THE VARIATION OF TWO SPECIES OF LYMNAEA

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The problem of the effects of isolation in relation to the establishment of subspecies and local races has been studied by many workers since the time of DARWIN and WALLACE, but in most instances it has been attacked only from the standpoint of geographical speciation. Little attention has been paid to the relationship existing between the type of variation in any one circumscribed locality, and that occurring over extensive geographical areas. The naturalists of sixty years ago were interested in the gross effects of isolation, as exemplified, for instance, in the fauna of oceanic islands, but paid no great attention to the possibility of studying this phenomenon over broad and continuous areas. The work presented in this paper covers an extensive territory in the Sub-Arctic region, and in certain respects runs parallel to the extensive researches of CRAMPTON (1916) upon the members of the genus *Partula* in certain Pacific islands, but with the important difference that CRAMPTON'S work covers a very small subtropical area. It appears that the differentiation of new species and races takes place in the first-mentioned region at a much slower rate than in that with the warmer climate, and this renders it possible, in certain respects, to follow the process with more precision. The analysis of this phenomenon in the northern part of North America may therefore be of interest.

The ideal animal with which to commence a study of this kind is one which has a very wide geographical range, a considerable tolerance of diverse environmental conditions, and a marked tendency toward variation. For comparison with this it is desirable to use a species which, while equally variable in form, is more specific in its habitat requirements. These conditions are admirably fulfilled by two species of fresh water mollusca, namely, *Lymnaea palustris* (MULLER), and *L. emarginata* Say. *L. palustris* is a hardy and widely distributed snail which is found in North America, Europe, and northern Asia; while *L. emarginata* is much more restricted in its range, being found only in the northern part of North America east of the Rocky Mountains. A comparison of the local and geographical variation of these two species shows that while in *L. palustris* the range of variation in one locality approximates that which occurs over almost the whole range of the species in North America, in *L. emarginata* there is a well marked tendency for the range of variation in any one locality to constitute only a small part of the range which is to be found over the whole

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geographical area inhabited by this species. That is to say, in the one instance local variation approximates geographical variation in range, while in the other it covers only a small part of it. In other words *L. emarginata* tends to split up into local races, whereas *L. palustris* does not.

THE SYSTEMATIC POSITION OF THE SPECIES STUDIED

The species dealt with in this account belong to the family Lymnaeidae, which in its old usage was believed to include not only the genus Lymnaea, but also Planorbis, Planorbula, and similar forms which are now placed in separate families. When the group came to be studied intensively in modern times, many new species were described, former varieties and sub-species were looked upon as species, and larger groups which had previously been regarded as sub-genera were raised to the rank of genera. As a result of this the name Lymnaea has tended to disappear from conchological literature in recent times, being supplanted by such names as Stagnicola and Fossaria, which while they may be more acceptable to the specialist, have the disadvantage of being less familiar to biologists in general. However, throughout these changes in nomenclature the relative status of the two groups designated here as *Lymnaea palustris* and *L. emarginata* has remained fairly constant, and there can be little doubt that they represent fundamental natural groups of the North American mollusc fauna. [BAKER (1934) considers that certain of the specimens here included as extreme variants of *L. palustris* are a new species.] Whether they are termed species or genera is of no great practical importance in the present connection. The animal referred to as *L. palustris* (MULLER) has been called *L. vahlii* ("BECK" MOLLER) in a number of publications (MOZLEY 1934), but it now appears to be desirable to revert to the more general name, *palustris*, of MULLER. The diverse forms of the species here called *L. emarginata* have been referred to by various names, but with the possible exception of certain races which approach *L. catascopium* their close mutual relationship is generally admitted by conchologists. The significant fact in this connection is that *L. palustris* and *L. emarginata* are well marked species, absolutely distinct from one another, and are not readily mistaken for any other members of the North American fauna.

MATERIAL AND METHODS

The material upon which this study is based is for the most part from my own collection, which is now in the UNITED STATES NATIONAL MUSEUM. The shells of many of the series have been individually numbered, so that it will be a relatively simple matter for later workers to refer to them in the museum collection for purposes of confirmation or making additional observations. In accordance with the scheme for the preserva-

tion of biological statistics too voluminous to permit of publication, a copy of the measurements which form the basis of this work will be deposited with the Secretary of the ROYAL SOCIETY OF EDINBURGH.

