Variation in the Northern Rough Periwinkle, *Littorina saxatilis* (Olivi) in Nova Scotia

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(Received for publication 28 June, 1973)

Abstract

Samples of *Littorina saxatilis* (Olivi) were taken at nine stations along the Atlantic coast in Halifax and Lunenburg Counties, Nova Scotia. The animals in these samples were examined for diagnostic characters in order to find the magnitude of variation that occurred and the relationships between Nova Scotian and European forms of *L. saxatilis*. On the basis of shell breadth to length ratio, shell sculpture, pigmentation of the head and tentacles and the form of the penis, it was possible to distinguish three forms of *L. saxatilis*, called A, B and C. These forms roughly correspond to named European forms as follows: Form A - *L. s. tenebrosa tenebrosa* (Montagu); Form B - *L. s. tenebrosa similis* (Jeffreys) and Form C - *L. s. neglecta* (Bean). More than one of these forms occurs in the populations at some of the stations. The populations examined showed some degree of variation but were apparently not as varied as certain populations described from Europe.

Introduction

The northern rough periwinkle, *Littorina saxatilis* (Olivi), occurs commonly on the shores of the North Atlantic and Arctic Oceans. It characteristically occupies the middle and upper tide levels on shores with a stable substratum.

In Europe, the species extends from the southern bays of Novaya Zemlya (Zenkevitch, 1963), south to Gibraltar, the Azores (Thorson, 1941) and the Mediterranean. It is present on all of the intermediate coast, including the British Isles, Faroes, Iceland and South Spitzbergen. In the Baltic Sea, the distribution is as far east as the west coast of Rügen (Stresemann, 1957).

In North America, *Littorina saxatilis* occurs in the Canadian Arctic, east of the MacKenzie Delta (Dall, 1919), West Greenland (Thorson, 1951) and Baffin Island (Ellis, 1955), and extends southward along the coast to New Jersey, U.S.A. (Bequaert, 1943). Stephenson and Stephenson (1952) give the most southerly record at Beaufort Inlet, North Carolina. Wells (1965), has shown that the extensive sand beaches and higher water temperatures south of New Jersey effectively prohibit the southerly extension of *Littorina littorea* (L.) populations. These barriers would similarly restrict *Littorina saxatilis*

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which has boreal-arctic distribution and lacks a planktonic laval stage for dispersal. Littorinids reported from the North American west coast as *Littorina saxatilis* are considered to be forms of *Littorina sitkana* Philippi (Bequaert 1943, and Urban 1962).

Over its wide geographic and habitat range, *Littorina saxatilis* shows great variation in the morphology of the shell as well as in ecology and reproductive biology. As a result many subspecies and varieties have been described. The complex synonymy that appeared in the earlier literature was effectively clarified by Dautzenburg and Fischer (1912), who redescribed the various forms as subspecies and varieties of a single species, *Littorina saxatilis*. Despite this, such synonyms as *Littorina rudis* (Maton) have continued in use by many authors. In Europe, there has been renewed interest in the variation of *Littorina saxatilis*, particularly of populations on the shores of France, the Iberian Peninsula and the British Isles (Fischer-Piette and Gaillard, 1960, 1961,1966 and 1968; Fischer-Piette *et al.* 1966; Fischer-Piette *et al.* 1963 and 1964, Fischer-Piette *et al.* 1961; and James 1968 a and b).

There are six subspecies of *Littorina saxatilis* and, of these, three have been further differentiated into varieties, largely on the basis of shape and sculpturing of the shell. These subspecies are listed in Table I. All other names referring to *Littorina saxatilis* are considered to be synonymous with the appropriate subspecies.

Table I

A list of the names and authors of subspecies and varieties of *Littorina saxatilis* (Olivi) currently in use. (After James, 1968).

SUBSPECIES	VARIETY
L. saxatilis saxatilis (Olivi, 1792).	
L. saxatilis rudis (Maton, 1797)	*rudis*, 1797.
	rudissima Bean, 1844
	nigrolineata Grey, 1839
	jugosoides James, 1968
L. saxatilis jugosa (Montagu, 1803)	*jugosa* Montagu, 1803
	rudissimoides James, 1968
	tenuis James, 1968
	attenuata Dautzenburg and Fischer, 1912
L. saxatilis tenebrosa (Montagu, 1803)	*tenebrosa* Montagu, 1803
	similis Jeffreys, 1865
	patula Thorpe, 1844
	elata Dautzenburg and Fischer, 1912
L. saxatilis neglecta (Bean, 1844)	
L. saxatilis gronlandica (Menke, 1830)	

In addition to the subspecies and varieties listed in Table I, there are 21 names assigned to distinct colour-forms. These are listed in Table II. Several of these colour-forms occur throughout the subspecies and varieties. Some are illustrated in the figures given by Dautzenburg and Fischer (1962).

Colour is one of the most variable characters of *Littorina saxatilis*. Fischer-Piette *et al.* (1963) describe two populations with extreme colour diversity; one having 164 colour variations in 400 specimens and the other, 155 variations in 468. Specimens were frequently found to have the characteristics of more than one of the colour-forms listed in the table.

Table II

A summary of the names of Colour-forms of *Littorina saxatilis* (Olivi), occuring in the literature. These colour-forms generally are found throughout the different subspecies and varieties.

NAME	COLOURATION	AUTHORITY
L. s. albida	Uniform white	Dautzenburg, 1887
L. s. zonaria	White or yellow with brown bands	Bean, 1844
L. s. bi-zonaria		James, 1963
L. s. tessellata	White and grey tesselations	Dautzenburg, 1893
L. s. interupta	White with dark brown hyphens	Fischer-Piette *et al.* 1961
L. s. bi-interupta		Fischer-Piette and Gaillard, 1963
L. s. flammulata		Dautzenburg and Fischer, 1912
L. s. hieroglyphica	White background with brown or grey designs	Fischer-Piette *et al.* 1961
L. s. lineata	Pale yellow with brown lines	Dautzenburg and Fischer, 1912
L. s. fusca	Uniform brown	Dautzenburg and Fischer, 1912
L. s. sanguinea	Uniform red	Dautzenburg and Duronchoux, 1900
L. s. mineata	Uniform brick red	Dautzenburg and Fischer, 1912
L. s. aurantia	Uniform yellow-orange	Dautzenburg, 1887
L. s. fulva	Uniform fawn	Monterosato, 1872
L. s. lutea	Uniform lemon	Dautzenburg and Duronchoux, 1900
L. s. tractibus	Light background with light brown hyphens	Fischer-Piette *et al.* 1961

Table II Continued

L. s. maculata	Black with light-yellow or grey patches	Fischer-Piette and Gaillard, 1963
L. s. trifasciata	Two light and two dark bands	Dautzenburg and Fischer, 1912
L. s. nojensis	Uniform green-grey to green-yellow	Fischer-Piette and Gaillard, 1964
L. s. nigrolineata	Light background with fine dark spiral lines, only in *L. s. rudis nigrolineata*	Grey, 1839

Tessellations may be described as alternately arranged light and dark areas, in a spiral mosaic.

Hyphens may be described as elongate, narrow, broken light and dark lines.

James (1968) has considered *L. s. trifasciata* and also a further colour form *L. s. fasciata*-Dautzenburg, as synonymous with *L. s. zonaria.*

Fischer-Piette *et al.* (1964) and James (1968a) have described the characteristics of shell, radula, number of penial glands, head pigmentation and size of emerging juveniles, together with the habitat and larval trematode parasites of each subspecies and variety. The authors admit, and in fact describe, the wide variation that occurs within a defined subspecies or variety. These variations are particularly apparent when different populations are contrasted. In their 1964 paper. Fischer-Piette *et al.* summarize as follows:

> "(a) some populations are homogeneous with respect to shell character and others in similar environmental conditions are heterogenous.
> (b) some heterogeneous populations have intermediates between extremes but others, again in similar conditions, do not.
> (c) stations with similar topography may have populations with widely different shell characters.
> (d) populations of varieties occur discontinuously and randomly in regions with apparently different topography.
> (e) some variations in shell characters, which are usually correlated with changes in the environment, may sometimes occur without, with apparent disregard for or even against, such changes.
> These observations further illustrate the extreme variation of *L. saxatilis* and the difficulty in trying to understand the causes of this variation."

Fischer-Piette and Gaillard (1966) have further shown that a progressive colour change toward darker forms has taken place during a period of from one to 16 years in some populations on the coasts of France and Spain. They do not, however, speculate on the causes for this change.

There have been very few descriptions of the variation of *L. saxatilis* in North America. Bequaert (1943), in a review of the genus *Littorina* in the western Atlantic, examined diverse *L. saxatilis* specimens but found it difficult to distinguish the different subspecies and varieties. No consistent differences were found between the southern forms and those northern forms that had been identified as *L.s. gronlandica*. *L. s. jugosa* was considered to be a form with few, but well-defined spiral ridges on the shell, whereas *L. s. vestita* (Say) and *L. s. obligatus* (Say) had similar shells but with less well-defined ridges. *L. s. tenebrosa* was described by Bequaert as having a thinner and more elongate shell, and as living in brackish water creeks and marshes. Gould (1870) has listed *L. s. obligatus* as a synonym of *L. s. rudis*, and *L. s. vestita* as a synonym of *L. s. tenebrosa*. Coleman (1932) considered the synonymy of *L. saxatilis* but confined his statistical treatment to a comparison of European and North American *Littorina obtusata* (L.).

