DEPARTMENT OF COMMERCE
BUREAU OF FISHERIES
HUGH M. SMITH, Commissioner

EXPERIMENTAL STUDY OF THE GROWTH AND MIGRATION OF FRESH-WATER MUSSELS

By Frederick B. Isely
Professor of Biology, Central College, Fayette, Missouri

APPENDIX III TO THE REPORT OF THE U. S. COMMISSIONER OF FISHERIES FOR 1913

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INTRODUCTION.

The growth lines of the Unionidæ have long been considered by many observers as "annual rings," marking the yearly increase in the shell diameter. On the other hand, proof of the correctness of this assumption has been lacking, and not a few investigators have questioned its validity.

If the so-called annual rings do mark yearly additions, the rate of growth may readily be ascertained in many species by inspection; if, however, two or three of these lines appear in one season, or prominent lines appear only at irregular yearly intervals, the importance of "growth lines" as definite indicators of rate of growth loses much of its significance.

The economic importance of fresh-water mussels has added a new stimulus to the study of the growth problem. Investigations [a] under direction of the Bureau of Fisheries during the past five years concerning various phases of and questions related to the problem of artificial propagation of the species valuable for use in the manufacture of pearl buttons, knife handles, etc., has promoted inquiry concerning the time required for an economic species to reach marketable size.

Israel and Haas, among German investigators, have recently given the growth question some attention in connection with their extensive study of the fresh-water mussels of streams of Germany. In this country Lefevre, Curtis, and Coker [b] have gathered experimental data concerning growth.

In my study of the ecology of the Unionidæ during the past five years, one of the perplexing problems has been the rate of growth and

[a] Various papers by Lefevre, Curtis, Coker, and other workers, in Bureau of Fisheries publications, the Journal of Experimental Zoology, and the Biological Bulletin for 1909, 1910, 1911, and 1912.

[b] Through the kindness of Dr. Coker, I have been permitted to read in manuscript the results of his experiments and observations.

the age question. After carrying on experimental work for some time on my own initiative, I was given opportunity in 1910 to undertake the work on a larger scale under the direction of the Commissioner of Fisheries.

PLAN OF INVESTIGATION.

In the experiments to be undertaken I proposed to ascertain the rate of growth, to inquire into the meaning of growth lines, to investigate the relation of age, maximum size, etc., and, as a secondary problem, to gather data concerning migration. The plan of work was, in brief, to collect a thousand specimens of as many species and sizes as could be secured in the region where the work was carried on; in some way mark them individually, weigh, measure, and make any other necessary records; and then return them to their usual habitat and at suitable intervals reclaim, weigh, and measure again.

To carry out this work, two questions of method had to be solved: (1) The marking of specimens and (2) the reclaiming of them.

MARKING OF SPECIMENS.

In 1909 I experimented with two ways of marking: One was to scratch a symbol (pl. I, H), as a Roman numeral, on the shell, and in this way identify it for future records; the second method was to fasten a serial-numbered tag to the shell and keep records by these numbers. In the final work both methods were used, the former for light shells, the latter for heavy ones.

The method of marking a shell by scratching a number on it is simple enough, as a mark cut through the epidermis of a mussel valve will be carried indefinitely. To get a satisfactory series for a large number of specimens, however, is difficult.

The tagging with serial numbers seemed to me to be more exact. For this method I used brass tags about the size of a dime and fastened them to the specimens with a light copper wire passed through a small hole made in the posterior edge of the valve. The hole in the valve was made with a very fine button-eye drill about 2 millimeters from the posterior edge of the shell (pl. I, II, and III). To hold the button-eye drill, a geared hand drill was used, and only a few seconds were needed to drill a hole even in a thick shell. By making a little hook on the wire it could be passed through the hole and out between the valves, usually without much difficulty. In large specimens it was found that the work of tagging could be more readily accomplished by wedging the valves open slightly before inserting the wire. A slight injury to the animal often resulted from the fact that the mantle was not sufficiently drawn back to avoid the drill point. While the irritation at the moment was doubtless severe, the ultimate effect upon the animal's future growth and activity was insignificant (p. 19).

FIELD RECORDS.

A tabular record was kept of all specimens tagged. The weights were taken in grams, a Harvard trip balance being used; the measurements, length, height, and breadth in millimeters with a steel caliper. The field record form, kept in duplicate, was ruled in columns with headings for number, weight, length, height, breadth, species, and remarks.

PLANTING SITES.

In most cases, after tagging and taking records, the mussels were placed directly back in their original habitats, but in some instances transplanting from river to creek or from pond to river was practiced.

Four different sites were selected for planting: One on Shoofly Creek, on the Corn farm in the north end of Kay County, Okla.; two on the Chikaskia River, on the Brewer and Esch farms near Tonkawa, Okla.; and a pond site on the Browne farm near Autwine. As the pond dried up, due to the unusual drought of 1910, this series does not figure in the results.

The Chikaskia River is a small, clear-water, sandy stream. The sand is coarse, and frequently there are stretches of gravel and occasionally mud banks and small, mud-bottomed side channels. In certain portions of the Chikaskia, Unionidæ are abundant.

Shoofly Creek is a tributary of the Chikaskia. In very dry weather the water stops flowing over the shallow, gravelly stretches; but the ponded sections, often a mile in length and with water 2 to 6 feet deep, have a constant water supply. In certain of these ponded portions mussels are fairly abundant.

PLANTING OF TAGGED SPECIMENS.

In all, about 900 specimens were tagged, weighed, measured, and listed for future observation. For convenience in further discussion these specimens may be grouped into seven lots.

SHOOFLY CREEK.

Shoofly, lot A, 140 specimens, and lot B, 80 specimens.—Nearly all of these were *Quadrula undulata* (three-ridge) and were taken from the direct site where they were planted after tagging. All of the *Q. undulata* (three-ridge) secured in the Shoofly were large; out of some 500 specimens handled in two days, only 4 weighed under 200 grams.

Shoofly, lot C.—Twenty-two specimens of *Anodonta grandis* (floater) were planted in a mud bank similar to the environment selected by this species in this creek.

Shoofly, lot D.—As already indicated, the Shoofly species were mostly *undulata,* with a few *grandis,* and all were large. In order to get a larger number of species and smaller specimens, I collected 168 mussels in the Chikaskia and planted them in the Shoofly. In this lot, *Q. undulata* (three-ridge), *Q. lachrymosa* (maple-leaf), *Q. pustulosa* (warty-back, pimple-back), and *Q. rubiginosa* were represented by fairly good numbers, and nearly all of the specimens were under 200 grams in weight. It should be stated here that a few specimens of all of the Quadrulæ were found native of the Shoofly, and in addition to these, *Lampsilis gracilis* (paper-shell), *Lampsilis anodontoides* (yellow sand-shell), *Symphynota complanata* (heel-splitter), and *Anodonta imbecilis* were found. Not counting *grandis* (floater), the ratio would be 25 *undulata* (three-ridge) to one of another species. This, however, is not unusual in dominance of species in certain streams.

