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THE AMNICOLIDAE OF MICHIGAN: DISTRIBUTION, ECOLOGY, AND TAXONOMY

BY
ELMER G. BERRY

ANN ARBOR
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FREDERICK M. GAIGE
Director of the Museum of Zoology
University of Michigan

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THE AMNICOLIDAE OF MICHIGAN: DISTRIBUTION, ECOLOGY, AND TAXONOMY*

INTRODUCTION

In 1933 a series of investigations was begun on snails belonging to the family Amnicolidae. Particular attention was given to the species in Michigan. The work was carried on for four years, and during this time information dealing with the character and comparative structure of the shells and comparative morphology of the animals, as well as data on distribution and ecology, was gathered. A complete synonymy has been listed for each species, and in certain instances the taxonomy has been revised. New techniques, which are believed to be an advance over older methods of study, are described. Since many of the findings are new or in disagreement with those of previous investigators, photographs rather than drawings are used as illustrations for the most part in this paper. The illustrations of the radulae are tracings made from photographs of the actual lingual ribbons; those of penes have been drawn from specimens which have been relaxed and killed with the animal extended.

Much useful material was available in the Division of Mollusks of the Museum of Zoology, University of Michigan, and I am particularly indebted to this institution for the use of its fine collection and library facilities so necessary to the study of this problem. During the course of the work helpful suggestions and criticisms were given by Mr. Calvin Goodrich and Dr. Henry van der Schalie, of the Museum of Zoology. Miss Crystal Thompson and Miss Dorothy Myers, of the University Museums, assisted with the photographic work. The text figures were drawn by Miss Grace Eager. Dr. George R. LaRue, of the Department of Zoology, kindly gave information on parasitological phases of the problem and also authorized the use of departmental microtechnique equipment. Dr. H. A. Pilsbry made valuable suggestions and assisted with facilities available in the Academy of Natural Sciences of Philadelphia. To these and others who gave encouragement and help I wish to express my sincere appreciation.

DISTRIBUTION OF THE FAMILY AMNICOLIDAE

These small operculate snails are among the most common of aquatic gastropods. They are found in various habitats and are distributed practically over the entire world. From paleontological findings it is known that the family is among the oldest of living fresh-water gastropods. More than seventy species and subspecies of Amnicolidae have been reported from

* A dissertation submitted in partial fulfillment of the requirements for the degree of doctor of philosophy in the University of Michigan.

North America alone. Of this number nine have been found in Mesozoic (Cretaceous) beds and sixty-seven in the Cenozoic. The few species reported from the Cretaceous do not necessarily imply that the Amnicolidae were less abundant then. Their scarcity in the earlier deposits is attributed to the comparatively few nonmarine Mesozoic outcrops that are known.

The Amnicolidae are world-wide in geographical distribution, a condition which hinders progress in gaining a complete knowledge of the family. Because of sparse collecting that has been done on this family in different parts of the world, it is impossible to determine at the present time in which of the hemispheres it is most abundant. Detailed information on the numbers of species occurring in various regions, which, if available, might give a clue to the center of geographical distribution, is lacking.

Few families of mollusks have a more diversified environment than does this one. Specimens belonging to this family have been collected from glacial cirques, more than 11,000 feet above sea level. In the Great Basin area of western United States they have been collected in a canyon creek from the headwaters to the stream's final termination—a brackish pool on the desert flat. They are abundant in rivers, fresh-water inland lakes, including the Great Lakes, and are continuous in their distribution from the headwaters of rivers all the way to the ocean. Furthermore, they are represented in tidal regions that are conditioned by both fresh and marine waters. They have been collected in rivers so near the ocean that the breaking of the waves could be easily heard, and where the tidal waters from the ocean have been seen rushing up an estuary changing the water from fresh to salt. A few genera of the Amnicolidae (*Peringia* and others) are truly marine.

To summarize: the family Amnicolidae is one of great antiquity, ranging in time from the Cretaceous to the present; it is cosmopolitan in geographic distribution and lives in a great variety of habitats.

CHRONOLOGY OF THE TAXONOMY OF THE AMNICOLIDAE

Thomas Say, the well-known pioneer student of invertebrates in America, was the first to give a name, popular or scientific, to an amnicolid mollusk. His specific designation was *limosa,* and it is interesting to note that this first described species has the widest distribution of all the New World amnicolas. Its colonies are also larger, as a rule, than those of any of the other species, and it occurs under more varied ecological conditions than does any other species. It was described in 1817 in Volume I of the *Journal of the Academy of Natural Sciences of Philadelphia.*

Say placed *limosa* under the genus *Paludina.* This was a genus established by Lamarck for fresh-water and brackish-water Mollusca which possessed an operculum and the lip of which was "simple, not dilated or re-

flected." Since the definition was very broad, the genus naturally came to include a great number of mollusks, varying exceedingly in shell characters, internal anatomy, physiological processes, habits, and habitats. Through the years it assumed the role of a catch-all. Authors who lacked an insight into contrasting characters, or an ability and industry to differentiate them, long continued to load the genus with a burden of specific names, many of which were generically unlike one another.

In 1837, when Michigan was admitted to the Union, one of the initial acts of the first legislature was the establishment of the State Geological Survey headed by Douglass Houghton as geologist and Abram Sager as zoologist. After two years of collecting and identifying, they published the first faunistic list, embracing both the vertebrates and invertebrates of Michigan. Although several species of minute snails are included in this list no species of Amnicolidae are cited. It seems reasonable to believe that many specimens of this family were collected in the survey. Either they were regarded as juvenile forms of the larger *Paludina* (such as *Campeloma*) or, possibly, they were put to one side for further study because of difficulties encountered in identifying these minute gastropods.

A period of more than twenty years elapsed before serious attention was again given to furthering knowledge of the Michigan fauna. During this interim, in 1841, the genus *Amnicola* was established by Gould and Haldeman and was placed in the family Peristomata. In 1861 a catalogue of the mammals, birds, reptiles, and mollusks of Michigan was published by Manly Miles. Three species of *Amnicola* are included in his list, *Amnicola grana* (which received all the very minute species, e.g., *A. walkeri* and juveniles of the larger species), *Amnicola lapidaria,* later placed in the genus *Pomatiopsis,* and *Amnicola pallida,* which was in all probability *A. limosa.*

In 1863 Theodore Gill described the family Amnicolidae, basing his conclusions on the shape of the animal, the foot, tentacles, branchiae, and genitalia. It was in 1865, however, that the greatest contribution to the study of the Amnicolidae of North America was made. In August of that year, William Stimpson published his "Researches upon the Hydrobiinae." He observed the close similarity of the members of the Amnicolidae with the extensive mundane marine family Rissoidae, and, therefore, united these two families under the name Rissoidae. Since the time of Stimpson little anatomical study has been made on either the marine family or the fresh-water Amnicolidae, although the number of species described, particularly of the latter, has made them major families in the Mollusca. One month after Stimpson published his researches on the Hydrobiinae, W. G. Binney published Part III of the "Land and Fresh-water Shells of North America." In this work he substantiated the research of Stimpson and employed the revised taxonomy of the preceding publication. These two classic works

form the basis for all subsequent study in this family. All of the then known species of North American Amnicolidae (twenty-six in number representing eight genera) were described and figured, the radulae were drawn and the dental formulae were given for nine species, and the genitalia of four other species were described and sketched.

Although adding little knowledge to the Amnicolidae of Michigan, these two works did provide a means by which students could more accurately classify specimens collected. Several faunal lists were published by various authors between 1865 and 1890: by Currier in 1865 and 1868, by Walker and Beecher in 1876, by Walker in 1879, and by DeCamp in 1881. In spite of the contributions of Stimpson and Binney the specimens collected by the above authors were often misidentified. DeCamp's list, for example, had thirteen species in four genera. At least ten of the thirteen species were incorrectly named.

One not familiar with the difficulties encountered in correctly classifying the Amnicolidae might unfairly criticize the above-mentioned list when it is contrasted with present knowledge of the Michigan species of this family. It must be remembered, however, that only one species listed by DeCamp is more than 5 mm. in height, and that the majority of the smaller species, although varying to a rather wide extent within a single species, have the same general contours. Three species which DeCamp very likely found were not described until after 1890. Even the best published works available at that time were very inadequate aids for one attempting to classify these minute mollusks. The figures of the shells were line drawings, for the most part, and the few radulae and genitalia which had been illustrated were inaccurate, because of limitations of the power of the microscopes.

The Amnicolidae of North America received a great deal of attention, especially during the latter part of the nineteenth century. More than twenty species were described, although few were figured. The major research work on this family was carried on by three of the foremost conchologists of that day, H. A. Pilsbry, C. E. Beecher, and Bryant Walker. In the descriptions of these new species Pilsbry frequently stated: "Illustrations of shell, operculum and dentition will be given in a Monograph of American Amnicolidae, now in preparation by Mr. Beecher and the writer." Unfortunately, this monograph never appeared. Pilsbry, to my knowledge, has not used the family name "Rissoidae" in referring to the group of gastropods under discussion. His reasons for not following Stimpson and Binney are, no doubt, contained in that monograph. The fresh-water rissoids of North America have been placed by Pilsbry and all subsequent workers in North America since 1881 in the family Amnicolidae.

From 1895 to 1912 many contributions, mostly in the form of short faunal lists of certain regions in Michigan, were published by various

authors, e.g., A. G. Ruthven (1904); T. L. Hankinson (1908); H. B. Baker (1909); and Bryant Walker (1896, 1898, 1911*b*). Walker's "Check-List of Michigan Mollusca," published in 1911, is a great advance over all previous lists. Twelve species representing six genera are cited in the family Amnicolidae by this author.

During the years between 1895 and 1912, forty-six species of Amnicolidae were described in North America. Of this number Walker described twenty-four and Pilsbry nineteen. The descriptions of these new species were largely based on shell characters alone.

Further increase in the knowledge of the Michigan fauna was made during the next twenty years (1912–32). Explorations within the state added considerably to distributional records of the group. Revision in taxonomy by several conchologists altered the nomenclature used by Walker in his check list of 1911. No new records of species of Amnicolidae, however, were discovered. A "Revised Check List of Michigan Mollusca," published in 1926 by Mina L. Winslow, included the more recent changes in taxonomy, but was based primarily upon the Walker check list of 1911.

Taxonomic studies of the Amnicolidae of North America, based mostly on the shell and rarely on the radulae and genitalia, have resulted in more change during the years 1912 to 1932 than in any preceding twenty years. The raising of varieties to species and subgenera to genera, not to mention the scores of species and subspecies described, has so completely changed the concept of this family that those not actively working with this group encounter great difficulty in attempting to determine even the most common *Amnicola*. An understanding of this change may be shown by contrasting the 1926 check list of Winslow with a listing of the newer taxonomic changes (see Table I).

TABLE I

1926		1936
Bithynia tentaculata (Linnaeus)		*Bulimus tentaculatus* (Linnaeus)
Amnicola cincinnatiensis (Anthony)		*Cincinnatia cincinnatiensis* (Anthony)
Amnicola emarginata (Küster)		*Vancleaveia emarginata* (Küster)
Amnicola leightoni (Baker)	(Extinct)	*Amnicola* (?) *leightoni* (Baker)
Amnicola limosa (Say)		(*Amnicola*) *limosa* (Say)
Amnicola porata (Say)		(*Amnicola*) *porata* (Say)
Amnicola lustrica Pilsbry		(*Marstonia*) *lustrica* Pilsbry
Amnicola gelida Baker		(*Marstonia*) *gelida* Baker
Amnicola walkeri Pilsbry		(*Marstonia*) *walkeri* Pilsbry
Paludestrina nickliniana (Lea)		*Fontigens nickliniana* (Lea)
Paludestrina attenuata (Haldeman)		*Fontigens attenuata* (Haldeman)
Pyrgulopsis letsoni (Walker)		*Pyrgulopsis letsoni* (Walker)
Somatogyrus subglobosus (Say)		*Birgella subglobosa* (Say)
Lyogyrus pupoideus (Gould)		*Lyogyrus pupoideus* (Gould)
Pomatiopsis cincinnatiensis (Lea)		*Pomatiopsis cincinnatiensis* (Lea)
Pomatiopsis lapidaria (Say)		*Pomatiopsis lapidaria* (Say)

At the present time about 150 species of Amnicolidae have been described from North America. The great majority of these are known from the shell

only. Comparatively little is known of the soft parts of any of them, particularly of the genitalia or of the radulae. As will be pointed out in a later section of this paper, the shell is the least reliable character for use in the determination of the species of this family, not only because of its minute size, but more particularly because all the shells have the same general shape and are often without constant characters. A revision of this entire family, based on the soft parts and radulae, has been needed for many years. In 1865, after completing his "Researches upon the Hydrobiinae," Stimpson wrote:

> The generic place of very many of these species, known as yet by the shell only, must remain undetermined until the soft parts and the lingual dentition are examined. Certain genera, as *Stenothyra, Tricula, Pyrgula,* and *Tryonia,* are indeed easily recognized by the shell alone, but no characters are found in it which will enable us to distinguish certain *Littorinellae* and *Hydrobiae* from *Bythinella* and *Paludestrina,* and the same difficulty will probably be found with *Gillia* and *Somatogyrus,* or with *Lithoglyphus* and *Fluminicola.* I shall therefore under each genus give as examples only a few species which certainly belong to it, without attempting to assign a place to every known species of the family. It would not, of course, be difficult to do this approximately, but rather than run the risk of adding to an already overburdened synonymy, I will leave the work to those who have proper opportunities for observing the entire animal in each case; and would beg my fellow-workers in this field to take the same course.

Unfortunately, Stimpson's sound advice has not been followed by most of the subsequent workers on the Amnicolidae.

A complete revision of the family Amnicolidae as it stands at the present would require many years. A careful investigation of any part of this complex family, however, would be a contribution to the larger whole. Because of the limitations which attend so vast a group, only those species known to occur in Michigan will be considered at the present time.

SIGNIFICANT CHARACTERS OF MICHIGAN AMNICOLIDAE

To identify species of this family correctly it is necessary to know what characters are considered significant. The features which are considered important, therefore, are discussed in some detail.

SHELL.—The shell is often one of the poorest characters to be used in determining species of Amnicolidae, yet, in most cases, it is the only character that has been employed in describing the species. The general shape of the shells of this group is duplicated in many families, both terrestrial and aquatic. They are dextral, unicolored, small in size, higher than wide, and have few whorls. The main objection to using the shell as the basis for determining a species is not so much its resemblance to that of another species, but rather the wide variation which occurs within any one species (see Pl. I, Figs. 8–10). Some species vary to such an extent that they have

been described three or four times and even placed in different genera. The environment seems to play a major role in the variation of the shell. Lake inhabitants, for example, are generally stunted in growth. This phenomenon may be due to many factors, such as the cramping of the body in the shell, a shorter growing season, or a reduction in biotic productivity.

It has been observed that lake-inhabiting *Amnicola limosa* and *lustrica* have their bodies just far enough out of the shell to allow a footing on the plants and often close their operculae when a wave rushes over them and fall to the lake bottom. In a fluviatile environment, particularly where the current is reduced, the species become adapted to the constant flow of water, and their bodies are more extended. The mantle, then being dilated, may secrete more shell material, resulting in a larger shell.

Amnicolidae have been found most active during the spring. Since the ice remains on lakes longer than in streams, the rise in the temperature of the water, the spring overturn, and the new growth of plants are delayed, and the activity of the snails is postponed. There is less delay in the rise of water temperatures of rivers, and the growing season is consequently longer.

Dwarfing may also be due to a reduction of biotic productivity in lakes, particularly in the diatoms, the food of these snails. Although this is somewhat questionable, there is a possibility that the current in rivers makes food more available for the fluviatile snails. All reasons given for stunting are theoretical. They are merely suggested as possibilities to account for the attainment of greater size of shells in rivers than in lakes.

It is not to be inferred that the shell is of no value in classifying Amnicolidae. When one becomes familiar with the range in variation for a given species, the shell is sometimes sufficient for determination. Certain Michigan amnicolids have distinctive shells, for example, *Bulimus tentaculatus* and *Somatogyrus subglobosus,* which are two or three times as large as most other species. In such species height serves as an index for determination. This character, however, can be used in determination only when the shell is mature or when the number of whorls is counted, which ensures one from confusing a juvenile form of a larger species with a mature shell of a smaller species.

The shape and position of the protoconch or first whorl is considered one of the best characters of the shell. This nuclear whorl may be elevated above the body whorl, coiled in the same plane as the following whorl (planorbid), or sunken below the following whorl (depressed). Significant characters are also found in the shape of the whorls since these vary from shouldered to inflated or flat. Other significant structures are the aperture, which may be round to oval, and the umbilicus, which may be wide or narrow, perforate or imperforate.

OPERCULUM.—Variation in the operculum within the species is too great to be a reliable character. It does have value, however, in separating certain subfamilies, e.g., Lyogyrinae (spiral); Buliminae (concentric); Amnicolinae and Lithoglyphinae (paucispiral or subspiral; see Pl. II, Figs. 3–5).

RADULA.—The radulae of members of the Amnicolidae are arranged in a series of transverse rows of teeth on the lingual membrane. As is true with all the members of the subclass Streptoneura, there are seven teeth to the row, and the number of rows varies to a wide extent. A single row of seven teeth is arranged so as to give the following formula: 2–1–1–1–2, with the central or rachidian tooth median, the lateral teeth on each side of the central, the first marginals lying next to the laterals, and the second marginal teeth being outermost.

An interesting correlation has been found between the size of the shell of a given species of amnicolid in Michigan and the length of the lingual membrane. Figures (Table II) have been computed to show this correlation.

TABLE II

CORRELATION OF THE HEIGHT OF SHELL (H. S.) WITH THE LENGTH OF RADULA (L. R.), THE CLASS VALUE (V), AND THE DEVIATION FROM THE CLASS VALUE (D)

	H. S.	L. R.	V	D
Amnicola (Amnicola) limosa	4.3	1.2	0.783	+.416
Amnicola (Amnicola) walkeri	2.5	0.76	0.4552	+.3047
Amnicola (Marstonia) lustrica	4.3	0.76	0.783	−.023
Amnicola (Cincinnatia) integra	5.0	0.95	0.9105	+.0395
Amnicola (Probythinella) binneyana	2.9	0.41	0.528	−.118
Pyrgulopsis letsoni	3.0	0.77	0.5463	+.2237
Hydrobia nickliniana	4.5	1.18	0.8194	+.3606
Somatogyrus subglobosus	9.2	1.25	1.6753	−.4253
Bulimus tentaculatus	11.1	1.25	2.0213	−.7713

By dividing the mean total average length of lingual ribbon of all the Michigan species of this family (0.947 mm.) by the mean total average height of shell (5.2 mm.), a comparison of the length of the radula with the shell then serves as a useful index in identifying the species. Such a correlation becomes of value if, for example, a juvenile of *Amnicola lustrica* with a height of 2.5 mm. resembles *Amnicola walkeri*. The radula of the juvenile *lustrica* would measure in length .44 mm. rather than .76 mm., which would be its length if it were *walkeri*. This becomes a very convenient and reliable index when the soft parts have been dried. Both characters, length of shell and lingual ribbon, are discussed under each species in the systematic section of this paper.

In describing the radulae a formula of the cusps is given. The figures represent an average number since variation occurs in all species. These figures are not as significant as certain authors have indicated. In the central or rachidian tooth the size and shape of the tooth and cusps are of

importance in identifying species. In the lateral tooth, size and shape of the tooth, peduncle, and cusps are significant characters. The general shape and size of the teeth and not the number of pectinate cusps present are the significant characters of the first and second marginal teeth.

In certain other families of gastropods the radula is sometimes considered of little importance as a basis for determining species. Fortunately, the radula in the Amnicolidae is remarkably constant and is of considerable value if these significant characters are employed correctly. The radula is composed of chitin, which often persists even when the animal dies and the soft parts decompose. Even in subfossil shells collected on the Great Salt Lake Desert, there were radulae within the shells although the soft parts were entirely desiccated. Generally, specimens received for identification are dried. Without the radula many of these would have been incorrectly identified.

ANIMAL.—In contrast to the shell itself, the animal offers several excellent characters which may be used in determining species. The color and pigmentation, the length of tentacles and rostrum, the length and shape of the foot, and the extent and position of the slime glands are all significant characters.

GENITALIA.—The Amnicolidae are dioecious. The male copulatory organ, known as the verge, is a very reliable character for determining species. This organ is exserted and lies some little distance posterior to the right tentacle. The snail must be fully expanded and its shell and mantle raised as normally seen when the animal is crawling before the verge becomes visible. It is essential, therefore, to have the specimen completely anesthetized and in a dilated condition before it is killed. Living specimens killed in alcohol contract to such a degree that the shape of the verge is distorted and becomes practically useless as a means of identifying the species. Unfortunately, snails are usually placed directly in alcohol when they are killed for study, and this may account for the errors which have been published regarding the verge in the Amnicolidae. For example, F. C. Baker (1928: Pt. I: 79) stated:

> In most of the groups of Amnicolidae the verge has a secondary lobe which forms the external opening of the flagellum. As this lobe seems not to have been named we have called it the flagellum sheath. This sheath varies in form and is said to be absent in some groups, although a careful anatomical search may lead to its discovery in some form.

J. W. Taylor (1900: 352, 361) also stated:

> The Exophallia embrace those dioecious species in which the males have acquired an external copulatory organ, projecting freely from the right side of the neck and arising as a muscular outgrowth from the body wall; . . . . It is strongly erectile and extensile by concentrated blood pressure, and though not eversible and retractile as in the Cryptophallia,

it can often be bent in a sigmoid form and hidden beneath the mantle folds, the spermatozoa being conveyed thereto. . . . The Flagellum is the blind diverticulum often found in highly organized Gastropods as a prolongation of the epiphallus or of the distal end of the penis-sheath, wherein is secreted a sheath or case for the safer transfer of the seminal element to the partner. It is very variously shaped, externally and internally, and the spermatophore moulded within it is an exact reproduction or cast of the shape and denticulations of the interior of the coecum.