LIST OF THE SERIES OF SHELLS MEASURED

Lymnaea palustris

NO. OF SERIES	LOCALITY	NUMBER OF SPECIMENS MEASURED	MEAN LENGTH OF SHELL
1.	Greenland	2	11.4 mm.
2.	Bernard Harbour	4	11.7
3.	Dall River, Alaska	2	12.0
4.	Fort Resolution	14	12.4
5.	St. Michaels, Alaska	24	12.4
6.	Yukon River	1	13.0
7.	St. Michaels, Alaska	2	13.2
8.	near Clair, Saskatchewan	4	13.6
9.	Little Quill Lake, Saskatchewan	50	14.0
10.	5 miles west of Fort Yukon	1	14.0
11.	Moose River, Ontario	2	14.1
12.	Paskweguin Brook, Saskatchewan	27	15.7
13.	Ironspring Creek, Saskatchewan	8	15.8
14.	Lake Mildred, Alberta	67	16.1
15.	Van Patten Creek, Saskatchewan	17	16.1
16.	Fishing Lake, Saskatchewan	20	16.5
17.	Atlin, British Columbia	7	16.5
18.	Milligans Creek, Saskatchewan	9	17.4
19.	Bernard Harbour	5	17.6
20.	Southern Twin Lake, Alberta	209	17.7
21.	Lake Mildred, Alberta	7	17.9
22.	Clair Brook, Saskatchewan	50	17.9
23.	The Grande Marais, Manitoba	29	17.9
24.	Atlin, British Columbia	2	19.6
25.	Shonts, Alberta	271	20.7
26.	Molson, Manitoba	6	21.0
27.	Duck Mountain, Saskatchewan	100	22.0
28.	Birtle, Manitoba	47	22.3
29.	Kelliher, Saskatchewan	25	24.3
Total number of shells		1012	

The shells of these gastropod molluscs are convenient objects for measurement, and the dimensions taken as standard for this work are those which are almost universally adopted by conchologists, and may be briefly defined as follows:

Length of shell—the distance from the apex to the lower edge of the lip.

Greater diameter—the greatest width of the shell as a whole, measured along a line at right angles to the axis of the shell, and in the same plane as the aperture.

Lesser diameter—the width of the shell on a plane at right angles to that of both the axis and aperture.

Aperture length—the length of the orifice along a line parallel to the axis.
Aperture width—the width of the orifice along a line at right angles to the axis.

Measurements of these five dimensions were made upon 1012 shells of *Lymnaea palustris* from the twenty-nine localities listed on page 454. Twenty-six series of *L. emarginata* were measured, the number of specimens being 452. The number of specimens in a series from a single locality varied from one to two hundred and seventy one.

Lymnaea emarginata

NO. OF SERIES	LOCALITY	NUMBER OF SPECIMENS MEASURED	MEAN LENGTH OF SHELL
1.	Grand Rapids of the Athabaska, Alberta	16	12.8 mm
2.	Aroostook River, Maine	8	13.8
3.	Lake Winnipegosis, Manitoba	31	14.3
4.	Eagle Lake, Minnesota	6	14.5
5.	Cross Lake, New York	12	14.9
6.	Rainey Lake, Ontario	40	15.4
7.	Madison, Wisconsin	6	16.5
8.	Douglas Lake, Michigan	12	16.7
9.	Sault Sainte Marie, Michigan	2	16.7
10.	Madison County, Montana	7	17.0
11.	Hell Gate, Montana	6	17.3
12.	Milwaukee, Wisconsin	3	18.6
13.	Victoria Beach, Lake Winnipeg, Manitoba	35	19.3
14.	Fish River, Maine	5	19.6
15.	Crystal Lake, Minnesota	20	20.2
16.	Lake Constance, Ontario	3	21.2
17.	Atikameg Lake, Hudson Bay Railway, Manitoba	100	21.9
18.	Douglas Lake, Michigan	5	22.1
19.	Crooked Lake, Michigan	5	22.4
20.	Bear Lake, Michigan	10	22.7
21.	Clear Lake, Riding Mountain, Manitoba	90	24.0
22.	Lake Michigan	6	24.4
23.	Brome Lake, Quebec	4	24.7
24.	Lake Higgins, Michigan	13	25.9
25.	Square Lake, Michigan	3	27.2
26.	Lake Houghton, Michigan	4	28.7
Total number of shells		452	

A convenient means of gauging the extent of variation in a series of shells lies in a comparison of the ratios of certain dimensions. The particular ratios here adopted for this purpose are the following:

$$\frac{\text{Length}}{\text{Greater Diameter}}, \frac{\text{Length}}{\text{Aperture Length}}, \frac{\text{Aperture Length}}{\text{Aperture Width}}, \frac{\text{Greater Diameter}}{\text{Aperture Width}}$$

It has been found that there is little change in these ratios during the latter part of the life of the animal.

