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Distribution of Aquatic Mollusks in Minnesota*

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Introduction

Although Minnesota is a state abounding in lakes and rivers of all sizes which contain a varied molluscan fauna, no general survey of its fresh-water mollusks has as yet been published. Such a survey is of interest from a geographical point of view because the waters of Minnesota drain in three directions, namely south through the Mississippi River to the Gulf of Mexico, east through Lake Superior to the St. Lawrence River, and north through the Red and Rainy Rivers to Hudson Bay. Moreover the rivers as well as the lakes, of which there are more than 10,000, present a wide range of size and of chemical and physical characteristics which make the distribution of mollusks interesting from an ecological standpoint.

The earliest published records of Minnesota mollusks are those of Thomas Say (1825) and William Cooper (1834) which are little more than lists of the species found on some of the early exploring expeditions sent into this territory. In 1885 U. S. Grant, a member of the staff of the Minnesota Geological and Natural History Survey, published a list of the mollusks of the Mississippi, Minnesota, and Red River systems, and in 1887 he reported on the mollusks of St. Louis County in the northern part of the state. In 1887 also John M. Holzinger published a paper on the mollusks of Winona County in the southern part of the state. Sargeant (1895, 1896), Stearns (1900), and Daniels (1909) listed the species found in some of the lakes and rivers in various parts of Minnesota and described their habitats and relative abundance. The mussels in the rivers of central and southern Minnesota were studied by Wilson and Danglade (1914) and Grier and Mueller (1922, 1926) in connection with investigations of the pearl button industry made by the U. S. Bureau of Fisheries. F. C. Baker (1929, 1935) published two studies on the mollusks of individual lakes in the northern part of the state.

The collection of shells in the Zoology Department of the University of Minnesota forms the basis for this study.** This collection was started seventy years ago by members of the staff of the Minnesota Geological and Natural History Survey and has since been augmented by persons in the Zoology Department and others. Its present organization and scope are largely due to Dr. Samuel Eddy of the Zoology Department. In 1931 a survey of Minnesota lakes was begun under his supervision, and many mollusks were brought in by field workers. The writer became interested in Minnesota mollusks in

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** The two groups of mollusks included in this paper are mussels and aquatic snails. The Sphaeriidae are omitted because of the uncertain condition of the taxonomy in this family.

the summer of 1936, and in order to make the survey more complete, made several collecting trips during the summers of 1938, 1939, and 1940 to parts of the state not previously studied. The data now include collections from 150 lakes in 44 of the 86 counties of the state, from 70 stations on 30 rivers and streams, and from 50 ponds in three different regions of the state.

In any study of animal distribution two ultimate questions to be considered are why certain species are found in some habitats but not in others, and what determines the geographical limits within which a species is found. Exact information concerning the geographical and ecological distribution of any species is necessary before such questions can be answered.

The environment of a mollusk must provide it with food, oxygen, and calcium for a shell. In addition it must furnish the proper conditions for reproduction. A mussel is more exacting in its requirements than a snail, being heavier and less motile. The bottom in which it lives may be sand, gravel, or mud, but not rock or soft muck because its foot cannot penetrate rock and it sinks too far into the muck and is smothered. It lives best where a current of water brings suspended food material, oxygen, and some form of calcium within reach of the cilia lining its mantle cavity. For this reason more species of mussels are found in rivers than in lakes. Snails, being smaller and lighter and more motile, are able to live almost anywhere where there is water and vegetation and therefore are the principal mollusks in lakes and ponds. Whereas mussel shells are almost pure calcium carbonate, snail shells in addition, contain chitin which probably accounts for the presence of snails in some waters containing very little calcium. Experience has shown that the calcium carbonate content of Minnesota waters can usually be measured as the total alkalinity (T.A.). The waters in this state vary in total alkalinity from less than twenty parts per million in some of the lakes on the Canadian border to more than 300 parts per million in the western part of the state. Where not otherwise noted, the total alkalinities quoted are taken from Dole and Wesbrook (1907).

The range of an animal may be limited by such environmental factors as food, temperature, or moisture, or by a physical barrier of some kind. In the case of freshwater animals land is a barrier and their range is limited by the discontinuous character of lakes, ponds, and even rivers—the rivers of one drainage system being separated from those of another. Unless an aquatic species can live temporarily on land or has some means of being transported over land, its distribution may be limited to one drainage system. Snails and fingernail clams, being small and light, can be transported by water birds in the mud which clings to their feet, and therefore are seldom restricted to any one drainage system, but mussels are too large and heavy to be carried by birds. Also the glochidial stage parasitic on fish makes the distribution of most mussels dependent on that of their fish host. The range of many mussels has undoubtedly been increased by migrating fish and it is even conceivable that in recent times man, by transplanting fish, might have accidentally transplanted mussels also. This, however, seems to be exceedingly rare. In general the range of a species of mussel is restricted to a single drainage system, and the presence of the same species in two or more separate drainage systems has been

considered evidence that the two systems were connected at one time (van der Schalie, 1939).

Distribution is of two types, geographical and ecological. In this study geographical distribution means distribution according to drainage system and is largely concerned with the effects of physical barriers on the migration of mussels. Snails seem to be able to surmount such barriers and their distribution does not show much relation to drainage systems in Minnesota. Ecological distribution is concerned with the effect on the distribution of both mussels and snails of the various sets of environmental conditions that are found within the boundaries of any one drainage system.

Geographical Distribution

At the present time the three drainage systems in Minnesota, namely the Mississippi, the Hudson Bay, and the St. Lawrence, are separate, but geological evidence shows that during the retreat of the last glacier, while the ice still blocked the north, all of the rivers in the state drained southward into the Mississippi River. Since most of the mussels in Minnesota are also found in the states farther south, it seems probable that most of them emigrated northward through the Mississippi River and its tributaries. Inasmuch as the post-glacial connections between these three major drainages were only temporary, the mussels which are today found in all three drainages must be the species which have the most efficient means of migration or the greatest powers of survival.

MISSISSIPPI DRAINAGE

The Mississippi River, which drains more than half of the state, rises in Lake Itasca in the north central part. It starts off northward, swings around eastward in a wide arc through Lake Bemidji, Cass Lake, and Lake Winnibigoshish to Grand Rapids, then southeast to Jacobson, southwest to Brainerd, south to Little Falls, and southeast again to Minneapolis where it passes over the St. Anthony Falls. A few miles below Minneapolis two important tributaries enter. One is the Minnesota River, a broad, shallow river which rises on the North Dakota border, flows across the western part of the state and enters the Mississippi just below Minneapolis at Fort Snelling. The other is the St. Croix River which rises in northern Wisconsin and after forming the boundary between that state and Minnesota for most of its course, enters the Mississippi at Hastings, thirty miles below Minneapolis. In the area around the town of Taylors Falls, the banks are steep and rocky and the river is turbulent and full of rapids, the largest being St. Croix Falls. Elsewhere there are quiet stretches and just before the St. Croix enters the Mississippi River at Hastings, it widens into a river-lake, Lake St. Croix. South of Hastings the Mississippi River, which forms the boundary between Minnesota and Wisconsin, is the largest river in the state. In this portion of the river is Lake Pepin, a large lake-like expansion between Red Wing and Reeds Landing.

Forty-four of the forty-five species of mussels found in Minnesota were found in the rivers or lakes of the Mississippi drainage. The one exception,

Elliptio complanatus, is common in the eastern part of the United States in the Atlantic drainage, but was found in Minnesota only in Lake Superior. Two species, *Anodonta marginata* and *Anodonta kennicotti*, although present within the Mississippi drainage area, were found only in lakes. The part of the Mississippi River below St. Anthony Falls contained thirty-nine species, which is the largest number of species found in a single river anywhere in the state. This is to be expected because the Mississippi is the largest river in the state and contains a variety of favorable habitats. Also the lower part of the river was not covered by the last glacier and was the channel through which the other rivers in the state were repopulated. The first four columns in Table 1 list the mussels found in the Mississippi River both above and below St. Anthony Falls and in its two principal tributaries, the St. Croix and Minnesota Rivers. The most striking thing about this comparison is the small number of species found in the Mississippi River above St. Anthony Falls as compared with the number in either the St. Croix or the Minnesota Rivers.

