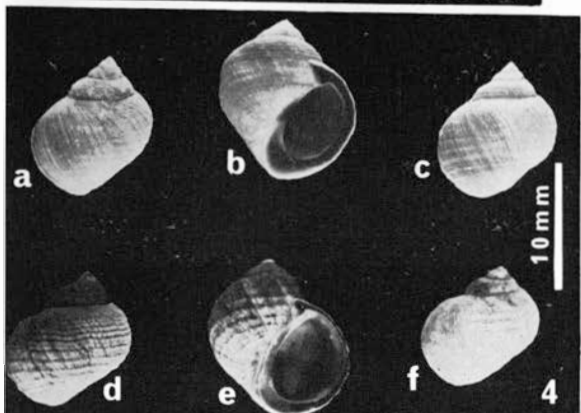
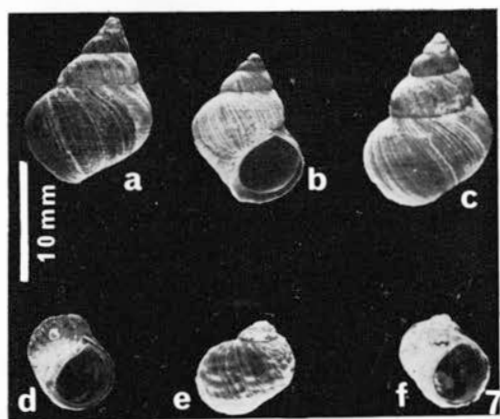
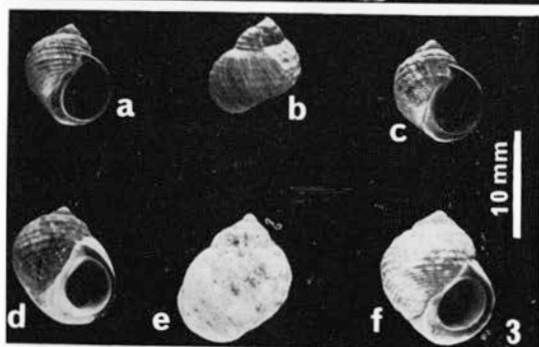
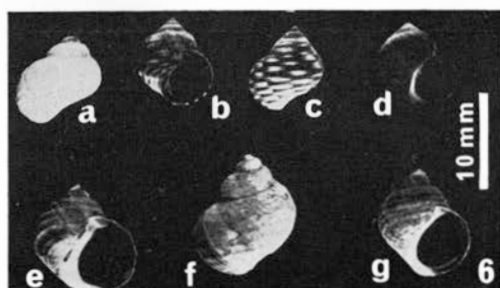
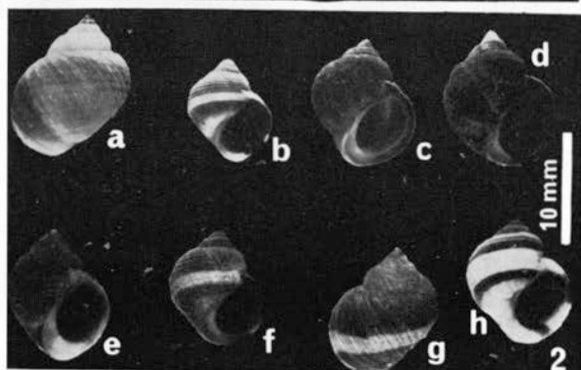
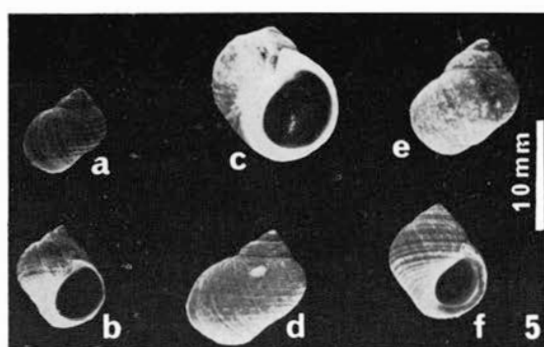
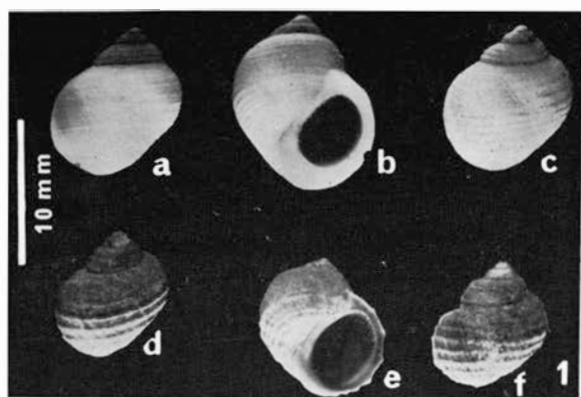
6 (a-h). Specimens from a semi-exposed (4) rocky headland near Thorny Pit, Dale peninsula, Wales. December 1960. a,b. subsp. *tenebrosa* var. *tenebrosa*, thin shelled form, ex.col. *fusca*. c,d. subsp. *jugosa* var. *tenuis*, yellowish brown. e,f. subsp. *neglecta*, ex.col. *interrupta*. g,h. subsp. *rudis* var. *nigrolineata*, white with purple lines.

