MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 64

GONIOBASIS LIVESCENS OF MICHIGAN

BY
CALVIN GOODRICH

ANN ARBOR
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DECEMBER 26, 1945

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INTRODUCTION

Goniobasis livescens (Menke) is more fully distributed over the region occupied by the state of Michigan than is any other species of aquatic mollusks, with the exception of the pulmonate *Helisoma trivolvis* (Say). It is also the most varied in size; the shell, irrespective of the "soft parts," takes the most varied forms and has possibly the widest range in coloration. The species is of interest also because the routes of its distribution can be fairly well traced and the period of its appearance, or reappearance, in the area after the recession of the glaciers set down with definiteness.

For about a century following the adoption of the Linnaean nomenclatorial system, the genus to which *livescens* was consigned was *Melania,* a name chosen apparently for the rusty blackness of untreated shells. *Melania* was made to comprehend the larger operculate fresh-water gastropods, other than the Viviparidae and Ampullariidae, the world around, taking in mollusks coarse, heavy or delicate, sculptured or unsculptured—no thought being given to possible differences in internal anatomy. It was in that period that Menke described and named the pleurocerid which came to him from the eastern end of Lake Erie. In 1858 H. and A. Adams set up a subgenus *Elimia,* which they meant to take in such species as *livescens,* but among the sixteen that they listed as illustrations were at least four of obviously different generic kinship. In 1862 Isaac Lea (1863) proposed a number of genera for American melanians, *Goniobasis* among them. The genus was accurately defined. Quite plainly, it constituted a natural differentiation among the Pleuroceridae. Pilsbry (1896) revived *Elimia* and raised it to generic rank, placing *Goniobasis* in the synonymy. Later, he "decided that *Goniobasis* should be restored to its former position as a generic term, on the ground that *Elimia* was a composite group" (Walker, 1918).

Dr. Abram Sager brought together in 1839 the names of vertebrates and invertebrates that were known to inhabit Michigan. In his list of the mollusks were *Melania virginica* and *M. depygis.* Both names represented erroneous identification, the first possibly being *G. livescens* or *Pleurocera acuta* (Rafinesque), the second *livescens* without doubt. Following Sager with this kind of cataloguing, but restricting themselves to the Mollusca, were Manley Miles (1861), A. O. Currier (1868), William DeCamp (1881), Bryant Walker (1879, 1893, 1895, 1911), and Mina L. Winslow (1926). Walker published also on the Mollusca of particular parts of Michigan. With Charles E. Beecher, in 1876, he compiled the names of species known to occur within four miles of Ann Arbor; with A. C. Lane, in 1900, the

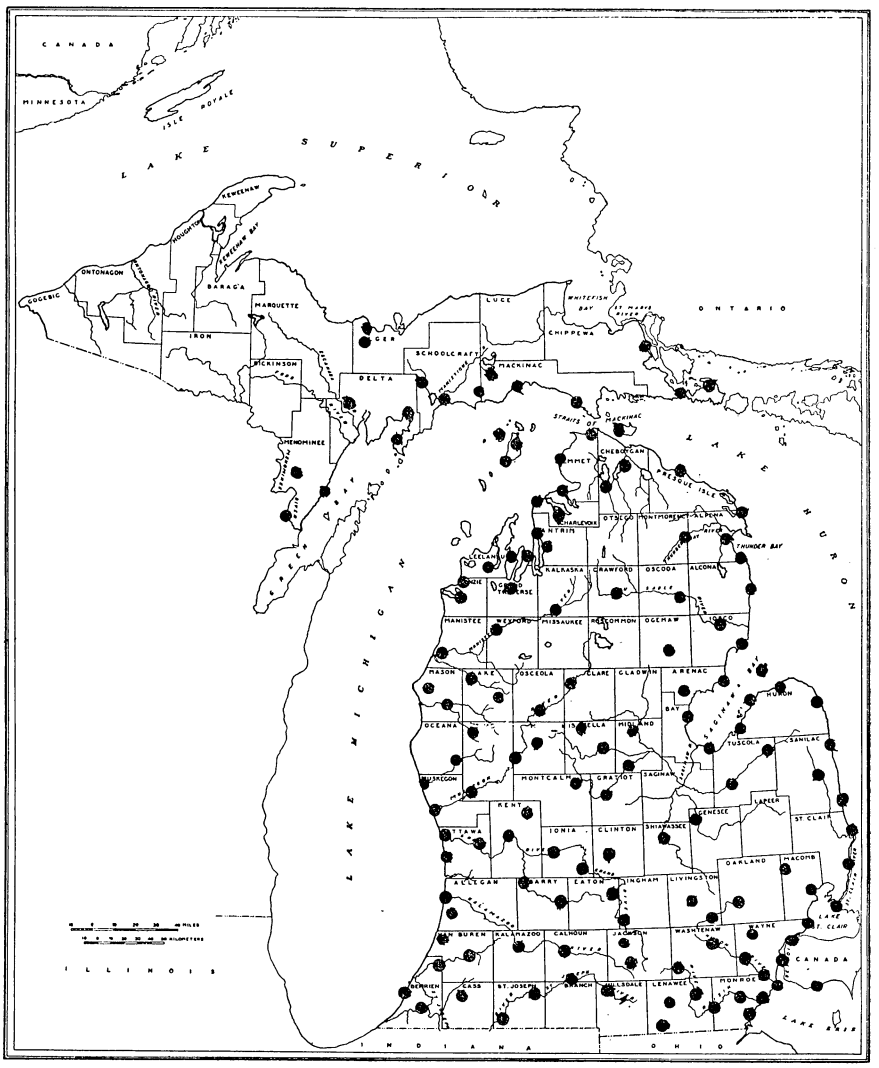
shells of the marls of Huron County. In all the compilations which are not restricted to terrestrial forms is mention of *Goniobasis,* indicative of its wide dispersal through the state.

It is interesting to observe in this printed matter the altering views on *G. livescens.* Sager considered it one species, or at most two. It was two species in the view of DeCamp and Currier. Walker thought it eight in 1893 and 1894 and four in 1911. Miss Winslow narrowed it to one, the present belief. Confusion in the determinations was natural enough, considering the variability of the species and that in earlier years of the state not much material was at hand for comparison. Repeated collections and repeated discoveries that the internal anatomy was everywhere the same, however varied the exo-skeletons were, have made it clear that *G. livescens* has certain basic characters that are constant, other characters that are inconstant and of relative unimportance, and that there exists in Michigan a single polymorphic species, and one only.

G. livescens has been found in Toleston deposits of glacial Lake Chicago (F. C. Baker, 1920*b*). This lake, in part at least, was contemporaneous with Lake Maumee, which formed at the sill of the retreating Erie lobe, and in one period in the history of the lakes, the two were connected by way of the Saginaw-Grand valleys. Up to this time, no Mollusca assignable to Lake Maumee have been discovered. Upon the present evidence, *livescens* made its entrance into the Great Lakes on the western side of Michigan first, although probably it had a second and later entry by way of early stages of the Maumee River of today. The species occurs in deposits of Huron County, Michigan, that are recognized as having formed on beaches of Lake Algonquin (Walker and Lane, 1900). That the Huron County localities may have been close to the northward limit of range of *livescens* in Algonquin time is indicated by the fact that, until introduced there, the species was absent from Douglas Lake, Cheboygan County—this lake being a part of Lake Algonquin, but isolated during the Nipissing stage. Mullet, Burt, and Crooked lakes, neighboring bodies of water, represent a Nipissing channel, and these lakes contain *G. livescens* (see H. B. Baker, 1912). Shells of *livescens* found in gravels at Cheboygan were believed by Frank B. Taylor to be of Nipissing Great Lakes age (F. C. Baker, 1920*b*). The Algonquin and Nipissing specimens are of the form existing now in Lake Huron.

Its offshoots counted out, *G. livescens* is the sole member of the goniobases in the drainage basin of the St. Lawrence River, the Great Lakes included. It occurs as far east as Lake Champlain and parts of Quebec. Through the Erie Canal, it has invaded the Hudson River basin. It has been found in all the Great Lakes except Lake Superior, yet is known from one stream of that body of water and within less than a mile of the stream's discharge, in addition to St. Mary's River connecting Lakes Superior and Huron. In

the Ohio River basin it occupies small streams of western Pennsylvania and rivers of Ohio, except the Scioto and the Little and Big Miami. Somewhat



MAP 1. Distribution of *G. livescens* is indicated on this map in a general way only. The absence of marks on a few counties of the Lower Peninsula means that collections have not been made there rather than that the species does not occur. The species is probably in more places in the Upper Peninsula than is shown by the black dots, but not in waters, other than those of Alger County, which flow into Lake Superior.

the same discontinuous distribution is observable in Indiana; *livescens* lives in streams of Lake Michigan and of the Erie drainage and in Wabash River and its northern tributaries, but not in the White River forks, nor in such

streams to the eastward of the Wabash as the Big Blue and Whitewater rivers. It is the *Goniobasis* of the Illinois River. F. C. Baker (1928) reported that in Wisconsin it is confined to Lake Michigan and streams discharging into it. In the Walker collection there are specimens credited to Des Moines River, Iowa.

