THE DISTRIBUTION AND KEYS OF SPECIES IN THE FAMILY LITTORINIDAE AND OF THEIR DIGENEAN PARASITES, IN THE REGION OF DALE, PEMBROKESHIRE

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I. Introduction

The family Littorinidae now includes only one British genus, *Littorina* Férussac, with four species, namely, *L. littorea*, *L. littoralis*, *L. neritoides* and *L. saxatilis* (Fretter and Graham, 1962). The history and synonymy of each species is discussed by Dautzenberg and Fischer (1912) and Colman (1932). The characteristic features of the subspecies and varieties of *L. saxatilis* and their distribution in Britain are described by Fischer-Piette, Gaillard and James (1964) and James (1968*a*).

The distribution of *Littorina* species on the Dale peninsula has been described previously by Moyse and Nelson-Smith (1963). The present account adds further details particularly about the subspecies and varieties of *L. saxatilis*.

New keys to the species and to the subspecies and varieties of *L. saxatilis* are included because it is difficult, using existing keys (Eales, 1952, Barrett and Yonge, 1958), to distinguish some specimens of *L. littorea* and *L. neritoides* from some varieties of *L. saxatilis*.

The larval Digenea which have *Littorina* species as first intermediate hosts are widely distributed (James, 1968*b*, *d*) but have received little attention and no keys have been published previously. Their morphology and, where known, their life cycles, are described by Lebour (1911), Stunkard (1930, 1932, 1950, 1957, 1966), Stunkard and Shaw (1931), Rees (1935, 1936*a*, *b*), Palombi (1938), Hunninen and Cable (1943) and James (1964*a*, 1968*b*–*d*) and their classification by Joyeux and Baer (1961) and Holliman (1961). The final hosts are marine birds or fishes; intertidal molluscs or crustacea may act as second intermediate hosts.

II. Methods

The topography and intertidal life of the rocky shores in the neighbourhood of Dale are described by Moyse and Nelson-Smith (1963) and Nelson-Smith (1965, 1967) and maps showing the shores examined by me are given by Moyse and Nelson-Smith (1963) and Fischer-Piette, Gaillard and James (1964). In addition, a number of shores were examined in the neighbourhood of St. Bride's Haven, St. Govan's Head, in Milford Haven, Daucleddau and on Skomer Island. The field work was carried out in December 1960, March 1962, September 1964 and September 1966.

Each shore was divided into the biologically defined zones of Stephenson and Stephenson (1949); the relationship between these and height above chart datum and tide levels having been established by Moyse and Nelson-Smith (1963). The degree of exposure to wave action on each shore was estimated by considering both physical and biological features as described by Ballantine (1961) and his exposure scale (1–8) is used throughout this paper.

The population density of juvenile and adult specimens of each *Littorina* species, subspecies or variety in each zone was measured and will be expressed in the six degrees of abundance defined by Moyse and Nelson-Smith (1963), who follow the work of Crisp and Southward (1958) and Ballantine (1961). The scale used for *L. neritoides* by Crisp and Southward (1958), however, is also used to express the population density of juvenile *L. littorea*.

A sample of each species, subspecies and variety was collected from each zone and later dissected for larval Digenea. The techniques used to examine and describe these parasites are given in detail by James (1964*a*, 1965, 1968*b*, *c*, *e*). A simple technique for the examination of larval Digenea is given below.

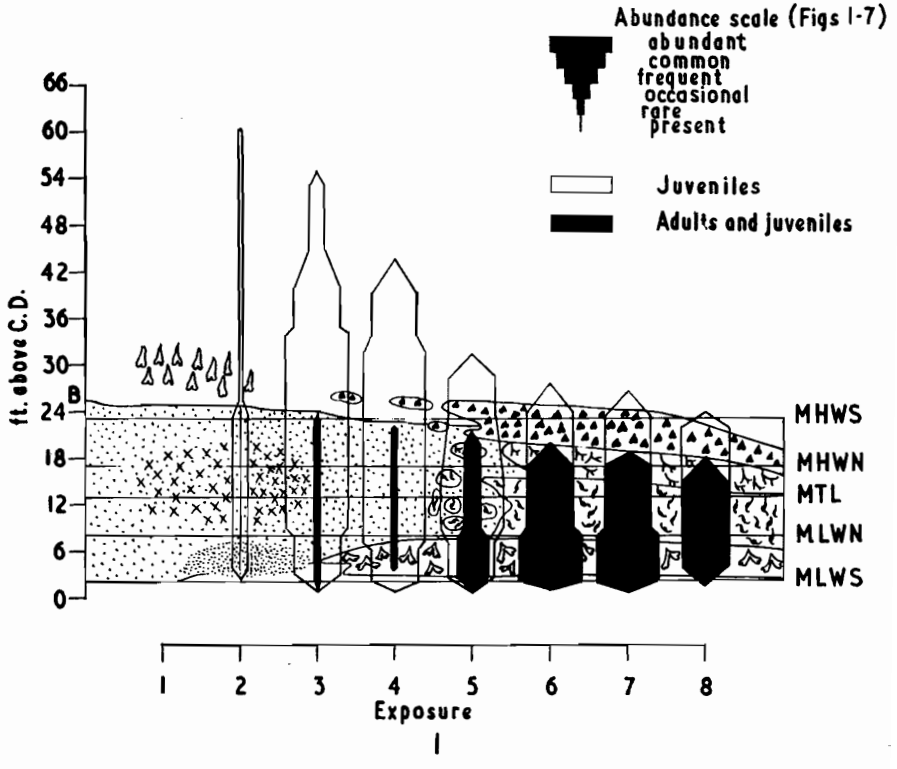
The host is removed from the shell and placed in a watch glass of sea water. The living parasites, which occur in the haemocoel, usually of the digestive gland and gonad in the spire, are teased from the host tissue with a pair of fine needles and transferred to a drop of sea water on a slide. The living cercariae and germinal sacs are then covered with a cover glass and examined under a microscope. In order to facilitate observation of the penetration glands, a drop of intravital stain, such as neutral red or bromocresol blue, may later be introduced at the edge of the cover glass and drawn over the living cercariae by means of filter paper placed at the opposite edge. Fixed cercariae and germinal sacs are very difficult to examine and often impossible to identify accurately.

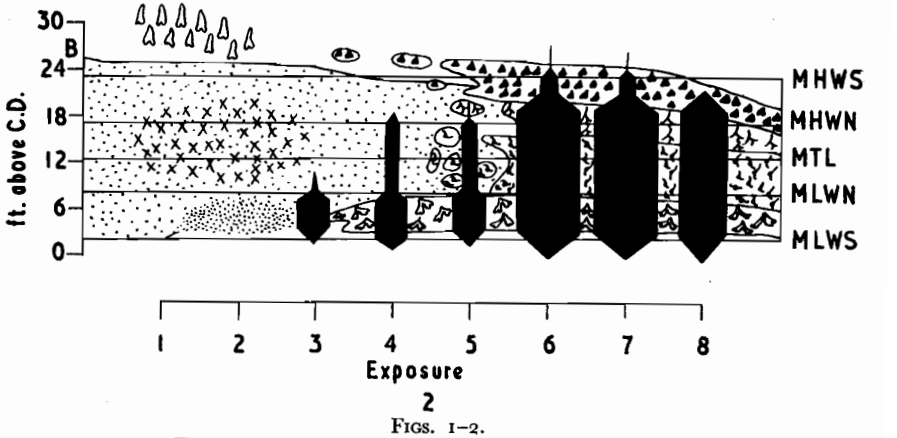
III. THE DISTRIBUTION OF *LITTORINA* SPECIES AND OF THEIR DIGENEAN PARASITES

(1) *Littorina littorea*

Adult specimens, over 12·0 mm. long, are abundant to common from M.L.W.S. to M.H.W.N. (Fig. 1), on sheltered (6) and very sheltered (7) shores; frequent to absent over a slightly wider vertical range, on fairly sheltered (5) rocky shores; being most abundant in the *Fucus serratus* zone on gently sloping shores. It is also rare to absent in deep crevices on semi-exposed (4) to very exposed (2) shores and common to present in the Haven, Daucleddau to Landshipping Ferry and on stones or on the surface of the mud in the Gann salt marsh.

Juvenile specimens (Fig. 1) are more widely distributed than the adults. This may be attributed to the fact that *L. littorea* has a planktonic larval stage. In addition to the habitats occupied by adults, juveniles are occasional to abundant in tiny crevices, in the empty shells of dead barnacles and under stones, throughout the midlittoral zone and abundant to absent in pools and in crevices throughout the supralittoral fringe on semi-exposed to very exposed shores. Presumably the juveniles die before developing into adults in the areas where adults are not found.





FIGS. 1–2.
The vertical and exposure range of two *Littorina* species.
1. *L. littorea* 2. *L. littoralis*

Only adult *L. littorea* are infected with larval Digenea. The rediae and cercariae of *Himasthla leptosoma* were found in 10 per cent and 18 per cent of the specimens examined from Black Rocks and North Haven, Skomer respectively. The metacercaria of *Himasthla leptosoma* was found in 20 per cent of *Mytilus edulis* L. collected from Marloes Sands and the adult, by Harris (1964), in the intestine of 2·2 per cent of *Larus argentatus* Pontopp., from Skomer and Skokholm.

Cercaria lebouri was found in 10 per cent of the specimens collected from Black Rocks and *Cryptocotyle lingua* in 3·0 per cent from Black Rocks and 6·0 per cent from North Haven, Skomer. The encysted metacercaria of *Cryptocotyle lingua* was found in *Gobius minutus* Pallas on Black Rocks and in *Blennius pholis* L. in Gatehold Sound. Harris (1964) found the adult in 33 per cent of *Larus argentatus* Pontopp., 17 per cent of *L. fuscus* L. and 20 per cent of *L. marinus* L. on Skomer and Skokholm. The complete life cycle of *C. lebouri* is unknown.

Additional species found in *L. littorea* elsewhere but not yet recorded from Dale are *Microphallus similis; Cercaria parvicaudata; C. emasculans; C. linearis; C. littorinae* and *C. buccini* (Table 1).

(2) *Littorina littoralis*

The adults and juveniles have similar distributions (Fig. 2) probably because the species has no planktonic stage.

The species (Fig. 2) is abundant to common on sheltered and very sheltered shores, in the *Fucus spiralis*, *Ascophyllum* and *Fucus serratus* zones, from M.H.W.N. to M.L.W.S. The numbers rapidly diminish above and below this vertical range. On the more exposed shores the distribution is more restricted, being frequent to absent on seaweed, from M.H.W.N. +2 ft. to M.L.W.S. on fairly sheltered and semi-exposed shores and from M.L.W.N. to M.L.W.S. on exposed (3) shores. Nelson-Smith (1967) has found the species in the Haven and in Daucleddau as far as Landshipping Ferry.

Recently Sacchi and Rastelli (1967) have subdivided *L. littoralis* into two species, namely, *L. obtusata* (L.) and *L. mariae* Sacchi and Rastelli. The latter has a more extended tip to the penis, is smaller and, according to Moyse (personal communication), occurs lower down on the shore than the former. Dr. John Moyse is preparing an account of the distribution of the colour varieties of both these species in the Dale area and Sacchi (1966) has reviewed the literature concerned with the distribution of the colour varieties.

No larval Digenea have yet been recorded from the species in the Dale area (Crothers, 1966) but elsewhere adults have been found to be infected with *Himasthla littorinae, Cercaria littorinae obtusatae, C. lebouri, Microphallus similis, C. parvicaudata* and *Notocotyloides petasatum*† (Table 1).

(3) *Littorina neritoides*

Both adults and juveniles (Fig. 3) occur on all of the extremely exposed (1) to very sheltered (7) rocky shores examined by me. In the upper Haven, the species is restricted to a narrow zone at about M.T.L. It is frequent to present, within the shells of dead barnacles and in tiny crevices, from M.H.W.S. to M.T.L. on sheltered and very sheltered shores. It becomes larger, more

† See addendum.

abundant and has a wider vertical range with increase in exposure to wave action (Fig. 3) but is still confined to empty barnacle shells or tiny crevices. The species is absent, for example, on completely smooth areas of rock near Skomer Head and St. Govan's Head. The upper limit of distribution is about 70 ft. C.D. (45 ft. above the barnacle line) on Hooper's Point, St. Ann's Head and Skomer Head.