In planting specimens, the bottom was cleared of the original occupants and the tagged specimens were put in their places. For example, for lot D, an area of bottom about 12 feet in diameter was cleared and the Chikaskia specimens spread out on the cleared bottom. The Shoofly bottom, where the sites were located, is made up of a mixture of broken blue shale, coarse sand, and mud. The water is still and cloudy and from 2 to 5 feet deep. The specimens were planted in water about 3½ feet deep. Results that follow indicate that the above is a favorable type of habitat for the species used.

As already indicated, the specimens were free in the stream; no obstruction of any kind was placed in their way, nor any effort made to confine them. The planting operation consisted in turning them out of a sack and spreading them around on the stream floor. In 24 hours after planting it was noticed that most of the specimens had righted themselves and were stuck in the bottom, foot end down, but seldom was a *Quadrula* found with the foot extended.

The Shoofly specimens, lots A, B, C, and D, were tagged, weighed, etc., June 13 to 16, 1910; reclaimed and first checked over in part June 14 and 15, 1911; and a second time some were reclaimed and checked over September 19, 1911.

CHIKASKIA RIVER.

In the Chikaskia two lots were planted. These were inclosed with a wire netting, as I was a little doubtful in regard to reclaiming free Unionidæ in the Chikaskia.

Chikaskia, lot E.—On the Brewer farm were planted 120 specimens of various sizes of Quadrulæ, and a few representatives of the other species mentioned for the Shoofly, with the addition of a few specimens of *Lampsilis purpuratus* and *Tritogonia tuberculata* (buckhorn, pistol-grip). The inclosure consisted of a triangular pen made of 3-foot, 1-inch mesh wire netting, run out from the bank and back again, 40 feet of netting being used in its construction. The bottom was a mud bank along the side and medium coarse sand farther out. The water was from 2 inches to 3 feet in depth, a portion of the main channel running across the lower end. The specimens were collected in part from the immediate vicinity of the inclosure, but, as they were by no means numerous in this portion of the river, about 90 of the 120 mussels were secured a mile farther down the stream. Lot E specimens were planted, weighed, etc., June 23 and 24, 1910, and checked over in part September 26, 1910, and June 22, 1911.

Chikaskia, lot F.—The second planting in the Chikaskia was on the Esch farm, and consisted of 330 specimens, collected mostly from the immediate vicinity, as the mussels in this portion of the river were abundant. The range of size was good, although really small specimens were rare in 1910. The species were about the same as noted under lot D, mostly Quadrulæ, as these are the only common species in this stream. Fifty specimens of *Unio tetralasmus*, a pond form never found in the Chikaskia, were placed in the Esch inclosure. This pen was made by fencing across a side channel formed by a long bar. The channel was 40 yards long and from 4 to 6 yards wide. The bottom was mostly coarse sand. At the time of its construction there was a regular flow of water through the channel, the depth of water varying from a few inches to 3 feet. Lot F mussels were planted June 23 to 28, 1910; examined and rechecked in part September 26, 1910, April 11, 1911, and June 20 and 21, 1911.

GROWTH RESULTS.

In discussing experiments and results, we will first consider growth, and second, migration (p. 19).

The results have shown that much could have been learned from a smaller number of specimens. It was not known, however, that we should be able to reclaim so large a per cent of the specimens first planted. Then, too, it was necessary to guard against loss by accidents, such as changes in course of streams, drifting sand, drying up of water, and other possible environmental changes. The Shoofly specimens were absolutely unmolested; only three dead specimens were found in the whole lot, and these had all started to grow, showing that the tagging certainly had no bad effects. The Chikaskia specimens suffered somewhat from all of the hostile environmental factors mentioned above; and, further, some were lost to the small boy interested in collecting brass tags.

On the whole, however, the specimens were reclaimed in such large numbers that all of the material could not be worked over for records in the time available when the rechecking and reclaiming was done.

In rechecking material as many specimens were handled as time would permit. As small specimens were few in number, these were always rechecked and care was taken to include representatives of all species. Aside from these influences in selection, specimens were rechecked as found. The left-over material was returned to the stream when it could not be handled. Where a lot was checked over several times, as lot F, naturally the ones worked over the first time they were reclaimed, September 26, 1910, were again followed up in subsequent work.

Far more data were gathered than can be included in this paper. In the tables given below I have stated the reasons for selecting the data presented. Nearly all the material used is selected from lots D and F, as the latter was more available for frequent recheckings, and lot D of the Shoofly material represented a larger number of species and more range as to size.

Table 1.—A Year's Growth in Young Quadrulæ from Lot D.

[Note.—All starred numbers in tables represent specimens shown in plate figures.]

Specimen No.[a]	Species.	Weight.		Length.		Height.		Breadth.	
		June, 1910.	June, 1911.	June, 1910.	June, 1911.	June, 1910.	June, 1911.	June, 1910.	June, 1911.
		Grams.	*Grams.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
323*	Q. undulata (three-ridge)	20	43	45	62	31	42	17	23
319	do	49.5	77	64	75	42	50	24	27
341	do	66	102	70	80.5	46	51	27	31
158*	Q. lachrymosa (maple-leaf)	22.5	47	45	56	35	45	19	25
149*	do	26	53	45	59	36	46	20	25.5
159	do	80	112	67	76	55	60	29	33.5
368	Q. rubiginosa	52	65	64	68.5	48	50	26	27
351	do	60	76	64	69	50	52	26	28
353	do	104	115	76	79	60	65	32	33.5
349*	Q. pustulosa (warty-back or pimple-back)	10	20	30	37	25	30	15	20
375	do	54	63	56	58	45	46	28	29
383	do	67	77	64	65	52	53	29	30

AVERAGE GAIN AND PER CENT OF AGGREGATE GAIN FOR EACH SPECIES.

Species.	Weight.		Length.		Height.		Breadth.	
	Grams.	*Per ct.*	*Mm.*	*Per ct.*	*Mm.*	*Per ct.*	*Mm.*	*Per ct.*
Q. undulata	28.8	63	12.8	21	8	20	4.3	19
Q. lachrymosa	27.8	64	11	21	8.3	19	5.3	23
Q. rubiginosa	13.3	18	4.1	6.1	3	5.6	1.5	5.3
Q. pustulosa	9.6	22	3.3	6	2.3	5.7	2	9.7

[a] Specimens listed in all tables according to size for each species.