Besides the Great Lakes, Superior excepted, the Michigan distribution is in streams, river lakes, and lakes connected with permanent streams that are neither swampy nor mucky, almost throughout the Lower Peninsula and in streams and some lakes of the Upper Peninsula which have Lake Michigan or Lake Huron connections. The one Lake Superior affluent that is known to contain *livescens* is Au Train River. The species is not in some of the "mud" streams of Monroe and Wayne counties, nor in those short ones of Lake Huron drainage which may be intermittent. The colony of Douglas Lake, Cheboygan County, is descendant of an introduction by H. B. Baker in 1912 or 1913 from Burt Lake (Baker, 1942). So far as has been learned, *livescens* is established in only one lake which is entirely without "outside" connections. This is Barney Lake of Beaver Island in Lake Michigan. A sand dune intervenes between this small lake and the large one. It seems possible that in some earlier day and during a period of high Great Lakes levels the two were joined, either by lagoon or running water. Just over the dune and in Lake Michigan, *livescens* is to be found on boulders and among gravel, the sites of which are more or less protected.

The causes of the appearance and disappearance of some of the colonies can only be conjectured from what is known of such phenomena elsewhere. An instance of the kind may be recited. In the 1880's, R. E. Call found Pleuroceridae in enormous numbers in Buck Creek, Helena, Alabama. After the passing of many years and following a flood, H. H. Smith visited the place and saw very few Mollusca. But in 1935, when van der Schalie and I went there, the pleurocerid population exceeded anything of the sort that either of us had seen before. *G. livescens* was collected in Saline River and Fleming Creek, Washtenaw County, about 1927. The colonies were of normal size. Searches made by Charles D. Dobrovolny in 1937 and 1938 failed to reveal the snail in these two localities. The disappearance cannot be accounted for by flood, since none of unusual size had occurred in the intervening ten or eleven years. Dobrovolny (1939*b*) reported the reappearance of *livescens* in the Huron River six months after the institution of a sewage disposal plant, this stretch of the river having been for a long time before this nearly barren of molluscan life. The recolonization was from upstream; migration from below was cut off by a high dam.

The distribution is from the basin of the Illinois River to waters of the Atlantic coastal plain—the Iowa record is taken as doubtful—from streams discharging into the Ohio River to one into Lake Superior. No other *Gonio-*

basis has so wide a dispersal. A group of species does occupy the coastal plain from Virginia to Texas, but the range of any one of them is not more than a hundred miles or so at most. How restricted distribution may be in the genus is illustrated by some of the goniobases of Coosa River, Alabama, most of which are restricted to the stream, some of which are limited to one or two sets of rapids. In short, *G. livescens* is of peculiar adaptiveness, made manifest by its early entrance into the glaciated areas, its wide distribution, and its broad choice of habitats.

In certain species of the genus the peripheral colonies are dwarfed, whorls are reduced in number, sculpture is reduced or other signs are afforded that the mollusks on these geographical boundaries are not wholly in harmony with their environment. Instances are the outliers of *G. laqueata* of Tennessee and *G. caelatura* of Georgia. Depauperate colonies exist in *livescens* of Michigan. These are not, though, in situations near the geographical border lines. Shells of Drummond's Island and of Au Train and Menominee rivers, marking the points of northward extension, are robust and, by their large numbers, give proof that the ability to reproduce is not circumscribed. The facts may be taken as further evidence of high adaptiveness and, again, that the glaciated area possesses the suitable kinds of habitats.

Mishaps during the period of shell secretion sometimes disturb regular and progressive growth. The mishaps may be registered as scars or blemishes in the epidermis, especially on the penultimate and final whorls. Deformation of the columella is occasionally brought about by trematode infestation, and to one such case Isaac Lea gave the name of *G. Lithasiodes,* mistaking the columellar deformity for a natural specific character. Almost as rare are spiral lines, usually incomplete, on maturing whorls. They appear to be brought about by defects in secreting glands. Some individuals have been seen in which part of a whorl is tumorous as though pressure had been applied at the time of secretion. Irregularities in the suture come oftener when a mollusk is completing growth than they do at juvenile stages. Gerontal growth is marked frequently by buckling of axial lines, an insufficient deposition of the epidermal chitin and other distortions. All these can be set down as individual singularities without specific or generic significance.

A corrosion of the epithelium affects entire colonies, all the epidermis being removed except upon the last whorl or part of it. This has been observed in *livescens* of streams of the Upper Peninsula and of the upper parts of the Lower Peninsula. These streams are of low pH so far as data are obtainable. The occurrence is rarer in lakes than in flowing waters.

Rarely, an adult specimen of *livescens* may be found with nucleus and spire entire. These parts of the shell may be lost in several ways. They

may be broken off mechanically; worn away by the attrition of silt wherein waves or flowing water supply the power, acting much as an emery grinding wheel does on articles of metal or stone; dissolved by chemical agencies in the water; or removed, again chemically, by blue-green algae of the class Myxophyceae which alter insoluble calcium compounds into soluble. Following a study of erosion in Pleuroceridae of Gunpowder River, Maryland, Baily, Pearl, and Winsor (1932) "provisionally" decided that this "is chiefly accomplished by the action of particles of silt carried along by the current, and that this action is somewhat retarded by the presence of sulphates in the water." Where one or more of the agencies may be active, as upon heavy rapids, all except the body whorls of the gastropods may be destroyed. The animal is not adversely affected, apparently, since with growth it abandons its occupancy of the earliest whorls. The phenomenon is fairly widespread in the Gastropoda of marine and fresh-water habitation and is known of several groups of terrestrial snails. Mature specimens of *Rumina decollata* (Linnaeus) have been observed in the act of swinging the spire of the shell smartly against hard substances in the endeavor to break off the whorls that are no longer tenanted and that have become encumbrances. A septum is formed which closes the ruptured convolution.

The reverse of this erosion and corrosion is the deposition of foreign substances upon the shell. *G. livescens* of Lake Erie, where it borders Michigan, is free of the deposits, and this is true to a somewhat lesser extent of the species in Lakes Huron and Michigan. But in the interior of the state, virtually all grown or half-grown shells are stained or roughened by one form or another of alien material. Algae are again the active causation. In parts of the Portage river lake of Washtenaw and Livingston counties shells bear a thick, compact, rounded deposit of calcium carbonate covering everything except the aperture, and even that may be encroached upon. On specimens of *livescens* in northern Michigan, the deposits are sometimes nodulous, irregular, and spongy and are easily scraped off. The difference points to differences in the species of algae. Almost universal on shells in the state, those of the Lake Erie border excepted, is a very fine layer of ferruginous material the exact nature of which appears not to have been studied. It is dissolved easily by oxalic acid.

The variation in *livescens* between colonies only a few miles apart may be illustrated by material from Millecoquins River, Mackinac County, Michigan. The upstream shells were taken near the discharge of Millecoquins Lake, the downstream shells not far from the discharge of the river into Lake Michigan:

Upstream Forms	Downstream Forms
Dark brown to nearly black	Some completely black
Ground color dull	Ground color shining

No revolving bands	No revolving bands
Encrusted with lime	Not encrusted
Spire tightly to moderately coiled	Spire loosely coiled
Whorls regularly rounded	Whorls tending to be shouldered
No revolving striae	Three shells out of twenty striate
Aperture slightly produced	Aperture distinctly produced
Obesity of ten largest specimens, 72.0 per cent	Obesity of ten largest, 74.4 per cent
Eight to nine whorls indicated	Ten to eleven whorls indicated

PROPORTIONS

Shells of three localities of Lake Erie have, to all intents and purposes, the same index of obesity, about 70.0, that is, the ratio of diameter to length. The index is slightly greater in shells of the Detroit River, and nearly the same in specimens collected in the River Rouge close to its mouth. More marked differences are to be noted in *livescens* of Lake St. Clair. The obesity index of Anchor Bay mollusks averages 73.7; of heavy, short-spired forms taken at Grosse Pointe, 81.3; and of an elongate phase living in strong currents in the flats, 65.6. Shells of Saginaw Bay of Lake Huron have a lower proportionate obesity than those of the open lake. No appreciable difference of proportions occurs between lots collected on the shores of Lake Michigan at Charlevoix and the material dredged off that point. A close relationship in the matter is shown between shells taken in Lake Michigan bays of the Upper Peninsula and those of more or less exposed stations farther south. Two lots from Lake Algonquin beaches near Lake Huron match, in obesity, shells now living at the present Lake Huron levels.

The obesity index of eight inland lakes ranges from 72.2, Crooked Lake, Charlevoix County, to 77.0, Platt Lake, Benzie County; that of the "drowned-river lagoons," 69.2, Kalamazoo River, Saugatuck, Allegan County, to 74.6, Spring Lake, Ottawa County. The average obesity of lots from two localities of Portage Lake, a river lake of Huron River, is 76.8, that at its discharge, 79.5. The obesity of shells of Commerce Lake, another expansion of the same river, is 76.4, virtually identical with the findings for Portage Lake, farther down stream. The discharge mentioned above is over boulders, the water fast and shallow.