Investigations on the Amnicolidae of Michigan are not in agreement with either of the above statements. It is true that a number of the groups in this family have a secondary lobe or flagellum sheath, but it is not true that all secondary lobes have an accessory duct or flagellum. Only four of the Michigan species have this peculiar diverticulum: *Amnicola limosa, A. walkeri, Hydrobia nickliniana,* and *Bulimus tentaculatus.* Furthermore, the flagellum has not been found to serve as a mold for a spermatophore. Serial sections of specimens collected at different seasons of the year reveal no spermatozoa nor the presence of a sheath in the accessory duct. Nor is the duct ciliated; and muscular tissues are lacking which would be necessary to force a sperm packet into the female if a spermatophore were present. The cells composing this blind diverticulum are glandular epithelium and produce some secretion, the function of which is, as yet, unknown.

As has been previously stated, the species of Amnicolidae sometimes have a confusing resemblance to one another in the general shape of the shell. For example, there is not enough distinction at times to differentiate the shells of *Amnicola limosa* from *A. lustrica* or *binneyana* or *integra.* The resemblances have suggested hybridization. Yet, nothing in the nature of interbreeding has been observed in the shape and structure of the verges of these species. Rather, it appears that such a phenomenon is well-nigh impossible, since the species have become markedly differentiated from one another in the structure of their verges.

It is interesting to note that both the radula and the verge indicate strongly that species are radically distinct and that hybridization has not taken place. Whenever the verge was unique in shape and structure the radula was likewise singular in its character.

In the majority of instances any one of the above significant characters would be sufficient for the determination of the Michigan Amnicolidae. Workers in other fields of biology, such as limnology, parasitology and faunistic zoology, have expressed a need for aid in their identification of the Amnicolidae. To the uninitiated the removal and mounting of the radulae of this family often proves a difficult task. Furthermore, one often lacks the facilities needed for relaxing the specimens collected, particularly when in the field. Consequently, a key to shell characters has been prepared which may make reasonable identification possible without resorting to a study of the soft parts.

KEY TO THE SHELL CHARACTERS OF MICHIGAN AMNICOLIDAE

I. Shell with nuclear whorl above following whorls.
  A. Umbilicus imperforate.
    1. Whorls flattened.
      a. Size large, 11 mm. in height ..... *Bulimus tentaculatus*
      b. Size small, 3 mm. in height ..... *Pyrgulopsis letsoni*
    2. Whorls inflated, size 5 mm. in height ..... *Hydrobia nickliniana*
  B. Umbilicus perforate.
    1. Shell attenuated, size less than 6 mm. in height.
      a. Columella not reflected, whorls inflated ..... *Amnicola lustrica*
      b. Columella reflected.
        (1) Whorls very inflated, aperture circular. *Pomatiopsis cincinnatiensis*
        (2) Whorls less inflated, aperture ovate ..... *Pomatiopsis lapidaria*
    2. Shell conical.
      a. Whorls increasing gradually in size.
        (1) Shell very small, 4 whorls, 2.5 mm. in height. *Amnicola walkeri*
        (2) Shell larger, 5 mm. in height ..... *Amnicola integra*
      b. Body whorl very large, size 9 mm. in height. *Somatogyrus subglobosus*

II. Shell with nuclear whorl planorbid or sunken below the following whorls, size less than 6 mm. in height.
  A. Shell with nuclear whorl coiled in the same plane with the following whorl, apex blunt.
    1. Shell conical, size more than 3.4 mm. ..... *Amnicola limosa*
    2. Shell turreted, size less than 3.4 mm. ..... *Lyogyrus brownii*
  B. Shell with nuclear whorl sunken below the following whorl, apex truncated. *Amnicola binneyana*

FIELD AND LABORATORY PROCEDURE

COLLECTING.—Amnicolids were collected for the most part by vigorously shaking aquatic vegetation over a pail of water. The various snails clinging to the plants dropped to the bottom of the pail and were later poured into cloth sacks where, if kept moist and cool, they remained alive for several days. Collections made at places where immediate examination was impossible were kept on ice in thermos bottles. The snails remained alive for more than two weeks in these cold storage chambers. Water from the melted ice was poured off and ice was added as needed.

LABORATORY PROCEDURE.—All snails, regardless of their genera, were separated from the plants. They were later classified and records of the various species were noted. Half of the individuals were killed in 70 per cent alcohol and were used for shell study, the other half were used for anatomical investigation.

CLEANING OF THE SHELL.—The shells were placed in a weak solution of oxalic acid for one-half hour. They were then scrubbed with a small brush and, after being rinsed in water, were allowed to dry.

PREPARATION OF THE OPERCULUM.—The operculum was removed from the operculigerous lobe, cleaned with oxalic acid, and stained with 1 per cent aqueous solution of crystal violet, dehydrated with alcohol, and mounted in euparol.

NARCOTIZATION.—One of the first problems encountered was the preparation of the animal in order that the soft parts could be examined. Alcohol and formalin caused the animals to withdraw far within their shells, thus distorting the soft parts and prohibiting correct anatomical studies. This has been the experience with all who have worked on the Amnicolidae. G. C. Robson (1920: 425) noted:

> Great difficulty was encountered in the preparation of material for study owing to the animal's contractility, small size, and power of resistance to anaesthetics. It was hence practically impossible to get satisfactory expansion of the anterior part of the body. Small shreds of tobacco and alcohol gave the most satisfactory results for this purpose; but it usually happened that after slow and careful narcotization extending over four or five days the animals would suddenly contract, or when at last properly expanded and insensitive to touch, they were found to be dead and already showing signs of maceration.

In the present investigation more than a dozen anesthetics were tried—ether, chloroform, chloretone, dilute alcohol, dilute formalin, tepid distilled water, epsom salts, ethyl urethane, and several others—all with indifferent success. It was finally discovered that menthol crystals, sprinkled on top of the water, caused the animal to become fully narcotized in an expanded condition.

KILLING AND FIXING.—The narcotized specimens were killed and fixed in Bouin's solution. The length of time they remained in the solution depended on the thickness of the shell; about eight hours was required for the majority of specimens.

PREPARATION FOR IN TOTO MOUNTS.—Specimens were stained in Mayer's paracarmine or Delafield's hematoxylin, cleared in xylene, and mounted in balsam.

MICROTECHNIQUE.—Histological studies were made from serial paraffin sections stained with Flemming's triple stain.

RADULAE TECHNIQUE.—The radula was freed from the buccal mass by a 2 per cent solution of potassium hydroxide and stained in Orange G for forty-five minutes with three volts of direct current obtained by the use of a step-down transformer and rectifier. The stained lingual ribbons were mounted in hyrax.

SYSTEMATIC DISCUSSION OF MICHIGAN AMNICOLIDAE

The following section is a systematic discussion of the living Amnicolidae of Michigan. Each species is discussed under the following outline:

1. Synonymy. So far as possible a complete synonymy is given.
2. Distribution. There is a record map for each species, and a general account is given. The records are based on published lists and on records of specimens in the Museum of Zoology, University of Michigan.
3. A description of the shell and figures of each species are given.
4. Description of the radula. A formula of dentition, the length of the radula, the number of rows in the lingual membrane, and a detailed and illustrated description of the central, lateral, and first and second marginal teeth are given.
5. Description of the animal and of the male genitalia. Characteristics of the animal and verge are discussed and figured.
6. Discussion. Items such as phases in life history, revision of nomenclature, and ecology are discussed.

Table III lists the classification employed in this section.

TABLE III

FAMILY AMNICOLIDAE GILL

Subfamily AMNICOLINAE Gill, 1871
- Genus *Amnicola* Gould and Haldeman, 1840
  - Subgenus Amnicola proper
    - *Amnicola* (*Amnicola*) *limosa* (Say)
    - *Amnicola* (*Amnicola*) *walkeri* Pilsbry
  - Subgenus Marstonia Baker, 1926
    - *Amnicola* (*Marstonia*) *lustrica* Pilsbry
  - Subgenus Cincinnatia Pilsbry, 1891
    - *Amnicola* (*Cincinnatia*) *integra* (Say)
  - Subgenus Probythinella Thiele, 1928
    - *Amnicola* (*Probythinella*) *binneyana* Hannibal
- Genus *Pyrgulopsis* Call and Pilsbry, 1886
  - *Pyrgulopsis letsoni* (Walker)
- Genus *Hydrobia* Hartmann, 1821
  - *Hydrobia nickliniana* (Lea)

Subfamily LITHOGLYPHINAE Fischer, 1885
- Genus *Somatogyrus* Gill, 1863
  - *Somatogyrus subglobosus* (Say)

Subfamily LYOGYRINAE Pilsbry, 1916
- Genus *Lyogyrus* Gill, 1863
  - *Lyogyrus brownii* Carpenter

Subfamily BULIMINAE (Hannibal), 1912
- Genus *Bulimus* Scopoli, 1777
  - *Bulimus tentaculatus* (Linnaeus)

FAMILY AMNICOLIDAE (TRYON, 1862) GILL, 1863

SHELL.—Small, dextral, conical, or attenuated, 4 to 8 whorls, apex elevated above the following whorls, or truncated; aperture entire, peristome usually continuous, acute and simple; umbilicus perforate or imperforate; periostracum without color markings.

OPERCULUM.—Corneous or calcareous; spiral, subspiral (paucispiral), or concentric.

RADULA.—From 30 to 80 transverse rows of teeth to the lingual membrane, with 7 (2–1–1–1–2) teeth to the row. Central tooth wider than high, with lateral angles bearing 1 to 6 or more basal denticles. Lateral teeth with the basal part usually lobed, peduncle long, slender, cusps few or many. Marginal teeth falcate, usually multicuspid.

ANIMAL.—Foot longer than wide, usually auriculated anteriorly, rounded posteriorly; operculigerous lobe well developed, wider than the foot; rostrum long; tentacles 2, long and usually cylindrical, eyes at their outer base; gills generally concealed beneath the mantle lobe, the right, or principal gill, pectinate, with 20 to 50 laminae, the left, simple, nonfunctional, and inconspicuous; genitalia dioecious; the copulatory organ (the verge) of the male exserted, arising from the posterior surface of the rostrum, near the margin of the mantle, median or slightly to the right; the uterus lying parallel to the left of the intestine, the vaginal opening not extending as far forward as the rectum. Oviparous or ovoviviparous. Eggs laid singly or in clusters. Lives in fresh, brackish, or marine water. Mundane.

SUBFAMILY AMNICOLINAE GILL, 1871

SHELL.—Less than 6 mm. in height, conical or attenuated; whorls 4 to 6, apex elevated above the following whorls or truncated; peristome continuous, acute and simple; umbilicus perforate or imperforate.

OPERCULUM.—Corneous, subspiral.

RADULA.—Central tooth wider than high with less than 4 basal denticles.

ANIMAL AND GENITALIA.—Foot auriculated anteriorly, longer than wide, dilated anteriorly, narrowed toward the middle, and expanded and rounded posteriorly. Tentacles cylindrical, gills pallial. Verge exserted, simple, bifid, or trifid; secondary lobe and accessory duct present or absent. Animal oviparous or ovoviviparous. Eggs laid singly. Lives in fresh, brackish, or marine water. Mundane.

GENUS *AMNICOLA* GOULD AND HALDEMAN, 1841

Amnicola Gould and Haldeman, 1841, pp. 228–29.

SHELL.—Usually less than 5 mm. in height, conical or ovate-conic, 4 to 5 whorls, nuclear whorl elevated above the following whorls, or planorbid, or depressed; aperture subcircular or ovate; umbilicus perforate.

RADULA.—Central tooth wider than high, with 1 to 3 basal denticles.

GENITALIA.—Verge simple or bifid, secondary lobe and accessory duct present or absent. Animal oviparous. Lives in fresh or brackish water. North America.

SUBGENUS AMNICOLA S. S.

SHELL.—Between 2 and 5 mm. in height, conical, 4 to 5 whorls; apex obtuse or planorbid; whorls rounded, shouldered, sutures well impressed; peristome continuous, lip thin; aperture subcircular, mainly basal; umbilicus perforate, deep.

RADULA.—Large for the size of the animal; central tooth broader than high, 1 basal denticle, lateral ridge strong, central cusp lanceolate or round, 4 side cusps, sharply pointed; lateral tooth with 2 inner cusps and 3 or 4 outer cusps; marginal teeth multicuspid.

GENITALIA.—Verge bifid; secondary lobe containing the accessory duct.

TYPE.—*Paludina limosa* Say.

Amnicola (*Amnicola*) *limosa* (Say)

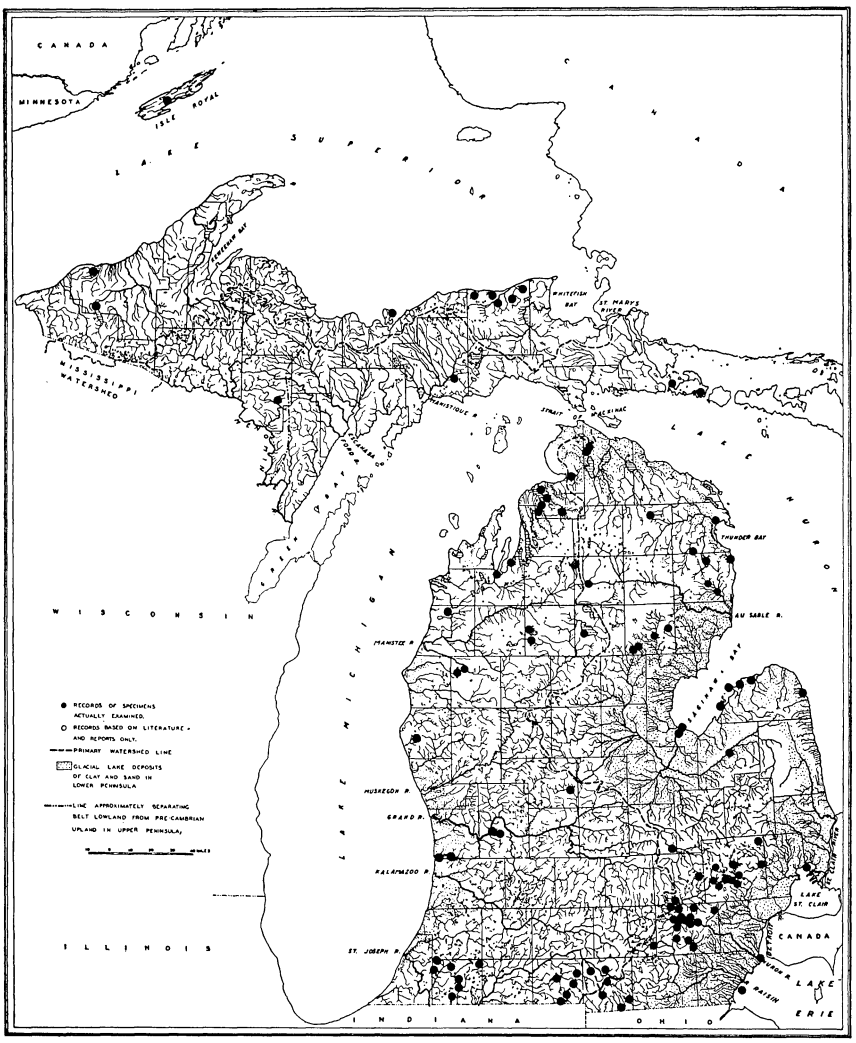
Paludina limosa Say, 1817, 1: 125–26.
Paludina porata Say, 1821, 2: 174.
Amnicola porata Gould, 1841, pp. 229–30, Fig. 157.
Amnicola porata De Kay, 1843, 5: 88, Pl. XXXV, Fig. 333.
Amnicola limosa De Kay, 1843, 5: 88.
Amnicola limosa Haldeman, 1845, pp. 10–11, Pl. I, Fig. 1.
Amnicola porata Haldeman, 1845, pp. 13–14, Pl. I, Fig. 8.
Amnicola limosa Stimpson, 1865, p. 52.
Amnicola porata Stimpson, 1865, pp. 12–16, Figs. 1–2.
Amnicola limosa Binney, 1865, p. 84, Fig. 166.
Amnicola limosa Gould, 1870, pp. 293–94, Fig. 559.
Amnicola limosa F. C. Baker, 1902, pp. 331–32, Pl. XXXI, Fig. 11.
Amnicola limosa porata Baker, 1902, pp. 334–35, Pl. XXVI, Fig. 13.
Amnicola limosa Baker, 1928, pp. 93–98, Pl. VI, Figs. 1–6.
Amnicola limosa porata Baker, 1928, pp. 98–101, Pl. VI, Figs. 7, 8, 18, Pl. VIII, Figs. 1–3.

Amnicola limosa is the most widely distributed species of the family in Michigan (Map 1). It is found in most lakes and streams where pollution or silt has not been an agent in prohibiting its existence. It is usually so common that other amnicolids in smaller numbers have been entirely overlooked. This species ranges from the Atlantic coast as far west as Utah, and from Labrador to Florida.

SHELL (Pl. I, Fig. 1).—Broadly conic in shape, about 4.5 mm. high, 3 mm. wide, 4.5 whorls; apex blunt, nuclear whorl planorbid, later whorls round and somewhat shouldered, increasing gradually in size; body whorl round; peristome continuous, joined to the body whorl by a thin callous; aperture subrotund, mostly basal (1.52 mm. wide by 1.88 mm. high). Umbilicus deeply perforate.

RADULA (Pl. III, Fig. 1).—Formula, $20 \pm : 15 \pm : 3\text{–}1\text{–}2 : \frac{4\text{–}1\text{–}4}{1\text{–}1} : 2\text{–}1\text{–}3 : 15 \pm : 20 \pm$. Sixty-four rows, long in proportion to the animal (1.2 mm. by 0.18 mm.). Central tooth almost twice as broad as high (45.0 μ by 23.7 μ).

Basal ridge strong, 1 prominent basal denticle at the arch and 1 tubercle (sometimes developing into a denticle) on the ridge. Central cusp broad, round, 4 side cusps, short and sharply pointed, basal lobe extending for a short distance below the arch. Lateral tooth with peduncle rather wide,



MAP 1. Records of *Amnicola* (*Amnicola*) *limosa* (Say) in Michigan.

base of tooth broad, pitted on ventral surface; central cusp rounded, 2 inner cusps, 3 outer cusps, all small and sharply pointed. First marginal tooth with a broad peduncle and blade; about 15 fine, rakelike cusps. Second marginal tooth with a more slender peduncle, blade narrower, about 20 fine pectinate cusps.

GENITALIA (Fig. 1; Pl. V, Figs. 1–3).—The verge is wide, somewhat flattened, arising slightly to the right on the back beneath the mantle lobe. It bifurcates about one-third of its total length. The penis, which is on the right-hand side of the organ, makes a complete coil around the secondary lobe and tapers to a sharp termination. The vas deferens, bordering the right margin of the verge, continues to the tip of the penis. The secondary lobe varies in shape from a small round knob (Pl. V, Fig. 1) to a long cylindrical organ truncated at its extremity (Pl. V, Fig. 3). This lobe has a secondary duct which terminates as a convoluted diverticulum.

EGGS (Pl. VII, Fig. 1).—Laid singly, lenticular in shape with a thin laminated crest extending across the dorsal margin; amber in color. Size: 1.3 mm. long, 0.9 mm. wide, 0.7 mm. high. Ten days are required for the eggs to hatch when the water is about 76° F.

BREEDING SEASON.—Stimpson (1865: 15) has given the months of April and May as the breeding season for *Amnicola limosa*. F. C. Baker (1928: 96) reported that egg capsules are deposited in July and August. The present investigation would indicate that there seems to be no particular time which might be designated as the breeding season for *Amnicola limosa*. In February, 1935, and again in January, 1936, *A. limosa* was collected from the Huron River near Ann Arbor. The river was partly covered with ice, and the snails were buried in the sand on the river bottom. Taken to a moderately warm room in the laboratory, the snails became active as the temperature of the water rose from near freezing to about 62° F. Males were separated from the females to determine whether the sperm was carried over in the female from the preceding season, or whether new impregnation was required for the fertilization of the eggs. Twelve days after collection, the females began depositing fertile eggs on the plants and on the sides of the aquarium.

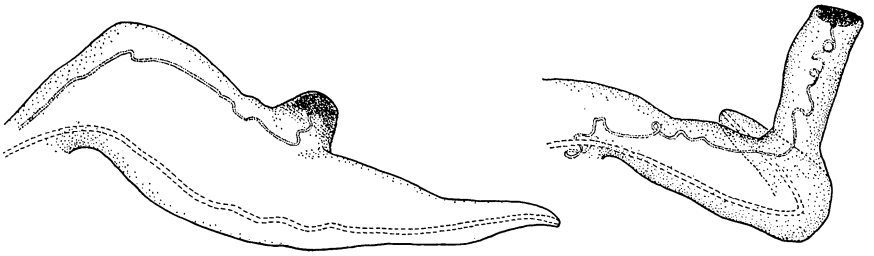


FIG. 1. Verge of *Amnicola* (*Amnicola*) *limosa* (Say), (see also Pl. V, Figs. 1–3). Left, with penis distended and secondary lobe (flagellum sheath) relaxed. The secondary duct (upper margin of verge) begins as a tortuous diverticulum back of the posterior region of the rostrum. The function of the secretion which is produced in the diverticulum is not known. Only four of the Michigan species of Amnicolidae have this peculiar structure. The duct along the lower margin of the verge is the vas deferens. Right, penis coiled around erected secondary lobe.

Consequently, there does not seem to be a definite breeding season in *Amnicola limosa*. Egg laying seems to be regulated by the temperature of the water, and the snails continue to lay eggs throughout the year if the water remains at an optimum temperature. The female does not need to be fertilized if she has been impregnated by the male during the preceding season.

Ecology.—*Amnicola limosa* has a wide range in distribution and is found in creeks, rivers, and fresh- and brackish-water lakes. It is most abundant where there are thick beds of *Chara, Potamogeton, Vallisneria,* and *Elodea.* These plants, however, are not used as food by the amnicolid, but they do harbor rich colonies of diatoms that the snails eat.

Discussion.—Say described *Paludina limosa* in 1817 and *P. porata* in 1821. Binney noticed the similarity and placed *porata* under synonymy of *limosa* in 1865. Other workers since Binney's time have considered *porata* as a species, a subspecies, a variety, and a form. The name is applied to a shell, in general shape like that of *limosa,* but attaining a greater size, which causes it to be more globular and increases the width of the umbilicus. *P. porata* is found with *limosa* and is more abundant in rivers, particularly where the current is comparatively slow, than in lakes. The radula and the verge are identical with those of *limosa,* and, consequently, the name *porata* is not recognized.

