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DISTRIBUTION OF SPHAERHDAE (PELECYPODA) IN MICHIGAN, U. S. A. <sup>1</sup>

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ABSTRACT

About half of the 31 species (and forms) of sphaeriid clams now inhabiting Michigan are of a more or less general distribution in the state, while the remainder have a geomorphologically or ecologically restricted range. During the Pleistocene Epoch those sphaeriids present in the basin of the Mississippi River presumably colonized the Michigan region from the south, as did the unionid mussels, by upstream migration through the post-glacial streams that drained the enormous water bodies occupying the region of the present Great Lakes. The major routes of migration from the Mississippi drainage were: (1) into Michigan's Upper Peninsula, the Fox River Valley in eastern Wisconsin and (2) into the Lower Peninsula, the Illinois-Des Plaines channel, which drained glacial Lake Chicago (the southern basin of the present Lake Michigan) and the glacial Maumee River which drained glacial Lake Maumee (the basin of the present Lake Erie). The subsequent formation of the present Great Lakes, with new watersheds and an eastward drainage, interrupted the former confluences and created a discontinuous distribution by isolating some species and preventing the progress of others at different times and with varying effectiveness. A striking example of such an obstacle was the glacial Grand River whose course transected the area of the Lower Peninsula; after the southern part of that Peninsula had been repopulated with sphaeriids, it effectively blocked the northward spread of three species: *Pisidium cruciatum*, *P. punctiferum* and *Sphaerium transversum*. Likewise, this stream formed the southern boundary for *P. insigne*, which did not enter the Peninsula directly from the south, but from the north by more devious routes. The glacial Grand River later divided into two streams running in opposite directions, the present easterly-flowing Saginaw River and the present westerly-flowing Grand River, before *P. cruciatum* and *P. punctiferum* could enter the Saginaw drainage from the west.

The distribution, restricted largely to the Great Lakes bordering the state, of *P. conventus*, *P. idahoense* and *S. nitidum*, which are species of deep and cold waters, can be explained on an ecological basis; that of *P. henslowanum*, *P. amnicum* and *S. corneum* which are restricted to the Great Lakes and their downstream drainage, by their probably only recent importation from Europe. The immediate causes for the localized occurrence of various other species or forms are, however, less apparent.

In general it is believed that both active migration during periods of alternate flooding and low water levels, which ultimately disrupted previous confluences, as well as passive transportation, partly in these waterways by other aquatic animals such as crayfishes, frogs and fishes, partly overland by aquatic birds, have obscured the original distribution of many of the sphaeriids in the inland waters of Michigan. The patterns of original distribution are still clearly evident only for *P. cruciatum*, *P. punctiferum* and *S. transversum*, while they are partially masked in *P. fallax*, *P. insigne*, *P. obtusale*, *P. walkeri* and *S. fabale*.

INTRODUCTION

At present all of the streams of the six principal watersheds in the two peninsulas of the State of Michigan belong to the Great Lakes - St. Lawrence River

drainage system. These watersheds comprise Upper (Northern) Peninsula streams flowing into (1) Lake Superior and (2) Lake Michigan, and Lower (Southern) Peninsula streams draining into (3) Lake Michigan, (4) Lake Huron, (5) the St. Clair River,

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Lake St. Clair, and the Detroit River, and (6) Lake Erie. The present account of the sphaeriids inhabiting Michigan is based primarily on the nearly 5000 lots in the collections in the Museum of Zoology, University of Michigan (UMMZ) from the major streams (Table 1) and their connected lakes in these watersheds.

The extensive list of 73 species and 36 varieties of fingernail (*Sphaerium*, including *Musculium*) and pill clams (*Pisidium*) recorded for Michigan by Winslow (1926) reflects the redundant taxonomy developed by Victor Sterki (1916). The present report reduces that list to 32 species and primarily follows the specific nomenclature of H. B. Herrington (1962); his assistance with identifications is gratefully acknowledged. In addition to good species several common "forms" are mentioned. These are at present considered to be ecological, but since they are incompletely known they are included here in the event that some of them might be raised to subspecific or even specific rank in the future. The generic and sub-generic classification of the Sphaeriidae presented here is that which is currently accepted by most malacologists. However, this classification is much in need of critical re-evaluation and will be the subject of a future report.