A certain uniformity is noticeable in the proportions of upstream shells of some of the rivers and creeks of Michigan, also a tendency toward a decrease in relative diameter as the discharges into the Great Lakes are neared or reached:

	Upstream	Discharge
Kalamazoo River	75.6–76.9	69.2
St. Joseph River	74.0–77.0	72.2
Grand River	71.3–73.6	70.3
River Rouge	78.6 (Birmingham)	71.2
Muskegon River	75.8 (Big Rapids)	72.9
Stony Creek, Monroe County	76.5	74.2

Varied ecological conditions of the Huron River appear to be reflected by differences in the proportions of the colonies of *livescens* which inhabit it. The index of obesity ranges from 73.2 to 81.3 in shells well upstream. It rises to 83.7 at Rockwood, near the mouth, and drops to 68.7 at the actual junction with Lake Erie. Specimens of a tributary, Mill Creek, Washtenaw County, near its discharge, have the index, 65.2, whereas those of the Huron River, a few yards below, have an average of 77.0. The records of five small streams on the west side of Michigan show a range of only 75.8 to 77.5. In some instances, tributaries have mollusks of larger relative diameter than those of the main streams; in other instances less.

In the Upper Peninsula, *livescens* of three lakes has an obesity index of 73.8 to 81.8. The last figure gives the proportions of shells of Au Train River, which discharges into Lake Superior. These shells are pyramidal in shape, and as a rule shells of that configuration are of greater relative diameter than are elongate individuals. As though to confound the rule, the pyramidal shells of Mt. Pisgah Bay, Beaver Island, have an obesity of 77.6, and the elongate inhabitants of Barney's Lake, just across the sand dunes from the bay, have virtually the same index.

G. livescens of Lake Erie varies in proportions as to whether the habitats are exposed to heavy wave action or are sheltered. The reaction to environmental conditions in the case is simple, direct, and demonstrable. Similar reactions have been observed in the Pleuroceridae of southern streams, downstream colonies as a rule having a greater relative diameter than upstream forms. The exceptions observed are sufficient to indicate that the governing factor is not mere volume of water, as has been concluded from some of the experiments with mollusks in aquaria. The study of relative proportions makes it clear that in a river the bulk of *livescens* may increase without necessarily increasing the ratio of diameter to heighth, although there is an apparent tendency in that direction.

SIZE AND SHAPE

The heighth, length, or altitude of *G. livescens,* the terms being interchangeable, varies with location, the amount of erosion which has been experienced, and, of course, with age. Through a count of numbers of whorls, it was learned that this heighth, length, or altitude depended in an adult snail, erosion ignored, upon the sizes of whorls. Thus, full-grown shells of two different colonies, even in the same stream or the same lake, might show the same number of whorls, but differ by several millimeters in the maximum size they have reached.

A subfossil example of *livescens,* still retaining shreds of its epidermis, was found by Clifford L. Blakeslee in excavated earth "at the exact junction of the old Clinton Canal (ditch) and the more recently abandoned Erie

Canal." Eight whorls remained. The apex was worn, yet still showed one of the juvenile carinae and the angulation of another. The altitude of the shell was 37.25 mm., the diameter, 16 mm. The aperture measurements were 15.25 mm. from edge of suture to base, 7.75 in diameter. Old age was indicated by the continuous and thickened columella, but otherwise there were no signs of senility, certainly none of the deformation which frequently attends on a senile condition in mollusks. This is by far the largest individual *livescens* I have seen. It is not to be considered to be even near average size, but rather as showing how large the species may grow (Fig. 1).

Shells taken in Lake Michigan in the Charlevoix area are nearly twice the size of the common Lake Huron form and of somewhat greater altitude than is usual with Lake Erie forms. The largest of Michigan stream shells are in downriver localities of the Grand River and the River Raisin. Specimens taken in a "side" channel of the flats of Lake St. Clair are of conspicuous altitude and small diameter, whereas in the case of others, taken in the lake at Grosse Pointe, the reverse is true.

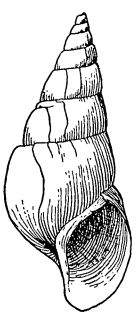


FIG. 1. A subfossil specimen of *G. livescens*.

"The size of the shell," Baily, Pearl, and Winsor (1932) wrote, "seems to be influenced by the chlorine, the food supply, and the silt toward the end of the year, and perhaps by other environmental factors."

The term "conic" can be used for all the shapes that *G. livescens* assumes in Michigan. This allows for a wide variation in the relative size of the base, the angle formed by sides of the whorls, and the heighth of the spire. In instances of very short spire as compared with the diameter of the body whorl, I have spoken of the shape as pyramidal, which still, of course, is conic. Certain goniobases of southern waters increase the size of whorls so little between the neanic whorls and the body whorl that the adjective "attenuate" suits them better than does conic. This shape may involve all members of a colony or only occasional individuals of one. No such instance has been observed so far among Michigan specimens of *livescens*. Again, the adolescent and adult growth of certain goniobases, especially marked in shells of the Coosa River, Alabama, and observed in *livescens* of the down-

stream parts of Tuscarawas River, Ohio, is somewhat constricted, two or three of the last whorls being almost of the same size. The shape has been called "cylindrical." This is attended by an extension of the aperture into something like a sinus. The nearest approach to cylindrical *livescens* in Michigan is among individuals of Lake Erie and Lake St. Clair, and is descriptive of shells taken by Bryant Walker in the River Rouge near its mouth.

Shape varies with age, an "infant" coming within the above definition of pyramidal. The juvenile may be elongate-conic, and the adult narrowly conic or broadly conic. These conformations may be stamped upon all individuals of a particular colony, or on only a few, but as a rule the shape of one adult of a colony of *livescens* is that of every other one. It is the variation in shape, apparently more than anything else, which has been productive of the many specific and subspecific names in the Pleuroceridae.

The two to two and one-half whorls which constitute the embryo or nucleus of *livescens* are rounded both above and below the periphery. The upper parts of the immediate postembryonic whorls are flattened. Convexity of these upper parts begins usually with the sixth or seventh whorl, and this, with exceptions later discussed, increases to some extent with each whorl thereafter. Shells with extremely gibbous body whorls have been observed in a lot from Lake Michigan, from two lakes on the west side of the Lower Peninsula of the state, and from two streams of the east side. The pronounced convexity is an individual variation. Thus, in a lot from the Huron River above Dexter, about one-half of thirty-two shells have conspicuously rounded body whorls; three out of sixteen from Thunder Bay River, Alpena County, are of this nature. In the great majority of Michigan specimens the adolescent and adult whorls are of moderate convexity, the sutures shallow and the peripheries regularly rounded.

Shouldered whorls are those which are slightly shelved or ledged just below the suture. They are of occasional occurrence and have been observed among stream shells only and to involve parts, not all, of a colony. Inasmuch as the amount of shouldering varies, it is difficult to make any positive pronouncement about it or to consider that it has ecological significance.

Colonies of *livescens* in which the flattened upper whorls of the juvenile stage are carried into the adult stage are established in Allegan, Ottawa, and Muskegon counties, a fairly circumscribed area on the west side of the state. All of the colonies except one are situated in lakes. Sink Lake is the most inland of the seven localities in which this form is known to occur. It is connected with Rabbit River. It is described as having a "sand and marshy beach." Goshorn and Duck lakes, Allegan County, two other stations, are close to the sand dunes bordering Lake Michigan, and in a period of very high Great Lakes levels would correspond to the river-lagoon type under

which the other lakes, Black Lake, Ottawa County; Little Black Lake, Duck Lake, and Mona Lake, Muskegon County, are classified. The single fluviatile location is Pigeon River, Ottawa County.

The shells are light to dark brown and are without revolving bands. Among the Black Lake shells are some having a sulcus immediately below the suture, in this resembling the subspecies *gracilior* of Ohio. The feature in land shells has been accepted as evidence of decadence. In the Goshorn Lake lot are specimens in which the juvenile carinae have been carried to the body whorl as a slight keel. Coiling is moderate. One shell only, from Pigeon River, is striate. The flattened upper whorls, though marking the most of the specimens, are not constant. Thus, among forty-one shells, old and young, of Little Black Lake, are six having slightly convex whorls. The averages of indexes of relative diameter to length among these forms range from 70.0 to 77.7, the general average being 73.7. The shells of greater proportional diameter, represented by the index 77.7, are rather smaller than the others, the spires lower.

F. C. Baker found similar shells of "very flat-sided whorls" in Red Cedar River, Barron County, Wisconsin, and gave them subspecific rank under the name of *barronensis*. He reported that the animal of *barronensis* is the same as in the typical form, the genitalia "as in *livescens*," and the radula "not differing particularly from *livescens*." In considering the great shell variation of *livescens* in Michigan there seems to be small justification for differentiating the form of the seven localities by name from those of the rest of the state.

VARIATIONS IN WHORL COILING

In the case of a loosely coiled shell of *G. livescens*, the postembryonic whorls drop below the peripheries of the preceding whorls. This is especially noticeable on the spires because the juvenile carinae are left projecting like the eaves of small pagodas. The term "tight coiling" is applied to those shells in which the whorls in their growth are, as it were, wrapped above the peripheries of preceding whorls. A third form of coiling is recognizable. In this, the carinae project little or not at all, each whorl fitting snugly against the periphery of the preceding whorl. For convenience, this coiling is spoken of here as "moderate."

Loose coiling, as observed in southern Pleuroceridae, is one of the manifestations of depauperization and may involve all the whorls from the protoconch to the body whorl. This extreme has not been seen in Michigan specimens of *G. livescens*, although it is approached by a single individual dredged from Lake Michigan off Charlevoix. Ecologically, loose coiling appears to be characteristic of the goniobases of sheltered situations, occurring more in inland lakes than in the Great Lakes, in river lakes rather than

in fast-moving parts of streams, and in millponds. Young shells of the upper parts of the Huron River are usually loosely coiled, those of the lower parts moderately coiled. A lot taken in the river at Ann Arbor is tightly coiled. Material from one of the channels of the flats of Lake St. Clair is loosely coiled, whereas that of a more open part of this lake is the opposite.

