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Distributional Features of Naiades in Tributaries of Lake Erie.

DR. A. E. ORTMANN.

The Naiad-fauna of Lake Erie is a glacial-postglacial offshoot of the Mississippi-Ohio-fauna, which has come chiefly by way of the Wabash-Maumee-route. This has been pointed out repeatedly (Ortmann, '12 p. 146; Walker, '13 p. 18, 58.) Some of the species are fully identical, but in other cases, Lake Erie proper contains more or less different forms, which, however, clearly take the place of the Ohio-types.

But one striking additional fact has been observed. The species of the Ohio, represented in the lake by different forms, generally present, in the tributaries of the lake, the common Ohio-phase, although this is not always the case. This fact has been commented upon by Walker ('13 p. 19), but he used it only in connection with the demonstration, that there are no pre-glacial relics in the lake basin. The present writer ('19) has pointed out several such cases*, and also Grier ('19 p. 163, 164) incidentally mentions this fact, although he does not take up this question in detail.

Several explanations have been suggested. (1) The one, that the types of shells of the lake tributaries identical with Ohio-types, are pre-glacial, has been finally disposed of by Walker. (2) Another suggestion is, that these forms, chiefly those of the southern tributaries of the lake, might have crossed over the divide from the tributaries of the upper Ohio (by stream-piracy or modern canals.) This has been hinted at by myself, ('19 p. 103),

* *Fusconaia flava*, p. 25; *Amblema costata*, p. 33; *Elliptio dilatatus*, p. 103; *Lasmigona costata*, p. 132; *Ligumia recta latissima*, p. 279; *Lampsilis siliquoidea*, p. 291; *Lampsilis ovata ventricosa*, p. 306.

but I was unable to find positive evidence for it. As will be shown below, this possibility *is positively excluded in certain cases, and surely does not apply in the case of northern and western tributaries of the lake.* (3) A third assumption is that these forms, having reached the lake by the Maumee route, and having changed in the lake, ascended then from the lake into the tributaries, and assumed again the identical characters which they had, when living in the upper Ohio. This idea has been indicated by myself ('19 p. 25, 33, 132), but it is hard to imagine, that in every tributary, into which one of these lake forms went, it always returned precisely to the ancestral Ohio form. Below we shall become acquainted with at least two cases, where *this assumption is positively excluded*, because the forms concerned are not at all found in the lake.

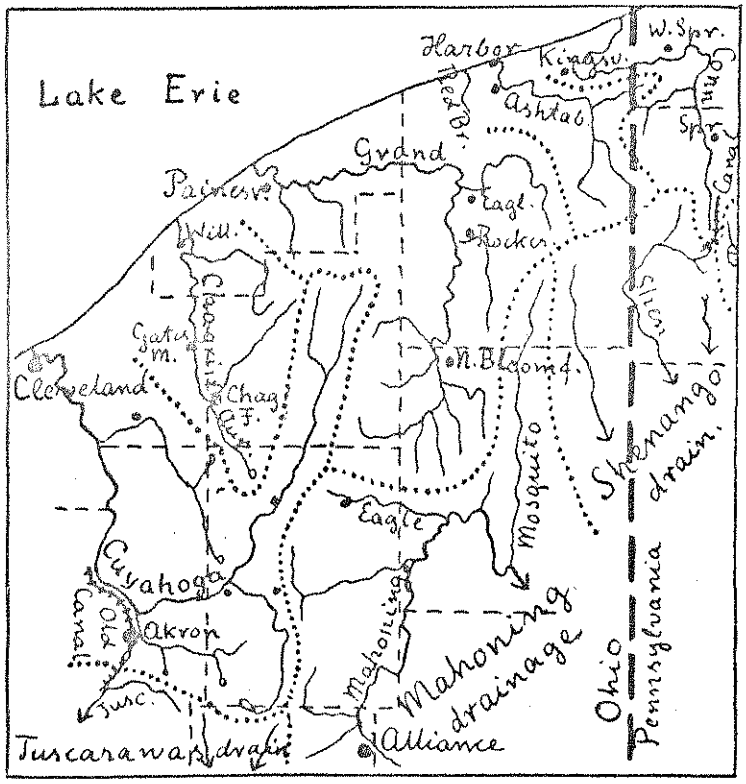
Thus there are objections to the assumption that any one of the above explanations is to be regarded as a *general* distributional law, and we are to look for another theory to which all of these cases might submit. And indeed, there is one, which has never been advanced. It is suggested by the *geological history* of the Lake Erie basin, and the present paper is written with the purpose to show, that there is another explanation, which *in several cases is the only possible one*, but which also can be applied very naturally to all other cases, although in some of them also the second idea, mentioned above, (crossing of the divide from the South) might be introduced as an additional possibility.