TABLES OF FREQUENCY DISTRIBUTION

The accompanying tables, which show the frequency distribution of the dimensional ratios mentioned above, are a convenient means of gauging the range of variation in the series of shells from different localities, and when all four ratios are considered together, they may perhaps be taken as an expression of the variability in growth of the organism as a whole.

In preparing the material for publication it has been considered desirable to present the data in as simple a form as possible. In the tables of frequency distribution each unit represents an individual animal, in which the proportion of the shell dimensions is of the magnitude indicated. The

SERIES NO.	LYMNÆA PALUSTRIS																		
	LENGTH																		
	GREATER DIAMETER																		
	1.60 TO 1.64	1.65 TO 1.69	1.70 TO 1.74	1.75 TO 1.79	1.80 TO 1.84	1.85 TO 1.89	1.90 TO 1.94	1.95 TO 1.99	2.00 TO 2.04	2.05 TO 2.09	2.10 TO 2.14	2.15 TO 2.19	2.20 TO 2.24	2.25 TO 2.29	2.30 TO 2.34	2.35 TO 2.39	2.40 TO 2.44	2.45 TO 2.49	2.50 TO 2.54
1.	1				1														
2.									1	1	1			1					
3.						1	1												
4.						5	2	3	3							1			
5.				2	4	5	8	1	3	1									
6.													1						
7.							1		1										
8.					1			1			1							1	
9.						1	1	11	10	10	6	5	1	2		1	2		
10.							1												
11.						1		1											
12.					2		4	2	7	3	4	2	3						
13.						1		3	1	2	1								
14.				2	3	12	21	12	6	6	5								
15.						3	6	4	3	1									
16.				1	2	2	3	5	3	1	1	1	1						
17.									3	2	1	1							
18.						2	4		1	1	1								
19.								1	2	1				1					
20.		1		1	2	7	22	42	43	38	31	10	9	2	1				
21.							1	3	2	1									
22.							2	9	12	8	7	4	5	2	1				
23.						1		4	7	5	8	3	1						
24.							1		1										
25.			1		2	15	26	43	50	57	42	17	12	2	1	2	1		
26.								2	1	1		2							
27.					1		1	6	6	17	18	22	16	5	5	1	1		1
28.					1	1	2	5	13	8	7	3	3	1	2	1			
29.								2	3	3	3	8	1	5					
	1	1	1	6	18	58	107	160	182	167	137	78	53	21	11	5	5		1

SERIES NO.	LYMNAEA PALUSTRIS																		
	APERTURE LENGTH																		
	APERTURE WIDTH																		
	1.20 to 1.24	1.25 to 1.29	1.30 to 1.34	1.35 to 1.39	1.40 to 1.44	1.45 to 1.49	1.50 to 1.54	1.55 to 1.59	1.60 to 1.64	1.65 to 1.69	1.70 to 1.74	1.75 to 1.79	1.80 to 1.84	1.85 to 1.89	1.90 to 1.94	1.95 to 1.99	2.00 to 2.04	2.05 to 2.09	2.10 to 2.14
1.							1	1											
2.							2	1			1								
3.				1			1												
4.								2	2	3	5	2							
5.						2	6	8	4	2	1				1				
6.									1										
7.					1				1										
8.				1			1		1		1								
9.							7	4	10	7	11	3	6	2					
10.								1											
11.								1		1									
12.							1	2	3	7	9	3	1	1					
13.							1	4				1	2						
14.							1		4	7	14	14	9	9	3	2	2		2
15.					1	2	3	4	2	3	2								
16.							4	2	2	4	6	2							
17.						2	3				1	1							
18.						1	1	3	2	1	1								
19.				1	1	1	1	1											
20.				1	5	13	19	37	63	37	22	7	2	2	1				
21.							1		1		1	1	2	1					
22.					1		2	9	5	10	13	7		3					
23.							2	2	7	6	7	2	3						
24.							1	1											
25.	1		1	1	1	5	19	41	60	56	44	23	10	5	2	1	1		
26.				1				2	3										
27.							6	6	16	18	23	20	7	1	2		1		
28.						1	3	9	6	10	8	9		1					
29.							2	3	1	10	2	1	5	1					
	1		1	6	9	28	88	144	194	182	172	96	47	26	9	3	4		2