Littorina saxatilis has been frequently reported from the shores of Nova Scotia. Published records are summarized by LaRocque (1953). Occurrences are also cited for the upper tidal zone of the Bay of Fundy, Minas Channel and Cobequid Bay by Bousfield and Leim (1959), and for southern and western shores as "very common along rocky shores at high water level, and in estuaries among eel grass", by Bousfield (1958). Gowanloch and Hayes (1926) give a brief description of *L. saxatilis* at Halifax, Nova Scotia and St. Andrews, New Brunswick. The wall of shells is described as thin, but thick in gross appearance due to the coarse texture and spiral ridges.

> "The shell is very variable in texture, ranging from a smooth appearance with no spiral ridges visible to the unaided eye, to a coarse looking shell with or without spiral ridges. The colour is extremely variable, and may be various shades of white, red or black, or a colour combination"

Stephenson and Stephenson (1954), during their studies of the intertidal zone in Nova Scotia and Prince Edward Island, recorded two distinct forms of *L. saxatilis* which they called "types A and B". "Type B" resembled *L. obtusata* in general shell form and was present at several localities including exposed rocks at Peggy's Cove, Nova Scotia. "Type A" had a more sharply pointed shell and was more widely distributed, though commonly occurring with type B.

The recent studies of variation in characters and ecology of *L. saxatilis* in Europe have provided a good basis for similar studies in North America. A study was made of some populations in Nova Scotia with the object of relating them to their European counterparts.

Methods

Studies were made of *L. saxatilis* populations at nine localities on a variety of shores in Halifax and Lunenburg Counties, Nova Scotia. These localities are

listed in table III and indicated on the map, Figure 1. Sample size varied from 50 to 250 individuals, with a total of 958 snails being examined. Collections were made at random, and without any special reference to tide level.

The individual snails in each sample were examined for anatomical characters and notes and measurements were made as follows:

(a) shell dimensions. Measurements of the length and breadth were made to the nearest 0.25 mm. Shell-length is the distance from the apex to the lower margin of the aperture, through the axis of the shell. Breadth is the greatest distance through the body whorl, at right angles to the shell axis.

(b) Shell whorls. The number of shell whorls was noted.

(c) Shell colour. The colour of each shell was described according to the list in Table II, or by direct reference to the colour or colour-combination where no trivial name is given.

(d) Shell sculpture. Shell sculpture is described by use of an index: 0 (smooth) to 3 (coarse ribbed) which roughly correspond to the stages shown in Figure 2.

Table III

The localities in Halifax and Lunenburg Counties, Nova Scotia where samples of *L. saxatilis* were collected for examination of variation in characters.

STATION NO.	LOCALITY	DATE	HABITAT	NUMBER OF SNAILS EXAMINED
1	Lawrencetown Lake	3 May 1967	Salt marsh	50
2	Point Pleasant Park, Halifax	12 Aug. 1968	Exposed boulder beach	100
3	Sandy Cove	28 Feb. 1968	Exposed rocky shore	107
4	Prospect Cove	28 Feb. 1968	Sheltered boulder beach	100
5	Peggy Point	29 Mar. 1968	Exposed rocky shore	97
6	Indian Harbour	29 Mar. 1968	Sheltered rocky shore	107
7	Mason Cove	28 Apr. 1968	Sheltered boulder beach	97
8	Queensland	29 Nov. 1967	Exposed boulder beach	50
9	Blue Rocks	3 Oct. 1967	Sheltered rocky shore	250

(e) Pigmentation of the head and tentacles. Indices have also been assigned to describe stages in the degree of pigmentation of the snail's head and tentacles. These stages, A to F, are shown in Figure 3. Intermediates occur but these have been grouped with the closest stage illustrated. In some males the penis is pigmented as well as the head and tentacles. This system was defined for use in the present investigation before James (1968) published a similar system for British *L. saxatilis*. The two systems are compared in Table IV.

(f) The number of penial glands. The number of mucus glands on the penis of each male was counted. These glands are arranged in one, two or rarely three rows.

(g) Brood pouch contents. *Littorina saxatilis* is ovoviviparous, and the eggs, embryos and larvae are retained during their development in a pouch-like expansion of the oviduct. The young were counted and any abnormalities such as sinistral and dentalioid shell forms, as described by Thorson (1946), were noted.

(h) Larval trematode infections. The infection of any individual snail by larval trematodes was noted. The parasites were named using the key and descriptions of James (1968b). Only specimens with a shell length greater than 3.0 mm were used in this study.

Parts of the nine samples taken for examination are now in the collection of the Nova Scotia Museum, under accession number 1968-z-60.

Table IV

The stages in the development of pigmentation on the head and tentacles of *Littorina saxatilis* used by James (1968a) and the approximately equivalent stages used in the present investigation.

JAMES (1968a) INDEX	RECENT INVESTIGATION INDEX
1	A
2	—
3	B
4	—
5	C
6	D
7	—
8	E
9	—
10	F
11	—

Results and Discussion

The nine samples of *L. saxatilis* collected along the Atlantic coast, in Halifax and Lunenburg Counties, Nova Scotia, were examined for anatomical characters. Each title (a to h) will be considered separately. Examples of the specimens from these stations are shown in Figure 10. These illustrate some of the shell characters encountered in the samples.

a) Shell dimensions. The maximum shell length and the ratio of shell breadth to shell length in each of the nine samples are shown in Table V.

The range in shell lengths is not great but at Station 1, a salt marsh, the snails are distinctly smaller than those at other stations. The maximum shell length was only 5.00 mm. The largest specimens, with a shell length of 14.00 mm were found at Station 5, a very exposed situation. The shells collected at the other stations, which were either sheltered or exposed, had maximum shell lengths of from 8.75 to 10.50 mm. The variation in maximum shell length between these stations is most probably related to environmental conditions.

Table V

The maximum shell length, average ratio of shell breadth to shell length and number of shell whorls of *L. saxatilis* collected at nine stations on the Atlantic coast of Nova Scotia.

STATION NO	MAXIMUM SHELL LENGTH (mm)	AVERAGE RATIO OF SHELL WIDTH TO SHELL LENGTH (Range of Ratios)	NUMBER OF SHELL WHORLS
1	5.00	1: 1.27 (1.00 - 1.67)	4
2	8.75	1: 1.29 (1.12 - 1.48)	4 - 5
3	10.50	1: 1.37 (1.13 - 1.57)	4 - 6
4	9.00	1: 1.41 (1.18 - 1.63)	5 - 6
5	14.00	1: 1.28 (1.14 - 1.44)	4 - 5
6	10.50	1: 1.33 (1.13 - 1.71)	4 - 6
7	10.00	1: 1.44 (1.16 - 1.67)	4 - 6
8	9.25	1: 1.30 (1.11 - 1.45)	4 - 6
9	12.00	1: 1.35 (1.16 - 1.69)	4 - 6

Remane and Schlieper (1958) recorded a decrease in the maximum size attained by *Buccinum undatum* (L.) from marine to brackish waters, and noted that this was also true, but to lesser degree, for littorinids. Such observations would indicate that the conditions of salinity, temperature, etc., found in brackish waters either reduce longevity or stunt growth in these animals.

The values for average ratio of shell breadth to shell length show a difference in the proportion of the shells between each of the nine samples. The ratios at sheltered marine localities such as Stations 4 and 9 are larger than those from exposed locations such as Stations 2 and 5 and from the salt marsh, Station 1. That is, the shells from sheltered marine locations have relatively higher spires than do those from exposed localities and the salt marsh.

Stephenson and Stephenson (1954) used shell shape to distinguish two forms of *L. saxatilis*, which they called "type A" and "type B". The difference in shell shape is shown by comparing the shell breadth to shell length ratios of specimens of "type A" from Mason Cove (Station 7) and of "type B" from Peggy Point (Station 5). The "type A" has a ratio of 1: 1.44, whereas the

"type B" has a ratio of 1: 1.28. The distinction of the two populations is clearly seen in Figure 4, where the shell breadth to length ratios have been plotted against shell length. It may be seen from the illustrations of the "type B" shell in Figures 10/11 and 12, that the smaller shell breadth to length ratio results from an enlargement of the body whorl and aperture. This aperture can accommodate a larger foot and since this character would be an advantage in situations exposed to wave action, selection would increase the proportion of "type B" in the population. Bequaert (1943) has suggested that a difference in the ratio of breadth to length that he observed in *L. saxatilis* was associated with the sex of the individual. Females would require a larger body whorl to accommodate the brood pouch. This hypothesis was tested in the sample collected at Sandy Cove (Station 3), which was a mixture of high-spired and short-spired individuals. The ratios of shell breadth to shell length are shown in Figure 5. No difference between the dimensions of males and females can be seen, although there is a wide range of breadth to length ratios in the sample.

b) Number of shell whorls.

The results show no great variation in the number of shell whorls. The range from four to six whorls shown in Table V, is associated with the range in shell length. That is, the number of shell whorls increases with shell length.

c) Shell colour.

The shell colour forms found in the nine samples are listed in Table VI, and some examples are illustrated in Figure 10. The majority of the forms distinguished could be associated with named forms which are included in Table II. A small proportion, however, are listed according to their colour because they could not be confidently associated with any of the named forms. One single example from Station 9, being white with a single brown spiral line apparently has not been previously described. (Figures 10/22). There was only little colour variation in most of the samples and in two cases this may have been a result of selection by predators. At Queensland (Station 8) and Mason Cove (Station 6) the only colour forms present were *L. s. fusca, L. s. fulva* and *L. s. lutea* all of which blend fairly well with the colour of the weathered granite. The more distinctly coloured forms would be more easily seen against this background. In direct contradiction to this situation, the greatest colour range was found at Blue Rocks (Station 9), where the snails are completely exposed and conspicuous against a dark slate background. Fischer-Piette *et al* (1963) found wide colour variation in some populations in Europe, both on exposed rock surfaces and in deep crevices. They attribute the wide range of colour in these populations to their isolation by physical barriers. The mode of reproduction and development of *L. saxatilis* does not allow wide dispersal of the offspring and mixing of populations. In the population, the various genetic combinations are always present and they are manifested in situations where there is little selection by predators. This, however, does not explain why such selection should be more severe in one population compared with another.