The new explanation entered my mind, when I explored certain tributaries of Lake Erie in northeastern Ohio and northwestern Pennsylvania, the basins of Chagrin River, Grand River, and Conneaut Creek (no Naiades were found in Ashtabula River.) Chiefly Grand River proved to be interesting for several reasons: it possesses a rather rich fauna; was never connected with the upper Ohio drainage by a canal; and, finally, it was found, that several Naiades present in this river could not have found their way into it by having been transferred from the upper Ohio drainage by stream piracy, simply because they are not present in this part of the Ohio drainage.

In order to present all the facts at my disposal, I first give

a list of my own (and previous) distributional records. (See: map fig. 1.)

Fig. 1.



TRIBUTARIES OF LAKE ERIE IN N. E. OHIO.

CHAGRIN RIVER. (Lower part polluted by paper mill at Chagrin Falls.)

1. Ch. R., Willoughby, Lake Co., O. (Sept. 10, '20.)
   Lampsilis siliquoidea (Barn.) · *Lampsilis ovata ventricosa (Barn.)*
2. Ch. R., Cuyahoga Co., O. (Hartman coll.)
   Lampsilis ovata ventricosa (Barn.)
3. Ch. R., Gates Mill, Cuyahoga Co., O. (seen, Sept. 9, '20.)
   Lasmigona costata (Raf.) *Lampsilis ovata ventricosa (Barn.)*
4. Ch. R., below Chagrin Falls, Cuyahoga Co., O. (seen, Sept. 8, '20.)
   Lampsilis siliquoidea (Barn.)
5. Ch. R., Russell Twp., Geauga Co., O. (above falls) (Sept. 8, '20.)

Lasmigona compressa (*Lea*)
Lasmigona costata (*Raf.*)
Anodonta grandis Say
Anodontoides ferussacianus (*Lea.*)
Strophitus rugosus (*Swains.*)

6. Aurora Branch, Chagrin Falls, Cuyahoga Co., O. (Sept. 8, '20.)
Lasmigona compressa (*Lea*)

GRAND RIVER. (Everywhere in good condition, without any pollution.)

1. Painesville, Lake Co., O. (Sept. 11, '20.)

Fusconaia flava (*Raf.*)
Amblema costata Raf.
Pleurobema cordatum coccineum (*Conr.*)
Elliptio dilatatus (*Raf.*)
Lasmigona costata (*Raf.*)
Alasmidonta marginata (*Say*)
Strophitus rugosus (*Swains.*)
Ptychobranchus fasciolare (*Raf.*)
Obovaria subrotunda lens (*Lea*)
Actinonaias carinata (*Barn.*)
Proptera alata (*Say*)
Micromya iris novi-eboraci (*Lea*)
Ligumia recta latissima (*Raf.*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

Of these, *Strophitus rugosus* and *Lampsilis ovata ventricosa* have been mentioned before from the same place by Simpson (in: Kirsch, '95.) The Carnegie Museum possesses *Actinonaias carinata* also from the Sterki collection.

2. Eaglesville, Ashtabula Co., O. (Sept. 16, '19.)

Fusconaia flava (*Raf.*)
Amblema costata Raf.
Pleurobema cordatum coccineum (*Conr.*) (seen)
Elliptio dilatatus (*Raf.*)
Elliptio complanatus (*Dillw.*)
Lasmigona costata (*Raf.*)
Anodonta grandis Say
Ptychobranchus fasciolare (*Raf.*)
Obovaria subrotunda lens (*Lea*)
Micromya iris novi-eboraci (*Lea*)
Ligumia recta latissima (*Raf.*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

3. Rockcreek, Ashtabula Co., O. (Sept. 8, '19.)

Fusconaia flava (*Raf.*)
Amblema costata Raf.
Elliptio dilatatus (*Raf.*)
Lasmigona costata (*Raf.*)
Anodonta grandis Say
Ptychobranchus fasciolare (*Raf.*)
Obovaria subrotunda lens (*Lea*)
Actinonaias carinata (*Barn.*)
Micromya iris novi-eboraci (*Lea*)
Ligumia recta latissima (*Raf.*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