#### SYSTEMATIC POSITION OF SPECIES AND THEIR DISTRIBUTION

##### *Species and Habitats*

Subfamily Pisidiinae F. C. Baker, 1927  
Genus *Pisidium* C. Pfeiffer, 1821

Only the anal siphon developed, the branchial siphon either rudimentary or represented by a mantle cleft; shell inequipartite: anterior end of shell longer than posterior end; beaks occasionally terminal.

Subgenus *Neopisidium* Odhner, 1921<sup>3</sup>

Complete absence of branchial siphon and of posterior gills; dorsal loop or lobe of the

TABLE 1. Major streams in the six watersheds of Michigan

WATERSHED	MAJOR STREAMS
UPPER PENINSULA	
Lake Superior	Ontonagon River Sturgeon River Tahquamenon River
Lake Michigan	Menominee River Ford River Escanaba River Manistique River
LOWER PENINSULA	
Lake Michigan	Manistee River Muskegon River Grand River Kalamazoo River St. Joseph River
Lake Huron	Cheboygan River Thunder Bay River Au Sable River Saginaw River
St. Clair River Lake St. Clair Detroit River	Black River Belle River Clinton River River Rouge
Lake Erie	Huron River River Raisin St. Joseph River of the Maumee River

nephridia united; constant retention of juvenile characters.

*Pisidium conventus* Clessin. The circumpolar *P. conventus* (= *abyssorum* Sterki) occurs in the Great Lakes (Lakes Superior, Michigan, and Ontario; Heard, 1962) and in the deep cold lakes of Isle Royale, an island in Lake Superior.

*Pisidium cruciatum* Sterki (Fig. 2). This minute sphaeriid (usually less than 2.0 mm in length) is known only from the lower portions of the Grand River (Ottawa and Kent Counties) and from the River Raisin and its tributaries (Washtenaw County). An explanation of this peculiar distribution is attempted in the section on Routes of Dispersal.

*Pisidium insigne* Gabb (Fig. 3). A rare sphaeriid found in lakes, ponds, bogs, and

<sup>3</sup>The morphology of *Pisidium cruciatum* Sterki and *P. insigne* Gabb is incompletely known. However, preliminary observations suggest that both species are members of *Neopisidium*, and they are placed here provisionally.



Fig. 1. Present drainage pattern in Michigan and surrounding areas.

streams, *P. insigne* is absent from the southern drainages of the Lower Peninsula.

*Pisidium punctiferum* (Guppy) (Fig. 2). The disjunct distribution of this sphaeriid in Michigan (i.e., Brown Lake, Dickinson County (Baker, 1922) and the North Branch of the Paint River, Iron County, in the Lake Michigan watershed of the Upper Peninsula, and the lower Grand River in Ottawa and Kent Counties in the western part of the Lower Peninsula) will be discussed later under Routes of Dispersal.

Subgenus *Eupisidium* Odhner, 1921

Partially fused mantle slit containing a short slit representing the branchial siphon; small posterior gills present in addition to larger anterior gills; posterior gills with inner lamellae only (outer lamellae entirely lacking); dorsal loop or lobe of the nephridia cleft.

*Pisidium adamsi* Prime. This common species occurs in the state of Michigan as the typical *P. adamsi* and as the form *sargenti* Sterki. Both types are more representative of lakes than streams.

*Pisidium aequilaterale* Prime. ". . . reported from Michigan and northward and westward, but I have seen no specimens from these regions" (Sterki, 1916). This species is typically found in the northeastern United States (Herrington, 1962). However, reliable records for Michigan are lacking. Although I have examined three different lots of *P. aequilaterale* from museum collections labeled Reed's Lake, Grand Rapids, Kent County, Michigan, the validity of this locality record must be subject to question because many other Grand Rapids citations are quite obviously mislabeled (some even include marine species). It would seem that, in the active exchange of samples conducted by the early naturalists, certain lots were tagged with the addresses of the sender and not the true place of origin.

*Pisidium casertanum* (Poli). The most common and widespread sphaeriid in the state, this variable species is composed of several dozen forms from a wide range of habitats: lakes, ponds, bogs, swamps, temporary woods pools, beach pools, and streams of all sizes.