The wide range of colour variation at Blue Rocks includes individuals with combinations of named forms. This may be a permanent combination with one

Table VI

The occurence of various colour forms of *L. saxatilis* collected at nine stations on the Atlantic coast of Nova Scotia. The named forms are defined in Table II. The values are percentages of the total number of individuals in each sample.

COLOUR FORM	STATION NUMBER								
	1	2	3	4	5	6	7	8	9
L. s. albida	—	12.0	0.9	10.0	—	0.9	—	—	10.5
L. s. zonaria	—	9.4	9.4	8.0	1.0	5.6	—	—	14.0
L. s. tessellata	+	25.0	—	11.0	24.8	33.6	—	—	9.5
L. s. interupta	—	—	—	2.0	—	—	—	—	18.5
L. s. fusca	—	27.0	0.9	18.0	—	24.3	78.4	—	23.5
L. s. sanguinea	—	—	—	—	—	—	—	—	1.0
L. s. aurantia	—	—	—	1.0	—	0.9	—	—	0.5
L. s. fulva	—	5.0	—	25.0	42.3	12.1	21.6	88.0	7.0
L. s. lutea	—	—	—	—	—	—	—	12.0	0.5
L. s. maculata	—	—	0.9	—	10.3	—	—	—	—
L. s. zonaria/tessellata	—	—	2.8	—	—	—	—	—	—
**L. s. zonaria/grey*	—	—	—	—	—	—	—	—	0.5
Uniform grey	—	10.0	—	4.0	—	—	—	—	7.5
Uniform olive green	—	4.0	—	—	—	—	—	—	—
Red brown	—	—	—	6.0	—	—	—	—	1.0
Yellow brown	—	—	—	3.0	—	1.9	—	—	—
Fawn with a dark band	—	—	—	—	—	2.8	—	—	—
Brown with dark spiral lines	—	15.0	—	12.0	—	17.8	—	—	5.0
White with a single brown line	—	—	—	—	—	—	—	—	0.5
Corroded shells	+	—	85.1	—	11.6	—	—	—	—

*showing a distinct colour change during life

Table VII

The shell sculpturing found in *L. saxatilis* collected at nine stations on the Atlantic coast of Nova Scotia. The extent of sculpturing is indicated by the reference numbers 0 to 3 (from no sculpturing to maximum sculpturing, see Fig. 2). The values are percentages of the total number of individuals in each sample.

STATION NO.	THIN SHELLS	SOLID SHELLS	OCCURRENCE OF EACH TYPE OF SCULPTURING %				SHELLS SHOWING CHANGE OF SCULPTURING DURING LIFE		
			0	1	2	3	1 to 0	2 to 0	3 to 0
1	+	—	100.0	—	—	—	—	—	—
2	+	—	84.0	11.0	4.0	1.0	—	—	—
3	—	+	94.4	2.8	2.8	—	—	—	—
4	+	—	—	8.0	41.0	51.0	—	—	—
5	+	—	34.0	—	57.7	8.2	—	—	—
6	+	—	61.7	2.8	15.9	17.8	—	—	—
7	+	—	1.0	—	3.1	95.9	—	—	—
8	—	+	78.0	22.0	—	—	—	—	—
9	+	—	24.5	9.5	7.5	49.5	1.5	1.0	6.5

Table VIII

The extent of head pigmentation found in *L. saxatilis* collected at nine stations on the Atlantic coast of Nova Scotia. The extent of pigmentation is indicated by the reference letters A to F (from minimum to maximum pigmentation, see fig. 3). The values are percentages of the total individuals in each sample.

EXTENT OF PIGMENTATION	OCCURRENCE AT EACH STATION, %								
	1	2	3	4	5	6	7	8	9
A	—	—	0.9	—	2.1	—	—	—	—
B	—	12.0	15.9	3.0	16.5	5.6	4.1	2.0	0.5
C	—	57.0	57.0	30.0	45.4	32.7	9.3	26.0	21.5
D	4.0	27.0	21.5	45.0	32.0	42.1	21.6	54.0	54.5
E	96.0	4.0	4.7	21.0	4.1	18.7	12.4	18.0	16.0
F	—	—	—	1.0	—	0.9	52.6	—	4.0
Undetermined	—	—	—	—	—	—	—	—	3.5

pattern imposed upon another as in the example with *L. s. zonaria* and *tessellata* (Figure 10/28), or a distinct change of colour following a seasonal growth interruption. An example of the latter is the change from *L. s. zonaria* to uniform grey. Such combinations of colour were also encountered by Fischer-Piette *et al* (1963).

d) Shell sculpture.

Shell sculpturing ranged from completely smooth (0) to coarse ridged (3) as illustrated in Figure 2. The sample from Station 1 contained only smooth shells, but the others had various sculptural forms (Table VII). When a comparison is made between populations from extremes of environmental conditions there is an indication of some relationship between ridged shells and exposure to wave action. The shells at Station 1 were all smooth (0), whereas at the exposed Station 5, 66% of the shells were ridged (2 and 3). It might be deduced that the shells are reinforced by the ridges and that this feature would be selected in very exposed habitats. However, a further comparison made with the shells from Station 7 does not support this. At this Station, in very sheltered conditions, 99% of the shells were ridged (2 and 3).

In the sample from Blue Rocks (Station 9) there were examples of change from ridged to smooth shell during the life of an individual. This change was always associated with a growth interruption, similar to the changes in shell colour observed in the same sample.

e) Pigmentation of the head and tentacles.

The extent of head pigmentation in *L. saxatilis* collected at the nine sampling Stations is shown in Table VIII. The stages (A to F) are illustrated in Figure 3. In all but two cases the most commonly occurring stages were C or D, being represented by from 42.0 to 57.0% of the individuals in each sample. At Station 7, a sheltered rocky shore, 52.6% of the snails had pigmentation at stage F, and at Station 1, a salt marsh, 96.0% had pigmentation at stage E. In all samples, except that from Station 1, there was a wide variation in the extent of pigmentation.

James (1968a) found some differences in the extent of pigmentation which could be related to the different subspecies of *L. saxatilis* in Britain. In the nine samples taken in Nova Scotia, only those populations at Stations 1 and 7 show any marked differences from the others.

It was also noted by James (1968a) that pigmentation became darker with age. Table IX shows the occurrence of pigmentation stages B to F throughout the size range of the sample taken at Station 9. The stages C and D are best represented in the sample and occur at all intervals of shell length. Darker forms, to stage F, occur less commonly in individuals of intermediate shell length, and the lightest form B, occurs only in one of the largest individuals. This result does not support the view that pigmentation becomes darker with age, but would apparently support the idea that the extent of pigmentation on the head and tentacles was characteristic for subspecies or forms of *L. saxatilis*.

f) The number of penial glands.

In the samples of *L. saxatilis* taken in Nova Scotia, males were found to have one, two or rarely three rows of penial glands. These results are given in Table

Table IX

The occurence of the stages B to F in extent of head pigmentation through the size range a sample of *L. saxatilis* collected at Station 9 on 3rd October 1967. These Stages are illustrated in Fig. 3.

SHELL LENGTH 0.6 mm INTERVALS	NUMBER IN EACH SIZE GROUP					
	n	B	C	D	E	F
1.75	1	—	1	—	—	—
2.25	11	—	4	7	—	—
2.75	13	—	7	6	—	—
3.25	23	—	7	15	1	—
3.75	9	—	4	5	—	—
4.25	13	—	3	7	2	1
4.75	10	—	2	3	3	2
5.25	16	—	3	11	2	—
5.75	15	—	5	6	3	1
6.25	17	—	4	10	3	—
6.75	18	—	2	11	4	1
7.25	10	—	3	4	3	—
7.75	11	—	3	7	—	1
8.25	8	—	2	4	2	—
8.75	13	—	5	6	2	—
9.25	12	—	3	6	1	2
9.75	13	—	3	8	2	—
10.25	10	—	2	8	—	—
10.75	8	—	1	5	2	—
11.25	7	1	1	5	—	—
11.75	1	—	—	1	—	—
12.25	4	—	—	4	—	—

X. Examples from specimens with glands in a short, single row (from Station 1), a long, single row (from Station 7) and a double row (from Station 5) are shown in Fig. 6.

At Stations 1, 2, 6, 8 and 9 all individuals had glands in a single row, the number varying from 0 to 18. The mean number of penial glands for all males in each sample ranged from 5 to 11, these extremes being for Stations 1 and 8 respectively.

At the other Stations (3, 4, 5 and 7) there was a mixture of individuals with single or multiple rows of penial glands. At Stations 4 and 7 there were only one and two examples respectively, with a double row of glands. At Stations 3 and 5 about half of the males in each sample had glands in double or triple rows. There were between 5 and 19 glands in the first row and 1 to 18 glands in the second row. The single example with three rows of glands, had four glands in the third row.

Table X

The penial gland arrangements in *L. saxatilis* collected at nine stations on the Atlantic coast of Nova Scotia. The mucus glands occur on the penis in either a single or multiple rows.