4. North Bloomfield, Trumbull Co., O. (Sept. 17, '19.)

Fusconaia flava (*Raf.*)
Amblema costata Raf.
Pleurobema cordatum coccineum (*Conr.*)
Elliptio dilatatus (*Raf.*)
Lasmigona costata (*Raf.*)
Obovaria subrotunda lens (*Lea*)
Micromya iris novi-eboraci (*Lea*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

In addition, Call ('85 p. 9) gives *Anodontoides ferussacianus buchanensis* (*Lea*) from Grand River, and Sterki ('07 p. 394) mentioned this under the varietal name of *subcylindracea* (*Lea*). This form is hardly different from the normal *A. ferussacianus*.

RED BROOK, 3 m West of Harbor, Ashtabula Co., O. (Sept. 13, '20.)
(A very small stream; shells found dead within a mile from the lake.)

Lasmigona compressa (*Lea*) *Anodontoides ferussacianus* (*Lea*)

CONNEAUT CREEK (in good condition for its whole length.)

1. Kingsville, Ashtabula Co., O. (Sept 12, '20.)

Pleurobema cordatum coccineum (*Conr.*)
Lasmigona compressa (*Lea*)
Lasmigona costata (*Raf.*)
Anodontoides ferussacianus (*Lea*)
Alasmidonta marginata (*Say*)
Strophitus rugosus (*Swains.*)
Ptychobranchus fasciolare (*Raf.*)
Micromya iris novi-eboraci (*Lea*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

2. West Springfield, Erie Co., Pa. (May 23, '09) (published in '19.)

Pleurobema cordatum coccineum (*Conr.*)
Elliptio dilatatus (*Raf.*)
Lasmigona compressa (*Lea*)
Anodonta grandis Say
Anodontoides ferussacianus (*Lea*)
Alasmidonta marginata (*Say*)
Strophitus rugosus (*Swains.*)
Ptychobranchus fasciolare (*Raf.*)
Micromya iris novi-eboraci (*Lea*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

3. Springboro, Crawford Co., Pa. (June 4, '08) (published in '19.)

Pleurobema cordatum coccineum (*Conr.*)
Strophitus rugosus (*Swains.*)
Lampsilis siliquoidea (*Barn.*)
Lampsilis ovata ventricosa (*Barn.*)

The Naiad-fauna of these streams consist of 19 species, and is rather uniform, with the qualification, that the largest (Grand River) contains more species than any of the others. Grand River has 6 species not found in the others (*Fusconaia flava, Amblema costata, Elliptio complanatus, Obovaria subrotunda lens, Actinonaias carinata, Proptera alata.*) Two species found in other streams (*Lasmigona compressa* and *Anodontoides ferussacianus*) have not been found recently in the Grand (the latter, however, has been reported by Call), but they apparently have been missed by myself only by accident. Since these two species are unimportant for our present purpose, we may safely take the *Grand River fauna as typical for this region,* and restrict our further discussion chiefly to this river.

Of the shells found here the following are found in the Ohio drainage, but differ more or less from the lake- in most cases, different names are in use, as indicated ow (see: Grier, '18, Ortman, '19, Grier, '19.)

In Grand and Ohio	In the lake
1. *Fusconaia flava* (*Raf.*)	*Fusconaia flava parvula Grier*
2. *Amblema costata Raf.*	*Amblema plicata* (*Say*)
3. *Pleurobema cordatum coccineum* (*Conr.*)	*Pleurobema cordatum pauperculum* (*Simp.*)
4. *Elliptio dilatatus* (*Raf.*)	*Elliptio dilatatus sterkii Grier*
5. *Lasmigona costata* (*Raf.*)	*Lasmigona costata erigaensis Grier*
6. *Strophitus rugosus* (*Swains.*)	*A dwarf form* (Ortmann, '19 p. 200)
7. *Ptychobranchus fasciolare* (*Raf.*)	*A dwarf, humped form* (Ortmann, '19 p. 210)
8. *Obovaria subrotunda lens* (*Lea*)	*Obovaria subrotunda leibi* (*Lea*)
9. *Proptera alata* (*Say*)	*A smaller, more swollen form* (Ortmann, '19 p. 254 and Grier, '19 p. 165)
10. *Ligumia recta latissima* (*Raf.*)	*Ligumia recta* (*Lam.*)
11. *Lampsilis siliquoidea* (*Barn.*)	*Lampsilis siliqoidea rosacea* (*DeKay*)
12. *Lampsilis ovata ventricosa* (*Barn.*)	*Lampsilis ovata canadensis* (*Lea*)

Thus it is seen, that in over half of the cases (12 out of 19) the fact is established, which has been indicated in the beginning: *that the Naiades of the Lake Erie tributaries resemble those of the Ohio drainage more closely than those of the lake itself.*

The other species of Grand River have the following distribution and affinities.