Amnicola (*Amnicola*) *walkeri* Pilsbry

Amnicola walkeri Pilsbry, 1898, p. 43.
Amnicola (*Marstonia*) *walkeri* F. C. Baker, 1928, p. 114.

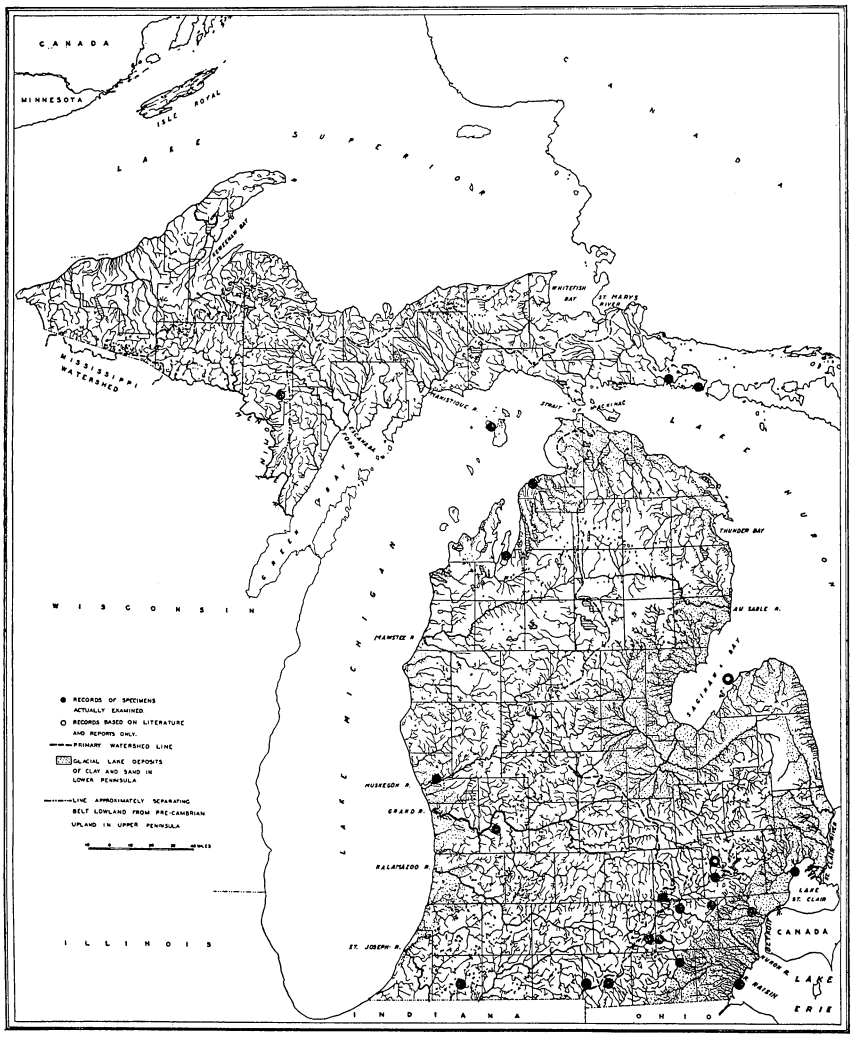
Type locality.—Lake Michigan at High Island Harbor, Beaver Island, Charlevoix Co., Michigan.

Amnicola walkeri appears to be most common in the Lake Erie drainage basin. A few widely scattered records have been made in western and northern Michigan (Map 2). When the entire state has been carefully surveyed, *walkeri* may be found to be more widely distributed than the present records indicate.

Shell (Pl. I, Figs. 2 and 3).—About 2.5 mm. high, 2.2 mm. wide, thin, broadly conic in outline. Four whorls increasing regularly in size. Apex obtuse, elevated, whorls shouldered, convex; sutures very deep. Aperture almost circular (1.04 mm. wide; 1.04 mm. high). Peristome continuous, adnate to the preceding whorl for only a short distance. Umbilicus rather wide, deep. Periostracum light tan, lines of growth crowded but distinct, often concealed with a deposit from its environment.

Radula (Pl. III, Fig. 2).—Formula, $20 \pm : 20 \pm : 4\text{–}1\text{–}2 : \frac{4\text{–}1\text{–}4}{1\text{–}1} : 2\text{–}1\text{–}4 : 20 \pm : 20 \pm$. Eighty-one rows, 0.76 mm. long, 0.096 mm. wide. About as

long as the radula of *A. lustrica,* but with almost twice as many rows, very much narrower. Central tooth less than half as high as wide (22.5 μ wide, 10.0 μ high). Ventral lobe pointed, basal ridge strong, central cusp lanceo-



MAP 2. Records of *Amnicola* (*Amnicola*) *walkeri* Pilsbry in Michigan.

late, 4 side cusps on each side, sharply pointed. Basals 1 on each side, placed high on the basal ridge. Lateral without a pit; central cusp spoon-shaped, 2 inner cusps, 4 outer cusps, all sharply pointed. First marginal scythe-shaped with about 20 cusps; second marginal slender with about 20 very minute cusps.

ANIMAL (Pl. V, Figs. 4 and 5).—The body of *Amnicola walkeri* is heavily pigmented, giving it a dark sooty color. This pigmentation is particularly noticeable on the head and becomes broadened toward the operculum. The slime gland is not concentrated in the fore part of the foot as in *limosa* and *lustrica*, but is loosely scattered, extending from the auriculation to the position of the pedal ganglia.

GENITALIA (Fig. 2; Pl. V, Figs. 4 and 5).—The verge is bifid, with the penis and the secondary lobe arising together, the penis directly anterior to the lobe. Both are about equal in length, the flagellum slightly thicker and truncated at its extremity. The penis gradually tapers to a sharp point. The flagellum has a diverticulum as described in *limosa*. The flagellum is

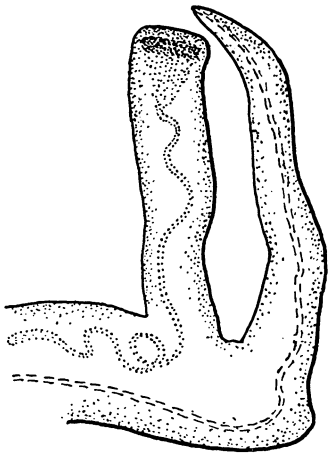


FIG. 2. Verge of *Amnicola* (*Amnicola*) *walkeri* Pilsbry with penis (right) enclosing the vas deferens; secondary lobe (left) with duct ending in a diverticulum.

retractile and occasionally is much shorter than the penis. This does not seem to be entirely seasonal, certain specimens exhibit the relaxation during the spring, summer and fall, and specimens collected beneath the ice during the winter months were found, when examined in the laboratory, to have the flagellum erected. The penis has never been observed to coil around the flagellum, as is usually the case with *Amnicola limosa*.

ECOLOGY (Pl. VIII, Fig. 2).—*Amnicola walkeri* inhabits sluggish streams and quiet ponds where the dead aquatic plants have accumulated to a thickness of several feet. The living animal has been collected deep in this accumulation of plants during the months of January and February. It has been observed that the dead vegetation, the sticks, and the stones were covered with a rusty brown deposit. The shells of this species were also coated, giving them a fine granulated appearance and obscuring the crowded growth lines. Although collected during every season of the year this species has not deposited egg capsules in the laboratory.

DISCUSSION.—*Amnicola walkeri* is the smallest of the Michigan Amnicolidae. Prior to 1898 the species was classified as *Amnicola granum* (=*Lyogyrus granum* [Say]). *L. granum* is known only from the Atlantic drainage basin in southeastern Pennsylvania and New Jersey. Walker and Pilsbry devoted much time to a study of the "*granum*" of Michigan, actually *walkeri,* and in 1898 Pilsbry described this species from specimens collected at a depth of 10 meters in Lake Michigan at High Island Harbor, Beaver Island, Michigan. The shell of *A. walkeri* has been frequently classified, together with other shells, as that of a juvenile form of larger species. The shell of young *Amnicola lustrica* (Pl. I, Fig. 4) and the adult shell of *walkeri* are sometimes difficult to separate with certainty. They are about the same height and are frequently found in the same region. The shell of *walkeri* may be distinguished from that of the juvenile *lustrica* by its more conic shape, deeper sutures, rounder aperture, and wider umbilicus. The dark pigmented animal and particularly the bifid verge will definitely separate *walkeri* from *lustrica.*

F. C. Baker (1928: 114) has placed *A. walkeri* under the subgenus *Marstonia* Baker, relating it to *A. lustrica.* His reasons for this are that the "operculum is similar to that of *lustrica* but rounder with coarse longitudinal and fine spiral striae; . . . the radula is essentially that of *lustrica;* . . . animal: as in *lustrica.*" Neither the radula nor the operculum justify separation of these forms, and the animal of *walkeri* is certainly very different from that of *lustrica.* The correlation of the shell and radula of *A. walkeri* (Table III), the bifid verge, and the secondary accessory duct bear more resemblance to *Amnicola limosa* than to any other Michigan species. For these reasons *walkeri* is considered a member of the subgenus *Amnicola.*

SUBGENUS MARSTONIA BAKER, 1926

SHELL.—Attenuated, almost twice as high as wide, apex elevated and acute, aperture ovate or subovate, peristome continuous, umbilicus narrow, perforate.

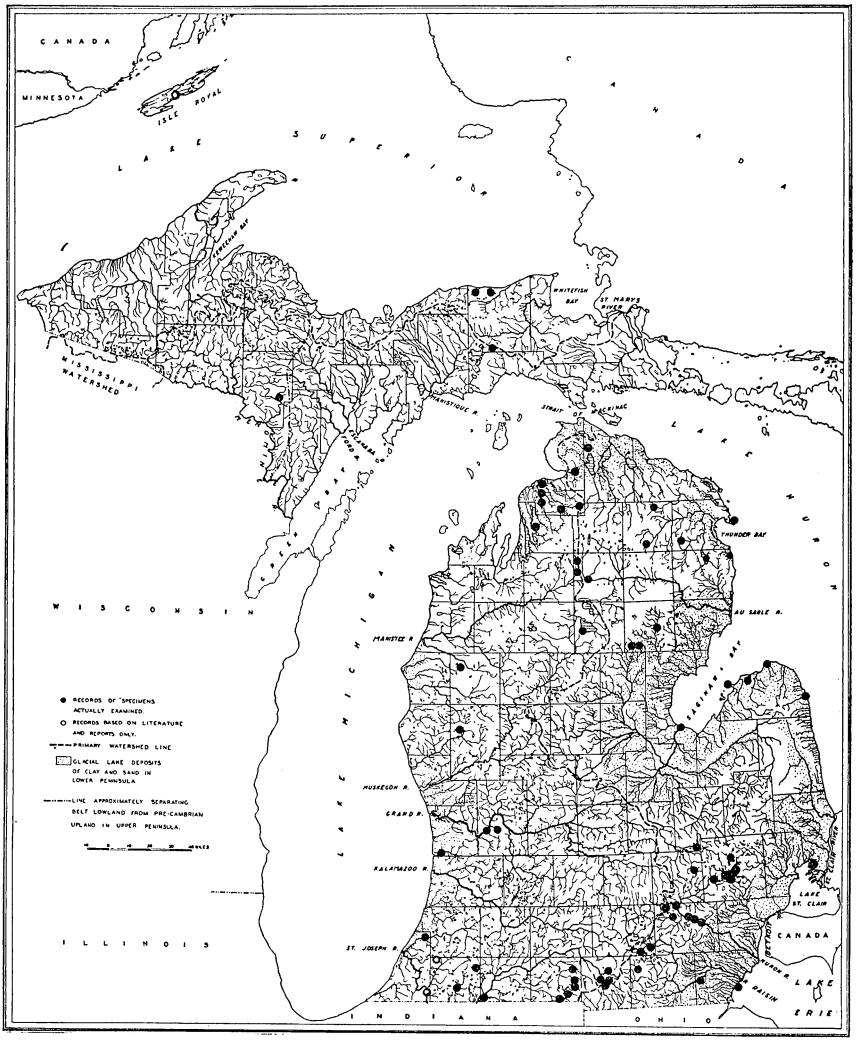
RADULA.—Length proportionate to the size of animal, central tooth with a single basal denticle, central cusp spade-shaped. Lateral tooth lobed on basal dorsal surface, pitted on median ventral surface, central cusp broadly trowel-shaped. First and second marginals multicuspid.

GENITALIA.—Verge broad at distal end, not bifid, penis at extreme right and projecting from rest of organ. Accessory duct lacking.

Amnicola (*Marstonia*) *lustrica* Pilsbry

Amnicola lustrica Pilsbry, 1890, p. 53.
Amnicola (*Marstonia*) *lustrica* Baker, 1926*b*, p. 195.
Lyogyrus (*Marstonia*) *lustrica* Thiele, 1928, p. 378.

Amnicola (*Marstonia*) *lustrica* Pilsbry, is the second most common amnicolid in Michigan (Map 3). It is distributed over the entire state and its ecology is similar to that of *limosa* Say, which is the most common form in Michigan.



MAP 3. Records of *Amnicola* (*Marstonia*) *lustrica* Pilsbry in Michigan.

SHELL (Pl. I, Figs. 4–6).—About 4 mm. high, 2.3 mm. wide, 5 whorls increasing gradually in size. Apex elevated, acute, sutures deeply impressed, whorls shouldered, rounded, growth lines prominent. Aperture ovate, angled above, round below; columella moderately curved; peristome continuous, joined to the body whorl from the umbilicus to the angle. Umbilicus narrow, perforate. Epidermis light tan.

RADULA (Pl. III, Fig. 3).—Formula, $15+:20+:4\text{–}1\text{–}3:\frac{4\text{–}1\text{–}4}{1\text{–}1}:3\text{–}1\text{–}4:20+:15+$. Forty-seven rows, 0.76 mm. long; 0.16 mm. wide. Very much smaller than the radula of *Amnicola limosa,* and only slightly longer than *Amnicola walkeri.* Central tooth twice as broad as high (42.5 μ by 20.0 μ). Central cusp spade-shaped, more sharply pointed than in *A. limosa.* Inner cusps 4, less than half as long as the central, sharply pointed. Basal ridge strong, with 1 basal denticle which is longer than the inner cusps. Ventral lobe tongue-shaped. Lateral tooth with a shallow pit, central cusp broadly trowel-shaped. Inner cusp often joined to the central cusp. Side

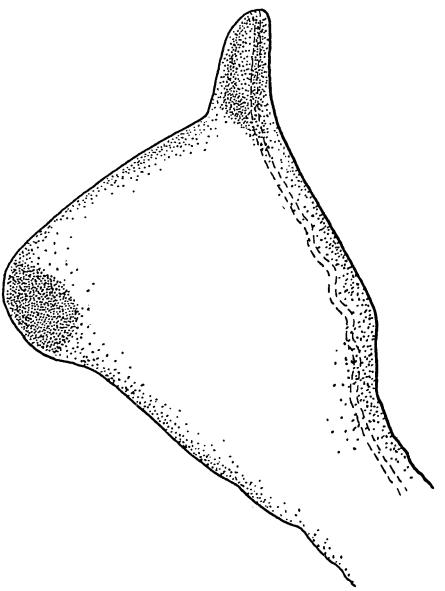


FIG. 3. Verge of *Amnicola* (*Marstonia*) *lustrica* Pilsby. Vas deferens lying along the right margin of the verge terminating in the penis.

cusps, 2 inner and 3 outer, long, slender, and sharply pointed. First marginal falcate, peduncle broad, about 20 cusps. Second marginal slender, peduncle narrow, more than 15 cusps.

ANIMAL AND GENITALIA (Pl. V, Fig. 6).—Very little has been published regarding the soft parts of *Amnicola lustrica.* In his description, Pilsbry (1890: 53) stated: "The animal and dentition are similar to [those of] *A. limosa.*" F. C. Baker (1928: 106) agreed with this statement in asserting "animal and genitalia: not differing materially from *limnosa.*" Studies on the soft parts of this species from a large series of *lustrica* collected in various parts of southern Michigan did not confirm this published information. The soft parts, particularly the male genitalia, are, in fact, very different

from those of *A. limosa.* In very young specimens of *lustrica* the verge is simple and crescent-shaped. As it matures, the extreme right side of the verge, the penis, elongates, forming a finger-like projection from the rest of the organ (Fig. 3). The vas deferens extends along the extreme right margin. The greater part of the verge grows in width rather than in length. Not only does it differ in general shape from that of *limosa,* but also the diverticulum in the accessory lobe of that species is entirely lacking in *lustrica.* There are no secretory cells or anything homologous to the structure which occurs in *limosa.* A loose connective tissue fills the verge in *lustrica,* with the exception of the extreme left tip, of epithelial tissue, staining very dark in prepared specimens.

EGGS (Pl. VII, Fig. 4).—F. C. Baker (1928: 106) figured and described the eggs of *Amnicola lustrica* as being "similar to those of *limosa,* but are often found on vegetation, especially *Vallisneria.*" In the case of several female specimens of *lustrica* that were isolated in an aquarium, eggs were laid singly on the plants and on the sides of the aquarium. They differ from those of *limosa* in being round and in lacking the laminated crest. As in *limosa,* the eggs are not always laid on stones or plants, but have been noted in clumps on the surface of the water of quite shallow pools. A similar deposition has been observed in the laboratory.

DISCUSSION.—*Amnicola lustrica* is often associated with *Amnicola limosa* and inhabits the same type of environment; it occurs on stones in rivers and lakes and on vegetation such as *Vallisneria, Potamogeton,* and *Chara.* As is also true of *limosa, lustrica* is sometimes a difficult shell to identify with certainty because of the wide range of variation. The river form is often so different from the lake form that the two have been regarded as distinct species (Pl. I, Figs. 5 and 6). Fortunately, the radula and particularly the verge, remain fairly constant and vary only slightly during the different seasons of the year.

SUBGENUS CINCINNATIA PILSBRY, 1899

TYPE.—*Paludina integra* Say, 1821, p. 174.

SHELL.—About 5 mm. high, 3 mm. wide, heavy, spire acute, elevated, never depressed. Whorls rounded, shouldered, sutures deep. Aperture roundly ovate, peristome continuous. Umbilicus wide and deep.

RADULA.—Minute in comparison with the size of the shell. The teeth are smaller and have more cusps, which are smaller than those in *Amnicola* s.s.

GENITALIA.—Verge bifid, penis very short and bluntly pointed; secondary lobe very much larger than the penis; accessory duct absent.

Amnicola (*Cincinnatia*) *integra* (Say)

Paludina integra Say, 1821, p. 174.
Paludina cincinnatiensis Anthony, 1841, p. 279, Pl. III, Fig. 3.

Amnicola cincinnatiensis Haldeman, 1845, p. 9, Pl. I, Fig. 4.
Amnicola (Cincinnatia)[1] *cincinnatiensis* Pilsbry, 1891, p. 327.
Cincinnatis[2] *cincinnatiensis* Baker, 1898, p. 64.
Amnicola (Cincinnatia) cincinnatiensis Pilsbry, 1899, p. 122.
Cincinnatia cincinnatiensis Walker, 1902, p. 35.

TYPE LOCALITY.—Not definitely known. "Inhabits the waters of the Missouri" (Say).

Amnicola (Cincinnatia) integra (Say), although represented by scattered records over the entire state of Michigan (Map 4), does not appear to be a common snail. It is interesting to note that this species has been collected in the first three tiers of southern counties from regions near Lakes Erie and Michigan only. Records from the interior counties are lacking, probably because its environment, so unlike that of the more common amnicolids, is not generally known.

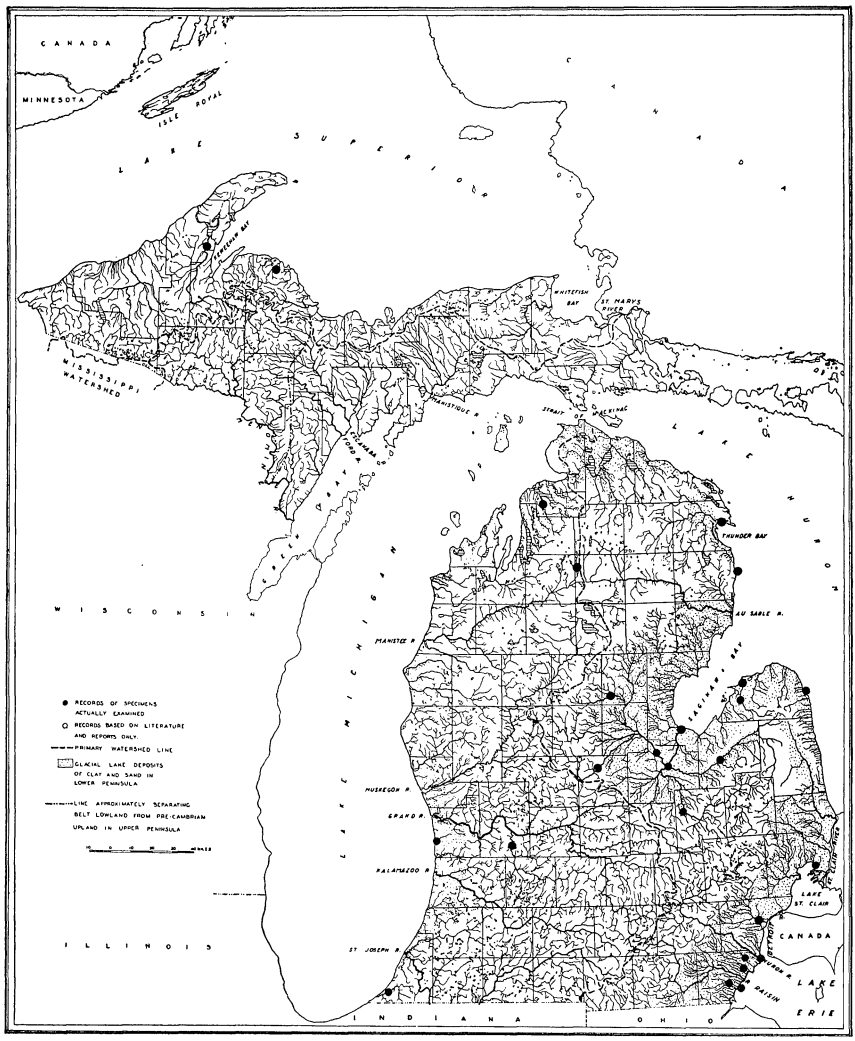
SHELL (Pl. I, Fig. 7).—About 5 mm. high, 3.5 mm. wide, heavy, spire acute, the nuclear whorl elevated above the other whorls. The second, third, and fourth whorls very shouldered, the body whorl round. Aperture (2.1 mm. high, 1.8 mm. wide), roundly ovate, angled above. Basal part not as convex as the rest of the aperture. Basal part of columella thickened, somewhat straight; upper part arched. Interior of aperture usually white. Peristome continuous, attached to the body whorl from the angle of the umbilicus. Umbilicus wide, deep. Epidermis light horn color, growth lines fine.