The foregoing tables relate to Unionidæ from lot D (p. 8) that were planted June 15 and 16, 1910, and reclaimed June 15 and 16, 1911. In the figures given, the first series under each number is the initial record, the second series the record a year later. These specimens show manner and extent of growth in one year's time for four species. They were killed at the time of reclaiming, and are preserved for future study should anyone wish to examine them. It can be seen at a glance that *undulata* (three-ridge) and *lachrymosa* (maple-leaf) are rapid growers in comparison with *pustulosa* (warty-back, pimple-back) and *rubiginosa*. Further averages and percentages are worked out for each species listed in table 1 and later tables on page 8.

TABLE 2.—TWO PERIODS OF GROWTH, OF ONE YEAR AND OF THREE MONTHS, RESPECTIVELY, IN SPECIMENS TAKEN FROM LOT D.

[NOTE.—Starred numbers represent specimens shown in plate figures.]

Specimen No.	Species.	Weight.			Length.			Height.			Breadth.		
		June, 1910.	June, 1911.	Sept., 1911.	June, 1910.	June, 1911.	Sept., 1911.	June, 1910.	June, 1911.	Sept., 1911.	June, 1910.	June, 1911.	Sept., 1911.
		Gms.	*Gms.*	*Gms.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
135	Q. lachrymosa (maple-leaf)	92.5	124	142	70	76	81	57	63	66.5	32	36	37.5
165	.....do	152	182	194	93	96	97	57	61	63	37	39	40
146	.....do	164	216	237	82	89	94	68	70	72	41	43.5	45
168	.....do	166	185	197	93	96	98	57	61	63	37	39	40
283	Q. undulata (three-ridge)	95	132	150	72	83	88	46	51	56	34	38	39
317	.....do	120	147	162	83	88	92	51	56	61	34	37	38
329	.....do	125	149	159	85	88	90	55	60	62	34	37	38
306	.....do	140	164	176	90	96	100	56	60	62	35	37	38
171	.....do	145	175	190	88	94	97	52	55	58	37	39	39.5
166	.....do	166	192	214	92	97	102	56	......	......	38	40	41
307	.....do	183	217	230	98	102	105	64	69	72	35	37	38
322	.....do	185.5	207	220	93	97	99	60	62	64	41	42	42.5
163	.....do	200	226	236	98	102	104.5	58	......	......	42	43	44
374	Q. pustulosa (warty-back, pimple-back)	35	45	50	51	55	57	43	45	47	24	25	27
363	.....do	60	73	80	55	57	59.5	49	51	52	29	31	32
384	.....do	87	102	112	63	65	66	55	57	57	34	36	36.5
377	.....do	90	107	114	79	82	85	57	59	60	31	32	33
358	.....do	135	145	152	88	89	90	65	66	67	33	35	35.5
355*	Q. rubiginosa[a]	68	75	84	64	67	70	49	50	52	29	30	31
371	.....do	87	97	104	76	78	80	53	55	55	31	32	33

[a] It should be noted that five of the specimens for the two last species were more nearly mature for these species than the specimens of *undulata* (three-ridge) and *lachrymosa* (maple-leaf).

The specimens shown in the preceding table were planted June 15 and 16, 1910, and were reclaimed June 15 and 16, 1911, put back in the stream, and reclaimed September 9, 1911. All of the specimens of lot D that were reclaimed twice, measured, and weighed, are shown in table 2.

In the figures given above, the first is the initial record, the second the record one year later, and the third a three months' summer record (June 15 and 16 to Sept. 9, 1911).

Table 2 simply adds to the data of table 1 in regard to annual growth, growth of species, etc. It adds the fact of seasonal growth, and gives data for comparison of yearly growth and summer months. The average yearly growth for 20 specimens shown in table 2, as well as the growth for three summer months (85 days) is shown below:

	Weight.		Length.		Height.	Breadth.
	Grams.	*Per cent.*[a]	*Mm.*	*Per cent.*[a]	*Mm.*	*Mm.*
Average gain for one year, 1910–11	23.2	18	4.2	5.2	3	2
Average gain for three months, 1911[b]	12.1	8.2	2.9	3.4	2.4	1

[a] Per cent of aggregate gain.
[b] It should be noted in this comparison that the 1910 and 1911 summer months were different in weather conditions. During 1910 there were no rains heavy enough to raise the creek and wash out the food supply of micro-organisms, while in 1911 there were two periods of high water, one in July and one in August.

Per cent of gain gives a truer basis for this kind of comparison than the average net gain. The lack of conformity in the height averages, when compared with other measurements, is doubtless due to error on account of the great difficulty in getting this dimension in rapid field measurements because of the circular ventral margins of these species.

TABLE 3.—SEASONAL GROWTH.

Specimen No.	Species.	Weight.				Length.			
		June, 1910.	Sept., 1910.	Apr., 1911.	June, 1911.	June, 1910.	Sept., 1910.	Apr., 1911.	June, 1911.
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
594	Q. undulata (three-ridge)	210	222	222	225	102	104	104	104
734	.....do	255	269	271	270	116	122	122	122+
678	.....do	261	273	272	277	110	112	112	112
573	.....do	290	305	305	305	118	125	125	125
644	Q. lachrymosa (maple-leaf)	104	116	114	116	76	76	76.5	77
753	.....do	105	115	117	123	66	67	68	70
665	.....do	154	167	167	172	84	86	86	86+
660	.....do	160	173	171	180	86	88	88	89
687	.....do	163.5	174	176	182	84	86	86	86.5
694	.....do	164	180	179	180	86	89	89	90
622	.....do	187	195	200	200	90	91.5	91.5	91.5
617	Q. pustulosa (warty-back, pimple-back)	91	98	98	99	64	64.5	64.5	64.5
689	Q. rubiginosa	141	146	146.5	147	84	86	86	86
721	.....do	148	154	156	156	84	86	86	86

While table 2 has given some good data concerning seasonal growth, table 3 gives more detail and permits a more exact location of the growth periods. Table 3 specimens are from lot F, Chikaskia River. These specimens were checked up, approximately, at the third, ninth, and twelfth months that they were under observation, and the results are shown by successive records. The initial records were taken June 23–28, 1910; second, September 26, 1910; third, April 11, 1911; and fourth, June 20, 1911. Only the weight[a] and length records appear in this table. The average gain for the different periods we find to be as follows:

[a] Some observers report weight measurements subject to a great deal of variation. In this investigation I have always kept the specimens out of water for short intervals and always under cover. Under these conditions I have found weight measures very satisfactory and stable under repeated reweighings.

Time.	Weight.	Length.
	Grams.	*Mm.*
June 28 to Sept. 26, 1910	10.9	2.4
Sept. 26 to Apr. 11, 1911	.5	.1
Apr. 11 to June 20, 1911	2.5	.3

For comparison with these averages we have the results from lot E, which I have not tabulated, for 14 specimens: 7 *lachrymosa* (maple-leaf); 4 *undulata* (three-ridge); and 3 *pustulosa* (warty-back, pimple-back). In this case the April reclaiming was not done.