13. *Alasmidonta marginata* (*Say*) 14. *Actinonaias carinata* (*Barn.*)

Both are species found in the identical form in the upper Ohio drainage, and are present in other tributaries of the lake; but in the lake itself they are absolutely missing. For our further studies, these two species will be very important.

15. *Micromya iris novi-eboraci* (*Lea*) (see: Ortmann, '19 p. 270.)

This species stands by itself. It is characteristic for the lake-drainage from New York to Michigan, both in Lake Erie and its tributaries, but it is not found in the upper Ohio drainage, where its place is taken by the typical *Micromya iris* (*Lea*). We have here a case of an identical form in the lake and its tributaries, but different from the Ohio-form.

16. *Lasmigona compressa* (*Lea*)

This is found in the upper Ohio drainage, in tributaries of the lake, and in the lake proper. Its value for distributional

studies is thus doubtful. But the fact that it is extremely rare in the lake (only 2 specimens ever recorded, one from Presque Isle, Pa., the other from Sandusky Bay, O.,) approaches this species to those which are not in the lake (Nos. 13 and 14 above.) It has the appearance, as if this species abundant and flourishing in tributaries and small streams in general, does not take kindly to the lake-environment.

17. *Elliptio complanatus* (*Dillw.*)

This is an abnormal case. It is an Atlantic species, not found in the upper Ohio and not elsewhere in the Erie drainage. I shall discuss this case at the end.

18. *Anodonta grandis Say* 19. *Anodontoides ferussacianus* (*Lea*)

These will be left out of consideration. Although in both the lake-form is somewhat different from that of the tributaries, and although the latter again generally resembles the Ohio-form, the various forms are not strictly separated along these lines. *Anodonta grandis footiana* (Lea), the lake-form, has been frequently reported from the Ohio-drainage, and in *Anodontoides* the same condition apparently prevails; but in this case the forms require further investigation, the var. *buchanensis Lea,* generally attributed to the lake, probably having been misunderstood.

THE THEORY OF THE CROSSING OVER THE DIVIDE.

(See: map fig.1)

There has never been a canal connecting the headwaters of Grand River with the Ohio system. This is true also of Chagrin River, but is different in the case of Conneaut Creek, where the headwaters come into contact with those of the upper Beaver (Shenango) River and French Creek (tributaries to Ohio, respective Allegheny.) This region was traversed by the old Beaver Canal, and I have suggested ('19) the possibility, that Conneaut Creek might have received some of its shells by this route (from Shenango River in Pennsylvania.) But since the species, which might have taken this route (*Pleurobema cordatum coccineum, Elliptio dilatatus, Lasmigona costata, Alasmidonta marginata, Strophitus rugosus, Ptychobranchus fasciolare, Lampsilis siliquoidea, Lampsilis ovata ven-*

tricosa) are not peculiar to this system, and possess all a rather general distribution, being also found in Grand River, where there was no canal, *this way of migration is for Grand River excluded*, although it should be admitted as a possibility for Conneaut Creek.

The canal-theory deserves more consideration in the case of Cuyahoga River, the next tributary of the lake to the West of Chagrin River. This was connected by a canal with the Tuscarawas-Muskingum system of the Ohio. In Cuyahoga River there is at least one species of the Tuscarawas drainage, *Lasmigona complanata* (*Barn.*), which is not found in the lake, and just this species favors the canal-environment.*

The headwaters of Grand River closely interlock with that of the Beaver drainage, in fact, they are almost surrounded by it (Mosquito and Eagle Creeks, tributaries to Mahoning River), with the exception of the western side, where they come into contact with the headwaters of Cuyahoga River.