7 (a-f). Specimens from a semi-exposed (4) rocky shore, near St. Mary, Channel Isles. July 1963. a-c. subsp. *tenebrosa* var. *tenebrosa*, ex.col. *albida*, very thin shelled form. d-f. subsp. *rudis* var. *nigrolineata*, yellow with dark brown lines.

8 (a-d). Specimens from a very sheltered (7) rocky shore, Black Rock, Dale, Pembrokeshire. December 1960. a,b. subsp. *jugosa* var. *jugosa*, ex.col. *fulva*. c,d. subsp. *rudis* var. *rudissima*, reddish brown.

Subsp. *neglecta* was also found on the same shores as the specimens shown in 4-8.







The shell shape varies with exposure to wave action (Figs. 20-22) from narrow to broader than long (Pl. 2, 7, a-c and d-f), the spire from very tall to very short and the aperture from fairly wide to very wide. The range in the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in adult specimens are 0.85—1.38, 1.18—2.25 and 1.05—1.50 respectively. The spire apex is blunt to very blunt and the sutures very deep. The humped ridges, when present, are few in number and the grooves shallow to very deep.

On the more exposed shores (Pl. 2, 7, d-f), on the open rock or in shallow crevices, the shell is smaller (Fig. 18 d), thinner (Fig. 19 d), broader (Fig. 20 d) and has a shorter spire (Fig. 21 d) and a larger, wider aperture (Fig. 22 c) than on the more sheltered shores (Pl. 1, 6, a-b). In deep crevices and/or above the influence of the waves, however, the shells may retain the characters of those from more sheltered shores (Pl. 2, 6, a-d) or even be larger, narrower and have taller spires (Fig. 18 a, 20 a, 21 a—Pl. 2, 7, a-c). Specimens on the open rock and in shallow or deep crevices may have shallow to very deep grooves but those in deep crevices may also have a completely smooth shell.

The shell colour is more variable in this subspecies than in any other. In addition to the colour forms, except *nigrolineata*, listed for

## PLATE 2

*Littorina saxatilis*, adult specimens (all the specimens in the same figure, except where stated otherwise, were collected from the same shore).

1 (a-f). Specimens from an exposed (3) rocky shore in Chapel Bay, near St. Govan's Head, Pembrokeshire. March 1962. a-c. subsp. *rudis* var. *rudissima*, uniform pale grey, from very deep crevices. d-f. subsp. *tenebrosa* var. *similis*, ex.col. *miniata*.

2 (a-h). Subsp. *rudis* var. *rudissima*, from a sheltered (6) rocky shore, Solway Firth. July 1960. a. ex.col. *fulva*. b,f. ex.col. *zonaria* (= *fasciata*). c-e. ex.col. *fusca*. h. ex.col. *zonaria* (= *trifasciata*).

3 (a-f). Specimens from an exposed (3) rocky shore on Constitution Hill Rocks, Aberystwyth. April 1960. a-c. subsp. *tenebrosa* var. *similis*, dark greyish green. d-f. subsp. *rudis* var. *rudissima*, distorted from, ex.col. *fulva*.