Tight coiling is the prevailing aspect of *livescens* of western Lake Erie, but not of all colonies of the Detroit River, ten to twenty miles to the north. Specimens from Charity Islands, Saginaw Bay, are tightly coiled. Of forty-five specimens from Stony Island, deeper in the bay, only eleven are of this phase. As against the loosely coiled shells of Commerce Lake, Huron River, are certain tightly coiled ones of Portage Lake, another river lake of the same stream. Shells that came through intake pipes of the Detroit water supply system are tightly coiled. This is characteristic of a few specimens of Burt Lake and not of those from a tributary Burt Lake stream.

Colonies known to include individuals both loosely and tightly coiled are in Crystal Lake, Benzie County, Grand and Kalamazoo rivers, the River Raisin, the south branch of Thunder Bay River, Alpena County, and Paw Paw River, Berrien County.

Moderate coiling characterizes about three-fourths of the several thousand specimens examined. Seemingly, all of the *livescens* of the Upper Peninsula of Michigan come within this description, the variations from the mean occurring in the Great Lakes bordering the Lower Peninsula and in the inland lakes and streams of this peninsula. It should be explained that many lots of Michigan are so eroded that it cannot be told what forms the whorls of their shells take. They have had to be ignored.

This part of the study does not permit assigning the forms that whorl coiling assumes to ecological factors with definiteness. Conditions in stream rapids would seem in this matter to correspond to those of exposed sections of the Great Lakes, but while most "exposed" examples of *livescens* of the Great Lakes are tightly coiled some occupying river rapids are not. It is probable that other factors than what we might call "exposure" govern in the case.

PERISTOME, SUTURE, AND COLUMELLA

In the Pleuroceridae, the peristome, or as it is most commonly called, the outer lip, varies from straight to fissured, and upon differing configurations of this character Lea gave his greatest emphasis in establishing three genera of the family. Straight peristomes have been seen as a constant in only one colony of *livescens*. These shells inhabited the shores of the whirlpool of Niagara River, a situation of violently disturbed waters. A lip so shaped permits close adherence to fixed objects such as boulders and slabs

of limestone. That the straight lip in the species is an environmental adaptation is borne out by the fact that peristomes of shells occupying exposed headlands of Lake Erie are only slightly incurved and in this feature contrast with the more or less conspicuously sinuous lips of mollusks of quiet parts of streams and lakes. The correlations are two-fold: ventricose individuals are especially the stamp of colonies of wave-beaten lake shores and the heavier rapids of streams, and their peristomes are broad, incurving arcs; elongate examples belong rather to sheltered places, the peristomes being sinuous. The lips in Michigan lots vary with the general shape of shells, and these, in turn, show variation in regard to habitats.

Occupants of exposed situations have relatively large clinging feet and ovate apertures to accommodate such soft parts. The apertures of elongate shells are elliptical rather than ovate, and sometimes the vent has the awl-like appearance which is characteristic of the feature in the genus *Pleurocera.* In certain colonies the aperture is extended into a slight sinus. Thus, shells taken at the mouth of the River Rouge are so marked, whereas those of the stream at Birmingham are not. What purpose, if any, the sinus fulfills when it occurs is not clear.

Descriptions of the Pleuroceridae usually mention the suture as lightly or deeply impressed, but since the character is not measurable, at least for comparative purposes, the statements are wanting in definiteness. About all that can be said of the suture in Michigan forms of *G. livescens* is that it is shallow and regular in the young and that it deepens rather more in adults, and in these is frequently rough and uneven. Accidents, deformations, and old age decadence are registered in the suture rather more than in other parts of the exoskeleton.

More often than not, the columella in *livescens* of Michigan is only partly developed, the upper part being a film of nacre, shining and translucent. Because of exposure to destructive salts of the water, a tendency, noticeable in adults, is toward alternation of the crystalline substance into amorphous, chalky calcite. This makes the columella more conspicuous than it is in younger specimens. The feature in *Goniobasis* has no distinguishing characteristics which aid in the differentiation of species.

SCULPTURE

The sculpture of *G. livescens* consists of axial growth lines, fine or nearly microscopic revolving lines, carinae and spiral striae, ridges or ribs.

The axial lines alter with growth, being fine and regularly spaced in young shells, irregular and sometimes rough in adults. A primitive sculpture of the Pleuroceridae is known as plicae, which are more or less evenly spaced thickenings, elevations, or intensifications of growth lines. It was probably common to all the species of *Goniobasis* in the geological past, or

at least to the stocks from which the species evolved. It has disappeared in many of the recent species, *livescens* among them. In the study of the Michigan material, a watch was kept for reversions to plication, but it was not seen in a single instance.

The fine revolving lines represent an absence of smoothness in the secretion of the chitin making up the periostracum. They are to be seen only in young shells or in older ones which have not been subjected to abrasion by silt in the moving water. Often these lines are not continuous, and sometimes they are slightly undulating rather than straight.

Carinae are formed at the periphery of whorls following the nuclear one and one-half to two whorls. They persist into adolescence and, as a rule, then disappear. In certain colonies of Lake Erie, the carinae persist as angulations or keels into fully adult life, and F. C. Baker (1920*b*) has reported this retention of a juvenile characteristic in the Niagara River shells. The carinae are sometimes double, and the basal one, as well as the upper, may sometimes be seen in specimens very loosely coiled. As the occurrence of carinae is generic, known to be absent in three species only, they have not been studied on this occasion further than to note their relation with whorl coiling.

Spiral sculpture, if present, appears near the suture of the fifth or sixth whorl. It rarely occupies more than a single whorl, and in *livescens* of Michigan, is seldom more than a single raised line. In three or four instances there are a few spiral ridges, corresponding to malleations, on the body whorls of individuals. In no one lot having shells with spiral lines were all the individuals so marked. They were as frequent as thirteen out of eighteen in one "spiraled" lot, as few as one in forty in another. The character was present in twenty-six stream lots, including a dammed area; this represents a fairly low percentage. It has been seen in shells from two localities of Lake Michigan and in occupants of a beach pool of Saginaw Bay of Lake Huron, but nowhere else among Great Lakes specimens of *livescens*. Shells of four inland lakes have these spiral lines. Of the twenty-six streams, all are in the lower tiers of Michigan counties with the exception of two, one of which is in Grand Traverse County and the other in Cheboygan County. Two of the inland lakes are near the southern border of the state, one in Charlevoix County, and one in Leelanau County. Spirals have been seen in no shells of the Upper Peninsula. The ridged revolving lines are probably caused by adventitious folds in the mantle which contains the shell-secreting glands, such as might be caused by the crowding of the animal within its exoskeleton. It seems unlikely that this sculpture is either a character in course of development or one that is disappearing. It is, in any case, of minor importance.

PIGMENTATION

The bulk of specimens of *G. livescens* of Michigan is within the lighter browns of Ridgway's *Color Standards* (1912), the fresher lots showing tints of green. Superficially, the brown shells seem to be varied of hue, but actually the range of color is narrow. Shades of dark brown from chestnut or bay to raw umber differentiate a number of the lots from hazel and brussels brown. Upstream mollusks of the Huron River are black while fresh. After a period of drying, they are dark brown. In river lakes of the Huron River, *livescens* is lighter than in fast water, as is also a colony near the mouth of the stream. Very dark brown shells of the Upper Peninsula appear to be correlated with the "bog-stain" characteristic of its waters. A similar depth of color is noticeable among shells of inland lakes of the Charlevoix area. With dark brown shells may be included some that are brownish black, or greenish black. These darker tints are more common in waters of the northern part of the Lower Peninsula and in the Upper Peninsula than in those of the extreme southern part of the state. Shells from two localities of Millecoquins River, Schoolcraft County, are more black than brown, the ones from the lower part of the stream being somewhat lighter than the upstream lot.

Mollusks that definitely can be called black are relatively rare. They occur from Paw Paw River to a millpond at Traverse City, comprise all from Barney Lake, Beaver Island, and Big Platt Lake, Emmet County. Material from three scattered streams is black.

Shells of western Lake Erie fall within varied shades of greenish yellow, the lightest agreeing with Ridgway's sulphur yellow. Yellow specimens with little hint of green in them inhabit parts of Lake St. Clair and Saginaw Bay of Lake Huron, Grand River, and the lower River Raisin. Shells of three of the "drowned-river lagoons" bordering Lake Michigan are yellow. A river lake of Washtenaw County contains colonies that are yellow, whereas the true stream has much darker shells. The outstanding yellow populations, those of Lake Erie, Lake St. Clair, and the three lagoons, are inhabitants of sandy bottoms, and that environment seems to have a bearing on the coloration.