Time.	Weight.	Length.
	Grams.	*Mm.*
June 23 to Sept. 26, 1910	9.1	1.0
Sept. 26 to June 23, 1911	5.4	.55

The second period shows a gain in the growth for lot E over lot F. The explanation is one of food and possibly oxygen, and appears later (p. 24) under the discussion of migration.

The following four tables show proportional rate of growth, at different ages, of a single species, *Q. undulata* (three-ridge). The fact that lot D mussels were transplanted (p. 5) brings in an additional factor (footnote, p. 23), but I am not sure that this is material. In making these comparisons weight and length are used.

TABLE 4.—INCREASE IN ONE YEAR OF SPECIMENS FROM LOT D, WEIGHING LESS THAN 100 GRAMS.

Specimen No.	Weight.		Length.		Specimen No.	Weight.		Length.	
	June, 1910.	June, 1911.	June, 1910.	June, 1911.		June, 1910.	June, 1911.	June, 1910.	June, 1911.
	Grams.	*Grams.*	*Mm.*	*Mm.*		*Grams.*	*Grams.*	*Mm.*	*Mm.*
323	20	43	45	62	313	70	101	74	83
319	49.5	77	64	75	287	85.4	107	79	85
299	50	70	67	76	283	95	132	72	83
341	66	102	70	80.5	282	100	124	82	....

TABLE 5.—INCREASE IN ONE YEAR OF SPECIMENS FROM LOT D, WEIGHING UNDER 200 GRAMS.

Specimen No.	Weight.		Length.		Specimen No.	Weight.		Length.	
	June, 1910.	June, 1911.	June, 1910.	June, 1911.		June, 1910.	June, 1911.	June, 1910.	June, 1911.
	Grams.	*Grams.*	*Mm.*	*Mm.*		*Grams.*	*Grams.*	*Mm.*	*Mm.*
336	120	135	79	(a)	304	145	163	89	92
317	120	147	83	88	292	149	172	94	....
329	125	149	83	86	331	163	182	91	....
290	131	160	87	94	310	187	222	95	....
333	134.5	160	89	(a)	339	195	225	99	102

a No record.

TABLE 6.—INCREASE IN ONE YEAR OF SPECIMENS FROM LOT B, WEIGHING OVER 200 GRAMS, SELECTED AT RANDOM FROM 20 SPECIMENS ONE YEAR FROM DATE OF PLANTING.

Specimen No.	Weight.		Length.		Specimen No.	Weight.		Length.	
	June, 1910.	June, 1911.	June, 1910.	June, 1911.		June, 1910.	June, 1911.	June, 1910.	June, 1911.
	Grams.	*Grams.*	*Mm.*	*Mm.*		*Grams.*	*Grams.*	*Mm.*	*Mm.*
216	193	215	110	111	244	282	300	114	115
239	226.5	246	101	101	201	291	302	119	120
211	240	263	115	116.5	242	308	322	114	114
251	250	265	110	111	205	323.5	335	115	116
219	258.5	270	110	111	249	378	394	119	120

TABLE 7.—INCREASE IN ONE YEAR OF SPECIMENS FROM LOT A, WEIGHING OVER 200 GRAMS, SELECTED AT RANDOM FROM 68 SPECIMENS RECLAIMED ONE YEAR FROM DATE OF PLANTING.

Specimen No.	Weight.		Length.		Specimen No.	Weight.		Length.	
	June, 1910.	June, 1911.	June, 1910.	June, 1911.		June, 1910.	June, 1911.	June, 1910.	June, 1911.
	Grams.	*Grams.*	*Mm.*	*Mm.*		*Grams.*	*Grams.*	*Mm.*	*Mm.*
70	199.5	216	96	97	9	266.5	277	125	125.5
80	223.5	235	107	108	5	270	285	114	115
10	240	260	106	107	15	273.5	304	120	120.5
12	252	270	125	125.5	2	316	342	120	120+
1	256.5	274	106	107	23	328	340	125	125.5

AVERAGES FOR ONE YEAR.

	Average increase in weight.	Average length.	Average increase in length.	Increase in length.
	Grams.	*Mm.*	*Mm.*	*Per cent.*[a]
Table 4	27.5	66.1	11.6	17.5
Table 5	24.55	88.9	3.5	3.9
Table 6	16.15	112.7	.8	.7
Table 7	17.75	114.4	.7	.6

[a] Per cent of aggregate increase.

The specimens under 100 grams make the largest increase in weight and length; those under 200 grams, the second; and those over 200, or fully mature specimens, fall short. A point of special interest in connection with tables 6 and 7 lies in the fact that while per cent of gain in length is almost negligible, weight goes steadily forward in fairly good proportion. From averages in tables 4 and 5, an average yearly growth for a young *undulata* (three-ridge) might be put at 25 grams in weight and from 5 to 25 millimeters in length; at this rate it would take about eight years to reach the weight of 200 grams and a length of 90 to 100 millimeters; as later growth is slower, about 12 to 15 years would be a fair estimate for the age of a Shoofly Creek *undulata* (three-ridge) of 300 grams in weight and 110 to 120 millimeters in length.

TABLE 8.—RATE OF GROWTH BY SPECIES.

[NOTE.—This table shows species not mentioned in other tabulations, because the number of individuals was too small for comparative study. The records are useful as indicative of what may be expected from these species. The Quadrulæ here listed are given because of their use in plate figures.]

Specimen No.	Species.	Time.	Weight.	Length.	Height.	Breadth.
			Grams.	*Mm.*	*Mm.*	*Mm.*
109	A. grandis (floater)	When planted	143	120	63	41
		1 year later	193	127	66	45
113	do	When planted	144	120	62	41
		1 year later	192	124	65	45
111	do	When planted	211	132	72	48
		1 year later	269	139	74	52
114	do	When planted	281.5	140	82	53
		1 year later	320	142	82	54
281*	Q. undulata (three-ridge)	When planted	16.5	40	27	16
		1 year and 3 months later.	51	65	41	25
564*	Q. lachrymosa (maple-leaf)	When planted	5	22	17	10
		1 year and 3 months later.	20.5	41	32	20
413*	do	When planted	8	27	22	13
		1 year later	18	42	35	19
430	T. tuberculata (buckhorn, pistol-grip)	When planted	128	87	56	31
		1 year and 3 months later.	138	90	58	32
431	do	When planted	470	136	76	50
		1 year later	489	136.5	76.5	50
XI	L. gracilis (paper-shell)	When planted	11	51	26	14
		3 months later	29	69	35	20.5
X	do	When planted	13	55	27	18
		3 months later	55	82	44	28
H*	do	When planted	22.5	63	32	19
		1 year and 3 months later.	84	97	50	33
566*	L. anodontoides (yellow sand-shell)	When planted	97	93	46	34
		3 months later	116	97.5	49	35.5
650	do	When planted	125	103	48	37
		1 year later	138	106	49	37.5
495	do	When planted	180	110	51	43
		1 year later	186	111	51.5	43
V	U. tetralasmus	When planted	25	65	33	20
		1 year later	30	71	36	22
LI	do	When planted	31	70	35	22
		1 year later	43	72	37	23

DISCUSSION OF DATA.

