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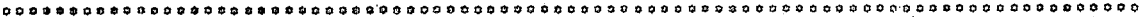
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THE FRESHWATER NAIADS OF THE LOWER END OF THE WABASH RIVER, MT. CARMEL, ILLINOIS TO THE SOUTH

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PRESENTATION OF DATA

The freshwater naiads of the Wabash River have been studied intermittently for over 100 years by both conchologists and commercial shell collectors. Dating from the 1820's, the papers of Thomas Say, of New Harmony, Indiana, are among the first published on the American freshwater Mollusca. Call (1900) referred to Say as the father of American conchology. The extensive work of Say facilitated the description of many new species of freshwater naiads, updated distribution data for others, and established the Mollusca of the Wabash River among the best known in the United States.

From the 1820's until the 1880's, little was published on the Wabash River. Stein (1881) issued a catalogue of Indiana naiads which listed species from the area but did not give exact collection locations. Most of the material of R. Ellsworth Call was published between 1885 and 1902. He assembled the scattered data on Indiana Mollusca and listed 92 species of naiads from the Wabash River. His descriptive catalogue of Indiana fauna (Call, 1900) is one of the most complete publications on the fauna of any state to date. Unfortunately, like most of the early conchologists, Call apparently considered unnecessary the delineation of collection locations. He did state that species and individuals abounded in the Wabash River below Terre Haute, Indiana; and that *Quadrula metanevra* (Raf.), *Q. nodulata* (Raf.), *Q. cylindrica* (Say) and *Cyprogenia irrorata* (Say) often were found in large numbers on gravel bars in fairly swift water (Call, 1900). Call (1896b) compared the molluscan faunas of ten drainage basins of Indiana, and demonstrated that the richest faunas occurred in the Wabash and Ohio drainages. He stated that he knew of beds of naiads, '... miles in length, /with/ enormous quantities of these animals' (Call, 1900).

Blatchley and Daniels (1902) published a supplement to Call's catalogue (based primarily on collections by Daniels) which added 91 species and varieties of land and freshwater Mollusca to the fauna of Indiana. They gave specific collection locations for only two species (Table 1). Daniels' (1903) report is a check list of Indiana Mollusca with the first extensive data on collecting sites (refer to Table 1).

Baker (1906) assembled the available information on the molluscan fauna of Illinois. He checked private and public collections and included data from unpublished lists provided by Illinois conchologists. Baker reported the collection of 11 species of naiads from Mt. Carmel, Illinois (refer to Table 1).

Goodrich and van der Schalie (1944) compiled the information on Indiana Mollusca, and analyzed it in relation to Ortmann's theories regarding the succession of mussels throughout drainage basins. This paper (Ortmann and Walker, 1922) provides the best coverage of the naiads of the Wabash River. It therefore has been used as a basis for Table 1 and for nomenclature throughout the report. Three transitional zones were noted in the Wabash River. The Southern Zone extends from Grand Chains to the mouth of the River (Zone of Influx), and the Large River Zone extends generally between Tippecanoe County and Posey County near the mouth. The Zone of Influx and the lower portion of the Large River Zone are in the study area: Mt. Carmel, Illinois to the mouth of the Wabash River. The Lower Zone is unique for it contains several species atypical of the Wabash drainage fauna. Fifty-two species are recorded from this zone (Goodrich and van der Schalie, 1944). Records for *Cumberlandia monodonta* (Say), *Dysnomia flexuosa* (Raf.), *D. personata* (Say), *D. sampsoni* (Lea), *Proptera capax* (Green) and *Simpsoniconcha ambigua* (Say) are restricted to this lower area of the Wabash River.

The most comprehensive study of the naiads of the Wabash River drainage was the survey of the commercially valuable mussels of the Wabash and White Rivers by Krumholz, Bingham, and Meyer (1970). During the years 1966 and 1967 they made 99 collections using a crowfoot bar, by scuba diving and hand-picking at 63 sites in the Wabash River, the White River, and the East Fork of the White River. Nine of these collections were made below Mt. Carmel at river miles 8-9, 16-17, 20-21, 30-31, 40-41, 51-52 (highway bridge at New Harmony, Indiana),

62-63 (Grayville, Illinois), 71-72, and 83-84 (Crawleyville, Indiana). Species taken at each listed site (personal communication, Dr. Krumholz, 1975) are included in Table 1. Unless the sites correspond with other categories listed in the table, they are listed primarily under the heading Mt. Carmel to the mouth.

Parmalee (1967) compiled the available literature on Illinois Mollusca (naiads) but his statement '... that systematic collecting in recent years ...' suggests considerable work had been done in the lower Wabash shortly before he prepared his paper. He specifically located the collecting site of *Dysnomia simpsoni* (Lea) at the Little Chains archeological site in White County, Illinois, thus indicating its ancient distribution in the lower Wabash River during prehistoric time. He assigns the distribution of many species to the lower Wabash River, but unfortunately does not note definite collection sites.

The report of Meyer (1968) was based on work done during the study made by Krumholz, Bingham, and Meyer (1970). His summarized data include the specific site locality for collected species (Table 1). Meyer (1974) reports the collection of several naiad species in the lower Wabash; but definitive site records are not included.

METHODS

In order to include all possible components of the naiad fauna of the study area, a complete literature survey was conducted. The preparation of a baseline for the present naiad population was complicated by the lack of definitive records from the early 1800's to the present. Generally specific location data are not given for most of the collection sites, collection methods are not detailed, and stream conditions at the time of collecting are not defined. Additionally, the synonymy is such that extensive library work was necessary to discriminate between species. For example, *Micromya nebulosa* Conrad, not included in this report, had been known by 26 names by 1944. Presently the generic name has been changed to *Villosa* (Burch, 1973).

In reviewing the data available from the time of Thomas Say in the 1820's, through the less intensive work of many other conchologists of Indiana prior to 1900, it appears that only the extensive field work of Call may have covered the part of the Wabash under consideration in this study. The comprehensive survey by Krumholz, Bingham, and Meyer (1970) was directed toward the commercial species; but their samples should have produced a representative collection of the species at each sampling station.

If a close correlation exists between the 1966-1967 and 1975 data, the report by Krumholz, Bingham, and Meyer should be representative of present day populations. Their data were of specific value in providing the baseline data for present day naiad fauna of the lower Wabash River. For these

purposes it was assumed that spot sampling of the section of the stream under study would permit a comparison with spot samples from the above mentioned collections, and thus provide a basis for speculating about the present naiad community.

It was recognized that, regardless of the type of survey, only a portion of the available stream bottom habitat could be sampled. Call (1894) sets a classical guide for comparisons and projections of data, 'Often in the case of the most common species, numbers of individuals are spasmodically great; then years go on and few of certain forms are to be found.' Apparently, speaking of rare species, Meyer (1974) wrote, 'They may live in unsampled habitats, or simply be rare and very difficult to obtain. ... their absence may be more apparent than real.'

In an effort to resample properly (in part) the areas sampled during the 1966-1967 survey, a long-time commercial mussel collector, buyer and button cutter was employed. A second collector, who operated the boat was utilized. Collectively, their experience on the Wabash River totaled 115 years.

Techniques used included a complete set of brail equipment as is used on the river today. A ¼ inch metal bar (a crowfoot bar) to which 56 strings of two hooks each were attached, was used for dragging the bottom for shells. The hooks were treble hook-like in nature, without barbs. A 'mule' made of a piece of plywood was used to steer the boat while floating with the bar on the bottom. It was not needed to increase the floating speed, because the current during high water transports the boat at ample floating speed. The brail was secured over the front end of the boat and the 'mule' was fitted behind the outboard motor where it could be used for the desired boat maneuverability.

It was believed that intensive brailing at eight locations from Mt. Carmel to the mouth of the Wabash (Figure 1) would provide sufficient data for a comparison with data of Krumholz, Bingham, and Meyer (1970). A spot sampling survey was conducted during the week of June 23-27, 1975. The collecting began at Mt. Carmel and a new location was sampled each day. Brail sampling varied from four 30 minute tows in productive areas to twelve 20 minute tows in less productive areas. The number of tows insured that bars, if they were present, would be sampled. Table 2 reflects the data resulting from the 1975 survey.

Mussel collectors, on the Wabash River, consider that high spring waters yield optimum brailing conditions; however, flood stage prevents brailing. Too much silt after sharp rises of water level in midsummer causes the shells to close; however, silt does not seem to have the same effects during the high spring waters. Increased water temperatures of midsummer either cause the mussels to bury themselves or close, indicated by the number of sample sizes which are diminished under such conditions. A greater variety of mussels can be taken during low water, when the bars were partially exposed. The Ohio River area on both sides of the mouth of

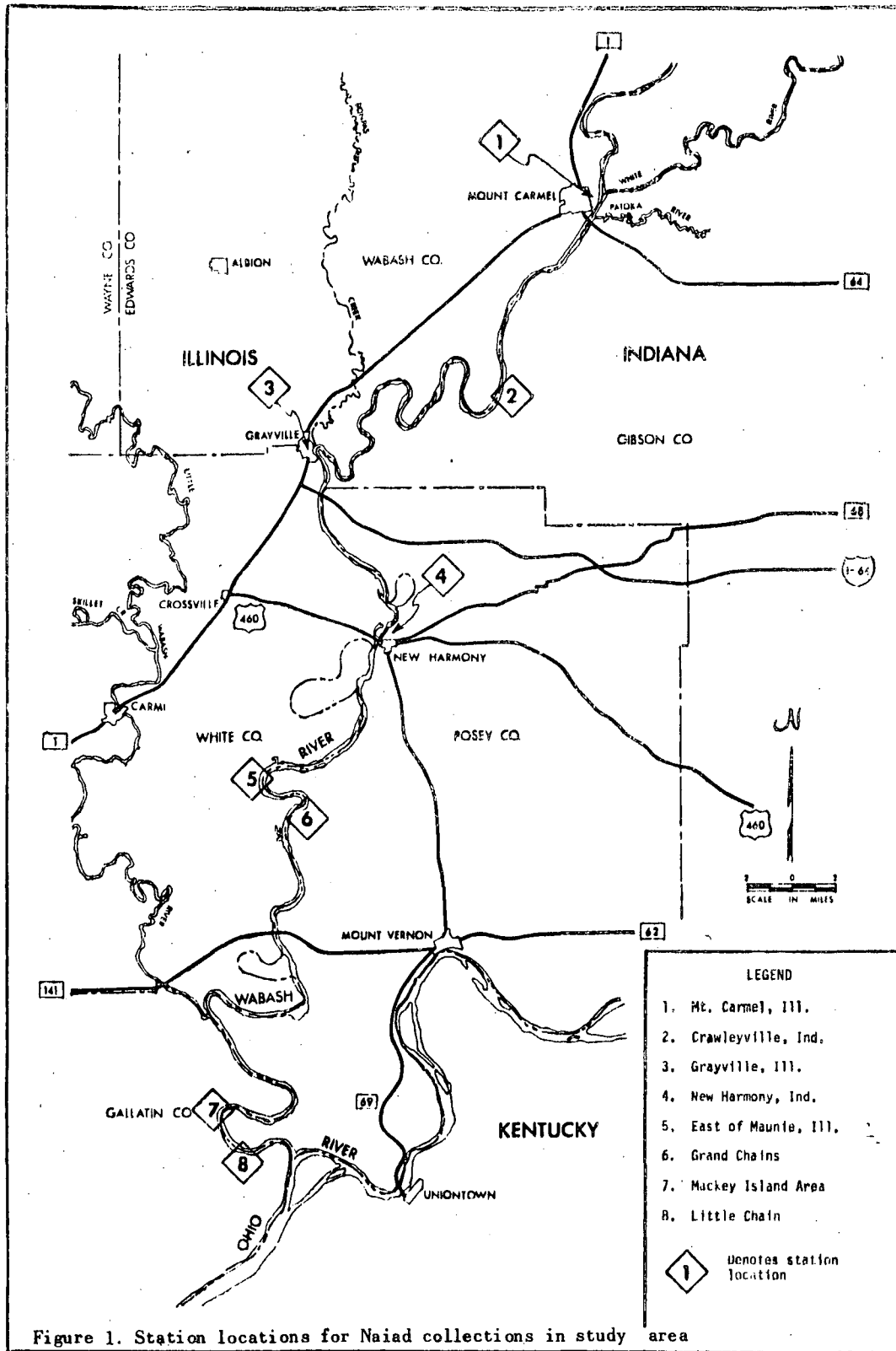


Figure 1. Station locations for Naiad collections in study area

Table 1. Species collected in study area with collector and site locations. (continued)

Species	Mt. Carmel, Ill.*	Crawleyville, Ind.	Grayville, Ill.	New Harmony, Ind.	East of Maunite, Ill.	Grand Chain	Above mouth Little Wabash	Mackey Isle Area	Little Chain 10 miles above mouth	Mt. Carmel to mouth
<u>Actinonaias carinata</u>	3									4
<u>Alasmidonta marginata</u>										9
<u>Amblema costata</u>			9							9
<u>Amblema peruviana</u>	10	10								
<u>Anodonta grandis</u>					4,8					
<u>Anodonta imbecillis</u>										
<u>Anodonta suborbiculata</u>										
<u>Anodontoides ferussacianus</u>										
<u>Arcidens confragosus</u>				2,1						
<u>Carunculina glans</u>				1						
<u>Carunculina parva</u>				1,2						
<u>Cumberlandia monodonta</u>						2,1,6,7				
<u>Cyclonaias tuberculata</u>										
<u>Cyprogenia irrorata</u>	3									
<u>Dysnomia flexuosa</u>										
<u>Dysnomia perplexa rangiana</u>				2,2						
<u>Dysnomia personata</u>				2,2						
<u>Dysnomia sampsoni</u>						1,2		6		
<u>Dysnomia sulcata</u>										
<u>Dysnomia trigueta</u>										
<u>Elliptia crassidens</u>	3,10	10			10	7				
<u>Elliptia dilatatus</u>										
<u>Fusconaia ebenus</u>	10,9				10	2				9
<u>Fusconaia flava</u>										
<u>Fusconaia subrotunda</u>										
<u>Fusconaia undata</u>	10	10		2						
<u>Lampsilis anodontoides</u>	3	10						9		
<u>Lampsilis anodontoides fallaciosa</u>					10					
<u>Lampsilis fasciola</u>										
<u>Lampsilis orbiculata</u>										
<u>Lampsilis ovata</u>								9		
<u>Lampsilis siliquoidea</u>										
<u>Lampsilis ventricosa</u>	3,9	9	9,10					9		9
<u>Lasmigona complanata</u>		10			10					4
<u>Lasmigona compressa</u>										
<u>Lasmigona costata</u>										
<u>Lastena lata</u>										
<u>Leptodea blatchleyi</u>				1,2		7,1				
<u>Leptodea fragilis</u>	10,9	9,10		9	10			9		9
<u>Leptodea laevissima</u>		10								4
<u>Leptodea leptodon</u>				1,2						
<u>Ligumia recta latissima</u>										
<u>Megalonaias gigantea</u>	10	10								
<u>Micromya iris</u>										
<u>Obliquaria reflexa</u>	10	10			10					4
<u>Obovaria olivaria</u>	10,9	10		2,1,9				9		9
<u>Obovaria retusa</u>				2,1						
<u>Obovaria subrotunda</u>										
<u>Plagiola lineolata</u>				2		2,1				

Table 1. Species collected in study area with collector and site locations. (continued)

Species	Mt. Carmel, Ill.*	Crawleyville, Ind.	Grayville, Ill.	New Harmony, Ind.	East of Maunite, Ill.	Grand Chain	Above mouth Little Wabash	Mackey Isle Area	Little Chain 10 miles above mouth	Mt. Carmel to mouth
<u>Plethobasus cicatricosum</u>										
<u>Plethobasus cyphus</u>										
<u>Pleurobema clava</u>				2,1						
<u>Pleurobema cordatum</u>				4,8	10					
<u>Pleurobema cordatum coccineum</u>										
<u>Proptera alata</u>			10							4
<u>Proptera capax</u>	3			2,10		1,2		10		
<u>Ptychobranchnus fasciolaris</u>										
<u>Quadrula cylindrica</u>	3									
<u>Quadrula metanevra</u>	10,9		9		10					9
<u>Quadrula nodulata</u>	10		10	2,1						
<u>Quadrula pustulosa</u>	3,10,9		10		10					
<u>Quadrula quadrula</u>	5,10,9		9,10	2,1,9	10					9
<u>Simpsoniconcha ambigua</u>						1,2				
<u>Strophitus rugosus</u>										
<u>Tritogonia verrucosa</u>	10		10							9
<u>Truncilla donaciformis</u>	5				10					
<u>Truncilla truncata</u>			9,10					9		4

- | | |
|---------------------------------------|---|
| (1) Blatchley and Daniels, 1902 | (6) Parmalee, 1967 |
| (2) Daniels, 1903 | (7) Goodrich and van der Schalie, 1944 |
| (3) Baker, 1906 | (8) Meyer, 1968 |
| (4) Krumholz, Bingham and Meyer, 1970 | (9) Personal conversation with Krumholz (1966-67 records) |
| (5) Hinckley, 1885 | (10) Clark 1975 records |

*Mt. Carmel 1975 and Crawleyville 1966-67 data combined

the Wabash River was not sampled. The Kentucky Department of Fish and Game, the Illinois Department of Conservation, the Indiana Department of Natural Resources, and several local mussel collectors were contacted for results of studies. After reviewing Williams (1969), it appeared that his findings might fill the disparity of information on the naiad population around the mouth of the Wabash River. Personal communication with Dr. Williams provided the information necessary to speculate about the present naiad population in the vicinity of the mouth of the Wabash River.

DISCUSSION OF DATA

Understandably, some of the species reported from the Wabash River in the early 1820's have not been collected for many years. Call (1894) stated, 'The habits of our mollusks are so peculiar that certain seasons present sometimes many forms which fail to appear again for several successive years.' His insight into present day problems of environmental concern is suggested by his interest in biological significance of the naiads in the total

faunal setting. He believed that many of the best collecting grounds sampled by Say and other early naturalists had been physically, chemically, and biologically altered by his time. He called attention to the need for more information. 'A further necessity for immediate action so that the original inhabitants of the state may be listed lies in the danger of extinction of very many forms' (Call, 1894).

Three of the species listed in Table 3 have been questioned. Goodrich and van der Schalie (1944) considered *Plethobasus cicatricosus* Say to be a deformed or 'unique' specimen. They also felt that *Leptodea blatchleyi* (Daniels) needed more study to determine the relationship between it and *L. leptodon* (Raf.). Daniels (1902) remarked about the similarities of anatomy and shell characters of the two species. It appears from the literature that specimens of the mentioned species have been collected only at the type locality listed in the Goodrich and van der Schalie report; '... more careful study may suggest that *Dysnomia sampsoni* (Lea) is a variant of *purpurea* representing a *rangiana* aspect of it as it appears in the larger rivers.'