4 (a-f). Specimens from an exposed (3) rocky shore, near Twr Gwylanod, Aberystwyth. December 1960. a-c. subsp. *rudis* var. *jugosoides*, large form, ex.col. *fulva*. d-f. subsp. *tenebrosa* var. *similis*, dark grey.

5 (a-f). Specimens from a semi-exposed (4) rocky shore in The Wick, Skomer Island, Wales. March 1962. a,b. subsp. *tenebrosa* var. *tenebrosa*, thin shelled form, ex.col. *fusca*. c,d. subsp. *jugosa* var. *attenuata*. c. ex.col. *albida*. d. ex.col. *fulva*. e,f. subsp. *rudis* var. *jugosoides*, large form, ex.col. *fulva*.

6 (a-g). Subsp. *tenebrosa*, from an extremely exposed (1) rocky shore, Grind of Navir, Shetland Islands. July 1963. a-d. var. *tenebrosa*, very thin shelled form, from pools on the horizontal rock surface of the Grind, from 100' to 130' above E.H.W.S., up to 100 yards from the sea. a. ex.col. *albida*. b. ex.col. *interrupta*, mustard and dark brown. c. ex.col. *interrupta*, black and white. d. ex.col. *fusca*. e-g. var. *similis*, ex.col. *fulva*, but with greyish dust covering surface, from deep crevices on vertical rock faces from M.H.W.N. to 100' above E.H.W.S.

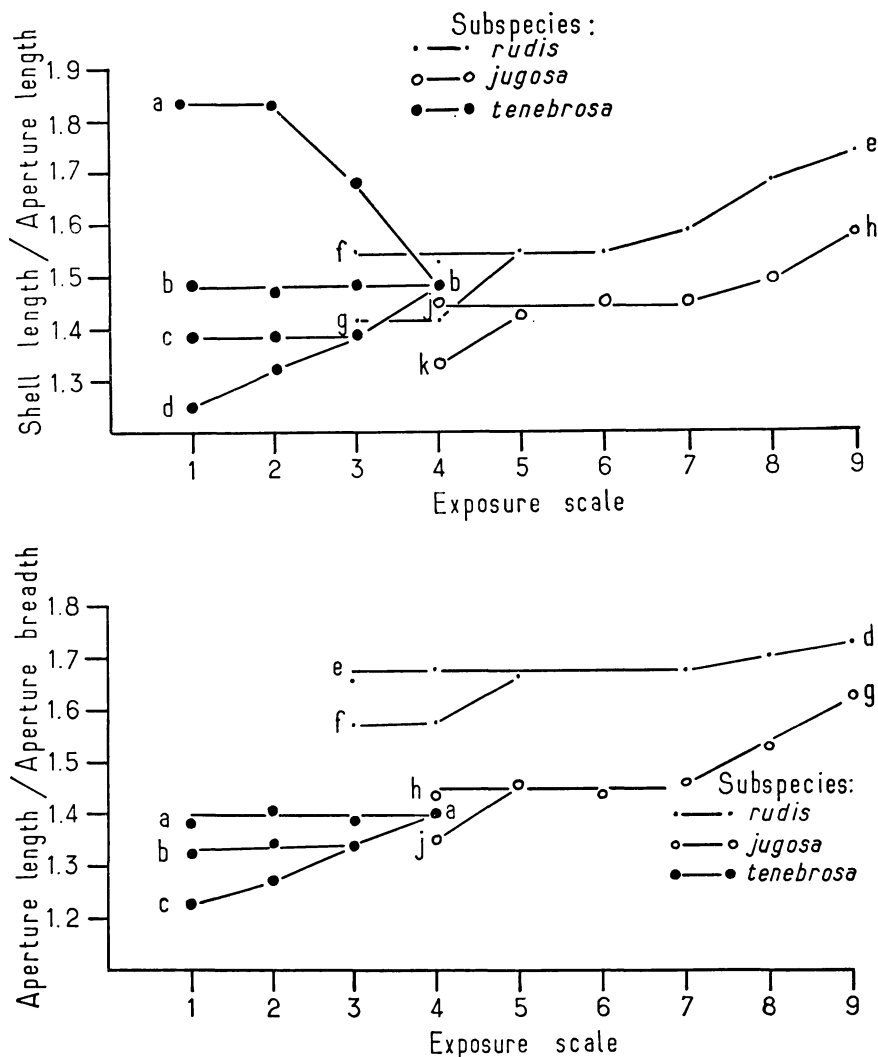
7 (a-f). Subsp. *tenebrosa* from an extremely exposed (1) rocky shore, Skomer Head, Wales. March 1962. a-c. var. *elata*, uniform brownish grey, from very deep crevices. d-f. var. *patula*, from shallow crevices. d. ex.col. *fulva*. e. ex.col. *interrupta*. f. ex.col. *zonaria* and *interrupta*.