The results set forth in the tables given above speak for themselves and need no extensive explanation.

One striking fact is the cessation of growth during the winter months of the Chikaskia specimens, especially in table 3. There are a number of cases in my field records where a loss is shown in weight for the six months from late September to early April, although in general they hold their own. It has been my observation for several years that the Chikaskia mussels, in the shallow water at least, burrow down into the sand in late October and become abundant again in late April.

For *undulata* (three-ridge), I have given rather complete averages of weight, and comparisons of rate of growth according to size in tables 5–8. From tables 1 and 2 (all lot D), I find the averages given below for the four species named: *Undulata* (three-ridge), 12 specimens; *lachrymosa* (maple-leaf), 7 specimens; *pustulosa* (warty-back, pimple-back), 8 specimens; *rubiginosa*, 5 specimens. From table 8, *grandis* (floater), 4 specimens; *tetralasmus*, 2 specimens; *gracilis* (paper-shell), 2 specimens; *anodontoides* (yellow sand-shell), 1 specimen.

AVERAGE INCREASES IN WEIGHT AND LENGTH, BY SPECIES.

AVERAGES FOR ONE YEAR.

Species.	Average weight.	Average increase in weight.	Average length.	Average increase in length.
	Grams.	*Grams.*	*Mm.*	*Mm.*
Lachrymosa (maple-leaf)	100	30.8	70	7.5
Undulata (three-ridge)	124	28	82	7.2
Rubiginosa	74	11.4	68.8	3.4
Pustulosa (warty-back or pimple-back)	67	11.5	60	2.7
Grandis [a] (floater)	194	48.6	128	5
Tetralasmus [b]	28	8.5	67	4
AVERAGES FOR THREE SUMMER MONTHS.				
Gracilis (paper-shell)	12	30	53	22.5
Anodontoides (yellow sand-shell)	97	19	93	4.5

[a] Large mature specimens, still the increase is good.
[b] In an unusual environment for this species (p. 9).

Juvenile Quadrulæ [a] of the above species double in size in a year, as shown by a number of examples (149, 158, 349, 323, in table 1; 281, 564, 413, in table 8). Averages here given and those taken from other sources indicate that a 100-gram, 75-millimeter *undulata* (three-ridge) (p. 14) or *lachrymosa* (maple-leaf) can develop in the Shoofly in about four years (averages for tables 1, 2, 4, and 5). A 300-gram specimen of *undulata* (three-ridge) or *lachrymosa* (maple-leaf) would doubtless be close to 15 years old. The largest *undulata* (three-ridge) rechecked weighed 407 grams in June, 1910, and 421 in June, 1911. This specimen was 123 millimeters long, and increased 1 millimeter in length. In *undulata* (three-ridge) and *lachrymosa* (maple-leaf), after the 100-millimeter length is reached, the increase in length is slow, and growth lines follow one another so closely that the differentiation of lines is difficult. *Pustulosa* (warty-back, pimple-back) and *rubiginosa* grow more slowly than the two preceding species. A 50-millimeter *pustulosa* (warty-back, pimple-back) has passed the age of rapid growth, and from this size on additions come slowly.

A light-shelled form, as *L. gracilis* (paper-shell) grows very rapidly; this would seem to indicate that the shell is built up at greater expense of food and energy than the soft parts of the mussel. In table 8, specimen X, during the three summer months, shows an increase of over four times in weight and 27 millimeters in length; 566, *L. anodontoides* (yellow sand-shell), in the same time, makes an increase of one-fifth its original weight, and 4.5 millimeters increase in length.

[a] Early juvenile forms grow even more rapidly as experimentally found (foot-note, p. 5) by Coker.

ARRESTED GROWTH RINGS.

"Growth lines," the conspicuous dark concentric rings of the shell, may be due to (1) thick epidermis, (2) double epidermis, and especially (3) to double epidermal and prismatic layers. It is well known that the epidermal and prismatic layers are formed by the

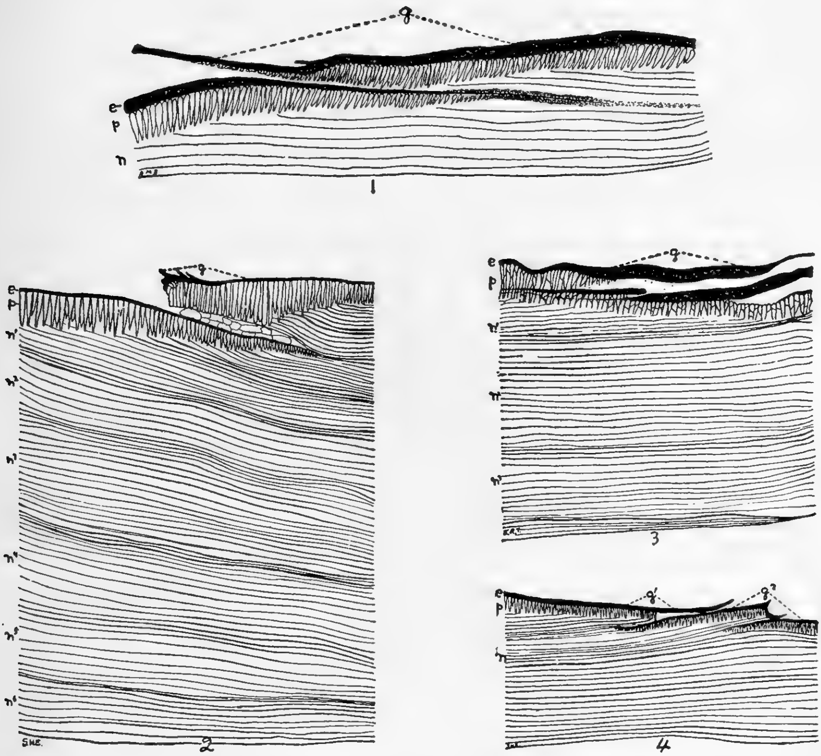

FIG. 1–4.—Cross-sections of shells of *Quadrula* showing structure in region of rest rings, all figures enlarged 20 times; *e*, epidermis; *p*, prismatic layer; *n*, nacreous layers; n^1, successive layers of nacreous structure; *g*, position and width of rest rings (growth lines).