Table 2. Species of Naiads collected in the lower Wabash River during the 1975 survey, with common names and estimated abundance in the area.

Scientific Name	Common Name	Abundance *
<u>Amblema peruviana</u>		Common
<u>Elleptio crassidens</u>	Elephant ear	Common
<u>Fusconaia ebenus</u>	Niggerhead	Rare
<u>Fusconaia undata</u>	Pig-toe	Rare
<u>Lampsilis anodontooides</u>	Yellow sand shell	Rare
<u>Lampsilis anodontooides fallaciosa</u>	Bank creeper	Rare
<u>Lampsilis ovata ventricosa</u>		Uncommon
<u>Lampsilis ventricosa</u>	Pocketbook	Uncommon
<u>Lasmigona complanata</u>	White heel splitter	Rare
<u>Leptodea fragilis</u>	Thin paper shell	Common
<u>Leptodea laevisima</u>	Pink paper shell	Common
<u>Megaloniais gigantea</u>	Washboard	Rare
<u>Obliquaria reflexa</u>	Three-horned Wartyback	Abundant
<u>Obovaria olivaria</u>	Glossy-back	Rather Common
<u>Pleurobema cordatum</u>		Rare
<u>Proptera alata</u>	Heel-splitter	Rare
<u>Proptera capax</u>	Pocketbook	Rare
<u>Quadrula metanevra</u>	Monkey-face	Rather Common
<u>Quadrula nodulata</u>	Warty-back	Rather Common
<u>Quadrula postulata</u>	Pimple-back	Abundant
<u>Quadrula quadrula</u>	Maple-leaf	Abundant
<u>Tritigonia verrucosa</u>	Buckhorn	Uncommon
<u>Pruncilla donaciformis</u>	Fawn's-foot	Rare
<u>Truncilla truncata</u>	Deer-toe	Rare

* Adapted from Meyer 1974 for comparison

Abundant--Found at 3 of 5 stations--one of the predominant species
 Common --Found at 3 of 5 stations--three or more specimens at each
 Rather Common--Found 2 of 5 stations--three or more specimens at each
 Uncommon--Found at 2 of 5 stations--one or two taken at each
 Rare--One one or two taken during the survey.

Table 3. Wabash River Naiads from the lower portion of the stream, which are reported as rare and endangered with estimates of abundance (from Stansbery, 1970).

Species	Abundance		
	Call (1900)	Goodrich & van der Schalie (1944)	Parnalee (1967)
<u>Cumberlandia monodonta</u> (Say)	Very rare	Rare	
<u>Fusconaia subrotunda</u> (Lamarck)	- - -		Of doubtful occurrence
<u>Lastena lata</u> (Rafinesque)	Rare	Rare	Of doubtful occurrence
<u>Plethobasus cicatriosus</u> (Say)	- - -	Relatively rare	Of doubtful occurrence
<u>Plethobasus cooperianus</u> (Lea)	Common	Rare	Of doubtful occurrence
<u>Plethobasus cyphus</u> (Rafinesque)	Common	Relatively rare	Uncommon to rare
<u>Pleurobema clava</u> (Lamarck)	Common		Of doubtful occurrence
<u>Quadrula cylindrica</u> (Say)	Common		Not common?
<u>Anodonta suborbiculata</u> (Say)	Common	Not common	Not common
<u>Simsoniconcha ambigua</u> (Say)	Very common		Of doubtful occurrence
<u>Carunculina glans</u> (Lea)	Rather common	Rather common	Uncommon to rare
<u>Dysnomia flexuosa</u> (Rafinesque)	Very rare	Relatively rare	Of doubtful occurrence
<u>Dysnomia personata</u> (Say)	Very rare	Rare	Rare
<u>Dysnomia perplexa</u> (Lea)	Abundant	"Quite well represented"	Uncommon to rare
<u>Dysnomia sampsonii</u> (Lea)	- - -	Rare	"Now absent?"
<u>Dysnomia sulcata</u> (Lea)	Rather rare	Relatively rare	Of doubtful occurrence
<u>Lampsilis orbiculata</u> (Hildreth)	- - -		Uncommon to rare
<u>Leptodea leptodon</u> (Rafinesque)	Rather common	Rare	Of doubtful occurrence
<u>Leptodea blatchleyi</u> (Daniels)	Described 1903	Rare	Not included
<u>Micromya fabilis</u> (Lea)	Common	Relatively rare?	Of doubtful occurrence
<u>Obovaria retusa</u> (Lamarck)	Rather common	Relatively rare?	Of doubtful occurrence
<u>Proptera capax</u> (Green)	Not common	Rare	

Table 4. Numbers of Species of mussel collected by crowfoot bar from the same 10 one-mile sections of the Wabash River in 1966 and 1967.

Species	1966 No. Taken	1967 No. Taken
<i>Alasmidonta marginata</i>	1	--
<i>Anodontoides terussaclanus</i>	1	--
<i>Lasmigona complanata</i>	8	2
<i>Lasmigona compressa</i>	1	1
<i>Strophitus rugosus</i>	5	--
<i>Actinonaias carinata</i>	43	9
<i>Lampsilis anodontoides</i>	2	--
<i>Lampsilis ovata ventricosa</i>	9	4
<i>Leptodea fragilis</i>	16	4
<i>Obliquaria reflexa</i>	--	1
<i>Obovaria olivaria</i>	44	15
<i>Obovaria subrotunda</i>	3	--
<i>Proptera alata</i>	5	--
<i>Truncilla truncata</i>	1	--
<i>Amblyma costata</i>	1	1
<i>Fusconaia ebenus</i>	1	--
<i>Fusconaia undata</i>	1	--
<i>Plethobasus eyphys</i>	1	--
<i>Quadrula metanevra</i>	15	--
<i>Quadrula pustulosa</i>	24	--
<i>Quadrula quadrula</i>	110	17
<i>Tritogonia verrucosa</i>	5	1
TOTALS	297	56

It is suspected that implications of Call (1894) concerning the extinction of many forms in Indiana may have become a reality during his life. He described two of the species listed in Table 3 as very rare. His comment that he had seen specimens of *Cumberlandia monodon* Say raises the questions as to whether he found one during his intensive collecting or if it for all practical purposes had become extinct in his day. *Dysnomia flexuosa* (Raf.) was considered by Call (1900) to be a species which was, '... by no means common in recently formed collections.' He only collected this species from the Ohio River. Call (1900) considered *Dysnomia personata* (Say) to be very rare; as he did not take a specimen during his intensive collecting. Additionally, he reported *Dysnomia sulcata* (Lea) to be, '... regarded as rare.' He stated that his description, '... is based solely on two females, the male not being at hand when it was made, though it was afterwards received for figuring.' Such a comment indicates a scarcity of specimens and raises questions as to whether Call actually collected it, for 'only two females were available when he wished to sketch it.'

Lastena lata (Raf.) was described as rare by Call (1900). Its habit of burying itself deep into mud and gravel bars may be why Call considered diffi-

culties in collecting were related directly to its apparent paucity. All Indiana authors have considered it rare.

Call (1900) commented that *Proptera capax* (Green) was by no means a common shell in Indiana, and was known only from the Wabash. Goodrich and van der Schalie (1944) restricted its distribution in Indiana to the lower part of the river and reported it rare.

It thus appears that at least five of the species included in Table 3 and in the list of rare and endangered species of naiads (Stansbery, 1970) were rare and endangered before 1900. From an analysis of Indiana literature on freshwater naiads, it appears that some of these may have been collected only once. The old records were carried through the literature each time a new list was prepared. Thus, only a few specimens of each were known from the State of Indiana.

Table 3 indicates that Call (1900) reported three of the listed species as Rather Common, six as Common, one as Very Common, and one as Abundant. The status of four others was not reported. Of those considered Rather Common by Call, one is reported

to be Uncommon to Rare by Parmalee (1967), and the other two to be of doubtful occurrence. Parmalee also considers three of Call's common species to be of doubtful occurrence and three more to be Uncommon to Rare. Table 3 shows that Call considered *Dysnomia perplexa* (Lea) to be Abundant, and *Simpsoniconcha ambigua* (Say) to be Very Common, as compared to Parmalee who reports the first to be Uncommon to Rare and the latter to be of doubtful occurrence.

It is evident that considerable change in the abundance of the Mollusca of the Wabash has occurred since the species were first studied. Others that could be added to the list of species discussed above are included in Table 3.

It is possible that such species as *Unio merus tetralasmus* (Say), *Anodonta grandis* (Barnes), *Proptera alata* (Say), *Lampsilis anodontoides* (Lea) and *L. ventricosa* (Barnes) have increased in abundance since many of the oxbows have become severed more completely from the main stream, and sand and silt have replaced the gravel bars.

None of the species listed in Table 3 were taken during the 1966-1967 collections. Only two specimens of *Proptera capax* (Green) were taken in 1975, one in the New Harmony area and the other in the Mackey Island area. This would indicate its rarity.

The 1966-1967 survey (Table 4) produced two species not taken during 1975 spot sampling: *Anodonta grandis* Say and *Actinonaias carinata* (Barnes). In general the conditions during the 1975 sampling period must have been exceedingly favorable, for nine species were collected in the study area which were not found by Krumholz, Bingham, and Meyer. These authors use *Amblema costata* Rafinesque, the small stream form, and the 1975 data use *Amblema peruviana* (Lamarck), the large stream form. Similar statements could be made about *Lampsilis ovata ventricosa* (Barnes) used in the 1966-67 survey data. Goodrich and van der Schalie (1944) stated, '*L. ovata* is definitely a species that inhabits large rivers and there are transitions into the headwaters that connect *L. ovata* through the form *L. o. ventricosa* with *L. ventricosa*.'

Only brail sampling was used in the 1975 survey as compared to that method plus scuba diving and hand-picking in the 1966-1967 survey. The effort made at the 'east of Maunie area' illustrates the incongruities of sampling in a large river. Six brail hauls were made at intervals across the stream so as to obtain a representative sample. The hauls were approximately one-half mile long. Mussels were obtained during two of the six hauls and these were collected in adjacent brailed areas. Each time hauls were made over a relatively hard bottom of gravel and rubble, shells were taken. Shells were not collected a few hundred feet on either side of the bar. The chances of finding these bars, known to mussel collectors as mussel beds, are remote unless the stream has been visited at low water. The vast experience of the two collectors used during the 1975 study is believed to have made

the differences in the hauls of the 1966-1967 and the 1975 collections. Sizes and ages of the specimens taken in the 1975 survey indicated they were available during the earlier study; but as previously suggested, every habitat in a stream cannot be sampled.

Two collectors brailing over the same area can reap different harvests quantitatively. The difference in harvest from the same area in two consecutive years is evident from data given by Krumholz, Bingham, and Meyer (1970). The sample dropped from 21 species and 297 shells in 1966 to 11 species and 56 shells in 1967. Only one species was taken in 1967 which was not found in the 1966 harvest. The reduction per collection site ranged from 10 down to 2 species and 45 down to 7 shells.

The abundance of the naiads of the Wabash River has been reported in general terms: Abundant, Very Common, Common, Rather Common, Rather Rare, Rare, and Very Rare. These terms are biased in accordance to the experience of each collector; but they offer some means of quantifying the populations as indicated in each study. Meyer (1974) has defined the use of these terms as they are related to his report. A comparison of data from Table 2 with Table 5 from Krumholz, Bingham, and Meyer (1970) indicates slight differences of minimal importance. Sampling problems discussed previously could account for differences found in the data of these two tables. The greatest difference is in the rating of *Obliquaria reflexa* (Raf.) -- (Rare in the 1966-1967 survey and Abundant in the 1975 reports). A review of the standards used by Meyer (1974) and those set up for the 1975 data, indicates that considerable error in judgement is possible. The reports agree that *Quadrula quadrula* (Raf.) and *Quadrula pustulosa* (Lea) are the most Abundant species, that *Obovaria olivaria* (Raf.) is Relatively Common to Abundant, and that the *Amblema*, *Leptodea fragilis* (Raf.), *Tritogonia verrucosa* (Barnes), and *Lampsilis ovata ventricosa* complex follow in order of abundance.

The 1975 take of shells revealed only a small number of immature mussels. Most of the shells collected would have satisfied the 2½-inch legal height required by Illinois law. For example, of 36 *Quadrula pustulosa* (Lea) taken east of the Maunie, only six were of illegal size. On the other hand most of the *Obliquaria reflexa* Rafinesque collected were undersize and many were under 1½ inches in height. Lopinot (1969) reported the percentages (by species) of shells under the 2½ inches in height in the stock piles of buyers. This information was collected by Illinois biologists and indicated that approximately 42 percent of the shells harvested from the Wabash River in 1967 were less than 2½ inches in height. Over 50 percent of the *Fusconaia undata* (Barnes), *Quadrula metanevra* (Raf.), *Q. pustulosa* (Lea), *Q. quadrula quadrula* (Raf.), *Q. nodulata* (Raf.), *Obliquaria reflexa* (Raf.), and *Obovaria olivaria* (Raf.) were of small sizes. If a crowfoot bar is designed for selectivity, larger specimens are collected more readily than the smaller ones.

Table 5. Distribution and abundance of unionid mussels in the Wabash, White, and East Fork of the White rivers of Indiana based on 99 collections in 1966 and 1967 (from Krumholz, Bingham and Meyer, 1970).

Species	Wabash River			White River	
	Upper	Middle	Lower	Main Stream	East Fork
Subfamily Anodontinae					
<i>Alasmodonta marginata</i>	R	-	-	-	-
<i>Anodonta grandis</i>	-	-	R	-	-
<i>Anodontoides ferussacianus</i>	R	-	-	-	-
<i>Lasmigona complanata</i>	C	C	C	C	C
<i>Lasmigona compressa</i>	R	-	-	-	-
<i>Lasmigona costata</i>	R	R	-	-	-
<i>Strophitus rugosus</i>	C	-	-	-	-
Subfamily Lampsilinae					
<i>Actinonaias carinata*</i>	A	A	C	C	C
<i>Cyprogenia irrorata</i>	-	R	-	-	-
<i>Lampsilis anodontooides</i>	C	C	C	-	-
<i>Lampsilis ovata ventricosa</i>	C	C	C	C	C
<i>Leptodea fragilis</i>	C	C	C	C	C
<i>Leptodea laevissima</i>	-	-	R	-	-
<i>Obliquaria reflexa</i>	R	R	R	R	C
<i>Obovaria olivaria*</i>	A	A	A	C	C
<i>Obovaria subrotunda</i>	R	-	-	-	R
<i>Proptera alata</i>	C	C	C	C	C
<i>Truncilla truncata</i>	R	R	R	R	R
Subfamily Unioninae					
<i>Amblesma costata*</i>	C	C	C	C	A
<i>Cyclonaias tuberculata</i>	-	-	-	-	R
<i>Elliptio crassidens</i>	-	-	-	-	C
<i>Fusconaia ebenus*</i>	R	R	R	C	C
<i>Fusconaia undata*</i>	R	R	-	R	C
<i>Megalonaias gigantea*</i>	R	C	-	R	C
<i>Plethobasus cyphus</i>	R	-	-	-	R
<i>Pleurobema cordatum</i>	-	-	-	-	R
<i>Quadrula metanevra*</i>	R	R	R	R	R
<i>Quadrula pustulosa*</i>	A	A	A	A	A
<i>Quadrula quadrula*</i>	A	A	A	A	A
<i>Tritogonia verrucosa*</i>	C	C	C	-	-

*The 10 species of greatest commercial value.

R, rare; --, not present; C, common; A, abundant. Upper Wabash River: Delphi to Terre Haute, Indiana; Middle Wabash River: Terre Haute to Mount Carmel, Illinois; Lower Wabash River: Mount Carmel to Ohio River

Table 6. Species and abundance of mussels collected on the Ohio River, miles 842-862, September 5, 6, 1967.

Location	Species	Abundance
Mile 843.2-844 (from mouth of Lost Creek to lower Highlands Rocks, ending one mile above Dam 49). Specimens taken 40 yards from Kentucky shore in water 12-17 feet	<u>Fusconaia ebenus</u>	1
	<u>Pleurobema cordatum</u>	1
	<u>Quadrula quadrula</u>	13
	<u>Quadrula pustulosa</u>	3
	<u>Lasmigona complanata</u>	1
Mile 857-858 (from directly opposite Millrace Slough to immediately above Shawneetown light). Specimens taken 125 yards from Illinois shore in water 12-18 feet deep.	<u>Fusconaia ebenus</u>	9
	<u>Pleurobema cordatum</u>	3
	<u>Amblema costata</u>	5
	<u>Quadrula quadrula</u>	12
	<u>Quadrula pustulosa</u>	5
	<u>Megaloniaias gigantea</u>	3
	<u>Elliptio crassidens</u>	2
	<u>Tritogonia verrucosa</u>	5
Mile 859-859.5 (SCUBA collections from 23 square yards, 10 yards from shore on Illinois side of river).	<u>Fusconaia ebenus</u>	2
	<u>Pleurobema cordatum</u>	4
	<u>Amblema costata</u>	65
	<u>Quadrula quadrula</u>	23
	<u>Quadrula pustulosa</u>	9
	<u>Lampsilis anodontoides</u>	2
	<u>Megaloniaias gigantea</u>	4
	<u>Plagiola lineolata</u>	2
	<u>Obliquaria reflexa</u>	5
	<u>Proptera alata</u>	1
	<u>Tritogonia verrucosa</u>	4
<u>Leptodea laevis</u>	4	
Mile 859-859.5 (brail samples taken 50-125 yards from the Illinois shore in 12-18 feet of water).	<u>Fusconaia ebenus</u>	10
	<u>Pleurobema cordatum</u>	5
	<u>Amblema costata</u>	19
	<u>Quadrula quadrula</u>	49
	<u>Quadrula pustulosa</u>	24
	<u>Quadrula metanevra</u>	1
	<u>Obovaria olivaria</u>	13
	<u>Megaloniaias gigantea</u>	1
	<u>Plagiola lineolata</u>	2
	<u>Elliptio crassidens</u>	3
	<u>Obliquaria reflexa</u>	25
	<u>Tritogonia verrucosa</u>	1
	<u>Lampsilis anodontoides</u>	1

These data suggest that natural recruitment exists in the Wabash for the species mentioned. We might add that three specimens of *Quadrula cylindrica* (Say), and listed on rare and endangered list of Stansbery (1970), were measured by the biologists. All three were under the 2½ inch measurement. Data by Lopinot (1968) indicate a large harvest of young mussels will affect the future harvest and possibly the obtaining of large shells.

Messrs. Collins and Carroll, who assisted in the 1975 spot sampling, stated that they rarely had seen a *Megaloniaias gigantea* (Barnes) or an *Amblema* spp. under three inches in length. Lopinot (1968) measured 896 of the former and 925 of the latter species. Most of the *Megaloniaias* and only three of *Amblema* were under 2½ inches in size.