8 (a-d). Subsp. *groenlandica*. a-b. from an extremely sheltered (8) rocky shore, Ingöy, Norway. August 1960. a. ex.col. *fusca*. b. ex.col. *zonaria*, orange and brown. c,d. from a salt marsh near Dublin. May 1963. ex.col. *fulva*.

Subsp. *neglecta* was also found on the same shores as the specimens shown in 1-7.

*I am grateful to Carl Stockton for help with the photographs.*

subsp. *rudis*, the subspecies has *nojensis* Fischer-Piette and Gaillard, 1964; *maculata* Fischer-Piette and Gaillard, 1963; *flammulata* Dautzenberg and Fischer, 1912; *lineata* Dautzenberg and Fischer, 1912;



FIGS. 21, 22.

Graphs showing variations in spire height, as measured by the mean shell length: aperture length ratio, and aperture width, as measured by the mean aperture length: aperture breadth ratio, of *Littorina saxatilis*, with changes in exposure to wave action. (21.) spire height. a-k as in Fig. 20. (22.) aperture width. a. var. *tenebrosa*, b. var. *similis*, c. vars. *elata* and *patula*, d. var. *rudis*, e. vars. *nigrolineata* and *rudissima*, f. var. *jugosoides*, g. var. *rudissimoides*, h. vars. *jugosa* and *tenuis*, j. var. *attenuata*.

*interrupta* Fischer-Piette, Gaillard and Jouin, 1961; *tractibus* Fischer-Piette, Gaillard and Jouin, 1961; *sellensis* Fischer-Piette, Gaillard and Jouin, 1961; *hieroglyphica* Fischer-Piette, Gaillard and Jouin, 1961; *bynei* Dautzenberg and Fischer, 1912; *bi-interrupta* Fischer-Piette and

Gaillard, 1963 and *bi-zonaria* James, 1963. The additional colours involved are greenish yellow, purple, mustard, greyish green and pink. Tricoloured and multicoloured shells occur and Fischer-Piette, Gaillard and James (1963) have described two multicoloured populations with as many as 155 and 164 colour patterns.

The mean radula length: shell length ratio (Fig. 3) is higher than in subsp. *jugosa*. The range in adults is 1.5–5.7. The pigmentation on the head and tentacles (Fig. 4) is less than in subspp. *rudis* and *jugosa* but there are more penial glands on the penis (Fig. 23). The mean number of penial glands, which may occur in a double row, is not affected by exposure to wave action (Fig. 23). The range