FIG. 1.—Section from near edge of shell, showing double layers and long underlying tongue of epidermal and prismatic structure, which formed the dark wide rest ring of a young rapid-growing *Quadrula lachrymosa*. Rings x^1 or x^2, specimens 149 or 158, plate II, would give similar sections.

FIG. 2.—Section of shell of mature mussel, taken about the middle of the valve. Rest ring not so wide as in 1, tongue shorter, prismatic layer thicker, and thick successive layers of nacreous structure.

FIG. 3.—A rest ring due chiefly to unusually thick, double layers of epidermis.

FIG. 4.—Two successive rest rings near together, undoubtedly formed in the same season, and probably only a few weeks apart, as specimen was young and at the rapid-growing age. (See description of specimen 413, pl. II.)

edge of the mantle only. Thus increase in shell diameter begins with the formation of the epidermal, followed by the prismatic layer. However, if the mantle is withdrawn from the edge of the shell, it often puts down new layers of epidermal and prismatic material underneath older layers [a] of the same structure, and sometimes underneath older layers of nacre as well. This is well shown in figures 1–4, showing sections of shells made through the growth lines.

In watching the growth of tagged specimens it was noted that a distinct growth line was formed at the time of tagging; the work of tagging, i. e., the drilling of the hole through the shell and the placing of the wire, caused considerable irritation, probably a strong contraction and partial breaking loose of the mantle from the edge of the shell, and, as a result, new epidermal and prismatic layers were put down underneath those already formed, as the mantle worked to its old position, and formed new layers over the wire holding the tag (pl. III, 763). Young specimens, especially, show a conspicuous and well-defined ring passing through the outer side of the wire holding the tag.

The so-called annual rings had better be called "arrested growth or rest rings," as they represent retarded growth, which may be very temporary, as in the case of the tagged specimens, and still leave a very marked ring. Ordinarily the prominent rest rings are presumably winter rings,[b] representing delayed growth, due to inactivity, a withdrawal of the mantle from the extreme edge of the valves, and the forming of double epidermal and prismatic layers as a result of renewed active growth in the following spring. Other rings may follow arrested growth, due to various unfavorable conditions that may arise in the life of the mussel, such as water shrinkage, temporary stranding due to migration, especially at flood periods; in the lighter species perhaps washing at flood times. It is possible that in certain pond forms, as *U. tetralasmus* and others that live in ponds that go dry for short periods during the summer season, the more prominent rings are summer rings.[c]

That the concentric rings are by no means dependable as absolute annual rings is well shown in many specimens under observation in this investigation.

A few specimens shown photographically (pl. I, II, III) will clear up some points in regard to growth. Rest rings are not always brought out clearly by photographic methods on account of the unequal or convex surface of the shell. A slight ridge that may have no connection with a rest ring will show as a shadow line beyond the ridge. This is shown in photograph H, plate I, in the line marked "o." Additional explanations are given with the plate figures.

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[a] This explanation was first suggested to me by Dr. Coker, and later verified in connection with my study of shell sections through arrested growth lines.

[b] While in this paper we have emphasized the point that "annual rings" are not annual rings absolutely, the statement that the prominent rest rings are usually, under stable environmental conditions, winter rings is clearly within the evidence of this investigation.

[c] Live specimens of this species were plowed up in the Browne pond (p. 7) three months after the pond had gone dry.

MIGRATION.

No end of speculation has been carried on as to the traveling ability of mussels. The long undulation tracks, often found upon the pond or stream floor, together with other field observations, and the active movements of specimens kept in aquaria have afforded data for discussion. While gathering information concerning growth, I have constantly kept in mind the migration question, as it was easy to carry on the two together.

As already indicated, the main reason for tagging a large number of mussels was the feeling that many would be lost through migration; and further to guard against this migration in the Chikaskia I inclosed the specimens in good-sized pens.

SHOOFLY.

The extent of actual migration is best shown in considering definite plantings. Lot D (see p. 8) of the Shoofly is good for this purpose. The 168 Quadrulæ planted here were from the Chikaskia, where they were collected from the sand bars in shallow water. From track-mark evidence these specimens had been actively moving about on the sandy bottom, stimulated to activity by unfavorable environmental conditions.

The 164 specimens were spread out on a small portion of the bottom of the Shoofly (p. 8), June 16, 1910, and left free to move. June 14 and 15, 1911, I reclaimed 139 of these specimens, or 84.8 per cent, in about three hours' work. Twelve of these specimens were reserved for records. On September 11, 1911, a cold rainy day, I again checked over lot D, and this time I secured 93 specimens in about one hour's time; the water was so cold that collecting was exceedingly difficult. Three specimens not found in June were found on this date, bringing the total number reclaimed from the original planting up to 142. When we consider that the water was cloudy and from 3 to 4 feet deep the experienced field collector will know that specimens could not be recovered in these numbers unless they were on the very spot [a] where they were planted. Lots A and B in the Shoofly gave similar results, although I did not attempt to recover these as thoroughly as in the case of lot D.

Lot C in the Shoofly is of especial interest, as these specimens were all *A. grandis* (floater). Of this lot 12 specimens were found directly on the site where they were planted. While this is rather a small per cent in comparison with lot D, I was surprised to find 46 per cent of *A. grandis* (floater), as it is well known to be an active

[a] It has been suggested that since lot D specimens were transplanted the inactivity may have been due to the changed environment. The relatively rapid growth and like inactivity of lots A and B, Shoofly specimens, which might very well be considered as control lots, should quiet any apprehensions on this point.

form. In all my reclaiming work in the Shoofly, which amounted to about 10 hours' actual hunting and collecting on three different days, I secured only one specimen that may be said to be off the planting plot; this was no. 141, found 15 feet from plot D.

CHIKASKIA.

In the Chikaskia lot E gave results similar to D. The Chikaskia River specimens were disturbed somewhat by curious people, and for this reason proportional figures can not be emphasized. The inclosure for lot E (p. 9) was rather small, but there was ample chance for movement. The results in this instance substantiate what I have often noticed in field work, namely, that the mussels, especially Quadrulæ and related species, are unable to help themselves if conditions become unfavorable, but, on the other hand, the power to endure these unfavorable conditions is remarkable.

Since the Chikaskia is a fairly swift stream, the lower end of the inclosure was undermined, making escape easy, while a sand bar was formed across the upper portion. Two-thirds of the mussels were caught in the drift bar and when I examined them on September 26, 1910, were helplessly stranded. Conditions of oxygen and food supply must have been unfavorable, and as a direct result the summer's growth was below the average for lot F.