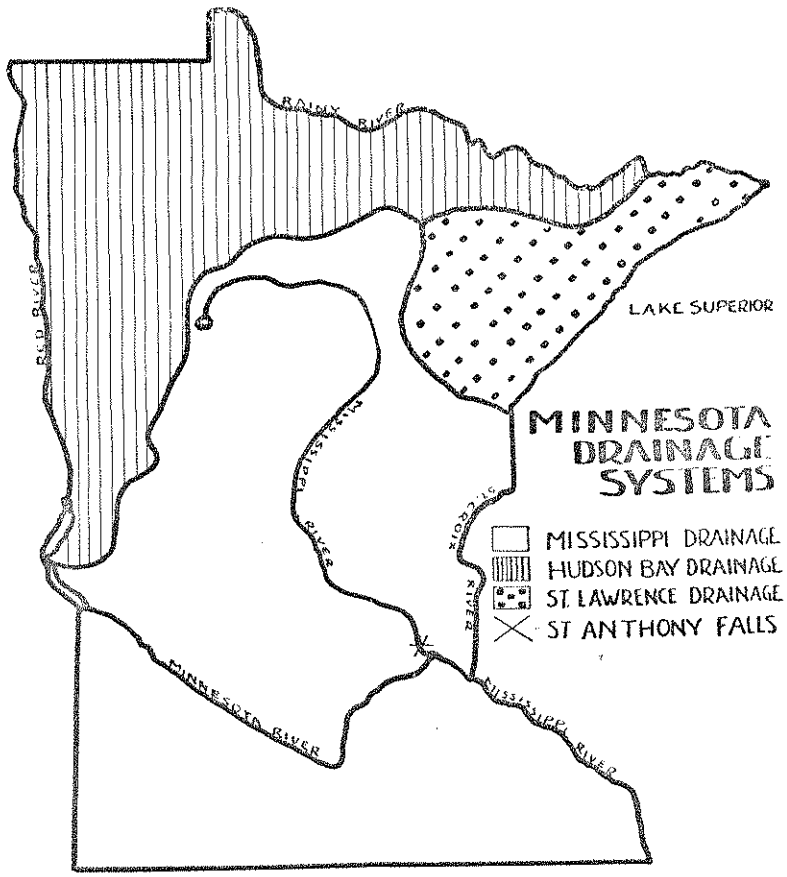

Table 1.—Distribution of mussels according to drainages.

	Mississippi R. below Minneapolis	Mississippi R. above Minneapolis	St. Croix R.	Minnesota R.	St. Lawrence	Hudson Bay
1. *Fusconaia undata*	X		X	X		
2. *Fusconaia ebena*	X					
3. *Fusconia flava*			X			
4. *Megalonaias gigantea*	X		X	X		
5. *Amblema peruviana*	X		X	X		
6. *Amblema plicata*	X		X	X		
7. *Amblema costata*	X		X			X
8. *Quadrula quadrula*	X			X		X
9. *Quadrula pustulosa*	X		X	X		
10. *Quadrula metanevra*	X					
11. *Tritogonia verrucosa*	X		X	X		
12. *Cyclonaias tuberculata*	X		X			
13. *Pleurobema cyphyus*	X		X	X		
14. *Pleurobema coccineum*	X		X	X		
15. *Elliptio dilatatus*	X		X	X		
16. *Elliptio complanatus*					X	
17. *Elliptio crassidens*	X			X		
18. *Lasmigona compressa*		X	X		X	X
19. *Lasmigona costata*	X		X	X		X
20. *Lasmigona complanata*	X		X	X	X	X
21. *Anodonta grandis*	X	X	X	X	X	X
22. *Anodonta marginata*		X			X	X
23. *Anodonta gigantea*	X			X		
24. *Anodonta corpulenta*	X		X	X		
25. *Utterbackia imbecillis*	X	X	X	X		
26. *Anodontoides ferussacianus*		X	X	X	X	X
27. *Alasmidonta marginata truncata*	X		X			
28. *Arcidens confragosus*	X			X		
29. *Strophitus rugosus*	X		X			X
30. *Obliquaria reflexa*	X		X	X		X
31. *Obovaria olivaria*	X		X	X		
32. *Actinonaias carinata*	X	X	X	X		X
33. *Truncilla truncata*	X		X	X		
34. *Truncilla donaciformis*	X			X		
35. *Plagiola lineolata*	X			X		
36. *Leptodea fragilis*	X		X	X		
37. *Proptera alata megaptera*	X		X	X		X
38. *Proptera laevissima*	X		X	X		
39. *Carunculina parva*	X		X	X		
40. *Ligumia recta latissima*	X	X	X	X	X	X
41. *Lampsilis fallaciosa*	X			X		
42. *Lampsilis siliquoidea*	X	X	X	X	X	X
43. *Lampsilis ventricosa*	X	X	X	X	X	X
44. *Lampsilis higginsi*	X		X	X		

Table 2.—Distribution of mussels in the Mississippi River.

		Alida	above Cass Lake	Brainerd	Fort Ripley	Little Falls	Clearwater	Elk River	Dayton	Anoka	Fridley	Nininger*	Red Wing*	Lake City**	Minneiska*	Winona*	Dresbach*
1.	*Fusconaia undata*												x	x	x	x	
2.	*Fusconaia ebena*												x	x	x	x	x
3.	*Megalonaias gigantea*												x	x		x	
4.	*Amblema peruviana*												x	x		x	x
5.	*Amblema rariplicata*												x				
6.	*Quadrula quadrula*											x	x	x			
7.	*Quadrula pustulosa*												x	x		x	x
8.	*Quadrula metanevra*											x	x	x		x	x
9.	*Tritogonia verrucosa*											x	x	x	x	x	x
10.	*Cyclonaias tuberculata*												x				
11.	*Plethobasus cyphyus*												x		x		x
12.	*Pleurobema cordatum coccineum*													x			
13.	*Elliptio dilatatus*											x	x	x	x	x	
14.	*Elliptio crassidens*												x	x		x	
15.	*Lasmigona compressa*	x	x														
16.	*Lasmigona costata*												x	x	x	x	
17.	*Lasmigona complanata*												x	x	x	x	
18.	*Anodonta grandis*		x					x	x	x			x	x			
19.	*Anodonta gigantea*												x	x			
20.	*Anodonta corpulenta*												x	x		x	
21.	*Utterbackia imbecillis*										x			x			
22.	*Anodontoides ferussacianus*	x	x														
23.	*Alasmidonta marginata truncata*												x			x	
24.	*Arcidens confragosus*												x		x		
25.	*Strophitus rugosus*												x	x			
26.	*Obliquaria reflexa*												x	x	x		x
27.	*Obovaria olivaria*												x			x	x
28.	*Actinonaias carinata*			x	x						x	x	x		x	x	x
29.	*Truncilla truncata*											x	x	x		x	
30.	*Truncilla donaciformis*												x				
31.	*Plagiolata lineolata*											x	x	x	x		
32.	*Leptodea fragilis*												x	x			
33.	*Proptera alata megaptera*											x	x	x		x	x
34.	*Proptera laevissima*												x	x			
35.	*Carunculina parva*													x			
36.	*Ligumia recta latissima*		x	x	x	x	x	x	x	x	x		x	x	x	x	x
37.	*Lampsilis fallaciosa*												x	x			
38.	*Lampsilis siliquoidea*		x	x	x	x	x	x	x	x	x		x	x	x	x	x
39.	*Lampsilis ventricosa*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
40.	*Lampsilis higginsi*												x				x

* below Minneapolis
** on Lake Pepin

Table 2 shows the species collected at ten stations above St. Anthony Falls and at six stations in the river south of the Falls, and Table 3 shows the species in the various tributaries both above and below St. Anthony Falls.

Beginning with the headwaters, the first mussel to appear in the river was *Anodontoides ferussacianus*, although *Anodonta marginata* and *Lampsilis siliquoidea* were in Lake Itasca. A few miles farther down *Lasmigona compressa* appeared. The four most common species, *Anodonta grandis*, *Lampsilis siliquoidea*, *Lampsilis ventricosa*, and *Ligumia recta latissima*, were first found about forty miles from Lake Itasca where the river was still small, and from there down they were almost always present. Above St. Anthony Falls,

Table 3.—Distribution of mussels in tributaries of the Mississippi River.

	Prairie R.	Crow Wing R.	Swan R.	Platte R.	Sauk R.	St. Francis R.	Elk R.	Crow R.	Rum R.	Coon Creek	Cannon R.*	Straight R.*	Zumbro R.*	Root R.*	Red Cedar R.*
1. *Amblema costata*															x
2. *Lasmigona compressa*					x				x	x					
3. *Lasmigona complanata*															
4. *Anodonta grandis*	x		x	x	x		x	x	x		x	x	x	x	x
5. *Utterbackia imbecillis*									x						
6. *Anodontoides ferussacianus*				x	x		x		x	x					x
7. *Strophitus rugosus*													x		x
8. *Actinonaias carinata*		x							x		x	x			
9. *Proptera alata megaptera*											x				
10. *Ligumia recta latissima*	x	x					x	x	x			x			
11. *Lampsilis siliquoidea*	x	x	x		x	x	x	x	x		x	x	x	x	x
12. *Lampsilis ventricosa*	x	x			x		x	x	x			x			

* below Minneapolis

Actinonaias carinata was found in a few places both in the main river and in two tributaries, but was not abundant. *Utterbackia imbecillis* was collected in fairly large numbers at Fridley and in the Rum River near Anoka, both places being about 500 miles below Lake Itasca, and about twenty miles north of St. Anthony Falls.