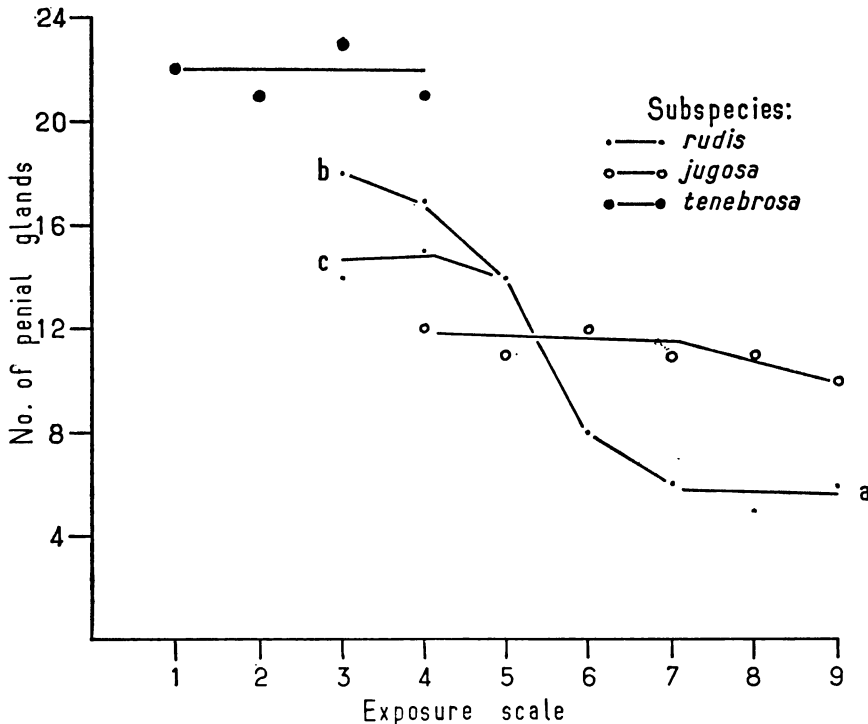


FIG. 23.

Graph showing variations in the mean number of penial glands occurring on the penis of *Littorina saxatilis* with changes in exposure to wave action. a. var. *rudis*, b. var. *jugosoides*, c. vars. *nigrolineata* and *rudissima*.

of pigmentation in adults is from stage 4 (Fig. 9) to stage 8 (Fig. 13) and the range in the number of penial glands is 10–30.

The specimens of this subspecies that occur in the supralittoral fringe on semi-exposed (4) and exposed (3) shores and in the lower supralittoral fringe on very exposed (2) and extremely exposed (1) shores, migrate down to the lower supralittoral fringe and upper midlittoral zone and give birth to their young in January–February and in July–August. The young and adults then migrate towards the upper supralittoral fringe (James, 1968 *b*). Specimens migrate when the rock is damp shortly after the tides have retreated or in showers of rain.

In Britain, the subspecies occurs in abundance throughout the supralittoral fringe, forming a zone above subsp. *neglecta* and sometimes subsp. *rudis* (Pl. 1, 7—Pl. 2, 1, 3, 4) and *jugosa* (Pl. 1, 6—Pl. 2, 5). No intermediates occur where the zones overlap. Subsp. *tenebrosa* occurs on all extremely exposed (1) to exposed (3) rocky shores except those which are completely devoid of crevices. It appears to be unable to cling on to completely smooth rock at these exposures. The subspecies also occurs on the open rock or in crevices on most semi-exposed (4) shores and, occasionally, in pools, between M.H.W.S. and E.H.W.S., in salt marshes. The upper limit of distribution increases, with exposure to wave action, from about 10-20' above the barnacle line on semi-exposed (4) shores to 100-130' on extremely exposed (1) shores. Exceptionally, Dacie (1917) found specimens about 450' above chart datum on St. Kilda.

The subspecies is also widely distributed in Europe and North America where it is sometimes the only subspecies present, occurring in the midlittoral zone on fairly sheltered (5) to extremely sheltered (8) rocky shores as well as in the habitats occupied in Britain.

Subsp. *tenebrosa* may be subdivided into four varieties namely, *elata* Dautzenberg and Fischer, 1912, *tenebrosa* (Montagu, 1803), *similis* (Jeffreys, 1865) and *patula* (Thorpe, 1844).

Var. *elata* (Pl. 2, 7, a-c) has a very thin, narrow shell which may be devoid of sculpturing or may have very shallow grooves and few humped ridges. The spire is very tall and the aperture relatively small but very wide. It occurs in very deep crevices on some very exposed (2) and extremely exposed (1) shores and, occasionally, in salt marshes.

Var. *tenebrosa* (Pl. 1, 6, a-b; 7, a-c—Pl. 2, 5, a-b, 6, a-d) has a thin to very thin, fairly broad to broad shell with shallow grooves. The spire is medium to short and the aperture fairly wide to wide. The thin shelled form (Pl. 1, 6, a-b—Pl. 2, 5, a-b) occurs on open rock or in crevices on some semi-exposed (4) shores. The very thin shelled form (Pl. 1, 7, a-c—Pl. 2, 6, a-d) is found on the open rock on other semi-exposed (4) shores and in deep crevices on some exposed (3) to extremely exposed (1) shores. Intermediates between var. *elata* and var. *tenebrosa* may occur in crevices on exposed (3) and very exposed (2) shores.