The upper Cuyahoga has a history of its own, and probably a rather complex one. It might once have belonged to the Tuscarawas drainage (Newberry, '73 pp. 204, 205); but the heavy, stratified gravels between the bend of the Cuyahoga and the Tuscarawas (near Akron) are considered glacial outwash by others (Leverett, '02, passim, and map. pl. 15.) There also might have existed here a large glacial lake, connected at different times toward the South and toward the North. For this reason it seems well to consider also this river in the following studies.

The Naiad-fauna of these rivers (Cuyahoga, Tuscarawas, and Mahoning) is well known† and of the shells mentioned above, the following distributional facts should be emphasized.

1. *Fusconaia flava.*—Missing in the whole Beaver (Shenango and Mahoning) drainage (Ortmann, '19 p. 17), but present in the uppermost Tuscarawas, near Akron; not in the upper Cuyahoga.

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*The Cuyahoga fauna has other peculiarities, which deserve special discussion, but I cannot go into detail here. Some of the facts will be alluded to below.

†See: Dean, '90, Sterki, '07, and my own collections, partially published in '19.

2. *Actinonaias carinata.*—Missing in the upper Mahoning (Ohio part of it), and in the Shenango above Sharon, Pa. (Dean, '90, Ortmann, '19 p. 236); present in the Tuscarawas, but not in the headwaters above New Philadelphia (Sterki collection in Carnegie Museum); not in upper Cuyahoga.

3. *Proptera alata.*—Missing in the whole Beaver drainage (Ortmann, '19 p. 256), missing in the Tuscarawas (Sterki, '07 p. 393), and missing in upper Cuyahoga.

4. *Ligumia recta latissima.*—Missing in the Beaver drainage (Ortmann, '19 p. 280); present in Tuscarawas, but not in the upper part (above New Philadelphia) (Sterki collection); not in upper Cuyahoga.

Thus these 4 species are not found in that part of the Ohio-drainage which comes into contact with Grand River, and they are also absent in the upper Cuyahoga. For these, at least, the assumption of a crossing of the divide by stream-capture is positively excluded.

For the other species the following facts of distribution have been ascertained.

The following species are found in the upper Mahoning, upper Tuscarawas, but not in the upper Cuyahoga:

1. *Amblema costata*
2. *Pleurobema cordatum coccineum*
3. *Elliptio dilatatus*
4. *Lasmigona costata*
5. *Alasmidonta marginata*
6. *Ptychobranchus fasciolare*
7. *Obovaria subrotunda lens*
8. *Lampsilis ovata ventricosa*

Two more species are in all three systems:

Strophitus rugosus — *Lampsilis siliquoidea*

The possibility must be granted that these last 10 species might have come into Grand River from the adjoining Ohio-tributaries, presumably by stream capture. However, in 8 of them, the upper Cuyahoga (if it ever was a tributary of the Tuscarawas) is excluded, and only in the last 2 species this latter river might come into question. But these two species are of such a general distribution, that they do not furnish any conclusive argument. The other 8 species, if they have

come from the South, could have come only from the Mahoning system.*

Although there are 8 cases, which would admit the theory that shells have been transferred from the upper Mahoning into Grand River by stream capture, there are 4 others, which are positively opposed to it. Moreover, there is no physiographical evidence for stream capture in this region. The divides are all ill-defined here, and, although a mingling of the waters is possible (and actually present at certain points), this concerns extremely small streams, into which no Naiades have advanced.

In order to support this conclusion, I may be permitted to introduce here the evidence furnished by the distribution of certain crayfishes (genus *Cambarus*). These creatures advance much farther toward the headwaters, than the Naiades, nevertheless their evidence is distinctly opposed to the theory that they have crossed the divide.

Grand River possesses the species *Cambarus propinquus Gir.*, characteristic for Lake Erie and many of its tributaries (also farther North and West), and this species is also in Ashtabula River and Chagrin River. The upper Mahoning River

*It might be interesting to say a few words about the upper Cuyahoga fauna. This consists of the following species (Dean, '90; Sterki and Ortmann collections in Carnegie Museum.)

