INTRODUCTION

Wisconsin contains a large and varied aquatic molluscan fauna. The State is favorably located for a diverse fauna, lying within the drainage areas of two of the largest of the Great Lakes and the great Mississippi basin. There are three major drainage areas, Lake Superior on the north, Lake Michigan on the east, and the Mississippi River on the south and west.

These three areas are divisible into several subareas of considerable importance, as noted below:

Lake Superior: There are several small rivers and creeks that drain into this Great Lake.

Lake Michigan: Fox River, Green Bay streams; Lake Michigan streams.

Mississippi River: St. Croix River; Chippewa River; Black River; Wisconsin River; Rock River; Fox River of Illinois.

Though few attempts have been made to prepare lists of the species of fresh water mollusks inhabiting the State, the literature relative to the fauna is extensive, about 50 papers having been published which refer definitely to Wisconsin species. These are indicated by an asterisk in the bibliography. The type localities of 49 species and varieties of aquatic mollusks are located within the state.

In the present monograph 327 species and varieties are recognized of which 40 are described as new. This number of species compares favorably with the fauna of neighboring states and ranks about with that of Michigan (see Winslow, 1926b) from which 316 species and varieties have been recorded. Illinois probably contains almost as many forms, but the last catalog was published many years ago (Baker, 1906) and lists but 240 species and varieties. Many additional species have since been added to the fauna of this state. The last list of Indiana Mollusca (Daniels, 1903) lists 215 species and varieties, but this number is doubtless much larger.

Only four catalogs of the Mollusca of Wisconsin have been published that attempt to list the species of the whole or a

considerable part of the state. In 1852 and 1860, Lapham published a list of the shells of Wisconsin in which 68 freshwater species are recorded. Some of these are synonyms of other species and a few are erroneously included in the state fauna. In 1897, Mrs. E. C. Wiswall published a list of the shells of southern Wisconsin, enumerating 65 aquatic forms. In 1906, Dr. Geo. H. Chadwick published an extended account of Wisconsin Mollusca in which are listed 129 species and varieties of freshwater forms. This is the first attempt to present a modern account of the aquatic molluscan fauna of the State. Several shorter papers by the writer have been published, dealing with restricted areas, the most important being one on the molluscan fauna of Tomahawk Lake Region (1911), in which 44 species are listed, and one on the fauna of the Lake Winnebago Region, in which 113 species are listed. Upwards of 50 papers refer definitely to Wisconsin aquatic Mollusca.

Our knowledge is yet too meager concerning the distribution of the aquatic fauna to form adequate generalizations. Generally speaking, the fauna of the Mississippi drainage is best represented, probably some 60–65 per cent. of the fauna being found here. The Lake Michigan drainage is also well represented, probably containing upwards of 60 per cent. of the total fauna. The Lake Superior drainage is least known, not more than 15 per cent. of the fauna occurring in this part of the State. When more collecting has been done in the unexplored portions of the State it may be possible to know just which species are peculiar to a given drainage.

The 327 species and varieties described and figured in this work are distributed among the following groups: Naiades 95; Sphaeriidae 77; Ctenobranch Gastropods, 62; Pulmoniferous Gastropods 93.

The species with type localities in Wisconsin are recorded below. Many of these are now considered synoynms of other species. The new groups diagnosed for the first time are also listed, together with the species and varieties published herein for the first time.

NEW GROUPS WITH THEIR TYPE SPECIES

Hinkleyia. Type: *Lymneus caperatus* Say.
Nasonia. Type: *Limnaea cubensis* Pfr.