	STATION NUMBER								
	1	2	3	4	5	6	7	8	9
With a single row of of glands. (n)	26	33	24	38	21	43	42	27	87
$\bar{x}$ number of glands	5	8	8	11	11	10	13	11	9
range of numbers	4-9	0-17	0-15	0-17	0-20	0-15	4-19	6-18	2-17
With a double or triple row of glands (n)	—	—	25	1	18	—	2	—	—
row No. 1 $\bar{x}$ number	—	—	11	11	12	—	8	—	—
range of numbers	—	—	5-19	11	5-19	—	7-9	—	—
row No. 2 $\bar{x}$ number	—	—	4	2	4	—	6	—	—
range of numbers	—	—	1-8	2	1-8	—	5-6	—	—
row No. 3 $\bar{x}$ number	—	—	4	—	—	—	—	—	—
range of numbers	—	—	4	—	—	—	—	—	—

Of the Stations sampled, 3 and 5 were the most exposed to wave action, and there may be an association between the *L. saxatilis* with multiple rows of penial glands and such habitats. The other distinct penial gland arrangement, a short, single row, found at Station 1, may also be associated with a form of *L. saxatilis* living in salt marshes. James (1968a) has shown that in *L. s. rudis*, the number of penial glands is reduced on sheltered shores as compared to exposed shores.

g) Brood pouch contents.

Although females carrying embroyonic snails or brood were found in all nine samples taken, examinations of the brood were only made at Stations 1, 3, 5, 6, 7 and 9.

The stages in the development of eggs and embryos of *L. saxatilis* were studied by Berry (1961). The periodic release of batches of eggs into the brood pouch and their retention during development results in there being a range of developmental stages within any individual female. The number of embryos present varies with the season of the year. The nine samples from Nova Scotia were not all taken at the same time of the year, but broods were always found.

All stages of development were observed, from eggs to juveniles about to be released. Various deformities were detected, including sinistral shell coiling and the open coiling (*dentalioid*) and plane spiral coiling (*planorbioid*) forms described by Thorson (1946). None of the abnormal forms was common however. Some examples are illustrated in Fig. 7. The shell breadth of juveniles at the time of release from the parents brood pouch was from 0.5 mm to 0.75 mm.

The mean number of brood occuring at 0.5 mm intervals of shell length of females at each station is given in Table XI. For all the stations there was an overall increase in the number of brood with increase in size (and age). The range extends from the minimum of three juveniles in adults of 3.50-3.99 mm shell length, to 206 in adults of 12.00-12.49 mm shell length. In Fig. 8 the mean number of brood have been plotted against shell length for the samples from station 1, 5, and 7. A relationship between the numbers of brood and the size of the female is clearly implied.

h)Larval trematode infections

The larvae of seven species of digenetic trematodes were found in *L. saxatalis* at the nine stations sampled. These species were *Parvatrema homeotecnum* James, *Himasthla littorinae* Stunkard, *Microphallus pygmaeus (Levinsen), Microphallus similis* (Jagerskiold), *cercaria roscovita* Stunkard, Podocotyle atomon (Rudolphi) and *Cryptocotyle lingua* (Creplin). All are previously known from *L. saxatalis* at other localities.

Table XI

The mean number of embryonic snails in brood pouches of female *L. saxatilis* at six stations on the Atlantic coast of Nova Scotia. The mean number is given for all snails in each group at 0.5 mm intervals of shell length.

SHELL LENGTH 0.5 mm INTERVALS	STATION NO.					
	1	3	5	6	7	9
3.50 - 3.99	11.3	—	—	3.0	—	—
4.00 - 4.49	12.1	—	—	20.5	—	—
5.00 - 5.49	13.5	—	—	7.0	—	26.5
5.50 - 5.99	25.5	—	—	23.3	—	23.2
6.00 - 6.49	—	—	—	27.7	9.0	48.4
6.50 - 6.99	—	22.0	—	37.2	13.7	35.3
7.00 - 7.49	—	26.0	—	31.6	4.0	74.7
7.50 - 7.99	—	12.3	—	79.5	26.0	41.0
8.00 - 8.49	—	39.3	23.0	—	21.0	4.0
8.50 - 8.99	—	25.8	42.8	113.0	34.0	63.0
9.00 - 9.49	—	33.0	55.0	79.0	60.5	49.7
9.50 - 9.99	—	31.6	46.6	52.0	48.5	35.3
10.00 - 10.49	—	22.0	60.1	—	7.0	6.0
10.50 - 10.99	—	29.3	61.7	—	—	144.3
11.00 - 11.49	—	18.0	76.0	—	—	3.0
11.50 - 11.99	—	—	102.7	—	—	78.0
12.00 - 12.49	—	—	206.0	—	—	—
12.50 - 12.99	—	—	55.0	—	—	45.0
13.00 - 13.49	—	—	—	—	—	—
13.50 - 13.99	—	—	—	—	—	—
14.00 - 14.49	—	—	179.0	—	—	—

One or more of these species was found at Stations 1, 2, 5, 6, 7 and 9. No parasites were found at Stations 3, 4 and 8. The results are summarised in Table XII. The greatest diversity of parasite fauna occurred at the most sheltered localities, Stations 1, 7 and 9. The high infection level of 39.2% at Station 9 was due to the presence of large numbers of gulls attracted by discarded wastes of local fish processors.

Of the seven trematode species, three occurred at only one of the stations. *Parvatrema homeotecnum* occurred at Station 1, *Himasthla littorinae* and *Cryptocolyle lingua* at Station 9. The other four species were found in *L. saxatilis* from a variety of shores.

Table XII

The occurence of larvae of seven species of digenetic trematodes in *L. saxatilis* collected at nine stations along the Atlantic coast of Nova Scotia. The number of *L. saxatilis* infected with each species is given. Some species were double infected with two species of parasite.

	STATION NUMBER								
	1	2	3	4	5	6	7	8	9
Total snails in sample	50	100	107	100	97	107	97	50	250
Parvatrema homeotecnum	2	—	—	—	—	—	—	—	—
Himasthla littorinae	—	—	—	—	—	—	—	—	1
Microphallus pygmaeus	1	3	—	—	—	—	1	—	3
Microphallus similis	—	—	—	—	1	—	2	—	22
Cercaria roscovita	—	—	—	—	—	4	2	—	—
Podocotyle atomon	2	—	—	—	—	—	1	—	1
Cryptocotyle lingua	—	—	—	—	—	—	—	—	63
double infections	—	—	—	—	—	—	1	—	7
Total snails infected	5	3	—	—	1	4	7	—	98
% infection (all species)	10.0	3.0	—	—	1.0	3.7	7.2	—	39.2

Intraspecific Classification of *L. Saxatilis* In Nova Scotia

Many of the descriptions of the subspecies and varieties of *L. saxatilis* in Europe have been based upon characters of the shell and habitats. The recent work of James (1968 a and b) has used many other characters for forms occurring in Britain, and this has been a most useful guide in the present study.

The examination of the nine samples for particular characters reveals the presence of three distinct forms of *L. saxatilis* in the Lunenburg-Halifax counties area of Nova Scotia. The size and shape of the shell, as used by Stephenson and Stephenson (1954) to distinguish their "Types A and B", were the most useful distinguishing characters. The distinction was made clearer, however, when shell proportions were related to the pigmentation of head and

tentacles, the number of penial glands and the shell sculpturing. These features have been combined in Fig. 9 for Stations 1, 5 and 7. Stations 5 and 7 are the recorded localities for "Types A and B". It will be seen that the three populations can be clearly distinguished.

The possible synonyms, and the characters of the three forms of *L. saxatilis* may be summarized as follows:

Form A. Synonyms: Type A (Stephenson and Stephenson, 1954), *L. s. tenebrosa tenebrosa* (Montagu, 1803). The shells were thin and either smooth or ridged with maximum length of 14.0 mm and breadth to length ratio of 1: 1.44. The head pigmentation was mostly of stages D, E and F and males had a mean number of nine penial glands arranged in a single row. This form was abundant on fairly exposed to sheltered rocky shores.

Form B. Synonyms: Type B (Stephenson and Stephenson, 1954), *L. s. tenebrosa similis* (Jeffreys, 1865). The shells were generally thin and smooth or ridged. The maximum recorded shell length was 14.0 mm and shell breadth to length ratio was 1: 1.28. The head pigmentation was mainly of stages B, C and D. Males had penial glands arranged in two rows with 12 glands in the long row and 4 glands in the short row. The form occurred on very exposed rocky shores.

Form C. Synonym: *L. s. neglecta* (Bean, 1844). The shells were thin and smooth, with maximum shell length of 5.0 mm and shell breadth to length ratio of 1: 1.27. The head pigmentation was mostly stage E and males had a mean number of five penial glands arranged in a single row. This form was extremely abundant in salt marshes and eel grass ponds.

From this preliminary examination and from the descriptions given by Bequaert (1943), *L. saxatilis* does not appear to be as variable in North America as it is in Europe. There is no geographic continuity between the European and North American populations but *L. s. gronlandica* is known from both continents and *L. s. gronlandica, L. s. rudis* and *L. s. tenebrosa* are known from Iceland (Thorson, 1941). In Iceland, *L. s. tenebrosa* is recorded as a brackish water form which intergrades with the other two subspecies. *L. s. tenebrosa* is the name commonly given to forms living in eel grass beds on both sides of the Atlantic, particularly in Denmark (Thorson, 1946 and Muus,1967) and New England (Dexter, 1947 and Hunninen and Cable, 1943). James (1968a) does not describe *L. s. tenebrosa* from this habitat in Britain but does record *L. s. neglecta* from salt marshes. The latter is the most common form in salt marshes and eel grass beds in Nova Scotia.