Lasmigona compressa (Lea)	*Anodontoides ferussacianus (Lea)*
Lasmigona costata (Raf.)	*Strophitus rugosus (Swains.)*
Anodonta grandis Say	*Ligumia nasuta (Say)*
Anodonta imbecillis Say	*Lampsilis siliquoidea (Barn.)*

There is no evidence in this fauna for the former connection of the upper Cuyahoga with the Tuscarawas. The presence of *Anodonta imbecillis*, which is a form also found in the Tuscarawas, preferring lake and canal environment, cannot be introduced in favor of this assumption, for this species has a rather erratic range (also in Lake Erie basin.) *Ligumia nasuta*, a characteristic form of the lake, is a very peculiar type of shell in this region; it also is a typical lake-dweller. It is found nowhere else in northern Ohio in tributaries of the lake (except some very small and sluggish ones close to the lake in the vicinity of Toledo), and is also absent in the Maumee River. Possibly both species, *Anodonta imbecillis* and *Ligumia nasuta* are remnants of the fauna of a lake of good size (mentioned above), which once existed in this region, and was connected with Lake Erie by the lower Cuyahoga.

(as well as the whole Beaver drainage) has *Cambarus obscurus Hag.*, the form of the uppermost Ohio-drainage (including Allegheny and Monongahela.) In Conneaut Creek, both species are found, and here we may take it for granted, that the old Beaver-canal has acted.

From the Cuyahoga, the lake species (*C. propinquus*) has not been reported (but it is in Rocky River, a little to the West): however, it may turn up here yet. In the upper parts of this drainage, in the Cuyahoga and its tributaries, as well as in several lakes, I found only *Cambarus propinquus sanborni* (*Fax.*), the form of the Tuscarawas and Muskingum Rivers: this surely indicates a closer connection of the upper Cuyahoga and the Tuscarawas, but it remains doubtful, whether this is due to old drainage-features, or to the modern canal.

This much is sure, that by the evidence furnished by both the Mussels and the Crayfishes of Grand River no stream piracy is probable in this region, and that there are cases which positively speak against it.

Of the four species of Naides, which could not have come from the Mahoning, none is found in Lake Erie. *Actinonaias carinata* is altogether missing there, and the three others (*Fusconaia flava, Proptera alata, Ligumia recta latissima*) are represented by more or less distinct forms. Yet all of these are present in other tributaries of the lake. Disregarding the Maumee (in which all four are present), but which is supposed to have been the route of immigration of all Ohio-types, we have them in the following rivers: Grand River in Ontario (all except *Ligumia*); lower Cuyahoga (all, but *Fusconaia* might have come from the Tuscarawas, which is excluded in the other three); Vermilion River (only *Proptera*); Sandusky River (all four); Raisin River, Mich. (*Fusconaia* and *Actinonaias*); Huron River, Mich. (*Actinonaias* and *Ligumia.*) In the cases of Grand River, Ont., Raisin and Huron Rivers, Mich, the argument also holds good, that these species could not have come from the Ohio drainage, since these systems do not come in contact with the latter.

This means that these four species, at present, have a *discontinuous distribution*, being found in a number of tribu-

taries of Lake Erie, but with the ranges separated by the body of the lake, and the same assumption, of course, is admissible, although not positively demonstrated, in all other cases here discussed. Thus a theory, which explains these four cases, also could be used in the others, although as an alternative it is not excluded, that they might have come across the divide from the upper Ohio at least in the state of Ohio.

Additional species which might fall under the same category with the above, and chiefly with *Actinonaias carinata*, are: *Alasmidonta marginata* (*Say*) and *Lampsilis fasciola Raf.* Both are not found in the lake. The former is in Grand R., Ont., in Raisin R., Mich., in Sandusky, Cuyahoga, Grand Rivers, O., and Conneaut Creek. The latter is known only from Raisin R., Mich., and Sundusky R., O. (both are in the Maumee.) Immigration into the tributaries of the lake in Ohio from the South is here also thinkable; but these species have the same *discontinuous* distribution in the lake tributaries, as the twelve mentioned above, and a theory explaining this discontinuity would also serve in their case.

It is clear, that such a theory should reconstruct a former connection of the now separated river-systems, a union of them into one system, to which they were tributaries.

THE NEW THEORY.