SPECIES WITH TYPE LOCALITIES IN WISCONSIN

Unio undatus Barnes *(Fusconaia undata).* Wisconsin and Fox Rivers.
Unio giganteus Barnes *(Megalonaias giganteus).* Prairie du Chien.
Unio nodosus Barnes (*Quadrula metanevra* Raf.). Wisconsin.
Unio prasinus Conrad *(Quadrula pustulosa prasina).* Fox River at Green Bay.
Unio schoolcraftensis Lea *(Q. pustulosa prasina).* Fox River at Green Bay.
Unio tuberculatus Barnes (*Tritogonia verrucosa* Raf.). Wisconsin.
Unio verrucosus Barnes (*Cyclonoias tuberculatus* Raf.). Wisconsin River.
Unio gibbosus Barnes (*Elliptio dilatatus* Raf.). Wisconsin River.
Unio mucronatus Barnes (*Elliptio dilatatus* Raf.). Wisconsin.
Alasmodonta rugosa Barnes (*Lasmigona costata* Raf.). Fox River.
Alasmodonta complanata Barnes *(Lasmigona complanata).* Fox River.
Utterbackia imbecillis fusca F. C. Baker. Sturgeon Bay, Door Co.
Anodonta footiana Lea *(Anodonta grandis footiana).* Asylum Bay, Lake Winnebago.
Anodontoides birgei F. C. Baker. Sturgeon Bay, Door Co.
Unio cornutus Barnes (*Obliquaria reflexa* Raf.). Fox River.
Unio ellipticus Barnes *(Actinonaias carinata).* Fox River.
Unio carinata Barnes *(Actinonaias carinata).* Fox River.
Unio gracilis Barnes (*Leptodea fragilis* Raf.). Prairie du Chien, Wisconsin River.
Unio planus Barnes (*Leptodea fragilis* Raf.). Prairie du Chien, Wisconsin River.
Paraptera gracilis lacustris F. C. Baker *(Leptodea fragilis lacustris).* Off Plummers Point, Lake Butte des Morts.
Unio parvus Barnes *(Carunculina parva).* Fox River.
Carunculina parva cahni F. C. Baker. Neosho mill pond, Dodge Co.
Unio praelongus Barnes (*Ligumia recta latissima* Raf.). Fox River.
Unio spatulatus Lea (*Ligumia ellipsiformis* Conrad). Rock River.
Unio siliquoideus Barnes *(Lampsilis siliquoidea).* Wisconsin River.
Unio inflata Barnes *(Lampsilis siliquoidea).* Wisconsin River.
Lampsilis siliquoidea pepinensis F. C. Baker. Lake Pepin, Lake City, Minn.
Unio ventricosus Barnes *(Lampsilis ventricosa).* Wisconsin River.
Sphaerium stamineum wisconsinense Sterki. Fox River, Brown Co.
Pisidium compressum limnicolum Sterki. Fox River, Brown Co.
Pisidium punctatum simplex Sterki. Fox River, Brown Co.
Pisidium minusculum Sterki. Fox River, Brown Co.
Pisidium fragillimum Sterki (*Pisidium complanatum* St.). Lake Geneva.
Pisidium abyssorum (Stimpson) Sterki. Off Racine, in Lake Michigan.
Pisidium medianum Sterki. Lakes in Wisconsin.
Amnicola judayi F. C. Baker *(Cincinnatia cincinnatiensis judayi).* Off Doemel Point, Lake Winnebago.

Amnicola sheldoni Pilsbry *(Hoyia sheldoni)*. Lake Michigan, off Racine.
Lymnaea stagnalis lillianae F. C. Baker. Tomahawk Lake, Oneida Co.
Lymnaea wisconsinensis F. C. Baker *(L. emarginata wisconsinensis)*. Tomahawk Lake, Oneida Co.
Lymnaea winnebagoensis F. C. Baker. *(Stagnicola winnebagoensis)*. Oshkosh, Lake Winnebago.
Lymnaea nashotahensis F. C. Baker *(Stagnicola nashotahensis)*. Lower Lake, Nashotah, Waukesha Co.
Stagnicola walkeriana F. C. Baker. Madeline Island, Lake Superior, Bayfield Co.
Planorbis bicarinatus striatus F. C. Baker *(Helisoma antrosa striata)*. Cold Spring Park, Milwaukee (fossil).
Stagnicola emarginata vilasensis F. C. Baker. Big Muskallonge Lake, Vilas Co.
Helisoma antrosa cahni F. C. Baker. Big Muskallonge Lake, Vilas Co.
Helisoma antrosa shellensis F. C. Baker. Shell Lake, Washburn Co.
Planorbis trivolvis pilsbryi F. C. Baker *(Helisoma)*. Tomahawk Lake, Oneida Co.
Planorbis trivolvis winslowi F. C. Baker *(Helisoma)*. Little Arbor Vitae Lake, Vilas Co.
Planorbis campanulatus wisconsinensis Winslow *(Helisoma)*. Little Arbor Vitae Lake, Vilas Co.
Valvata tricarinata mediocarinata. Lake Winnebago, Lower Asylum Bay.
Lioplax subcarinata wisconsinensis. Fox River, Brown Co.
Campeloma brevispirum. Mirror Lake, Sauk Co.
Viviparus intertextus illinoisensis. Havana, Ill.
Bulimus tentaculatus magnalacustris. Lake Winnebago, near Oshkosh.
Amnicola limosa superiorensis. Bayfield, Shore of Lake Superior.
Amnicola lustrica decepta. Silver Lake, Waukesha Co.
Amnicola lustrica perlustrica. Lake Michigan shore, east of Sturgeon Bay.
Amnicola greenensis. Green Lake, Green Lake Co.
Amnicola walkeri foxensis. Fox River, mile north of Portage, Columbia Co.
Amnicola precursor. Green Lake, Green Lake Co. (fossil).
Cincinnatia emarginata lacustris. Winnebago Lake, near Oshkosh.
Cincinnatia emarginata canadensis. Lake Kakiska, near Great Slave Lake.
Goniobasis livescens michiganensis. Lake Michigan, east of Sturgeon Bay.
Goniobasis livescens barronensis. Red Cedar River, west of Chetek.
Fossaria sayi. Niagara River near Buffalo, N. Y.
Helisoma antrosa sayi. Tomahawk Lake, Oneida Co.
Physella laphami. Hancock, Waushara Co.
Physella latchfordi. Meechs Lake, Ottawa Co., Quebec.
Physella chetekensis. Moose Ear Creek, near Chetek, Barron Co.
Physella bayfieldensis. Pike Creek, near Bayfield, Bayfield Co.