In Nova Scotia there seems to be a close relationship between the forms described. Certainly there is mixing of forms A and B at some localities (e.g. Station 3) and possibly also between forms A and C in sheltered situations (e.g. Station 9). James (1968) has suggested lines of evolution of the subspecies and varieties of *L. saxatilis* in Britain. He indicates a gradation between *L. s. tenebrosa similis* and *L. s. tenebrosa tenebrosa* with different grades of exposure to wave action. Also, a main evolutionary line from *L. s. tenebrosa tenebrosa* to *L. s. neglecta* is indicated. Both of these ideas are supported by the forms and habitats of *L. saxatilis* in Nova Scotia.

Acknowledgments

This study was carried out at Dalhousie University, with support from a Dalhousie graduate award, and at the Nova Scotia Museum. I would like to thank Dr. J. Farley for his helpful suggestions and Drs. I.A. McLaren and E.T. Garside for reading the manuscript.

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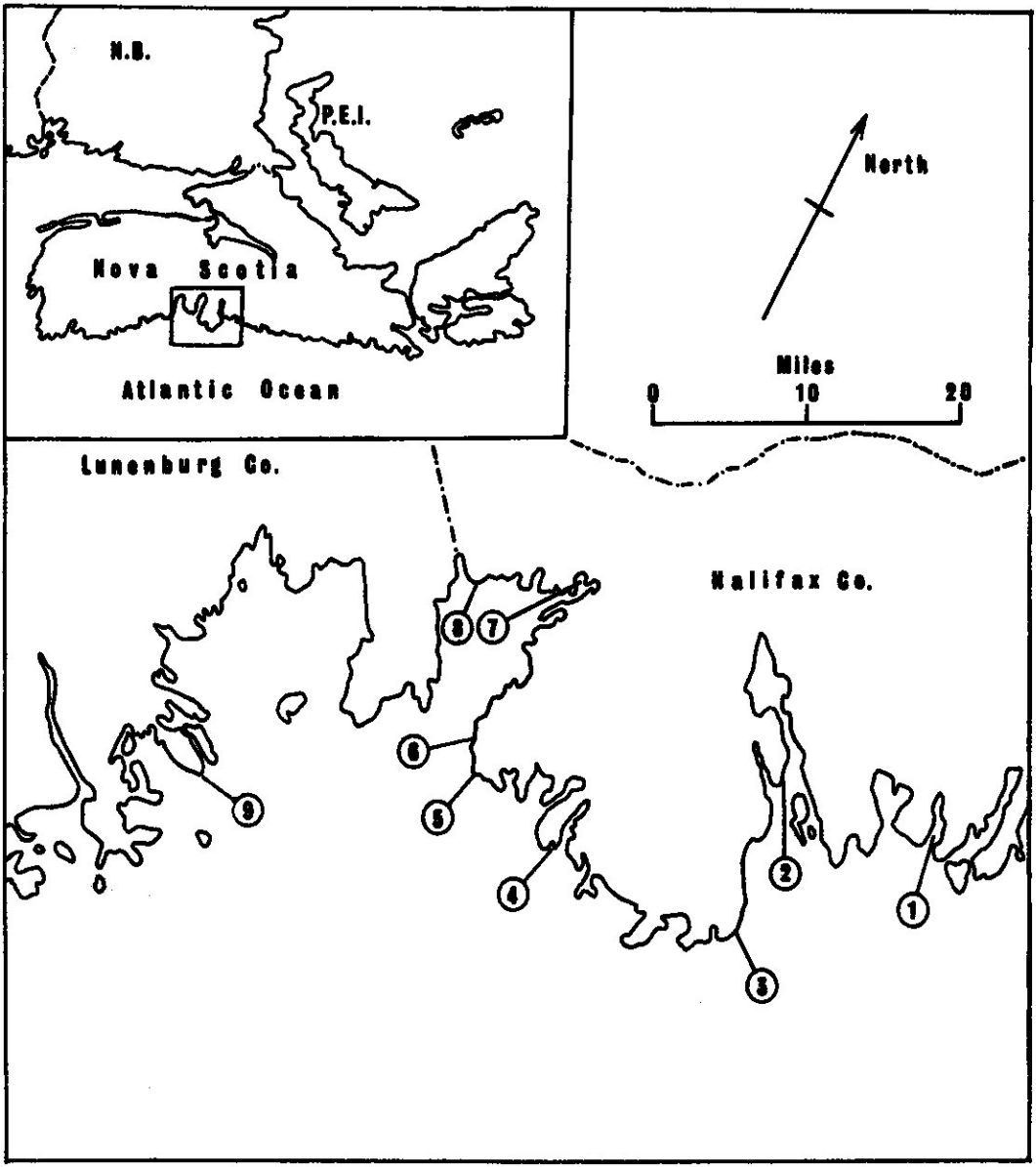

Fig. 1 A map of part of the shore line of Halifax and Lunenburg Counties, Nova Scotia. Single samples of *L. saxatilis* were collected at each of the stations, 1 to 9 between May 1967 and August 1968, for determination of variation in characters.

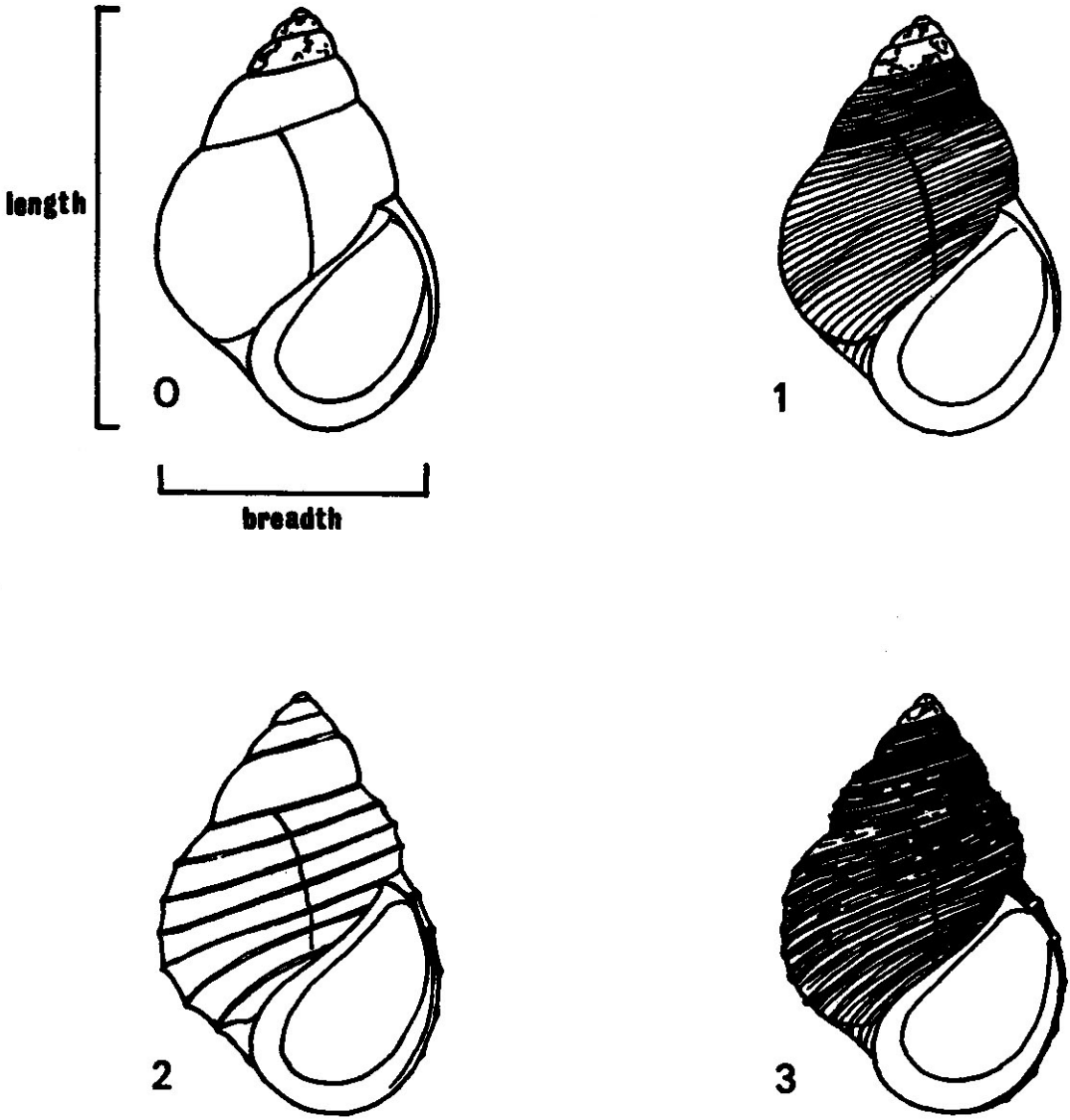

Fig. 2 Shell sculpture in *L. saxatilis*. The four stages in degree of development of shell sculpturing observed in Nova Scotia specimens are shown. The index numbers 0-3 are used to describe the sculpturing of individual specimens. The main shell dimension, length and breadth, used to describe shell shape are shown.