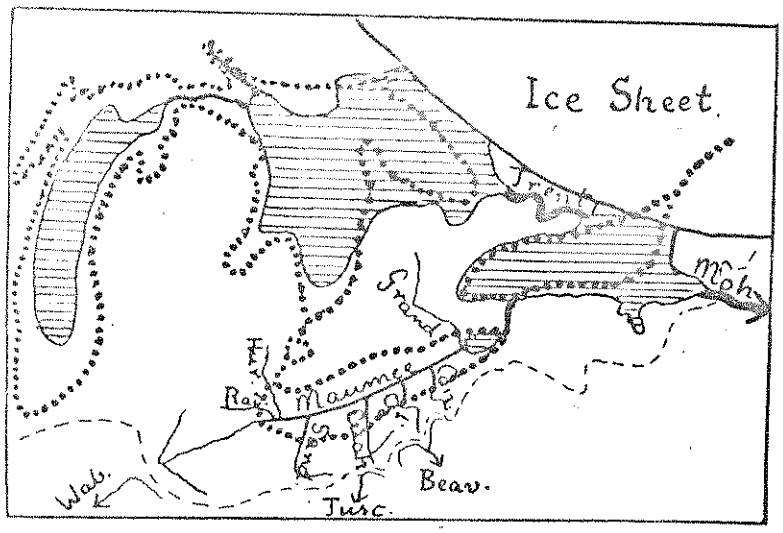
Turning to the glacial history of the lake, we find that indeed there was once such a drainage condition represented during the stages of the so called *Trent* and *Nipissing Outlets*, the former a little earlier, the latter a little later toward the end of the Glacial time. Both are characterized by the peculiarity, that the waters of the upper lakes (Superior, Michigan, Huron, at a certain time called Lake Algonquin) did not flow to Lake Erie (Detroit River route), but were flowing, in the Trent stage, from Georgian Bay of Lake Huron directly to Lake Ontario (Lake Iroquois), and, in the Nipissing stage, by way of Lake Nipissing to the lower St. Lawrence valley (at that time invaded by the Champlain Sea) (See map fig. 2)*

At this time, Lake Erie, at present a rather shallow body of

* See maps: Chamberlin & Salisbury, 3. '06 p. 401 fig. 521 and p. 404 fig. 522; also: Walker, '13 p. 44 fig. 4.

water, was practically dry, possibly only with a small remnant of a lake at its eastern end (near Buffalo), and, consequently, Maumee River, entering the basin at its western end, must have traversed it in the direction of its long axis, so that all the present tributaries of the lake (except possibly the most eastern ones) *must have been tributaries of this continuation of Maumee River.*

Fig. 2.



TRENT OUTLET STAGE OF GREAT LAKES.

Adapted from Walker, Naut. 27, 1913, p. 44 fig. 4.

Thus we obtain a system of connected rivers, an enlarged Maumee-system, collecting all the tributaries in which the Naiades here discussed are found, and this system had a continuous fauna, the Maumee fauna, which, as Walker has shown ('13) was mainly derived from the Wabash River, a tributary of the Ohio.

Later on, after the Trent and Nipissing Outlets were closed (the latter by a re-elevation of the continent in the North-East), the waters of the upper lakes were turned again, by way of Detroit River, into the Lake Erie basin, filling it up, and drowning the lower Maumee and the lower parts of its

tributaries. Only the upper parts of the latter persisted as rivers, becoming tributaries of the lake, and containing, up to the present time, the remnants of the once continuous fauna, now become *discontinuous*. In the new Lake Erie, the fauna either died out (*Actinonaias carinata, Alasmidonta marginata, Lampsilis fasciola*), or (in most cases) changed under the influence of the different lake environment, producing those forms, which we know now as the representative lake-forms of the original river-types.

Of course, we should expect the old Maumee-fauna best preserved in the present Maumee (upper part of Maumee of Trent-stage), and this is actually the case: all the species discussed here (and many additional Ohio-types) are found in the Maumee.*) But this requires no special discussion, since this river formed the highway along which the Ohio-fauna migrated into the Erie basin.

For the other tributaries of Lake Erie, however, we are justified in drawing the following conclusion. The fact, that they contain a number of Ohio-types, which are represented in the lake by different forms, or not at all, must be explained, in the Grand River of Ohio and in the Grand River of Ontario, and also in tributaries at the western end of the lake in Michigan, by the assumption *that these rivers were at a certain time tributaries of an old Maumee River, continued along the Erie basin*, which was dry. This was towards the end of the Glacial Period, at the stages in the development of the Great Lakes known as the *Trent and Nipissing Outlet stages*. This continuous and connected river-system was rendered discontinuous by the re-filling of Lake Erie in Post-Champlain time. In the rivers named, this assumption is *imperative*, because an immigration from the Ohio-system (other than by the Wabash-Maumee route) is excluded.