SERIES NO.	GREATER DIAMETER																	
	LYMNAEA PALUSTRIS																	
	APERTURE WIDTH																	
	1.25 TO 1.29	1.30 TO 1.34	1.35 TO 1.39	1.40 TO 1.44	1.45 TO 1.49	1.50 TO 1.54	1.55 TO 1.59	1.60 TO 1.64	1.65 TO 1.69	1.70 TO 1.74	1.75 TO 1.79	1.80 TO 1.84	1.85 TO 1.89	1.90 TO 1.94	1.95 TO 1.99	2.00 TO 2.04	2.05 TO 2.09	2.10 TO 2.14
1.							1				1							
2.							2			1			1					
3.					1		1											
4.			1		1	1	4	5	2									
5.					1	1	5	8	3	4	1							1
6.					1													
7.				1		1												
8.			1				1		1	1								
9.			1	1	6	4	8	15	7	3	1	3	1					
10.						1												
11.							1		1									
12.						4	10	5	4	4								
13.					1	4		2		1								
14.			1		1	6	9	21	14	11	3	1						
15.				2	5	3	4	1	1	1								
16.			1	1			4	8		1								
17.					1	1	1	2	1		1							
18.					1	3	3	1		1								
19.					1	1		2			1							
20.					5	16	29	62	61	22	11	3						
21.							1	1	1	3	1							
22.			1			5	5	14	11	7	4	2	1					
23.			1		2	4	11	4	4	2	1							
24.					1		1											
25.	1			1	7	27	59	63	68	30	6	6	2	1				
26.					1	3	1	1										
27.			1		2	2	8	15	21	24	17	6	3	1				
28.				2	2	1	13	10	13	4	2							
29.					2	3	5	8	5	2								
	1	8	8	42	96	187	248	218	122	50	21	8	2					1

SERIES NO.	LYMNAEA EMARGINATA																		
	LENGTH																		
	APERTURE LENGTH																		
	1.25 TO 1.29	1.30 TO 1.34	1.35 TO 1.39	1.40 TO 1.44	1.45 TO 1.49	1.50 TO 1.54	1.55 TO 1.59	1.60 TO 1.64	1.65 TO 1.69	1.70 TO 1.74	1.75 TO 1.79	1.80 TO 1.84	1.85 TO 1.89	1.90 TO 1.94	1.95 TO 1.99	2.00 TO 2.04	2.05 TO 2.09	2.10 TO 2.14	2.15 TO 2.19
1.							4	4	4	2	2								
2.						2	4	1		1									
3.							1	4	6	8	7	5							
4.									2	1	2		1						
5.										2	2	2	5	1					
6.			2	4	12	16	4	1		1									
7.				1	1		2		2										
8.			3	3	4	1	1												
9.							2												
10.									1	2	4								
11.						3		1	1			1							
12.									1		1	1							
13.					2	2	9	16	5	1									
14.		1	2	1	1														
15.					1		2		2	3	4	4	1	3					
16.															2				1
17.								4	7	16	19	28	13	5	8				
18.				1		3	1												
19.								1	1	1	2								
20.										4		1	2	1	1		1		
21.					1	6	10	19	17	21	10	4	1		1				
22.									1		1	1			1			2	
23.		1	2					1											
24.					1	2	1	3	3	2	1								
25.		2				1													
26.	2		1		1														
	2	4	10	10	24	36	41 *	55	53	65	55	47	23	10	13		1	2	1

SERIES NO.	LYMNAEA EMARGINATA															
	APERTURE LENGTH															
	APERTURE WIDTH															
	1.10 to 1.14	1.15 to 1.19	1.20 to 1.24	1.25 to 1.29	1.30 to 1.34	1.35 to 1.39	1.40 to 1.44	1.45 to 1.49	1.50 to 1.54	1.55 to 1.59	1.60 to 1.64	1.65 to 1.69	1.70 to 1.74	1.75 to 1.79	1.80 to 1.84	1.85 to 1.89
1.				1		2	3	8		2						
2.						1	1	3	2	1						
3.								1		6	7	6	9	1	1	
4.	1	1	1		2	1										
5.						1		3	1	5		1		1		
6.					1	2	4	11	17	4						1
7.							1	1		3		1				
8.					2	3		2	1	3	1					
9.								1	1							
10.						3	1	1	1	1						
11.						1	1	4								
12.							2	1								
13.						1	5	5	8	10	3	1	2			
14.						1	1			2		1				
15.					1	1	1	5	4	2	3	2	1			
16.							2	1								
17.						2	12	29	27	20	9			1		
18.				2		1	1			1						
19.							1	1		2			1			
20.								1	2	1			2	2	2	
21.					2	20	18	24	12	9	5					
22.				1			1	2	1		1					
23.				1			2				1					
24.					3	3	2	2	2			1				
25.								1		1		1				
26.				1			1				1	1				
	1	1	1	6	11	43	60	107	79	73	31	15	15	5	3	1