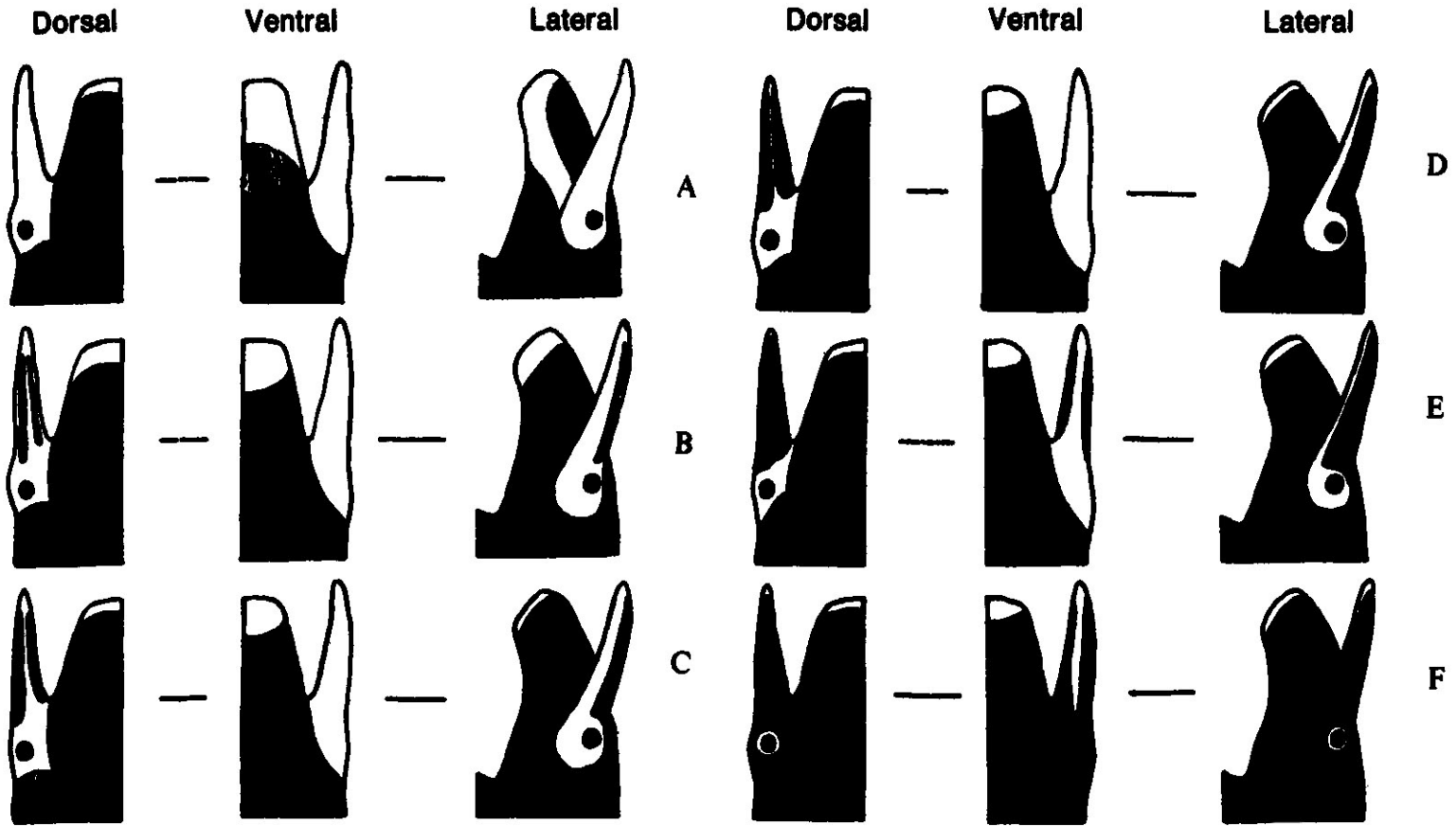

Fig. 3 Pigmentation patterns on the head of *L. saxatilis*. The six stages shown occured throughout samples collected at nine stations in Nova Scotia. The index letters A-F are used to define the degree of pigmentation.

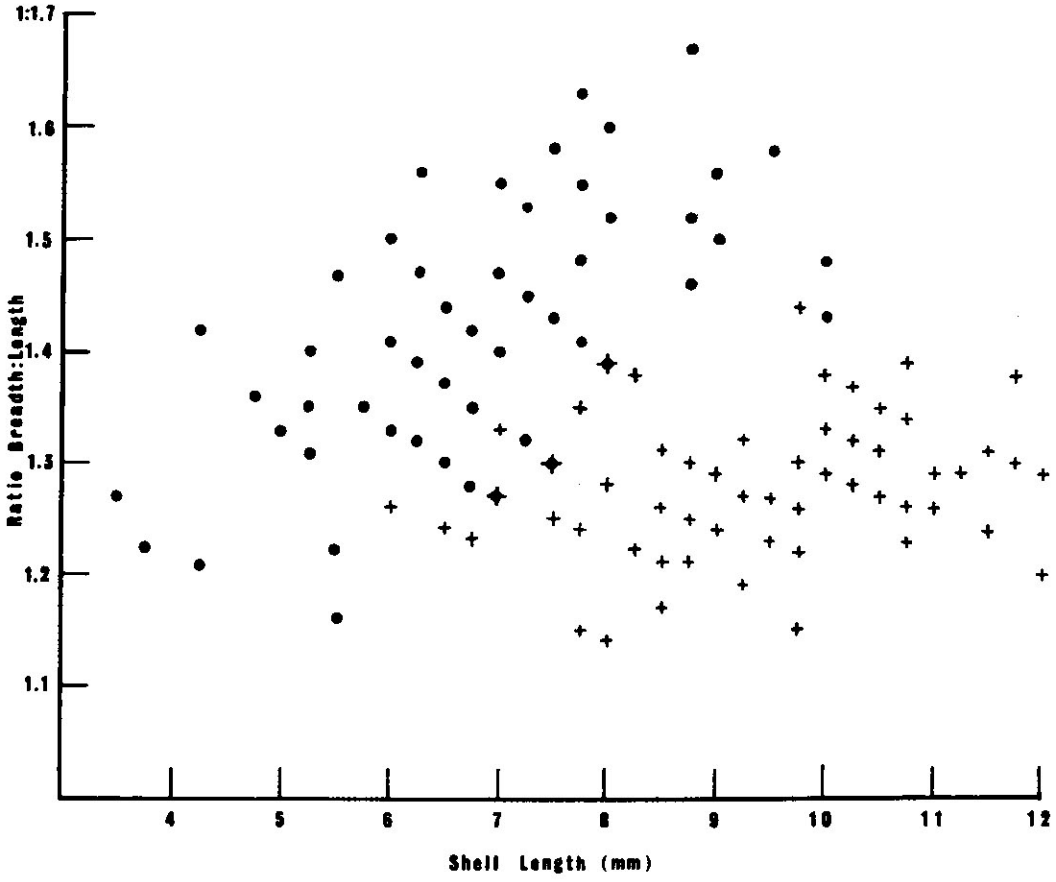

Fig. 4 The relationship between shell length and shell breadth to length ratio of *L. saxatilis* at two stations with different environmental conditions. Station 5, at Peggy Point, is a rocky shore exposed to wave action. Station 7, at Mason Cove, is a sheltered rocky shore. Both samples were taken in March 1968. Peggy Point data are plotted as crosses (+), Mason Cove data, as dots (●).

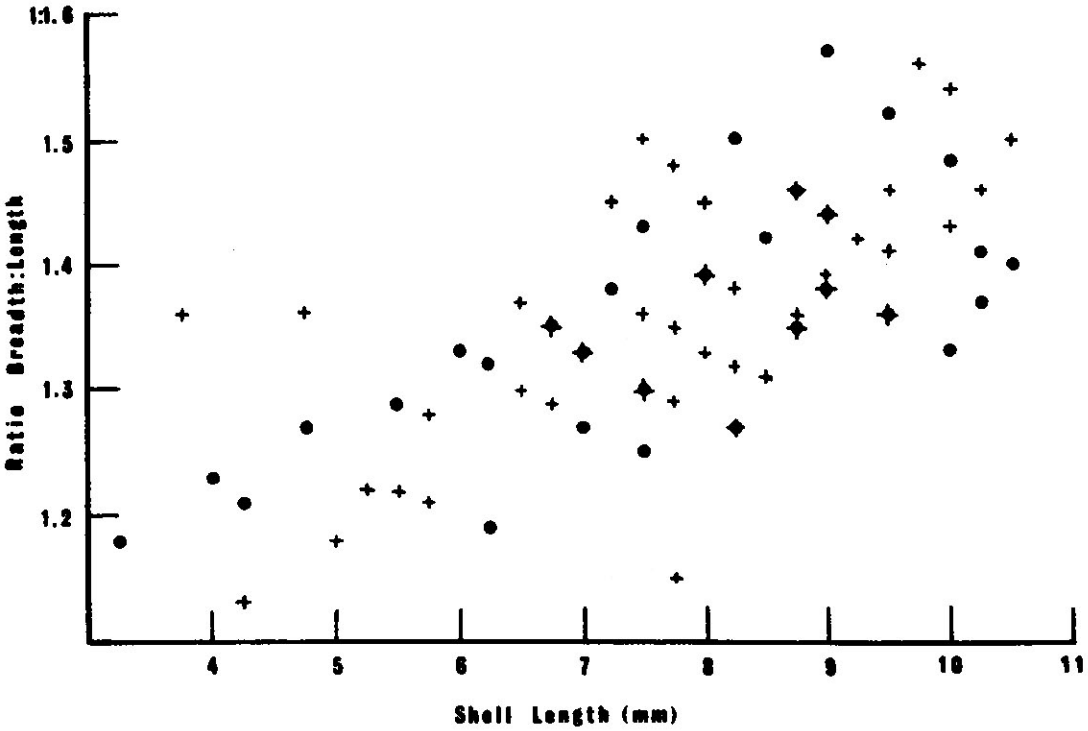

Fig. 5 The relationship between shell length and shell breadth to length ratio of male and female *L. saxatilis*. The values are all taken from the same sample, collected at Sandy Cove (Station 3) on 28 February 1968. Males are plotted as crosses (+), females as dots (●).