The bed of Ohio River naiads, closest to the mouth of the Wabash was studied by Williams (1969). Although not considered to be a large bed, its inhabitants are commercial species (Table 6). Williams believed the bed to have been a part of the larger bed downstream.

In June 1975, Dr. Williams spot sampled some of the beds of naiads which he had worked during a 1967 survey. He found them to be essentially the same as when first sampled. Species composition was about the same and recruitment was occurring. He is of the opinion that conditions in the Ohio, near the mouth of the Wabash, are approximately the same as in 1967, and that there is little reason to believe the mussel beds of the area have been altered since that survey.

REASONS FOR CHANGES IN THE WABASH RIVER NAIAID POPULATION

Call (1894) found that factors existed at least 100 years ago which could have caused the demise of the less adaptive and/or tolerant species of freshwater naiads. Call further stated, 'The sewage of towns and villages, the refuse of factories and other manufacturing plants, the gradual encroachment on the primitive forest, the drying up of streams, the drainage of swamps, the general increase in tilled lands, these all conspire against the chances of perpetuity of a rich molluscan fauna.' He described man as the greatest enemy of molluscan life, and added, 'It is believed that many of the collecting grounds known to Say and the early naturalists have in this way been completely destroyed' (Call, 1900). Further, he implicates dam building, which prevents free fish migrations, as causing the almost complete extinction of some forms of unionids. A report by van der Schalie (1938) stated that M. M. Ellis found the Mississippi River from the mouth of the Missouri to the Gulf of Mexico to be practically devoid of mussels. Ellis (1931) attributed this condition to the tons of silt carried downstream and deposited in the Mississippi River by the Missouri. As van der Schalie stated, 'Mussels, for the most part, are extremely sensitive to such changes . . . relatively few species adapt themselves to the altered habitats.'

Wurtz (1956) stated that unionid mussels were quite intolerant to pollution of any kind and reported unequivocally that freshwater mussels disappear from streams carrying moderately heavy burdens of pollutants. Krumholz, Bingham, and Meyer (1970) cited the work of Forbes and Richardson (1919) which directly correlated the increasing levels of pollution and decreasing ranges and numbers of mollusks in the Illinois River. Starrett (1971) documented changes in the distribution of the more common mussels of the Illinois River. Meyer (1974) wrote, 'A trend toward restrictions of ranges and declines in abundance of many members of the unionid fauna of the Wabash and White Rivers is clearly indicated, as is extirpation of certain species.'

Parmalee (1967) commented that, 'Species adapted to sand and gravel bottom environments cannot long survive in one composed of mud and they are quickly destroyed by the smothering effects of silting.' He also considered the changing structure of stream beds as one of the major factors causing changes in mussel populations. A constantly changing or shifting bottom will limit and/or prevent the establishment of mussel beds. 'Each species has evolved its own combination of optimum habitat requirements and these differ considerably among the various kinds' (Parmalee, 1967). He speaks of pollution and silting as if they were not synonymous, but of equal importance.

During the 1975 survey on the Wabash, at least twenty-five of the older mussel collectors, who had spent their lives along the Wabash River, were contacted to learn the causes for the decline of the

gravel removal operations as the chief cause. They explained that the gravel companies employed many of the mussel collectors to aid with the removal. The collectors knew the locations of the good gravel bars because these were also the good mussel collecting sites in the stream. When the gravel was removed the sand and silt washed from it was carried downstream.

Very little of the bottom sampled in the 1975 study was composed of gravel. Most of the bottom was sand with varying amounts of silt. Every specimen of *Megalonias gigantea* (Barnes) and *Amblema peruviana* (Lamarck), taken during 1975, contained large amounts of silt in and around the gills. The heavy silt load derived from cultivated fields in the drainage area, the continuous disturbance of the bottom by removal of gravel and the resulting release of sand and silt have combined to produce a tremendous sediment load, especially during high waters. Stream bottoms of silt and sand are usually unstable and constantly changing. Such conditions are not suitable for the establishment of mussel beds.

Call (1900) provides us with one of the early causes for the reduction of the mussel populations, a cause which has received little attention. He stated, 'I have seen hogs rooting the largest of the mollusks from their beds in the rivers of the south and crushing them as they would apples, rejecting the shells and using only the soft portion.'

Call (1900) also emphasized the importance of mollusks as food for wildlife, '... raccoons and muskrats destroy thousands yearly, so many indeed that one wonders how they manage to perpetuate their species.' The 'kitchen middens' have long been known by conchologists as a source from which many of the smaller and rarer shells of a stream may be found. *Simpsoniconcha ambigua* (Say) at one time were located by finding a pair of shells in a 'midden' on the shore. In their specialized habitat, the smaller and rarer shells which were possibly rare or endangered in the time of Call, were of the sizes most often collected for food by muskrats and raccoons. The vast populations of these predators in early days, their habits of underwater food collection, and their use of small shells may have made them a greater factor in the demise of many species than has received consideration.

Call (1900) ranked man as the greatest enemy of mollusks but did not list commercial collecting of mussels as one of his crimes. Both Virgil Carroll and Charles Collins of Mt. Carmel, Illinois stated that mussel collecting started in 1905 on the bar below the bridge at Mt. Carmel. Since the first pearl button factory was established in Muscatine, Iowa in 1892 (Lopinot, 1967), it would seem that the Wabash, especially near the Mt. Carmel area, has been collected for as long or longer than most areas in the United States. Carroll and Collins related experiences of early collecting when up to 1000 pounds of mussels were collected per day in this area. The 1975 survey included eight 20 minute hauls over this bar. This sampling net-

ted a total of 16 species and 54 specimens. The total weight of the live mussels was approximately 25 pounds.

The total weight of shells taken per day during the 1975 spot sampling never exceeded 40 pounds. Total brailing time per day did not exceed 4 hours. Thus, in an 8-hour day, 80 to 100 pounds of shells, including non-commercial species, might be collected.

The presence of a population of freshwater mussels large enough to support a profitable commercial collecting industry is doubtful. Table 4 is a presentation of the harvest from 10 one-mile sections in the upper Wabash where shells are said to be more abundant. Only 297 specimens were collected during the 10 miles of brailing. The 18 plus actual hours of brailing during the 1975 survey produced 178 naiads (less than 10 per hour). Some were not of legal size or of commercial value.

Messrs. Carroll and Collins of Mt. Carmel described a combination commercial fishing and mussel collecting industry which supported approximately 50 families in the Mt. Carmel area in the 1930's. Mr. Collins, who has purchased shells since 1945, estimated that he purchased about 600 tons of shells in 1964 as compared to 14 to 15 tons in 1974. Homer Booton of Grayville, Illinois, has collected shells for 40 years, but had difficulty in collecting enough shells to make 10 to 15 dollars a day in 1974. Other collectors spoke of earning \$30.00 per day when shells brought only 3¢ per pound (today they bring 10¢ to 15¢ per pound). Residents along the river, east of Maunie, estimated that they could collect \$10.00 to \$15.00 in shells per day; but this does not cover the cost of equipment and labor.

Lopinot (1968) reported a decrease in the Wabash River harvest from 919 tons in 1965 to 317 tons in 1967. Collins paid between \$350 and \$400 per ton for mussels in 1965 as compared to \$300 for three ridge (*Amblema* spp.) and niggerheads (*Fusconia ebenus* (Lea), and \$200 for muckets (*Actinonaias carinata* (Barnes) in 1975. According to Lopinot (1968), 4,688 mussel collecting licenses were sold in 1934; but the sale dropped to a few hundred, or less, for a period of nearly 30 years. Sales returned to 1,279 in 1966. These figures reveal the pressures which may have been exerted on the Wabash mussels by licensed Illinois clammers. Indiana sales of licenses may have been equivalent. At least sales probably followed a similar trend because Wabash River shells brought a higher price than those from other streams, and would have attracted mussel collectors.

Collins recalled that one year, probably during the late 1920's or early 1930's, his uncle sold nearly \$1500 in pearls from mussels collected in the Wabash. He stated that his father collected several times as many mussels as his brother, but he found very few pearls of any value. Collins stated that he paid \$500 for a pearl in 1963, but he recalled two or three that had sold for \$800 to \$900 in earlier years.

Regardless of the factors discussed which would

contribute to the decline in the Wabash River naiad fauna, contacts with numerous commercial fishermen revealed that a considerable quantity of 'hacklebacks' (*Scaphirhynchus platorhynchus* (Rafinesque), or shovelnose sturgeon are taken in the lower part of the Wabash. One fisherman stated that he could show weigh bills for 1500 pounds taken during the spring of 1975. This fish could act as a major predator on small naiads. Their presence would indicate that the stream bottom in many areas still provides desirable habitats for the small mussels. Trautman (1957) quoted several fishermen as reporting that this sturgeon congregates wherever there are large quantities of small clams and snails. Most of the fishermen contacted along the Wabash reported that the sturgeon were taken in large numbers only in the lower part of the river, probably below the Grand Chains area.

CONCLUSIONS

The history of mussel collecting in the Wabash River was reviewed to determine the species reported in early collections. Some of the species which are considered 'rare and endangered or extinct' (Stansbery, 1970) may have been taken only once in the Wabash or were rare or endangered 75 years ago. Thus, factors which caused the demise of several species have existed for possibly 100 years, and are not necessarily of recent origin.

Changes have occurred in the naiad fauna, from 70 listed by Call (1900), 75 by Goodrich and van der Schalie (1944), and 30 in the 1966-1967 survey by Krumholz, Bingham, and Meyer (Meyer, 1974). However, no recent intensive and extensive survey has been made of the entire Wabash River drainage from which comparisons can be made with the state-wide compilations of Call (1900) and Goodrich and van der Schalie (1944) who included all known records. Krumholz, Bingham, and Meyer (1970) proved that different collecting methods produced different results, and that sampling the same area in different years produced dissimilar results. Each method has its value under different stream conditions; and only a combination can provide the most reliable data. Thus, the comparisons of the data on Indiana naiads are not necessarily valid unless the methods used to collect them are the same.

The 1975 data compare quite favorably with those obtained during the 1966-1967 survey when compared on the basis of abundance used during the earlier survey. These data from the two surveys indicate that a population of commercially valuable mussels exists in the area of the Wabash from Mt. Carmel to the mouth; but the numbers are such that they cannot support a viable collecting industry. The data also suggest that few if any of the rare or endangered species exist, although intensive collecting during low water stages would add considerably to the credibility of this supposition.

The shifting sand and silt bottom of this lower section of the Wabash River does not present a desirable habitat for most of the rare or endangered species of freshwater naiads, or the more commercially valuable shells. The constant and systematic removal of the better habitat (gravel bars),

the resulting resuspension of sand and silt, plus that carried by the stream during high waters, suggest a degradation in the habitat in the future, considering no control measures.

The suggested possibility of the construction of one or more locks and dams, in the Mt. Carmel to the mouth area, raises the question of their detrimental effects on the mussel population. Clark (1971) raised the question if the large beds of mussels in the Muskingum River in Ohio were present prior to the construction of the dams, or did the dams create a set of conditions downstream which resulted in the creation of the favorable habitat, and thus the establishment of the mussel beds. There seems to be a definite correlation between the locations of the mussel beds and the dams.

Impoundments do not have the same effects on different species of mussels. The 38-foot power dam in the Auglaize River near Defiance, Ohio, in the area collected by Clark and Wilson (1912) created an impoundment behind it. Personal collections from the area would indicate that *Quadrula quadrula* (Raf.), *Q. pustulosa* (Lea), *Lasmigona complanata* (Barnes) and *Proptera alata* (Say) were benefited by the impoundment and were reproducing in large numbers. Undocumented information coming from work in the TVA reservoirs indicates that mussel fisheries are becoming reestablished in some reservoirs where species have thrived under impoundment conditions. Even some of the rare or endangered species seem to be abundant in muddy bottoms. Call (1900) stated that *Dysnomia flexuosa* (Raf.), "... should be sought in deep and muddy bottoms ...". It is inconceivable that impounding the Wabash behind relatively low dams will bring back such rare species, but some could thrive under conditions similar to those which may be created both above and below dams and locks.

Finally, a quick appraisal of the area would seem to indicate that most of the rare or endangered species of mussels already are extinct, and that the populations of commercially valuable species are too low to provide a viable mussel economy. Both the removal of the gravel bars and the heavy sediment load are rapidly destroying the desirable habitat so that the future for the survival of the mussels which are present is rather dim. The installation of locks and dams, the building of stable bars unmolested by dredging barge channels, and the discontinuation of dredging operations on existing bars, might stimulate a recovery of at least a few of the remaining species of naiads.

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LAND SNAILS FROM NORTHERN MISSOURI

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INTRODUCTION

The state of Missouri has a rich land snail fauna. However, the knowledge of those species comprising the fauna and the details of their distribution are far from adequate. As pointed out by Miles (1969) and, more recently, Hubricht (1972a), the details of the northern fauna are particularly scanty. Locality records from north of the Missouri River are scattered in the literature, most reports having concerned the southern half of the state. A partial review of the literature devoted to Missouri land snails is included here.

The present study was initiated to contribute to our knowledge of the distribution of land snail species in all of northern Missouri. The records presented here are from the northeastern part of the state. Data from the northwest will hopefully be tabulated soon. All of the specimens listed herein have been deposited in the Mollusk Collection of the University of Missouri - Kansas City with the exception of those from locality no. 40 which are in the collection of the senior author.

HISTORICAL ACCOUNT

F. A. Sampson was the earliest serious student of Missouri land snails. His first paper (Sampson, 1883a) included a brief discussion of shells collected in the vicinity of Lamar in Barton County and near Springfield in Greene County. A second paper reported 51 species of snails, including aquatics, from near Sedalia, Pettis County, Missouri (Sampson, 1883b). Sampson also contributed other shorter reports on snails collected in Pettis County in 1885 and 1890.

Pilsbry (1891) published a short report on zoni-tids from Arkansas, and on the paper he mentioned *Helix appressa* Say (= *Mesodon appressus*) from Boonville, Missouri. The next year, Sampson (1892) reported *Mesodon andrewsae* Binney from St. François

County. A year later in a long list of North American collections, Stearns (1893) reported eight species of land snails from Stone County in southern Missouri.

The first paper supplying records of a wider scope was by Sampson (1894) in which he reported 11 species from 14 southern counties. Four years later a short paper on snails from Iron County appeared (Baker, 1898). This was the last paper devoted to Missouri gastropods before 1900, although a short paper by Pilsbry (1899) on species of *Polygyra* from Arkansas contained a few records from extreme southern Missouri.

Pilsbry, in 1903, reported a few Missouri records in another work devoted mainly to Arkansas; and Greger (1905) published the first paper containing records from northern Missouri (Callaway County). Then Pilsbry and Ferriss (1906) published a major paper devoted to land snails of Missouri, Arkansas, and 'Indian Territory' (Oklahoma). In regard to Missouri, this work dealt mostly with the southern part of the state, although there were a few records listed from north of the Missouri River (notably from Boone, Callaway, and St. Charles Counties).

Six years later, Sampson produced two more short reports. The first (Sampson, 1912a) concerned records of some polygyrids and included measurements of *Polygyra albolabris* (Say) (= *Triodopsis*) from Jackson County and elsewhere. The second was a more extensive report of locality records from seven counties in southeast Missouri (Sampson, 1912b).

A year later, Sampson (1913) contributed what could be called the most important and extensive paper on Missouri snails. This consisted of locality data and notes on most of the species known to occur in the state at that time. This report was the last major paper devoted to Missouri gastropods. It is particularly important because it included more data on the northern fauna than had been published previously and was the only source of information in this regard until recently.

Since 1913, most information in the literature pertaining to Missouri snails has been brief. Samp-

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son (1914) published a short paper concerning fossil shells from Providence and Lupus. Greger (1916, 1917) published papers referring to fossil species of Missouri gastropods. Baker (1932) mentioned a collecting trip but gave no data, and Hubricht (1941) published a study dealing with Mollusca from caves in the Ozarks. It included aquatic as well as terrestrial forms.

Nearly all of the records in the works discussed thus far were summarized by Pilsbry (1940, 1946, and 1948), and the number of reports since his monumental work has been few, and, as before, devoted to southern and central Missouri. Dowdy (1950), in a report on ecological studies of invertebrates, mentioned several species collected from the flood plain of the Osage River in central Missouri. Hubricht (1962) described a new species of *Helicodiscus* (*H. notius* Hubricht) and listed six Missouri counties where it had been found, including St. Charles and Boone. In the same year, Branson (1962) reported four species of polygyrids from Jasper County in southern Missouri.

Hubricht has contributed two other short papers. In the first (Hubricht, 1963) he discussed the genus *Discus* in the state, while in the second, (Hubricht, 1964a) he gave several southern localities for *Strobilops aenea* Pilsbry. He also published a long list of records on the Pleistocene fauna of parts of Missouri and Illinois (Hubricht, 1964b). This last paper is most interesting as it indicates that the Pleistocene fauna of northeastern Missouri has survived to the present essentially unchanged.

A brief paper by Grimm (1968) reported *Catinella oklahomaram* Grimm from Barry County. In the same year, a rather extensive study of terrestrial gastropods from part of Jackson County was completed (Hershey, 1968). A year later, attention was turned to the northern part of the state with two short preliminary reports (Miles, 1969; Miles and Reeder, 1969). Recently Hubricht (1972a) reported all of the Missouri land snails in his collection, mostly from southern and central Missouri and (Hubricht, 1972b) discussed fossil *Gastrocopta* including some Missouri records.

A perusal of all of these reports brings home the paucity of information on northern Missouri land snails. Only the works of Sampson (1913) and Miles and Reeder (1969) reported substantial information with regard to recent land snail distribution north of the Missouri River.

GAZETTEER

The following is a list of localities in northeastern Missouri from which the specimens of the present study were collected. They are listed by counties, the latter arranged alphabetically. Each locality is assigned a number from one through 67. These assigned numbers are used in the Accounts of Species to indicate the localities where each species occurred.

1. Adair Co. On Chariton River, 1.0 mi E Novinger.
2. Adair Co. Thousand Hill State Park, 4.0 mi W and 3.0 mi S Kirksville.