There seems to be no reason for this scarcity of species on grounds of chemical or physical conditions because the few species that were present were abundant. The total alkalinity in this part of the river ranges from 100 to 200 parts per million. Extensive collecting has been done in the upper Mississippi by survey crews of the University of Minnesota and the Department of Conservation, and although large numbers of mussels have been brought in and examined, the results from a taxonomic standpoint were monotonous—only eight species in the 500 miles of river and ten tributaries between Lake Itasca and St. Anthony Falls. The most likely explanation is that St. Anthony Falls has acted as a barrier to post-glacial migration up the river. In 1885 Grant reported 27 species from Fort Snelling a few miles below St. Anthony

Falls, and although at the present time pollution has eliminated the mussels from this area which is just below St. Paul and Minneapolis, this record is evidence that at least 27 species had migrated this far. Only five species have ever been reported from Fridley about five miles above St. Anthony Falls.

Table 4 shows the thirty-three species of mussels which have been collected from four stations in the St. Croix River and from six tributary streams. The total alkalinity ranges from 50 to 150 parts per million, which is lower than for other parts of the upper Mississippi drainage. The St. Croix Falls, located at the town of Taylors Falls, does not seem to have been much of a barrier to the migration of mussels. Although collecting has not been as extensive as in the upper Mississippi, seventeen species have been found in the

Table 4.—Distribution of mussels in the St. Croix River and its Tributaries.

	Federal Rec. Area in Pine Co.	Taylors Falls	Marine	Lake St. Croix	Kettle R.	Big Sand Creek	Rush Creek	Sunrise R.	Snake R.	Gristmill R.
1. *Fusconaia undata*		x	x	x						
2. *Fusconaia flava*		x				x	x			
3. *Megalonaias gigantea*				x						
4. *Amblema peruviana*				x						
5. *Amblema plicata*			x							
6. *Amblema costata*					x			x	x	
7. *Quadrula pustulosa*		x	x	x						
8. *Tritogonia verrucosa*		x		x						
9. *Cyclonaias tuberculata*				x				x		
10. *Plethobasus cyphyus*		x								
11. *Pleurobema cordatum curtum*		x							x	
12. *Elliptio dilatatus*	x		x							
13. *Lasmigona compressa*							x	x		x
14. *Lasmigona costata*									x	
15. *Lasmigona complanata*				x						
16. *Anodonta grandis*				x			x			
17. *Anodonta corpulenta*			x							
18. *Utterbackia imbecillis*			x							
19. *Anodontoides ferussacianus*							x			
20. *Alasmidonta marginata truncata*								x	x	
21. *Strophitus rugosus*	x	x		x	x	x		x		x
22. *Obliquaria reflexa*		x		x						
23. *Obovaria olivaria*	x	x						x		
24. *Actinonaias carinata*	x		x		x	x		x	x	
25. *Truncilla truncata*		x		x						
26. *Leptodea fragilis*		x		x						
27. *Proptera alata megaptera*				x					x	
28. *Proptera laevissima*			x							
29. *Carunculina parva*			x							
30. *Ligumia recta latissima*	x		x	x	x				x	
31. *Lampsilis siliquoidea*	x			x				x	x	
32. *Lampsilis ventricosa*	x		x					x	x	
33. *Lampsilis higginsi*				x						

Table 5.—Distribution of mussels in the Hudson Bay drainage, Minnesota River, and the St. Lawrence drainage.

	Hudson Bay drainage				Minn. R. drainage						St. Lawrence drainage		
	Red Lake R.	Red R.	Bear R.*	Sturgeon R.*	Minn. R.**	Ft. Snelling	above New Ulm	Blue Earth R.	Cottonwood R.	Chippewa R.	St. Louis R. and tributaries	Lake Superior
1. *Fusconaia undata*						x	x					
2. *Fusconaia flava*	x	x										
3. *Megalonaias gigantea*						x						
4. *Amblema peruviana*						x						
5. *Amblema variplicata*						x	x					
6. *Amblema costata*	x	x										
7. *Quadrula quadrula*		x				x						
8. *Quadrula postulosa*						x	x					
9. *Tritogonia verrucosa*						x						
10. *Plethobasus cyphyus*							x					
11. *Pleurobema cordatum coccineum*					x							
12. *Elliptio dilatatus*						x		x				
13. *Elliptio crassidens*					x							
14. *Elliptio complanatus*												x
15. *Lasmigona compressa*											x	
16. *Lasmigona costata*	x				x							
17. *Lasmigona complanata*	x			x		x	x					x
18. *Anodonta grandis*	x	x		x		x					x	x
19. *Anodonta gigantea*						x						
20. *Anodonta corpulenta*						x						
21. *Utterbackia imbecillis*						x						
22. *Anodontoides ferussacianus*			x	x			x		x		x	
23. *Alasmidonta marginata truncata*					x							
24. *Arcidens confragosus*						x						
25. *Strophitus rugosus*	x	x										
26. *Obliquaria reflexa*		x				x						
27. *Obovaria olivaria*						x						
28. *Actinonaias carinata*		x		x			x					
29. *Truncilla truncata*						x	x					
30. *Truncilla donaciformis*						x						
31. *Leptodea fragilis*						x	x					
32. *Proptera alata megaptera*	x	x				x						
33. *Proptera laevissima*						x				x		
34. *Carunculina parva*						x						
35. *Ligumia recta latissima*	x	x					x	x				x
36. *Lampsilis fallaciosa*						x						
37. *Lampsilis siliquoidea*	x	x	x	x		x					x	x
38. *Lampsilis ventricosa*	x	x		x	x	x	x					x
39. *Lampsilis higginsi*							x					
40. *Plagiola lineolata*						x						

* Tributaries of the Rainy R.
** No location designated

river and its tributaries above the falls. Geological evidence furnished by the pot holes and old channels around Taylors Falls suggests that in the early post-glacial period before the river cut the gorge, it flowed through a series of cascades and there were no abrupt falls to act as a barrier.

Table 5 shows the thirty-four species of mussels which have been collected from the Minnesota River and its tributaries. The total alkalinity ranges from 150 to 300 parts per million. Very little recent collecting has been done in this river, and very little collecting has ever been done in the upper part or in its smaller tributaries. All species found occurred abundantly in the Mississippi below the mouth of the Minnesota River.

HUDSON BAY DRAINAGE

About one-third of Minnesota, the northern and western portions, drains north into Hudson Bay. The two principal rivers of this drainage are the Rainy River which separates Minnesota from Canada and the Red River which rises close to the Minnesota River on the North Dakota border but flows northward. Fourteen species of mussels have been found in this drainage —thirteen from the Red River and its tributaries and six from the Rainy River drainage. They are listed in Table 5. The small number of species reported from the Rainy River drainage may be due either to its remoteness from the source of post-glacial migration or to the fact that only a few rivers in this drainage have been explored for mollusks. Almost all of the collecting has been done in the Sturgeon River in St. Louis County. Very few chemical analyses have been made of the waters of the Rainy River drainage, but in some places at least the total alkalinity is much lower than in the Red River, which varies from 150 to 200 parts per million.

Eleven of the fourteen species from the Red River drainage were found also in the Minnesota River, the other three, *Fusconaia flava*, *Amblema costata*, and *Strophitus rugosus*, being small river forms which might be found in the Minnesota drainage if the tributaries were more thoroughly explored. This similarity in species is easily explained by the extensive post-glacial connection between their headwaters. At present, Bigstone Lake on the North Dakota border, the source of the Minnesota River, and Lake Traverse which drains into the Red River are only a few miles apart, and are sometimes connected during periods of extremely high water. After the last glacier, the whole northwestern part of the state, which now drains north through the Red River, was occupied by Lake Agassiz, a huge glacial lake which drained southward through the River Warren in the present valley of the Minnesota River. During this period considerable migration of mussels could have taken place. The discovery of shells of *Amblema costata*, *Lampsilis siliquoidea*, *Lampsilis ventricosa*, *Lasmigona complanata*, and *Ligumia recta latissima* in the debris excavated from the bed of glacial Lake Agassiz is further proof that the conditions were suitable for mussels.