RADULA (Pl. III, Fig. 4).—Formula, $20 \pm : 25 \pm : 9\text{–}1\text{–}4 : \frac{4\text{–}1\text{–}4}{1\text{–}1} : 4\text{–}1\text{–}9 : 25 \pm : 20 \pm$. Fifty-seven rows, 0.95 mm. long, 0.096 mm. wide. Central tooth quadrangular in outline, nearly two-thirds as high as broad (31.25 μ wide, 17.5 μ high). Lateral angle less flaring than in *Amnicola limosa*. Lateral ridge terminating at its upper limit with a single basal denticle. Basal denticle triangular with the cusp pointing downward. Central cusp short, triangular, sharply pointed. Side cusps 4 on each side, small and sharply pointed. The tongue-shaped process is broad and blunt on the ventral lobe. Lateral tooth with the inner margin nearly straight, ventral margin broadly concave, peduncle narrow at its attachment and broadening without a definite demarcation between the peduncle and the blade. A shallow pit beneath the cusps. Central cusp broad, but sharply pointed. Inner cusps 4, the first and second attached to the central. Outer cusps 9 and graduated in size, the largest adjacent to the central. First marginal with about 25 cusps, fine and sharply pointed, peduncle narrow. Second marginal narrow, cusps too minute to be accurately counted.

[1] *Cincinnatia* as a section under the Genus *Amnicola*.

[2] Probably a typographical error for *Cincinnatia*.

ANIMAL AND GENITALIA (Pl. VI, Fig. 1).—F. C. Baker (1928: 123) has described the soft parts of *integra* as follows: "Generally as in *limosa* externally . . . tentacles, eyes and verge as in *Amnicola limosa.*" From two localities, each representing distinct habitats (Stony Creek, Monroe County,



MAP 4. Records of *Amnicola* (*Cincinnatia*) *integra* (Say) in Michigan.

and Lake St. Clair), more than 70 specimens of *integra* have been collected and later fully relaxed with the use of menthol crystals. Even the female specimens differ structurally from the females of *limosa*. It is not until the male external genitalia (the verge) are examined, however, that a very striking difference is noted between *limosa* and *integra*. The foot in

A. (*Cincinnatia*) *integra* is broad, not auriculated, the mucous gland bordering the anterior end. Pigment is scattered over the head except on the rostrum, which is grayish white. Tentacles short, cylindrical. The verge is bifid (Fig. 4), the penis, at the extreme right, is very small, round, terminating in a blunt point and staining darker than the rest of the organ. Secondary lobe very large, more than 6 times as high or wide as the penis. Structurally the secondary lobe is composed of loose connective tissue with several condensed bands of epithelial tissue on the dorsal surface. The diverticulum, which is present in *Amnicola limosa,* is absent in *integra.*

ECOLOGY.—This species was found crawling on the soft muddy ooze in Stony Creek, Monroe County. At this locality the current was slow, and

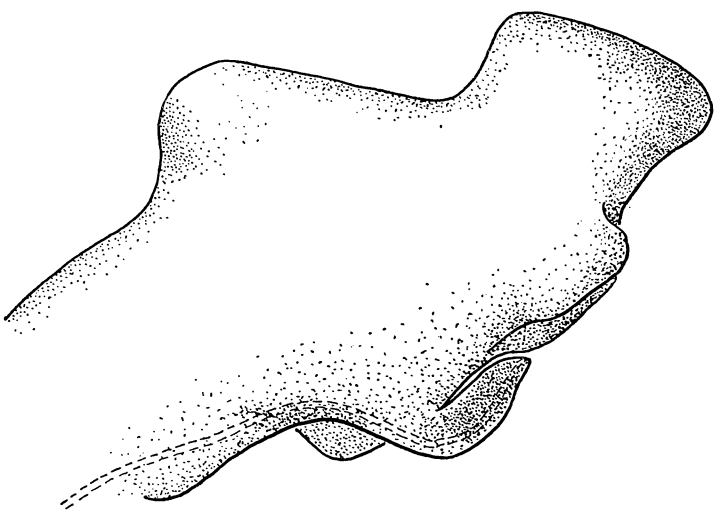


FIG. 4. Verge of *Amnicola* (*Cincinnatia*) *integra* (Say). Penis, containing vas deferens, at lower right.

aquatic vegetation was practically absent. No other amnicolids were taken, although both above and below this locality, where the stream becomes more swift and *Potamogeton* and *Vallisneria* grow in extensive patches, *Amnicola limosa* was collected. At these places, however, no specimens of *integra* were taken. One would not ordinarily select ooze from which to collect Amnicolidae. This is perhaps one reason why the species has not been taken in some of the counties of Michigan. In Lake St. Clair the specimens were collected from a sandy bottom. Microscopic examinations of sections through the intestine reveal that the food of *integra* consists mainly of diatoms.

DISCUSSION.—*Amnicola* (*Cincinnatia*) *integra* (Say) is widely distributed over the United States, occurring as far west as Utah. It has commonly been classified as *Amnicola cincinnatiensis* (Anthony). Pilsbry has

examined the type of Say's *integra* and has informed me that Anthony's *cincinnatiensis* and *integra* are one and the same species. Since Say's description of *integra* (1821) antedates Anthony's description of *cincinnatiensis* (1841) by 20 years, *cincinnatiensis* is considered a synonym of *integra*. The shell of *integra* has been confused with that of 3 other species in Michigan, *Amnicola limosa* (Say), juvenile forms of *Bulimus tentaculatus* (Linnaeus), and *Campeloma integrum* (Say). The nuclear whorl of *limosa* is depressed or planorbid, whereas *integra* has its nuclear whorl elevated above the other whorls. The wide umbilicus of *integra* separates this species from the young of *Campeloma* or *Bulimus*. The animals of all 4 species, as described elsewhere in this paper, are distinctive.

SUBGENUS PROBYTHINELLA THIELE, 1928

TYPE.—*Cincinnatia binneyana* Hannibal, 1913.

SHELL.—Subcylindrical, apex blunt or truncate, about 4 whorls, 3 mm. high, 2 mm. wide. First and sometimes second whorls planorbid, depressed below the following whorl. Aperture subovate, peristome continuous, adnate to the body whorl for a very short distance and occasionally unattached. Umbilicus perforate and narrow.

RADULA.—Very minute, much smaller than the radula of members of the subgenus Cincinnatia, although the teeth bears some resemblance to those of this subgenus.

ANIMAL.—Rostrum very elongated; foot slender, auriculated.

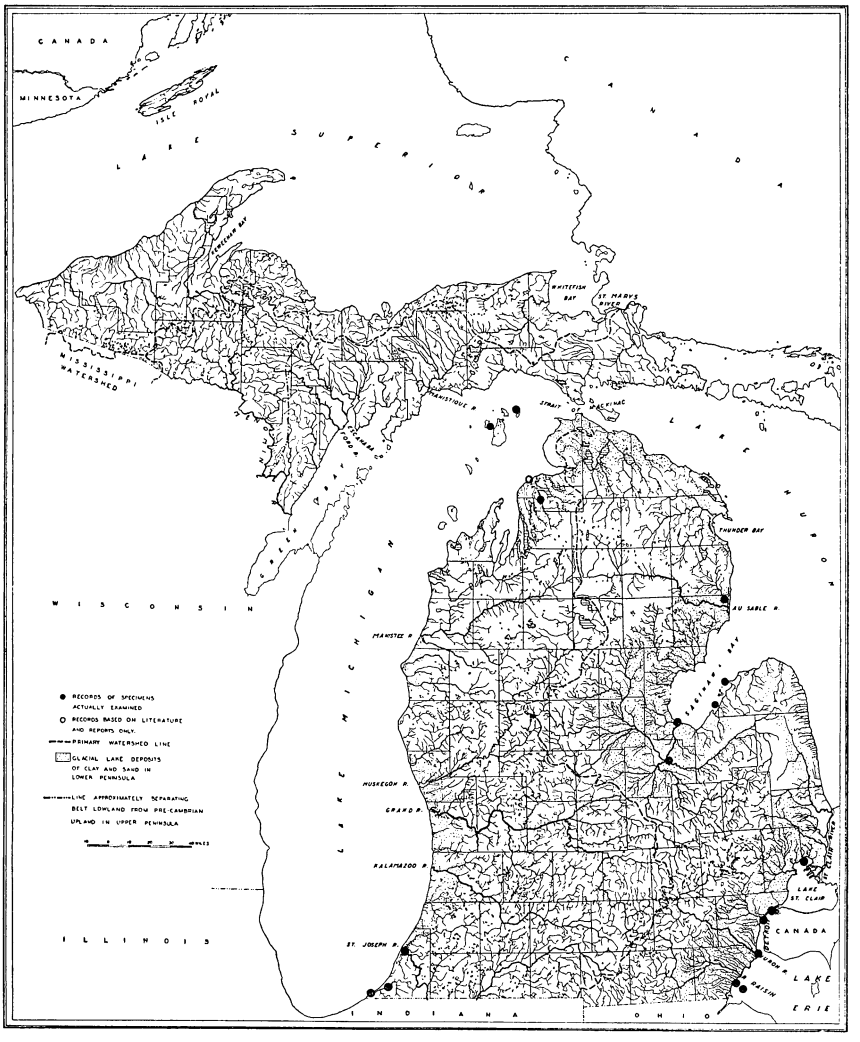
GENITALIA.—Verge bilobed, but not bifurcate as in the subgenus Cincinnatia; right lobe longer than left; accessory duct absent.

Amnicola (*Probythinella*) *binneyana* Hannibal

Paludina obtusa Lea, 1841, p. 34. Not *Paludina obtusa* Troschel, 1837.
Paludina emarginata Küster, 1852, p. 50, Pl. X, Figs. 3, 4.
Amnicola emarginata (Say) Frauenfeld, 1863, p. 1030.
Bythinella obtusa Stimpson, 1865, p. 20.
Cincinnatia emarginata Walker, 1901, pp. 30–32.
Amnicola (*Cincinnatia*) *emarginata* Baker, 1902, pp. 336–37, Pl. 26, Fig. 10.
Cincinnatia Binneyana Hannibal, 1913, p. 190.
Cincinnatia emarginata Baker, 1928, pp. 126–27, Fig. 54: 1, 2.
Cincinnatia (*Probythinella*) *emarginata* Thiele, 1928, pp. 369–70.
Hoyia (*Probythinella*) *emarginata* Thiele, 1929, p. 140, Fig. 115.
Vancleaveia emarginata Baker, 1930, p. 191, Fig. 2: 1, 2, 9.
Probythinella binneyana Pilsbry, 1934, p. 562.

Amnicola (*Probythinella*) *binneyana* is not common in Michigan (Map 5). It is restricted to the Great Lakes and the immediate vicinity, and, according to the records, has been collected only 3 times from rivers. Even at these stations the distance is not more than 20 miles inland from the Great Lakes.

SHELL (Pl. I, Figs. 8–12).—Subcylindrical, apex blunt or truncate, about 4 whorls, 3 mm. high, 2 mm. wide. First and second whorls planorbid, sunken below the third whorl; sutures well impressed. Spire slightly longer



MAP 5. Records of *Amnicola (Probythinella) binneyana* Hannibal in Michigan.

than the body whorl. Aperture subovate, mainly basal, 1.44 mm. high, 1.36 mm. wide. Columella reflected, peristome continuous, adnate to the body whorl for a very short distance and occasionally detached. Umbilicus perforate, very narrow. Periostracum light tan, gray, or white. Growth lines very fine.

RADULA (Pl. III, Fig. 5).—Formula, $0:25\pm:12\text{–}1\text{–}6:\frac{6\pm\text{–}1\text{–}6\pm}{3\text{–}3}$:6–1–12:25 ±:0. Fifty-one rows, 0.41 mm. long, 0.13 mm. wide. *Amnicola* (*Probythinella*) *binneyana* possesses the smallest radula of any Michigan amnicolid examined. *A. walkeri,* the smallest representative of this family in Michigan, has a shell only one-half as high as that of *binneyana,* but has a radula nearly twice as large as that of this species. The cusps on the different teeth are so microscopic that it is difficult to designate the formula. The above formula and the following description of the teeth were determined by means of a 1.8 oil immersion objective and a 15× ocular.

Central tooth twice as broad as high (17.04 μ × 7.81 μ); lateral ridge absent, the 3 basal denticles arising from the ventral margin of the lateral

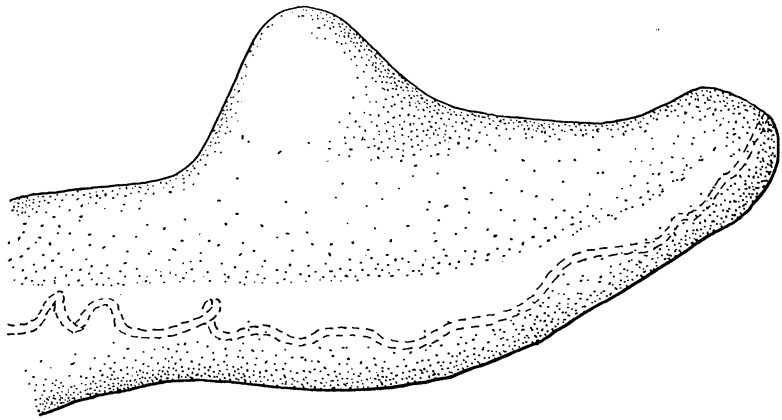


FIG. 5. Verge of *Amnicola* (*Probythinella*) *binneyana* Hannibal with vas deferens along lower margin.

wing. Central cusp comparatively long, narrow and sharply pointed with usually 6 fine needle-like cusps on each side of the central. Lateral tooth with the general outline of the lateral of *A. integra.* Peduncle very narrow, and from the base of attachment the interlocking ridge lies median to the peduncle, continues through the body of the tooth, and projects beyond the inner margin, forming a hook. The distal end of the ridge is joined to the inner margin near the reflection and on the under side. From the central cusp, causing it to be much serrated, 3 inner and 2 outer cusps arise. There are 6 inner cusps and 12 outer cusps. First marginal scythe-shaped, with about 25 fine sharply pointed cusps; peduncle comparatively broad. Second marginal consisting of a single blade. Peduncle moderately large at its attachment to the lingual ribbon and tapering to a point at its distal end. Reflection and cusps entirely absent, a character which has not been observed in any other species of Amnicolidae.

ANIMAL (Pl. VI, Figs. 2 and 3).—White, waxy in appearance. Rostrum long and slender; tentacles cylindrical. A small patch of light tan pigment at the base of each tentacle. Foot long and narrow, auriculated. Slime glands chalky white and scattered loosely in the anterior part of the foot.

GENITALIA (Fig. 5; Pl. VI, Fig. 3).—Verge bilobed, but the 2 parts not bifurcate. Right lobe longer than the left, and during seasonal activity the right lobe becomes increasingly long as the left correspondingly decreases. The vas deferens tortuous and situated along the right lobe, terminating at the extreme tip. Paralleling this duct is a blood vessel which might easily be mistaken for the diverticulum in the secondary lobe as found in other species of this family, e.g., *A. limosa.* Not only is the diverticulum absent in *binneyana,* but neither are there concentration areas of epithelial tissue in the verge (as in *A. integra*) or at the tips (as in *A. lustrica*). Baker's (1928: 128) statement that the genitalia and animal are "similar to [those of] *limosa*" is incorrect.

ECOLOGY.—This species has seldom been taken alive in Michigan, the majority of specimens are from drift along the shores of the Great Lakes. A series of *binneyana* was taken at Fair Haven Beach (north shore of Lake St. Clair) in November, 1935. The shells were collected only at depths of water greater than 5 feet. Here they were living on *Potamogeton* and also on the sandy bottom. A series of more than 200 specimens was dredged from La Plaisance Beach, Lake Erie, at a depth of 18 feet. At this station no plants were taken, and the snails were living on the marl and coarse sandy bottom. This species appears to be most common in the major large lakes of the northern United States and southern Canada. From dredgings it seems to be most abundant at depths of more than 10 feet of water. Evidence of this is also substantiated by the examination of stomachs of the whitefish from Clear Lake, Manitoba, and Humboldt Bay, Lake Nipigon, Ontario. *A. binneyana* made up the main bulk of the food contents of these stomachs. It is known that whitefish inhabit water which is near the thermocline and generally at depths of 60 feet or more.

Specimens of *A. binneyana* from Lake St. Clair and La Plaisance Bay, when brought into the laboratory, repeatedly exhibited a positive phototropism, migrating from the darkened side of the aquarium toward the light. *A. limosa,* which were collected from the same region, but nearer the shore, did not respond phototropically. Fecal pellets demonstrate that the food of *binneyana* consists primarily of diatoms.

DISCUSSION.—The complete synonymy of *Amnicola* (*Probythinella*) *binneyana* is complex but interesting. Lea (1841: 34) described this species as *Paludina obtusa,* from specimens collected in Ohio. Four years before this, Troschel (1837: 173) described a *Vivipara* from Bengal under the name *Paludina obtusa.* Because of this homonym, Lea's species needed renam-

ing. Conchologists were slow in detecting this error, and the name *obtusa* became well established. Tryon, as late as 1870, was still using Lea's name, although the genus *Paludina* had been broken into several genera, "*obtusa* Lea" being placed under the genus *Bythinella.*

In 1852 Küster (1852: 50) redescribed this species as "*Paludina emarginata* Say" from specimens which had been wrongly identified by Bronn as "*Limnaeus emarginatus* Say." Küster did not propose a new specific name in assigning these specimens to "*emarginata,*" but merely gave a new combination to Say's species of *Lymnaea.* This error also became entrenched in the literature. In fact, this species is still known by most conchologists as "*emarginata* Küster."

Hannibal (1912: 190) pointed out the error in using either "*obtusa* Lea" or "*emarginata* Küster" and substituted the name "*Cincinnatia Binneyana.*" Pilsbry (1934: 562) reviewed the synonymy of this species, again pointed out the mistake in using either Lea's or Küster's names, and stated "the species long known as *obtusa* Lea should therefore be called *Probythinella binneyana* (Hannibal)."

As may be seen from the complete synonymy, *binneyana* has been placed under several genera. Because of the minuteness of the radula and particularly the shape of the lateral tooth, it was regarded by Hannibal and others as belonging to the genus *Cincinnatia.*

Thiele (1928: 370) erected the subgenus *Probythinella* for *emarginata* (Küster). This he first placed under the genus *Cincinnatia,* but later in the discussion (1928: 378) he listed it under the genus *Hoyia* Baker. Baker (1930: 189) disregarded Thiele's subgenus and named the genus *Vancleaveia* with *emarginata canadensis* (Baker) as the type.

It is apparent from the above discussion how muddled this group has become. Baker (1930: 191) stated: "The whole family of Amnicolidae is in need of revision, based on examination of genitalia and radula, and until such revision is made such groups as offer differences in radula or genitalia must be considered as genera. When this has been done it may be advisable to reduce some genera to sub-genera." The opposite point of view has been taken in the present study. Until the entire family of Amnicolidae of North America has been completely studied, and the relationship that one species, or one genus, bears to others is established, it seems better to keep the family as simple and as unified as possible. This species is, therefore, called *Amnicola* (*Probythinella*) *binneyana* (Hannibal).

As is true with the majority of Amnicolidae which inhabit both lake and river environments, there is a marked difference between the shell of the Great Lakes *binneyana* and that of the river form. The lake form has been given specific rank by Baker (1930: 191) as *Vancleaveia lacustris.* There is a regular transition of the shell from the river form (Pl. I, Fig. 8) to the

Great Lakes form (Pl. I, Figs. 10–12). This transition stage is represented by specimens collected from Lake St. Clair just below the St. Clair River (Pl. I, Fig. 9). The radula, the animal, and the genitalia are constant in the specimens from the 3 localities and at present are to be regarded as ecological forms and not subspecies.

GENUS *PYRGULOPSIS* CALL AND PILSBRY, 1886

Pyrgulopsis Call and Pilsbry, 1886, 5: 9–10.

SHELL.—Minute, ovate, or conically turreted, elongated, imperforate. Apex acute, aperture ovate, peristome continuous. Whorls 4 to 6. Operculum subspiral, ovate, thin, corneous, with nucleus well forward and approximating the columella. Spiral sculpture absent or very faint.

RADULA.—Central twice as broad as high, lateral angles attenuated, ventral lobe rounded, basal denticles 1 or 2, central cusp long and pointed, 4 lateral cusps, small and pointed. Lateral tooth lobed on dorsal basal surface, pitted on ventral median surface, peduncle slender, central cusp spade-shaped, 2 or 3 inner cusps, 4 or 5 outer cusps. First and second marginals falcate, multicuspid.