3. Audrain Co. On state rt. J, 6.4 mi W of U.S. Rt. 54.

4. Audrain Co. North city limits of Mexico (on Missouri Rt. 15).

5. Audrain Co. 1.2 mi W and 3.9 mi N Mexico (on Missouri Rt. 15).

6. Boone Co. 0.5 mi E Boone-Howard County line on U.S. Rt. 40.

7. Boone Co. 2.5 mi E and 0.5 mi N Hallsville (on Missouri Rt. 124).

8. Boone Co. 0.6 mi S and 3.6 mi E Rocheport (junction of Interstate 70 and state rt. O).

9. Callaway Co. 1.8 mi W Wainwright (on Missouri Rt. 94).

10. Callaway Co. 4.0 mi S and 0.2 mi W Toledo (on state rt. O).

11. Callaway Co. 3.7 mi W and 0.3 mi S Portland (on Missouri Rt. 94).

12. Callaway Co. 3.0 mi S and 3.8 mi E Toledo (on state rt. O).

13. Callaway Co. Auxvasse River, 1.3 mi E and 0.7 mi N Kingdom City (on U.S. Rt. 54).

14. Knox Co. 1.7 mi N Shelby County line (on Missouri Rt. 15).

15. Knox Co. 3.0 mi N of Missouri Rt. 156 on Missouri Rt. 15.

16. Lincoln Co. 0.6 mi S and 0.8 mi E Truxton (on state rt. A).

17. Lincoln Co. 3.1 mi W and 3.7 mi N Troy (on state rt. H).

18. Lincoln Co. 2.5 mi W and 3.3 mi N Troy (on state rt. H).

19. Lincoln Co. Cuivre River State Park, 2.0 mi E and 2.0 mi N Troy (on Missouri Rt. 147).

20. Lincoln Co. Cuivre River State Park, 3.2 mi S and 2.0 mi N Troy (on Missouri Rt. 147).

21. Lincoln Co. 3.5 mi S and 0.8 mi E Elsberry (junction of state route M and Missouri Rt. 79).

22. Lincoln Co. 0.8 mi W and 2.7 mi N Elsberry (on Missouri Rt. 79).

23. Marion Co. 1.3 mi S Hester (on state rt. A).

24. Marion Co. 1.8 mi W Palmyra (on Missouri Rt. 168).

25. Marion Co. approx. 2.0 mi NW Woodland (on state rt. E).

26. Marion Co. 2.5 mi S and 0.5 mi W Woodland (on state rt. E).

27. Marion Co. 2.8 mi N Ralls County line (on Missouri Rt. 79).

28. Monroe Co. 3.3 mi E and 2.5 mi N Granville (on Missouri Rt. 15).

29. Monroe Co. 0.2 mi S and 3.2 mi E Middle Grove (northern junction of state rt. M and Missouri Rt. 151).

30. Monroe Co. 2.5 mi S Paris (on Missouri Rt. 15).

31. Monroe Co. 1.5 mi S and 4.7 mi E Paris (on Missouri Rt. 154).

32. Monroe Co. 0.7 mi S and 1.6 mi W Florida (on state rt. U).

33. Monroe Co. Mark Twain State Park, 0.3 mi S and 0.3 mi E Florida.

34. Monroe Co. 2.3 mi S and 2.3 mi W Florida (on Missouri Rt. 154).

35. Monroe Co. Mark Twain State Park, 0.5 mi S and 0.5 mi E Florida.

36. Monroe Co. 6.5 mi S and 0.8 mi E Paris (on state rt. D).

37. Monroe Co. 1.2 mi W and 0.6 mi N Santa Fe (on state rt. D).
38. Montgomery Co. 4.0 mi E Wellesville (on state rt. CC).
39. Montgomery Co. 1.0 mi S and 1.0 mi E Big Spring (on Missouri Rt. 19).
40. Montgomery Co. Graham Cave State Park, just E of Danville exit on Interstate Rt. 70).
41. Montgomery Co. on state rt. Y, 6.0 mi E Missouri Rt. 19.
42. Pike Co. 1.7 mi S and 3.4 mi W Frankford (on state rt. C).
43. Pike Co. 2.0 mi SE Louisiana (on Missouri Rt. 79).
44. Pike Co. 3.0 mi S and 3.5 mi E Louisiana (on Missouri Rt. 79).
45. Pike Co. 3.7 mi S and 4.5 mi E Louisiana (on Missouri Rt. 79).
46. Pike Co. Cuivre River, 1.0 mi S and 1.3 mi W Ashely (on Missouri Rt. 161).
47. Pike Co. 2.4 mi S and 1.0 mi E Ashely (on state rt. KK).
48. Ralls Co. 4.1 mi S and 2.0 mi W Huntington (on state rt. A).
49. Ralls Co. 6.0 mi N Perry (on state rt. J).
50. Ralls Co. 4.6 mi N Perry (on state rt. J).
51. Ralls Co. 0.5 mi W and 2.4 mi N Perry (on state rt. J).
52. Ralls Co. 3.8 mi S and 3.6 mi E Center (on state rt. F).
53. Ralls Co. 4.1 mi E and 2.9 mi N New London (junction of state rt. T and Missouri Rt. 79).
54. Randolph Co. Junction of U. S. Rt. 24 and state rt. Y (near Monroe County line.)
55. Randolph Co. Approx. 1.5 mi E Leveck Mill (on state rt. J).
56. Schuyler Co. 0.5 mi W of U.S. Rt. 136 on state rt. AA.
57. Schuyler Co. 0.8 mi E Chariton River on U.S. Rt. 136 (near Livonia).
58. Shelby Co. 1.4 mi N of Shelbina (at city park).
59. Shelby Co. 3.7 mi N of Shelbyville on Missouri Rt. 15.
60. Shelby Co. 6.2 mi N Duncan's Bridge (on state rt. J).
61. Shelby Co. North Fork of Salt River, 4.3 mi S Shelbyville (on Missouri Rt. 15).
62. Warren Co. 1.2 mi N Warrenton on Missouri Rt. 47.
63. Warren Co. 0.7 mi S and 0.5 mi E New Truxton (on state rt. A).
64. Warren Co. 0.3 mi S and 0.3 mi W Case (on Missouri Rt. 94).
65. Warren Co. 2.5 mi W and 1.0 mi N Treloar (on Missouri Rt. 94).
66. Warren Co. 0.3 mi NE Treloar (on state rt. N).
67. Warren Co. North city limits of Holstein (on state rt. N).

ACCOUNT OF SPECIES

Family Pupillidae

- Gastrocopta armifera* (Say): Adair (2); Boone (7); Callaway (9); Lincoln (21); Monroe (28, 37); Ralls (50); Shelby (58).

- Gastrocopta contracta* (Say): Adair (2); Boone (7, 8); Lincoln (21); Monroe (28); Montgomery (38); Pike (46); Shelby (61).
- Pupoides albilabris* (Adams): Adair (2); Ralls (50).

Family Strobilopsidae

- Strobilops labyrinthica* (Say): Audrain (3); Lincoln (21); Monroe (33); Montgomery (38); Ralls (49, 50, 52); Randolph (54); Warren (62, 63).

Family Succineidae

- Catinella vermeta* (Say): Audrain (3); Knox (15).
- Succinea concordialis* Gould: Boone (6).
- Succinea ovalis* Say: Adair (1, 2); Shelby (61); Warren (64).

Family Endodontidae

- Anguispira alternata* (Say): Audrain (4); Knox (14); Lincoln (16, 17, 19, 20); Marion (24, 26); Monroe (28, 29, 30, 31, 34, 35, 37); Montgomery (38, 39); Pike (42, 46, 47); Ralls (51); Schuyler (57); Warren (64, 65).
- Anguispira kochi* (Pfeiffer): Callaway (9); Lincoln (20); Montgomery (40).
- Discus patulus* (Deshayes): Warren (67).
- Helicodiscus parallelus* (Say): Adair (2); Marion (23, 27); Monroe (31, 32, 37); Montgomery (38); Ralls (51); Schuyler (56).

Family Zonitidae

- Retinella electrina* (Gould): Adair (1, 2); Audrain (5); Knox (14); Shelby (60); Warren (67).
- Retinella indentata* (Say): Adair (1, 2); Audrain (3, 5); Boone (6, 8); Callaway (12, 13); Knox (15); Lincoln (21); Marion (23, 26, 27); Monroe (31, 32, 33, 35, 37); Montgomery (38, 39, 41); Pike (47); Ralls (50, 51, 53); Randolph (54); Schuyler (56); Shelby (59, 61); Warren (62, 65, 66, 67).
- Paravitrea capsella* (Gould): Lincoln (20).
- Paravitrea simpsoni* (Pilsbry): Lincoln (17, 19).
- Euconulus chersinus* (Say): Warren (62).
- Euconulus fulvus* (Müller): Warren (64).
- Ventridens ligera* (Say): Monroe (34); Montgomery (39).
- Ventridens demissus* (Binney): Boone (6).
- Zonitoides arboreus* (Say): Adair (1); Audrain (3, 4, 5); Boone (7, 8); Callaway (10, 12, 13); Knox (15); Lincoln (16, 18, 19, 21); Monroe (29, 30, 31, 32, 37); Montgomery (38, 39); Pike (43, 46, 47); Ralls (50, 51, 53); Randolph (54); Schuyler (56, 57); Shelby (58, 59, 60, 61); Warren (66, 67).

Family Haplotrematidae

- Haplotrema concavum* (Say): Callaway (11, 13); Lincoln (19, 22); Marion (23, 24, 27); Monroe (33); Pike (42); Schuyler (57); Warren (65).

Family Polygyridae

- Stenotrema fraternum* (Say): Boone (8); Callaway (11); Lincoln (17, 19, 20); Marion (27); Montgomery (39, 41); Pike (42); Ralls (49, 50, 51, 53); Warren (64, 65, 66, 67).
- Stenotrema hirsutum* (Say): Adair (2); Boone (8); Marion (27); Monroe (30); Ralls (53).
- Stenotrema leai aliciae* (Pilsbry): Adair (1, 2); Knox (15); Lincoln (21); Monroe (29); Montgomery (38); Shelby (59, 60, 61).

- Allogona profunda* (Say): Lincoln (2); Marion (27).
Mesodon clausus (Say): Adair (2); Boone (6); Marion (23, 24); Monroe (28); Pike (47); Shelby (58).
Mesodon elevatus (Say): Lincoln (19); Marion (27); Montgomery (40); Pike (42, 43, 44, 45, 46); Ralls (52).
Mesodon inflectus (Say): Callaway (9, 10, 11, 12, 13); Lincoln (17, 19); Monroe (31); Montgomery (39, 41); Warren (62, 65, 66, 67).
Mesodon thyroideus (Say): Audrain (4); Callaway (11); Lincoln (19, 20, 21, 22); Marion (23, 24, 26); Monroe (29, 31, 32, 34); Montgomery (41); Pike (42, 44, 45, 46); Ralls (49, 52, 53); Randolph (55); Warren (62).
Triodopsis albolabris alleni (Sampson): Callaway (10, 12); Lincoln (20); Marion (23, 24, 25); Monroe (32, 33, 34); Ralls (49, 53).
Triodopsis fosteri (F.C. Baker): Lincoln (20, 22); Marion (24, 27); Monroe (35); Pike (43, 44); Warren (64).
Triodopsis multilineata (Say): Marion (27).

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CECILIOIDES ACICULA (MÜLLER): LIVING COLONIES ESTABLISHED IN TEXAS

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Many exotic land gastropods have become established in the United States. One of the smallest to be introduced is *Cecilioides acicula* (Müller), an achatinid snail native to central and western Europe (Pilsbry, 1909: 9). Previous U. S. records of established colonies include Florida, Maryland, and Pennsylvania; numerous interceptions have occurred at East Coast ports on materials from Europe and Central America (Dundee, 1974).

Previous U. S. records have been spotty and confused with the related *C. aperta* (Swainson). A Florida record by Bartlett in the A. Binney collection was reported by W. G. Binney (1885: 429), but no further specimens have been reported in the area (Pilsbry, 1946: 186). In the same area, Clapp (1915) reported *C. aperta* (as *C. gundlachi* Pfr.) two miles north of Miami, Florida. Maryland specimens of *C. acicula* occur along railroad tracks (Grimm, 1959, 1971). Pennsylvania records include stream drift (undoubtedly from a garden) reported by J.L. Baily (see Pilsbry, 1946: 186). Sine (1966) found a shell of *C. acicula* under a rock above another Pennsylvania creek. New Jersey specimens reported by Binney (1885: 429) were said to be *C. aperta* by Pilsbry (1946: 186).

Although much confusion appears to exist between *C. acicula* and *C. aperta*, shells of the two species are readily separable. Burch (1960) lists shell characteristics of *C. acicula* as follows: 1) abruptly truncate columella, 2) no parietal callus, 3) nearly flat-sided whorls, and 4) weakly striate surface. Pilsbry (1946: 186, fig. 89) illustrates both species side by side, thus demonstrating the differences between them. Pilsbry (1909) gives line drawings of several species of *Cecilioides*; all my specimens are like those of *C. acicula* (pl. 1, fig. 1, 2) and do not compare with those of *C. aperta* (pl. 4, fig. 73-74, as *C. gundlachi* Pfr.).

Previous Texas records of the genus *Cecilioides* are restricted to *C. aperta* except for the report of Hubricht (1960) of a single beach drift shell of *C. acicula* on South Padre Island, Cameron County.

Fullington and Pratt (1974) suggested that this might also be *C. aperta*. C. D. Orchard collected shells of *C. aperta* in and near San Antonio, Bexar County (Pilsbry, 1950). Fullington and Pratt (1974) added the counties of Cameron, Kendall, and Tarrant for *C. aperta*. Thus, the specimens collected by me are the first living specimens of *C. acicula* (Müller reported from Texas).

Collections of *C. acicula* were made at two widely separated localities in Texas. On 14 December 1974, several living specimens were collected in an urban garden in Brownsville, Cameron County. Snails were found in soil attached to the underside of a brick which was part of the garden edging. On 25 January 1975, a single living snail was found along the edge of a small boulder in the bank of Tannehill Branch in Bartholomew Park in northeastern Austin, Travis County. Brownsville is at the southern tip of the state while Austin is in the central section some 500 kilometers to the north.

The ability of *C. acicula* to survive the hot, dry summers characteristic of these areas is unknown. The Brownsville locality receives substantial supplementary watering while the Austin site is a semi-natural area in an urban setting. Residences occur within 40 meters of the latter locality; supplementary groundwater undoubtedly reaches the Austin site. *C. acicula* is a blind snail which lives underground and requires much moisture (Meeuse & Hubert, 1949; Pilsbry, 1909). Moquin-Tandon (in Binney, 1885) reported it in rock crevices as well as under moss and dead leaves. Meeuse and Hubert (1949) report that in open sites this species is found living 'at some distance below the surface of the soil.' These snails in central and south Texas most likely must burrow to some depths if they are to survive drought periods.

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REPRINTS OF RARE PAPERS ON MOLLUSCA:

LEFEVRE AND CURTIS CONTINUED

The last 30 pages of this issue of Sterkiana are a continuation of the reprint of *Studies on the Reproduction and Artificial Propagation of Fresh-water Mussels* by George Lefevre and Winterton C. Curtis (1912).

The reprinting of this important work began in Sterkiana 47 (September, 1972) and continued intermittently, as space permitted. The reprinting was interrupted because priority has been given to original papers. It was thought that a summary of the instalments so far published might prove useful. The complete list to date follows:

Title page and	105-114	STERKIANA	47
	115-134		48
	135-146		49
	147-154		51
	155-162		57
	163-192		61

The remaining 10 pages of text and the 12 plates will be reprinted in a future number of Sterkiana. Once the entire work has been reprinted in these pages, extra copies of all the instalments will be gathered together in one volume and offered for sale at a reasonable price.

A. L.

In the case of the carp, while the fish is admirably suited to carrying the hooked glochidia of *Anodonta* and *Symphynota*, we have never been able to secure a successful infection of the gills with the hookless glochidia of the genus *Lampsilis*. The disappearance of the hooked glochidia of *Anodonta* and *Symphynota* from the gills of the carp may be due to the pulling away of these large and heavy glochidia from the delicate gill filaments, as suggested in our consideration of the survival of the two types of glochidia upon fins and gills, respectively. The disappearance of the hookless glochidia of *Lampsilis* from both gills and fins of the carp can not be explained in this manner; it suggests rather that there may be some reaction of the host's tissues comparable to the processes which confer immunity against parasitic bacteria in higher vertebrates. With minnows (*Notropis cayuga* and *N. lutrensis*) 2 to 4 inches in length, we have not been able to secure any considerable infection with the glochidia of *Symphynota complanata*, for, although they will attach in large numbers during infection, they all drop from the fins and gills within a few days. The fins of these minnows are much more delicate than those of the carp, and the explanation is perhaps that so large a glochidium is easily torn away; but the large-mouth black bass has hardly a delicate fin, and for this fish we have records of infections where no glochidia of *S. complanata* became attached during an exposure sufficient for the attachment of many to the gills. In this latter case, the extreme activity of the fish must be considered as a factor which might keep the hooked glochidia from attachment to the fins.

Darters (*Etheostoma caeruleum spectabile*) 1½ to 2 inches in length can not be infected successfully with the glochidia of *Lampsilis*, for although they may fasten so thickly to the fins that many fish die during the first day after their exposure, the surviving fish will slough off considerable portions of the fins and within a week show only the healed and regenerating parts as an indication of their recent experience. The gill slits were so small in these fish that only an occasional glochidium was found upon them.

Such cases as these are of great importance and should be followed up to determine whether the simple mechanical conditions like over-infection, delicacy of fin, or configuration of the mouth parts can give a satisfactory explanation; or whether the histological changes of which the fish is capable, under stimulation by the glochidium, must be regarded as the cause of its immunity. We have not carried out a sufficient number of experiments to feel sure that the simpler explanations can be excluded. In any case, it is interesting that fish like the minnows and darters, which live close to the bottom, are not likely to become heavily infected by some of our most common glochidia.

BEHAVIOR OF FISHES DURING INFECTION.

The behavior of the fish during infection is a matter of some importance and has been already mentioned in an incidental manner. The rock bass, large-mouth black bass, and blue-gill sunfish, which are very active and which consequently exhibit powerful respiratory movements, are well adapted to artificial infection, and the proper suspension of the glochidia in the water is secured by the movements of the fish alone. The crappie, which are sluggish and easily killed by handling, require some special device to

insure the optimum infection and are not well suited for work on a large scale because of their behavior during infection. Fish which rest upon the bottom are sometimes not so favorable as they might seem because they do not move about enough to keep the glochidia in motion. While other features may be of greater importance, the behavior of the fish as affecting the distribution of the glochidia in the water should always be considered in deciding how useful any fish may be for purposes of infection.

INFECTION OF FISH IN LARGE NUMBERS.

The infection of fish in large numbers has been attempted with a view to determining the feasibility of extending the methods described above to wholesale infections of fish in a hatchery. As a result of two such attempts, we have no doubt that the successful development of the methods needed for infection in connection with the artificial propagation of mussels is only a matter of a little study in a properly equipped station. In December, 1907, about 25,000 small fish, under 6 inches in length, were placed at our disposal at the substation of the Bureau at La Crosse, Wis., and we were able on this occasion to infect by wholesale methods about 12,000 blue-gill sunfish, 3,700 yellow perch, 7,000 catfish, 2,000 crappie, 150 rock bass, 150 carp, and 100 roach. The greater number of these fish were infected with the glochidia of *Lampsilis ligamentina*, and, considering the fact that this was our first experience with so large a number of fish, the results were satisfactory. Smaller lots were infected with the glochidia of *L. anodontoides* and *L. recta*, the results giving every indication that these two species are essentially like *L. ligamentina* in the conditions of their development. The most successful infections were obtained by placing from 100 to 200 fish in a common galvanized iron washtub about two-thirds full of water. It was found that by adding to this body of water the glochidia obtained from two or three specimens of *Lampsilis*, and, when it seemed necessary, stirring the water by hand, tolerably constant results could be secured. Our difficulties were with over- rather than with under-infection. It was also possible to use the same tub a number of times without changing the water or adding to the stock of glochidia. Infection was also attempted by lowering the water in the large retaining tanks of the station to a depth of 4 inches and confining the whole number of fish which had been held in the full tank to this much smaller body of water. This method was found, in the absence of any attempt to keep the glochidia properly distributed through the water, quite inadequate and it became necessary to re-infect these fish in the tubs.