ST. LAWRENCE DRAINAGE

About a tenth of the state, the northeastern part, drains into Lake Superior either through the St. Louis River at the extreme western end or through

many small rivers running directly into the lake on its northern border. Two species, *Anodonta marginata*, and *Elliptio complanatus*, probably entered Minnesota through this drainage. *Elliptio complanatus* is common in the Atlantic drainage but not in the Mississippi and Walker (1913) who first reported this species in Lake Superior, thought that it had migrated in early post-glacial times from the St. Lawrence River through the Trent outlet into Lake Huron and from there into Lake Superior. *Anodonta marginata* is widely distributed in the northern part of the United States and in Canada in both the St. Lawrence and upper Mississippi drainages.

Mussels are not abundant in the St. Lawrence drainage in Minnesota. They are entirely absent from the rushing, turbulent streams which run into Lake Superior on its north shore. The total alkalinity of these streams is low, from 30 to 85 parts per million (Smith and Moyle, 1944). But the total absence of mussels is probably due to the fact that these streams have rocky bottoms and also that just above the mouths of most of them there are falls over which it would be impossible either for adult clams or for glochidia-bearing fish to migrate. The St. Louis River at the western end of the lake is a placid, winding stream flowing through bogs and pine woods and in most places its soft, muddy bottom is not firm enough for mussels. Thin and badly eroded specimens of *Anodonta grandis*, *Anodontoides ferussacianus*, *Lampsilis siliquoidea*, and *Lasmigona compressa* were occasionally found in this river and its tributaries. The total alkalinity is about 60 parts per million.

The north shore of Lake Superior in Minnesota is mainly rock, but even in the few sandy coves there were no mussels. According to Eddy (1943) in a report on limnological studies in Lake Superior "The marginal plant and animal life was practically absent from most of the Minnesota shore due to the heavy wave action". The only part of the south shore which is in Minnesota is Minnesota Point, a narrow spit of sand projecting into the lake at the mouth of the St. Louis River in Duluth. On this point dead shells of *Elliptio complanatus*, *Anodonta grandis*, *Lampsilis siliquoidea*, *Lampsilis ventricosa*, *Lasmigona complanata*, and *Ligumia recta latissima* have recently been collected. With the exception of *Elliptio complanatus* these are all species which are common in the Mississippi drainage and which might have entered during the retreat of the last glacier when glacial Lake Duluth in the Lake Superior area drained southward through the present St. Croix valley. An outline of the mussels found in this drainage is given in tables 1 and 5.

Ecological Distribution

Within the boundaries of any one drainage system are to be found many different types of environments. In Minnesota the aquatic environments include not only streams of various sizes, but also lakes and ponds. These different environments differ in such characteristics as movement or stillness of the water, chemical composition, depth, kind of bottom, amount of vegetation, etc. Some species of mollusks have a wide range of tolerance of such conditions and are found in a variety of habitats, while others are limited to one or two.

Fresh water environments fall easily into two groups—1) moving waters, such as rivers and streams, and 2) standing waters such as lakes and

ponds. This classification is not rigid for the parts of rivers along the edges and behind barriers become pond-like and many lakes with an inlet and outlet have a considerable flow of water at these points. Moving waters have been divided into four categories. The division is made primarily on the basis of size, but size is correlated in most instances with differences in depth, current, and bottom.

Habitat 1. Small Streams

Small streams are usually less than ten feet wide and shallow enough to be waded. Inlets and outlets of lakes, headwaters of rivers, and streams flowing through the bottoms of ravines belong to this category. Streams which have been studied in Minnesota are: Nicollet and Chambers Creeks flowing into Lake Itasca and the Mississippi River flowing out, Rice and Coon Creeks north of Minneapolis, and the outlet of Tanners Lake in Washington County. The chemical composition of these streams varies with the local conditions of the region in which they are found, but the physical characteristics are fairly constant. The current is swift, the water shallow, and the bottom made of stones or gravel. In the pool-like stretches vegetation is abundant. Mussels were rare, but fingernail clams and snails were abundant, although only a few species were found at any one place. Below is a composite list of the species found.

Mussels

Anodontoides ferussacianus
Lampsilis siliquoidea
Lasmigona compressa

Snails

Amnicola limosa
Ferrissia tarda
Gyraulus deflectus obliquus
Gyraulus parvus
Helisoma antrosa
Helisoma campanulata
Helisoma trivolvis
Lymnaea caperata
Lymnaea modicella
Lymnaea palustris
Lymnaea stagnalis appressa
Physa gyrina
Physa integra
Physa michiganensis
Planorbula armigera
Valvata tricarinata

Probably the two species most characteristic of small streams in Minnesota are the mussel, *Anodontoides ferussacianus*, and the snail, *Physa integra*. *Physa michiganensis*, which is purely a small creek form (Clench, 1926), has been found only once in Minnesota. Most of the species found in small streams were forms which could live in many different environments or they were lake forms which have spread to the connecting streams.

Habitat 2. Small Rivers

These rivers range in width from ten to fifty feet. In places there are deep, quiet pools, but elsewhere the bottom is stony, the water shallow, and the current swift. Vegetation is confined to areas near the shore. In Minnesota the Mississippi River from Alida to Cass Lake, the Prairie River, the Zumbro River at Kenyon, and the Sturgeon River in St. Louis County are examples of small rivers which have been studied. In these rivers mussels are abundant, the following being a composite list:

Alasmidonta marginata truncata
Amblema costata
Anodonta grandis
Anodontoides ferussacianus
Fusconaia flava
Ligumia recta latissima
Lampsilis ventricosa
Lasmigona complanata
Lasmigona compressa
Lampsilis siliquoidea
Strophitus rugosus

The following snails were found in small rivers:

Amnicola limosa
Campeloma decisum
Ferrissia parallela
Ferrissia tarda
Helisoma antrosa
Helisoma campanulata
Helisoma trivolvis
Lymnaea megasoma
Lymnaea modicella
Lymnaea palustris
Lymnaea stagnalis appressa
Physa gyrina
Physa integra

Habitat 3. Medium-sized Rivers

These rivers are from fifty to one hundred feet wide and quite deep in the center. They offer at least two types of environment, deep pools where the current is slow and the bottom sand or mud, and shallow rapids where the bottom is stony and the current swift. Examples of medium-sized rivers in Minnesota are the Rum River where it enters the Mississippi, the St. Croix River above Taylors Falls, the Red Lake River, and the Mississippi River from Jacobson to Little Falls. The following mussels were found:

Actinonaias carinata
Amblema costata
Amblema rariplicata
Anodonta grandis
Elliptio dilatatus
Fusconaia flava
Lampsilis siliquoidea
Lampsilis ventricosa
Lasmigona complanata
Lasmigona costata
Ligumia recta latissima
Pleurobema cordatum coccineum
Proptera alata megaptera
Quadrula pustulosa
Strophitus rugosus
Utterbackia imbecillis

The following snails were found in medium-sized rivers:

Amnicola integer
Amnicola limosa
Campeloma decisum
Helisoma antrosa
Helisoma trivolvis
Lymnaea catascopium
Lymnaea megasoma
Lymnaea stagnalis appressa
Physa gyrina
Physa integra
Pleurocera acuta tracta
Somatogyrus subglobosus

Habitat 4. Large Rivers

This category includes the largest rivers in Minnesota, namely the Mississippi River below Little Falls, and the lower parts of the Minnesota and St. Croix Rivers. They are broad and deep and for the most part are bordered by sandy beaches or broad flood plains often filled with sloughs and marshes. River-lakes such as Lake Pepin and Lake St. Croix which are simply widenings of the river are included. In general, the larger the river the greater the number of species of mollusks, especially mussels. The following were found in large rivers in Minnesota:

Actinonaias carinata
Alasmidonta marginata truncata
Amblema peruviana
Anodonta corpulenta
Anodonta grandis
Anodonta gigantea
Arcidens confragosus
Carunculina parva
Cyclonaias tuberculata
Elliptio dilatatus
Elliptio crassidens
Fusconaia ebenus
Fusconaia undata
Lampsilis fallaciosa
Lampsilis higginsi
Lampsilis siliquoidea
Lampsilis ventricosa
Lasmigona complanata
Lasmigona costata
Leptodea fragilis
Ligumia recta latissima
Megalonaias gigantea
Obliquaria reflexa
Obovaria olivaria
Plagiola lineolata
Plethobasus cyphyus
Pleurobema cordatum coccineum
Proptera alata meg ptera
Proptera laevissima
Quadrula metanevra
Quadrula pustulosa
Quadrula quadrula
Strophitus rugosus
Tritogonia verrucosa
Truncilla donaciformis
Truncilla truncata
Utterbackia imbecillis