Pyrgulopsis letsoni (Walker)

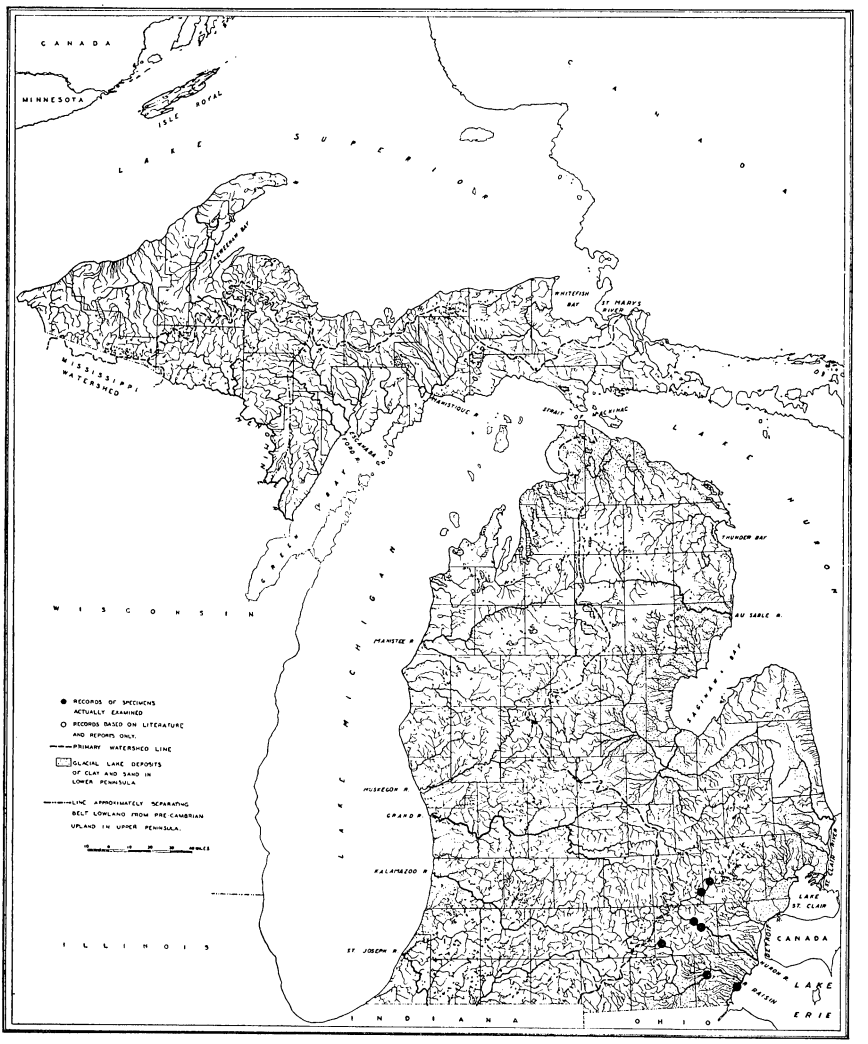
Amnicola letsoni Walker, 1901, p. 113.
Pyrgulopsis letsoni Walker, 1918, p. 139.

Pyrgulopsis letsoni (Walker) has been collected from Michigan only in the southeastern counties (Map 6). This species had a greater range during the Pleistocene than it seems to have at present. During that time it ranged from New York to Illinois, whereas today it has been taken only in regions near Lake Erie, or from streams which empty into this lake.

SHELL (Pl. I, Fig. 13).—About 3 mm. high, 1.5 mm. wide, $5\frac{1}{3}$ whorls, increasing gradually in size. Apex blunt, elevated, obtuse, sutures moderately impressed; the first 3 whorls shouldered, the flattened sides becoming more pronounced with the maturity of the shell. Aperture (1.6 mm. high, 1.2 mm. wide) small, ovate, angled above, rounded below; columella straight and oblique to the axis; peristome continuous, adnate or entirely free from the body whorl. Umbilicus subimperforate. Epidermis light horn color, growth lines prominent and occasionally developed as striae.

OPERCULUM (Pl. II, Fig. 7).—Paucispiral, ovate, thin, basal margin slightly convex; a little more than 2 whorls, horn-colored except at basal and right margin, which are colorless; growth lines strong, spiral sculpture faint; nucleus one-fourth distance from the base to the summit and toward the left (columellar margin). Attachment to the operculigerous lobe occupying the greater part of the left half of the operculum. Height, 0.95 mm., width, 0.62 mm.

RADULA (Pl. IV, Fig. 1).—Formula, $25+:25+:4\text{–}1\text{–}2:\frac{4\text{–}1\text{–}4}{2\text{–}2}:2\text{–}1\text{–}4:25+:25+$. Thirty-six rows, 0.77 mm. high, 0.08 mm. wide. Slightly smaller than in *Pyrgulopsis scalariformis* Wolf. Central tooth twice as broad as high (21.3 μ by 10.6 μ). Central cusp very long and pointed, more than



MAP 6. Records of *Pyrgulopsis letsoni* (Walker) in Michigan.

twice as long as side cusps. Side cusps 4 on each side of central, fine and sharply pointed. Basal denticles 2 on each side, the admedian basals being the larger. Lateral tooth with a distinct triangular lobe beneath a shallow pit. The center cusp spade-shaped, the outer and inner cusps sharply

pointed. The first inner cusp usually attached to the center cusp. First and second marginals falcate, with 25 or more fine sharp cusps, too minute to be accurately counted.

ANIMAL (Pl. VI, Fig. 4).—Head dusky brown, body gray, tentacles long and cylindrical, foot auriculated, light gray with dense patches of mucous glands anteriorly.

GENITALIA (Fig. 6; Pl. VI, Fig. 4).—Verge bilobed, penis black, long, pointed at its extremity. Secondary lobe short, truncated, light gray, but retaining the pigment at the tip in stained specimens. Accessory duct absent.

Since the soft parts of no member of the genus have been known heretofore, a comparison of the animals of *P. letsoni* and of other species of *Pyrgulopsis* is impossible.

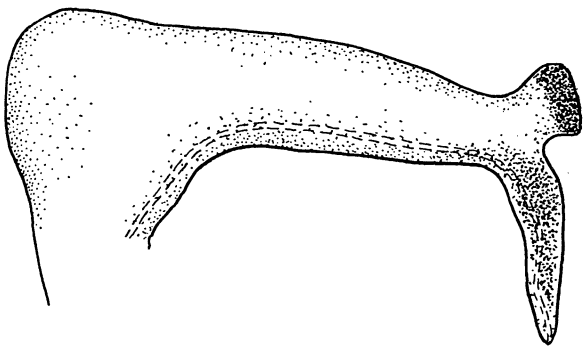


FIG. 6. Verge of *Pyrgulopsis letsoni* (Walker) with vas deferens lying along the lower margin and terminating in the end of the penis.

EGGS (Pl. VII, Fig. 2).—Laid singly, round, without the laminated crest as in *A. limosa,* light gray. Size, 0.4 mm.

DISCUSSION.—*Pyrgulopsis letsoni* (Walker) was described from subfossil specimens collected by Miss Elizabeth Jennie Letson from Goat Island, Niagara River, New York, in 1901. The shells of this species have been found in various parts of southeastern Michigan from the west end of Lake Erie, the River Raisin, to the Huron River above Milford. In spite of extensive search in regions where the dead shells were collected, no living specimens were found. This, it is now clear, was due to the peculiar ecology of *letsoni,* which differs from that of any other amnicolid of Michigan. A clue to its environment was obtained when the Argo Pond (an artificially dammed area in the Huron River above Ann Arbor, Michigan) was drained (Pl. VIII, Fig. 1). This created more suitable conditions for collecting in the river bed. While working there, several fresh shells of *P. letsoni* were taken, although the bodies and opercula were gone. A search in the thick beds of *Chara, Potamogeton,* and *Vallisneria* which bordered this channel did not reveal even a dead shell.

On returning to the river bed, I discovered more dead specimens. An examination of the larger stones presented another problem. These glaciated igneous stones are encrusted with thick deposits of calcium carbonate laid down by aquatic plants. The lime has undergone partial solution, forming deep honeycombed cavities (Pl. VII, Fig. 6), which serve as reservoirs for silt, mud, and algae and conceal any small shells which might be present. The contents of these cavities were carefully examined and finally the first living specimen of *P. letsoni* was discovered in the deep recess of a cavity on the underside of a stone. By vigorously shaking the stones in a pail of water and then pouring the contents of the pail into a fine sieve more than 40 specimens were collected.

This shell, although distinct when its characters are known, might be confused with that of juvenile forms of *Amnicola lustrica* or *Hydrobia nicklinia-ana*. It may be distinguished from *lustrica* by its flattened sides, ovate aperture, and subimperforate umbilicus. It may be separated from *nickliniana* by the flatter whorls, more shallow sutures, and the elevated nuclear whorl. The soft parts of these species are even more distinct. Each of the three has a characteristic environment, although in collecting *letsoni* several *lustrica* were seen on the same stones, but not in the cavities.

GENUS *HYDROBIA* HARTMANN, 1821

Hydrobia Hartmann, 1821, p. 47.
Paludina Lea, 1839, p. 92.
Paludestrina D'Orbigny, 1840, p. 381.
Bithinie Moquin-Tandon, 1851, p. 239.
Bythinella Stimpson, 1865, p. 19.
Bythinella Binney, 1865, pp. 67–68.
Stimpsonia Clessin, 1878, p. 151.
Paludestrina Pilsbry, 1899*b*, p. 22.
Stimpsonia Baker, 1928, pp. 131–32.
Fontigens Pilsbry, 1933, p. 12.
Hydrobia Pilsbry, 1934, pp. 559–60.
Hydrobia Henderson, 1935, p. 194.

SHELL.—Averaging about 3 mm. in height, elongate-conic or attenuate, whorls inflated, sutures well impressed, apex elevated, peristome continuous, aperture subovate, umbilicus subperforate.

RADULA.—Comparatively large for the size of the animal, central tooth with a single basal denticle, lateral lobed on basal dorsal surface, pitted on ventral median surface. First and second marginals multicuspid.

GENITALIA.—Bifid or trifid verge.

ECOLOGY.—Generally found in cold springs.

Hydrobia nickliniana (Lea)

Paludina nickliniana Lea, 1839, p. 92, Pl. XXII, Fig. 109.
Amnicola attenuata Haldeman, 1842, p. 200.

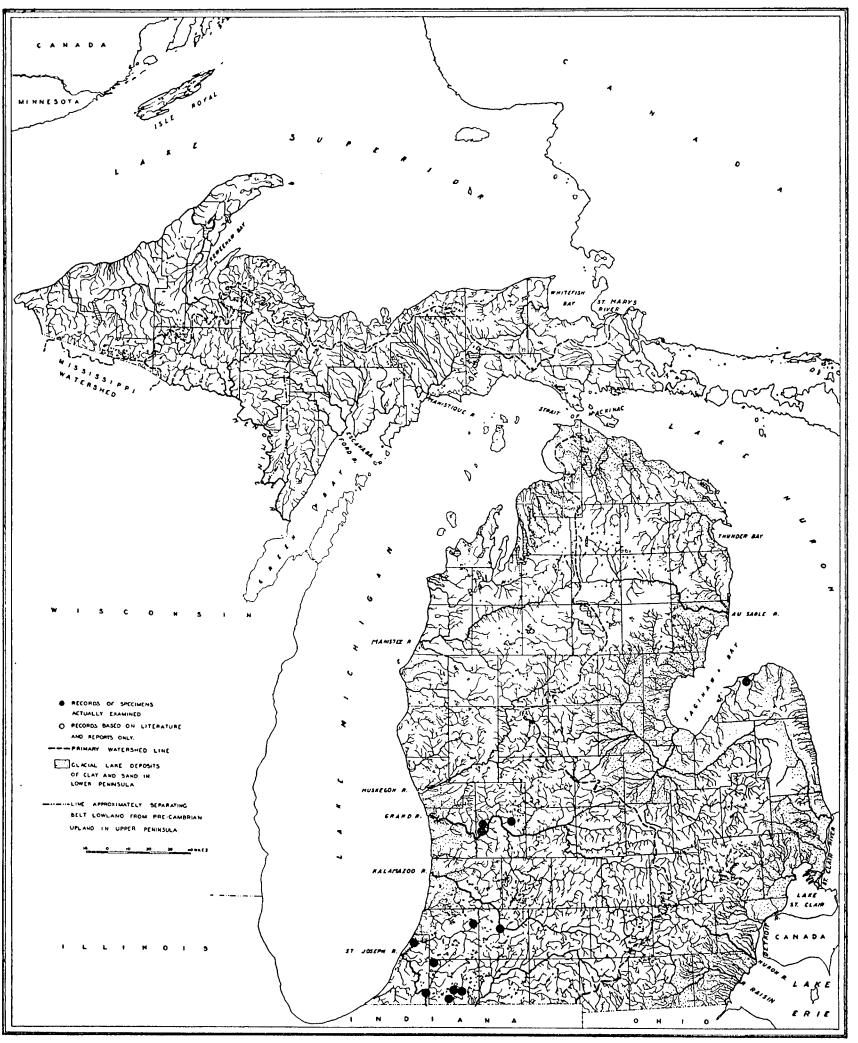
Amnicola nicliniana Haldeman, 1845, pp. 19–20.
Amnicola attenuata Haldeman, 1845, p. 22, Pl. I, Fig. 13 (named *elongata* on plate).
Bythinella Nickliniana Stimpson, 1865, pp. 19–20.
Bythinella attenuata Stimpson, 1865, p. 20.
Bythinella nickliniana Binney, 1865, pp. 68–69, Figs. 133–34.
Bythinella attenuata Binney, 1865, p. 68, Fig. 132.
Bythinella attenuata Tryon, 1870, p. 46.
Bythinella nickliniana Tryon, 1870, p. 46.
Paludestrina nickliniana attenuata Pilsbry, 1899*b*, p. 22.
Paludestrina nickliniana Baker, 1902, pp. 338–39, Pl. XXVI, Fig. 11.
Stimpsonia nickliniana Baker, 1928, pp. 132–36, Pl. VII, Figs. 9–12.
Stimpsonia nickliniana attenuata, Baker, 1928, pp. 136–37, Pl. VII, Figs. 13, 14.
Fontigens nickliniana, Pilsbry, 1933, p. 12.

Hydrobia nickliniana (Lea) has a rather wide distribution in the United States, occurring from Pennsylvania to Wisconsin and from Ontario to Alabama. It has been collected in western and southwestern Michigan and also at Port Austin and Rush Lake, Huron County (Map 7). There are two possible explanations for the Huron County records. The species may have been introduced with water cress. A more probable explanation is based on the position of the late glacial lakes, Arkona and the Grand River outlet, Lake Whittlesey and the Ubley outlet; and, finally, Lake Warren and the Grand River outlet. During the late history of the glacial lakes the Saginaw Bay region drained westward through the Grand River channel emptying into Lake Chicago. It seems reasonable to suppose that this continuous waterway system had much the same fauna throughout its length. Supporting evidence of this is found among certain naiads of Michigan. *Actinonaias ellipsiformis* (Conrad), for example, is present in the western drainage basins of Michigan but not in such rivers as the Rouge, Clinton, Huron, and Raisin. Curiously enough, this species inhabits the Saginaw River drainage basin, which now discharges its waters into Saginaw Bay. *Hydrobia nickliniana* may have migrated up the Grand River outlet or, possibly, the stock came from Ontario drainage basins.

Shell (Pl. I, Fig. 16).—Attenuate, more than twice as high as wide (about 4.5 mm. high, 2 mm. wide), $5\frac{1}{4}$ whorls, inflated, sutures deep, apex bluntly elevated above the following whorls. Aperture ovate (1.44 mm. high by 1.16 mm. wide), peristome continuous, umbilicus subimperforate. Lines of growth somewhat coarse. Periostracum light horn color.

Radula (Pl. IV, Fig. 2).—Formula, $25 \pm : 20 \pm : 3\text{–}1\text{–}2 : \frac{4\text{–}1\text{–}4}{1\text{–}1} : 2\text{–}1\text{–}3 : 20 \pm : 25 \pm$. Comparatively long (1.18 mm. by 0.125 mm.), 87 rows. Central more than twice as wide as high (32.5 μ by 15 μ), lateral ridge strong with a single basal denticle, basal lobe deep and narrow, central cusp narrow and sharply pointed, lateral cusps sharply pointed, generally 4, occasionally

5, the fifth being blunt and small. Lateral tooth with a strong dorsal basal lobe and a deep ventral median pit, central cusp wide, spade-shaped, 2 small inner cusps, the innermost being sharply pointed and longer than the other, which is blunt; 3 outer cusps, all sharply pointed, the innermost being the



MAP 7. Records of *Hydrobia nickliniana* (Lea) in Michigan.

largest. First marginal tooth multicuspid with about 20 fine comblike cusps, peduncle somewhat broad. Second marginal tooth with numerous short, fine cusps, too minute to be accurately counted.

GENITALIA (Fig. 7; Pl. VI, Fig. 5).—Verge arising as a large single organ from the posterior end of the rostrum directly beneath the mantle.

Remaining as a single organ for a comparatively short distance, the verge usually splits into 3 units, occasionally 2, the penis being at the extreme right. Each of the other 2 lobes has an accessory duct which is tortuous, the extreme left duct being the smaller in diameter. The middle duct terminates as a large blind sac. The 3 lobes that comprise the external verge vary greatly in shape. Usually, the middle lobe is the longest, but at times the penis exceeds the length of the other 2 lobes and is gyrate. Occasionally, the 3 may be of equal length. In a large series of *nickliniana* a few

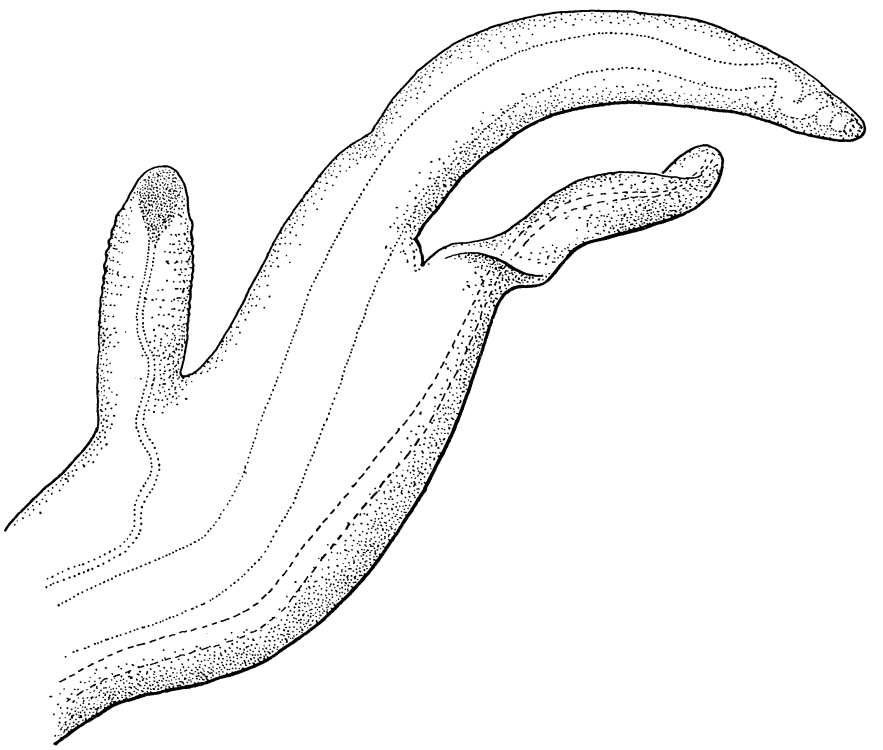


FIG. 7. Trifid verge of *Hydrobia nickliniana* (Lea). The extreme right lobe is the penis. The function of the other two ducts in the left and middle lobes is unknown.

specimens possessed a verge of only 2 lobes, the extreme left lobe being absent.

ECOLOGY (Pl. IX, Fig. 1).—*Hydrobia nickliniana,* because of its environment, has been popularly called the "water cress snail." It is usually present in cool, shallow springs where water cress grows in a thick mat; water an inch or so deep allows this species to thrive in such numbers as to blacken the stems of the cress. As many as 20 specimens were removed from a small sprig of water cress from the spring near Button Lake.

DISCUSSION.—The use of the generic name *Hydrobia* was abandoned for a time. It was considered preoccupied by *Hydrobius,* a genus of Coleoptera. Recent rulings of the International Commission on Nomenclature, however, have made valid the use of similar *a* and *us* endings, e.g., "*Conulinus* von Martens (1895) is not preoccupied by *Conulina* Bronn (1835),"[3] and, consequently, the name *Hydrobia* has again been established for this genus.

The species under discussion has been classified by most workers in this century as *Paludestrina nickliniana.* There is some doubt that this group of nearctic amnicolids is congeneric with the European *Paludestrina. Hydrobia* has priority over *Paludestrina* by almost 20 years. Baker (1928: 132–36) revived Clessin's *Stimpsonia* (1878) for *nickliniana. Stimpsonia* is preoccupied in Hemichordata (Girard, 1853) and also in Crustacea (Bate, 1862), and, therefore, is rejected in Mollusca. Pilsbry (1933: 12) substituted the genus *Fontigens* for Clessin's *Stimpsonia. Hydrobia,* like the other fresh-water rissoids, is only slightly known. The genitalia and radulae have been studied in only a few of the many species consigned to the group. It seems a sound policy to leave *nickliniana* within this genus until such time as a more complete knowledge and truer concept of the Amnicolidae may be had.

In large colonies some specimens of *H. nickliniana* become more attenuated than average individuals. These forms have been given the varietal name *attenuata* Haldeman. There is no difference in the radula, genitalia, or ecology to warrant the use of this trinomial, and it is therefore discarded.

SUBFAMILY LITHOGLYPHINAE FISCHER, 1885

Shell ranges from minute (*Cochliopa*) to comparatively large (*Fluminicola*). Spire short, body whorl large, columella usually thickened; operculum corneous, subspiral. Central tooth of radula with several basal denticles.

GENUS *SOMATOGYRUS* GILL, 1863

Paludina Say, 1825, p. 125.
Amnicola Tryon, 1862, p. 276.
Somatogyrus Gill, 1863, p. 2.
Somatogyrus Baker, 1902, pp. 339–40.
Somatogyrus Walker, 1918, p. 32.
Birgella F. C. Baker, 1926*b*, p. 196.
Somatogyrus F. C. Baker, 1928, pp. 146–47.
Birgella F. C. Baker, 1928, pp. 154–55.

Shell usually thick, imperforate or narrowly perforate, spire short, body whorl large, round, columella thickened. Operculum corneous, subspiral.

[3] See "International Rules of Zoological Nomenclature," *Proc. Biol. Soc. Wash.,* 39 (1926), Opinion 86: 102.

Radula with several basal denticles on central tooth; lateral tooth lobed and pitted; marginals multicuspid.