These stranded specimens were now taken and put in the outer corner of the pen, where they could escape under the wire net through an opening 5 feet long. Six months later, June 22, 1911, I again examined lot E. A large number of the specimens were recovered, about half being along the wire net inside, and half along the net outside; not a specimen was found over 5 yards from the pen. Clear water and sandy bottom made the finding of specimens easy.

Lot F specimens of the Esch inclosure (p. 9) had a good opportunity for migration; in fact, the inclosure was not needed, as only two specimens reached either lower or upper cross fences. One of these was a *gracilis* (paper-shell), and the other a *grandis* (floater). The Quadrulæ did not come within 25 yards of the lower fence. If they were placed in water over 3 feet deep, the migration was slight in any case, as far as the Quadrulæ were concerned. Those placed in water as shallow as 1 foot moved to deeper water, which was easily reached in this case. The *Lampsiles* were more active, and the percentage recovered was small by comparison. Of the 50 *U. tetralasmus*, not a single specimen or shell was found at the first examination, September, 1910; but in the June, 1911, examination, three specimens were found. I am not able to explain the disappearance of the *tetralasmus*; however, they are great burrowers, and may have escaped my extensive digging for them.

DISCUSSION OF MIGRATION DATA.

The migration results came as a surprise to me. The very fact that I was willing to risk specimens free in the Shoofly would indicate that I hoped to make some kind of recovery; but to go back and find specimens by the score—apparently in the exact spot where they were planted—was not to be expected. The Quadrulæ in these plantings show little migration; the Shoofly specimens may be said to be nearly stationary in water over 3 feet deep. Those placed in shallow water in the Chikaskia always moved until water 2 to 3 feet deep was found. Specimens found on shoals and bars in nature are there by chance distribution, not choice, although breeding reactions may cause migration in some species.

ECONOMIC BEARING OF EXPERIMENTS—RELATED PROBLEMS.

While the scientific interest in the growth and migration problems was the real motive that prompted this investigation, it was the relation of the problem to the practical question of artificial propagation of mussels for commercial purposes that made funds available to carry on the work. That the results will be of service as preliminary to further investigation is a matter of satisfaction. The man interested in commercial propagation will continue to ask the question, How long will it take to grow a mussel to marketable size? Much more work will be needed to get at all the facts in the case of the various economic species; and where the work of propagation is to be conducted on a large scale, preliminary experiments will be of value in testing the fitness of a particular region for commercial operations. Some of the methods of procedure have been indicated by the series of experiments here outlined.

I wish to call the attention of the field students of the Unionidæ to the transplanting of adult mussels from the Chikaskia to the Shoofly, where young specimens were not to be found, yet these transplanted mussels averaged higher in rate of growth than the regular Chikaskia specimens. If the Shoofly is so favorable a habitat for mussels, why are young specimens absent from the beds?

Again, notice the transplanting of over a hundred specimens from the vicinity of lot F, where mussels are so abundant, to lot E: The transplanted specimens did as well in growth as the specimens that were near the region of abundant mussels in the Chikaskia. This difference in abundance was by no means slight. It is a fact that in the vicinity of lot F one could, in a few hours, collect a wagonload of mussels, while for a quarter of a mile above and below the Brewer inclosure two of us were able to get only 30 specimens in several hours' careful collecting.

The distribution of mussels within individual streams, and in the Chikaskia in particular, is not easy to explain. Little or negligible migration among the Quadrulæ, at least, has not cleared the situation.

SUMMARY.

1. Rate of growth is exceedingly variable for individuals of a single species in the same stream and in different streams, depending, as in other invertebrates, upon season, food, oxygen supply, and other conditions. Juvenile mussels grow much more rapidly than adult or near-adult individuals. *Lampsilis* species grow very much faster than Quadrulæ. Specimens in stable conditions seem to have a fairly definite rate of growth from year to year. The rate, after sexual maturity, is slowed down, but growth goes on steadily, though the proportional increase in length is so slow as to make appreciable additions very slight, so that growth lines in Quadrulæ, after a size of 100 millimeters (4 inches) has been reached, can not be ascertained by inspection.

2. From April to September may be designated as growth months, most specimens showing very slight increase during winter.

3. Lines of arrested growth may be called rest rings, the conspicuous ones being usually winter rest rings; very often, however, the rings may be two or more years apart, or several equally prominent rings may be formed in one year. Prominent lines are generally due to double prismatic and double epidermal layers. Winter rings, especially where environmental conditions are stable, are usually sufficiently regular for use as indicators of age in estimating roughly the time required for a commercial species to reach marketable size.

4. Under favorable conditions there is little migration among the Quadrulæ. Some of the Lampsiles and other light-shelled species move about quite actively, but probably seldom migrate far from the point where they were dropped from the fish, although their total wanderings may be considerable. Water of sufficient depth is essential to optimum conditions. The minimum depth seems to be at least 2 feet; the range up to the maximum has not been studied. Quadrulæ prefer water over 2 feet deep. The reason they are found on the shoals in many of our streams may be explained as chance distribution, due probably to the fact that the particular individuals have never found optimum conditions after their parasitic development, and the reason they move about is that they do not find the right environment.

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[a] Dr. A. E. Ortmann and Dr. F. Haas have called my attention to Dr. Haas's monograph, "Die Unionidæ in Martini-Chemnitches Conchyliencabinet," 1910. I have not had access to this paper.

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EXPLANATION OF PLATES.

All photographs are about natural size. For actual measurements see tables. As already explained (pp. 10, 11, and 15), tags were fastened on with a small copper wire passed through a small hole made about 2 mm. from the edge of the shell, usually along the edge of the posterior umboidal ridge; x marks the tagging ring, i. e., the ring formed when the specimen was marked and measured. This ring was formed without exception in all specimens handled and thus marks the diameter of the mussel at the time of tagging and making initial records; x^1, rest rings formed by natural processes between tagging time and reclaiming of specimen; o, shadow line due to a ridge on the valve and in photographic copy may be mistaken for a rest ring.

Plate I.

Specimen H, *Lampsilis gracilis* (table 8), shows 3[illegible] mm. growth in length in 15 months (June, 1910, to Sept., 1911); x marks the rest ring formed when the specimen was marked and measured; x^1 is probably the 1910–11 winter rest ring; o, shadow line.

Specimen 323, *Quadrula undulata* (table 1), shows 17 mm. increase in one year's growth (June, 1910, to June, 1911). A new ring appears at x^1 near the margin. Notice the two rings, y^1 and y^2, near together, formed before the specimen was tagged.

Specimen 281, *Quadrula undulata* (table 8), shows 25 mm. growth in 15 months (June, 1910, to Sept., 1911); x^1 is probably the winter rest ring.

Plate II.