Cercaria littorinae saxatilis I was found in 0·76 per cent of adult *L. neritoides* on

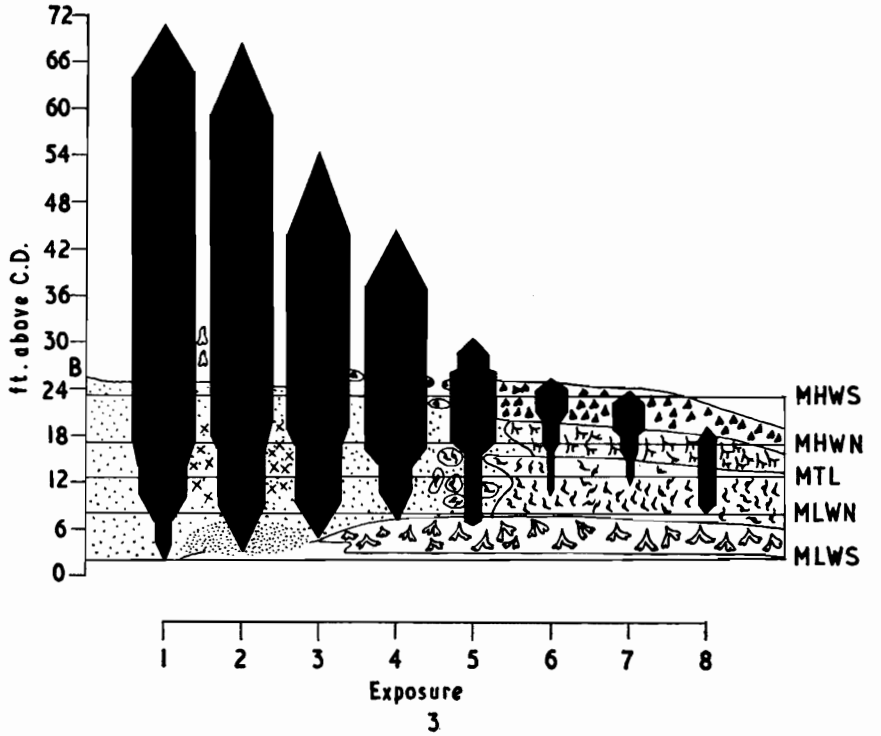


FIG. 3.
The vertical and exposure range of *Littorina neritoides*.

Skomer Head. *C. roscovita* and *C. lebouri* have been recorded from this host in other parts of Britain by James (1968*b*). Lysaght (1941) and Rothschild (1941) have recorded but not described or named a microphallid monostome xiphidiocercaria, a plagiorchioid distome xiphidiocercaria and a notocotylid monostome cercaria from this host.

(4) *Littorina saxatilis*

Only four of the six subspecies distinguished by James (1964*b*, 1968*a*) occur in the Dale area. Subspecies *saxatilis* (Olivi, 1792) occurs in the lagoons of

Table 1. *A list of species, subspecies and varieties in the genus* Littorina, *together with their known digenean parasites*

Littorina littorea (L.)
1. *Himasthla leptosoma* (Creplin, 1829) Dietz, 1909 (=Cercaria of *Echinostomum secundum* Nicoll, 1896 *sensu* Lebour, 1911).*
2. *Cercaria lebouri* Stunkard, 1932.*
3. *Cryptocotyle lingua* (Creplin, 1825) Fischoeder, 1903 (=*Cercaria lophocerca* (*non* Filippi) Lebour, 1911; life cycle described by Stunkard, 1930).*
4. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943 (=*Cercaria ubiquita* Lebour, 1907; *Cercaria ubiquitoides* Stunkard, 1932; *Cercaria* sp. Rees, 1936*a*; Cercaria of *Spelotrema excellens* Nicoll, 1907 *sensu* Lebour, 1911; life cycle described by Stunkard, 1957 and James, 1968*d*).
5. *Cercaria emasculans* Pelseneer, 1906.
6. *Cercaria parvicaudata* Stunkard and Shaw, 1931.
7. *Cercaria linearis* Lespés, 1857 (*non* Lebour, 1911).
8. *Cercaria littorinae* Rees, 1936*b* (=*C. buccini* Lebour, 1911 *sensu* Rees, 1935).
9. *Cercaria buccini* Lebour, 1911.

Littorina littoralis (L.)
1. *Himasthla littorinae* Stunkard, 1966.
2. *Cercaria littorinae obtusatae* Lebour, 1911.
3. *Cercaria lebouri* Stunkard, 1932.
4. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.
5. *Cercaria parvicaudata* Stunkard and Shaw, 1931.
6. *Notocotyloides petasatum* (Deslongchamps, 1824) Dollfus, 1966.†

Littorina neritoides (L.)
1. *Cercaria roscovita* Stunkard, 1932.
2. *Cercaria lebouri* Stunkard, 1932.
3. *Cercaria littorinae saxatilis* I James, 1968*d*.*

Littorina saxatilis (Olivi)
subsp. *saxatilis* (Olivi, 1792)
1. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.

subsp. *rudis* (Maton, 1797)
var. *rudis* (Maton, 1797)

var. *rudissima* (Bean, 1844)
1. *Cercaria lebouri* Stunkard, 1932.
2. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.*
3. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943 (=*Cercaria littorinae rudis* Lebour, 1906; *Microphallus claviformis* (Brandes, 1888) Baer, 1943 *sensu* James *in* Crothers, 1966; life cycle described by James, 1968*c*).
4. *Cercaria littorinae saxatilis* I James, 1968*d*.*
5. *Cercaria littorinae saxatilis* III James, 1968*d*.
6. *Cercaria roscovita* Stunkard, 1932.*
7. *Podocotyle atomon* (Rudolphi, 1809) Odhner, 1905 (Cercaria and life cycle described by Hunninen and Cable, 1943).

var. *nigrolineata* (Gray, 1839)
1. *Cercaria lebouri* Stunkard, 1932.*
2. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.*
3. *Cercaria roscovita* Stunkard, 1932.*
4. *Podocotyle atomon* (Rudolphi, 1809) Odhner, 1905.*

var. *jugosoides* James, 1968*a*
1. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.
2. *Cercaria roscovita* Stunkard, 1932.

subsp. *jugosa* (Montagu, 1803)
var. *rudissimoides* James, 1968*a*

var. *jugosa* (Montagu, 1803)
1. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.*
2. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943.
3. *Cercaria roscovita* Stunkard, 1932.*

var. *tenuis* James, 1968*a*
1. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943.*

var. *attenuata* (Dautzenberg and Fischer, 1912)
1. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.*
2. *Cercaria roscovita* Stunkard, 1932.*

subsp. *tenebrosa* (Montagu, 1803)
var. *tenebrosa* (Montagu, 1803)
1. *Cercaria lebouri* Stunkard, 1932.
2. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.
3. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943.
4. *Cercaria littorinae saxatilis* I James, 1968*d*.
5. *Cercaria roscovita* Stunkard, 1932.*
6. *Cercaria brevicauda* Pelseneer, 1906.*

var. *similis* (Jeffreys, 1865)
1. *Cercaria lebouri* Stunkard, 1932.
2. *Parapronocephalum symmetricum* Belopolskaia, 1952.
3. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.
4. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943.
5. *Cercaria littorinae saxatilis* I James, 1968*d*.
6. *Cercaria littorinae saxatilis* II James, 1968*d*.
7. *Cercaria littorinae saxatilis* IV James, 1968*d*.
8. *Cercaria roscovita* Stunkard, 1932.
9. *Parvatrema homoeotecnum* James, 1964*a*.*

var. *patula* (Thorpe, 1844)

var. *elata* Dautzenberg and Fischer, 1912
1. *Microphallus pygmaeus* (Levinsen, 1881) Baer, 1943.*
2. *Cercaria littorinae saxatilis* I James, 1968*d*.*

subsp. *neglecta* (Bean, 1844)

subsp. *groenlandica* (Menke, 1830)
1. *Microphallus similis* (Jägerskiöld, 1900) Baer, 1943.

In addition, the germinal sacs and cercariae of *Himasthla littorinae* Stunkard, 1966, *Cryptocotyle lingua* (Creplin, 1825) Fischoeder, 1903, *Cercaria parvicaudata* Stunkard and Shaw, 1931 and *Cercaria emasculans* Pelseneer, 1906, have been recorded from unidentified subspecies of *L. saxatilis*.

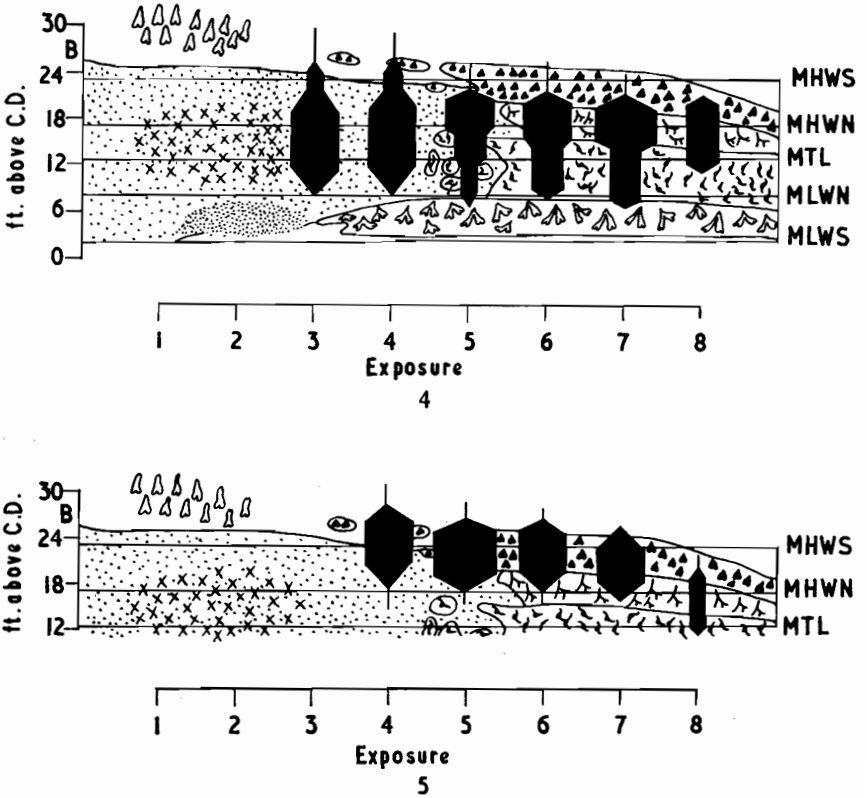
* Recorded in region of Dale.

† See addendum

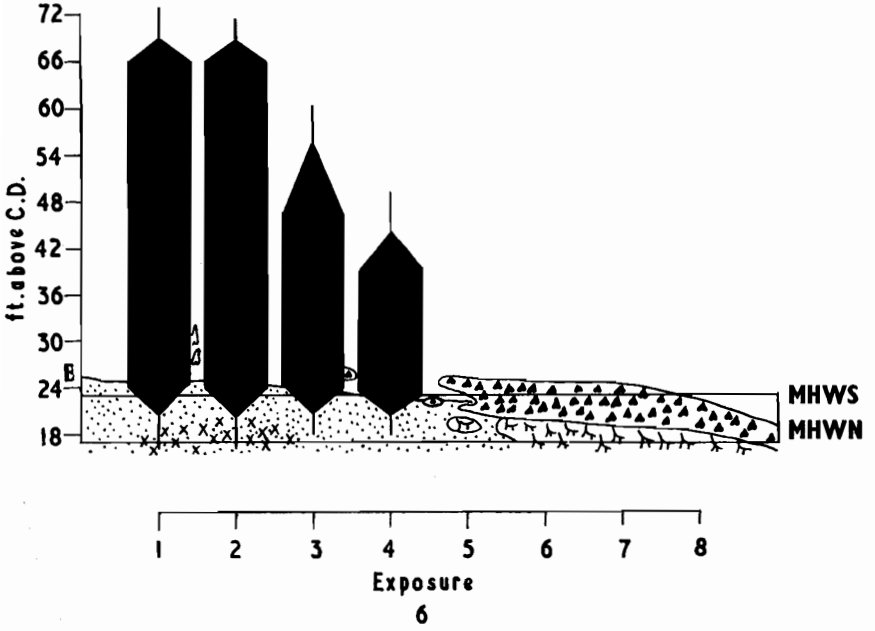
Venice, the type locality for the species, and has not been recorded in Britain. Subsp. *groenlandica* (Menke, 1830) is a northern subspecies which is found in the Shetland Islands and occasionally in saltmarshes further south in Britain. In addition to a characteristic shell, each of the remaining subspecies has a characteristic zonation and exposure range (Figs. 4–7). In the Dale area, as in other parts of Britain, usually two or three subspecies occur on each shore. Exceptionally, four subspecies occur on the semi-exposed shores near Swallow's Hole and Thorny Pit and in The Wick, Skomer (Fischer-Piette, Gaillard and James, 1964). The subspecies frequently overlap in distribution when two or more occur on the same shore but no intermediates exist between them.

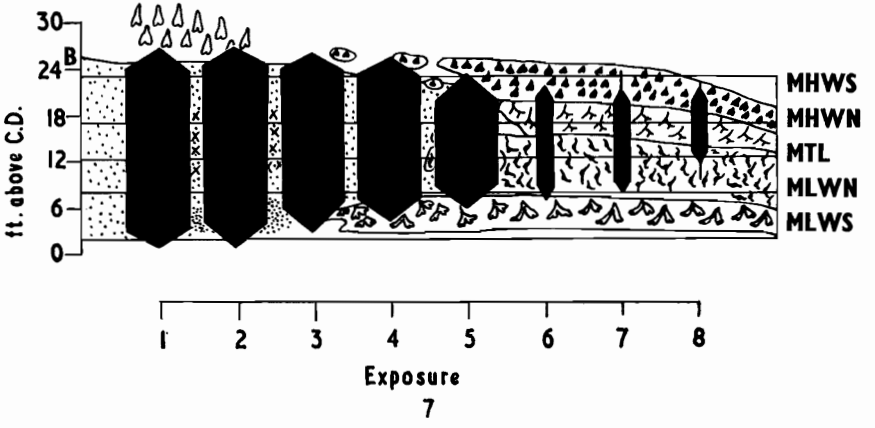
(a) subsp. *rudis* (Maton, 1797)

This subspecies (Fig. 4) occurs, usually from M.H.W.S. to M.L.W.N., on all very sheltered to semi-exposed shores, in deep crevices on exposed shores and



FIGS. 4–5.
The vertical and exposure range of two subspecies of *Littorina saxatilis*.
4. *rudis* 5. *jugosa*





FIGS. 6–7.
The vertical and exposure range of two subspecies of *Littorina saxatilis*.
6. *tenebrosa* 7. *neglecta*

on stones and in the mud at the mouth of the Gann salt marsh, in the Haven, Daucleddau, and in the lower reaches of the rivers Cleddau. The subspecies may be subdivided into four varieties, namely, *rudis* (Maton, 1797), *rudissima* (Bean, 1844), *nigrolineata* (Gray, 1839) and *jugosoides* (James, 1968*a*). The change in form from one variety into another is often associated with changes in exposure to wave action. Thus, var. *rudissima*, which occurs on the very sheltered Black Rocks, is replaced by var. *jugosoides* on the exposed Dale Point. Intermediates between the varieties occur on shores of intermediate exposure grades. Sometimes more than one variety of the same subspecies may occur on the same shore as, for example, var. *jugosoides* and var. *nigrolineata* on Dale Point. When this occurs, intermediates may or may not exist between the varieties (Fischer-Piette, Gaillard and James, 1964). Dale Point is an example of a shore on which intermediates between varieties do exist.