Menke devised his name *livescens* from the adjective *lividus,* meaning "bluish." As many of the shells thrown on the Great Lakes beaches alter from brown or yellow to blue or purplish, and, in the case of *Campeloma* and some land shells, even to red, desiccation, sunlight, and perhaps heat acting as forces of disintegration, it is probable that Menke's specimens were "dead" ones. Still, blue is the color of some colonies of living *livescens,* and it may involve the shells entirely or only in part. Thus, mollusks of Lake Michigan in the Charlevoix area are more distinctly blue than they are any other color. This may be said also of specimens collected on the

shores of islands of Saginaw Bay. Blue has been noted as the prevailing coloration in specimens of six inland lakes north of the Saginaw and Grand valleys and in shells of one lake of Cass County. In the Museum of Zoology collection are bluish specimens marked simply "Ann Arbor," presumably from the Huron River. This is an off color for the stream. Of forty-eight shells from the Grand River, three are blue, the rest brown; of seventeen from near the mouth of Kalamazoo River, twelve are blue, and the others yellowish brown. The bluish pigmentation, so far as it affects living animals, is a localized phenomenon, and in instances, as in stream occupants, it is restricted to certain individuals of a colony.

The word texture is loosely applied to describe the surface structure of shells as it appears to the human eye unaided by the microscope. Thus, shell texture may be coarse or fine, shining or silky, dull, tarnished, glossy, opaque, or translucent. Color is sometimes brought within the meanings of texture, especially where that is indefinite. With this inclusive definition in mind, it may be stated that *livescens* varies in texture between colonies, between members of any given colony, between individuals of different ages, and, finally, between occupancy of a protected position among aquatic weeds and one subject to stream erosion.

Revolving bands, ribbons, or belts of pigmentation darker than the color of the periostracum are present throughout the Pleuroceridae with the exception of the genus *Lithasiopsis* which possibly belongs to the family Pachychilidae. Glands secreting this pigment occupy a part of the mantle. In most of the banded individuals, the color is deposited both in the crystalline shell substance and in the epidermis. It happens occasionally that only the epidermis receives the banding pigment. Again, instances are known in which banding pigment permeates the entire shell material, giving a deep purplish effect. This appears to be due to oversecretion, the result of some pathological defect.

The color bands in *G. livescens* of Michigan, where they occur, are mostly in the epidermis and disappear as the ground color fades. It is highly probable that numbers of the lots which have been examined in this study and that are without bands may yet have had them at the time of collection—in the case of many of the shells that was more than a quarter century ago.

Bands have been found in shells of the Grand, Red Cedar, and Looking Glass rivers, and of Sandstone Creek, of the same stream system. Banded shells of the Grand River amount to 50 per cent of all collected at Grand Rapids, varying in other parts of the river, the highest percentages being in downriver sections. They are 58 per cent of collections in Red Cedar River at East Lansing, about 10 per cent of Looking Glass River shells, and 3.3 per cent of those of Sandstone Creek.

While no bands have been observed in specimens from Cass River of

the Saginaw River basin the banded shells of Pine River, another tributary of the Saginaw River, are 85 per cent of a lot of sixty-nine. In contrast are shells of Flint River at Birch Run, the Flint belonging also to the Saginaw—two banded shells in twenty-eight. Specimens with bands were noted in *livescens* from the Kalamazoo River and the tributary Battle Creek River; the White Pigeon River of the St. Joseph River, Paw Paw River, the River Raisin and its branch, the Saline River. In only one locality of the Huron River does the species seem to be banded. This is at Portage Lake, a river expansion. One lot of Lake St. Clair shells has the bands; an occasional shell of Detroit River is so pigmented; the character is absent in Lake Erie *livescens*. So far as the study gives indication, the feature is not present in *livescens* of the Upper Peninsula.

In some places nearly all the members of a colony have these revolving color bands, in other places only a few individuals are pigmented in this way, and in still other waters no pigmentation of the kind occurs; or pigment glands may be highly active, slightly active, or inactive. The cause of the differences has not been learned with certainty, but it is indicated by experiments carried out by H. B. Moore (1936) with *Thaias lapillus,* a marine mollusk. Banded mollusks that were feeding on *Mytilus* were transferred to locations having no *Mytilus*. As these shells continued their growth pigmentation was reduced. Retransfer to *Mytilus* beds was followed by a resumption of pigmentation. It might be assumed that *G. livescens* requires certain substances for the synthesis of banding pigment and that these substances are obtainable only in certain foods—such foods are more often wanting than they are present in the Michigan area.

Baily, Pearl, and Winsor (1932) tabulated the occurrence of bands in Pleuroceridae of Gunpowder River, Maryland. Analysis of the tables shows that 6.2 per cent of upstream *Goniobasis* are banded, 25.9 per cent of downstream shells. In *Nitocris* the banded upstream shells amounted to 22.6 per cent, the downstream inhabitants with bands to 41.3 per cent. The authors are of the opinion that the pigmented stripes "seem to be influenced by the chemical constitution of the water, and perhaps particularly by the relative amount of alkali generally, and of bicarbonates more specially."

In a few descriptions of goniobases, mention is made of a light band just beneath the suture. The pigmentation is less than that of the epithelium, much less than in the revolving bands discussed above. It is observable in fresh specimens and not very often in old museum lots. This is to say that the ground color becomes uniform through fading. The sutural band was observed in several lots of Michigan *livescens,* but in no instance were all the specimens of a given lot so marked. This pigment is laid down at the upper margin of the gland which secretes the chitinous epidermal material. It is apparent that in some shells the secretion thins out at the glandular

verge, and so what to the observer seems to be a revolving band is, in fact, simply the basic shell substance showing through the epithelium. Occasionally, such a reduction of coloration appears on the base of the shell; thus it is clear that both margins of the glands of the mantle can be affected in this way.

THE OPERCULUM

The chitinous, protective operculum of *G. livescens* is attached to the ends of the fibers of the columellar muscle. It develops from a nucleus into constantly widening spirals, the number of spirals being three and a little more. The apex, acute in the young, may be obtusely rounded in adult mollusks; the basal margin is apparently invariably broadly rounded. Usually, the operculum is unequilateral, but examples have been seen in which the sides are equal, making the organ ovate in shape. Clean, unstained opercula are thin, reddish brown.

Growth is by a series of underlappings, narrow at the left margin, broadened at the right. In growing, the operculum is so rotated that the most recent laminae are at right angles to those immediately postnuclear. In the juvenile stage of the shell, the early lines of growth of the operculum are the most delicate. With additional growth, these lines coarsen and alter from curves on the left margin to nearly straight lines. The heavier growth lines represent rests or pauses of longer duration than those for which the finer lines stand. The nucleus is called neomelanian. It is very tightly coiled and tends to be indistinct as though destined, in the course of its evolution, for complete elimination. Commonly, the nucleus is close to the left margin, but new growth, in instances, leaves it near the center of the operculum, though still close to the basal margin. The area of attachment is elongate-elliptical; the marginal borders form a continuous low ridge of callus.

There are some slight differences of thickness in the opercula as between colonies, the thickness as well as the size being correlated with the size of the aperture. These differences do not seem to have any bearing as to whether the examples came from the east or the west side of Michigan or from the Lower or the Upper Peninsula.

G. livescens in many respects resembles *G. semicarinata* (Say). The two species occupy contiguous waters in Ohio and Indiana. Superficially, it might seem that the one developed out of the other. Yet if the operculum is a primitive character, and, as in the case of axial plicae of the shell, undergoes a limited alteration, then these species are more unlike each other than appears from the exoskeletons. The operculum of *semicarinata* has a phase of spiral coiling which is about midway between paleomelanian and neomelanian. The lines of the spiral are so distinct as to give no suggestion that the operculum was tending toward obsolescence. The operculum of

livescens is closer to that of *Lithasia obovata* than to that of most goniobases; the nucleus of each is tightly coiled, and the operculum in both is probably of limited protective value.

THE RADULA

The median teeth of the dozen radulae of Michigan *G. livescens* that have been examined are symmetrical, but Howe (1930) found irregularities in the medians of the species in Illinois. This is not uncommon among the Pleuroceridae. It seldom affects more than two or three rows of the radula, and it is clearly indicated that malformations, once occurring, do not persist nor do they involve the whole ribbon. Medians in the central part of the radula are at their best development. They are likely to have fewer and weaker cusps at the secreting termination and to betray senility at the other termination. The median formula is 2–1–2, 3–1–3, or 4–1–4.

In this species as in other Pleuroceridae, the lateral teeth are the most constant of all. Their position alters with growth. The broad face of the teeth is offered to the observer at the beginning; a twisting takes place at an early stage, and thereafter it is a partial "side-view" which the observer obtains. When a lateral of *G. livescens* radula is flattened out it is seen to have five denticles, and this number does not vary, apparently. In making this count, the end of the right margin is taken to be a cusp, although it does not always seem to be sharply differentiated from the cusp next to it. This may be due to incomplete staining.

The inner marginal commonly has five denticles, but as many as eight have been noted. Where the edges of the transparent extensions of the denticles have taken the stain properly, the tooth is rakelike in appearance. This is true also of outer marginals. F. C. Baker (1928) gave a denticle count of 8–9 in the outer marginal teeth of Wisconsin *G. livescens,* Howe (1930) gave one of 9–12 in the case of Illinois shells. I found these variations in Michigan lots:

Lake Erie, La Plaisance Bay	9 denticles
Manistee River, Crawford County	9–10 denticles
Detroit River	10–11 denticles
Grand River, Eaton County	10–11 denticles
Saginaw Bay, Huron County	12–14 denticles

Howe thought such differences might "serve as a basis for distinguishing ecologically distinct variations in *Goniobasis livescens.*" In the absence of extensive data, no opinion is here offered in the matter.