The following snails were collected from large rivers:

Amnicola emarginata
Amnicola integer
Campeloma decisum
Ferrissia tarda
Helisoma trivolvis
Lioplax subcarinata
Lymnaea modicella
Lymnaea stagnalis appressa
Planorbula armigera
Pleurocera acuta tracta
Somatogyrus subglobosus
Somatogyrus tryoni
Valvata tricarinata
Viviparus intertextus illinoisensis

When we compare the mussel fauna of the rivers of different size, we find that the larger rivers have a greater number of species than the smaller rivers. This is probably due to the greater variety of environments for the adult mussel and the larger number of species of fish hosts for the glochidia. The two species that seem to be restricted to small rivers and streams are *Anodontoides ferussacianus* and *Lasmigona compressa*. *Amblema costata* and *Fusconaia flava* are found only in small and medium sized rivers, but closely related species, *Amblema rariplicata* and *Amblema peruviana*, *Fusconaia undata* and *Fusconaia ebenus* are found in large rivers. Several species (*Arcidens confragosus*, *Carunculina parva*, *Leptodea fragilis*, *Quadrula metanevra*, *Tritogonia verrucosa*, *Truncilla truncata*) have apparently never migrated beyond the larger rivers in Minnesota although they are found in both small and large rivers in states farther south. The two most widespread species are *Anodonta grandis* and *Lampsilis siliquoidea* which were found in rivers of all sizes and also in lakes. Other species which were found in small, medium and large rivers are *Lampsilis ventricosa*, *Lasmigona complanata*, *Ligumia recta latissima*, and *Strophitus rugosus*. *Actinonaias carinata* and *Proptera alata megaptera* were found in small rivers in the St. Croix drainage, but elsewhere were species of medium-sized and large rivers.

The species of snails found in rivers can be divided into two groups, those which were found only in rivers, and those which were found in lakes and ponds as well. Most of the members of the first group breathe by gills and were found where the current was fairly swift. The only common example of this group is *Pleurocera acuta tracta* which was found in many of the large

and medium-sized rivers of the Mississippi drainage. It is the only member of the Pleuroceridae found in Minnesota. The species *Amnicola emarginata, Amnicola integer, Lioplax subcarinata, Lymnaea catascopium, Physa michiganensis, Somatogyrus subglobosus,* and *Somatogyrus tryoni,* also restricted to rivers, have been found only once or twice. *Physa integra,* although found in both lakes and streams, was more common in streams. Members of the second group, *Amicola limosa, Campeloma decisum, Ferrissia parallela, Ferrissia tarda, Gyraulus parvus, Gyraulus deflectus obliquus, Helisoma antrosa, Helisoma campanulata, Helisoma trivolvis, Lymnaea caperata, Lymnaea megasoma, Lymnaea modicella, Lymnaea stagnalis appressa, Physa gyrina, Planorbula armigera,* and *Valvata tricarinata* were not restricted to rivers, but were found as often in lakes and ponds, and were either found close to where the stream entered or left the lake, or were found in the shallow edges of the river which were stagnant and pond-like. In general the larger rivers contain more of the species which are restricted to a river habitat while the streams and smaller rivers contain more of those species which can live either in standing or flowing waters.

Standing waters have been classified into five groups on the basis of size, total alkalinity, and flow of water.

Habitat 5. PONDS

While there is no sharp distinction between a large pond and a small lake, any shallow body of water less than an acre in area with a mucky, weedy bottom is considered a pond. They usually become smaller or dry up completely in midsummer, and they freeze solid in winter. Minnesota ponds have been studied mainly in three regions. The first is Itasca Park where George Klak in the summer of 1936 collected mollusks in 33 ponds and turned them over to the writer for identification. These ponds were mainly coniferous forest pools and the most common species found were *Aplexa hypnorum, Gyraulus parvus* and *Lymnaea exilis.* This is almost the only habitat for *Aplexa hypnorum* in Minnesota although in other states it may be found near springs and on the walls of wet, shady ravines. It seems to require shade and can endure drought. In addition mollusks were collected by the writer from nine ponds in the region near St. Paul and Minneapolis and from about the same number near Hibbing in St. Louis County. These ponds were either roadside ditches or located in meadows with few if any trees around them. The most common species were *Helisoma trivolvis* and *Physa gyrina.*

No mussels were found in Minnesota ponds, but the three genera of Sphaeriidae, Sphaerium, Musculium, and Pisidium, were common. The following is a complete list of the snails found:

Aplexa hypnorum
Gyraulus parvus
Helisoma trivolvis
Lymnaea caperata
Lymnaea exilis
Lymnaea megasoma
Lymnaea modicella
Lymnaea palustris
Lymnaea reflexa
Menetus exacuous megas
Planorbula armigera
Physa gyrina

All of these species are lung breathing. Since they do not depend on dissolved oxygen in the water, but come to the surface to breathe, they are more suited to shallow stagnant water. Usually not more than three species of snails were found in any one pond.

Habitat 6. Soft-water Lakes

Soft-water lakes ranging in total alkalinity from 7.5 to 75 parts per million are found in the northeastern part of Minnesota in the Rainy River and St. Lawrence drainages. Drainage is poor in this region and lakes are numerous and of different sizes. Those in which mollusks have been collected are principally of two types—they have either a rocky or a sandy shoreline. Lake Vermillion and Sturgeon Lake, both in St. Louis County northwest of Lake Superior are the two lakes which have been studied most extensively.

Lake Vermillion, a large, irregularly shaped lake with an area of 37,915 acres and a total alkalinity of 25 parts per million has a rocky shoreline. Mollusks were collected in this lake in 1881 by U. S. Grant, in 1927 by F. C. Baker, and in 1939 and 1940 by the writer and also by a survey crew from the Minnesota Department of Conservation. Sturgeon Lake is smaller, with an area of 1659 acres, and has gently sloping sandy beaches. The total alkalinity is about 35 parts per million. Extensive collecting was done in this lake by the writer during the four years between 1938 and 1942.

The following mollusks were found in these two lakes:

	Lake Vermilion	Sturgeon Lake
Mussels		
Anodonta grandis	x	x
Anodonta kennicotti	x	–
Anodonta marginata	x	rare
Lampsilis siliquoidea	x	x
Snails		
Amnicola limosa	x	x
Campeloma decisum	–	x
Ferrissia parallela	x	x
Ferrissia tarda	x	–
Gyraulus deflectus obliquus	x	x
Helisoma antrosa	x	x
Helisoma campanulata	x	x
Helisoma corpulenta vermilionensis	x	–
Lymnaea haldemani	x	x
Lymnaea megasoma	x	–
Lymnaea stagnalis appressa	x	–
Lymnaea stagnalis lillianae	x	–
Menetus exacuous megas	x	x
Physa gyrina	x	x
Planorbula armigera	x	x
Planorbula crassilabris	x	–
Valvata tricarinata	x	x

In spite of the low total alkalinity of the lakes in this area, many of them contain large numbers of mussels, usually *Lampsilis siliquoidea* and one or two species of *Anodonta*. It is difficult to state just what the relationship is between the total alkalinity of a lake and the number of mussels produced. In some of the lakes, such as Clearwater Lake, St. Louis County, with a

total alkalinity of 15 parts per million there were no mussels. In others near by, such as Rock Lake, 20 parts per million, and Robinson Lake 22.5 parts per million, mussels were plentiful. It would seem that unless the total alkalinity is very low, it is not the limiting factor in determining the presence of mussels in a lake. Most of the species of snails found in these soft-water lakes were found also in hard-water lakes and sometimes in ponds or rivers. *Helisoma corpulenta* is restricted to the northern part of the state, but not to soft-water lakes, as it was abundant in Lake Itasca, a medium-hard-water lake described in the next group. *Campeloma decisum*, which was found in both lakes and rivers, was more abundant in soft-water lakes than in lakes with a higher total alkalinity.

Habitat 7. MEDIUM-HARD-WATER LAKES

Most of the lakes in the central part of Minnesota in the Mississippi drainage belong in this category. The total alkalinity varies from 75 to 175 parts per million. Two lakes that have been studied in detail from this area are Lake Itasca in Clearwater County in the north central part of Minnesota, and Snail Lake just north of St. Paul in Ramsey County. Lake Itasca is a Y-shaped lake with an area of 1,152 acres and a total alkalinity of 165 parts per million. Its outlet is the beginning of the Mississippi River. The shore of the lake is either sand or mud and is filling in with wild rice and bulrushes. The University of Minnesota Biological Station is located in Itasca Park, and consequently the mollusks in the lake have been thoroughly studied. Snail Lake near St. Paul, 200 miles south of Lake Itasca, a small lake of 155 acres, has a total alkalinity of about 165 parts per million. Most of the bottom and much of the shore is mucky and filled with weeds, but at one end is a shallow sandy beach where snails are plentiful. The writer explored various parts of the lake during 1939 and 1940.