Var. *rudis* is occasional from midway between M.H.W.S. and M.H.W.N. to M.T.L. on stones and in the mud in the drainage canals, which occur between dense growths of *Halimione portulacoides*, on the Gann salt marsh. The shells in this region reach a maximum of 18·0 mm. long and are a uniform dark brown in colour and are, thus, examples of the colour variety *fusca* Dautzenberg and Fischer, 1912.

The variety is also frequent to occasional over a similar vertical range in the Daucleddau near Landshipping Ferry where it reaches a maximum length of 20·0 mm. and is a bright yellow or dark brown in colour. It also penetrates the lower stretches of the rivers Cleddau where it has to withstand drops in salinity to 5‰ (Nelson-Smith, 1965).

No larval Digenea have been recorded from this variety in Britain (James, 1968*d*).

Var. *rudissima* is frequent to abundant on very sheltered to fairly sheltered shores between Cliff Cottage and Dale Point. Maximum population density and the largest specimens, measuring up to 23·0 mm. long, occur in the *Fucus spiralis* zone on very sheltered shores but slightly smaller and fewer specimens also occur in the *Pelvetia* and *Ascophyllum* zones. The variety also decreases in size with increase in exposure to wave action. It is common, and measures up to 18·0 mm. long, on the fairly sheltered shores and, in shallow crevices, semi-exposed shores near St. Bride's Haven and, in deep crevices, in the exposed Chapel Bay near St. Govan's Head. The variety is a reddish brown in colour on the Dale peninsula; brown near St. Bride's Haven and a uniform light grey near St. Govan's Head.

Cercaria roscovita, *Microphallus similis* and *C. littorinae saxatilis* I were found in 0·6, 0·6 and 0·3 per cent respectively of var. *rudissima* on Black Rocks. In contrast, 63·6 per cent were infected with *Microphallus similis* near St. Bride's Haven. Additional species of larval Digenea recorded from this variety in other parts of Britain include *C. lebouri*, *Microphallus pygmaeus*, *C. littorinae saxatilis* III and *Podocotyle atomon* (Table 1). *C. littorinae saxatilis* I occurs in juvenile hosts but the other species only in adults.

Var. *nigrolineata*, which has a similar vertical range to var. *rudissima*, is common to occasional in the *Fucus spiralis* and *Ascophyllum* zones on fairly sheltered shores on Marloes Sands and Gateholm Sound. The shell measures up to 20·0 mm. long and has white ridges with brown, black or purple grooves.

Similar specimens, but with a slightly thinner shell, are abundant to absent in deep crevices, from M.H.W.S. +2 ft. to M.L.W.N., on the semi-exposed and exposed shores between Thorny Pit and St. Ann's Head.

A small form of this variety, measuring up to 8·0 mm. long, occurs between E.H.W.S. and M.L.W.N. on the semi-exposed headlands near Thorny Pit and Swallow's Hole and on the exposed Dale Point.

The colour form of var. *nigrolineata*, which has yellow ridges and black lines, does not occur in the Dale area but is found, together with the white and brown, black or purple form, on Anglesey and the Scilly Isles. Intermediates between these two colour forms are found on Anglesey.

Cercaria lebouri, *Microphallus similis*, *C. roscovita* and *Podocotyle atomon* were found in 0·9, 0·4, 0·4 and 0·4 per cent respectively of adult var. *nigrolineata* in Gateholm Sound. The adult of *Podocotyle atomon* was recorded from the intestine of *Cottus scorpius* L. on Marloes Sands. The encysted metacercaria, which occurs in amphipods, has not been recorded in the Dale area. The adult of *Microphallus similis* was found by Harris (1964) in 3·5 per cent of *Larus marinus* L. and 8·8 per cent of *L. argentatus* Pontopp. from Skomer and Skokholm. The encysted metacercaria was recorded from the hepatopancreas of 98 per cent and 100 per cent of *Carcinus maenas* (L.) on Skomer and in Dale Roads respectively (Crothers, 1966).

Var. *jugosoides* is common to occasional from E.H.W.S. to M.L.W.N., on semi-exposed and exposed shores near Dale Point. It is a reddish brown in colour, measures up to 11·0 mm. long and, as already described, occurs over the same range and forms intermediates with the small form of var. *nigrolineata*.

Microphallus similis and *Cercaria roscovita* have been recorded from this variety in other parts of Britain (James, 1968*d*).

(b) subsp. *jugosa* (Montagu, 1803)

This subspecies (Fig. 5) is found, mainly in the *Pelvetia* zone, between M.H.W.S. and M.H.W.N. on most of the very sheltered to fairly sheltered shores in the region and on the semi-exposed shores near Thorny Pit, Swallow's Hole and in The Wick, Skomer. On the semi-exposed shores, the upper limit of distribution is higher than on the more sheltered shores. The subspecies is also found, in the same habitat as subsp. *rudis*, in the Gann salt marsh, Landshipping Ferry, in the lower reaches of the rivers Cleddau and, according to Nelson-Smith (1967), throughout the Haven, particularly on salt marshes fringing tributary pills.

Subsp. *jugosa* may also be subdivided into four varieties, namely, *rudissimoides* (James, 1968*a*), *jugosa* (Montagu, 1803), *tenuis* (James, 1968*a*) and *attenuata* (Dautzenberg and Fischer, 1912).

Var. *rudissimoides* together with var. *rudis*, is occasional from midway between M.H.W.S. and M.H.W.N. to M.T.L. on stones and in the mud in the drainage canals on the Gann salt marsh and in a similar habitat at Landshipping Ferry and in the lower reaches of the rivers Cleddau.

The shell grows to a maximum of 10·0 mm. long and, on the Gann salt marsh, is a uniform lemon colour (ex. col. var. *lutea* Dautzenberg and Durouchoux, 1900) or has white and grey tessellations (ex. col. var. *tessellata*

Dautzenberg, 1893). At Landshipping Ferry, the shell is fawn in colour (ex. col. var. *fulva* Monterosato, 1872).

In other parts of Britain this variety occurs on extremely sheltered rocky shores in addition to salt marshes and estuaries.

No larval Digenea have been recorded from var. *rudissimoides*.

Var. *jugosa* is abundant on the fairly sheltered rocky shores on Marloes Sands and Gateholm Sound, where it forms a zone above var. *nigrolineata*. The shell reaches a maximum of 15·0 mm. long and, on Marloes Sands, is a uniform dark brown in colour (ex. col. var. *fusca*) and, in Gateholm Sound, a uniform brick red in colour (ex. col. var. *miniata* Dautzenberg and Fischer, 1912).

The variety is common to occasional on the fairly sheltered to very sheltered shores between Dale Point and Cliff Cottage, where the shell colour is fawn or light brown (ex. col. var. *fulva*) and where it forms a zone above var. *rudissima*. Yellowish brown specimens are common on the fairly sheltered shores in Mill Bay and a multicoloured population occurs on the fairly sheltered rock faces and crevices at the base of The Wick, Skomer.

Cercaria roscovita and *Microphallus similis* were found in 1·2 and 0·3 per cent respectively of adult var. *jugosa* from Gateholm Sound. *Microphallus pygmaeus* has also been recorded from this variety in other parts of Britain.

Var. *tenuis* is common to abundant on the semi-exposed shores near Thorny Pit and Swallow's Hole. It forms a zone between subsp. *tenebrosa* var. *tenebrosa* in the supralittoral fringe and subsp. *neglecta* and subsp. *rudis* var. *nigrolineata* in the midlittoral zone. The vertical distributions of the subspecies overlap considerably. Var. *tenuis* was discovered on these shores and has not yet been found elsewhere. The shell is a yellowish brown in colour and measures up to 10·0 mm. long on the more exposed rock faces and up to 14·0 mm. long within the relative shelter of the bays or in honeycomb erosion pits.

Intermediates between var. *tenuis* and var. *jugosa* occur on some of the fairly sheltered shores between Mill Bay and Thorny Pit. Thus, the change in form from var. *jugosa* to var. *tenuis* and, as shown below, from var. *jugosa* to var. *attenuata* appear to be correlated with an increase in exposure to wave action.

Microphallus pygmaeus was found in 1 per cent of adult var. *tenuis* taken from a headland near Thorny Pit. The adult which occurs in shore birds (James, 1968*c*) has not yet been recorded in the Dale area.

Var. *attenuata* is common to abundant on semi-exposed rock faces in The Wick, Skomer, where it forms a zone between subsp. *tenebrosa* and subsp. *neglecta*. The shells are white (ex. col. var. *albida* Dautzenberg, 1887), orange (ex. col. var. *aurantia* Dautzenberg, 1887), yellow (ex. col. var. *lutea*), purple, light brown or dark brown and measure up to 15·0 mm. long.

Intermediates between var. *jugosa* and var. *attenuata* occur in the slightly more sheltered rock faces or in crevices and, as stated earlier, var. *jugosa* alone occur on the fairly sheltered rock faces in The Wick.

Cercaria roscovita and *Microphallus similis* were found in 2 and 1 per cent respectively of adult var. *attenuata* from The Wick.

(c) subsp. *tenebrosa* (Montagu, 1803)

This subspecies (Fig. 6) is found in the supralittoral fringe on almost all of the semi-exposed to extremely exposed shores in the region. The only exceptions

are exposed, very exposed and extremely exposed smooth rock faces which have no crevices to shelter the subspecies from pounding by the waves. The upper limit of distribution is raised with increase in exposure to wave action.

The subspecies is subdivided into four varieties, namely, *tenebrosa* (Montagu, 1803), *similis* (Jeffreys, 1865), *patula* (Thorpe, 1844) and *elata* Dautzenberg and Fischer (1912). In general, the varieties replace each other successively with increases in exposure to wave action, with intermediates occurring on shores of intermediate exposure grades. Deep, relatively sheltered crevices on very or extremely exposed headlands, however, may contain varieties which are characteristic of more sheltered shores.

Var. *tenebrosa* is common to abundant on smooth rock faces and in shallow crevices from 2 feet below to up to 20 feet above the barnacle line on the semi-exposed shores near Dale Point, Mill Bay, Swallow's Hole, Thorny Pit, St. Bride's Haven, The Wick and the mouth of The Haven. The shell measures up to 14·0 mm. long and is usually a uniform light or dark brown in colour.

Cercaria brevicauda was found in 2 per cent of adult var. *tenebrosa* from a semi-exposed shore near St. Bride's Haven and *C. roscovita* in 2 per cent from St. Bride's Haven and West Angle Bay. *Cercaria lebouri*, *Microphallus pygmaeus*, *Microphallus similis* and *C. littorinae saxatilis* I have been recorded from this variety in other parts of Britain (James, 1968*d*).

Var. *similis* is occasional to abundant, from 2 feet below to 30 feet above the barnacle line, in shallow crevices on all exposed shores in the area. It is also abundant in deep crevices on the very exposed Hooper's Point and St. Govan's Head. The shell measures up to 14·0 mm. long and is usually brownish in colour. However, in the exposed Chapel Bay, near St. Govan's Head and on St. Govan's Head, the shell is brick red in colour (ex. col. var. *miniata*).

Parvatrema homoeotecnum was found in 0·4 per cent of var. *similis* from Hooper's Point. Unlike the other species of larval Digenea infecting *Littorina* species, *Parvatrema homoeotecnum* occurs exclusively in juvenile hosts. The adult, which occurs in *Haematopus ostralegus occidentalis* Neumann has not been recorded from the Dale area. *Cercaria lebouri*, *Parapronocephalum symmetricum*, *Microphallus pygmaeus*, *Microphallus similis*, *C. littorinae saxatilis* I, *C. littorinae saxatilis* II, *C. littorinae saxatilis* IV and *C. roscovita* have been recorded from this variety in other parts of Britain (James, 1968*d*) (Table 1).