Somatogyrus subglobosus (Say)

Paludina subglobosa Say, 1825, p. 125.
Melania isogona Say, 1829, p. 277.
Paludina subglobosa Haldeman, 1845, pp. 10–11, Pl. X, Fig. 7.
Somatogyrus isogona Stimpson, 1865, pp. 10–11.
Somatogyrus isogonus Binney, 1865, p. 77.
Somatogyrus subglobosus Tryon 1870, pp. 60–61.
Somatogyrus subglobosus Baker, 1902, pp. 340–41.
Birgella subglobosus Baker, 1928, pp. 155–59.

Somatogyrus subglobosus (Say) is a deep water inhabitant. It has seldom been taken alive in Michigan, most records representing beach drift. This species is restricted to the Great Lakes and deep rivers, e.g., the Grand River (Map 8).

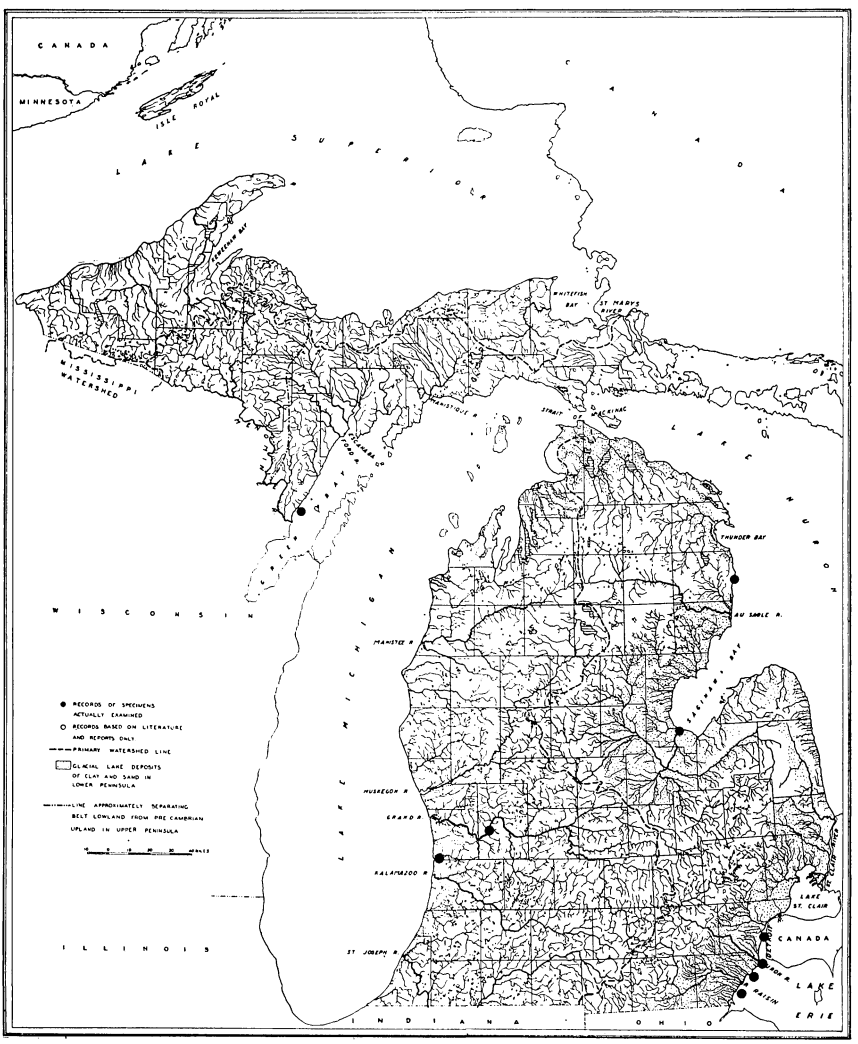
SHELL (Pl. II, Fig. 1).—Comparatively large, subglobose (9.2 mm. high, 6.8 mm. wide), $4\frac{1}{4}$ whorls, rounded, shouldered, sutures impressed, spire short, body whorl large; peristome continuous, lip not thickened, columellar axis reflected; aperture subovate (5.1 mm. high, 3.8 mm. wide); umbilicus narrow, perforate; lines of growth fine, somewhat crowded; periostracum light horn color. Operculum subspiral (Pl. II, Fig. 3).

RADULA (Pl. IV, Fig. 3).—Formula, $10 \pm : 13 \pm : 5\text{–}1\text{–}2 : \frac{4\text{–}1\text{–}3}{3\text{–}3} : 2\text{–}1\text{–}5 : 13 \pm : 10 \pm$. Length of lingual ribbon, 1.25 mm., width, 0.325 mm. Forty-eight rows. This radula is larger than that of any other Michigan amnicolid, including *Bulimus tentaculatus*. Central cusp broader than high (57.75 μ by 34 μ), 3 basal denticles, the innermost being the largest; central cusp bifurcate, producing an asymmetry in the central tooth,[4] the main cusp unusually long and dagger-shaped, lateral cusps (3 on the right, 4 on the left) are smaller and sharply pointed; basal part round. Lateral tooth with basal part of the blade lobed on the dorsal surface and pitted on the median ventral surface; central cusp long, somewhat slender, sharply pointed; 2 inner and 5 outer cusps all sharply pointed, peduncle short in comparison to the blade. First marginal with about 15 sharply pointed rakelike teeth, peduncle with 2 strongly supporting ribs. Second marginal with about 10 sharply pointed cusps.

GENITALIA (Fig. 8).—Verge proportionate to the size of the animal, arising some little distance behind the tentacles, slightly to the right. Bifur-

[4] This condition was at first thought to be a malformation of the lingual ribbon. It appears, however, to be a constant character inasmuch as every ribbon examined thus far (material from widely separated localities) has this curious splitting of the central cusp, a condition heretofore unreported in the Amnicolidae.

cating at about half its length, the penis extends only a short space past the forking. It is short and fleshy and terminates bluntly. The vas deferens is tortuous throughout most of the verge, becoming straight at its distal end. The accessory lobe is larger and extends farther than the penis. The distal part is usually reflexed. There is some variation in the general shape of



MAP 8. Records of *Somatogyrus subglobosus* (Say) in Michigan.

the verge of *subglobosus*. At times the secondary lobe retracts, becoming about the same length as the penis. This alters the width of both lobe and penis, causing an increase in width and thickness in each. The species does not have a secondary blind duct in the accessory lobe as do *A. limosa* and *B. tentaculatus*.

ECOLOGY.—*Somatogyrus subglobosus* is a deep water inhabitant. Specimens have been dredged from a depth of 15 feet in La Plaisance Bay, Lake Erie, during the course of this study. It was taken with *Amnicola* (*Probythinella*) *binneyana* (Hannibal).

DISCUSSION.—F. C. Baker (1926*b*: 193–205) erected the new genus *Birgella* for the reception of *subglobosus* for the reason that "the penis [is] much longer than the flagellum sheath which is short and conical or compressed" and that the central tooth of the radula has "a long pointed central cusp which reaches nearly to the base of the tooth, the lateral ridge with but one large denticle and two smaller ones below." He further added: "The verge does not appear the same in different individuals (in spirit) and these probably represent different degrees of contraction." No verge in the Amnicolidae could appear natural after the live animal has been killed in alcohol. The verge should always be examined from living specimens, which, after being narcotized with the animal in a fully relaxed condition, should be killed, fixed, and the verge re-examined. Only those specimens

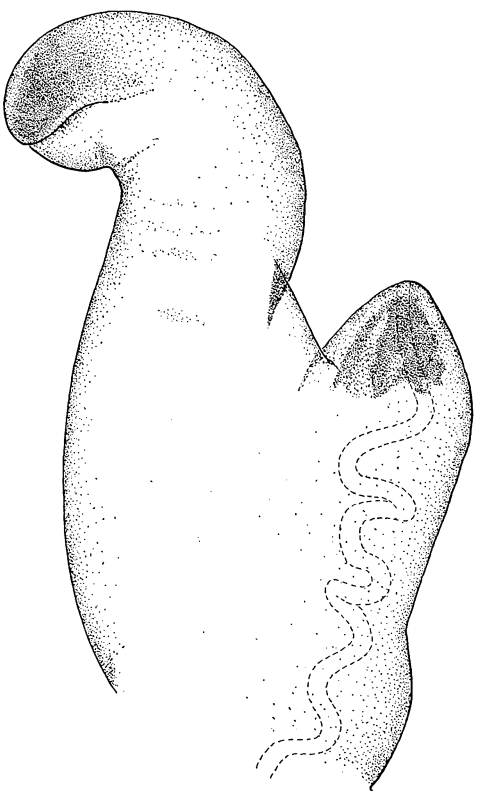


FIG. 8. Verge of *Somatogyrus subglobosus* (Say). Penis, containing vas deferens, is at the right.

which exhibit the same general features as those in the live animal should be described and figured as typical representatives of the species. Since the large majority of species of *Somatogyrus* are known from the shell only, there is insufficient evidence at present to warrant a separation of this genus and the establishment of *Birgella* for the reception of the single species *subglobosus*.

Subfamily Buliminae (Hannibal), 1912

Bythininae, Gill, 1863.
Bulimidae, Hannibal, 1912.

Shell ovate, comparatively large (10 mm.), peristome generally thickened. Operculum calcareous, concentric.

Genus *Bulimus* Scopoli, 1777

Bulimus Scopoli, 1777, p. 392. Type by designation: *Helix tentaculata* Linnaeus, Pilsbry and Bequaert, 1927: 214.
Bithynia Leach, 1818, Abel, p. 362. Type: *Helix tentaculata* Linnaeus.
Bithinia Gray, 1824, p. 277. Monotype: *Helix tentaculata* Linnaeus.
Bythinia MacGillivray, 1844, p. 124. Monotype: *Helix tentaculata* Linnaeus.
Elona Moquin-Tandon, 1855, pp. 516, 527. Type by designation: *Helix tentaculata* Linnaeus.
Bythinia Gray, Stimpson, 1865, p. 4.
Bulimus Scopoli, Dall, 1892, pp. 334–35. Type by elimination: *Helix tentaculata* Linnaeus.
Bulimus Scopoli, Pilsbry, 1895, pp. 2–4.
Bythinia Gray, F. C. Baker, 1902, pp. 328–30.
Bulimus Scopoli, Hannibal, 1912, pp. 183–84.
Bythinia Leach, Walker, 1918, p. 28.
Bulimus Scopoli, Pilsbry and Bequaert, 1927, pp. 214–15. Type by designation: *Helix tentaculata* Linnaeus.
Bithynia Leach, Thiele, 1929, p. 154.
Bithynia Leach, Kennard, 1941, pp. 262–63.

Shell comparatively large (10 mm.), imperforate, aperture ovate. Radula with central tooth broader than high, basal denticles numerous. Verge bifid.

Type.—*Helix tentaculata* Linnaeus.

Discussion.—The synonomy of this genus clearly indicates that there is a question whether the name should be *Bulimus* or *Bithynia* (*Bythinia, Bithinia*). The very involved history of these names has been published by several authors: Dall (1892: 335), Pilsbry (1895: 2–5; 1927: 214–15), Hannibal (1912: 183–84). These men came to the conclusion that *Bulimus* must be used in place of *Bithynia*, and that the genotype should be *Helix tentaculata* Linnaeus. Smith (1894: 636) and Kennard and Woodward (1924: 125–28) have claimed, however, that *Bulimus* is not valid and that *Bythinia* is the proper genus of *tentaculata*. Pilsbry presented the problem

to the International Commission on Zoological Nomenclature. The commission voted (see Opinion 116, 1931: 6–17) that it "does not interpret *Bulimus* Scopoli, 1777, as an obvious typographical error" of *Bulinus* Adanson, 1757, as was claimed by Woodward. Kennard (1941: 262–63) stated: "The continued use of this name [*Bithynia* Leach] instead of *Bulimus* Scopoli is urged for it is clear that all the facts were not submitted to the Commission and their decision was against the evidence." He does not mention what facts were withheld which would have altered the decision. Therefore, in conformity with the decision of the International Commission on Zoological Nomenclature, the genus *Bulimus* Scopoli, 1777, is recognized and *Bithynia* is considered a synonym. Pilsbry (1927: 214) has named *Helix tentaculata* Linnaeus as the type of *Bulimus*.

Bulimus tentaculatus (Linnaeus)

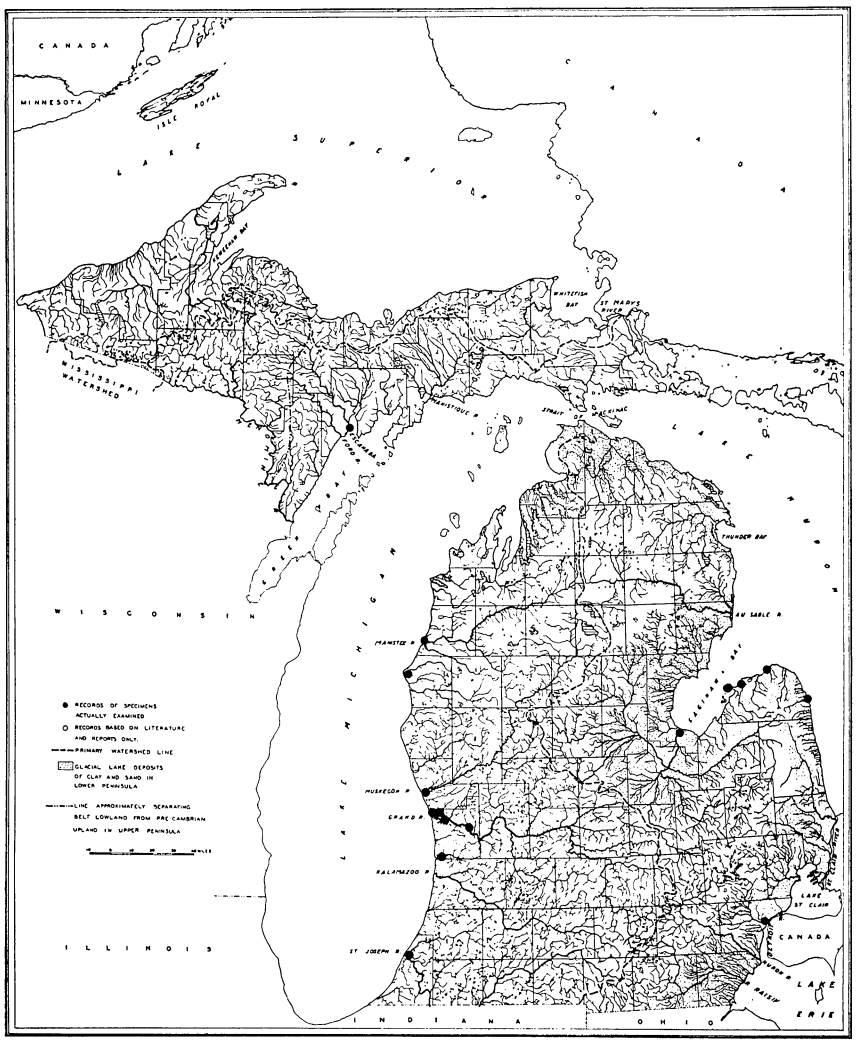
Helix tentaculata Linnaeus, 1758, p. 774.
Bulimus tentaculata (Linnaeus) Scopoli, 1777, p. 392.
Bithynia tentaculata (Linnaeus) Leach, in Abel, 1818, p. 362.
Bithinia tentaculata (Linnaeus) Gray, 1824, p. 277.
Bythinia tentaculata (Linnaeus) MacGillivray, 1844, p. 51.
Elona tentaculata (Linnaeus), Moquin-Tandon, 1855, pp. 516, 527.
Bulimus tentaculatus magnalacustris F. C. Baker, 1928, pp. 81–89.

Bulimus tentaculatus (L.) was introduced into the eastern United States from Europe. It has spread into the Great Lakes, possibly through the Erie Canal or the St. Lawrence River. As yet it seems to be limited to Lakes Erie, St. Clair, Huron, and Michigan, and the territory adjacent thereto (Map 9). It probably is living in Lake Superior, although it has not been reported from there.

SHELL (Pl. II, Fig. 2).—*Bulimus tentaculatus* (Linnaeus) is the largest species of Amnicolidae known in America. About 11 mm. high, 6.5 mm. wide; $5\frac{3}{4}$ whorls, somewhat flattened, sutures shallow, nuclear whorl prominent and well above succeeding whorls. Aperture oval (4.5 mm. high, 3.3 mm. wide), peristome continuous, lip somewhat thickened. Umbilicus imperforate. Periostracum horn color.

OPERCULUM (Pl. II, Fig. 5).—Concentric in growth, calcareous in composition. In its embryonic development the operculum of *B. tentaculatus* is subspiral and corneous as are the opercula of North American amnicolids. After hatching, the secretory part of the operculigerous lobe is not limited to the parietal-marginal side only, but new growth is added in concentric rings. Accompanying this growth, calcium carbonate is laid down between the dorsal and ventral surfaces, producing a thick opaque operculum. This type of operculum is unknown in any native North American species of Amnicolidae.

RADULA (Pl. IV, Fig. 4).—Formula, $12 \pm : 15 \pm : 4\text{–}1\text{–}2 : \frac{4\text{–}1\text{–}4}{6\text{–}6} : 2\text{–}1\text{–}4 : 15 \pm : 12 \pm$. Fifty-six rows, 1.25 mm. long, 0.207 mm. wide. Central tooth broader than high (72.5 μ wide, 41.25 μ high). Lateral ridge strong, with



MAP 9. Records of *Bulimus tentaculatus* (*Linnaeus*) in Michigan.

about 6 basal teeth, the largest being innermost. Basal lobe pointed or blunt, thicker than the middle part of the tooth. Central cusp sharply pointed, becoming spade-shaped with wear. Lateral cusps 4, comparatively small, pointed. Lateral tooth lobed on the outer surface, pitted on the underside. Peduncle slender, central cusp broad and spade-shaped, 2 inner cusps, with

an occasional third very small and blunt. Outer cusps 4, sharply pointed. First marginal, multicuspid, has about 15 sharply pointed cusps and is more sturdy in structure than that of any other Michigan amnicolid. Peduncle more robust toward the middle. Second marginal, multicuspid with about 12 slender cusps which circumscribe the tip of the blade.

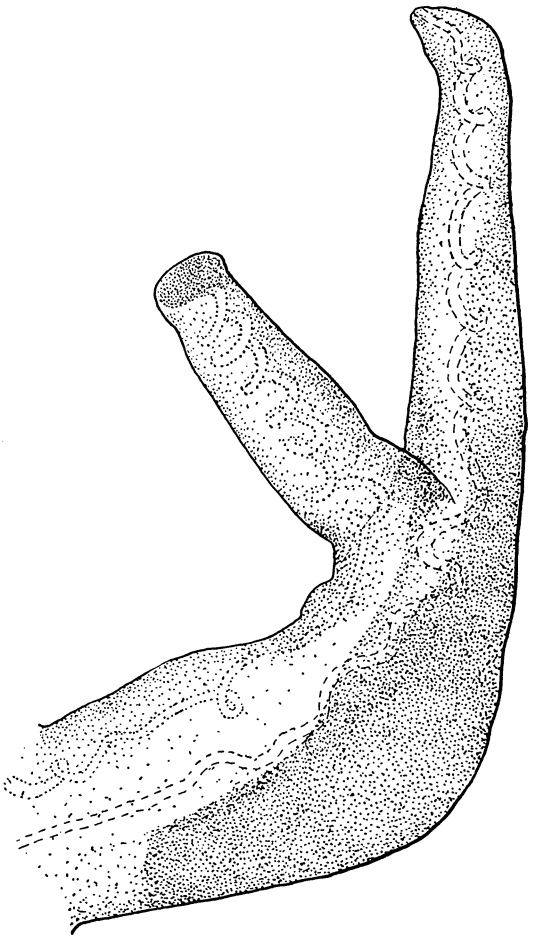


FIG. 9. Verge of *Bulimus tentaculatus* (Linnaeus). The secondary lobe (left) contains an accessory duct. Right lobe is the penis with the vas deferens.

GENITALIA (Fig. 9).—Verge bifid, the penis and secondary lobe are about equal in length. The forking is situated about the middle of the verge. The penis is more slender than that in *Somatogyrus subglobosus*. The secondary lobe, truncated at its extremity, contains an accessory duct which ends blindly, as in *Amnicola limosa*.

EGGS (Pl. VII, Fig. 3).—Deposited in a cluster of 8 to 12 eggs to the mass. This disposition has not been observed in any native North American amnicolid.[5]

DISCUSSION.—*Bulimus tentaculatus* (L.) is a European species, introduced into America about 1870. It was reported from the southeastern shore of Lake Ontario at Oswego, the Erie Canal at Syracuse, and from West Troy in the year 1888. Its spread has been continuous since that time, and it has invaded Toronto, Canada, the shores of Lake Erie, the Detroit River, Lake St. Clair, Lake Huron, and Lake Michigan. As early as 1891 it was reported from Black Lake, Ottawa County, Michigan. Its shells are now among the most abundant of those in the Great Lakes. Not only has its spread been rapid, but the species has thrived in its new environment, its shells in this country are larger and more handsome than are those in Europe. Beauchamp (1888: 114–15) wrote:

> It (*B. tentaculatus*) has now become the most abundant shell in the canal in that vicinity (Syracuse, N. Y.). I collected, last spring on a gravelly bottom in the canal, favorable to *Goniobasis Virginica* and *livescens,* but found only dead shells of these, while every stone was occupied by the Bythinias. I think they devoured the food of the others, and so starved them out.

Baker (1902: 330) reported:

> The Lake View water supply [of Chicago] has been seriously threatened by the presence of the snail (*B. tentaculatus*). The small service pipes became choked and in many private houses a tumblerful of these animals was taken from the faucet. Investigation at the Lake View crib showed that the screens were provided with such a large mesh that the eggs gained access to the main tunnel and there developed, the force of the water drawing them farther and farther into the tunnel until they finally appeared in the service pipes.

This species, when mature, is one of the easiest to identify of Michigan amnicolids. Its large size, imperforate umbilicus, and concentric operculum readily reveal its identity. Juvenile specimens, however, bear some resemblance to other species of *Amnicola,* e.g., *limosa* and *integra.* By means of a hand lens one may notice that there are fewer whorls in the young *Bulimus,* a narrower umbilicus, and the outer margins of the operculum are concentric.