*Pisidium compressum* Prime. Also of widespread range, this species is common in lakes and streams of all sizes. Specimens from streams usually exhibit a pronounced diagonal ridge on the beaks; shells from lakes are stunted, have an atypical shape, and the ridge is inconspicuous if it is present at all. Several forms are represented in the state: *P. compressum arrosum* Sterki (streams), *P. c. confertum* Sterki (lakes), *P. c. laevigatum* Sterki (a very common form inhabiting both lakes and streams), *P. c. pellucidum* Sterki (primarily a stream form), and *P. c. rostratum* Sterki (lakes).

*Pisidium fallax* Sterki. *P. fallax* occurs throughout the Lower Peninsula but is found only in the Lake Michigan watershed of the Upper Peninsula. More commonly found in streams than lakes, this species frequently exhibits tubercular beaks, a feature in which the beaks appear to have been pushed down, creating a concentric pseudo-ridge or bar at their base.

*Pisidium ferrugineum* Prime. Rarely taken in quantity, *P. ferrugineum* and its form *medianum* Prime are typically inhabitants of standing waters. This species occurs throughout the state.

*Pisidium henslowianum* (Sheppard). Presumably introduced from Europe, this sphaeriid is restricted to the Great Lakes in Michigan and occurs more abundantly in the lower lakes. Its presence as far inland as Lake Erie is well documented. Its extended range has been recorded for Lake Michigan (Heard, 1961), and recent dredging by Dr. Frank F. Hooper, Institute for Fisheries Research, University of Michigan, has also turned up living animals of *P. henslowianum* from Saginaw Bay of intervening Lake Huron.

*Pisidium lilljeborgi* Clessin. Predominantly a lake dweller, this species ranges widely in Michigan and occurs only infrequently in streams. The typical *P. lilljeborgi* is found in all drainages but the Lake Michigan watershed of the Upper Peninsula; the form *cratum* Sterki does not inhabit the southern streams of the Lower Peninsula.

*Pisidium milium* Held. This species is uncommon but has a wide range. It inhabits lakes and small streams in all watersheds.

*Pisidium nitidum* Jenyns. Typically occupants of lakes, *P. nitidum* and the form *pauperculum* Sterki occur throughout Michigan. However, the form *contortum* Sterki is found only in the Muskegon, Saginaw and Rouge drainages of the Lower Peninsula.

*Pisidium obtusale* C. Pfeiffer. This frequently globular species is found throughout the state, inhabiting lakes, ponds, and sluggish, protected areas of streams. The typical *P. obtusale*, however, is absent in the Northern Peninsula where it is replaced by the forms *rotundatum* Prime and *ventricosum* Prime, the former occurring only in the Lake Michigan watershed and the latter only in the Lake Superior watershed.

*Pisidium subtruncatum* Malm. A species found in few but widespread localities, *P. subtruncatum* occurs in all



Fig. 2. The distribution of *Pisidium (Neopisidium) cruciatum* and *Pisidium (Neopisidium) punctiferum* in Michigan.



Fig. 3. The distribution of *Pisidium (Pisidium) dubium* and *Pisidium (Neopisidium) insigne* in Michigan.



Michigan watersheds, inhabiting lakes and small streams.

*Pisidium variable* Prime. This species is commonly encountered in all state watersheds in both lakes and streams.

*Pisidium walkeri* Sterki. Occupying lakes and streams throughout the Lower Peninsula, *P. walkeri* and its form *mainense* do not occur in the Upper Peninsula.

Subgenus *Pisidium* s.s. C. Pfeiffer

Branchial siphon rudimentary (*P. dubium*) or represented only by a slit in the partially fused mantle (*P. amnicum* and *P. idahoense*); large posterior gills present in addition to large anterior gills; posterior gills with inner lamellae as well as outer lamellae; dorsal loop or lobe of nephridia cleft.

*Pisidium amnicum* (Muller). This large species (length greater than 5 mm) is known only from certain waters bordering the state in the east: Lake Erie, the Detroit River, and Saginaw Bay of Lake Huron. Introduced from Europe and at present common only in the Great Lakes - St. Lawrence River drainage, *P. amnicum* has advanced into Lake Huron and may eventually extend its range upstream into Lake Michigan, as did *P. henslowanum*, and possibly into Lake Superior.

*Pisidium dubium* (Say) (Fig. 3). Typically living in very small colonies, this widespread species is rarely found in lentic habitats. Its large size (length more than 5 mm) may lead to some confusion with *P. amnicum* and *P. idahoense*. However, the coarse striae of *P. dubium* are absent from the beaks while remaining prominent in *P. amnicum*; the striae in *P. idahoense* are fine. In addition the beaks are more terminal in *P. dubium*, and the hinge teeth are different from those of the two other species as described in detail by Herrington (1962).