ANATOMY

The body of a male specimen taken in the first week of November, 1942, was rather short and rounded posteriorly and had a blunt wedge-shaped rostrum. The mouth was a narrow, vertical slit. The tentacles were short,

thick at the base, and tapering to a blunt termination. Strongly pigmented eyes at the base of the tentacles were conspicuous. The mantle covered about three-fourths of the body; its margins were smooth. A trenchlike line extended from the palial cavity to the right tentacle. The color in general was grayish to nearly black.

A female of the same colony, taken at the same time, differed in showing faint, discontinuous stripes of tallowish coloration on top, not greatly contrasting with the leaden hue of the body mass. Irregular spots occurred here and there on the sides of the foot. The tip of the tentacles was translucent, nearly colorless. In the extended animal, the operculum rested in a fold or pocket, showing only its edges. The edges of the mantle were slightly yellow. Sex was determined by a noticeable sinus on the right side of the foot.

No copulatory organ has been found in the Pleuroceridae. The male genitalia were noted in *G. laqueata* by Woodard (1934) as consisting of a sperm duct, or vas deferens, "and two long narrow laminae which communicate with the mantle cavity along their free ventral margins." From January through May, he found genitalia swollen, testes and ovary "in a state of thorough depletion from June to late August." The findings correspond very closely to those of Jewell (1931) in *G. livescens* of Illinois. Capsules containing three or four eggs glued to stones and shells were observed before the present study was undertaken, but no further attention was given to them. When search was made for them, none was to be found. For details, therefore, dependence is placed on Miss Jewell. She recorded the eggs to be "in lines of two or three with no covering except the simple shell membrane which remained until time for hatching." These were on stones to June 8. The veliger stage was reached in seven days; the membrane was broken about the eleventh day.

The body pigmentation of *livescens* of the Huron River in the autumn of 1942 was seen to be different from that of specimens collected in the Manistee River of western Michigan at about the same time. Through the rest of 1942 and the whole of 1943, observations were made on the subject as opportunity offered. The findings may be summarized as follows: Late fall and winter specimens are either uniformly grayish black on top of the rostrum or marked with light and dark stripes of irregular lengths. No hue that could be called bright is present. By May 1, the prevailing tone is yellow, the pigmentation either involving most of the upper part of the body or occupying areas of the rostrum and mantle or bordering mantle and foot. Material examined through July and August, about fifty specimens in all, showed an increase in distribution and intensity of the yellow color, so that in some animals it could be described as golden. An October, 1943, lot was losing the yellow, some specimens lacking it altogether. No streaks,

stripes, or mottlings were to be seen in examples collected on November 18, 1943, and in only one specimen was there a slight tinge of yellow.

Woodard (1934) found the testes of *G. laqueata* "when active" to be "a golden yellow in color, owing to the presence of numerous pigment granules in the ectodermal covering." There are a few other observations which, like those on *G. livescens,* show differences in coloration as between breeding and sexually inactive periods. Thus, the fresh-water bivalve *Fusconaia* is high yellow in tone in the egg-laying months, and *Pleurobema* is distinctly reddish. Writing from Cedar Bluff, Alabama, in October, 1910, H. H. Smith said of *Goniobasis hartmaniana,* "in all that I have observed, the animal is dull orange in color," and again, "the animal is orange-colored, unlike any other *Goniobasis* known to me." It seems likely that the species was a fall breeder, in this differing from others of the genus whose breeding and pigmented season came at a high-water time in which they were least likely to be collected and examined.

FOOD

The food of the goniobases as indicated in their feces consists of diatoms and those desmids which inhabit alkaline waters. As sand is in these excrements and has been found in the alimentary tract, Baily, Pearl, and Winsor (1932) are of the opinion that the sharp particles of inorganic matter serve as triturating agencies, whereas "finer and smoother particles of argillaceous alluvium" serve poorly in this aspect. Their conclusion is that this has a correlation with choice of habitat; fine silt cuts off access to food and at the same time fails to supply the proper material for trituration.

Stomachs of brook trout from fifteen localities in Michigan were examined in 1929. They contained, among other substances, shells or parts of shells of eight genera of fresh-water mollusks. These ranged from the minute and delicate shells of *Gyraulus* to the thick *Campeloma.* The stomach of one fish ten and one-half inches long contained two specimens of *G. livescens.* In one example digestion had advanced so far as to remove the epithelium, part of the outer lip, and most of the juvenile whorls. In the other, the epithelium was gone and the shell substance was pitted, but the apex remained, its growth lines being plain without the aid of the glass. Soft parts of neither mollusk had as yet been attacked, and in each instance the operculum was attached and unaffected by the digestive agencies. The brook trout had been taken in the East Branch of Black River, Montmorency County. *G. livescens* was found in the gizzard of a white-winged scoter, shot at Fish Point, Tuscola County, by N. A. Wood, May 12, 1926.

PARASITISM

As in other groups of aquatic mollusks, the Pleuroceridae are subject to trematode parasitism. F. C. Baker (1928) observed in Wisconsin that

"some of the [*Pleurocera*] *acuta* from the outlet of Lake Oconomowoc (Oconomowoc River) are heavily infested with rediae of a trematode worm. The parasites completely fill the rectum of the animal, causing it to be greatly distended. The infested snails were found only in certain parts of the river, other colonies being quite free from the parasite."

Zetek (1918), quoting Faust, recorded that the *Goniobasis pulchella* [*livescens*] of Big Vermilion River, Illinois, was the host of cercaria *aurita* Faust. Detailed studies of parasitized *livescens* of Huron River, Michigan, have been carried out by Charles G. Dobrovolny. He found (1938) that the mollusk serves as the first and second intermediate host of *Plagioporus sinitsini huroni* Dobrovolny, the subspecies being erected because of peculiarities that are absent in the typical form which occupies Oneida Lake, New York. In this lake Baker (1919) came upon infested *livescens;* doubtlessly the parasite was *P. sinitsini.* Dobrovolny (1939*a*) also discovered sporocysts and daughter sporocysts of *P. lepomis* in the Huron River *livescens:* "After developing, the mature cercariae leave the daughter sporocyst by way of the birth pore and emerge from the snail . . . without discrimination these larvae, as *C. dictorenalis,* will often attach themselves to any organism with which they come in contact." A fairly low degree of parasitism is indicated by the findings, since of 43,189 examples of the gastropod only 1.25 per cent shed cercariae. As metacercariae, the trematodes developed into sexual maturity "in most of the local centrarchid fishes."

HABITATS

The writings of several authors who have observed the habitats of *G. livescens* are quoted:

F. Baker (1902), referring to the Chicago area: ". . . on a muddy (sometimes sandy) bottom, in water from two to ten or more feet in depth. Prefers a bottom with water weeds."

H. B. Baker (1911), Saginaw Bay, Michigan: "Unprotected, rocky, littoral habitats off the north shores of both North and Stony islands, both on the limestone rock that forms the bottom, and on piers of wharves, etc. . . . Rock pools. Off Sand Point in deep water." Pigeon River: "On stones, on Potamogeton of ox-bow pond."

A. D. Robertson (1915), Georgian Bay of Lake Huron: "Obtained abundantly where there are currents, in sand runs or along rocky shores and on rocky shoals near the outer islands. Occurs also but not plentifully in muddy bays."

F. C. Baker (1916), Oneida Lake, New York: "Young individuals, a few millimeters in length, have been noted on a sandy bottom."

F. C. Baker (1918), Oneida Lake, New York: "Found only on boulder and gravel bottoms, on exposed shores or points, in water one-half to four

feet in depth. Most abundant in water one to two feet deep on a boulder shore."

A. H. Wiebe (1926), Lake Erie, in vicinity of Put-in-Bay, Ohio: On pebbles and small stones of a bar "subject to almost continuous wave action." On the protected side of bars in a few inches to four feet of water. On timbers and stones of a protected bay in a few inches of water. On boulders and timbers of dock. " . . . snails migrate into less protected areas during fair weather, then when it gets rough they seek a sheltered place."

Scott, Hile, and Spieth (1928), Lake Wawasee, Indiana: "*Goniobasis* forms by weight 97 per cent of all the snails in the open littoral and 74 per cent of all snails in the weedy littoral."

F. C. Baker (1928), Sturgeon Bay of Lake Michigan: "On marly clay bottom in water .3–1–3 m. deep, among Chara, on sand bottom."

Certain habitats recorded by C. L. Blakeslee of Pittsford, New York, are listed:

Swift water; sides of partly submerged boulders
On rocks in water up to three feet in depth
Bridge abutments and embankment just below. Water deep, current moderate
Vertical ends of rock layers constantly drenched with fast water; in rock crevices; young in pools at the edge of the creek
On the sloping side of a dam with a good volume of water pouring over them
Just above the brink of Niagara Falls; fast water
Quiet water along the shores
Pool in midstream at foot of a length of fast, shallow water
Face of vertical dam
Supports of a boat landing. No noticeable current
Old Welland Canal; rock shoring on embankment; hardly any current

Additional habitats are: In joints, cracks, and holes of the limestone of the shore of Lake Erie at Port Maitland, Ontario, the rock covered by a thin film of algae. A habitat contrasting with this situation is the sandy shallows of the western loop of Lake Erie, the water so subject to changes of level that depths vary one to four feet in the course of a few hours. A few miles north of this locality, *livescens* has been seen on slimy wharf piling and on the exposed faces of concrete piers. In streams of Michigan the shells may sometimes be observed among water-soaked leaves, branches, and logs. The young in many thousands have been seen on the limestone rocks of rapids of Maumee River, Ohio; adults in slower water at the banks. The same age differentiation has been noted in the discharges of lakes in Lake County, Michigan, and also in the genus *Pleurocera* of the upper Clinch River of Virginia. Old clam shells with films of algae appear to have more attraction for the young of *livescens* in Michigan rivers than they do for adults.