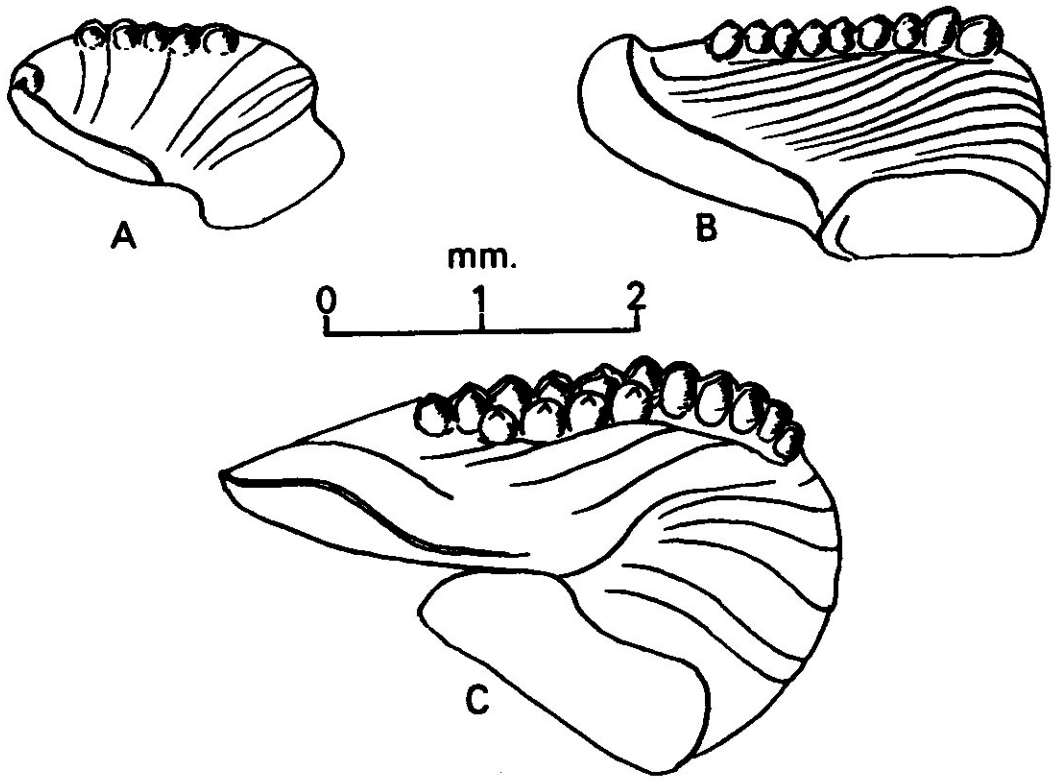

Fig. 6 The form of the penis in selected examples of *L. saxatilis* from three localities in Nova Scotia. A. A specimen from Lawrencetown (station 1) which has a single row of five glands. B. A specimen from Mason Cove (station 7) which has a single row of nine glands. C. A specimen from Peggy Point (station 5) which has a double row of glands; eleven in the long row and four in the short row.

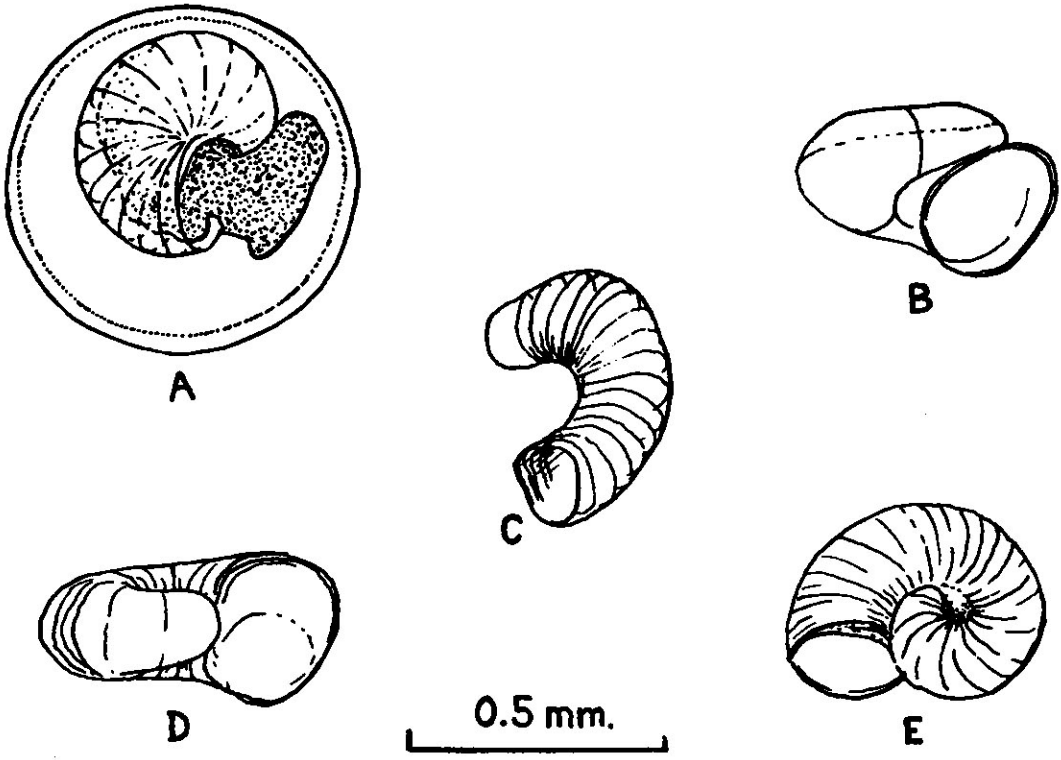

Fig. 7 Examples of juvenile *L. saxatilis* taken from the brood pouches of selected females collected from stations along the Atlantic coast of Nova Scotia. A. An embryo developing inside an egg capsule. B. A juvenile shell at the time of hatching. C. An embryonic shell with open coiling (named *dentalioid* by Thorson, 1946). D. An embryonic shell having a plane spiral (named *planorbioid* by Thorson, 1946). E. An embryonic shell having sinistral coiling.

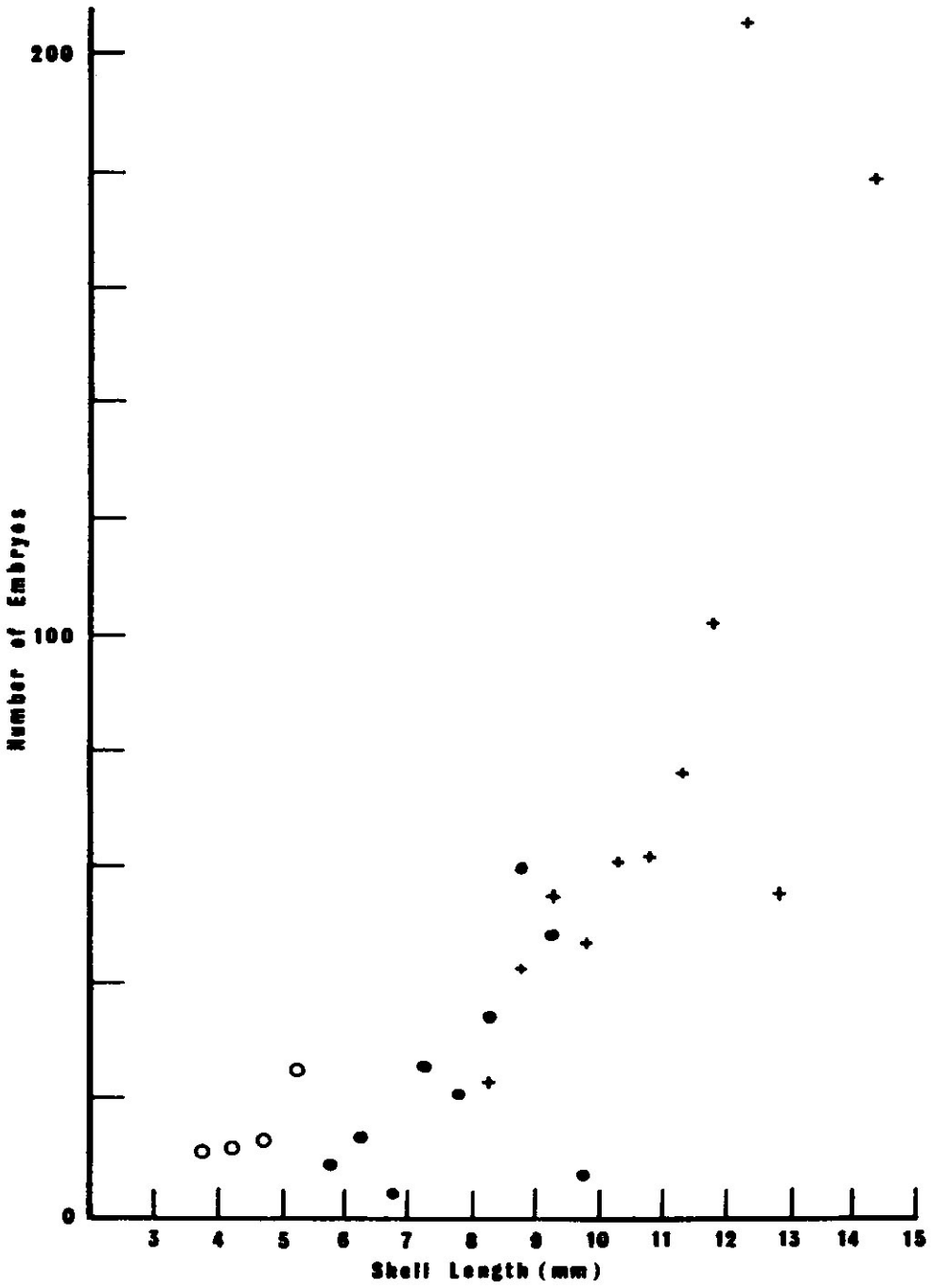

Fig. 8 The mean number of embryonic snails in brood pouches of female *L. saxatilis* at three Stations on the Atlantic coast of Nova Scotia. The mean number is given for all snails in each group at 0.5 mm intervals of shell length. Lawrencetown Lake (Station 1) data are plotted as circles (o), Peggy Point (Station 5) data as crosses (+) and Mason Cove (Station 7) data as dots (●).