Because of the subspiral operculum in the embryonic *Bulimus,* it is reasonable to believe that the ancestors of this species were paucispiral-operculates, as are the majority of Amnicolidae living at the present time. *Bulimus,* therefore, seems to have evolved further than the other members of its family. This is substantiated by the fact that the basal denticles are more numerous in this genus than they are in its relatives.

[5] Stimpson, 1865, described and figured eggs in a capsule which he thought were those of *Fluminicola.* This genus lays its eggs singly and not in clusters.

Subfamily Lyogyrinae Pilsbry, 1916

Shell minute, conical, turreted or subdepressed. Operculum spiral. Radula comparatively long, central tooth with 1 or 2 basal denticles.

Genus *Lyogyrus* Gill, 1863

Lyogyrus Gill, 1863, p. 34.

Shell about 2.5 mm. high, conical or turreted. Operculum spiral (Pl. II, Fig. 4). Radula comparatively long, similar to that of *Amnicola walkeri;* the central tooth has 1 or 2 basal denticles.

Lyogyrus brownii (Carpenter)

Amnicola brownii Carpenter, 1872.
Valvata (Lyogyrus) brownii Carpenter, 1889, p. 67.
Lyogyrus brownii Pilsbry, 1892, p. 83.

The genus *Lyogyrus* is known from Michigan by a single specimen (Univ. Mich. Mus. Zool. No. 91723) collected by DeCamp about 1880 from Eagle Mill Springs, a few miles west of Grand Rapids (Map 10). *Lyogyrus brownii* is at present known only from the Atlantic states (Massachusetts, Rhode Island). Since DeCamp's time, Grand Rapids has expanded, and several other conchologists and I have visited the springs near the city, but this species has never been rediscovered. Because of the fact that only 1 specimen has been collected, and that far removed from its known range, doubt is entertained that *Lyogyrus* is native to Michigan. It is possible that this specimen came from Kent County, Rhode Island.

Shell (Pl. I, Fig. 15).—Turreted, $\frac{3}{5}$ as wide as high (2.4 mm. high, 1.5 mm. wide), $4\frac{1}{2}$ whorls, inflated, sutures very deep, apex blunt, first whorl of protoconch planorbid. Peristome continuous, separated from the body whorl by a narrow margin, aperture subcircular (0.88 mm. high by 0.80 mm. wide), columella reflected. Umbilicus comparatively wide, deep. Shell thin, lines of growth fine, periostracum light horn color when cleaned from the adhering deposit.

Operculum.—Spiral, chitinous.

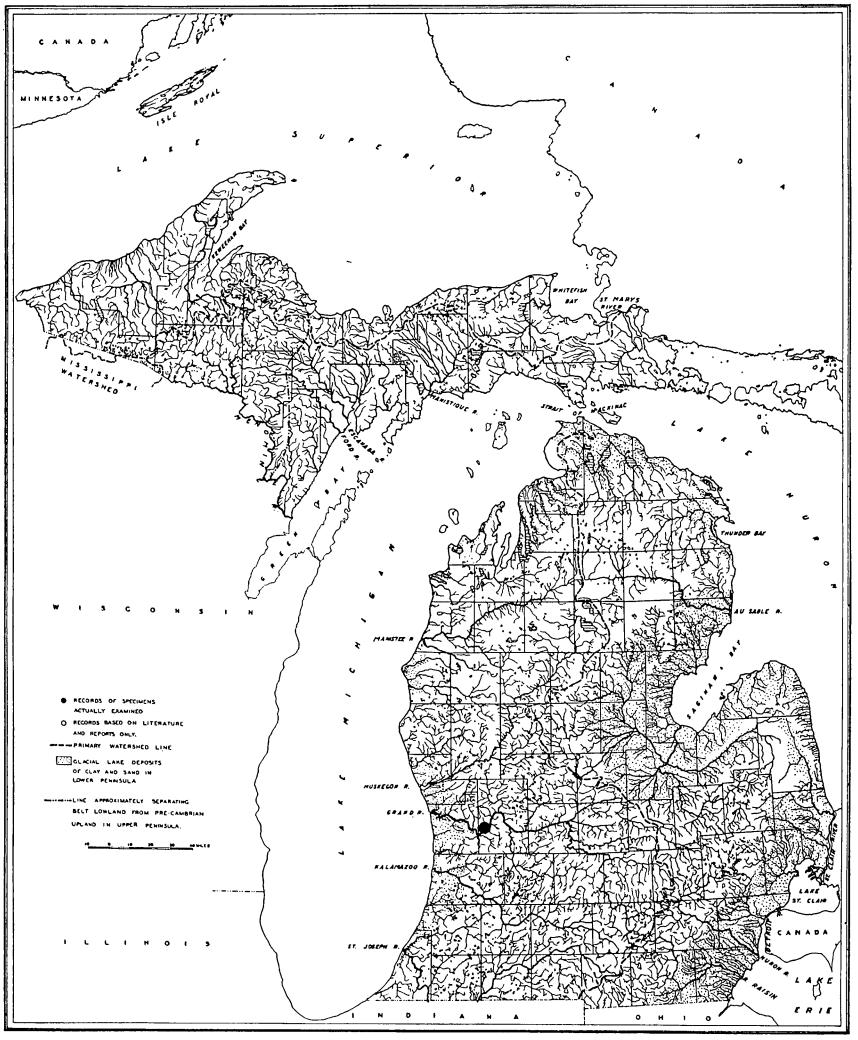
Radula.—Unknown.

Animal and genitalia.—Unknown.

Discussion.—This specimen has been classified in preceding publications (Walker, 1895, 1911; Winslow, 1926) as *Valvata pupoidea* Gould (DeCamp, 1881) and *Lyogyrus pupoideus* (Gould). *Lyogyrus brownii* differs from *pupoideus* (Pl. I, Fig. 14) in the turreted spire, the depth of the sutures, the greater inflation of the whorls, and in the shape of the umbilicus.

The genus *Lyogyrus* has 5 described species and belongs to the fauna of the eastern and southern United States. Since this genus has the general

shell contour and the radula of an *Amnicola* but the operculum of a *Valvata,* it has been revised from *Paludina* to *Valvata* to *Amnicola* and is at present regarded as a member of the subfamily Lyogyrinae. There has been no opportunity to examine living material of this genus.



MAP 10. Records of *Lyogyrus brownii* (Carpenter) in Michigan.

THE GENUS *POMATIOPSIS* TRYON

Two species of *Pomatiopsis* are known from Michigan: *lapidaria* and *cincinnatiensis.* Since these shells bear some resemblance to certain species of Amnicolidae and have been regarded as belonging to that family, under the

subfamily Pomatiopsinae, they are briefly discussed in this study of Michigan Amnicolidae.

It is believed, with Gill (1871), Pilsbry and Ferriss (1906), and Baker (1926*b*) that *Pomatiopsis* belongs to a separate family, Pomatiopsidae, rather than to a subfamily of the Amnicolidae. *Pomatiopsis cincinnatiensis*

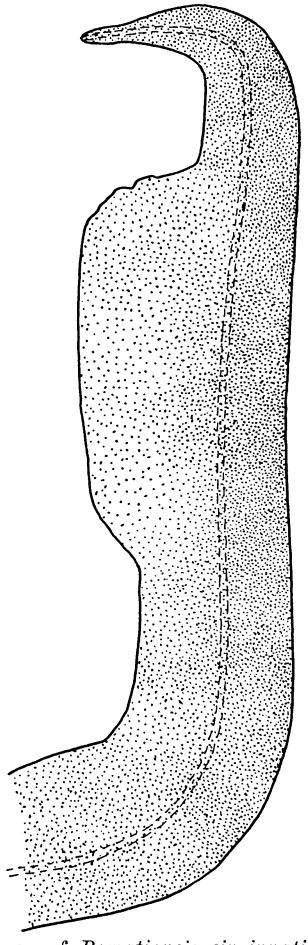


FIG. 10. Verge of *Pomatiopsis cincinnatiensis* (Lea).

is less common than *lapidaria,* and little has been published regarding its soft parts. For this reason *cincinnatiensis* has been chosen to represent the characters of the radula and verge of the genus.

SHELL (Pl. II, Figs. 6 and 8).—Elongated or conical; sutures impressed; 6 to 7 whorls, inflated, nucleus elevated above the following whorls; aperture subcircular to ovate. Peristome entire, columella reflected; unbilicus wide and deep. *Pomatiopsis lapidaria* differs from *cincinnatiensis* in being more

attenuated and greater in height, and having whorls less inflated and aperture more ovate. *P. cincinnatiensis* has been found in the southern counties of Michigan, whereas *lapidaria* ranges over the entire Lower Peninsula.

RADULA (Pl. IV, Fig. 5).—Very different from that of members of the Amnicolidae. The central tooth has the basal wing terminating as a cusp, and a single basal denticle projects down from the lateral ridge. The few large cusps on the central, lateral, and marginal teeth are distinct characters of *Pomatiopsis* and not of Amnicolidae.

GENITALIA (Fig. 10; Pl. VI, Fig. 6).—The verge is large, simple, cylindrical, and longer than in the Amnicolidae. The secondary lobe and duct are absent.

ECOLOGY.—*Pomatiopsis* has a wide range. I collected living specimens of *P. lapidaria* on a mountain side in southern Kentucky more than 500 feet from water, and I also found them completely submerged in water during the spring. Whether the species should be regarded as a terrestrial, an amphibious, or an aquatic mollusk has been the object of controversy with a number of conchologists. H. A. Pilsbry (1896: 37) stated: "*P. lapidaria* Say is as much a terrestrial mollusk as most of the *Succineas*. They cannot live for any length of time immersed in water, and I have drowned specimens, just as land snails may be drowned, by confining them in a vessel full of water." During the course of this study some experimentation on this matter was undertaken. In a wire screen trap (Pl. IX, Fig. 2) completely submerged in a small creek, *P. lapidaria* remained alive from February to May, indicating that this species is much more tolerant of aquatic conditions than is *Succinea*. It is true, however, that *Pomatiopsis* is most common near streams and is generally found on the river bank, preferring an amphibious type of environment, whereas the Amnicolidae are confined to the water.

AMNICOLIDAE IN RELATION TO BIOLOGICAL SCIENCES

ECONOMIC IMPORTANCE.—Amnicolidae are of economic importance in that they are consumed as food by fresh-water fish. Their minute size, their occurrence in great quantities, and their wide range of habitat, from shallow streams to bodies of water of considerable depths (such as the Great Lakes, where food is at a premium) have placed this family near the top of the list of mollusks which serve as natural fish food. Investigators (Baker, 1916; DeRyke and Scott, 1922; Covey, 1935) have noted that yellow perch, rock bass, trout, and whitefish commonly eat amnicolid snails. Practically all of the food found in the stomach of whitefish (*Coregonus clupeaformis*) sent for identification to the Museum of Zoology of the University of Michigan, from Humboldt Bay and Clear Lake, Manitoba, Canada, was *Amnicola limosa* and *A. binneyana*. In most publications on natural food of fishes the general term "small snails" is used. More often than not these "small snails" are Amnicolidae.

In many areas where water cress is grown for human consumption, certain amnicolids, e.g., *Hydrobia nickliniana,* have become so abundant as to be an annoyance to the housewife in the preparation of the water cress for the table. Others may cause considerable trouble, as did *Bulimus tentaculatus* when its eggs entered water pipes through improper filters of reservoirs, and after hatching, appeared in great numbers in the water pipes of Chicago homes.

PARASITOLOGY.—The study of Mollusca bears intimate relationship to the study of parasitology. Both snails and bivalves are known to serve as intermediate hosts for families of internal helminths. The digenetic trematodes have particular interest for specialized students of Mollusca, since in their life histories, complex as they are, involving an alternation of 2, 3, or 4 hosts, snails or bivalves are 1 or 2 of the intermediate hosts. Certain of these parasites are very specific in the host involved in their life cycles. The life of the free-swimming miracidium is limited to only a few hours unless it successfully enters a particular species of mollusk. Parasitologists may be able to predict, within certain limits, whether a particular parasite will be found in a given area if they are furnished reliable data on the molluscan fauna which inhabits that territory. In spite of the knowledge which has resulted from the research interest in life histories of parasites within recent years, there are still comparatively few life cycles which are completely known. Any additional information that the conchologist may offer, whether in faunistic lists or ecological notes, should, therefore, be of aid to the parasitologist.

Among the mollusks which serve as intermediate hosts in the life cycle of trematodes, the Amnicolidae are not well represented. It is believed, however, that the lack of representatives is due, not to the fact that few parasites choose these minute snails as hosts, but rather that investigators, in selecting life cycles as problems are more attracted to larger gastropods, e.g., Pleuroceridae, Lymnaeidae, and Planorbidae. George R. LaRue, of the Department of Zoology, University of Michigan, has suggested that when more life history work has been completed, especially on the trematodes of fish, it is expected that the Amnicolidae will be considered as centers of radiation for many parasites, infecting directly or indirectly, all classes of vertebrates. Lundahl (1941: 461) wrote:

> A survey of the cercariae parasitizing this group of snails [Amnicolidae] near Ann Arbor was accordingly undertaken, partly in anticipation of obtaining material for life history studies and partly to determine the species of cercariae and the extent of cercarial infection in these snails. Several cercariae not before noted in this locality were encountered. . . . Among these cercariae was a pleurolophocercous form, parasitizing *Amnicola* (*Marstonia*) *lustrica* Pilsbry at the Argo Dam, Huron River, and penetrating and encysting in centrarchid fishes.

Members of the family Pomatiopsidae also serve as intermediate hosts for trematodes. Ameel (1938: 704) stated: "Four species of tailed cercariae in addition to *Paragonimus* have been recovered from *P. lapidaria.*"

Investigations carried on under the direction of LaRue, on the cercaria which emerged from *Amnicola,* revealed that more than 20 species of the Strigeidae, Echinistomidae, Schistosomoidea, Plagiorchidae, Heterophyidae and (?) Opisthorchidae, and other families, used amnicolids as their first intermediate host. These data were obtained from no more than 3 species of Amnicolidae.

While observing specimens of Amnicolidae in the laboratory, I frequently saw cercariae emerging from the snail host. Snails which have been stained and mounted often reveal both cercaria and metacercaria in their bodies. Specimens heavily infected with cercaria suffer a loss of tissue. This becomes a critical factor when the cercariae inhabit vital regions of a snail's body. Large parts of the digestive gland and genitalia are destroyed (Pl. VII, Fig. 5). It is known that certain developing cercariae, even though the sporocyst is not in the gonadal tissue, may cause parasitic castration of the host. Unquestionably, if the infection becomes too great and the genitalia and digestive gland are destroyed the condition leads to sterility and even to death of the snail. In one instance mature cercaria have been observed to migrate down the alimentary canal of *Amnicola* and to be liberated by way of the anus (Pl. VII, Fig. 5).

Encysted larval trematodes have been found in the foot and rostrum of certain species of Amnicolidae (*binneyana*). From one snail dredged from 15 feet of water in Lake Erie 21 cysts were removed. The majority of snails from this locality were heavily infected, each cyst being a potential parasite to the definitive host (likely a fish). One realizes the importance which the Amnicolidae bear to parasitology from the fact that 98 *A. binneyana* were taken from the stomach of 1 whitefish. This number represents only a single feeding, and if each snail was as heavily infected as the one examined, more than 1000 parasites gain entrance to the final host at each feeding.

SUMMARY

In the Amnicolidae shell characters alone are in many instances unreliable for species determination. An analysis of the radula and animal is here presented as a new approach to the systematic classification.

In the species investigated the structure of the radula is a reliable character for the determination of species.

The verge (male copulatory organ) has a characteristic shape and definite structure in each species considered and serves as a significant character for differentiating species and as a basis for tracing phylogenetic relationship.

Certain forms, previously considered species and subspecies, have been found to be ecological or other kinds of variants of well-established species.

The radula and verge of *Pomatiopsis* are not amnicolid in character. This genus is, therefore, consigned to a separate family, Pomatiopsidae.

Ten species of Amnicolidae are recognized as occurring in Michigan. The 16 species and subspecies reported in the most recent check list (Winslow, 1926) have been reduced to 9, and 1 is added (through earlier misidentification).

Pyrgulopsis letsoni, previously known from dead shells, is here treated with a description of the operculum, radula, soft parts (including the verge), ecology, and phases of its life history. This species is the only representative of the genus *Pyrgulopsis* of which the anatomy is known.

There is no definite period which might be termed a breeding season in *Amnicola limosa*, but egg laying is continuous throughout the year, provided the temperature is suitable. Experimentation has proved that the sperm in *Amnicola limosa* is carried over in the female from the fall to the spring, and once the female is impregnated, she may continue to lay fertile eggs for at least a year.

Amnicolidae serve as primary and secondary intermediate hosts for digenetic trematode parasites.

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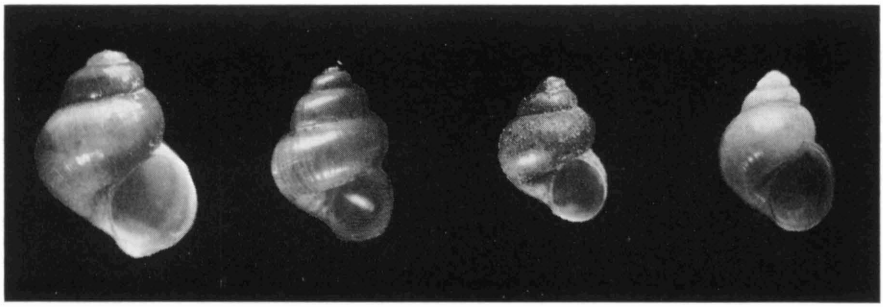
PLATES

PLATE I

FIG. 1. *Amnicola* (*Amnicola*) *limosa* (Say).
FIGS. 2 and 3. *Amnicola* (*Amnicola*) *walkeri* Pilsbry.
FIG. 4. *Amnicola* (*Marstonia*) *lustrica* Pilsbry. River form, juvenile.
FIG. 5. *Amnicola* (*Marstonia*) *lustrica* Pilsbry. River form, adult.
FIG. 6. *Amnicola* (*Marstonia*) *lustrica* Pilsbry. Lake form, adult.
FIG. 7. *Amnicola* (*Cincinnatia*) *integra* (Say).
FIG. 8. *Amnicola* (*Probythinella*) *binneyana* Hannibal. River form.
FIG. 9. *Amnicola* (*Probythinella*) *binneyana* Hannibal. Lake St. Clair.
FIGS. 10–12. *Amnicola* (*Probythinella*) *binneyana* Hannibal. Lake Erie.
FIG. 13. *Pyrgulopsis letsoni* (Walker).
FIG. 14. *Lyogyrus pupoideus* (Gould).
FIG. 15. *Lyogyrus brownii* (Carpenter).
FIG. 16. *Hydrobia nickliniana* (Lea).

PLATE I



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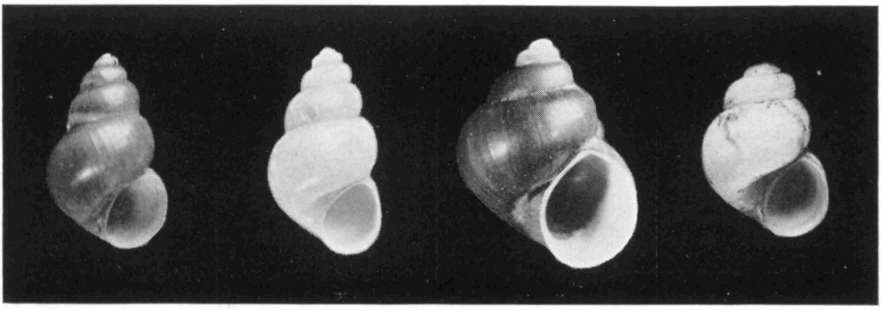

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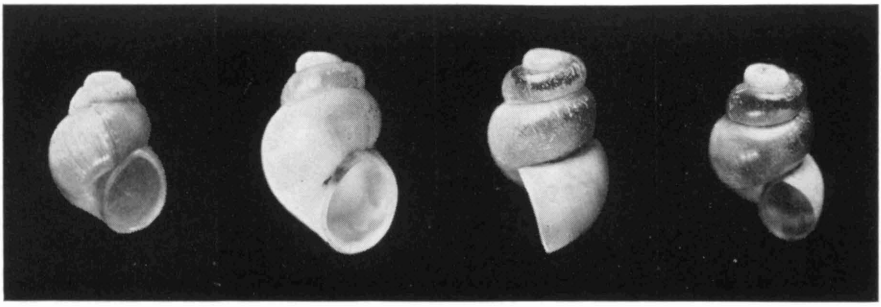

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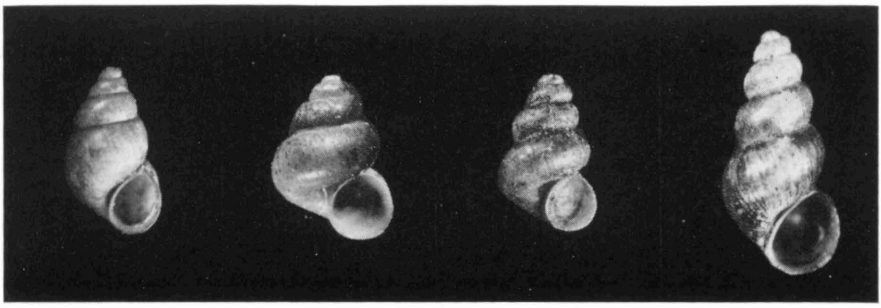

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PLATE II

FIG. 1. *Somatogyrus subglobosus* (Say).
FIG. 2. *Bulimus tentaculatus* (Linnaeus).
FIG. 3. Paucispiral operculum. *Somatogyrus subglobosus* (Say).
FIG. 4. Spiral operculum. *Lyogyrus pupoideus* (Gould).
FIG. 5. Concentric operculum. *Bulimus tentaculatus* (Linnaeus).
FIG. 6. *Pomatiopsis lapidaria* (Say).
FIG. 7. Operculum of *Pyrgulopsis letsoni* (Walker).
FIG. 8. *Pomatiopsis cincinnatiensis* (Lea).