SERIES NO.	GREATER DIAMETER													
	APERTURE WIDTH							LYMNAEA EMARGINATA						
	1.25 TO 1.29	1.30 TO 1.34	1.35 TO 1.39	1.40 TO 1.44	1.45 TO 1.49	1.50 TO 1.54	1.55 TO 1.59	1.60 TO 1.64	1.65 TO 1.69	1.70 TO 1.74	1.75 TO 1.79	1.80 TO 1.84	1.85 TO 1.89	1.90 TO 1.94
1.			1	1	2	4	6	2						
2.						2	5		1					
3.						1	5	5	6	7	4	1	1	1
4.	1		1	2	1		1							
5.				2	1	3	1	4	1					
6.		2	11	17	8		1				1			
7.					1	2	2		1					
8.		3	1	1	5	1	1							
9.						2								
10.				1	3	2	1							
11.				2	2	2								
12.			1			1	1							
13.	1	1	4	2	9	11	7							
14.						3	1			1				
15.						4	4	7	4		1			
16.			1		1		1							
17.			4	4	37	29	18	5	2	1				
18.			1	2	1		1							
19.		1			2	1		1						
20.					1	1	5	3						
21.		1	7	13	23	25	16	5						
22.				2	1	2	1							
23.						2	2							
24.					2	3	3	1	4					
25.				1			1	1						
26.					1	2				1				
	2	8	32	50	101	103	84	34	19	10	6	1	1	1

COMPARISON OF THE VARIATION OF THE TWO SPECIES

A study of the preceding data indicates with a considerable degree of certainty that there is an important difference in the type of variation exhibited by the two species investigated. In *Lymnaea palustris* the range of variation in any one locality tends to approximate that which occurs over the whole of the territory occupied by this animal. This is particularly remarkable in view of the fact that the collections of this species came from a wide variety of habitats. Series Nos. 25 and 27 came from ponds; Nos. 12 and 15 from intermittent streams; Nos. 16 and 20 from fresh water lakes; and No. 9 from a saline lake in which the concentration of mineral salts was 9688 parts per million (MOZLEY 1930). It is also interesting to observe that the same general principle regarding the relationship of local to geographical variation holds for all four ratios. It is particularly to be noted that this relationship holds true only in the particular region in which this work was done, and is known not to hold in other regions. In contrast to this, in *L. emarginata* the range of variation in any one locality forms only a part of the geographical variation.

The explanation of this diversity is believed to lie in the differences in the local distribution of the two species. Within the territory included in the scope of this paper, *L. palustris* occurs in a high proportion of the very numerous ponds and small lakes; for example, it was found in 238 of a series of 315 examined. These ponds and small lakes are often situated close together, and it is easy to understand that there are frequent opportunities for the mixture of stock. Under these conditions the appearance of recessive characters would be sporadic, the variation in all localities would be expected to be very similar, and its range wide.

In contrast to this continuous type of variation, is that of *L. emarginata*, which is found for the most part only on the rocky or bouldery shores of large lakes, a type of habitat which is of relatively rare occurrence in many parts of the country, sometimes being situated one or two hundred kilometers apart. There is thus little opportunity for genetic intermixture between the members of different colonies. Under these conditions recessive characters might be expected to appear in the bulk of the population in certain localities, and thus to form the basis of local races.

These facts may quite conceivably form the basis upon which many other natural experiments in isolation have taken place, and give some insight into a mechanism by means of which endemic faunas may have arisen.

It seems reasonable to suppose that this diversity is a matter of multiple factor inheritance. Many of the morphological characters which form the basis of the local races are in all probability recessive, and are masked,

or at least not much in evidence under conditions of free interbreeding, as occurs in *L. palustris* in this region. In *L. emarginata* the role of isolation appears to be connected with the segregation into colonies of small groups of individuals, in many cases the progeny of a single immigrant individual. Among these the selective action of the environment sometimes results in the predominance of a recessive character. The results of this work are therefore in accordance with those of SUMNER's extensive investigations (1932) of the geographical races of deer mice. His results seem to lead to the conclusion that the extension of the Mendelian principle to include the inheritance of characters governed by multiple genetic factors is an adequate explanation of the transmission of subspecific differences. The present work may possibly give some further insight into the mechanism of a process by which such varieties may arise.

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