Var. *patula* is common to abundant in shallow crevices, in the lower supra-littoral fringe from 3 feet below to 12 feet above the barnacle line, on the extremely exposed shores near Skomer Head and on Grassholm. Intermediates between vars. *patula* and *similis* are common in shallow crevices, over a similar vertical range, on the very exposed shores near Skomer Head, St. Ann's Head and Hooper's Point. Var. *patula* measures up to 10·0 mm. long and the intermediates to 11·0 mm. long. The shell of var. *patula* is light brown (ex. col. var. *fulva*), dark brown (ex. col. var. *fusca*), orange (ex. col. var. *aurantia*) or white with dark brown hyphens (ex. col. var. *interrupta* Fischer-Piette, Gaillard and Jouin, 1961) or has dark or light brown and white tessellations (ex. col. var. *tessellata*), has brown or black and white bands (ex. col. var. *zonaria* Bean, 1844) or has mixtures of these colours. The shells of the intermediates between *patula* and *similis* near St. Ann's Head are white (ex. col. var. *albida*), dark brown (ex. col. var. *fusca*), light brown or orange with dark brown or black lines (ex.

col. var. *lineata* Dautzenberg and Fischer, 1912) or light brown with dark brown hyphens (ex. col. var. *interrupta*).

No larval Digenea have been found in var. *patula*.

Var. *elata* is common to abundant in very deep crevices in the supralittoral fringe from 2 feet below to 45 feet above the barnacle line, on the very exposed headlands near Hooper's Point and St. Ann's Head and on the extremely exposed headlands near Skomer and Grassholm Heads. The shells of specimens taken from near Skomer Head measure up to 16·0 mm. long and are a uniform brownish grey in colour. Those of specimens from St. Ann's Head measure up to 13·0 mm. long and are dark brown (ex. col. var. *fusca*), black, brown with mustard hyphens (ex. col. var. *interrupta*) or have white and grey tessellations (ex. col. var. *tessellata*).

In other parts of Britain var. *elata* is sometimes found in salt marshes.

Intermediates between var. *elata* and *tenebrosa* are occasional to rare in crevices on exposed shores near St. Ann's Head and Dale Point.

Microphallus pygmaeus was found in 2 per cent of adult var. *elata* from St. Ann's Head and *C. littorinae saxatilis* 1 in 0·9 per cent of juveniles from Skomer Head.

(d) subsp. *neglecta* (Bean, 1844)

This subspecies, which has been erronously referred to as subsp. *saxatilis* (Johnston, 1841) in previous publications (Fischer-Piette, Gaillard and James, 1964; Moyse and Nelson-Smith, 1963; Nelson-Smith, 1965; Crothers, 1966), is abundant (Fig. 7), throughout the barnacle zone, in the empty shells of dead barnacles, in tiny crevices or amongst the byssus threads of mussels, on all extremely exposed to fairly sheltered shores in the region. It is occasional to absent on sheltered and very sheltered shores and, according to Nelson-Smith (1965, 1967), throughout the lower Haven to Newton Noyes and Martin's Haven.

The shell measures up to 5·0 mm. long and is usually pale yellow (ex. col. var. *lutea*), light brown (ex. col. var. *fulva*), pale yellow with brown lines (ex. col. var. *lineata*) or has grey and white or brown and mustard tessellations (ex. col. var. *tessellata*), frequently with a dark brown band running into the shell aperture.

In other parts of Britain this subspecies is occasionally found, in enormous numbers, in salt marshes (James, 1968*a*).

No larval Digenea have been found in this subspecies (James, 1968*d*).

Himasthla littorinae, *Cryptocotyle lingua*, *Cercaria parvicaudata*, *C. emasculans* have each been recorded once from unidentified subspecies of *L. saxatilis* in France or U.S.A. (Stunkard, 1930, 1932, 1950, 1966). In addition to the three subspecies mentioned above, *Microphallus similis* has been recorded from subspecies *saxatilis* (Olivi) and *groenlandica* (Menke) (James, 1968*d*).

Fourteen of the twenty-two species of larval Digenea found in *Littorina* (Table 1) occur only in one host species and five, *Cryptocotyle lingua*, *Himasthla littorinae*, *Cercaria roscovita*, *C. emasculans* and *C. littorinae saxatilis* 1, in two host species. Two, *Microphallus similis* and *C. parvicaudata*, occur in three host species and one, *C. lebouri* in all four host species. Similarly, seven of the twelve species of larval Digenea found in *L. saxatilis* are known to occur only in one host subspecies.

Two, *C. littorinae saxatilis* 1 and *C. lebouri*, occur in two subspecies, two, *C. roscovita* and *Microphallus pygmaeus*, in three subspecies and one, *Microphallus similis* in five subspecies.

At present, it is not known if this (*a*) indicates that many species of larval Digenea are strictly host specific or (*b*) reflects the paucity of records of larval Digenea from *Littorina* species.

IV. The identification of *Littorina* species and of their digenean parasites

It is necessary, in order to compare the shells of young *Littorina* species and subspecies and to give an adequate key to the adults, 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 species or subspecies in hand. Since this is unlikely, diagrams (Figs. 8–50) and definitions, based on shell measurements, are provided to clarify the meaning of the comparative terms.

(1) *The definition of some terms used to describe the shell of* Littorina *species*

(a) *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	over 1.40

(b) *spire height*	*shell length/aperture length*
spire absent	1.0 –1.2
very short	1.2 –1.35
short	1.35–1.50
medium	1.50–1.65
tall	1.65–1.80
very tall	over 1.80

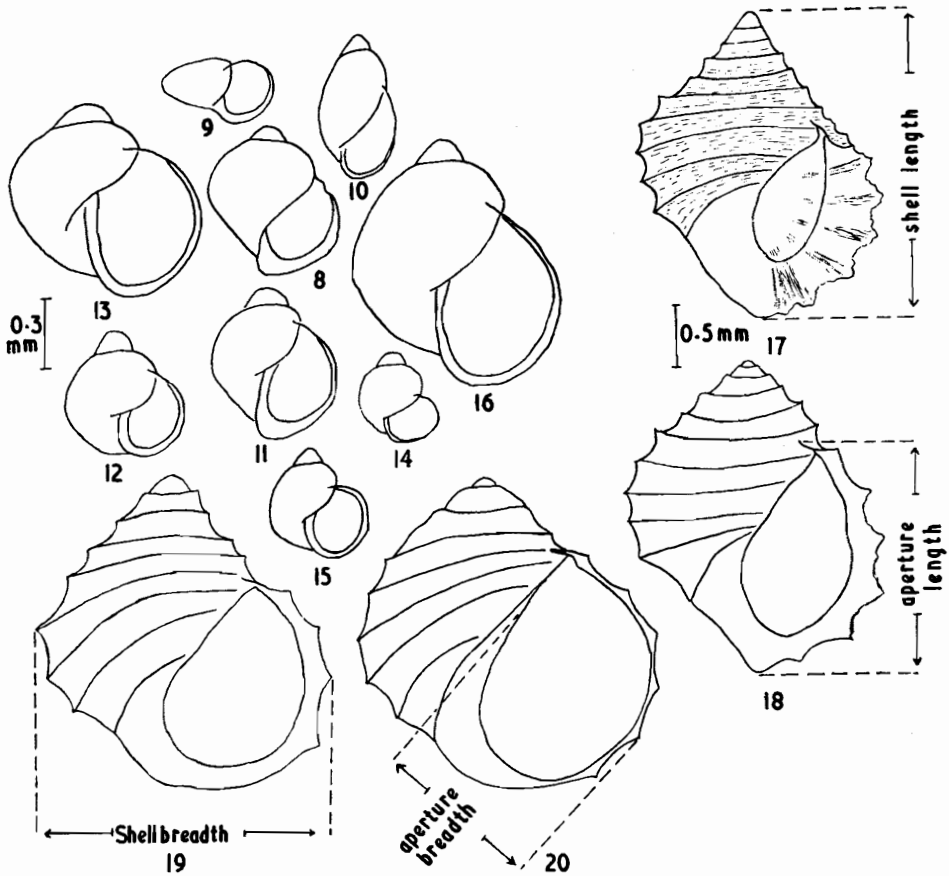
(c) *aperture width*	*aperture length/aperture width*
very wide	less than 1.30
wide	1.30–1.40
fairly wide	1.40–1.50
narrow	1.50–1.60
very narrow	more than 1.60

(d) *shell thickness*	*density of shell and contained animal in gm./c.c.*
very thick	more than 1.75
thick	1.75–1.60
thin	1.60–1.45
very thin	1.45–1.30
fragile	less than 1.30

(e) *shell size*	*shell length of largest adult in population in mm.*
very large	over 30.0
large	30.0–20.0
medium sized	20.0–10.0
small	10.0– 5.0
very small	less than 5.0

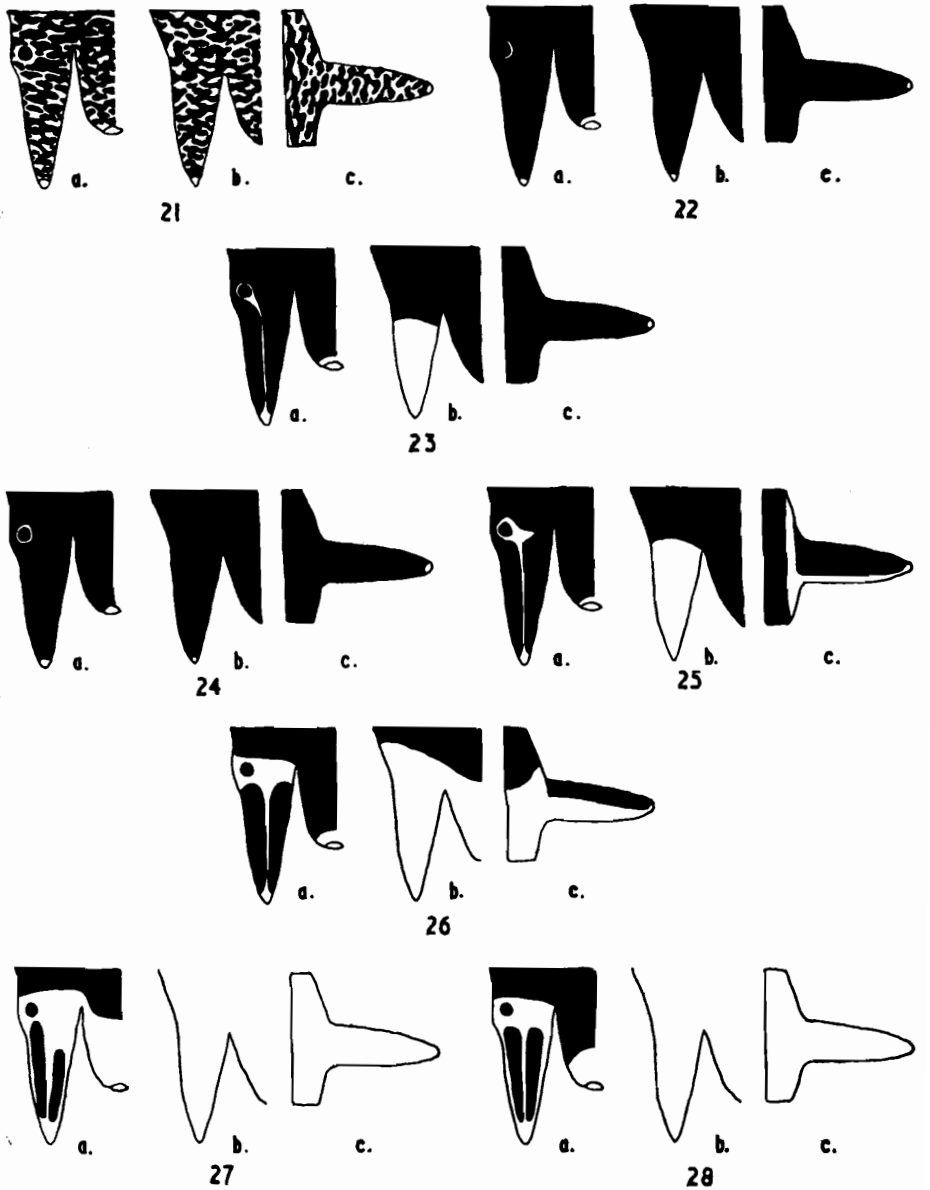
(2) *The identification of young* Littorina *species*

When they first settle on the shore, the young of the four *Littorina* species (Figs. 8–16) have an extremely thin, completely smooth, semi-transparent shell with two whorls. They are pale yellow to light brown in colour, except for *L. neritoides* which may be dark brown or black. No pigmentation occurs on the



FIGS. 8–16.
The shells of young *Littorina* specimens at the stage in development attained when they first settle on the shore.
8. *L. littorea* 9. *L. littoralis* 10. *L. neritoides* 11. *L. saxatilis rudis*
12. *L. saxatalis jugosa* 13. *L. saxatilis tenebrosa* 14. *L. saxatilis neglecta*
15. *L. saxatilis saxatilis* 16. *L. saxatilis groenlandica*