The mortality of the fish in these experiments was decidedly in excess of what one might expect for uninfected fish kept under similar conditions, a result clearly due to the over-infection which is the one thing most to be guarded against. At the end of six weeks some of the remaining fish were liberated in the west channel of the Mississippi River at La Crosse, a locality which we then believed might be suitable for this species of *Lampsilis*.

These infections were made under conditions of limited time and equipment and were wholly tentative, the aim being to make a test of our methods on a large scale. We revisited La Crosse a month after the infection, making careful examinations of the

fish and by shipping several hundred to Columbia were able to follow the development of the glochidia under the conditions in our laboratory. The results were probably as favorable as could have been expected under the circumstances.

In December 1908 a similar infection was attempted with about 6,200 large-mouth black bass and 3,800 crappie in the station of the Bureau at Manchester, Iowa. Upon this occasion the glochidia of *Lampsilis ligamentina* were again used in a majority of the infections, similar results being obtained with *L. anodontooides, recta*, and *ventricosa*, which were used for the minor infections. The black bass took the glochidia very readily and, having had only a limited experience with this species of fish, we gave them an amount of infection equal to that which had been carried successfully by the rock bass infected at La Crosse in the previous experiments. The infection was estimated at from 2,000 to 2,500 glochidia to a fish 4 or 5 inches in length. This proved entirely too heavy for the large-mouth black bass and the mortality among them amounted to about 55 per cent in the 30 days they were under observation. By the third day after the infection the hypertrophy of the gill tissue was so great as to be at once noticeable to the eye, and this was clearly the cause of death. An infection of not more than 1,000 glochidia per fish would have been more nearly the optimum load.

The crappie did not take the infection well despite longer exposure, the reason for this being the size of their gill slits and their behavior as already discussed, and we do not consider small fish of this species favorable for infection with any of the glochidia from mussels which are of commercial importance.

Thirty days after these infections the surviving fish were liberated in the Maquoketa River near Manchester, in a situation where the conditions were favorable for mussels and where the presence of a dam below the point of liberation, together with the absence of mussels of this species, made it seem possible that at some later period their appearance in this locality might be traced to this experiment. We have never made any subsequent examination of this stretch of the river with this in view, a thing which should be done by one of the parties engaged in the field work of the mussel investigation.

These two experiments in the wholesale infection of fish, while disappointing in some respects, give no indication of any insurmountable difficulties. It is fair to conclude that a little experimentation under hatchery conditions will make it as easy to carry the glochidia through their metamorphosis in large numbers as we have found it in small lots of fish kept in aquaria. The high mortality of the fish, being so clearly a matter of over-infection, is a thing which can be guarded against without reducing too greatly the load of glochidia which the fish may carry. It is then only a matter of discovering the most suitable species of fish and finding out how best to handle them in large numbers.

One thing which seems necessary for the rapid and uniform infection of fish in large numbers is a device which will bring about a uniform distribution of the glochidia in the water during the whole period of the fishes' exposure. Without something of the sort it will hardly be possible to handle large numbers of fish with constant and uniform results. We have tried, though not very extensively, two means of effecting

this. The first consisted of a two-bladed propeller fastened in the middle of the bottom of a tub and rotated slowly, there being enough space in the water above the blades to allow the fish room to escape the stroke. This device was not very satisfactory, but as it was operated by hand and the blades roughly constructed, effective use might be made of a more carefully adjusted mechanism of this type. A second and more promising device consists of a branched system of iron pipes bored with many small holes (text fig. 3), through which fine jets of water are forced out at the bottom of a tank. The amount of pressure in these fine jets can be easily regulated from the main supply pipe, and the height to which the glochidia will be driven from the bottom is thus controlled. The tank may be allowed to overflow at the top and the glochidia

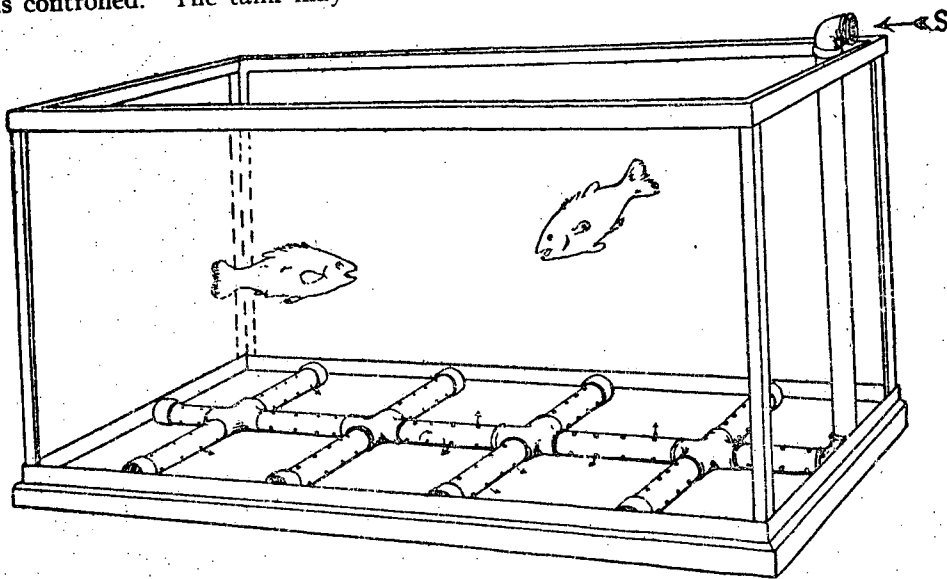


FIG. 3.—Apparatus for keeping glochidia suspended in water while fish are being exposed to them for gill-infections. Tap water entering at S issues in fine jets through the very small holes placed along the top and sides of the pipes on the bottom of the aquarium, and an even distribution of glochidia throughout the water is thereby maintained. By regulating the force of the water entering the pipes at S the glochidia are prevented from rising to the top of the aquarium and escaping with the overflow.

prevented from being carried off in the overflow by so adjusting the force of the jets that the glochidia will not rise quite to the surface. This device keeps the glochidia suspended in a very uniform way, and it may prove to be just what is needed for the uniform infection of large numbers of fish.

CONDITIONS NECESSARY FOR SUCCESSFUL INFECTION.

Three factors should be considered in attempting the infection of any species of fish with glochidia, namely, the uniform suspension of the glochidia in the water, the reaction of the glochidia when stimulated by mechanical or chemical contact with the fish, and the reaction of the fish's tissues after the glochidium has become attached.

In any attempted infection of fish in large numbers, careful tests should first be made upon a few fish in small dishes, with microscopic examination of the infected parts from fish killed during the time of infection and for several days following, or until it is clear that the glochidia have become safely established in their host's tissues. After even limited experience one learns approximately the number of glochidia needed and can determine roughly their suspension in the water by taking samples at random in a pipette, which when held against the light shows clearly the individual glochidia. During infection it is possible to pick out individual specimens and by lifting up the operculum of the living fish, examine the gills with a hand lens. The glochidia are then seen individually and the progress of the infection can be watched. Fin-infecting glochidia may be seen individually if a fish is placed in a small dish against a black background.

It is not difficult to determine by these means the optimum time for the exposure. When 100 fish 5 to 6 inches in length are taken and the contents of a single marsupium of a large *Lampsilis* is placed in an ordinary washtub, infections may be obtained somewhat as follows: Rock bass, exposed 30 to 40 minutes, 2,000 to 2,500 glochidia on gills of each fish; large-mouth black bass, exposed 15 to 20 minutes, 500 to 1,000 glochidia on gills; crappie, exposed 20 to 30 minutes, 200 to 400 glochidia on gills; yellow perch, exposed 20 minutes, 400 to 600 on gills; German carp (with *Anodonta*), exposed 30 to 40 minutes, 200 to 500 on fins. These figures are given as starting points for anyone attempting artificial infections and can not be taken as representing the results of precise determinations of optimum infections for the fish in question, because the means for determining the numbers and distribution of the glochidia have been only approximate. It will probably always be necessary, in the practice of artificial infection on a large scale, to have the fish examined microscopically by a properly trained observer, and this will be particularly true in the beginning of this work in hatching establishments, because the practical details of artificial infection on a large scale have yet to be solved.

DURATION OF THE PARASITIC PERIOD.

According to the experience of previous observers, the duration of the parasitic period varies inversely with the temperature of the water (Schierholz, 1888; Harms, 1907-1909). Although we have found this to be true in general, our experiments have not shown so definite a relation between temperature and parasitism as has been described by Harms, for example, and it is quite possible that other factors, which are obscure, exert a modifying influence upon the length of time the glochidia remain on the fish. Harms found that the glochidia of *Anodonta* completed the metamorphosis in 80 days at a temperature of 8° to 10° C; in 21 days at 16° to 18°; and in 12 days at 20°; while in the case of the hookless glochidia of *Unio* (which are gill parasites) the period was 26 to 28 days at a temperature of 16° to 17°. He is inclined to attribute the somewhat longer time required for the metamorphosis of *Unio* to the fact that the glochidia in this genus when discharged are in a less advanced stage of development than are those of *Anodonta*—a difference that exists between all hookless and hooked glochidia.

A few typical cases, selected from our records of infections are given in the accompanying table, which illustrates the far greater variability in the parasitic period than that observed by Harms.

TABLE SHOWING INFECTIONS WITH GLOCHIDIA.

Experiment.	Date.	Mussel.	Fish.	Exposure.	Young mussels liberated.	Duration of parasitism.	Av. temp. during parasitism.
HOOKEED GLOCHIDIA.							
1.....	Dec. 3, 1909	<i>Symphynota complanata</i> .	<i>Apomotis cyanellus</i>	Min.	Dec. 17-19.....	Days. 14-16	°C. 16.0
2.....	Dec. 17, 1909	do.....	do.....	15	Jan. 1-4.....	15-18	16.3
3.....	Jan. 7, 1910	do.....	<i>Pomoxis annularis</i> .	12	Jan. 18-21.....	11-14	16.0
4.....	Apr. 5, 1910	do.....	<i>Apomotis cyanellus</i>	30	Apr. 14-18.....	9-13	17.8
HOOKLESS GLOCHIDIA.							
5.....	Feb. 19, 1910	<i>Lampsilis ligamentina</i> ...	<i>Apomotis cyanellus</i>	9	Mar. 5-12.....	14-21	17.8
6.....	Mar. 6, 1909	do.....	do.....	10-15	Apr. 7-11.....	32-36	19.1
7.....	Apr. 8, 1909	do.....	<i>Micropterus salmoides</i> .	10-15	Apr. 27-May 1.....	19-23	20.3
8.....	Apr. 13, 1910	<i>Lampsilis subrostrata</i> ...	<i>Apomotis cyanellus</i>	8-15	May 2-8.....	19-25	18.1
9.....	May 2, 1910	<i>Lampsilis ligamentina</i> ...	do.....	7-10	May 15-26.....	13-24	18.1
10.....	May 3, 1910	<i>Lampsilis subrostrata</i> ...	<i>Micropterus salmoides</i> .	50	May 17-25.....	14-22	18.1
11.....	July 29, 1909	<i>Unio complanatus</i>	<i>Apomotis cyanellus</i>	7-14	Aug. 12-14.....	14-16	23.0
12.....	Aug. 5, 1908	<i>Quadrula plicata</i>	<i>Perca flavescens</i>	30	Aug. 17.....	12	24.4

In the case of *Symphynota complanata*, which has hooked glochidia essentially like those of *Anodonta*, the period varied from 9 to 18 days at average temperatures of 17.8° to 16° C., as compared with Harms's 21 days at practically the same temperature. At lower temperatures, about 10°, we have recorded a period of 74 days for *S. costata*.

The absence of a close correspondence between the temperature and the duration of the parasitism has been much more conspicuous in the case of hookless glochidia, which have shown not only a remarkable range in the period but a considerable irregularity in different experiments made at about the same temperature. The shortest period recorded by us was seven days in an infection of black bass with the glochidia of *Lampsilis subrostrata* and *L. recta* in April when the average temperature during the parasitism was 20.5°, but this unusual time was only observed in this one instance. A still more remarkable case, but at the opposite extreme, was an infection of black bass and crappie with the glochidia of *L. ligamentina* and *L. recta* which remained on the fish for 13 to 16 weeks. The infection was made in November and the young mussels were liberated during a period of about three weeks in the following February and March; during the parasitism the temperature varied from about 16° to 18°. The cause of the extreme duration in this case is not known, for in no other experiment at the same temperature has the parasitism lasted for more than 25 days.

As may be seen in the table, with hookless glochidia (aside from the extreme cases mentioned) the variation in the period has been from 12 to 36 days at average temperatures ranging from 24.4° to 17.8°; but even at practically the same temperature the difference may be quite marked, as in experiments no. 8 and no. 9. Experiment no. 6 should be noticed as being a case in which, contrary to expectation, quite a long period (32 to 36 days) was recorded at 19.1°, whereas in other experiments (no. 5 for example) the time was only 14 to 21 days at the lower temperature of 17.8°.

It would seem clear that, although within certain wide limits the duration of the parasitism is dependent upon the temperature of the water, nevertheless other factors may enter into the case to either accelerate the metamorphosis or prolong it over a period which is much longer than the usual duration of the parasitism. These factors would seem to be associated with individual physiological differences in the interaction between the fish and the parasite and are probably nutritive in nature, for on one and the same fish some glochidia may remain several days longer than others.

As may be seen from an examination of the table, in which the period of liberation is given in each experiment, not all of the young mussels leave the fish at the same time, but, on the contrary, the liberation may occupy a week or more. Harms found that it required from 5 to 6 days, the greater number leaving the fish during the middle of the period. Our experience has usually been in accord with these observations, but we have found the period to be somewhat more variable, from 2 to 11 days, or even much longer.

IMPLANTATION AND CYST FORMATION.

As has been described, the glochidium attaches itself to the fish by closing its shell firmly over some projecting region which can be grasped between the valves, like the free border of a fin or a gill filament. In so doing, a portion of the epithelium and underlying tissue, including blood vessels and lymphatics and varying in amount with the extent of the "bite," becomes inclosed within the mantle space of the glochidium. This tissue early disintegrates into its cellular constituents, which are taken up by the pseudopodial processes of the larval mantle cells, and, as Faussek (1895) has described, are utilized as food during the early stages of metamorphosis. In figure 60, plate xv, drawn from a glochidium six hours after attachment to a fin, the disintegrated tissue, consisting of loose epithelial cells, blood corpuscles, and fibers which lie scattered in the mantle cavity, is seen in the process of being ingested by the mantle cells. Figure 61, plate xv, shows a later stage, 24 hours after attachment, in which the detritus has been entirely taken up, and the mantle cells are now heavily charged with food material.

Almost immediately after attachment proliferation of the epithelium begins as the initial step in the formation of the cyst which eventually incloses the entire glochidium. The overgrowth of the larva has been described by Faussek (1895) and Harms (1907-1909) as a healing process on the part of the fish's tissues, resulting from the irritation caused by the wound. The proliferation starts around the line of constriction produced by the pressure of the edges of the valves on the epithelium, and, since the glochidium lies between and prevents the immediate closure of the lips of the wound, the extending

epithelium is forced to slide up over the surface of the shell on all sides, until the free margins meet and fuse over the back of the larva, as may be understood by reference to figures 59 to 61, plate xv, and 35 to 38, plate xi.

So rapid is the overgrowth, especially in the case of implantation on the gills, that it would seem that something more than the mere mechanical irritation produced by the glochidium is concerned in causing the proliferation of the epithelium. We have, therefore, carried out a series of experiments with a view to determining whether or not a chemical stimulus is provided by the larva, and by using various methods have studied the action of glochidial extracts on the epithelium of both fins and gills. The results have been entirely negative, although the question has by no means been settled by the experiments which have been thus far attempted. By further improvements in the technique, some of the difficulties involved in the investigation, which is still in progress, may be overcome.

The process of implantation and cyst formation may be readily observed on the filaments of an excised gill, which under favorable conditions will live long enough in a dish of water to enable one to see the glochidium completely covered by the proliferated epithelium. Figure 54, plate XIII, drawn from the living excised gill, shows the distal end of a single filament bearing a glochidium of *Unio complanatus* which has become nearly covered by the walls of the cyst. In this case the gill was cut from the fish two hours after the infection and the drawing was made an hour later; immediately after the excision of the gill this particular glochidium was hardly half covered. The same glochidium was kept under observation, and two hours later (five hours after the infection) the sketch was made which is reproduced in figure 55, plate XIII. By this time the cyst, which is seen to have very thick walls, was completed, and formed a prominent mass near the end of the filament. Shortly afterwards the tissues of the gill began to disintegrate, but for at least three hours they remained alive and the proliferation of the epithelial cells proceeded rapidly, the entire process of cyst formation taking place in a perfectly normal manner.

The histological changes which the epithelium undergoes in the formation of the cyst have been studied in this laboratory by Miss Daisy Young, and, as her results will soon be published in detail, only a brief reference will be made in this place to the essential points involved in the cellular changes occurring during implantation of the glochidium.

Figure 59, plate xv, shows a very early stage, 15 minutes after attachment, in the formation of the cyst on the fin of a fish which had been infected with the glochidia of *Symphynota complanata*. The section is taken transversely through the glochidium and the free border of the fin on which the parasite has a firm grip. The mass of tissue, consisting of epithelial cells, connective tissue, and blood vessels in the mantle chamber of the glochidium, is the edge of the fin which was inclosed between the valves when attachment was effected. Already the proliferation of the epithelium is beginning in the neighborhood of the constriction, where two mitoses may be seen on the right in the figure. At the edges of the wound caused by the closure of the shell some of the

epithelial cells are undergoing degeneration, while on the left of the section quite a patch of these cells is sloughing off, a not infrequent occurrence. The region of most active growth and multiplication of cells is just below the line of constriction, and, as the cells at this level increase in number, they appear to push those lying above them up over the outside of the shell, so that the actual covering of the glochidium is due largely to this mechanical gliding of the epithelium over its surface. Sections give no conclusive evidence of amitotic division, while mitoses are generally abundant in the region of active proliferation. An intermediate step in the process of implantation is illustrated in figure 60, plate xv, less highly magnified than the last figure, which shows a glochidium about half covered in six hours after attachment. The free edges of the cyst wall eventually meet over the dorsal side of the glochidium, where they then fuse. Figure 61, plate xv, shows a case of complete implantation on a fin at the end of 24 hours; now the epithelial covering is continuous and the glochidium entirely inclosed. The wall of the cyst is seen at this time to be quite thick, but it usually becomes thinner later on as the cells composing it flatten down. In the last two figures the mantle cells of the larva clearly show epithelial nuclei and cell detritus which have been ingested.