PLATE II

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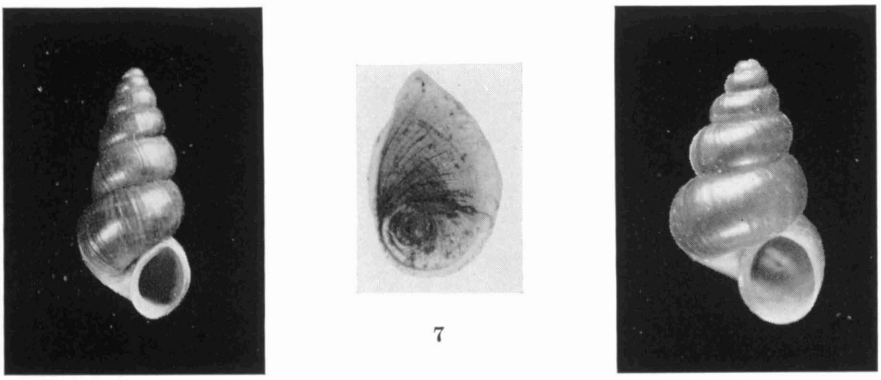

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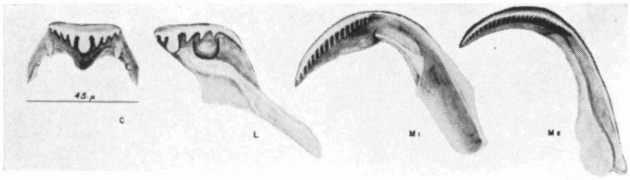
PLATE III

FIG. 1. Radula of *Amnicola* (*Amnicola*) *limosa* (Say).
FIG. 2. Radula of *Amnicola* (*Amnicola*) *walkeri* Pilsbry.
FIG. 3. Radula of *Amnicola* (*Marstonia*) *lustrica* Pilsbry.
FIG. 4. Radula of *Amnicola* (*Cincinnatia*) *integra* (Say).
FIG. 5. Radula of *Amnicola* (*Probythinella*) *binneyana* Hannibal.

PLATE III



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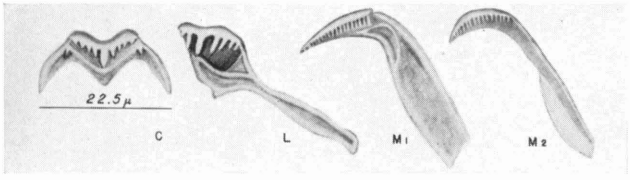

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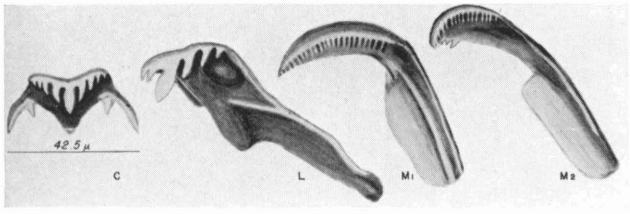

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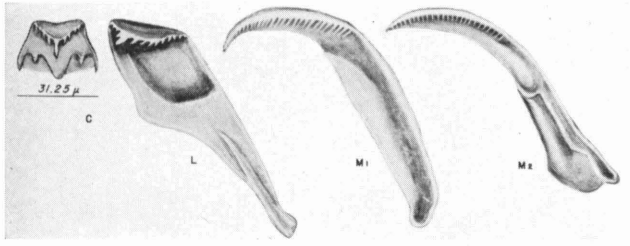

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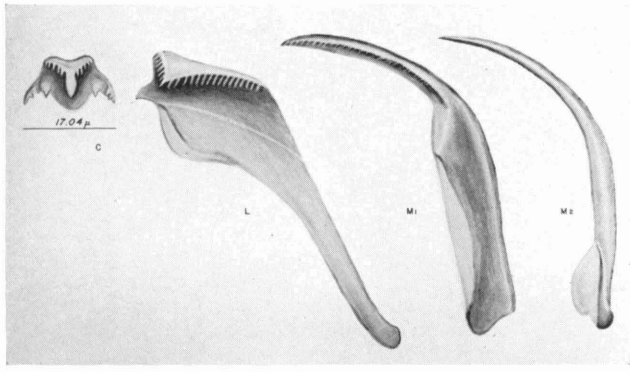

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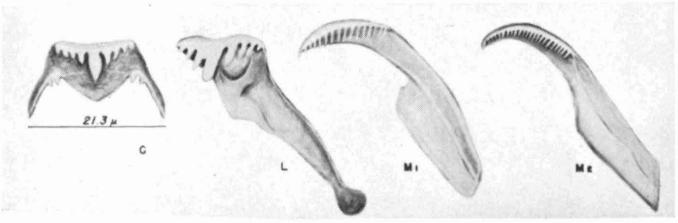
PLATE IV

FIG. 1. Radula of *Pyrgulopsis letsoni* (Walker).
FIG. 2. Radula of *Hydrobia nickliniana* (Lea).
FIG. 3. Radula of *Somatogyrus subglobosus* (Say).
FIG. 4. Radula of *Bulimus tentaculatus* (Linnaeus).
FIG. 5. Radula of *Pomatiopsis cincinnatiensis* (Lea).

PLATE IV



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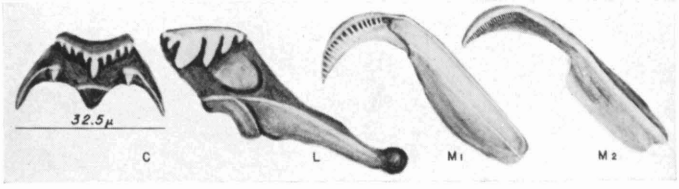

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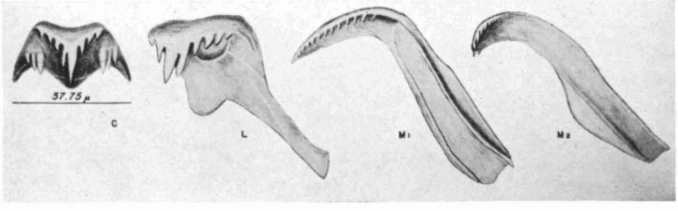

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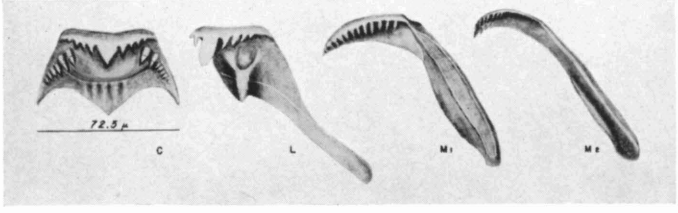

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PLATE V

FIG. 1. Animal of *Amnicola* (*Amnicola*) *limosa* (Say), with verge pulled forward (upper right).

FIG. 2. Animal of *Amnicola* (*Amnicola*) *limosa* (Say), with penis coiled around erected secondary lobe.

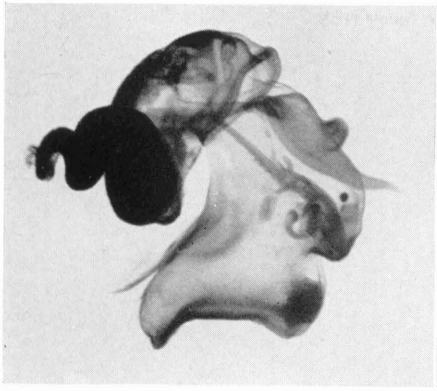
FIG. 3. Animal of *Amnicola* (*Amnicola*) *limosa* (Say), with penis (right center) distended and erected; secondary lobe showing secondary duct ending in diverticulum.

FIG. 4. Animal of *Amnicola* (*Amnicola*) *walkeri* Pilsbry, showing pigmented body.

FIG. 5. Animal of *Amnicola* (*Amnicola*) *walkeri* Pilsbry; bifid verge (upper right) and diverticulum from duct in the secondary (left) lobe.

FIG. 6. Animal of *Amnicola* (*Marstonia*) *lustrica* Pilsbry, with verge (upper left).

PLATE V



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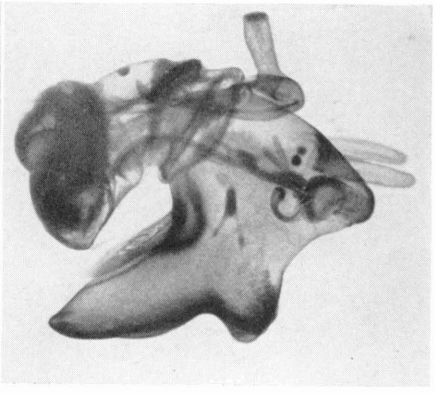

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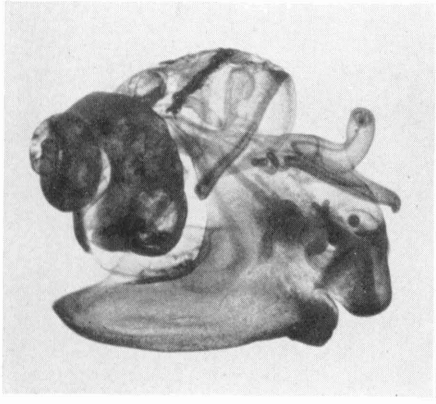

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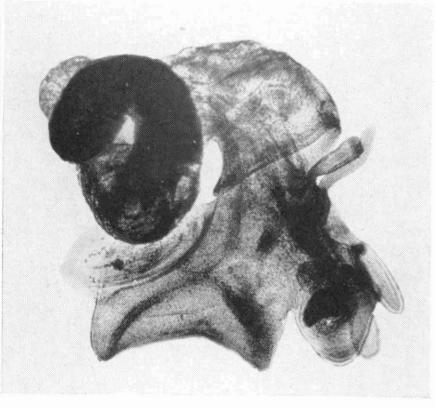

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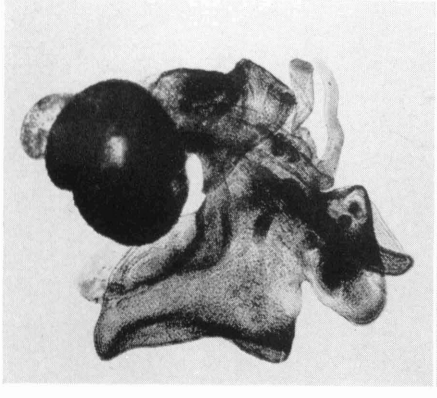

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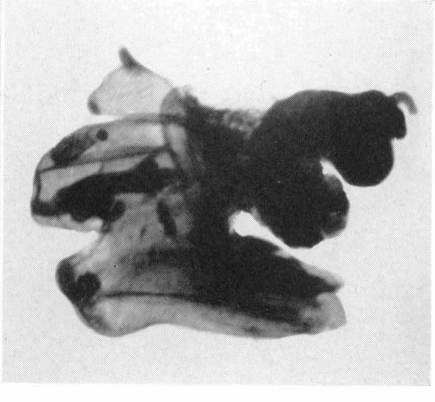

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PLATE VI

FIG. 1. Animal of *Amnicola* (*Cincinnatia*) *integra* (Say), with verge (upper right).

FIG. 2. Animal of *Amnicola* (*Probythinella*) *binneyana* Hannibal, with verge (upper right).

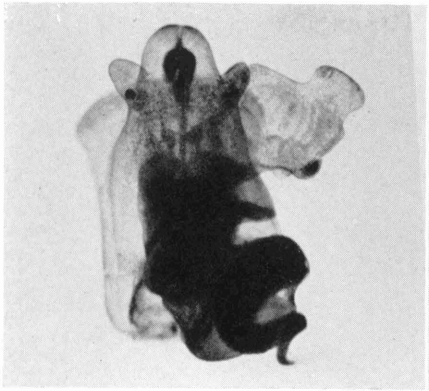
FIG. 3. Animal of *Amnicola* (*Probythinella*) *binneyana* Hannibal, showing long rostrum (left center).

FIG. 4. Animal of *Pyrgulopsis letsoni* (Walker), with verge (right center).

FIG. 5. Animal of *Hydrobia nickliniana* (Lea), with trifid verge at right.

FIG. 6. Animal of *Pomatiopsis cincinnatiensis* (Lea), with verge anterior.

PLATE VI



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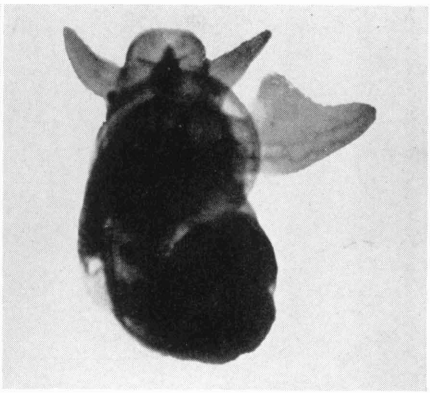

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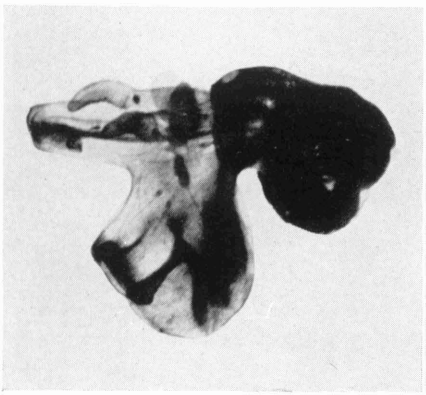

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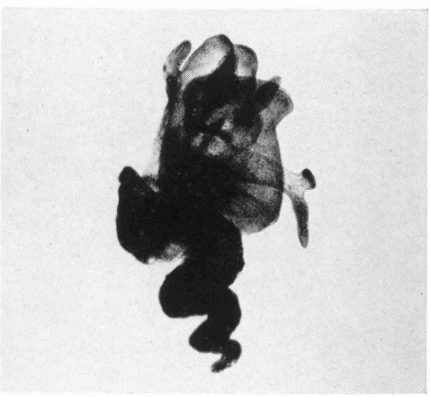

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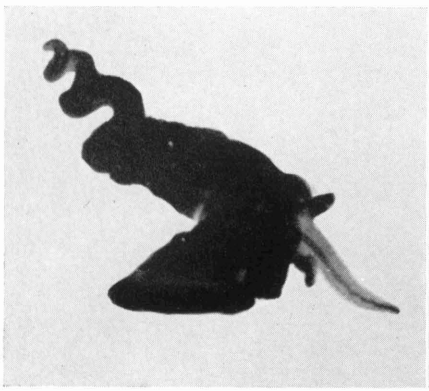

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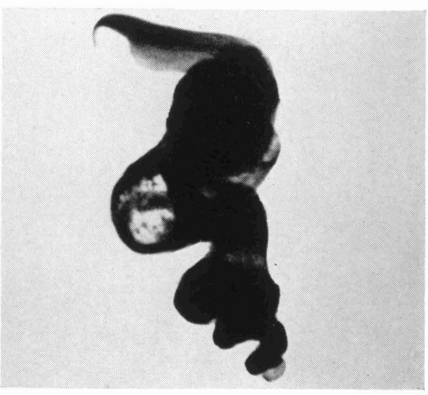

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PLATE VII

FIG. 1. Eggs of *Amnicola* (*Amnicola*) *limosa* (Say).

FIG. 2. Eggs of *Pyrgulopsis letsoni* (Walker).

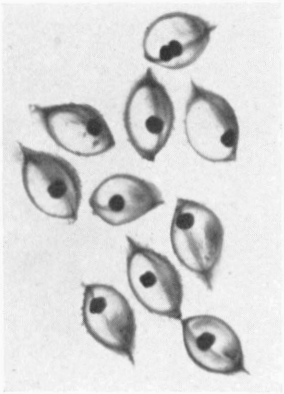
FIG. 3. Eggs of *Bulimus tentaculatus* (Linnaeus).

FIG. 4. Eggs of *Amnicola* (*Marstonia*) *lustrica* Pilsbry.

FIG. 5. *Amnicola* (*Probythinella*) *binneyana* Hannibal serves as intermediate host for trematodes. Cercaria in liver (extreme left); emerging from alimentary canal (above foot, behind rostrum, within mantle). The dark rodlike object just below the alimentary canal is a *Chaetogaster*. The dark rounded objects in foot and rostrum are metacercaria.

FIG. 6. Cavities in a lime-encrusted stone in which *Pyrgulopsis letsoni* (Walker) was found living.

PLATE VII



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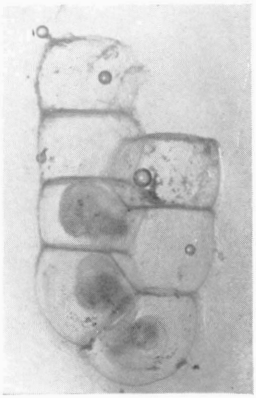

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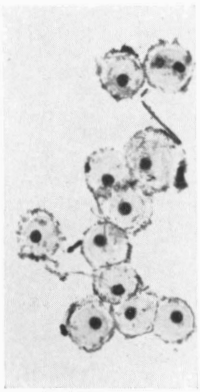

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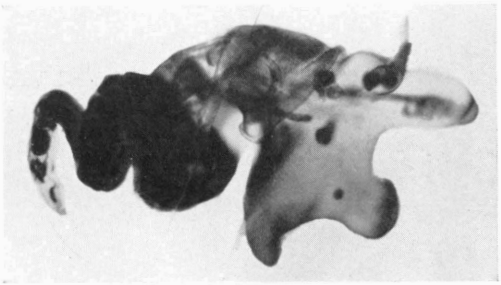

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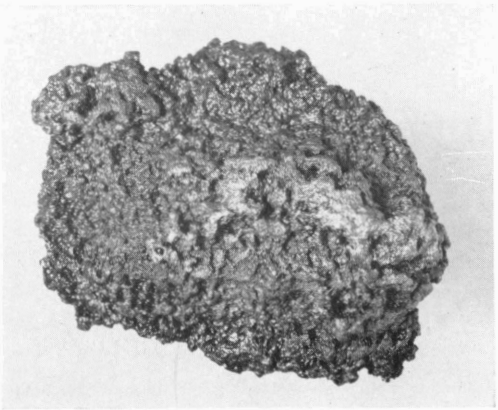

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PLATE VIII

FIG. 1. Argo Pond (after being drained), Huron River at Ann Arbor, Michigan. *Pyrgulopsis letsoni* (Walker) lives in the cavities in rocks along the middle of the river.

FIG. 2. A pond below Highland Lake, Livingston County, Michigan, where specimens of *Amnicola walkeri* Pilsbry were present in great numbers.

PLATE VIII

FIG. 1

FIG. 2

PLATE IX

FIG. 1. Spring near Button Lake, Kent County, Michigan. *Hydrobia nickliniana* lives on the water cress.

FIG. 2. Submerged trap for experiments on *Pomatiopsis lapidaria* (Say).

PLATE IX

FIG. 1

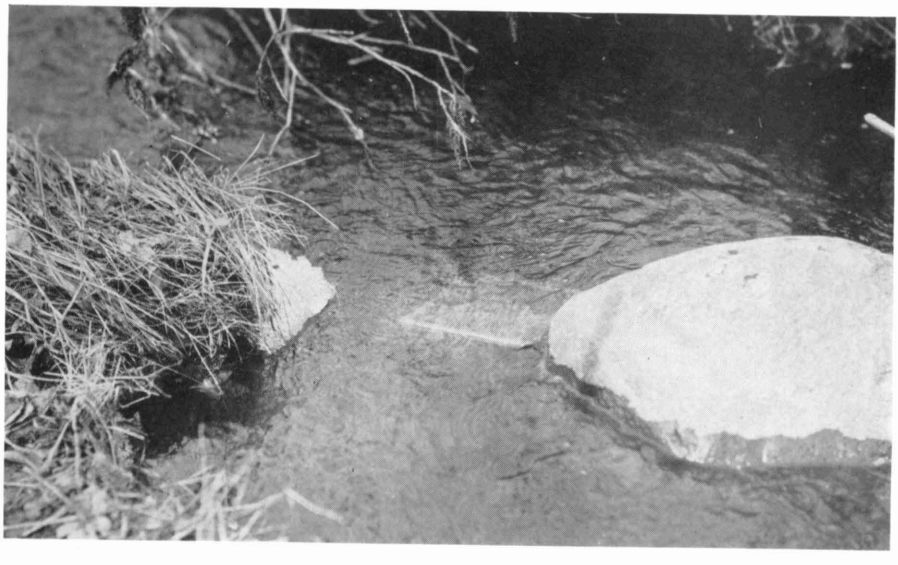

FIG. 2

No. 24. **A Comparative Life History Study of the Mice of the Genus Peromyscus.** By ARTHUR SVIHLA. (1932) Pp. 39 ..... $0.50

No. 25. **The Moose of Isle Royale.** By ADOLPH MURIE. (1934) Pp. 44, 7 plates $0.70

No. 26. **Mammals from Guatemala and British Honduras.** By ADOLPH MURIE. (1935) Pp. 30, 1 plate, 1 map insert $0.35

No. 27. **The Birds of Northern Petén, Guatemala.** By JOSSELYN VAN TYNE. (1935) Pp. 46, 2 plates, 1 map $0.45

No. 28. **Fresh-water Fishes Collected in British Honduras and Guatemala.** By CARL L. HUBBS. (1935) Pp. 22, 4 plates, 1 map $0.25

No. 29. **A Contribution to a Knowledge of the Herpetology of a Portion of the Savanna Region of Central Petén, Guatemala.** By L. C. STUART. (1935) Pp. 56, 4 plates, 1 figure, 1 map $0.50

No. 30. **The Darters of the Genera Hololepis and Villora.** By CARL L. HUBBS AND MOTT DWIGHT CANNON. (1935) Pp. 93, 3 plates, 1 figure $0.50

No. 31. **Goniobasis of the Coosa River, Alabama.** By CALVIN GOODRICH. (1936) Pp. 60, 1 plate, 1 figure $0.35

No. 32. **Following Fox Trails.** By ADOLPH MURIE. (1936) Pp. 45, 6 plates, 6 figures $1.00

No. 33. **The Discovery of the Nest of the Colima Warbler (Vermivora crissalis).** By JOSSELYN VAN TYNE. (1936) Pp. 11, colored frontis., 3 plates, 1 map $0.35

No. 34. **Mollusca of Petén and North Alta Vera Paz, Guatemala.** By CALVIN GOODRICH AND HENRY VAN DER SCHALIE. (1937) Pp. 50, 1 plate, 1 figure, 1 map $0.50

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