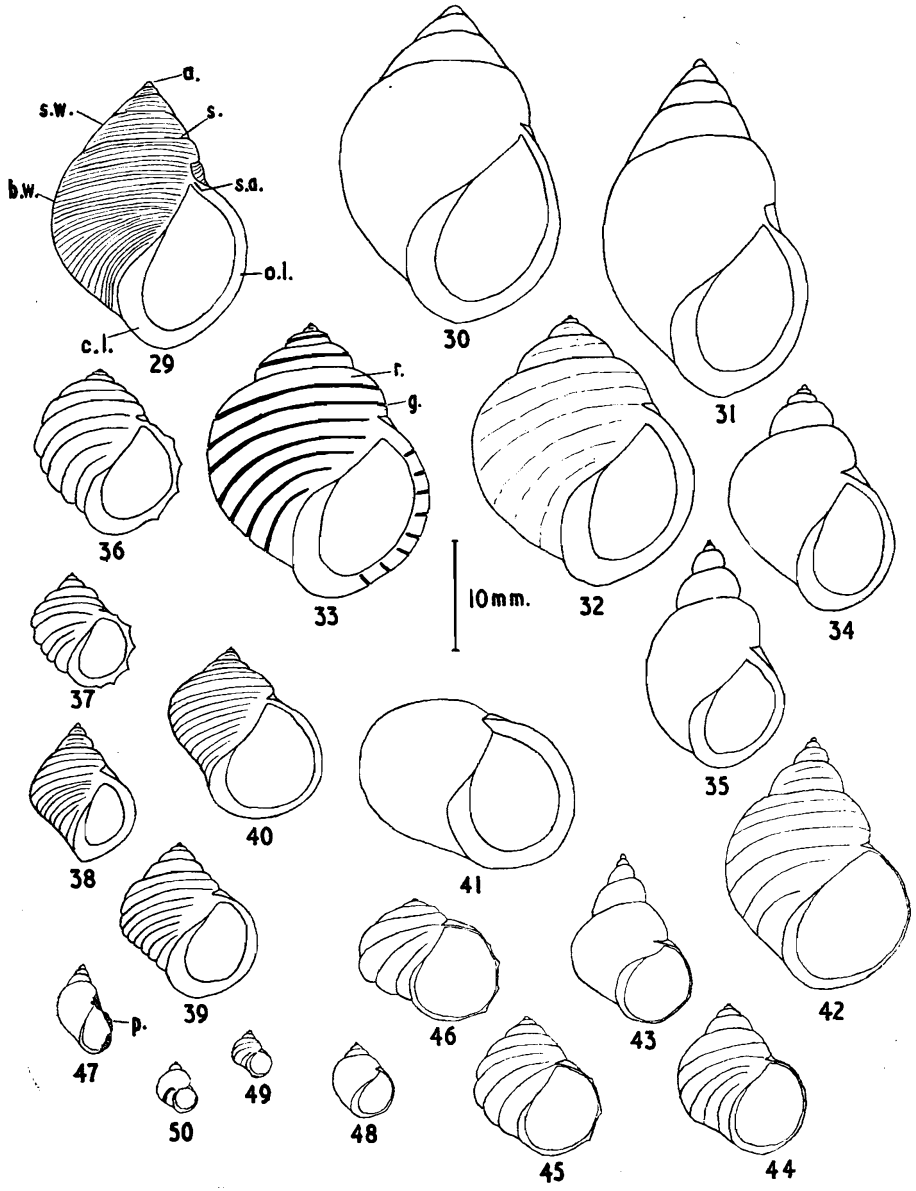
FIGS. 17–20.
Deeply grooved shells of young *Littorina* specimens, measuring 2·5 mm. long.
17. *L. littorea* 18. *L. saxatilis rudis* 19. *L. saxatilis jugosa* 20. *L. saxatilis tenebrosa*



FIGS. 21–28.

Pigmentation on head and tentacles of largest adult specimens of four *Littorina* species. (*a*) Dorsal view of right side of head and tentacle. (*b*) Ventral view of left side of head and tentacle. (*c*) Lateral view of right tentacle.

21. *L. littorea* 22. *L. littoralis* (pigmentation may be absent in some forms)
23. *L. neritoides* 24. *L. saxatilis rudis* and *L. saxatilis groenlandica*
25. *L. saxatilis jugosa* 26. *L. saxatilis tenebrosa* 27. *L. saxatilis neglecta*
28. *L. saxatilis saxatilis*



FIGS. 29–50.
The shells of adult *Littorina* specimens.

head and tentacles at this stage. The species and subspecies can be distinguished from each other by the shape of the shell and aperture and by the relative height of the spire. The varieties of the subspecies of *L. saxatilis* are indistinguishable at this stage.

Littorina littorea (Fig. 8) has a broad shell with a short spire and a narrow aperture. The outer lip is slightly crenated, indicating the beginning of groove formation. The angle between the outer lip of the aperture and the body whorl (the shell angle) is acute. *L. littoralis* (Fig. 9) has a broader than long shell with no spire and a wide aperture. The shell angle is obtuse. The shell of *L. neritoides* (Fig. 10) is very narrow, has a tall spire, a very narrow aperture and an acute shell angle. The shell of *L. saxatilis rudis* (Fig. 11), very similar to that of *L. littorea*, is broad to fairly broad, has a very short spire, a very narrow aperture and an acute shell angle. The shell shape, spire height, aperture shape and shell angle respectively in subsp. *jugosa* (Fig. 12) is broad to very broad, short, fairly wide and almost a right angle; in subsp. *tenebrosa* (Fig. 13) very broad, very short, wide to very wide and a right angle; in subsp. *neglecta* (Fig. 14) broad, very tall, very wide and a right angle; in subsp. *saxatalis* (Fig. 15) broad, medium, wide and a right angle and in subsp. *groenlandica* (Fig. 16) fairly broad to broad, short, narrow and acute.

The shell of most species and subspecies has attained the adult form (Figs. 29–50) by the time they have grown to 2·0–3·0 mm. long. However, the shell of *L. littorea* and *L. saxatilis* subspp. *rudis*, *jugosa* and *tenebrosa* at this stage may be quite different from that of the adult. The shells (Figs. 17–20) of these four forms are invariably deeply grooved but they can be distinguished from each other as shown below.

The shell of *L. littorea* (Fig. 17) has five whorls and a medium to tall, very sharply pointed spire. It is very thick, broad and a dark brown in colour. The

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29. *L. littorea*, grooved form from a sheltered rocky shore
30. *L. littorea*, smooth form from a sheltered rocky shore
31. *L. littorea*, smooth form from a salt marsh
32. *L. saxatilis rudis* var. *rudissima*, from a very sheltered rocky shore
33. *L. saxatilis rudis* var. *nigrolineata*, from a very sheltered rocky shore
34. *L. saxatilis rudis* var. *rudis*, wide form from on mud in an estuary
35. *L. saxatilis rudis* var. *rudis*, narrow form from a salt marsh
36. *L. saxatilis rudis* var. *jugosoides*, from an exposed rocky shore
37. *L. saxatilis jugosa* var. *tenuis*, from a semi-exposed rocky shore
38. *L. saxatilis jugosa* var. *rudissimoides*, from on mud in an estuary
39. *L. saxatilis jugosa* var. *jugosa*, from a fairly sheltered rocky shore
40. *L. saxatilis jugosa* var. *attenuata*, from a semi-exposed rocky shore
41. *L. littoralis*, from a sheltered rocky shore
42. *L. saxatilis groenlandica*, from a salt marsh
43. *L. saxatilis tenebrosa* var. *elata*, from very deep crevices on an extremely exposed rocky shore
44. *L. saxatilis tenebrosa* var. *tenebrosa*, from a semi-exposed rocky shore
45. *L. saxatilis tenebrosa* var. *similis*, from an exposed rocky shore
46. *L. saxatilis tenebrosa* var. *patula*, from shallow crevices on an extremely exposed rocky shore
47. *L. neritoides*, from an exposed rocky shore
48. *L. saxatilis saxatilis*, from a canal in Venice
49. *L. saxatilis neglecta*, grooved form, from empty shells of dead barnacles on an exposed shore
50. *L. saxatilis neglecta*, smooth form, from empty shells of dead barnacles on an exposed shore

aperture is narrow to very narrow and the shell angle acute. The columellar lip is very broad and translucent white in colour. The outer lip is crenated, deflected tangentially before meeting the body whorl and has white and dark brown pigment bands on the inner edge. The shell of *L. saxatilis rudis* (Fig. 18) has five whorls and a short bluntly pointed spire. It is very thick and fairly broad to broad. The aperture is very narrow. The columellar lip is not as broad as in *L. littorea* and the outer lip is not deflected tangentially before meeting the body whorl. The shell angle is acute. The shell of subsp. *jugosa* (Fig. 19) has four whorls and a short pointed spire. It is thick and broad to very broad. The aperture is fairly wide and the shell angle almost a right angle. The shell of subsp. *tenebrosa* (Fig. 20) has four whorls and a short to very short, very blunt spire. It is thin to fragile and very broad. The aperture is wide to very wide, the shell angle a right angle and the columellar lip is thin. The varieties of subspp. *rudis*, *jugosa* and *tenebrosa* are still indistinguishable at this stage.

Further development of the shell particularly in the varieties of the subspecies of *L. saxatilis* is dependent on environmental conditions. With increase in size, however, the shells soon develop the characteristic adult form (Figs. 29–50).

In addition to their shell characters, the adults of the species and subspecies can be distinguished from each other by the pigment on the head and tentacles (Figs. 21–28). Since the extent of pigmentation increases with age (James, 1968*a*), the diagrams (Figs. 21–28) apply only to the largest specimens of each species and subspecies.

In the following key to adults, the shell characters in 1. and in the lower line of 2. are invariable and shared by two or more species and subspecies. The shell characters in **bold** print occur in every specimen of the species concerned and only in that species. Those in CAPITALS also occur in every specimen but identify the species or subspecies concerned only when considered together with the characters given earlier in the key.

The shell characters given in SMALL CAPITALS, if present, occur only in one species or subspecies but those in *italics*, if present, identify the species or subspecies concerned only when considered together with the characters given earlier in the key. A number of these characters are given for most of the species and subspecies because when present they are usually more distinctive than the characters which occur in every specimen and one or another is nearly always present. Sometimes two or more occur on a single shell.

With some experience, each species, subspecies and variety can be recognized at a glance, *in situ*, on the shore.

(3) *A key based on shell characters, for the identification of adult* Littorina *species and subspecies*

1. Shell heavy and thick to very thick — 2
   Shell light and thin to fragile — 5

2. BROADER THAN LONG; **apex flat; spine absent** (Fig. 41) **L. littoralis**
   very broad to very narrow; apex pointed; spire present — 3

3. Large to VERY LARGE; OUTER LIP OFTEN DEFLECTED TANGENTIALLY BEFORE MEETING BODY WHORL; COLUMELLAR LIP OFTEN TRANSLUCENT WHITE AND OUTER LIP WITH VERY MANY ALTERNATING WHITE AND BROWN PIGMENT BANDS; apex VERY SHARPLY to bluntly pointed; SUTURES SHALLOW TO FAIRLY DEEP; SPIRE WHORLS FLAT; sculpturing, if present, consists of VERY MANY humped ridges separated by narrow shallow grooves (Figs. 29–31) **L. littorea**

Small to large; outer lip never deflected tangentially; columellar lip never translucent white and outer lips never with very many alternating white and brown pigment bands; apex sharply to *very bluntly pointed*; SUTURES DEEP TO VERY DEEP; SPIRE WHORLS HUMPED; sculpturing, if present, consists of *few to very few* FLATTENED or humped ridges separated by narrow or very wide shallow or *deep* grooves (**L. saxatilis**) 4

4. *Small* to *large*; thick to *very thick*; *very narrow* to very broad; apex bluntly to *very bluntly pointed*; spire short to *very tall*; SUTURES VERY DEEP; aperture fairly wide to very narrow; grooves and ridges may be *absent*, but if present, grooves shallow to deep with very few humped or FLATTENED ridges (Figs. 32–36) (a) subsp. **rudis**

Medium sized; thick; fairly broad to very broad; apex *sharply* to bluntly pointed; spire *very* short to medium; SUTURES DEEP; aperture very narrow to *wide*; grooves and ridges always present; ridges FEW, always humped and separated by shallow to *very deep* grooves (Figs. 38–40) (b) subsp. **jugosa**