In figures 62 and 63, plate xv, two stages are represented in the formation of the cyst on gill filaments, taken at one hour and three hours, respectively, after attachment. The glochidia are those of *Lampsilis ligamentina*. In figure 62, plate xv, the proliferation has made some progress, especially on one side, and three or four mitotic figures are seen just below the glochidium and near the raw edge of the constricted epithelium. A large mass of the tissues of the filament is also shown in the figure inclosed within the mantle chamber of the glochidium. Figure 63, plate xv, represents a stage when the process is nearly completed and the edges of the epithelial covering have met but not yet quite fused. The cyst wall in this case is much thinner than that shown in figure 61, plate xv, but its thickness is quite variable.

In about one week after attachment, as a rule, the wall of the cyst begins to assume a looser texture, the intercellular spaces becoming infiltrated with lymph, and from this time on to the end of the parasitic period there is little further change in its structure.

Before liberation of the young mussel, the valves open from time to time and the foot is extended. By the movements of the latter the cyst is eventually ruptured, its walls gradually slough away, and the mussel thus freed falls to the bottom.

Portions of the wall of the cyst often adhere to the shell after liberation, while, if the young mussel has hooks, it may hang for a time by shreds of the fin in which the hooks are embedded, as seen in figure 24, plate ix.

METAMORPHOSIS WITHOUT PARASITISM IN STROPHITUS.

In a brief paper (1911) we have recently announced the discovery that in the genus *Strophitus* Rafinesque the metamorphosis takes place in the entire absence of parasitism, and, since the life history of this form is without a parallel in the Unionidæ, so far as is known, reference may be made again to the interesting conditions which obtain in its development.

It has been known for a long time that in *Strophitus* the embryos and glochidia are embedded in short cylindrical cords which are composed of a semitranslucent, gelatinous substance, and that these cords, which are closely packed together, like chalk crayons in a box, lie transversely in the water tubes of the marsupium. The blunt ends of the cords are seen through the thin lamella of the outer gill, which in this genus, as in *Anodonta* and others, constitutes the marsupium. The position of the masses of embryos, while contained within the gill, is so unusual that Simpson in his "Synopsis of the Naiades" established a special group, the Diagenæ, for *Strophitus*—the only genus of the family in which this peculiarity exists. In other genera the embryos are conglutinated more or less closely to form flat plates or cylindrical masses, each one of which is contained in a separate water tube and lies vertically in the marsupium.

So far as we are aware, Isaac Lea (1838) was the first to observe this interesting arrangement which he described and figured, rather crudely to be sure, in *Strophitus undulatus* (*Anodonta undulata*). In several subsequent communications (1858, 1863) he added further details and illustrations, and also mentioned the occurrence of the transversely placed cords, or "sacks," as he called them, in *S. edentulus*. He recorded the former species as being gravid from September until March, and described the extrusion of the cords from the female, as well as the remarkable emergence of the glochidia from the interior of the cords after the latter have been discharged.

The sacks were discharged into the water by the parent from day to day, for about a month in the middle of winter. Eight or ten young were generally in each sack, but some were so short as only to have room for one or two. Immediately when the sacks came out from between the valves of the parent, most of the young were seen to be attached by the dorsal margin to the outer portion of the sack, as if it were a placenta.

The essential points in these observations have since been verified by other investigators. Sterki (1898), following the suggestion of Lea, has called the cords, which differ strikingly from the conglutinated masses of *Unio* and other genera, "placenta," thus indicating that he considered them to have a nutritive function. He also described the extrusion of the glochidia, when placed in water, and their attachment to the cord "by a short byssus thread whose proximal end is attached to the soft parts of the young." He further states that the glochidia are inclosed in the placenta when the latter are first discharged, and that after their extrusion they remain attached for some time.

Strophitus edentulus, which Ortmann (1909) regards as identical with *undulatus*, is a rare species in all of the localities in which we have collected mussels, and, until recently, our only observations on this form were made upon a few gravid individuals which were taken in the Mississippi River near La Crosse, Wis., during the summer of 1908. Mention has already been made of our records with reference to the breeding season of *Strophitus*.

After verifying the main observations of Lea and Sterki, so far as was possible at that season of the year, we examined the glochidia carefully with a view to determining whether their subsequent life history would exhibit any peculiarities, as might be suspected from their relation to the cords. At that time we did not observe the normal

discharge of the cords by the female; but we removed them from the marsupium, placed them in water, and, after the glochidia had emerged (fig. 46, pl. XII), employed various means to bring about their attachment to fish. None of these attempts, however, was successful, although the fish were left in small dishes containing many cords for as long a time as 12 hours. In the light of these results, which indicated the inability of this glochidium to attach itself to fish, and in view of the fact that the cords so evidently seemed to be a nutritive device, we felt it to be highly probable that in this species the metamorphosis would be found to occur in the absence of parasitism—a prediction which has been recently verified.

On February 6, 1911, a single female of *Strophitus edentulus*, which had been kept in the laboratory since the preceding November, was seen discharging its cords from the exhalant siphon. The discharge continued until March 25, and during that time the cords were thrown out in varying numbers from day to day. They measured from 2 to 10 mm. in length and about 1 mm. in diameter, although they became more or less swollen after lying in the water for a time. Each cord contained from 10 to 24 glochidia arranged in an irregular row. In many cases the glochidia emerged from the cords in a few minutes after the latter were discharged, and then usually remained attached by the thread in essentially the same manner as has been described by Lea and Sterki (fig. 46, pl. XII). The thread, which is apparently a modified larval thread, is continuous at its distal end with the egg membrane, which generally remains embedded in the cord; so intimate, in fact, is the union between the two that at times the membrane, adhering to the thread, is dragged out of the cord when the glochidium is extruded, in which case, of course, the glochidium becomes entirely detached from the cord.

All attempts to infect fish with these fully formed glochidia were again unsuccessful, even when the exposure was of long duration. Within a few days the extruded glochidia died in spite of every effort to provide the most favorable conditions for their maintenance.

When the cords first began to be discharged, one of our students, Miss Daisy Young, happened to notice that not all of the larvæ were extruded, and that among those which remained in the cords some had lost the larval adductor muscle, possessed a protrusible foot, and showed other signs of having undergone the metamorphosis. Upon careful examination this was found to be true, and it was discovered that these young mussels—for such they undoubtedly are—are subsequently liberated by the disintegration of the cord *after having passed through the metamorphosis in the entire absence of a parasitic period*. We, therefore, have concluded that the emergence from the cords in the glochidial stage is premature, due possibly to some change which has taken place in the gelatinous substance surrounding them as a result of free contact with the water, or to release from the pressure to which they are subjected while in the marsupium. It is perfectly evident that these glochidia neither become attached to fish nor undergo any further development; they have simply come out too soon and are lost.

The young mussels, on the other hand, which have developed inside the cords, when liberated by the disintegration of the latter or removed directly by teasing, are found to

have reached as advanced a stage of development as is attained by any unionid at the time it leaves the fish. They closely resemble the young of *Anodonta* at the close of the parasitic period, and upon examination have been found to possess the following structures: The anterior and posterior adductor muscles; the ciliated foot; two gill buds on each side; a completely differentiated digestive tract, including mouth, esophagus, stomach intestine, and anus; liver; the cerebral, pedal, and visceral ganglia; otocysts; the rudiments of the kidneys, heart, and pericardium; while they also show a slight growth of the permanent shell around the margin of the shell of the glochidium (fig. 45, pl. XII). The larval muscle has completely disappeared, although some of the mantle cells of the glochidium, as well as the hooks of the shell, are still present. They crawl slowly on the bottom of the dish by the characteristic jerking movements of the foot, after the manner of the young of other species at a corresponding stage, although the valves of the shell gape more widely apart and the foot is shorter and less extensible. We have not succeeded as yet in keeping them alive for more than 10 days, but it is difficult in the case of any species to maintain young mussels of this age under laboratory conditions.

One of these young mussels after removal from the cord is shown in figure 45, plate XII, in which many of the organs of the adult or their rudiments are clearly indicated. A comparison will show that it is essentially as advanced in its development as the young of *Anodonta* when it is liberated from the fish (cf. Harms's figures, 1909, and also our fig. 47, pl. XII, of *Symphynota costata*).

The conclusion is inevitable that we have here to do with a species which has no parasitism in its life history, although the presence of hooks and other typical glochidial structures would indicate that it has originated from ancestors which possessed the parasitic stage like other fresh-water mussels. The cord is undoubtedly to be interpreted as a nutritive adaptation which arises in the marsupium during the early stages of gravidity, since the young embryos are at first contained in an unformed viscid matrix and the cords are a later product.

The whole history of this exceptional species warrants a more detailed study, and Miss Young is now engaged in such an investigation. When her work is completed we hope that it may include the entire course of development, the method of formation of the cords, and the rearing of the young mussels during a much longer period than has thus far been possible.

V. ATTEMPT TO REAR GLOCHIDIA IN CULTURE MEDIA.

Since the relation of the glochidium to the fish is essentially a nutritive one, it seemed to us that it should be possible to rear the larvæ through the metamorphosis artificially, provided a suitable nutritive medium could be found, and accordingly a series of experiments, with this object in view, were undertaken at our suggestion by one of our students, Mr. L. E. Thatcher. Although the result has thus far been entirely negative, we have not despaired of ultimate success, and, since the experiments are to be continued, a brief mention of the methods employed may be made in this place.

It was natural to suppose that the blood of the fish would offer the most favorable nutritive conditions for the development of the glochidia, and hence it has been used in most of the experiments, which, moreover, have been made in the spring, when the water in the laboratory was comparatively warm and the metamorphosis, if it had occurred, would have taken place as rapidly as possible.

The glochidia of *Lampsilis ligamentina* and *L. subrostrata* were carefully removed from the marsupium with a sterilized pipette and then repeatedly washed in distilled water in order to obtain them as free as possible from bacteria and other organisms. A drop of blood was next taken from a fish's heart and placed on a cover glass and a few glochidia immediately introduced into it. The cover glass was then inverted over a hollow slide containing a moist piece of filter paper, and the chamber sealed with vaseline. Every precaution was taken to avoid contamination by bacteria. As soon as the glochidia came into contact with the blood, of course they snapped shut in the manner already described and in doing so inclosed some of the corpuscles, which it was to be presumed would be ingested by the mantle cells. Although in some cases bacteria and infusoria, probably introduced with the glochidia, appeared, in a majority of the cases the cultures remained free from foreign organisms. In the latter event the glochidia lived for a few days, but finally died without showing any indication of further development. Experiments were tried with the blood of the frog and of *Necturus*, and also with extracts of fish's tissues, bouillon and other nutritive media. In all, however, the results were negative. The failure may possibly have been due to insufficient aeration, and experiments are now being devised in which oxygen is to be introduced into the moist chambers, and it is hoped that we shall yet succeed in rearing the glochidia in nutritive media through the metamorphosis.

VI. POST-LARVAL STAGES.

BEGINNING OF THE GROWTH PERIOD AND LIFE ON THE BOTTOM.

The changes occurring during the parasitism and by means of which the glochidium becomes transformed into the young mussel, ready for life on the bottom, are more properly described by the term development than by the word growth. The latter process becomes the conspicuous feature only when the miniature mussel has left the fish. From this time onward there are very few changes to which the term development may be strictly applied; for, with the exception of the outer gill, all the important organs of the animal have been laid down and have assumed something of their definitive structure (fig. 47, pl. XII).

As soon as they are liberated from the fish the young mussels become quite active and move about on the bottom of a dish by means of the foot (fig. 18, pl. VIII, and fig. 48, pl. XII), securing a hold by flattening the ciliated distal end against the bottom, and then drawing up the body after the characteristic fashion of lamellibranchs. In these movements the cilia of the foot play an active part; they beat vigorously while the foot is being extended, and apparently are effective in part at least in causing the protrusion. When

the foot reaches its limit of extension, the cilia stop abruptly and remain quiet while the forward movement of the body is taking place, only to resume their activity when the extension begins again. Figure 18, plate VIII, furnishes an excellent illustration of the various positions assumed as the young mussels crawl about in their twisting, jerking movements, and also shows the extent to which the shell has grown beyond the limits of the glochidial valves by the end of the first week of free life.

In the great majority of forms, as appears from the work of other investigators and our own observations, the mussel leaves the fish with only a very narrow margin of adult shell protruding beyond the glochidial outline. The shape is still that of the glochidium, although all other resemblances to this larval stage have disappeared. In the larva of *Symphynota costata* this margin of the adult shell is so narrow, even after some days upon the bottom (fig. 47, pl. XII), as not to protrude beyond the glochidial outline when the young mussel is slightly contracted. Exceptions to this supposedly universal condition have been observed by Coker and Surber (1911) in the young of *Plagiola donaciformis* and *Lampsilis (Proptera) lævissima*—forms in which there is a considerable growth of the definitive shell and presumably of the other organs during the parasitic period. These cases are unique so far as known, but in view of the small number of species which have been observed at all during this period of their existence other such exceptions may be looked for. No data bearing upon the duration or other conditions of the parasitic life are given in the paper in question, since the material studied was from the gills of a fish which had been preserved after its infection under natural conditions.

These stages immediately following the parasitism and until the mussels are about 20 mm. in length are less known than any others. They have seldom been found by collectors, and the reasons for this are made clear by the work of Isely (1911), to which we shall presently refer. Pfeiffer first observed and figured in 1821 a small shell having the glochidial outline still visible at its umbo, and other cases have been recorded, notably by Schierholz (1888). Such specimens were taken from nature and not from mussels artificially reared. Indeed, no one has yet succeeded in following individual specimens for more than a few weeks beyond the beginning of life on the bottom. Recently Harms (1907, 1908, and 1909) has obtained these stages, by rearing, more extensively than his predecessors and has figured (1907a, p. 811) the young of *Anodonta* with a very substantial increase in size at an age of six weeks after the parasitism, beyond which they could not be reared because of their destruction by small Crustacea. He concludes that the latter constitute a serious danger to the life of the young mussel.

In our own work repeated attempts have been made to rear these stages to a size which can be more easily handled, but without success. Specimens of *Symphynota costata* (fig. 47, pl. XII) and of *Anodonta cataracta* have been kept alive in small dishes containing green plants for a period of from one to two weeks after they had left the fish, and *Lampsilis ligamentina* and *subrostrata* for a period of six weeks. Little or no growth was observed after the first week. The two species of *Lampsilis* formed a conspicuous border of new shell during the first few days of bottom life (fig. 18, pl. VIII, and fig. 48,

pl. XII) and then ceased growing although they continued to move actively about. This would indicate that the difficulty lies in the lack of a suitable food supply. Crustacea were not observed to play an important rôle, though we do not doubt the correctness of Harms's observations in this respect.

Figures 18, plate VIII, 47 and 48, plate XII, will illustrate the appearance of the young mussels at this period and an examination of figure 47 will show how extensively the organs of the future adult have been laid down. Nothing remains to suggest the glochidium save the shell, and structure and habit alike indicate that the organism is now ready for a life on the bottom essentially like that of the adult.

JUVENILE STAGES AND THE ORIGIN OF MUSSEL BEDS.

For the sake of completeness, we shall discuss briefly at this point the present state of our knowledge regarding the stages between the one last mentioned and that represented by the young mussels over 20 mm. in length, which are often found upon the natural beds. In common with the experience of other collectors, we have seldom found mussels under 20 mm. It would therefore seem clear that these early stages are not at all common in localities where the slightly later stages and the adults are found. Isely (1911) has published a preliminary note upon his study of this "juvenile" period. We shall refer to his results rather fully, since there are no other recorded observations which deal with these stages save in the way of incidental reference to single specimens. This author states the problem by saying (p. 77) that: "Much difficulty was experienced in finding young mussels for study and experimentation. I have collected many specimens from the size of a nickel (20 mm.) to a quarter (24 mm.), but mussels under the size of a dime (17 mm.) have been rare." The latter he terms the "early juvenile" stages, including in this "the period following the time when the mussel completes the parasitic stage and leaves the fish to lead an independent life until it is about 15 mm. in length. This would cover, in most species, approximately the first year of independent existence. Other periods may be designated as later juvenile and adult life." He then reports the finding of 32 specimens in this early juvenile stage representing four genera and nine species, as follows: (1) *Lampsilis luteola*, two; (2) *Lampsilis fallaciosa*, one; (3) *Lampsilis parva*, four; (4) *Lampsilis gracilis*, three; (5) *Plagiola elegans*, one; (6) *Plagiola donaciformis*, sixteen; (7) *Anodonta imbecillis*, two; (8) *Ptychobranchus phaseolus*, two; (9) unnamed species, one.

All these specimens were found in places where the water was fairly swift, from 1 to 2 feet in depth, and on a bottom of coarse gravel, the particles of which were 10 to 25 mm. in diameter. They were anchored by the threads of a byssus gland "strong enough to support the mussel in a rapid current" and capable of sustaining "the weight of a number of small pebbles without breaking."

Here then, as Isely concludes, we have the clue to the habits and ecology of these so little-known stages. The finding of representatives from so many genera and species, both heavy and light shelled, under identical environmental conditions and the presence of the functional byssus in all cases is pretty good evidence that this is the normal

condition for early juvenile life in a wide range of forms. It is, moreover, interesting to find in the Unionidæ, as in many other lamellibranchs (e. g., *Mya* and *Pecten*) a functional byssus in the early stages, though there is no such organ in the adult.

As these results are very important and of convenience for reference in this paper we may here quote Isely's conclusions in full.

The facts noted above are closely related, not only to the ecology of the juvenile mussel, but also to the ecology of the adult.

1. They indicate the conditions essential for the most successful growth and early development of the Unionidæ. This kind of an environment gives a constant supply of oxygen and sufficient food; is frequented by suitable fish; is free from shifting sand and silt accumulation. Those mussels that drop from the fish in these favorable situations develop in large numbers, while the less fortunate, that drop in shifting sand and silt, die early.

2. In the study of the ecological factors that are inimical to mussel life more attention should be given to the consideration of the juvenile habitat. Absence of gravel bars and stony situations may sometimes explain the scarcity of the Unionidæ in certain streams and lakes where frequently water content has been thought the chief unfavorable factor.

3. It is a well-known fact that in many streams certain stretches of mud bottom are found loaded with mussels, while other areas, in the same stream, equally favorable from the standpoint of the habitat of the adult mussels, have only scattering specimens.

This distribution of the adults may be explained by the assumption (which is fairly well established by experimental study and will be discussed in a later paper) that the average mussel seldom travels far up or down the stream from the place where it begins successful development. Stretches favorable for juvenile development thus come to be the centers of dispersal in the streams where they occur. As a result, areas of mud bottom near these favorable habitats become loaded with mussels by migration.