The following mollusks were found in these two lakes:

	Lake Itasca	Snail Lake
Mussels		
Anodonta grandis	x	–
Anodonta marginata	x	x
Anodontoides ferussacianus	x	–
Lampsilis siliquoidea	x	–
Snails		
Amnicola limosa	x	x
Amnicola lustrica	x	–
Ferrissia tarda	x	–
Gyraulus deflectus obliquus	x	–
Gyraulus hirsutus	x	–
Helisoma antrosa	x	x
Helisoma campanulata	x	x
Helisoma corpulenta	x	–
Helisoma trivolvis	x	x
Lymnaea exilis	–	x
Lymnaea stagnalis appressa	x	x
Menetus exacuous megas	x	–
Physa gyrina	x	x
Physa integra	–	x
Planorbula armigera	x	–
Valvata lewisi	x	–
Valvata tricarinata	x	–

There were many more mussels in Lake Itasca than in Snail Lake, possibly because of its larger size or because its beaches suffer less from human disturbances. It is generally true that it is easier to find mussels in the more isolated lakes than in those close to the more populous area around St. Paul and Minneapolis. Snails were abundant in both lakes and many of the most common species were common also in soft-water lakes. Perhaps the most striking feature was the number and variety of the planorbid snails. In Lake Itasca all nine of the species of the family Planorbidae common in Minnesota were present.

Habitat 8. Hard-water Prairie Lakes

These lakes are found in the western part of Minnesota in the region drained by the Red River, the Minnesota River, and the western tributaries of the upper Mississippi. The lakes vary in size but are often large and shallow. The total alkalinity varies from 150 to 300 parts per million and the water often contains other salts in addition to calcium salts. No lake of this group has been studied extensively, but in the summer of 1940 the writer spent a week collecting in this area. The lakes were very low that summer due to a series of dry years, and in many lakes there was a wide stretch of exposed beach covered with mussel shells. A combined list of mollusks found in lakes in Pope, Ottertail, and Todd Counties gives the following:

Mussels
Anodonta grandis
Lampsilis siliquoidea

Snails
Amnicola limosa
Gyraulus deflectus obliquus
Helisoma antrosa
Helisoma campanulata
Helisoma trivolvis
Lymnaea emarginata
Lymnaea emarginata canadensis
Lymnaea emarginata angulata
Lymnaea palustris
Lymnaea stagnalis appressa
Lymnaea stagnalis lillianae
Physa gyrina
Valvata tricarinata

As in the previous groups *Amnicola limosa*, *Valvata tricarinata*, the three species of *Helisoma*, and *Lymnaea stagnalis appressa* were common. *Physa gyrina*, although present, was noticeably less abundant than in other parts of the state, and *Campeloma decisum* and *Anodonta marginata* were missing entirely. But most striking of all was the abundance and variety of the larger Lymnaeidae. Two varieties of *Lymnaea stagnalis* and at least two varieties of *Lymnaea emarginata*, as well as *Lymnaea palustris* were present in large numbers in these lakes. There was much variation in these three species in these lakes agreeing with Baker (1936) who stated of *L. emarginata* "Almost every large lake has its own peculiar form which is often quite distinct from the same species from nearby lakes."

Habitat 9. River Lakes

River lakes are lakes in which there is at least a slight current due to their being a part of a river system. They are of two kinds: 1) true river-lakes like Lake Pepin or Lake St. Croix which are simply widenings of a river behind a natural or artificial barrier, and in which the river influence is strong, and 2) lakes with a good sized river for an inlet and outlet, but in which the lake influence predominates. Examples of the second class are Lake of the

Woods and other border lakes in the Rainy River, Cass Lake, Lake Bemidji and Lake Winnibigoshish in the upper Mississippi River, and Cross Lake and Lake Pokegama in the Snake River.

One effect of close relationship with a river system is an increase in the number of species of mussels. The thirty-five species of mussels in Lake Pepin and the fourteen in Lake St. Croix (Tables 2, 4) were the same as those in the Mississippi and St. Croix Rivers respectively. The following snails were found in these two river-lakes:

Amnicola limosa	*Lymnaea exilis*
Campeloma decisum	*Physa gyrina*
Helisoma antrosa	*Planorbula armigera*
Helisoma trivolvis	*Pleurocera acuta tractı*
Lioplax subcarinata	*Valvata trizarinata*

The effect of the river is shown in the presence of *Pleurocera* and *Lioplax*, typical river snails. This, together with the large number of species of mussels proves that this type of river-lake is more like a river than a lake in its molluscan fauna.

The second type of river-lake is more like a lake than a river, but the effect of having a good sized river for inlet and outlet is to increase the number of species of mussels. In most Minnesota lakes with little or no river connections, the mussels found were limited to *Lampsilis siliquoidea*, *Anodonta grandis*, *Anodonta marginata*, and *Anodontoides ferussacianus*, and usually not more than two species were found in any one lake. The following species were found in three of the second type of river-lake:

	Lake Pokegama	Cross Lake	Lake of the Woods
Mussels			
Amblema rariplicata	x	x	–
Anodonta grandis	x	–	x
Anodonta marginata	–	–	x
Actinonais carinata	–	x	–
Fusconaia undata	x	x	–
Lasmigona complanata	–	–	x
Lampsilis siliquoidea	x	x	x
Lampsilis ventricosa	x	x	–
Leptodea fragilis	–	x	–
Ligumia recta latissima	–	x	x
Proptera alata megaptera	–	x	–
Quadrula pustulosa	x	–	–
Quadrula quadrula	x	x	–
Strophitus rugosus	x	–	–
Snails			
Amnicola limosa	x	x	–
Campeloma decisum	–	–	x
Gyraulus deflectus obliquus	–	–	x
Helisoma antrosa	x	–	x
Helisoma campanulata	x	–	x
Helisoma trivolvis	x	–	x
Lymnaea exilis	x	–	–
Lymnaea emarginata	–	–	x
Lymnaea palustris	–	–	x

Lymnaea stagnalis appressa	–	–	x
Physa gyrina	–	–	x
Planorbula armigera	x	–	–
Valvata tricarinata	x	x	x

The typical river snails, *Pleurocera* and *Lioplax*, were not found in these lakes, and many typical lake species, i.e. *Helisoma campanulata*, *Lymnaea stagnalis appressa*, *Amnicola limosa*, and *Volvatat tricarinata* were found. (The small number of snails reported from Cross Lake is probably due to lack of collecting in that lake.) It would seem that in this type of river-lake the number of species of mussels is increased due to its close relationship to a river, but that the snail population is not noticeably affected.

Distribution of Individual Species

Below is a list of the 45 species of mussels found in Minnesota with a brief summary of the geographical and ecological distribution of each.

Subfamily UNIONINAE

1. *Fusconaia flava* (Rafinesque).—in the Red River and St. Croix River systems, in streams and small rivers.

2. *Fusconaia undata* (Barnes).—in the St. Croix and Minnesota Rivers and in the Mississippi River south of St. Anthony Falls, restricted to large rivers and river lakes. It is the most common species of Fusconaia in Minnesota.

3. *Fusconaia ebenus* (Lea).—in the Mississippi River south of St. Anthony Falls, apparently a large river species. It has not been seen for some years and may be extinct in Minnesota.

4. *Megalonaias gigantea* (Barnes).—in the lower Minnesota and St. Croix Rivers, and in the Mississippi River south of St. Anthony Falls, apparently confined to large rivers.

5. *Amblema peruviana* (Lamarck).—in the lower Minnesota and St. Croix Rivers and Mississippi River south of St. Anthony Falls, a species confined to large rivers.

6. *Amblema rariplicata* (Lamarck).—in the Minnesota and St. Croix Rivers and in two river-lakes in the St. Croix drainage, apparently a species of medium-sized rivers.

7. *Amblema costata* (Rafinesque).—in the Cedar River, a tributary of the lower Mississippi, in the Kettle, Snake and Sunrise Rivers, tributaries of the St. Croix, and in the Red River drainage, apparently confined to small rivers.

8. *Quadrula quadrula Rafinesque*.—in the Red and Minnesota Rivers and in the Mississippi south of St. Anthony Falls, a species of large rivers.

9. *Quadrula pustulosa* (Lea).—in the Mississippi River south of St. Anthony Falls, and in the Minnesota and St. Croix Rivers, all large rivers.