Specimen 355, *Quadrula rubiginosa* (table 2), shows 6 mm. increase in 15 months (June, 1910, to Sept., 1911) in a mature slow-growing species. No evidence of rest rings beyond x.

Specimen 349, *Quadrula pustulosa* (table 1), shows 10 mm. increase in one year (June, 1910, to June, 1911). A rest ring, not well brought out by the plate figure, shows very near the margin; o, on the anterior slope, is a shadow line.

Specimen 564, *Quadrula lachrymosa* (table 8), shows 19 mm. increase in length in 15 months (June, 1910, to Sept., 1911). Tag pulled off (t) after specimen was reclaimed.

Specimen 413 (table 8), shows 16 mm. increase in one year (June, 1910, to June, 1911). Two rest rings, x^1, x^2, in addition to the regular, x, formed at the time of tagging. If we count the one at the tagging line we have three rest rings for one year.

Specimens 149 and 158, *Quadrula lachrymosa* (table 1 and as shown here about two-thirds natural size). These specimens are from the Shoofly, the two *lachrymosa* above from the Chikaskia. The rest rings are about the same as 413 and the time (June, 1910, to June, 1911) is the same.

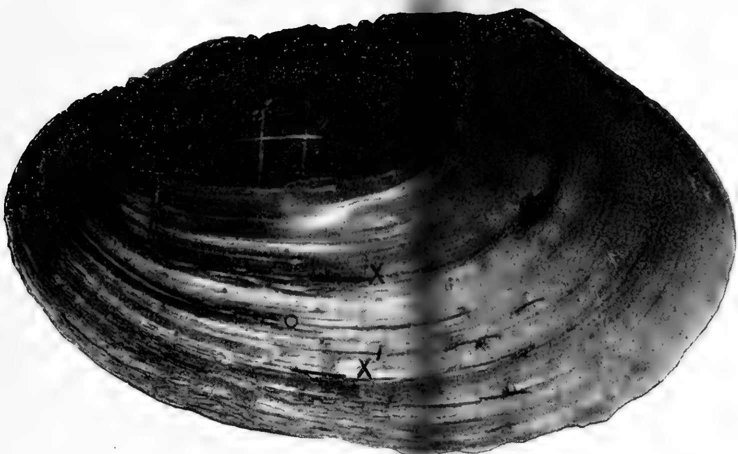
Specimen 158 is the left valve and also does not show the tag or mark.

PLATE III.

Specimen 566, *Lampsilis anodontoides* (table 8) ,shows 5 mm. increase in length in nearly three months (June 27, 1910, to Sept. 19, 1910). A mature Chikaskia specimen growing in rather unfavorable environment.

Specimen 763, *Quadrula lachrymosa*, shows how the tag wire is overlaid with nacre (*t*) nearly three months after tagging (June 27, 1910, to Sept. 19, 1910).

Specimen 200, *Quadrula undulata*. In the Shoofly (p. 7) no *Q. undulata* under 193 grams was found in June, 1910. In 1911 two specimens were secured that may be called young. No. 200 is one of these and is interesting on account of the regularity of rest rings, four in number. The specimen measures 80 mm. in length and, according to estimates worked out upon known growth of this species in the Shoofly, was 4 or 5 years old when taken (p. 14).



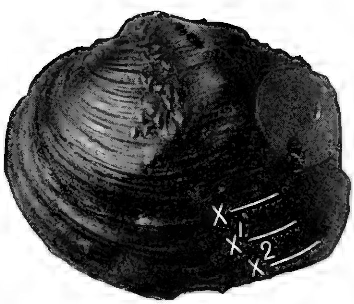
SPECIMEN H.

SPECIMEN 323.

SPECIMEN 281.

SPECIMEN 355.

SPECIMEN 349.



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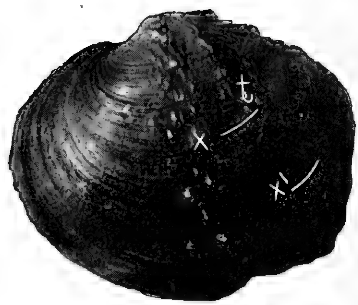

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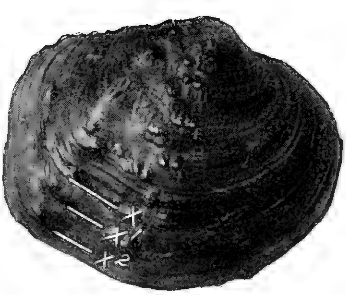

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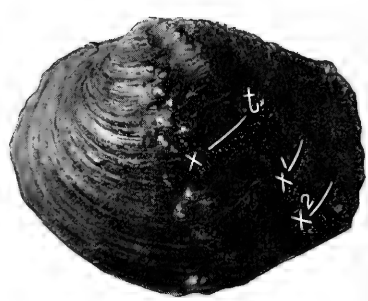
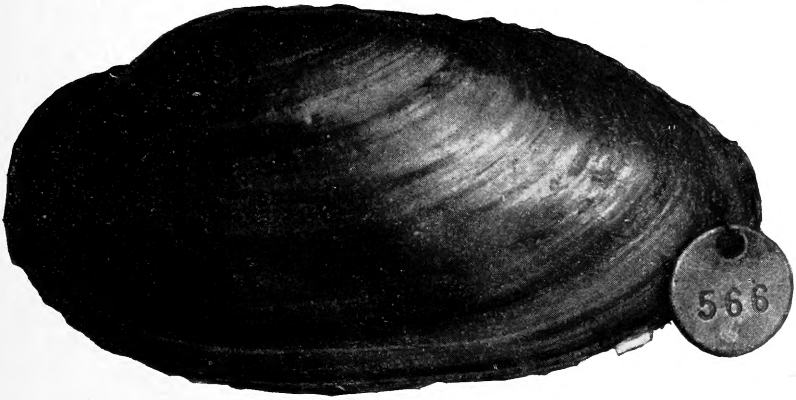
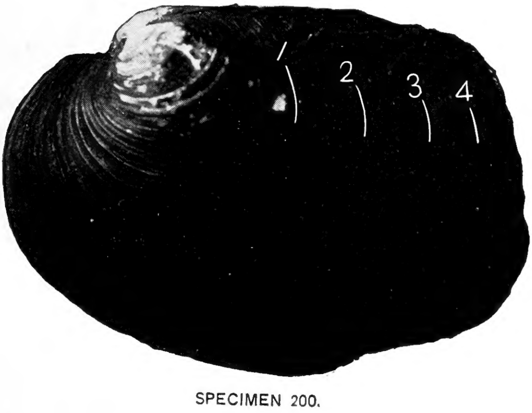


SPECIMEN 413.



SPECIMEN 566.

SPECIMEN 763.



SPECIMEN 200.