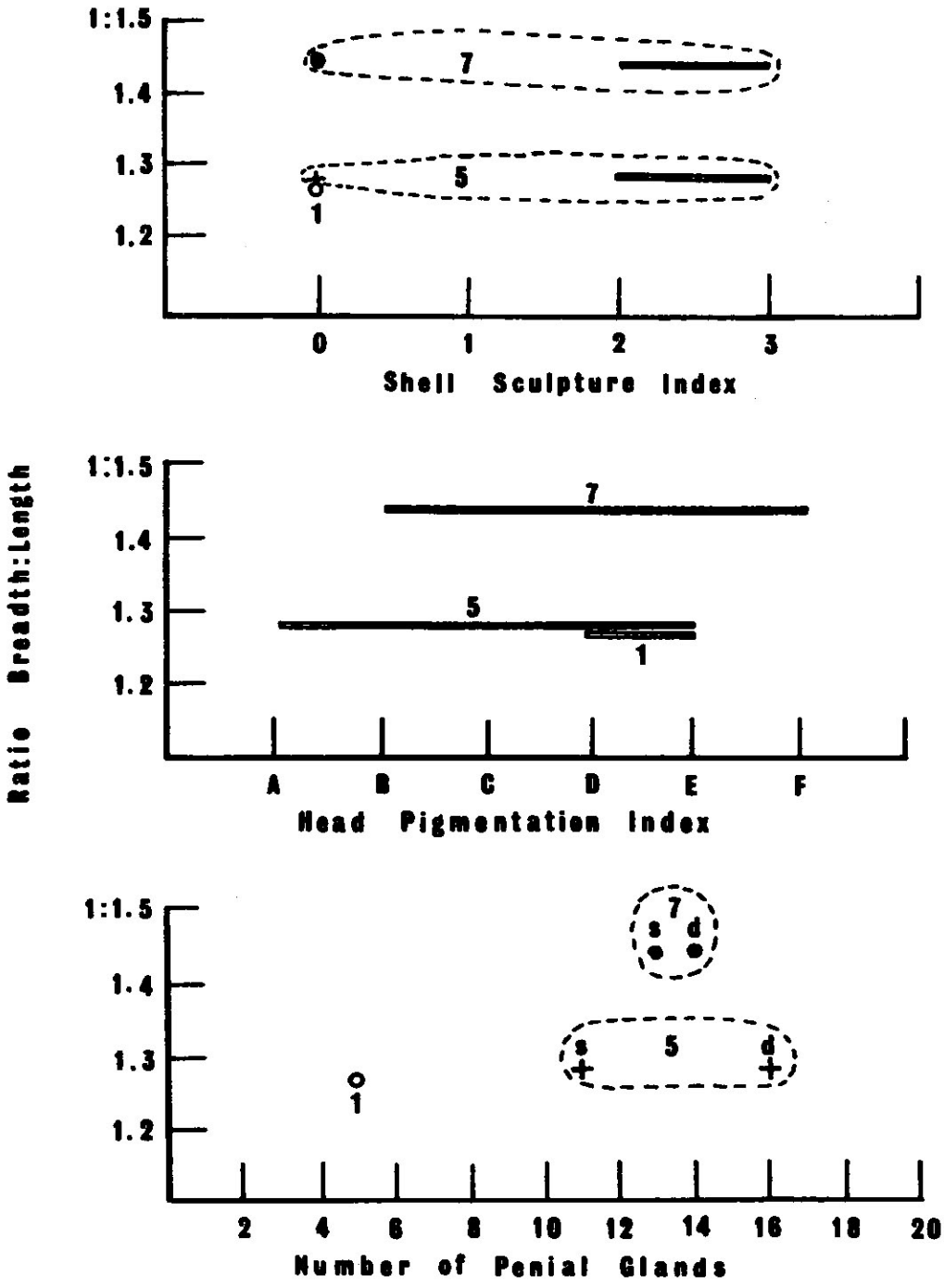

Fig. 9 Shell sculpturing, head pigmentation and number of penial glands shown in relation to shell breadth to length ratios for samples from Stations 1, 5 and 7. The mean numbers of penial glands in specimens with a single row(s) and those with a double row (d) are shown separately.

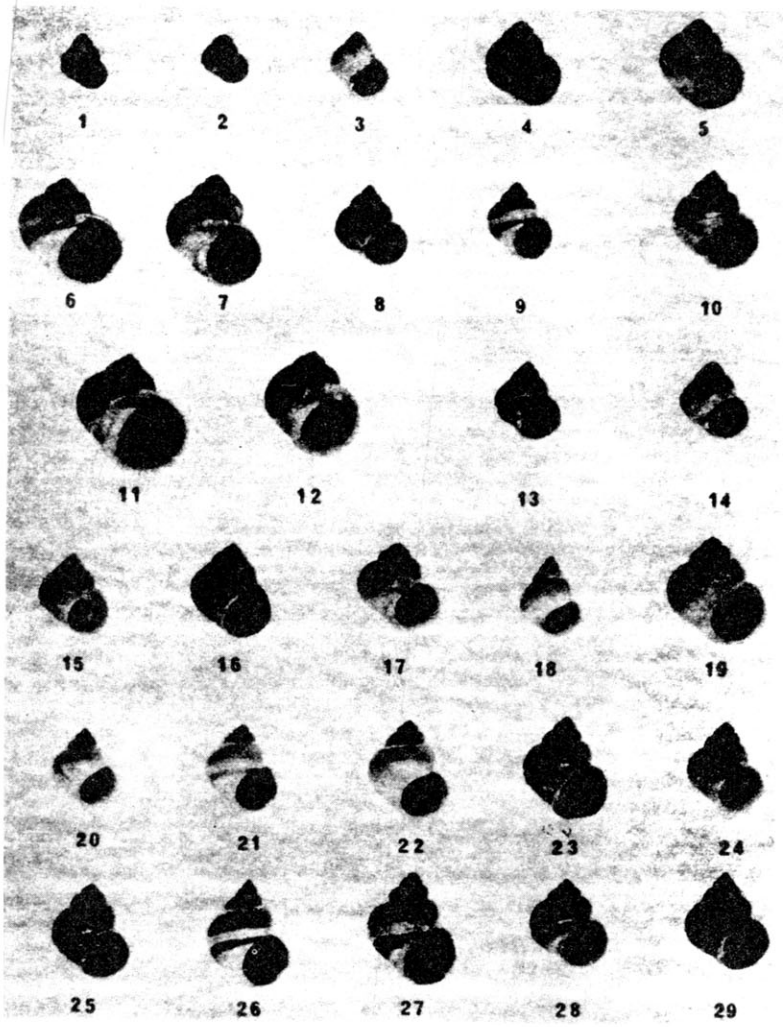

Fig. 10 Examples of the shells of *L. saxatilis* collected at nine stations along the Atlantic coast of Nova Scotia, from May 1967 to August 1968. These examples illustrate the range of shell proportions, sculpturing and colour encountered in the collections. Photograph is approximately life size.

1 and 2.	Station 1, Lawrencetown Lake, Halifax Co. Form C.
3 and 4.	Station 2, Black Rock, Point Pleasant Park, Halifax. Both are form A. Specimen 3 is *L. s. albida*.
5, 6 and 7.	Station 3, Sandy Cove, Halifax Co. Specimens 5 and 6 are form B and 7 is form A.
8, 9 and 10.	Station 4, Prospect, Halifax Co. All are form A. Specimen 9 is *L. s. zonaria*.
11 and 12.	Station 5, Peggy Point, Halifax Co. Both are form B.
13 and 14.	Station 6, Indian Harbour, Halifax Co. Both are form A.
15 and 16.	Station 7, Mason Cove, Halifax Co. Both are form A.
17.	Station 8, Queensland, Halifax Co.
18 to 29.	Station 9, Blue Rocks, Lunenburg Co. All are form A. 18 is *L. s. albida*, 19 and 20 are *L. s. fulva*, 21 is a pale *L. s. zonaria*, 22 is unnamed (white with a thin brown line), 23 is *L. s. interupta*, 24 is *L. s. maculata*, 25 is *L. s. tessellata*, 26 and 27 are *L. s. zonaria*, 28 is a combination of *L. s. zonaria* and *tessellata*, and 29 is *L. s. fusca*.