10. *Quadrula metanevra* (Rafinesque).—only in the Mississippi River south of St. Anthony Falls, the largest river in Minnesota.

11. *Tritogonia verrucosa* (Rafinesque).—in the Mississippi River south of St. Anthony Falls and in the Minnesota and St. Croix, all large rivers.

12. *Cyclonaias tuberculata* (Rafinesque).—in the Mississippi River south of St. Anthony Falls and in the St. Croix River, not found in large numbers anywhere.

13. *Plethobasus cyphyus* (Rafinesque).—in the Mississippi River below Lake Pepin where it was abundant at ane time, and in the Minnesota and St. Croix Rivers where it is apparently rare.

14. *Pleurobema cordatum coccineum* (Conrad).—in the St. Croix River, and the Snake River, one of its tributaries, in Lake Pepin and in the Minnesota River, but not abundant anywhere.

15. *Elliptio dilatatus* (Rafinesque).—in the Mississippi River south of St. Anthony Falls, in the Minnesota and St. Croix Rivers, restricted to large rivers except in the St. Croix, and abundant where found.

16. *Elliptio crassidens* (Lamarck).—in the Mississippi River south of St. Anthony Falls, and in the Minnesota River, restricted to large rivers and comparatively rare.

17. *Elliptio complanatus* (Dillwyn).—in Lake Superior, found in large numbers on Minnesota Point in Duluth.

Subfamily ANODONTINAE

18. *Lasmigona compressa* (Lea).—widespread and abundant in streams and small rivers of the Mississippi drainage north of St. Anthony Falls and also found in the St. Croix, St. Louis, and Rainy River drainages.

19. *Lasmigona costata* (Rafinesque).—in the Mississippi River south of St. Anthony Falls, and in the Snake River and Red Lake River, being found in medium-sized as well as large rivers.

20. *Lasmigona complanata* (Barnes).—in small medium, and large rivers of the Mississippi drainage south of St. Anthony Falls, the Minnesota, St. Croix, Hudson Bay and St. Lawrence drainages as well as in Lake of the Woods and Lake Superior.

21. *Anodonta grandis* Say.—in both lakes and rivers in all parts of Minnesota. Special lake and river varieties can sometimes be distinguished. It is one of the most common species in Minnesota.

22. *Anodonta gigantea* Lea.—sometimes considered a variety of *A. grandis*, in the Mississippi River south of St. Anthony Falls and in the Minnesota River, restricted to large rivers.

23. *Anodonta kennicotti* Lea.—in several large lakes in the northern part of the state. It is rare.

24. *Anodonta marginata* Say.—in many lakes in northern Minnesota in the Mississippi, Hudson Bay, and St. Lawrence drainages.

25. *Anodonta corpulenta* Cooper.—in the Mississippi River south of St. Anthony Falls, in the Minnesota and St. Croix Rivers, apparently restricted to large rivers and not common.

26. *Utterbackia imbecillis* (Say).—in the Mississippi, Minnesota and St. Croix Rivers, often in lake-like areas. It surmounted the barrier of St. Anthony Falls but has never been found north of Anoka, about twenty miles above the Falls.

27. *Anodontoides ferussacianus* (Lea).—in all parts of the state in small tributary and headwater streams, and also in lakes, especially in the northern part. It is common and widespread in Minnesota.

28. *Alasmidonta marginata truncata* (B. H. Wright).—in the Mississippi River south of St. Anthony Falls, the Minnesota River, and the Sunrise and Snake Rivers. Not common, but found in both small and large rivers.

29. *Arcidens confragosus* (Say).—in the Mississippi River south of St. Anthony Falls and in the Minnesota River, restricted to the largest rivers in Minnesota and not common.

30. *Strophitus rugosus* (Swainson).—in small rivers in the St. Croix and Red River systems, and in the Mississippi River south of St. Anthony Falls, not common but found in both small and large rivers.

Subfamily LAMPSILINAE

31. *Obliquaria reflexa* Rafinesque.—in the Mississippi River south of St. Anthony Falls, and in the Minnesota, St. Croix, and Red Rivers, widely distributed but not abundant.

32. *Obovaria olivaria* (Rafinesque).—in the Mississippi River south of St. Anthony Falls and in the Minnesota and St. Croix Rivers, large and medium sized rivers, not common.

33. *Actinonaias carinata* (Barnes).—in all parts of the Mississippi drainage and in the Hudson Bay drainage, widely distributed in medium sized and large rivers, but not present in large numbers.

34. *Truncilla truncata* Rafinesque.—in the Mississippi River south of St. Anthony Falls, and in the Minnesota and St. Croix Rivers, all large rivers.

35. *Truncilla donaciformis* (Lea).—in the Mississippi River at Red Wing and in the Minnesota River at Fort Snelling, a rare species and limited to the largest rivers in the state.

36. *Plagiola lineolata* (Rafinesque).—in the Mississippi River south of St. Anthony Falls and in the Minnesota River, confined to large rivers and not common.

37. *Leptodea fragilis* (Rafinesque).—in the Mississippi River south of St. Anthony Falls, in the Minnesota and St. Croix Rivers and in Cross Lake, apparently confined to large rivers and river-lakes.

38. *Proptera alata megaptera* (Rafinesque).—in the Mississippi River south of St. Anthony Falls, the Minnesota, St. Croix and Red River drainages, in both large and medium-sized rivers.

39. *Proptera laevissima* (Lea).—in the Mississippi River south of St. Anthony Falls and in the Minnesota and St. Croix Rivers, a rare species limited to large rivers.

40. *Carunculina parva* (Barnes).—abundant in Lake Pepin, found also in the St. Croix and Minnesota Rivers.

41. *Ligumia recta latissima* (Rafinesque).—in all drainages, common in all but the smallest rivers and found also in Lake of the Woods and Lake Superior.

42. *Lampsilis fallaciosa* (Smith) Simpson.—in the Mississippi River south of St. Anthony Falls and the Minnesota River at Fort Snelling, restricted to large rivers.

43. *Lampsilis siliquoidea* (Barnes).—in rivers and lakes in all parts of the state, not restricted to any stream type but showing growth forms or varieties in lakes and rivers.

44. *Lampsilis ventricosa* (Barnes).—in all parts of the Mississippi drainage, in the Hudson Bay drainage, and in Lake Superior, common in small, medium, and large rivers.

45. *Lampsilis higginsii* (Lea).—in the Mississippi River south of St. Anthony Falls, and in the Minnesota and St. Croix Rivers, not common and restricted to large rivers.

Below is a list of snails found in Minnesota with a brief statment of the distribution of each.

Family VALVATIDAE

1. *Valvata tricarinata* (Say).—common in lakes in all parts of the state, on shallow, sandy beaches, or on vegetation, more rare in streams connected with lakes.

2. *Valvata sincera* Say.—reported by Daniels from Cannon Lake in Rice County and by Goodrich from Medicine Lake in Hennepin County.

3. *Valvata lewisi* Currier.—in Lake Itasca and several other lakes in the northern and eastern parts of the state, not common.

Family VIVIPARIDAE

4. *Viviparus intertextus illinoisensis* Baker.—in the Mississippi River near Winona and in White Bear Lake and a few other connecting lakes and streams in Ramsey County.

5. *Lioplax subcarinata* (Say).—in Lake Pepin and in the Minnesota River at Fort Snelling, limited apparently to large rivers.

6. *Campeloma decisum* (Say).—common in lakes and rivers in the northern, eastern, and central parts of the state where the waters have a low total alkalinity. Often found buried in mud of river banks or in sand of lake shores. Most of the Campelomas found in the state are considered to belong to this species, but *Campeloma subsolidum* was reported by Goodrich in the southern part of the state in a lagoon off the Mississippi River.

Family AMNICOLIDAE

7. *Amnicola limosa* (Say).—common in lakes throughout the state, usually attached to vegetation, and also found in some rivers where the current is slow and there is attached vegetation.

8. *Amnicola lustrica* Pilsbry.—in a few lakes in the central part of the state, attached to vegetation.

9. *Amnicola integer* Say.—in three rivers: Rum River in Anoka County, Rainy River on the Canadian border, and the Minnesota River at Fort Snelling, in shallow water attached to gravel and small stones.

10. *Amnicola emarginata* (Kuster).—in the Minnesota River at Fort Snelling (1885).

11. *Somatogyrus tryoni* Pilsbry and Baker.—in the St. Croix River at Marine, collected from rocks at water's edge (1939).

12. *Somatogyrus subglobosus* (Say).—in the Kettle River and in the Minnesota River on mud flats.