4. In the study of the life history of the Unionidæ we may consider the embryonic, the glochidial, the parasitic, the early juvenile, and the adult as distinct periods for separate and special study.

These results of Isely's are clearly of very great importance in the problem of artificial propagation and it is to be hoped that his observations may be greatly extended in the near future. The number of different species which he has found is a most promising sign that he is on the right track, and we may hope that we shall soon reach a satisfactory understanding of this stage of the life cycle hitherto so little known.

At this point a word regarding the formation of beds may be opportune. It is a familiar fact that many species are most likely to be found congregated in beds which in some of the larger streams must have contained, before the shells came into commercial use, numbers of mussels which are hardly conceivable. Elsewhere in the stream the mussels are found scattered and wandering over the bottom. In the absence of any indication that the individuals of a species are in some manner attracted to one another, the simplest explanation of the formation of beds would be the same as that given in other cases of this sort. The conditions of food supply, current, character of bottom, etc., must differ considerably, and we may reasonably suppose that some places present the optimum conditions over an extended area and that in such a place a bed may be formed. As the mussels wander over the bottom they may by chance enter such an area of optimum conditions and will then move about less actively or come to rest, because in the absence of unfavorable conditions there is no stimulus to continued locomotion. The result is that individuals which enter are likely to remain and more keep

coming in. This kind of an explanation has been offered, by the students of animal behavior in recent years, to account for the formation of aggregates in a great variety of the lower organisms; and it appears the most reasonable one in such cases as the one in hand, where there is no evidence that the gregariousness is due to a definite recognition of the presence of other individuals.

RATE OF GROWTH.

It has been quite generally believed, by those investigators who have given their attention to this matter, that the mussel shell grows during the warmer months of the year and that in winter there is no appreciable addition to its margin. When growth begins again in the spring, the winter's rest has left a mark which appears as a dark line on light-colored shells or as a deeper groove in others where the color is not so conspicuous. Finer lines may be found between these rings of growth, but the latter, like the rings of a tree, mark the years. It is certain that these more conspicuous lines or "rings," as we may term them, indicate an alternation of growing and resting periods in the formation of the shell. It is not entirely certain that a single growth period must always correspond to a single year; for, when any lot of shells is carefully examined, some will be found in which the "rings" are distinct and strongly suggestive of an annual increment, while others of the same size may not show these rings in any such distinct fashion, and one is forced to conclude either that the annual rings, if such they be, are not always clearly to be seen or that some mussels may grow at a very different rate from others. The examination of any considerable number of shells leads to the belief that even if the annual-ring theory can be proved conclusively the rings are often not sufficiently distinct from the intervening lines to give an unquestionable record of the age.

Assuming that these rings, when clearly seen, do represent years, it would seem that the shell grows very rapidly during the first few years of the mussel's life and after that much more slowly. To judge from the lines alone, we should say that many of the large *Quadrula* shells had reached one-half their size in ten or a dozen years and then taken forty or fifty for the remainder, so closely set are their later rings of growth; and that shells of these species can not reach the most desirable commercial size in a less period than twenty or thirty years. Since these are regarded as the best of all button shells, the outlook may seem discouraging, because, like hardwood timber, the best shells take too long to grow.

The "ring theory" if proved would not, however, make the situation so discouraging as might seem from the species of *Quadrula*; for we have in some members of the genus *Lampsilis* shells which are almost if not equally desirable, and such evidence as we have from the rings indicates that shells like these may reach a commercial size in a very few years and that even forms like the quadrulas may become marketable within a period of four or five years.

In a recent paper, Israël (1911) has reported his conclusion that there is no winter-rest period and that more than one ring may be formed in a single year. This statement

is based upon the examination of the shell margin in mussels collected at various seasons of the year and of mussels which had been placed in wire inclosures on the bottom of the stream after having been accurately measured. The results from these plantings were fragmentary because of the accidental destruction of most of the inclosures. In one case, however, he found specimens which "when placed in the inclosure in August, 1909, and measuring 18 mm. in length, had reached, at the time of their examination in June, 1910, a length of 26 mm." He reports that other similar investigations are in progress, the results of which we shall await with interest.

Since no accurate observations on the rate of growth of fresh-water mussels have ever been made, we have attempted to secure definite data bearing upon this problem. The data obtained are derived from two entirely different lines of observation, as indicated by the headings of the sections which follow, and although meager they show that with better facilities it should not be difficult to follow individual mussels from the juvenile to the adult stages, and thus to determine their rate of growth in an accurate manner.

GROWTH OF MUSSELS IN WIRE CAGES.

While engaged in mussel investigations at La Crosse, Wis., during the summer of 1908, we collected a number of young clams (fig. 68, pl. xvii) belonging to 16 different species, and after weighing and measuring them accurately they were distributed in wire cages, which were then anchored by long wires in midstream to the piers of a bridge over the west channel of the Mississippi River opposite La Crosse. One hundred and sixty-three small mussels, belonging to the following genera and representing both thin and thick shelled forms, were planted out in this manner: *Alasmidonta*, *Anodonta*, *Lampsilis*, *Obliquaria*, *Obovaria*, *Plagiola*, *Quadrula*, and *Unio*.

Some of the cages contained only a single specimen of each species represented in it, in which case an absolute identification would be possible, should the cage be recovered later, while, if two or more individuals of a species were put in a cage together, only specimens of practically the same size were selected. In the latter case it would of course be impossible to subsequently distinguish an individual mussel, and only the average rate of growth could be determined for the individuals present. It was assumed that mussels of the same size and under the same conditions would grow at practically the same rate.

These plantings were made at intervals from June 29 to August 10, 1908. An opportunity did not present itself to make an attempt to recover the cages for over two years, but in November, 1910, Dr. R. E. Coker, who knew of the experiment, made a search while on a visit to La Crosse and was fortunate enough to find 2 of the 11 cages planted by us in 1908. One of the cages was deeply buried in the mud and all of the mussels in it were dead; as they showed little or no growth, they were evidently killed shortly after the planting. In the other cage, however, 6 living mussels were found, as follows: 3 *Lampsilis ventricosa*, 1 *Obovaria ellipsis*, 1 *Quadrula solida*, 1 *Anodonta imbecillis*. These 6 mussels, with the exception of the specimen of *Obovaria ellipsis*, were readily referred to definite individuals as recorded at the time the cage was set out. The comparative measurements and weights are given below.

June 29, 1908.	November 15, 1910.
<i>Lampsilis ventricosa</i> :	
(1) 45 by 36 mm., 16 grams.....	85 by 65 mm., 129.85 grams.
(2) 47 by 32 mm., 15 grams.....	81 by 57 mm., 115.5 grams.
(3) 47 by 30 mm., 16.5 grams.....	96 by 67 mm., 145.2 grams.
<i>Obovaria ellipsis</i> :	
(1) 52 by 52 mm., 59.1 grams.....	57 by 55 mm., 74.6 grams.
(The identification of this specimen is somewhat uncertain.)	
<i>Quadrula solida</i> :	
(1) 35 by 36 mm., 27 grams.....	45 by 46 mm., 46.3 grams.
<i>Anodonta imbecillis</i> :	
(1) 30 by 25 mm., 8 grams.....	61 by 28 mm., 13.3 grams.

In each case, the first measurement is the greatest antero-posterior length of the shell, and the second the distance from the top of the umbo to the ventral margin taken approximately at right angles to the lines of growth. An interesting and important feature of these specimens is the fact that the original margin is clearly indicated by a conspicuous line on the shell of each, and as the measurements within this line correspond with the original measurements, the identification is made sure for each individual.

We quote below an analysis of the results sent us by Dr. Coker, who made the second series of measurements after the recovery of the cages:

Lampsilis ventricosa.—They have increased in length by 34 to 39 mm. and in height by 25 to 37 mm., and they now weigh approximately 7, 8 and 9 times as much, respectively, as when first put out. Furthermore, the added area of shell is divided by a conspicuous dark ring and a less distinct ring which, one is tempted to assume, represent the periods of cessation of growth during the two winters. If such an interpretation is made, the growth was accomplished chiefly during 1908 and 1909, while during the present year (1910), the mussel having reached adult size, the growth has been considerably less.

Increase in size stated by percentage (present measurements compared with original measurements).
 Period, June 29, 1908, to November 15, 1910, 2 years, 4½ months:

	Length.	Height.	Weight.
Specimen no. 1..... per cent.....	188	217	812
Specimen no. 2..... do.....	172	178	770
Specimen no. 3..... do.....	204	223	880

The proportion of increase is slightly greater in height than in length, and the coefficient of increase in weight is, as might be expected, something like the cube of the coefficient of increase in either dimension.

Obovaria ellipsis.—The specimen has probably gained very little in length or height but materially in weight. It was nearer its adult size, is doubtless a slower growing species, and has probably gained in weight by increase of thickness of shell. But we are not so sure of the identity of this specimen.

Quadrula solida.—Has gained nearly 30 per cent in length and height and 70 per cent in weight.

Anodonta imbecillis.—Has more than doubled in length, with negligible increase in height, while it has increased 66 per cent in weight. This is particularly interesting as showing a marked change in form from the young to the adult.

Text figure 4, A and B, represents outline sketches of two of the three specimens of *L. ventricosa* described above, showing the exact size of each after the completion of the growth in the fall of 1910; the line marked *a* is the margin of the shell at the time the planting was made in 1908; while lines *b* and *c* are the two successive rings indicating cessation of growth. The two areas inclosed between these lines, representing the two chief periods of growth which have occurred, are not of equal extent in the three speci-

mens. In A they are of about equal width, while in B the second area is much greater than the first. The area between line *c* and the margin of the shell is in all three cases very narrow, showing that, as the mussel approaches the adult size, further increase in the shell must take place very slowly. The recovered specimen of *Q. solida* shows only one broad area of growth, and a very narrow one around the margin. This mussel was relatively much nearer adult size when put in the cage than the specimens of *ventricosa*.

Dr. Coker comes to the following conclusion with respect to the age of the specimens of *L. ventricosa*:

They are very significant, as they show clearly that growth is much more rapid than is generally suspected. Considering what the growth has been since the cages were put out, it is fair to assume that the specimens had only one year's growth at that time. That is to say, they were glochidia in the spring of 1907, and, since they must have been carried in the gills of the mother over the preceding winter, their complete age at this time (Nov. 15, 1910) is a little over four years.

Their age since the metamorphosis would therefore be about three years. Their probable history, on the above assumption, is as follows:

1. Eggs fertilized in August, 1906.
2. Glochidia discharged in spring or early summer, 1907.
3. Liberated from fish in summer, 1907.
4. Collected at age (since metamorphosis) of about one year and placed in cages June 29, 1908.
5. Recovered and remeasured, November 15, 1910.

The rate of growth of these individuals is probably typical of the genus *Lampsilis*, and the experiment indicates at least that commercial mussels may reach a marketable size in three years from the time they leave the fish. With the heavier shelled species (those of *Quadrula*, for example) the rate of growth is probably slower and a longer time must elapse before they are large enough for commercial use.

These experiments, meager as they are, are quite significant and furnish the first definite data, so far as we know, relating to the rate of growth of fresh-water mussels. With the proper facilities and the opportunity of examining the mussels at closer intervals, similar plantings could readily be made and exact information obtained on the growth of all the important species. To prevent the cages from being buried in the sand or mud would seem to be the chief precaution that should be taken in future experiments of this kind.

AN ARTIFICIALLY REARED MUSSEL.

Another experiment, although it does not throw light upon the question of the rate of growth in nature, might be mentioned in this connection on account of its significance for the problem of artificial propagation. A lot of black bass which had been infected with the glochidia of *Lampsilis ligamentina*, *ventricosa*, and *recta* at Manchester, Iowa, on December 2, 1908, were brought to Columbia, Mo., and placed in a large tank containing sand. The fish were left in the tank, where the young clams were allowed to fall off in the hope that some would survive and be later recovered. The sand was examined at intervals thereafter but never thoroughly, as the chance seemed very slight that any of the young clams were still living. On December 26, 1910, however, a single

small individual of *Lampsilis ventricosa* was found alive and active in the sand of the same tank. There can be no doubt that it was derived from the infection referred to, as no young clams of this species had ever been in the laboratory, and no subsequent infections were made in that tank. The exact size of this young mussel was 41 by 30 mm. on December 26, 1910. It is still alive, but as late as June, 1911, it was practically of the same size. Since it is over two years old, it is evident that it is quite a dwarf, and, had it been reared under favorable conditions, it undoubtedly would have been much larger by this time. The tank in which it has spent all of its life is supplied with tap water, which is obtained from deep wells and contains little that a mussel could utilize as food, and its small size is undoubtedly due to the fact that it has been underfed from the beginning. The shell shows no indication whatever of lines of interrupted growth, but this is only what might have been expected, as the mussel has never been exposed to low temperatures. It is evident, therefore, that it has been growing continuously, but very slowly, throughout its entire life.

This individual, however, is of no little interest, as it is

the first fresh-water mussel actually reared artificially from the glochidium, and in a sense

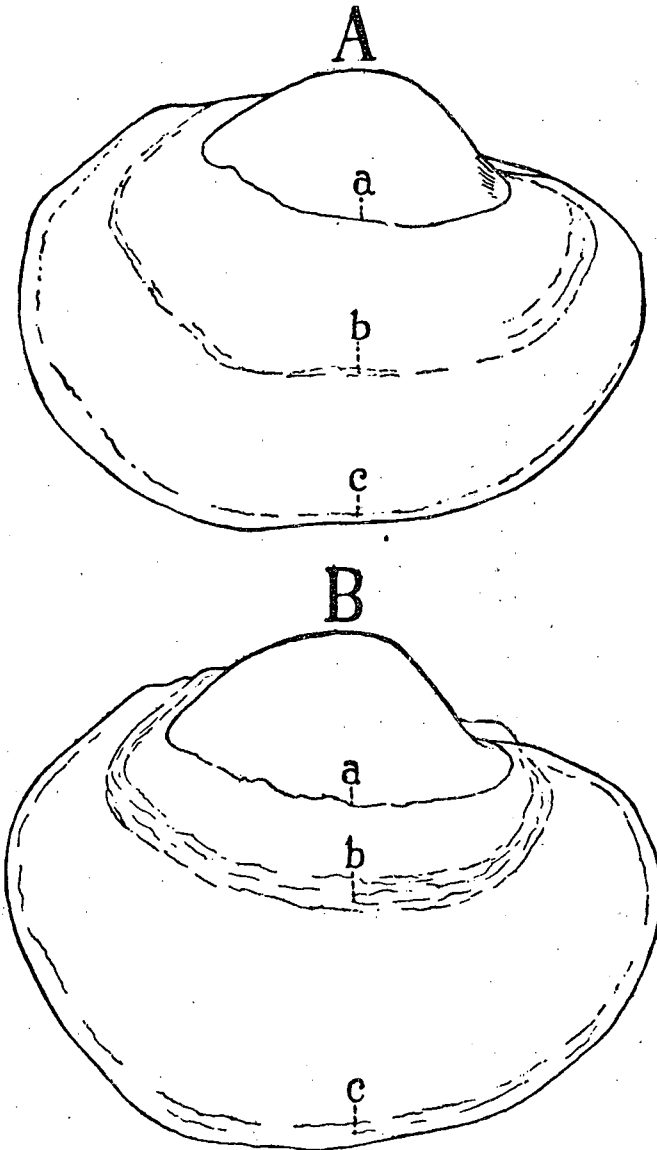


FIG. 4.—Two individuals of *Lampsilis ventricosa* recovered on November 15, 1910, after having been confined in a wire cage in the Mississippi River for two years and four and a half months. The line a is the original margin of the shell at the time of planting, June 29, 1908, and the lines b and c represent the "rings" which are due to the periods of cessation of growth. Natural size.

furnishes a demonstration of the feasibility of artificial propagation. Had the food supply in the tank been adequate, it would now be a mussel of about two-thirds the adult size.

THE ORIGIN AND AGE OF MUSSELS IN ARTIFICIAL PONDS.

A second line of evidence bearing upon the rate of growth has been obtained in connection with an examination of certain artificial ponds in the vicinity of Columbia, Mo. In this region it is customary for the farmers to construct, for the watering of cattle, ponds in which water is held the year round by the impervious clay soil. We have examined many of these small bodies of water and have records of the approximate, if not the exact, dates of their construction. In 12 of these ponds, the ages of which are from 5 to 40 years, we have found specimens of *Lampsilis subrostrata* and *Unio tetralasmus* in some numbers, and in two of the ponds the mussels are present in very great numbers.

The occurrence of the mussels in the different ponds has been considered, first, with a view to the question of their original introduction into a given pond, and, second, their rate of growth. The first of these two considerations will be discussed here as a matter of convenience, although it should more properly be considered in a section dealing with the introduction of mussels into favorable localities.

As to their origin in the ponds, we find the facts interesting because it is quite clear that a majority, if not all of the ponds, must have been stocked with mussels which were first introduced as parasites upon fish. The significant facts in this connection are: That we have never found a pond containing mussels but no fish, although there are a number of ponds containing fish in which we have thus far failed to discover any mussels, and that none of the ponds have outlets or other immediate connections with streams in which the mussels occur, but are situated, for the most part, on high ground far from the watercourses, making it impossible that the mussels could have worked their way into these bodies of water by any ordinary process of migration. Since it is very unlikely that persons have introduced adult mussels into so many places by intent or accident, the mussels must have appeared in these ponds by natural means and the most probable of these is their introduction while parasites upon the fish with which the ponds were stocked. The transportation of small individuals attached to the mud on the feet of birds or of terrestrial animals, so often suggested as a means of dispersal in a case like this, is a possible mode of origin, although it seems hardly a probable one in view of the excellent chance the mussels would have of being introduced while still parasites.

One of the above ponds, which is about 40 by 60 feet in area and 10 feet in depth, is particularly interesting since it contains great numbers of *Lampsilis subrostrata* and also of the sunfishes (*Lepomis humilis* and *Apomotis cyanellus*), which we have found in our laboratory experiments to be very favorable hosts for the glochidia of this mussel. The mussels are of all sizes and the pond has existed for many years. We do not know its exact age nor how long ago fish were introduced. The mussels were first discovered in 1907 and have ever since been found in abundance. Their success is doubtless due,

in large part, to the abundance of a fish favorable for their parasitism. Nothing in these specimens, nor in what we know of the history of this pond, gives a clue to the age of the mussels.