Var. *similis* (Pl. 2, 1, d-f; 3, a-c; 4, d-f; 6, e-g) has a very thin, broad to very broad shell with shallow to very deep grooves. The spire is short and the aperture is wide. It occurs in shallow crevices on most exposed (3) shores and, rarely, in deep crevices, on very exposed (2) and extremely exposed (1) shores. Intermediates between var. *similis* and var. *tenebrosa* are found occasionally in crevices on extremely exposed (1) to exposed (3) shores.

Var. *patula* (Pl. 2, 7, d-f) has an extremely thin, very broad to broader than long shell with shallow grooves. The spire is very short and the aperture relatively large and very wide. The shell shape enables this variety to exist in only very shallow crevices or in hair-line cracks on gently sloping ledges in the lower supralittoral fringe on extremely exposed (1) shores. Intermediates between var. *patula* and var. *similis* occur in a similar habitat on very exposed (2) shores.

Subspecies *groenlandica* (Menke, 1830) (= *Littorina groenlandica* Menke, 1830; *Turbo obligatus* Say, 1821; *L. saxatilis* subsp. *groenlandica* (Menke) Dautzenberg and Fischer, 1912; *L. saxatilis* var. *groenlandica* (Möller) Thorson, 1941) (Pl. 2, 8, a-d), the least common subspecies in Britain, measures 0.95–1.2 mm long on leaving the brood pouch of the adult. The maximum size attained in each population varies slightly with exposure to wave action. The largest specimens, up to 25.0 mm long, occur in salt marshes or on extremely sheltered (8) rocky shores and the smallest, up to 15.0 mm long, on fairly sheltered (5) shores and, in crevices, on semi-exposed (4) and exposed (3) shores.

Shell thickness is unaffected by exposure to wave action. In adults the shell is thin and has a density range (and mean) of 1.48–1.60 (1.51). The shape, which does not vary with exposure to wave action, may be narrow to broad, the spire medium to tall and the aperture narrow to fairly wide. The range (and the mean) of the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in adults are 1.15–1.4 (1.31), 1.5–1.8 (1.70) and 1.4–1.6 (1.52) respectively. The spire is bluntly to very bluntly pointed, the sutures deep and the whorls may have no sculpturing or have very shallow grooves and few widely separated humped ridges.

The only shell colour forms found were *albida*, *fusca*, *fulva*, *aurantia*, *zonaria* and *tessellata*.

The pigmentation on the head and tentacles (Fig. 4) is slightly more developed than in subsp. *rudis*, the range in adults being from stage 6 (Fig. 11) to stage 11 (Fig. 16). A range of 3–28 penial glands occurs in a single row on the penis. The mean number (12) is not affected by changes in exposure to wave action. The radula length: shell length ratio, the migratory behaviour and breeding cycle was not investigated.

In Britain, the subspecies occurs on some shores in the Shetland Islands and has the same vertical and exposure range as subsp. *rudis* but is found only in deep crevices on the more exposed shores. It was also found in a salt marsh near Dublin.

The subspecies is widely distributed in northern Europe particularly in Greenland and Iceland. In these regions the subspecies may be benthic and may occur in mixed populations and form intermediates with subspp. *tenebrosa* or *rudis*.

Subspecies *neglecta* (Bean, 1844) (= *Littorina saxatilis* Johnston, 1841; *Littorina neglecta* Bean, 1844; *L. saxatilis* (Johnston) Forbes and Hanley, 1850; *L. rudis* var. *saxatilis* (Johnston) Jeffreys, 1865; *L. saxatilis* subsp. *saxatilis* (Johnston) James, 1963, 1964 a, b) (Pl. 1, 6, e-f), the smallest subspecies, measures 0.35–0.4 mm long, on leaving the brood pouch of the adult. The maximum length attained is up to 5.0 mm long on extremely exposed (1) to extremely sheltered (8) rocky shores and in estuaries but, occasionally, up to 7.0 mm long, on salt marshes.

The shell is extremely thin, the range of shell density in adults being 1.2–1.35 (1.28). It is fairly broad to broad, the spire tall to very tall and the aperture small but very wide. The shape and thickness is not influenced by changes in exposure to wave action

probably because the subspecies always occurs in the shelter of crevices or in empty barnacle shells. The range (and the mean) of the shell length: shell breadth, shell length: aperture length and aperture length: aperture breadth ratios in adults are 1.15—1.3 (1.21), 1.65—2.1 (1.8) and 1.05—1.3 (1.22) respectively. The spire apex is very blunt, the sutures very deep and the whorls may have no sculpturing or have shallow grooves and many humped ridges. The outer lip frequently meets the body whorl below the mid-line.