G. virginica (Gmelin) has been taken from tidal pools of the Raritan River, New Jersey, where the water has a brackish taste. In the Potomac at Mount Vernon, Virginia, the same species is subject to alternating fresh-water and saline conditions. It lives in Gunpowder River, Maryland, where the salinity is 50 per cent of that of the ocean (Baily, 1929). *Goniobasis* in general can endure the periodical silting of streams during freshets. That prolonged or continuous turbidity coupled with a reduction of oxygen content is inimical is indicated by the absence of colonies in millponds. The disappearance of *livescens* and almost all other mollusks from heavily polluted parts of Huron River points to another man-made agency of destruction. A certain amount of domestic sewage, however, is not deleterious and may, at least indirectly, serve as fertilizer. The shallow section of Lake Erie contains diluted parts of the sewage discharges of Toledo, Ohio, and perhaps to a smaller extent those of Monroe, Michigan. The phytoplankton count of the section is the highest known of the Great Lakes and also, so far as known, the area has the largest molluscan population. Particularly in spring, waves form windrows of shells on the beaches, the Pleuroceridae amounting to hundreds of thousands. Of several possible causes of the destruction, one is suggested from the findings of limnologists. The winter ice cover shuts off that oxygen which is supplied through wave movement. Prescott (1939) has observed in certain lakes an oxygen depletion of 4.5 to 5.5 p.p.m. to 1.5 to 2.0 p.p.m. "within a day or a few hours. The exhaustion of the oxygen brings about the death of both micro-fauna and phytoplankton and the decay by bacteria of this mass of organic matter quickly reduces further the oxygen content and then fish and other aquatic animals are suffocated." Complete destruction of the Pleuroceridae of western Lake Erie does not occur, but there is sufficient havoc to make itself manifest and striking.

During his study of the naiad fauna of the Huron River, van der Schalie (1938) found the alkalinity ranging from 133 p.p.m. to 233 p.p.m. The lowest reading was in the tributary Portage River, the highest in Fleming Creek, another affluent. Both streams, as well as the Huron River, are or have been occupied by *G. livescens*. From data kindly supplied by the Institute for Fisheries Research, the following results of alkalinity tests have been taken: Crystal Lake, Benzie County, 111 to 120 p.p.m.; Muskegon Lake, Muskegon County, 132 p.p.m.; Van Ettan Lake, Iosco County, 136 to 148 p.p.m.; Big Platte Lake, Benzie County, 141 to 156 p.p.m., Round Lake, Benzie County, 139 to 150 p.p.m., and Muskegon River, Clare County, 87 to 89 p.p.m. In each instance, high or low, sufficient amounts of carbonates are available for the production of shell material.

The hydrogen-ion concentration of shallows of Huron River was found by van der Schalie to range from 7.8 to 8.4. It was not less than 7.9 or

higher than 8.5 in the lakes above mentioned that were examined by the Institute for Fisheries Research, and for Muskegon River the pH was 7.6 to 7.8. A drop in pH much below 7.0 does not permit of pleurocerid life, to judge by studies made by C. S. Shoup in the Obey River in 1939. A fork of the stream showing pH readings above 7.0 was extensively colonized by these mollusks. In another fork the average of five tests was 6.1, one of its tributaries indicated a pH of only 2.6. This fork was barren of Pleuroceridae (Goodrich, 1940*a*).

Wiebe (1926) remarked the migration of *livescens* back and forth as waves of Lake Erie were of moderate force or turbulent. There are other movements which can be called migratory. As winter advances there is a seasonal retreat from positions near the water surface to deeper situations; some details of this will be given later. There is also sometimes retreat from high temperatures. On three occasions in midsummer, snails were found crowded together under boulders in the Huron River, while, at the same time, few were seen on the tops of the stones. The same thing has been observed in the lower Wabash River in Indiana and in small streams of Kentucky; this movement is apparently a general pleurocerid habit. That even in the course of a few hours the mollusks may move a few feet is shown by the tracks in the silt on stones and in the mud and sand of beach pools. The general absence of *livescens* near stream borders during periods of high water indicates its tendency toward quiescence similar to that on exposed parts of the Great Lakes, but that a few have been found at flood margins and others have been left stranded after recession of the water levels is proof that an occasional individual adventures out of depths to which the mass of the colonies keep. At one time in the upper Cumberland River while the stream was high about a dozen pleurocerids were obtained by feeling along the bank in the discolored water. In a low-water period and at the same spot, the snails were seen in thousands.

Frequently, shells taken from sheltered positions are seen to have small streamers of algae. The attachment is seldom below the adolescent whorls. The filaments act in instances as entanglements, holding a snail to a single boulder or to a narrow space among aquatic weeds, restricting even the limited migration of which it is capable. Inasmuch as *G. livescens* has been discovered on four species of the vegetation in Van Ettan Lake, Iosco County, Michigan, there is, seemingly, no choice as to habitat except as the requisite food is present.

The lowest water temperature at which the snails have been seen on the upper sides of stones in the Huron River drainage basin is 5° C. That the seasonal quiescence was approaching seemed proved by the absence of the tracks which mark movement or feeding in silt and algae. Colonies, apparently of normal size, were observed at water temperatures of 6.1° to 6.6° C.

By the time the next observation was made, the temperature had dropped to 1.1° C., registered in the Huron River at two localities on December 8, 1942. The mollusks had disappeared. Hibernation is under stones in water too fast to freeze, as noted by myself in the Huron River at Delhi, or in gravel and sand, as remarked by Leo Jackowski in the Huron River at Ann Arbor. A winter visit to rapids of the lower Maumee River several years ago disclosed no living goniobases on the upper surfaces of the rocks, but many hundreds were crowded together in joints of the limestone; the apertures were tightly closed by the opercula and over the shells was a film of whitish material, which doubtless was gelatinous algae. The earliest spring date at which the shells have been seen in what may be called the active stage was May 1, 1943. The end of hibernation may have come much earlier, but could not be perceived with anything approaching exactness because of high waters and flood turbidity.

THE TAXONOMIC RECORD

Melania livescens Menke. *Synopsis Methodica Molluscorum,* Pyrmont (1830). Lake Erie, New York, "Communicavit am. Hoeninghaus." The name suggests that Menke's material had undergone the change, common in the Great Lakes, which appears to be an effect of sunlight and weathering. The description does not mention carinae; this would indicate Menke's specimens were beach worn. Tryon, in figuring *livescens,* showed the carinae, and thus his illustration does not conform to the description. It is probably not that of a Lake Erie shell.

Melania rufula Haldeman. *Monograph Limniades,* No. 2 (1841) : 3 of cover. Lake Pepin, now part of an artificial expansion of Cuyahoga River, near Kent, Portage County, Ohio, and probably once connected with the river by a small stream. In every likelihood, Haldeman received the specimens from Benjamin Tappan, founder of the town of Ravenna in Portage County, judge of a circuit court of common pleas and United States senator who "devoted his last years to an interest in mineralogy and conchology."

Melania Niagarensis Lea. *Proc. Amer. Phil. Soc.,* 2 (1841) : 12. Falls of Niagara. Lea said that his shells were obtained at the foot of the Falls. *G. livescens* of Niagara River is of several forms and is variously colored within a fairly narrow range; this unquestionably is due to varying ecological conditions. F. C. Baker (1920*b*) distinguished *niagarensis* "from the variety as found elsewhere in the persistence of the peripheral keel in the adult stage." This is not true of shells I have taken at the foot of the Falls, or of the ones taken by Lea, but may be of colonies elsewhere in the river. The retention of carinae or keels into adult life marks material dredged in deep water off Put-in-Bay in Lake Erie and of some specimens thrown on the beaches of the lake in Ottawa County, Ohio.

Melania bizonalis DeKay. *Nat. Hist. N. Y.,* Pt. 5 (1843): 91, Pl. 7, Fig. 140. Lake Champlain, New York. Considered a synonym of *G. virginica* (Gmelin) by Tryon (1873). Apparently, the Lake Champlain colonies mark the easternmost limit of the range of *livescens.*

Melania gemma DeKay. *Nat. Hist. N. Y.,* Pt. 5 (1843): 91, Pl. 7, Fig. 142. Mud Creek, Onondaga County, New York; Erie Canal. The description is of young individuals. The water of the creek connects with Lake Ontario, that of the canal with Lake Erie and Lake Ontario.

Melania inornata Anthony. *Proc. Boston Soc. Nat. Hist.,* 3 (1850): 360. Lorain County, Ohio. The county borders on Lake Erie, and all streams of the county have their discharges in the lake. Of the shell, Anthony said that "its pale, sutural region is perhaps the most obvious character." Even if obvious in the instance, the character is far from being specifically distinct.

Melania brevispira Anthony. *Proc. Boston Soc. Nat. Hist.,* 3 (1850): 361. Ohio. Specimens labeled by Anthony and in the collection of the University of Cincinnati are marked as coming from "Coasking" [Kokosing] River, Gambier, Ohio. The *Goniobasis* of the drainage basin is *livescens,* but the types, which are in the Museum of Comparative Zoology, are reduced to such simple terms that, lacking opercula, they might be taken either for this species or *G. semicarinata* (Say). Another lot from the same basin and named *brevispira* by Anthony, for a time in the Wetherby collection, is *livescens* without question. With the type lot, Anthony wrote: "New species det. while I was blind, by touch alone."