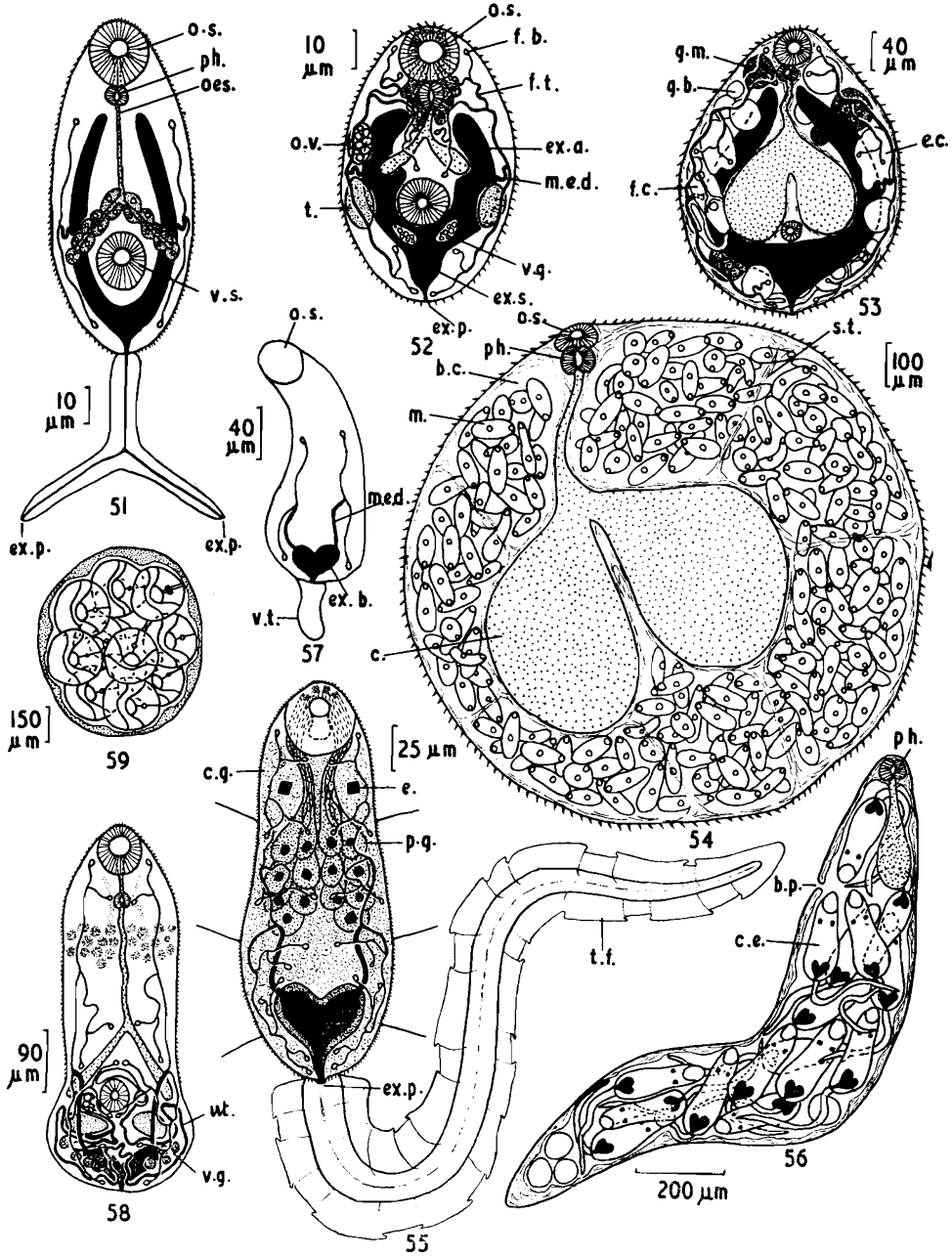
5. VERY NARROW; APERTURE VERY NARROW; ANGLE BETWEEN OUTER LIP AND BODY WHORL VERY ACUTE; THE PERIOSTRACUM EXTENDS BEYOND THE EDGE OF THE OUTER LIP TO FORM A THIN FLEXIBLE MEMBRANE; SUTURES SHALLOW; SPIRE WHORLS FLAT; grooves and ridges absent; colour black but older parts of shell frequently have an EPIZOOIC ORGANISM (POSSIBLY A LICHEN) WHICH GIVES THE SHELL A DUSTY BROWN APPEARANCE (Fig. 47) **L. neritoides**

NARROW TO BROADER THAN LONG; APERTURE NARROW TO VERY WIDE; ANGLE BETWEEN OUTER LIP AND BODY WHORL ALMOST A RIGHT ANGLE OR A RIGHT ANGLE; the periostracum does not extend beyond the edge of the outer lip; SUTURES DEEP TO VERY DEEP; SPIRE WHORLS HUMPED; grooves and humped ridges *present* or absent; colour variable; without noticeable epizooic organisms (**L. saxatilis**) 6

6. LARGE; thin (Fig. 42) subsp. **groenlandica**
MEDIUM SIZED; thin to fragile 7
SMALL TO VERY SMALL; fragile 8

7. Thin; broad; APEX SHARPLY TO BLUNTLY POINTED; spire medium; aperture fairly wide; FEW VERY DEEP GROOVES (Fig. 37) subsp. **jugosa** var. **tenuis**

Thin to *fragile*; *narrow* to *broader than long*; APEX BLUNT TO VERY BLUNT; spire *very tall* to *very short*; aperture fairly wide to *very wide*; GROOVES VERY FEW TO ABSENT, SHALLOW OR DEEP (Figs. 43–46) (c) subsp. **tenebrosa**


o.s.
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g.b.
40 µm
e.c.
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40 µm
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ex. b.
57
o.s.
ph.
b.c.
m.
s.t.
100 µm
c.
54
150 µm
59
c.g.
e.
p.g.
25 µm
ph.
b.p.
c.e.
t.f.
90 µm
ut.
v.g.
58
ex.p.
55
56
200 µm

8. VERY SMALL; APEX VERY BLUNT; SPIRE TALL TO VERY TALL; aperture **small**, VERY WIDE; OUTER LIP FREQUENTLY MEETS BODY WHORL WELL BELOW THE SUTURE BETWEEN BODY WHORL AND FIRST SPIRE WHORL; *frequently a dark brown or black band of pigment on body whorl running into shell aperture* (Figs. 49, 50) subsp. **neglecta**

SMALL; APEX SHARPLY TO BLUNTLY POINTED; SPIRE MEDIUM; APERTURE LARGE, NARROW TO WIDE; outer lip meets body whorl near the suture between body whorl and first spire whorl; no dark brown or black band of pigment on body whorl (Fig. 48) subsp. **saxatilis**

(a) *A key to the varieties of* L. saxatilis rudis

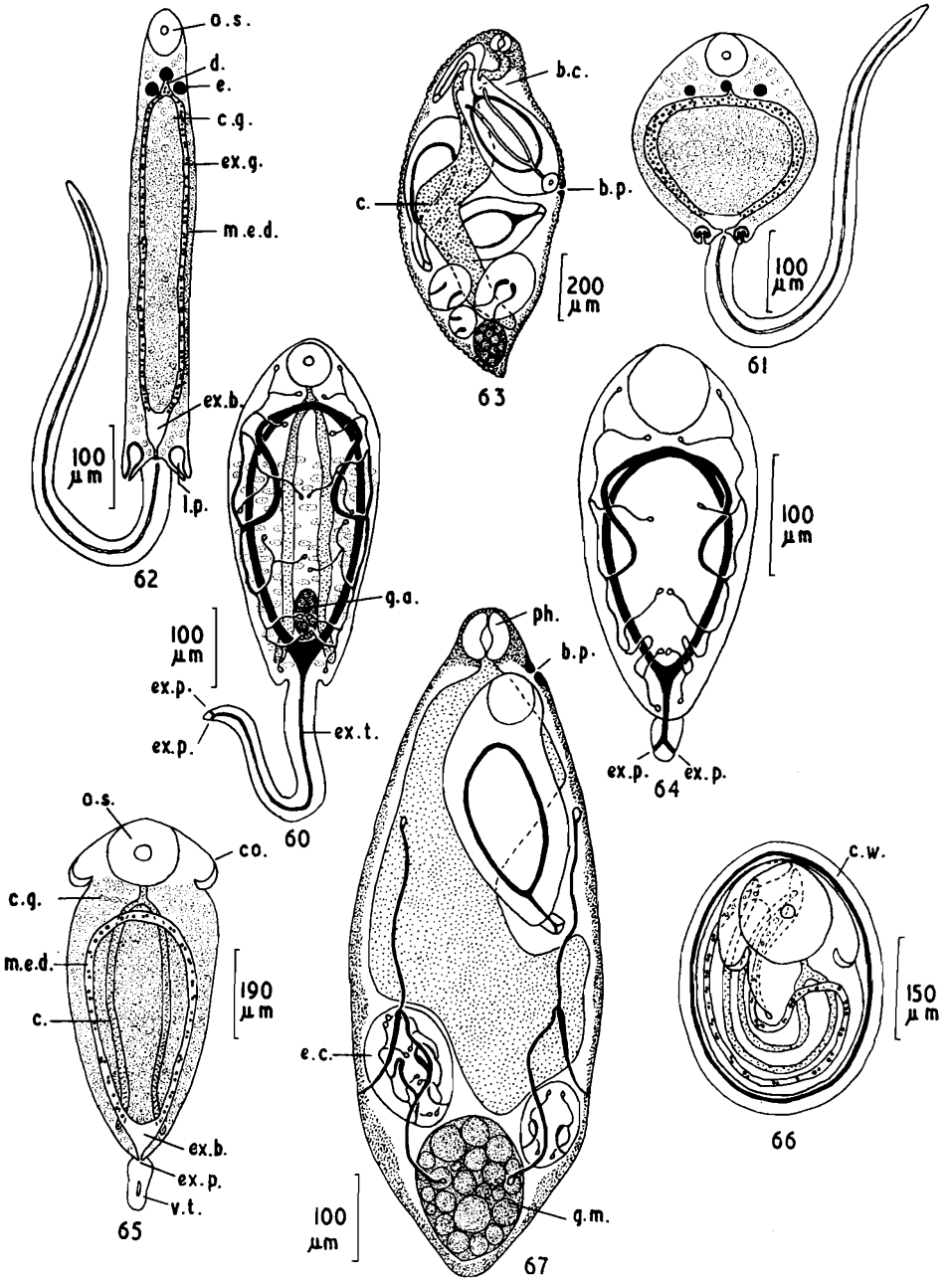
Since intermediates exist between the varieties the following keys distinguish only the extremes in form.

1. Sculpturing absent; fairly broad to very narrow; spire medium to very tall (Figs. 34, 35) **rudis**
   Sculpturing present; fairly broad to very broad; spire medium to short 2
2. Ridges broad and flat; grooves narrow, deep and usually a different colour from the ridges (Fig. 33) **nigrolineata**
   Ridges narrow and humped; grooves wide, deep or shallow and usually the same colour as ridges 3
3. Fairly broad to very broad; spire medium to short; aperture very narrow; grooves very shallow (Fig. 32) **rudissima**
   Broad to very broad; spire short; aperture narrow to fairly wide; grooves shallow to very deep (Fig. 36) **jugosoides**

(b) *A key to the varieties of* L. saxatalis jugosa

1. Thin (Fig. 37) **tenuis**
   Thick 2
2. Fairly broad; spire medium; aperture very narrow; grooves very shallow (Fig. 38) **rudissimoides**
   Broad; spire medium; aperture fairly wide; grooves very shallow to very deep (Fig. 39) **jugosa**
   Very broad; spire medium to very short; aperture wide; grooves very shallow (Fig. 40) **attenuata**

FIGS. 51–54.
Parvatrema homoeotecnum.
51. cercaria 52. metacercaria
53. Young germinal sac containing cercariae at various stages in development
54. Fully formed germinal sac containing metacercariae
FIGS. 55–56.
Cryptocotyle lingua.
55. cercaria
56. Redia containing cercariae at various stages in development
FIGS. 57–59.
Microphallus pygmaeus.
57. cercaria 58. metacercaria
59. Daughter sporocyst containing metacercariae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c.w.
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(c) *A key to the varieties of* L. saxatilis tenebrosa

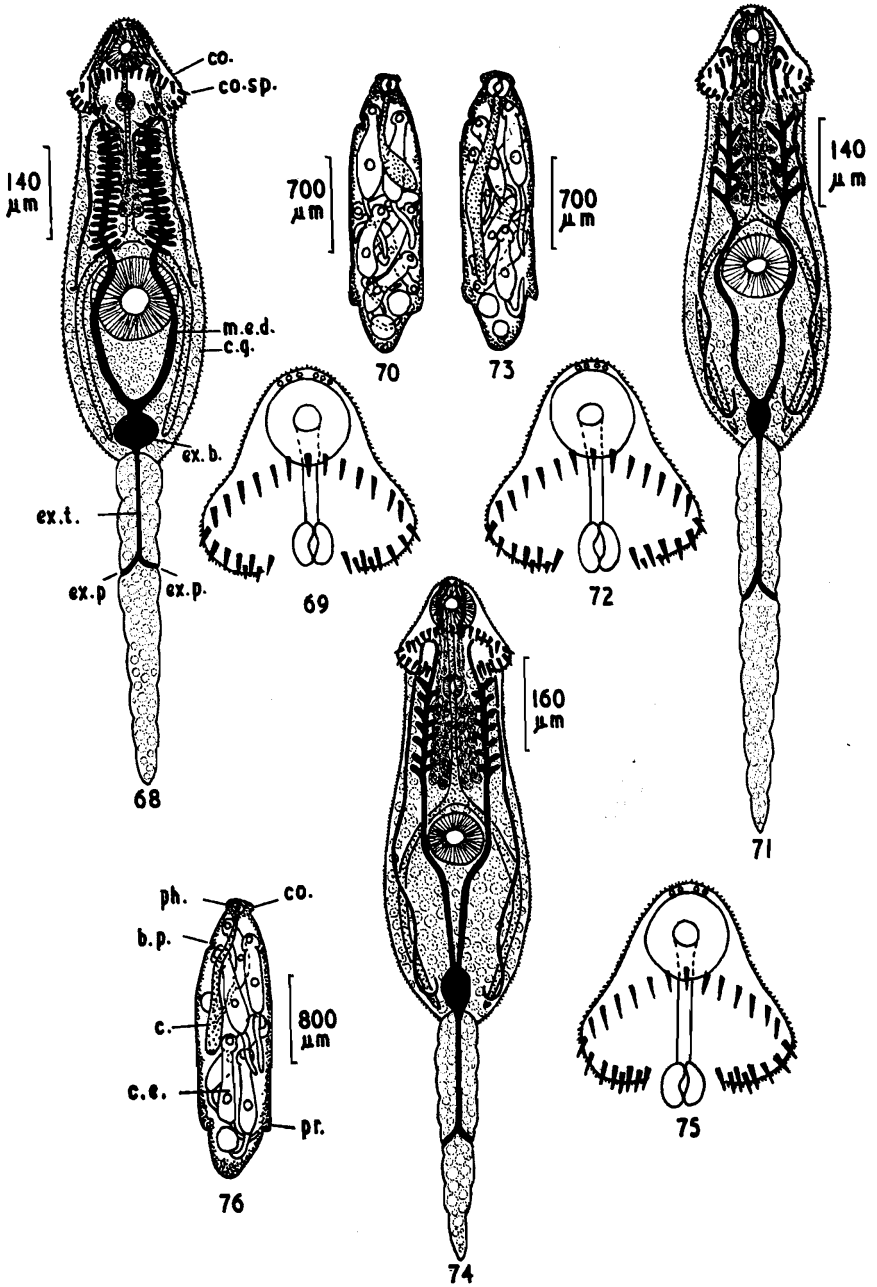
1. Very thin; narrow; spire very tall; aperture small, very wide; sculpturing absent or very shallow grooves (Fig. 43) **elata**
   Thin to fragile; fairly broad to broader than long; spire medium to very short; aperture large, fairly wide to very wide; sculpturing always present, with very shallow to deep grooves 2
2. Thin to very thin; fairly broad to broad; spire medium to short; aperture fairly wide to wide; shallow grooves (Fig. 44) **tenebrosa**
   Very thin; broad to very broad; spire short; aperture wide; shallow to deep grooves (Fig. 45) **similis**
   Fragile; very broad to broader than long; spire very short; aperture very wide; shallow grooves (Fig. 46) **patula**