The only shell colour forms recorded for the subspecies are *albida*, *fusca*, *fulva*, *lutea*, *lineata*, *flammulata*, *interrupta* and, most frequently, *tessellata*, often with a dark brown band running into the shell aperture.

The radula length: shell length ratio (Fig. 3) is lower in adults but higher in juveniles than in the other subspecies. The range in adults is 1.6—3.9. The pigmentation on the head and tentacles (Fig. 4) is poorly developed in adults, the range being only from stage 2 (Fig. 7) to stage 6 (Fig. 11). A range of 2-10 penial glands occurs in a single row on the penis. The mean number (4-5) is not affected by changes in exposure to wave action.

In Britain, the subspecies is abundant throughout the midlittoral zone, from M.L.W.S. to M.H.W.S., in the empty shells of dead barnacles and in tiny crevices on all extremely exposed (1) to semi-exposed (4) rocky shores. It is slightly less common on fairly sheltered (5) rocky shores and is sometimes found on sheltered (6) to extremely sheltered (8) rocky shores on stones or on wooden piles in estuaries and, occasionally, in enormous numbers on salt marshes. In these areas, it frequently occurs on the same part of the shore as subsp. *rudis*, *jugosa* or *tenebrosa* but no intermediates are formed in Britain.

## DISCUSSION

*Littorina saxatilis*, the most widely distributed intertidal mollusc in Britain, occurs throughout the littoral zone on the most sheltered to the most exposed rocky shores. It is almost terrestrial in places on the Atlantic seaboard, benthic in Iceland, and survives almost in fresh water in estuaries. The wide distribution and the corresponding variation in morphology may be attributed to the fact that the species is viviparous. The absence of a planktonic dispersal stage allows each population to become isolated and precisely adapted to local environmental conditions. The absence of migration and the very limited movements of most subspecies and varieties also contribute to this isolation. In some areas, perhaps because of local conditions, the isolation appears to be more effective or longer established than in others.

Thus, in Britain, the difference in morphology of the subspecies may be due to the fact that they usually occur in different habitats. Subsp. *groenlandica* occurs further north and subsp. *tenebrosa* and *jugosa* occur in a different zone than subsp. *rudis* and subsp. *neglecta* occupies a separate environmental niche in the same zone. In Britain, the isolation has apparently been sufficiently well established for the

subspecies to retain their morphological identity and to prevent interbreeding when their zones overlap on rocky shores or when they occupy the same habitats in estuaries and on salt marshes (Fischer-Piette, Gaillard and James, 1964). In other parts of Europe, however, this is not so, for the subspecies appear to interbreed and intermediates frequently occur in mixed populations.