Another pond has great numbers of *Unio tetralasmus*. This pond was constructed in 1901 and during the first year was stocked with fish (the exact species unknown). In 1907 it contained a great many mussels as long as 4 inches, and since that year the largest individuals have slightly exceeded this size, which is near the maximum as we know it for this species. It is inconceivable that these unios were introduced as adults, for they are present in great numbers, and the farmer who owned the land was astonished to find them there four or five years after the pond was established, because it was near the entrance to his dooryard and he knew that no one had introduced mussels in any such numbers and that there was no watercourse connecting the pond with any creek in which mussels occurred. These mussels evidently came as parasites upon the fish with which this pond was stocked during the first year and they had reached a length of 4 inches in a period of five years. The abundance of the adults when the pond was six years old and the presence of some smaller specimens made it seem that more than one generation was represented, and hence some may have reached this size in a shorter time. The shell of *Unio tetralasmus* is light and is by no means a good button shell. Still it is not an impossibility, commercially speaking, for we have been assured by one of the leading button manufacturers, Mr. J. E. Krouse, of Davenport, Iowa, to whom we sent shells from which buttons were cut, that a marketable button could be made from them and would be made if there were no other shells available.

The appearance of *Lampsilis subrostrata* and *Unio tetralasmus* and no other species in all the ponds examined suggests the question, why have these two species and no others become established? If they were introduced as glochidia infecting fish, is it likely that the different lots of fish placed in so many ponds were infected solely with the glochidia of these two species? It seems much more probable that other mussels were introduced in the parasitic stages and that they were not able to survive long upon the bottom of these ponds. We have introduced large adult specimens of *Quadrula metanevra* and *Symphynota complanata* into one of the ponds in question and found some of them still alive after two years. This pond had a very soft mud bottom well covered with a layer of black muck filled with the soft coal soot from the smoke of a neighboring power-house chimney and seemed unsuitable for any variety of mussel. It had become, in spite of this, well stocked with *Lampsilis subrostrata* and is the pond referred to in detail in a previous paragraph. The survival here of these specimens of heavy shelled mussels for a period of two years shows that the adults are not at once killed even by unfavorable conditions, and we are therefore inclined to believe that when these species are introduced into the ponds on fish their destruction occurs in the early juvenile stages.

If a small body of water can be so fully stocked by the scant infection of glochidia obtained by fish in nature, we should be able to introduce mussels like these into a pond far more effectively by the use of fish which had been artificially infected and to rear

them to adult size within a short term of years. Accordingly, we have attempted the introduction of *Lampsilis ligamentina* into one of the ponds where no mussels had ever been found by placing in the pond several hundred fish well infected with the glochidia of this species; but several examinations of the mud and silt from the bottom, made during the 18 months following, have failed to show anything as a result of the experiment.

The conclusions drawn from these observations are encouraging because they indicate, first, that other species, like those of the genus *Lampsilis*, whose shells are of excellent quality for the best of buttons, may be reared to commercial size in about the same length of time, and, second, that restricted localities can be stocked with mussels by the introduction of fish infected with glochidia. The members of the genus *Lampsilis* have shells which are evidently not much heavier than the shell of *Unio tetralasmus*, a fact which better fits them for life upon soft bottoms where there is little current, and in such localities they often occur. They move about more actively than the heavier shelled species and this, doubtless, enables them readily to seek out the most favorable food conditions in any body of water, instead of remaining long in one place where the conditions are very stable, as do the heavier shelled species. The study of any mussel which can live in small ponds like those in question and from which button shells can be obtained should be followed up with care, since the extensive culture of mussels would be a far simpler matter in ponds than in any stream where high and low water and the shifting of the bottom might so largely interfere with the most carefully located beds. For this purpose the species of *Lampsilis* which give good button shells would seem the most desirable, because they are better adapted for the conditions and because our planting experiments indicate that they reach a marketable size in a shorter time than the quadrulas.

We feel that there is nothing discouraging in what is at present known regarding the rate of growth under the average natural conditions. Moreover, it should be remembered that in most invertebrates where the growth rate has been studied this may be modified to an astonishing degree by the food supply and that the actual size of an individual furnishes no trustworthy clue to its age. It is not at all unlikely that proper study of the food and other conditions necessary for the maximum rate of growth will enable us to obtain shells of commercial size in even slow-growing varieties within a reasonable number of years. To judge from the supposed annual rings of specimens taken in nature, *Quadrula ebena* may take from 20 to 30 years to reach, under natural conditions, the size which is most desirable. The question whether this is a necessity, or only a result of the poverty of food conditions which most mussels meet in nature, is one which must wait upon the proper scientific analysis of the mussel's food and rate of growth in this and other species, and there is no problem in connection with the attempted artificial propagation which has more pressing importance.

VII. INVESTIGATIONS ON THE UPPER MISSISSIPPI RIVER.

A brief reference may here be made to certain field studies which were carried on in connection with our mussel investigations during the months of June, July, and August, in 1908, on the upper Mississippi River. The Bureau of Fisheries put at our disposal for this purpose its substation, a small building provided with tanks and running water, at La Crosse, Wis., and also its steamboat, the *Curlew*, which not only furnished us with living quarters, but was of invaluable service for transportation from place to place on the river (fig. 65, pl. XVI). The boat, which is ordinarily used in the work of reclaiming young fish from the overflow of the river during the floods which occur in the spring and early summer, is equipped with aerated tanks, seines, and other apparatus and provided us with what was essentially a floating laboratory. With these facilities much was accomplished that would have otherwise been impossible. In addition to the usual crew of the *Curlew*, the party consisted, besides ourselves, of Messrs. W. E. Muns, Howard Welch, F. P. Johnson, and W. E. Dandy, students in the University of Missouri, who served as assistants.

The primary object of the expedition was a determination of the breeding seasons of the commercial species of mussels as far as possible at that time of the year and an examination of the depleted mussel beds in the upper Mississippi River, which have been all but destroyed as a result of the ravages of the mussel fisheries.

With a clamming outfit of our own (fig. 69, pl. XVII), consisting of a flat-bottomed skiff and "crow-foot" dredges—the usual apparatus employed by the mussel fishermen—we were able to secure thousands of mussels, which were examined microscopically for the purpose of determining their sex and the stage of development of the embryos. The data thus obtained furnished a mass of detailed information, especially with respect to those species which breed in the summer, but as they are incorporated in the account already given of the breeding seasons, there is no need to refer to the subject again.

The planting of young mussels in cages for a determination of the rate of growth was also made during this summer, with the result as described in a preceding section.

Some attempts were made to infect fish with glochidia, but this phase of the work was greatly interfered with by the high water of the river, which remained at flood stage unusually late in the summer of 1908 and made the seining of fish very difficult. Some infections, however, were carried out with the glochidia of a few summer-breeding species, the fish being retained in the tanks at the La Crosse station throughout the parasitic period and the duration of the parasitism determined.

A thorough survey of the mussel beds from Winona, Minn., to Lansing, Iowa, was made, and records taken at each locality where mussels were collected. No large beds at all were discovered, and in every instance where mussels were found indications of the ravages worked by the clammers were apparent. An account of the distribution of the species throughout this section of the Mississippi River and their relative abundance is not presented here, as the results of our observations in these respects will be incorporated in the work of the several field parties which have been engaged in the study of

the geographical distribution of the Unionidæ throughout the Mississippi Valley under the direction of the Bureau of Fisheries during the past four or five years.

While working in the neighborhood of La Crosse, we made a careful investigation of the west channel of the river at this locality, with a view to determining whether places of this nature presented favorable conditions for experimental rearing of young mussels. As is usually the case with the accessory channels of the river in this region, the west channel at La Crosse is dammed across its head for the purpose of confining the water in the main channel, and, although at high-water stages of the river the dam is submerged, during the greater part of the year the volume of water in the channel is greatly reduced and the current retarded. These dams, however, are never tight, and a greater or less quantity of water constantly seeps through them. A thorough study of this channel showed that it contained very few mussels indeed, and of those species that were found living in small numbers under these conditions, the majority belonged to *Lampsilis, ventricosa* being by far the most abundant form. Whenever a channel of the river is dammed, the slackening of the current causes an enormous sedimentation to take place, and in these "sloughs," as such obstructed channels are called, sand and mud bars and shoals have been formed to an extent varying with the length of time since the dam above them was built. The more sluggish species of mussels, like the quadrulas, are especially ill adapted to these conditions and are frequently buried and destroyed by the deposits of silt in the river, an occurrence of which we found abundant evidence. With the more actively moving and burrowing species, as those of *Lampsilis*, the case is different, for apparently they may adjust themselves more readily and by their far greater ability to move from place to place they may avoid the danger of being buried. We found little evidence that the quadrulas, for example, move about at all, while, on the contrary, the tracks of slowly wandering individuals belonging to the species of *Lampsilis* were everywhere conspicuous on the sandy bottoms of the shallow sloughs.

An interesting case of the destruction of mussel beds *in situ* by sedimentation is shown in figure 70, plate xvii, which is a photograph taken on the bank of a slough, near Muscatine, Iowa, which was exposed by a gully washed out by rains and cut directly through an extinct mussel bed. The photograph shows the surface of the cut where the mussels are exposed as they lie embedded in the muddy bank. The bed is buried under about a foot of mud, and it is interesting to note that the valves of the mussels are closed and lying together in pairs. The latter fact proves conclusively that this is not an old shell heap, for the valves of the shells would be found scattered and separated in that event, but a mussel bed which had once existed in the river near the bank. It was probably buried under the deposits of sand and mud which followed the building of the dam across the head of the slough. An investigation of the species represented in the bed showed that they all belonged to *Quadrula*, being chiefly *ebena*, *pustulosa*, and *trigona*, while not a single individual belonging to *Lampsilis* could be found in it. It is probable, as already stated, that it is the sluggish species, like those of *Quadrula*, that are the principal sufferers in catastrophies of this nature, and are caught and smothered in the process of sedimentation, while the propensity to wander possessed by the more active species

enables them to move out into deeper water when the deposit of silt becomes a menace.

The result of our study of the conditions obtaining in sloughs like the west channel at La Crosse, which are closed by dams at their heads, proves conclusively that such waters afford a very unfavorable habitat for mussels, and that therefore they are not adapted to experimental uses.

VIII. ECONOMIC APPLICATIONS.

It may not be inadvisable to discuss briefly certain applications of the results obtained in the foregoing investigations to the practical work of artificially propagating fresh-water mussels on a commercial basis. It must be emphasized at the outset that the ultimate object of the investigations—the restocking of depleted waters with commercial species of mussels—is not dependent for its realization solely upon the success of rearing mussels artificially from the glochidia, but that other methods of attaining the same end may be employed which are of equal, if not greater, importance.

PROTECTIVE LAWS.

Much can undoubtedly be done by securing the passage of laws by State legislatures for the closing of certain streams or sections of streams against all clamming for a period of years of sufficient length to allow of a natural increase of the mussels; by laws prohibiting the use of the ordinary "crow-foot" dredge, which takes immature and adult individuals indiscriminately,^a and by laws prohibiting the discharge of sewage and factory refuse in the neighborhood of mussel beds. By these and other protective measures of a legal nature, a great deal might be accomplished in the way of conserving the supply of mussels in the more important waters, but, since in the case of many rivers the control is in the hands of two or more States, the passage of such laws would require, to be effective, similar action on the part of several legislatures, and such cooperation might not be obtained without the greatest difficulty.

The utter futility of laws which would establish a closed season of the year against clamming is apparent in the light of our knowledge of the breeding seasons of the Unionidæ. We have already seen that there is no month in the year when some species are not bearing embryos or glochidia, and as species of commercial value are found in both groups—those with the long and those with the short period of gravidity—a closed season at any time would be of little or no avail. Several species of *Lampsilis*, for example, which bear embryos or glochidia from August to July, furnish valuable shells for the pearl-button industry, while the species of *Quadrula* and other summer breeders, gravid from May to August, supply shells of the best quality. Any law then, designed to relieve the situation, which prohibits the taking of mussels during a supposed breeding season is based on ignorance of the facts, for the entire year is the breed-

^a Mussels caught on a hook of the "crow-foot" are generally so badly injured internally in the process that, even if they are afterwards thrown back into the river, the majority probably die. A special form of hook has been devised by Mr. J. P. Buepple which is so constructed that small mussels can not be caught by it. The use of some such selective apparatus should be required by law.

ing time of the Unionidæ. A law, however, which would close a river or large section of a river for a period of five years or more would be most beneficial, for in that time much could be accomplished both by artificial and by natural means to restore normal conditions. Even artificial propagation, unaided by certain protective measures, could hardly become effective on however extensive a basis it might be carried on, for unless some means can be devised for saving the young mussels it is difficult to see how much headway could be made against the destruction of the supply. It therefore becomes of vital importance not only to make illegal the use of any apparatus which will catch or injure young mussels, but to see that the law is rigidly enforced.

Certain requisite conditions for the artificial culture of fresh-water mussels, based upon our knowledge of their life history and habits, may now be briefly referred to.

SELECTION AND MAINTENANCE OF A FISH SUPPLY.

Although only a comparatively few kinds of fishes have been thus far used in our experimental infections, and doubtless as our experience widens many more will be found to be favorable for the purpose, success has been attained chiefly with the black basses, rock bass, and the sunfishes. All of these fishes have proved to be extremely resistant to the injurious effects of gill infections (practically all of the commercial species of mussels have hookless glochidia, which are gill parasites); to be able to carry large numbers of glochidia through the parasitic period; and to be easily kept in confinement—three necessary conditions for the success of propagation. It is to be hoped that other fishes will be found to be equally useful, but at present those just mentioned afford the most promising material for the work. As has already been shown, some species of fishes are very easily killed even by light gill infections, while others, according to our experience, have resisted all attempts to bring about permanent implantation of glochidia on their gills. The latter is particularly true of German carp and catfishes.

Fortunately, the basses and sunfishes can be obtained in large quantities without serious difficulty. In the reclamation work conducted by the Bureau of Fisheries along the upper Mississippi River, immense numbers of young bass are annually seined from the sloughs and "lakes" into which they are carried when the river rises over its banks during the flood stages of early summer. When the water recedes these young fish are caught outside the banks of the river, and only the small fraction of them which is reclaimed in the seining operations is saved from the wholesale destruction (fig. 67, pl. xvi). There is no limit to this supply of material for the work of mussel culture, and doubtless extensive use will be made of it at the Fairport station.

Even more valuable for the purpose are the species of sunfishes which we have used (probably other species of the same group are equally good), for, besides being just as resistant and as readily infected as the black bass, they are more easily kept and are less subject to disease in confinement. An adequate number of breeding ponds, in which sunfishes could be left to multiply naturally, would insure a large and constant supply of these fish for artificial infections.

THE BEST SEASONS FOR INFECTIONS.

It has already been stated that the duration of the parasitic period of the mussel is inversely proportional to the temperature of the water. This fact is obviously important for mussel culture, since the longer the fish have to be kept while carrying the glochidia the greater is the loss from disease and other causes. The loss not only involves the fish but the potential mussels which they are nourishing as well. It therefore becomes desirable to reduce, as far as possible, the length of time that the infected fish must be retained, and this we have seen depends upon the temperature. Late spring and summer, consequently, are the seasons when the maximum efficiency from artificial infections should be obtained, for in the warmer water at that time the duration of the parasitism will be at the minimum—about two weeks or even less. The glochidia of *Lampsilis* are available all through the spring and as late as July, while those of *Quadrula* can be obtained during the summer months, and most of the commercial species of mussels fall in these two genera. Of course infections can successfully be made in the fall and winter and the duration of the parasitism reduced by keeping the water artificially warmed, but the difficulty of maintaining the fish alive under these conditions is greatly increased.

THE MUSSEL SUPPLY.

By far the greater number of species of commercial value, as has already been stated, belong to the genera *Lampsilis* and *Quadrula*, and, as both of these genera are widely distributed, practically all of the mussel-bearing streams of the Mississippi Valley may be drawn upon for a supply of material for cultural purposes. We have found that living mussels may be shipped even long distances with little or no mortality, especially in cool weather, and it is therefore possible to obtain breeding material from places at quite a distance from the station where the infections are to be made, should the local supply be inadequate. We have had on several occasions large numbers of gravid mussels shipped from Terre Haute, Ind., to La Crosse, Wis., to Manchester, Iowa, and to Columbia, Mo., with scarcely the loss of an individual, and have successfully used the glochidia obtained from them in infecting thousands of fishes.

According to our experience mussels thrive very well in confinement, in small ponds and laboratory tanks, and that without any special attention to a food supply. We have for years been keeping both pond and river forms alive in the laboratory for months at a time in tanks containing a few inches of sand on the bottom and supplied by tap water. Under such conditions mussels have frequently been retained in the laboratory from the fall to the following summer. It should therefore be an easy matter to keep mussels for breeding purposes in ponds with natural bottoms in any quantity desired, and, if the ponds are fed with river water, a natural food supply should be present in abundance.

Since, as has been pointed out above, the species of *Quadrula*, *Unio*, and other summer breeders abort their embryos and glochidia with astonishing ease when disturbed, it will be necessary, when making infections with the glochidia of forms exhibiting this peculiarity, to collect the material at a time prior to the fertilization of the eggs and to

allow them to enter upon the breeding season after being placed in the ponds of the station. We have had females of different species of *Quadrula* become gravid in the tanks of the laboratory after they had been held in confinement for weeks or even months, and therefore no difficulty should be encountered in obtaining a supply of glochidia from these forms under the conditions mentioned.

REARING AND DISTRIBUTING YOUNG MUSSELS.

After the fish have been infected, one of two things may be done in distributing the young mussels resulting therefrom: Either the fish, after having been retained in tanks or ponds until near the end of the parasitism, may be taken to the stream which is to be restocked and the clams allowed to drop off there, or the liberation may take place in ponds where the young mussels may be reared until they are of considerable size, say until they are a year old, and then distributed as desired. Both methods might be used successfully, but in the first case it is to be supposed that only a very small proportion of individuals thus liberated would succeed in reaching maturity, as they would be exposed to the same destructive agencies as are encountered under natural conditions. The difficulty and expense of transporting the infected fish, the mortality among the fish themselves resulting from shipment, and the subsequent loss of large numbers of the young mussels are considerations which lead one to regard this method as not an efficient one. It should be stated, however, that in using this method of distribution it would not be necessary to liberate the fish and thus lose them for subsequent infections, for they could be confined in wire-bottomed fish cars set out in the streams, and after the mussels had all fallen off and dropped through the bottoms of the cars the fish could be returned to the station. This would of course involve a very large amount of labor and much expense.

It would, therefore, seem to be a far more effective practice to retain the young clams in ponds with natural bottoms until they could with safety be liberated in the streams. After infection, in this event, the fish could be set free in these ponds at once, and allowed to remain there throughout the parasitism of the glochidia, at the close of which they could be seined out and made to do service again. Supplied with river water, the ponds should furnish an adequate amount of food for a practically normal rate of growth of the young mussels, which at the end of a year at latest should be of sufficient size to be placed in favorable localities in the rivers. When ready for distribution, the water in the ponds could be drawn off and the juvenile mussels raked carefully from the sand or mud. If properly packed, it should be possible to ship them in large numbers to considerable distances. It is only reasonable to suppose that a large proportion of the mussels thus reared would reach maturity after distribution, and it is certain that the number coming through would be far greater than would be the case if the first method should be pursued.