Melania napella Anthony. *Proc. Boston Soc. Nat. Hist.,* 3 (1850): 362. Ohio. An adolescent shell of pyramidal shape.

Melania cuspidata Anthony. *Proc. Boston Soc. Nat. Hist.,* 3 (1850): 362. Maumee River, Ohio. Distinguished by Anthony from *napella* by being "much more elongated."

Melania elata Anthony. *Proc. Boston Soc. Nat. Hist.,* 3 (1850): 362. Maumee River, Ohio. A "thin, gracile, elongate" form, such as occurs in quiet water rather than in rapids.

? *Melania varicosa* Haldeman. *Monograph Limniades,* No. 3 (1854): 3 of cover. Ohio. "Allied to . . . *M. exilis.* It may prove to be a variety of *M. rufula,* Hald." Types not seen. Tryon's figure of the mollusk is suggestive of *livescens* rather than of *semicarinata,* the other Ohio species of *Goniobasis.*

? *Melania tecta* Anthony. *Ann. Lyc. Nat. Hist. N. Y.,* 6 (1854): 105, Pl. 3, Fig. 4. Ohio. The three types are broken shells, having the texture of *livescens.* An author's example in the Academy of Natural Sciences of Philadelphia, also from Ohio, is *livescens.*

Melania cubicoides Anthony. *Proc. Acad. Nat. Sci. Phila.,* 12 (1860):

60. Wabash River, Indiana. The juvenile carinae have been carried into adult life as a keel. Not infrequent in individuals of the upper Wabash River, but apparently not involving entire colonies.

Melania occulta Anthony. *Proc. Acad. Nat. Sci. Phila.,* 12 (1860) : 5. Wisconsin. ". . . apparently referable to the river form [of livescens], which appears to be rather restricted in its distribution" (F. C. Baker, 1928).

Melania correcta Brot. *Catalogue systématique famille des Mélaniens* (Geneva, 1862), p. 39. A name proposed as substitute for *M. cuspidata* Anthony, preoccupied. F. C. Baker (1928) has employed *correcta* as a subspecies of *livescens,* applying particularly to "a small river form."

Goniobasis Grosvernorii Lea (in part). *Proc. Acad. Nat. Sci. Phila.,* 14 (1862) : 263. Lea named two localities, Fox River, Illinois, one specimen; Quincy, Ohio, "about a dozen specimens." The Fox River shell is *livescens,* the other shells are *semicarinata* (Say).

Goniobasis lithasiodes Lea. *Proc. Acad. Nat. Sci. Phila.,* 15 (1863) : 154. Changed by Lea in the same year to *G. lithasioides.* Named for a single specimen from Ohio the columella of which is more thickened than usual. Otherwise, the type has the characters common in *livescens.*

Goniobasis Milesii Lea. *Proc. Acad. Nat. Sci. Phila.,* 15 (1863) : 154. Tuscola County, Michigan. Named for Manly Miles, state zoologist of Michigan. One of the stream forms of *livescens.*

Goniobasis translucens Anthony. *Amer. Journ. Conchol.,* 1 (1865) : 36, Pl. 1, Figs. 1, 2. Canada. ". . . distinguished by its coloration and thin texture from *G. livescens,* which it otherwise greatly resembles" (Anthony).

Goniobasis columbiensis Whiteaves. *Nautilus,* 19 (1905) : 61–2, Pl. 2, Figs. 11, 12. Assigned by error to headwaters of the Columbia River, British Columbia. Paratypes that I have seen are identical in shell characters and opercula with *livescens* of Lake Erie.

Goniobasis livescens michiganensis F. C. Baker. *Wis. Acad. Sci.,* Pt. 1 (1928) : 183–84, Pl. 9, Figs. 27–32. "Lake Michigan shore, east of Sturgeon Bay, north of Ship Canal, Door Co." The name was put forth for the "Great Lake form of *livescens,* characterized by a bulbous body whorl, a wider spire, and thick shell and lip." The studies of Wiebe of Lake Erie *Goniobasis* indicate that variations in shell form represent adaptions to ecological conditions rather than true subspecific modifications. Baker found the animal and radula "as in typical form."

Goniobasis livescens barronensis F. C. Baker. *Wis. Acad. Sci.,* Pt. 1 1928) : 186–87, Pl. 9, Figs. 33–36. Red Cedar River, Barron County, Wisconsin. Apparently corresponds with flat-whorled forms of *livescens* occurring in a few places on the west side of the Lower Peninsula of Michigan.

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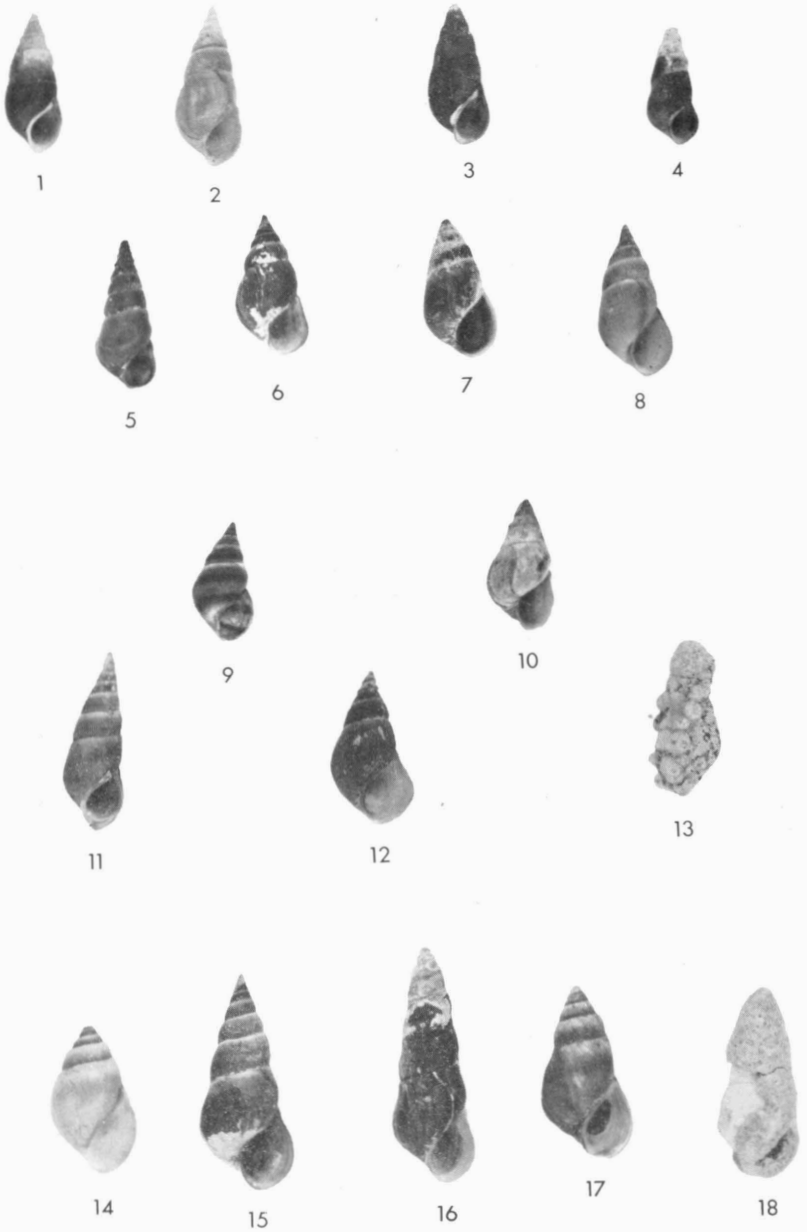
PLATE I

Variations in *Goniobasis livescens* in Michigan. All figures are natural size.

FIG. 1. Crystal Lake, Beulah, Benzie County.
FIG. 2. Lake Huron, Stony Island, Saginaw Bay, Huron County.
FIG. 3. Lake Michigan, Ludington, Mason County.
FIG. 4. Sink Lake, south of Hamilton, Allegan County.
FIG. 5. Round Lake, Emmet County.
FIG. 6. Cass River, three miles east of Frankenmuth, in Tuscola County.
FIG. 7. Lake Michigan, Grand Traverse Bay, Grand Traverse County.
FIG. 8. Lake Erie, La Plaisance Bay, La Salle Township, Monroe County.
FIG. 9. Looking Glass River, two miles southwest of DeWitt, Clinton County.
FIG. 10. Little Black Lake, Muskgeon County.
FIG. 11. Lake St. Clair, New Baltimore, Macomb County.
FIG. 12. River Raisin, one mile above Monroe, Monroe County.
FIG. 13. Bass Lake, Mason County. Calcareous deposit irregularly nodulous, friable.
FIG. 14. Lake St. Clair, Grosse Pointe, Wayne County.
FIG. 15. North Barr Lake, three miles north of Empire, Leelanau County.
FIG. 16. Side channel of St. Clair Flats, St. Clair County.
FIG. 17. Grand River, Grand Rapids, Kent County.
FIG. 18. Baseline Lake, Washtenaw County. Calcareous deposit even, smooth, and coherent.

PLATE I



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