Furthermore, if this is correct, nothing prevents the assumption that also in other tributaries the same explanation holds good. There is, indeed, the possibility, that in other

* A remarkable exception is *Ligumia nasuta*, which is not in the Maumee; this species stands by itself. It is of western origin, but apparently has a history of its own, being possibly one of the oldest immigrants into the lake-basin.

rivers in the state of Ohio some faunal elements of the upper Ohio drainage may have reached the lake-tributaries by stream-piracy in the region of the headwaters. But such forms cannot be singled out, since they do not differ from those which used the Maumee-route. In addition, some forms may have reached the lake-basin in very recent times, coming from the upper Ohio by canals, as in the cases of Conneaut Creek and Cuyahoga River, but such cases seem to be very few (one has been indicated above.) The Miami-Maumee and the Wabash-Maumee canals of recent times may also have helped to introduce additional Ohio-types into the lake-basin, and, indeed, there are several species known, where this might be suspected. But this is outside of the scope of the present paper, and, moreover, it concerns the same region covered by the old Wabash-Maumee route of immigration.

THE CASES OF MICROMYA IRIS NOVI-EBORACI AND ELLIPTIO COMPLANATUS.

Of the shells which compose the fauna of Grand River, two additional cases require further discussion.

Micromya iris novi-eboraci is found in the lake, in the Maumee, and a number of the lake-tributaries, but it is not in the upper Ohio-drainage, being represented there by *Micromya iris* (*Lea.*) The lake-form is not distinguishable from the form of the tributaries. In this case we may assume, that the form *novi-eboraci* came in recent times from the Maume into the lake, and then ascended into the tributaries. But, of course, there is no objection to the assumption, that it also is a remnant of the Trent-Nipissing stage, but that here the form has not changed in the lake. A few additional, similar cases are known: *Quadrula pustulosa prasina* (*Conr.*) (represented in the upper Ohio by *Quadrula pustulosa* (*Lea*); *Dysnomia sulcata delicata* (*Simp.*) (not in upper Ohio); and the following species which, although present in the Ohio-drainage, are not found in the tributaries in northeastern Ohio and northwestern Pennsylvania: *Quadrula quadrula* (*Raf.*), *Obliquaria reflexa Raf.*, *Truncilla truncata Raf.*, *Truncilla donaciformis* (*Lea*). For all these the same holds good as for *Micromya iris novi-eboraci.*

Finally, *Ellipto complanatus* (*Dillw.*) in Grand River is an anomalous case. This is a common Atlantic species, missing in the whole interior basin. Yet I have found a single individual, and Sterki ('07 p. 393) has reported a single shell from the Tuscarawas drainage near New Philadelphia, O., (collected in 1898; the specimen is now in the Carnegie Museum.)

This species is known from the St. Lawrence and Lake Ontario along the Nipissing and Trent routes to northern Lake Huron and the eastern part of Lake Superior (see map given by Walker, '13 p. 30 fig. 2), but does not go thence southward into the southern part of Lake Huron, and has never been found in Lake Erie.

Walker ('13 p. 45) connects this range with the *Trent Outlet stage*, and thinks that this species came from the Mohawk Outlet of Lake Iroquois (Ontario) up the Trent River into Lake Huron. This undoubtedly is correct, and it should be added that another species took the same route: *Lampsilis radiata* (*Gmel.*) (often called *borealis Gray.*) It is found practically in the same region, from New York state and the St. Lawrence to Lake Huron in the Georgian Bay region, but it does not go farther West.

The occasional presence of *Elliptio complanatus* in Grand River, and even in the Tuscarawas, is very astonishing. The only explanation I can think of, is the following.

Since there is, apparently, no natural barrier to the dispersal of this species from Lake Huron southward into Lake Erie, *Elliptio complanatus might be expanding its range in this direction at the present time*, not only into Lake Erie, but also into some of its tributaries, for instance Grand and Cuyahoga Rivers, and from the latter it might have reached the Tuscarawas by the canal. But only the forerunners, occasional individuals, are arriving. They might be also in the lake, but have not yet been discovered. It would be interesting to watch the further progress of this colonization. Of course we know that here, as generally among mussels, the dispersal probably is by transport in the larval stage by fishes.

but what we know about this shell in this respect does not furnish any additional information.*)

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*) The fish-host of this species is not positively known. Lefevre & Curtis (Bull. Bur. Fish. 30. '12 p. 168) have succeeded in *artificially* infecting the Yellow Perch (*Perca flavescens*) with the glochidia of *Lampsilis complanatus*.