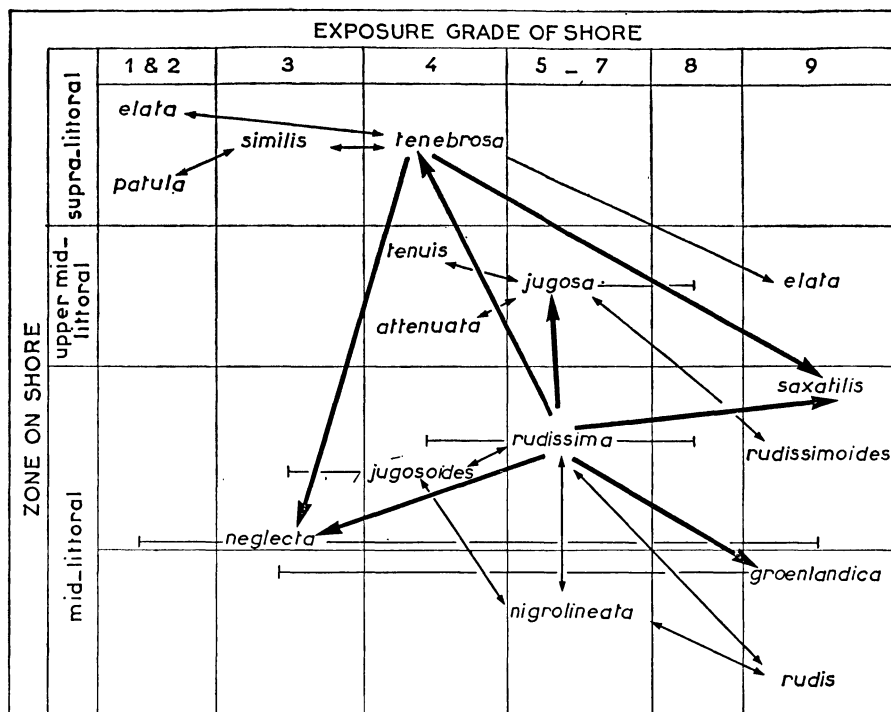


FIG. 24.

Diagram of hypothetical evolution of subspecies and varieties of *Littorina saxatilis* in Britain.

Similarly, the differences between the varieties of subspp. *rudis*, *jugosa* or *tenebrosa* can be attributed to their occurrence usually on shores with different grades of exposure to wave action. It is possible that a very large, wide aperture is necessary on the more exposed shores because the animal has to have a large powerful foot which can grip the substratum firmly. A short spire may offer little resistance and grooves break up the force of the waves. Finally, an animal with a small, thin and light shell may find it easier to hold on to the rock in exposed conditions than with a large, thick and heavy shell.

In Britain, the varieties usually appear to interbreed as intermediates often occur in mixed populations. However, some varieties, such as *elata* and *patula*, never occur in mixed populations and others may interbreed in some areas and not in others. For example, at Roscoff, vars. *nigrolineata* and *rudissima* occupy different but overlapping zones and retain their identity and do not interbreed in the areas of overlap in distribution (Deyglun, 1955). In Britain, however, the two varieties occupy the same zone and may interbreed and form intermediates in mixed populations. Examples of varieties which appear to interbreed in some areas and not in neighbouring, topographically identical areas are given in the text and by Fischer-Piette, Gaillard and James (1964).

Consideration of those shores without intermediates suggests that *Littorina saxatilis* should be divided into at least a dozen different species. In contrast, consideration of other shores with similar forms but with intermediates, suggests that the concept of a single variable species should be retained. In my opinion, the latter is preferable until more is known, particularly about the genetics. In addition, attempts, similar to those described by Gaillard (1965), should be made to rear the subspecies and varieties in the laboratory and to transfer the young experimentally from one shore or zone to another.

The fact that speciation appears to have proceeded further in some areas than in other neighbouring areas, suggests that the subspecies and varieties may evolve independently in each area in response to similar environmental conditions. It is possible that they could all evolve from subsp. *rudis* (Fig. 24) which is the most variable and widely distributed subspecies. The similarity of the young of subsp. *rudis* to the adults of the other subspecies (see Figs. 4-16 and James, 1968 a) suggests that they could have evolved initially by the process of paedogenesis. In addition, subspp. *neglecta* and *saxatilis* could evolve in this way from subsp. *tenebrosa*. Evidence for this hypothesis is provided by the examination of populations on newly constructed sea walls and breakwaters. When these form the supralittoral fringe on semi-exposed (4) and exposed (3) shores, specimens of subsp. *rudis* appear to move from the midlittoral zone and colonise the crevices. On new constructions these specimens are similar but slightly smaller than those in the midlittoral zone. Examination of older constructions suggests that they become progressively smaller and thinner shelled and may evolve eventually into subsp. *tenebrosa* which occurs on very long established constructions.

### Summary

Six subspecies and twelve varieties of *Littorina saxatilis* (Olivi) are distinguished on the basis of their shell characters, morphology and distribution in Britain. The effect of changes in exposure to wave action on their shell characters is described and their taxonomic status and evolution is discussed briefly.

### Zusammenfassung

Es werden sechs Subspecies und zwölf Varietäten von *Littorina saxatilis* (Olivi) aus Grossbritannien auf Grund ihrer Schalenmerkmale, ihrer Morphologie und ihrer Verbreitung unterschieden. Es wird der Effekt verschiedener Wellenaktivität auf die Schalenstruktur beschrieben und der taxinomische Status und ihre Evolution werden kurz diskutiert.



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