Family PLEUROCERIDAE

13. *Pleurocera acuta tracta* (Anthony).—in many parts of the Mississippi, Minnesota, and St. Croix Rivers and their tributaries, common in large and medium sized, and rare in smaller rivers, it is the most common river snail in Minnesota.

Family LYMNAEIDAE

14. *Lymnaea stagnalis appressa* Say.—in many lakes throughout the state, in large numbers on shallow, sandy beaches. Especially common in northern and eastern parts. Also found in a few streams, usually inlets or outlets of lakes. Two other varieties, *L. stagnalis lillianae* Baker and *Lymnaea stagnalis perampla* Walker were occasionally found in large lakes.

15. *Lymnaea palustris* Müller.—in western and southern parts of the state in ponds, lakes, and slow-moving edges of rivers.

16. *Lymnaea umbrosa* Say.—in several lakes in the state, rare.

17. *Lymnaea reflexa* Say.—in a few lakes and ponds in central and southern Minnesota, also rare.

18. *Lymnaea exilis* Lea.—in many ponds and a few lakes in the northern, eastern and central parts of Minnesota, sometimes present in large numbers, especially in ponds.

19. *Lymnaea emarginata* Say.—and the two varieties *L. emarginata angulata* (Sowerby) and *L. emarginata canadensis* (Sowerby) in many large lakes in western and northern Minnesota, seems especially adapted to large, hard-water lakes.

20. *Lymnaea lanceata* Gould.—in two lakes in the northern part of the state.

21. *Lymnaea walkeriana* (Baker).—from the north shore of Lake Superior.

22. *Lymnaea woodruffi* (Baker). from two lakes on the Canadian border.

23. *Lymnaea catascopium* Say.—from the Rum River, Anoka County.

24. *Lymnaea caperata* Say.—from lakes, ditches, ponds, and small streams, often filled with vegetation and drying up in summer.

25. *Lymnaea haldemani* Deshayes, Binney.—in several lakes in central and northern Minnesota, usually found attached to sticks or rushes, often found in only one spot in a lake, and probably easily overlooked.

26. *Lymnaea megasoma* Say.—in central and northern Minnesota, in parts of lakes, ponds, and rivers where vegetation is abundant and the bottom mucky.

27. *Lymnaea humilis modicella* (Say).—in central and eastern Minnesota on edges of rivers, lakes, and ponds especially on flat muddy beaches that are drying up.

28. *Lymnaea obrussa* Say.—in central, eastern and north central Minnesota, in lakes or ponds, sometimes on water plants and sometimes on the bottom. The variety *L. obrussa decampi* Streng was found in two lakes in the central part of the state.

Family PLANORBIDAE

29. *Helisoma antrosa* (Conrad).—in all parts of Minnesota in both lakes and rivers, very common. One very distinct variety, *H. antrosa royalensis* Walker, was found in a few northern lakes.

30. *Helisoma trivolvis* (Say).—in all parts of Minnesota, in lakes, ponds, and rivers, often in thick masses of water plants. The large, high variety, *H. trivolvis pilsbryi* (Baker) was found in a few northern lakes.

31. *Helisoma corpulenta* (Say).—in many northern lakes, both in the upper Mississippi and Hudson Bay drainages. The variety *H. corpulenta vermilionensis* (Baker) has been found only in Lake Vermilion.

32. *Helisoma campanulata* (Say).—in lakes in all parts of the state, very common both alive and as a white dead shell in beach debris.

33. *Planorbula armigera* (Say).—in the stagnant parts of lakes, ponds, and rivers in all parts of the state.

34. *Menetus exacuous megas* (Dall).—in lakes in all parts of the state, attached to sticks or larger floating wood.

35. *Gyraulus hirsutus* (Gould).—in a few lakes in northern Minnesota.

36. *Gyraulus deflectus obliquus* (DeKay).—in lakes in central and north central Minnesota.

37. *Gyraulus parvus* (Say).—in northern and central Minnesota, in lakes, ponds or streams attached to aquatic plants, especially common on the under side of water-lily leaves.

38. *Gyraulus umbilicatellus* (Cockerell).—from the central and northern part of the state in lakes and ponds.

39. *Gyraulus circumstriatus* (Tryon).—reported by F. C. Baker from North Star Lake in Itasca County.

40. *Gyraulus altissimus* (Baker).—reported by F. C. Baker from North Star Lake in Itasca County.

41. *Gyraulus crista* (Linneus).—reported by F. C. Baker from North Star Lake in Itasca County.

Family ANCYLIDAE

42. *Ferrissia parallela* (Haldeman).—attached to water plants in rivers and lakes

in widely separated parts of Minnesota, probably easily overlooked because of its small size.

43. *Ferrissia tarda* (Say).—attached to shells or sticks in lakes in central and northern Minnesota.

44. *Ferrissia rivularis* (Say).—reported once or twice mainly from northern lakes and rivers.

45. *Ferrissia fusca* (Adams).—reported once or twice mainly from northern lakes or rivers.

Family PHYSIDAE

46. *Physa gyrina* Say.—in all parts of the state, and in all kinds of habitats, the most common species of *Physa* in the state.

47. *Physa sayii* Tappan.—in several large lakes in different parts of the state.

48. *Physa integra* Haldeman.—in many parts of Minnesota in streams and lakes, but more often in streams.

49. *Physa laphami* (Baker).—in two northern lakes, rare.

50. *Physa michiganensis* Clench.—in a stream near Minneapolis.

51. *Aplexa hypnorum* (Linneus).—in temporary pools in coniferous forests especially in the northern part of the state.

Summary

The distribution of mollusks is influenced by both geographical and ecological factors. The separation of one drainage system from another, and barriers such as water-falls within a single drainage serve to limit the geographical distribution of mussels. Snails can surmount such barriers more easily. Ecological factors, such as size, current, chemical content, kind of bottom, and presence of vegetation are important in the distribution of both snails and mussels.

The three drainage systems in Minnesota are described and the mussels in each are listed. The largest number of species was found in the Mississippi River south of St. Anthony Falls which has apparently proved a barrier to the Northward migration of many of these species since only eight were found above the falls while 27 species were found at Fort Snelling a few miles below and 20 species were found in the upper St. Croix drainage. The rivers of the St. Lawrence drainage had the smallest number of species. Most species of mussels in Minnesota apparently migrated into the state from the lower Mississippi River after the retreat of the glacier, but *Anodonta marginata*, found in many northern lakes, and *Elliptio complanatus*, found only in Lake Superior in Minnesota are species characteristic of the St. Lawrence drainage and apparently have come in through the Great Lakes. There is a similarity between the mussels of the Minnesota and Red Rivers which is explained by their long post-glacial connection.

The waters of Minnesota are divided ecologically into flowing waters and standing waters. The flowing waters are further subdivided into small creeks, small rivers, medium-sized rivers, and large rivers, and the standing waters into ponds, soft-water lakes, medium-hard lakes, prairie hard-water lakes, and river-lakes. The mollusks in each are listed.

Although some species of mussels, such as *Lampsilis siliquoidea* and *Anodonta grandis* can live in a wide variety of habitats, most species are adapted to a more or less limited environment. *Anodonta marginata* was found only in lakes, *Anodontoides ferussacianus* only in lakes and small rivers, *Lasmigona compressa* only in small rivers. *Amblema costata, Fusconaia flava,* and *Strophitus rugosus* also seemed to prefer small rivers. Several species were found only in larger rivers in Minnesota, although farther south they were found also in medium-sized and even small rivers.

Most snails found in lakes, ponds, and even in small rivers were lung breathing and belonged to the Order Pulmonata, although a few gill-breathing snails of the Order Ctenobranchiata, such as *Valvata tricarinata, Amnicola limosa,* and *Campeloma decisum* were common in large lakes. Most of the snails found only in rivers were gill-breathing, the most common one being *Pleurocera acuta tracta*. Only lung-breathing snails were found in Minnesota ponds, and usually not more than three different species in any one pond. *Aplexa hypnorum, Gyraulus parvus,* and *Lymnaea exilis* were the most common species in the more or less temporary coniferous forest pools of Itasca Park, while *Helisoma trivolvis* and *Physa gyrina* were more common in the less shaded and more permanent ponds in other parts of the state. In lakes the common species were *Amnicola limosa, Helisoma antrosa, Helisoma campanulata, Lymnaea stagnalis appressa, Physa gyrina,* and *Valvata tricarinata. Campeloma decisum* was common in soft-water and medium-hard lakes, while in the prairie hard-water lakes in the western part of the state *Lymnaea palustris* and *Lymnaea emarginata* were abundant and varied. In river-lakes the river influenced the molluscan fauna in two ways—the number of species of mussels increased and the snails *Pleurocera acuta tracta* and *Lioplax subcarinata* appeared.

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