(4) *A key based on the characters of cercariae, for the identification of larval Digenea using* Littorina *species as first intermediate host*

1. Stylet absent 2
   Stylet present 8
2. Oral sucker, ventral sucker and pharynx present 3
   Only oral sucker or oral sucker and pharynx present 4
3. Forked tail; collar and cystogenous gland cells absent; develops directly into unencysted metacercaria in a germinal sac which is similar in structure to an adult digenean (Figs. 51–54) **Parvatrema homoeotecnum**
   (Fellodistomatoidea: Gymnophallidae)
   Simple tail; collar with 29 collar spines; cystogenous gland cells present; develops in a redia with collar and procuscula, escapes from redia and first intermediate host before developing into encysted metacercaria
   echinostomate cercaria (a)
   (Echinostomatoidea: Echinostomatidae)
4. Body spinose; tail with well developed fin; two eye spots
   (Figs. 55, 56) **Cryptocotyle lingua**
   (Opisthorchioidea: Heterophyidae)
   Body aspinose; tail simple; three or no eye spots 5
5. No eye spots; excretory vesicle V-shaped, main excretory ducts do not extend to near level of oral sucker; develops directly into unencysted distomate, pharyngeate metacercaria within sporocyst
   (Figs. 57–59) **Microphallus pygmaeus**
   (Plagiorchioidea: Microphallidae)
   Three or no eye spots; excretory vesicle sacculate, main excretory ducts extend to near level of oral sucker; escapes from redia before developing intoencysted monostomate, apharyngeate metacercaria 6

FIGS. 60–63.
Cercaria lebouri.
60. Cercaria from body cavity of redia at stage in development attained just prior to birth
61. Fully formed cercaria from haemocoel of host, contracted specimen
62. Fully formed cercaria from haemocoel of host, expanded specimen
63. Redia containing cercariae at various stages in development

FIGS. 64–67.
Parapronocephalum symmetricum.
64. Cercaria from body cavity of redia at stage in development just prior to birth
65. Fully formed cercaria from haemocoel of host, relaxed specimen
66. Encysted metacercaria from haemocoel of host
67. Redia containing cercariae at various stages in development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pr.
76
75

6. 3 eye spots; locomotor pockets present; tail well developed; main excretory ducts fuse anteriorly and have anterior diverticulum; free-living, encysts on substratum (Figs. 60–63) **C. lebouri**
(Notocotyloidea: Notocotylidae)

Eye spots and locomotor pockets absent; tail vestigial; main excretory ducts may or may not fuse anteriorly but without diverticulum; encysts in haemocoel of first intermediate host (Notocotyloidea: Pronocephalidae) 7

7. Main excretory ducts fuse anteriorly (Figs. 64–67) **Parapronocephalum symmetricum**

Main excretory ducts do not fuse anteriorly **Notocotyloides petasatum**†

8. Oral sucker, ventral sucker and pharynx present 9

Oral sucker only present Microphallid monostome xiphidiocercaria (b)
(Plagiorchioidea: Microphallidae)

9. Body spinose; tail simple, caudal gland cells absent; cystogenous gland cells present; excretory vesicle Y-shaped, excretory granules in intercellular spaces throughout body Plagiorchioid distome xiphidiocercaria (c)
(Plagiorchioidea: family unknown)

Body aspinose; tail modified to form a protrusible adhesive organ, caudal gland cells present; cystogenous gland cells absent; excretory vesicle sacculate, excretory granules intracellular, within cells lining the excretory vesicle Opecoelid cotylomicrocercous xiphidiocercaria (d)
(Allocreadioidea: Opecoelidae)

(a) *A key to echinostomate cercariae*

1. End collar spines much smaller than other collar spines; develops in redia with a large pharynx 2

End collar spines almost as large as other collar spines; develops in redia with a small pharynx 3

2. Tail about three-quarters as long as body; oral sucker: ventral sucker ratio about 1 : 2; develops in colourless redia in which the caecum does not extend to midbody (Figs. 68–70) **Himasthla littorinae**

Tail almost as long as body; oral sucker: ventral sucker ratio about 2 : 3; develops in orange redia in which the caecum extends into posterior third of body (Figs. 71–73) **Himasthla leptosoma**

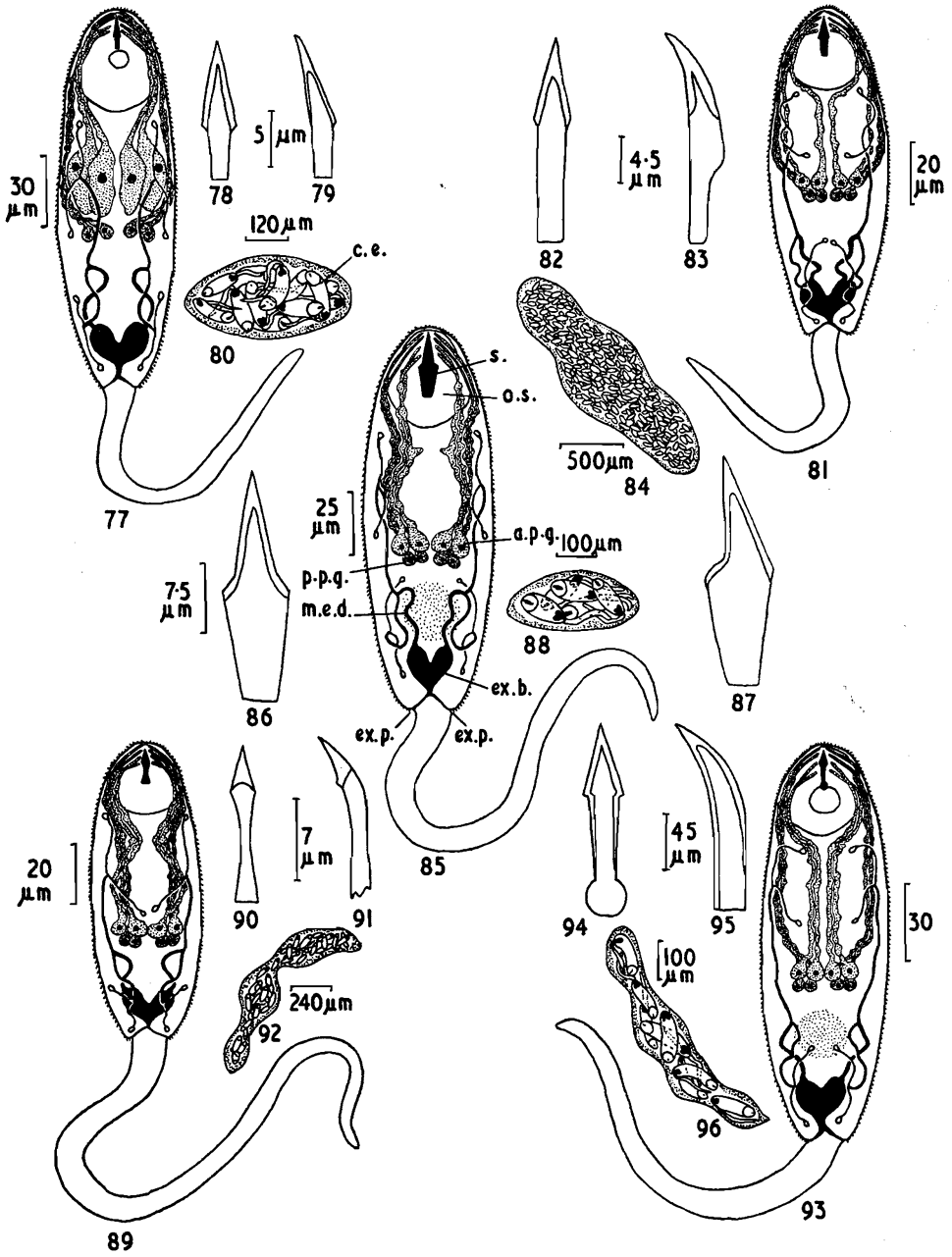
3. Tail about half length of body; oral sucker: ventral sucker ratio about 3 : 4; develops in colourless redia in which caecum extends to midbody (Figs. 74–76) **C. littorinae obtusatae**

† See addendum.

FIGS. 68–70.
Himasthla littorinae.
68. Cercaria 69. Anterior end of cercaria
70. Redia containing cercariae at various stages in development

FIGS. 71–73.
Himasthla leptosoma.
71. Cercaria 72. Anterior end of cercaria
73. Redia containing cercariae at various stages in development

FIGS. 74–76.
Cercaria littorinae obtusatae.
74. Cercaria 75. Anterior end of cercaria
76. Redia containing cercariae at various stages in development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(b) *A key to microphallid monostome xiphidiocercariae*

1. Anterior penetration gland cells more than four times as large as posterior penetration gland cells; stylet less than half the length of oral sucker; develops in immobile orange sporocyst (Figs. 77–80) **C. littorinae saxatilis IV**

   Anterior penetration gland cells only about twice as large as posterior penetration gland cells; stylet about half or more than half length of oral sucker; develops in contractile, colourless, pale yellow or cream sporocyst 2

2. Stylet simple; develops in oval, pale yellow or cream sporocyst 3

   Stylet with narrow waist or posterior knob; develops in elongate oval, colourless sporocyst 4

3. Extended tail shorter than body; stylet 17–21 μm. long, about half length of oral sucker; develops in large cream sporocyst containing 200–1,050 cercariae (Figs. 81–84) **C. littorinae saxatilis II**

   Extended tail longer than body; stylet 23–26 μm. long, more than two-thirds length of oral sucker; develops in small pale yellow sporocyst containing 4–30 cercariae (Figs. 85–88) **Microphallus similis**

4. Extended tail about twice as long as body; stylet with narrow waist; develops in medium sized sporocyst containing 30–110 cercariae (Figs. 89–92) **C. littorinae saxatilis I**

   Extended tail about same length as body; stylet with posterior knob; develops in small sporocyst containing 3–20 cercariae (Figs. 93–96) **C. littorinae saxatilis III**

(c) *A key to plagiorchioid distome xiphidiocercariae*

1. Body longer than tail; ventral sucker behind midbody 2

   Body shorter than tail; ventral sucker in front of midbody 4

2. Tail only slightly shorter than body; oral sucker: ventral sucker diameter ratio about 10 : 9; stylet 13–18 μm. long; 12 or numerous penetration gland cells; cystogenous gland cells extend to level of mid-oesophagus; main excretory ducts enter stem of excretory vesicle; develops in immobile sporocyst; free-living, encysts in a second intermediate host 3