Physella obrussoides. Oshkosh, Winnebago Lake, in hatchery bay.
Fusconaia undata wagneri. Lake Pepin, near Lake City, Minn.
Quadrula quadrula bullocki. Fox River, near DePere, Brown Co.
Pleurobema coccineum mississippiensis. Lake Pepin, near Lake City, Minn.
Lasmigona costata pepinensis. Lake Pepin.
Lasmidonta costata nuda. Red Cedar River, near Chetek, Barron Co.
Alasmidonta calceolus danielsi. Moots Creek, Indiana.
Alasmidonta calceolus magnalacustris. Sturgeon Bay, Door Co.
Alasmidonta marginata variabilis. Red Cedar River, west of Chetek.
Strophitus rugosus winnebagoensis. Long Point Island, Lake Winnebago.
Strophitus rugosus pepinensis. Lake Pepin, near Lake City, Minn.
Strophitus rugosus lacustris. Oconomowoc Lake, Waukesha Co.
Truncilla truncata lacustris. Long Point Island, Lake Winnebago.
Lampsilis siliquoidea chadwicki. Doemel Point, Lake Winnebago.
Lampsilis ventricosa perglobosa. Lake Pepin, near Lake City, Minn.
Lampsilis ventricosa winnebagoensis. Winnebago Lake, near Oshkosh.
Sphaerium solidulum winnebagoense. Lake Butte des Morts, near Plummers Point.
Sphaerium flavum foxense. Lake Butte des Morts, near Plummers Point.
Sphaerium bakeri Sterki. Green Lake.

Species and Varieties Influenced by the Environment

For many years a controversy has existed between different fields of biological science concerning the part played by the environment in the evolution of life and the formation of species. Some biologists deny that the environment has any effect or plays any part in the evolution of species while others, notably the paleontologists, affirm that the environment is the chief factor, and some students, with Lamarck, believe that the acquired characters are inherited. It is now admitted by all biologists that it is the germ plasm that transmits new characters through the genes of the chromosomes. It is held by many zoologists and paleontologists, however, that, while the heredity characters are transmitted through these determinators, the environment performs a directive stimulus and in some manner shapes the new organism so that it is in harmony with its environment.

Paleontologists who have studied the great changes that have taken place during the long period of geological time, and field zoologists who have observed the multitude of living things in their diverse environments, cannot but believe that the en-

vironment has played a large part in the production of this infinite variety of living organisms. The geneticists who confine their studies to laboratory experiments on a few animals, usually under abnormal conditions, are not in as good position to judge of the effect of environmental changes as are the students who have spent years in field observations. The truth of the matter is probably best expressed in a recent statement that the "environment permits and directs evolution but does not cause it" (Coe, Organic Adaption to Environment, p. 147, 1924).

Some zoologists—especially ecologists—may affirm that the environment, in directing evolution, does in large measure cause the change, as for example, when a normal river or creek species is forced to inhabit a lake, and in a sense this may be true, the changed environment *compelling* the organism to change its structure so that it may be in harmony with the changed conditions of its environment. Such reactions between the environment and the organism have been observed in many places in North America and these features must be recognized in attempting to unravel the puzzle of organic evolution.

Everyone who has spent much time studying large quantities of animal life is soon drawn to the conclusion that the most notable and fundamental characteristic of living organisms is their inherent tendency to vary. Gather a few thousand snails from any locality and the first observation made is the great number of different forms included, no two specimens, perhaps, being exactly alike, and many of them being so different as to confuse the observer as to their specific relationship. It logically follows that the conclusion suggested is that the changing of an environment, acting upon or directing this inherent tendency to vary, results in the production of a new variety or species which is better adapted to the changed environment.

During the progress of the field work incident to the preparation of this monograph it has become increasingly apparent that each stream has a faunal facies of its own which is not shared to a similar degree by other streams. It was repeatedly observed, also, that the size of the stream governed in a measure the character of the fauna. The small rivers and creeks, such as the Fox, parts of the Rock, the headwaters of

the Chippewa, and the Red Cedar River, contained a type of mollusks which was different from that of the medium sized rivers, as the Wisconsin and Rock; and these two systems were still different from the large rivers, as the Mississippi and lower Wisconsin Rivers. The fauna of the small lakes, also, was somewhat different from that of Lakes Michigan and Superior, and totally different from that of the streams and rivers. This variation of the fauna, coordinate with the size of the stream and the character of the water body, appears to be a universal law. It has been noted by Ortmann in Pennsylvania and Tennessee, Adams in the Tennessee River system, Grier in the Ohio and Lake Erie systems, and Baker in Illinois and Wisconsin (see Ortmann, 1920, 1924; Grier, 1926, Adams, 1915, Baker, 1926).

The early naturalists, Say, Lea, Haldeman, Tryon, did not pay any attention to the precise habitat relations of species, but separated them on the basis of individual differences, and often these simply represented individual variations in the same species. Species were based on one, two, or a few specimens and the broad relationships of habitat association had not yet been realized. Indeed, it was not possible in these early days to obtain the data for such generalizations, the new species being founded upon specimens picked up by exploring parties and others, usually but slightly interested in the mollusks, and gathering the specimens for conchological friends. At the present time, with transportation available to all parts of the country and with the great interest in ecology it is possible to consider the animals in groups as they bear relationship to certain natural types of territory. This is the natural method and gives the best results in trying to interpret the relationships of varying types of animal life.

Wisconsin is peculiarly well situated for studies of animal life from the standpoint of environmental evolution, having hundreds of lakes of various sizes, streams of all sizes connecting with each other, and each water body having an almost endless combination of ecological characteristics. In this monograph an attempt has been made to interpret some of this habitat variation and all species have been viewed from this standpoint.

In an address given not so long ago, Jennings makes certain statements which should be borne in mind when attempting to

generalize on the laws of evolution from any one series of factors. He says (1927, p. 22) "Different organisms, different societies of organisms, are diverse emergents, showing diverse systems of relations and consequent diverse methods of action. No longer must it be held that what is true for one organism is necessarily true for another. No longer will the investigator expect by a single crucial experiment to settle a question for the whole organic world. Knowledge of the biology of the oyster is practically not a solid basis for judgment of that of the social insects; this practical fact will be recognized as theoretically significant; as a fact typical of biological science; not something to be minimized and explained away. Organic evolution will be seen as emergent evolution in its most conspicuous and manifold display. * * * To generalize will be recognized as the most laborious task in biology, instead of the lightest and simplest. * * * To discover what organisms have in common becomes an object for wide-extended comparative investigation; not a matter for assumptions".

With these statements the writer is in full accord, for it has seemed that to assume that the changes in environmental complexes can be understood by a study of social insects or that any organism other than a creature influenced by the same environmental complex is absurd to the last degree, and generalizations based on such assumptions must, as Jennings remarks, be filled with error. It has been observed that the water breathing mollusks respond to this lake-river-creek ecological complex much more closely than the air-breathing freshwater forms, again clearly demonstrating that an assumption based on one of these organisms will not be entirely true for another. Much light would undoubtedly be thrown on this subject by experimental study of material transferred from one environment to another, or by long-continued examination of animals which have been forced to adapt themselves to a changed environment by the formation of artificial lakes by damming creeks and rivers. Such a condition has been created at Chetek in Barron County, Wisconsin, and a study of the molluscan life of the resulting lakes and the near-by creeks and small rivers has been productive of much information on this point. Attention is called to this particular territory in many places in this monograph (see Baker, Ecology, IX, July, 1928).

It is believed by the writer that the mass variations of the creeks, small rivers, large rivers, etc., should be distinguished as ecological varieties and given definite names, and in this monograph this has been done. In many cases the change has been of a most decided character while in others it is not as distinctly apparent. As systematic zoology is an attempt to interpret the animal life of the earth in its relationship to related forms and to the environment, no other course seems satisfactory.

The freshwater mollusks of Wisconsin have evolved from several different sources at different times during geological time. The ancestral forms were probably all marine. Among the gastropods, the Ctenobranchiata have descended more or less directly from marine forms which became adapted to a freshwater habitat through gradual change from marine through brackish to fresh water. These forms retain the ancestral gills, with, in some groups, the addition of a lung. The freshwater pulmonates (Basommatophora) have descended from terrestrial mollusks through an adaptation to aquatic conditions. In some forms (Planorbidae) there is a secondary gill (pseudobranch) which may exist with the lung, or the secondary gill may replace the lung almost entirely (Ancylidae). All of these adaptations attest the influence of the environment, at least as a directive stimulant.