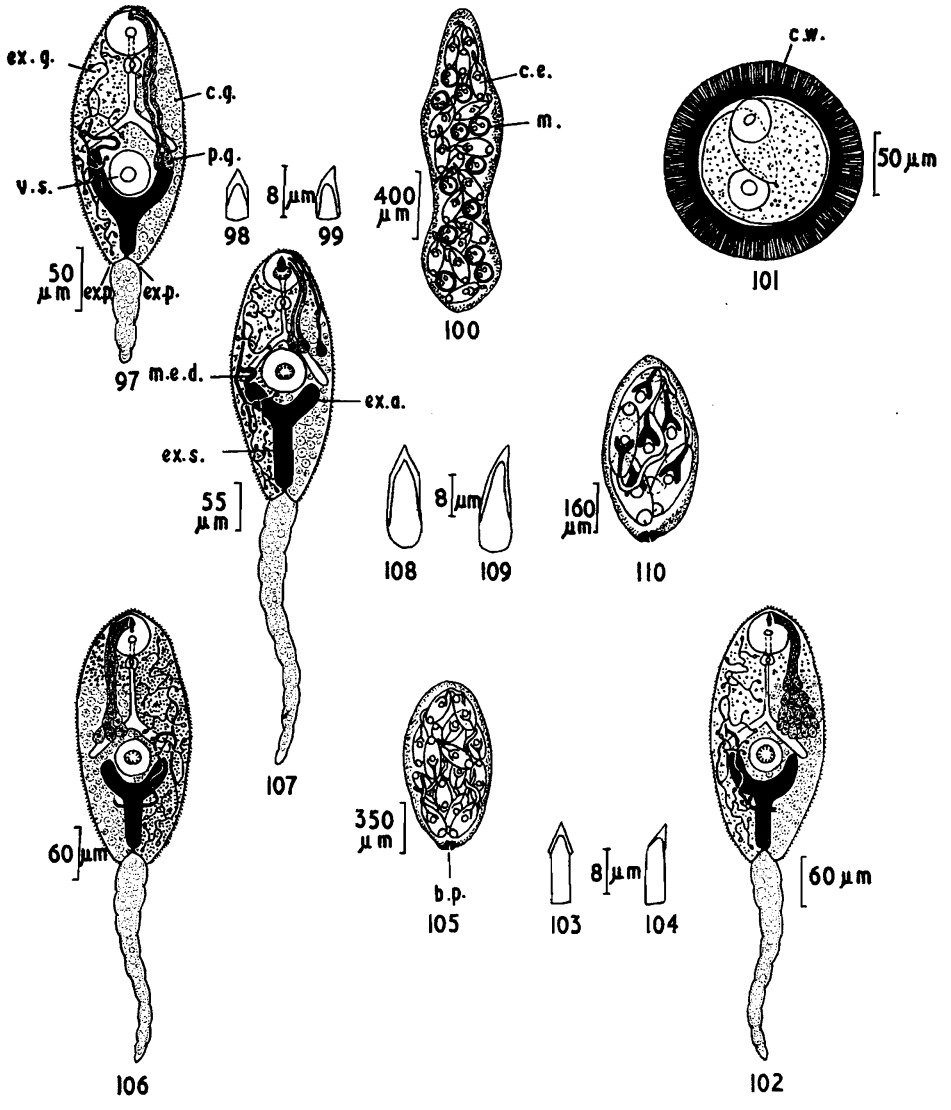
FIGS. 77–80.
Cercaria littorinae saxatilis IV.
77. Cercaria 78. Stylet, dorsal view 79. Stylet, lateral view
80. Fully formed daughter sporocyst containing cercariae

FIGS. 81–84.
Cercaria littorinae saxatilis II.
81. Cercaria 82. Stylet, dorsal view 83. Stylet, lateral view
84. Fully formed daughter sporocyst containing cercariae

FIGS. 85–88.
Microphallus similis.
85. Cercaria 86. Stylet, dorsal view 87. Stylet, lateral view
88. Fully formed daughter sporocyst containing cercariae

FIGS. 89–92.
Cercaria littorinae saxatilis I.
89. Cercaria 90. Stylet, dorsal view 91. Stylet, lateral view
92. Fully formed sporocyst containing cercariae

FIGS. 93–96.
Cercaria littorinae saxatilis III.
93. Cercaria 94. Stylet, dorsal view 95. Stylet, lateral view
96. Fully formed daughter sporocyst containing cercariae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Tail vestigial, much shorter than body; oral sucker: ventral sucker diameter ratio about 1 : 1; stylet 6–8 μm. long; 4 penetration gland cells; cystogenous gland cells extend to level of pharynx; main excretory ducts enter arms of excretory vesicle; develops in contractile (orange) sporocyst; not free-living encysts in sporocyst or in haemocoel of first intermediate host (Figs. 97–101) **C. brevicauda**

3. Numerous penetration gland cells; develops in lemon or cream sporocyst (Figs. 102–105) **C. roscovita**

12 penetration gland cells; develops in orange sporocyst (Fig. 106) **C. parvicaudata**

4. Oral sucker: ventral sucker diameter ratio about 6 : 7; stylet 17–25 μm. long; 6 penetration gland cells; main excretory ducts enter arms of excretory vesicle; develops in immobile colourless sporocyst (Figs. 107–110) **C. emasculans**

(d) *A key to opecoelid cotylomicrocercous cercariae*

1. Stylet with single point; 14 penetration gland cells; develops in orange-red sporocyst (Figs. 111–113) **C. linearis**

Stylet with two points; 6 penetration gland cells; develops in white or cream sporocyst (Figs. 114–115) **Podocotyle atomon**

Stylet with four points; 6 or 18 penetration gland cells; develops in pale yellow or colourless sporocyst 2

2. 18 penetration gland cells in 6 groups of 3 cells, each group with a single duct to the exterior; develops in pale yellow sporocyst (Figs. 116–117) **C. littorinae**

6 penetration gland cells each with a separate duct to the exterior; develops in pale yellow or colourless sporocyst (Figs. 118–119) **C. buccini**

V. Summary

The distribution of *Littorina littorea*, *L. littoralis*, *L. neritoides*, the subspecies and varieties of *L. saxatilis* and of their larval digenean parasites is described for the rocky shores in the neighbourhood of Dale, Pembrokeshire.

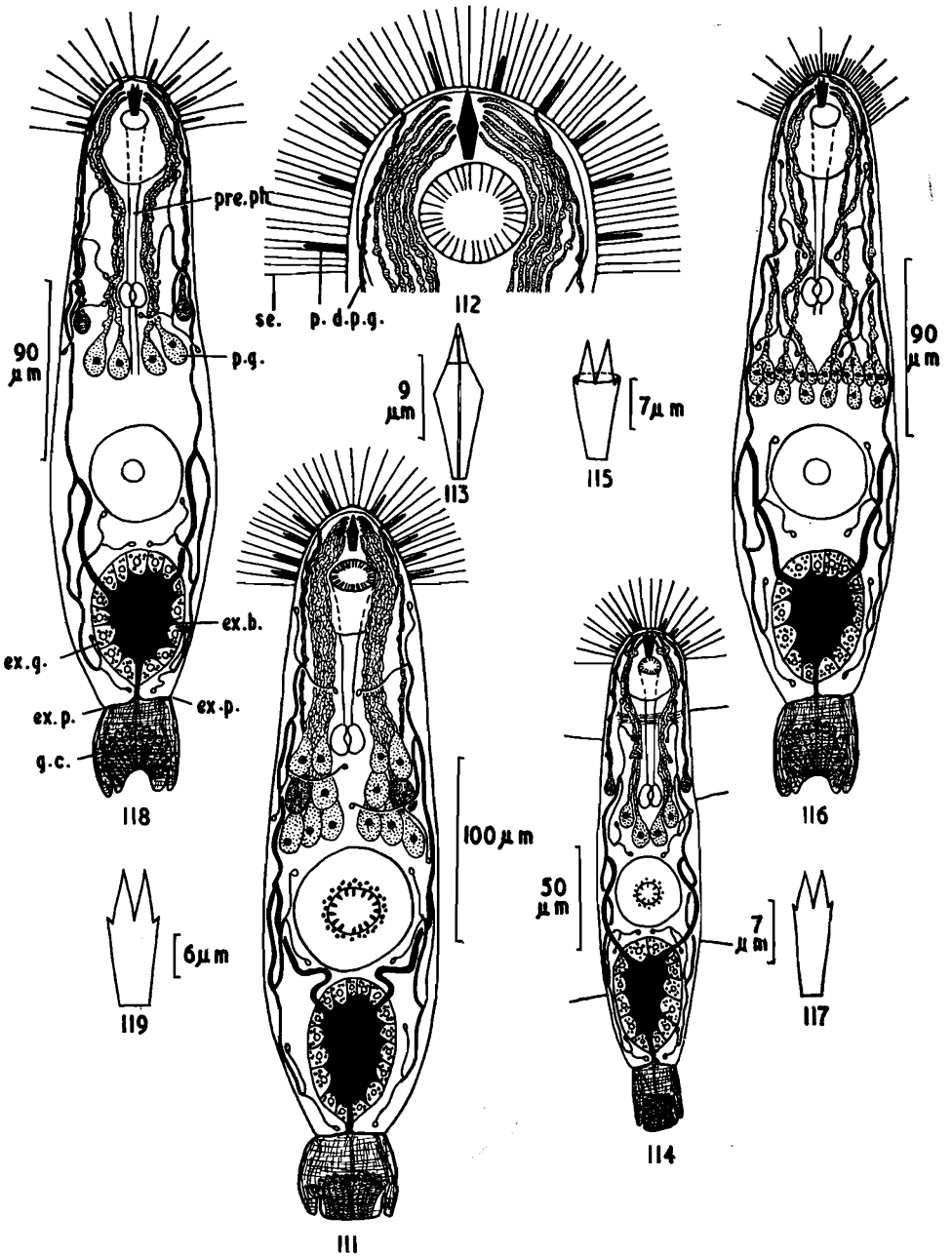
Figs. 97–101.
Cercaria brevicauda
97. Cercaria* 98. Stylet, dorsal view 99. Stylet, lateral view
100. Fully formed daughter sporocyst containing cercariae and encysted metacercariae
101. Encysted metacercaria

Figs. 102–105.
Cercaria roscovita
102. Cercaria* 103. Stylet, dorsal view 104. Stylet, lateral view
105. Fully formed daughter sporocyst containing cercariae

Fig. 106.
Cercaria parvicaudata, cercaria.*

Figs. 107–110.
Cercaria emasculans
107. Cercaria* 108. Stylet, dorsal view 109. Stylet, lateral view
110. Fully formed daughter sporocyst containing cercariae

* The excretory system is drawn only on one side of the diagram and the gland cells only on the other.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50 µm
7 µm
6µm
119
117
111
114

The shells of young *Littorina* species and subspecies are described and keys are included for the identification of adult *Littorina* species, subspecies and varieties and for twenty-two species of larval digenean parasites.

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FIGS. 111–113.
Cercaria linearis.

111. Cercaria 112. Anterior end of cercaria 113. Stylet, dorsal view

FIGS. 114–115.
Podocotyle atomon

114. Cercaria 115. Stylet, dorsal view

FIGS. 116–117.
Cercaria littorinae

116. Cercaria 117. Stylet, dorsal view

FIGS. 118–119.
Cercaria buccini

118. Cercaria 119. Stylet, dorsal view

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ADDENDUM

After this paper was sent to the printers, I became aware of the description by Dollfus (1966) of the redia, cercaria and metacercaria of *Notocotyloides petasatum* (Deslongchamps, 1824) Dollfus, 1966 (Pronocephalidae) from *Littorina littoralis* (L.) collected at St. Vaast-la-Hougue, France. The adult occurs in the intestine and caeca of the oystercatcher, *Haematopus ostralegus* (L.) and the turnstone, *Arenaria interpres* (L.). The larval stages would be indistinguishable from those of *Parapronocephalum symmetricum* (Figs. 64–67) but for their slightly smaller size,

the much narrower caecum in the redia and for the fact that the main excretory ducts do not fuse anteriorly in the cercaria.

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KEY TO LETTERING AND SYMBOLS OF FIGURES

(Figs. 1–7)

B	upper limit of barnacles in abundance (barnacle line)
MHWN	level of high water on mean neap tides
MHWS	level of high water on mean spring tides
MLWN	level of low water on mean neap tides
MLWS	level of low water on mean spring tides
MTL	mean tide level


the distribution of *Porphyra umbilicalis*


the distribution of *Fucus vesiculosus* f. *evesiculosus*


the distribution of *Balanus balanoides* and/or *Chthamalus stellatus*


the distribution of *Himanthalia elongata*


the distribution of *Pelvetia canaliculata*


the distribution of *Fucus spiralis*


the distribution of *Ascophyllum nodosum*


the distribution of *Fucus serratus*

1–8 Ballantine's (1961) exposure scale; 1-extremely exposed, 2-very exposed, 3-exposed, 4-semi-exposed, 5-fairly sheltered, 6-sheltered, 7-very sheltered, 8-extremely sheltered

(Figs. 29–50)

a.	apex
b.w.	body whorl
c.l.	columellar lip
g.	groove
o.l.	outer lip
p.	periostracum
r.	ridge
s.	suture
s.a.	shell angle (angle between outer lip and body whorl)
s.w.	spire whorl

(Figs. 51–117)

a.p.g.	anterior penetration gland cell
b.c.	body cavity
b.p.	birth pore
c.	caecum
c.c.	fully formed cercaria
c.g.	cystogenous gland cell
c.w.	cyst wall secreted by cystogenous glands of cercaria
co.	collar

co.sp.	collar spines	m.	metacercaria
d.	diverticulum of main excretory ducts	m.e.d.	main excretory duct
		o.s.	oral sucker
d.p.g.	ducts of penetration gland cells	oes.	oesophagus
e.	eye spot	ov.	ovary
e.c.	cercarial embryo	p.	sensory papillus
ex.a.	arm of excretory vesicle	p.g.	penetration gland cell
ex.b.	excretory vesicle	p.p.g.	posterior penetration gland cell
ex.g.	refractile excretory granule	ph.	pharynx
ex.p.	excretory pore	pr.	procusculum
ex.s.	stem of excretory vesicle	pre.ph.	prepharynx
ex.t.	caudal excretory vessel	s.	stylet
f.b.	flame cell	s.t.	tissue strand supporting caecum
f.c.	furcocercous cercaria	se.	sensory seta
f.t.	excretory tubule	t.	testis
g.a.	gonad anlage	t.f.	tail fin
g.b.	germinal ball	ut.	uterus
g.c.	caudal glandular cell	v.g.	vitelline gland
g.m.	germinal mass	v.s.	ventral sucker
l.p.	locomotor pocket	v.t.	vestigial tail