*Pisidium idahoense* Roper (Fig. 4). This large species (length greater than 5 mm; see *P. dubium*) is typical of cold and deep waters such as Lake Superior and Lake Michigan (Heard, 1962), although it occurs as well in suitable "inland" localities: Isle Royale (Lake Superior),

Keweenaw County; Sturgeon River and Douglas Lake, Cheboygan County; Hunt Creek, Ogemaw County; Bass Lake, Livingston County.

Subfamily Sphaeriinae F. C. Baker, 1927  
Genus *Sphaerium* Scopoli, 1777

A distinct anal and branchial siphon present, either fused only at their base or for the greater part of their length; shell nearly *equipartite*, anterior end of shell shorter than posterior end.

*Sphaerium corneum* (Linnaeus). Another sphaeriid introduced from Europe and restricted to the lower Great Lakes - St. Lawrence drainage, *S. corneum* is presently found only in waters outside the boundaries of the state: Lake Erie.

*Sphaerium fabale* Prime. This species is very widespread in the streams of the Lower Peninsula watersheds but does not occur in the Northern Peninsula.

*Sphaerium lacustre* (Muller). Although the typical *S. lacustre* ranges throughout all watersheds of Michigan, the form *ryckholti* (Normand) is not found south of the Grand-Saginaw Valley, while the form *jayense* (Prime) does not occur north of it.

*Sphaerium nitidum* Clessin. Typical of deep and cold waters, *S. nitidum* occurs in Lake Michigan and Lake Huron, and the inland lakes of Isle Royale (Lake Superior) in Keweenaw County (Heard, 1961).

*Sphaerium occidentale* (Prime). A characteristic part of the fauna of woods pools, *S. occidentale* ranges throughout Michigan.

*Sphaerium partumeium* (Say) (Fig. 5). This species is very widespread in temporary woods ponds and muddy substrates of lakes and sluggish streams of Michigan.

*Sphaerium rhomboideum* (Say) (Fig. 6). Of wide range in all Michigan watersheds, this peculiar species, which has a rhomboid shape, inhabits muddy areas in lakes and streams.

*Sphaerium securis* (Prime). Widely ranging throughout the state, *S. securis* is found in lakes and ponds with muddy substrate, swamps, and woods pools.



*Sphaerium striatinum* (Lamarck). This variable species is the most commonly encountered of all the sphaeria in the state. It has many forms which are found in lakes and streams of all sizes.

*Sphaerium sulcatum* (Lamarck). This is one of the largest of all sphaeriids, sometimes reaching one inch in length. It has a more rectangular shape and more consistent striae (in spacing and height) than *S. striatinum* with which it is frequently associated. Although *S. sulcatum* includes several forms, it is considerably less variable than most sphaeriid clams. It occurs commonly in lakes and streams throughout Michigan.

*Sphaerium transversum* (Say) (Fig. 4). This sphaeriid occupies streams rather than the usual habitats of its more closely related fellow species, i.e., *S. lacustre*, *S. partumeium* and *S. securis*. In Michigan *S. transversum* occurs only in the southern streams of the Lower Peninsula.

#### Distribution Patterns

In summary, a review of the locality records available to me reveals that the Sphaeriids in Michigan fall into two categories: species of general distribution of which 3 representatives have been mapped, and species with a restricted range.

Sphaeriids with general distribution (i.e., found in all watersheds of both peninsulas) are, as follows:

*Pisidium adamsi*  
*P. case rtanum* and its forms  
*P. compressum*  
*P. dubium* (Fig. 3)  
*P. ferrugineum*  
*P. milium*  
*P. nitidum* s.s. and form *pauperculum*  
*P. subtruncatum*  
*P. variabile*  
*Sphaerium lacustre* s.s.  
*S. occidentale*  
*S. partumeium* (Fig. 5)  
*S. rhomboideum* (Fig. 6)  
*S. securis*  
*S. striatinum*  
*S. sulcatum*

The sphaeriid species or "forms" with restricted range can be grouped into the following categories:

- (a) Species present in all drainages except (1) the Lake Superior Watershed of the Upper Peninsula in the very north: *P. fallax* and *P. obtusale* s.s. with its form *rotundatum*, or except (2) the Lake Michigan Watershed of that Peninsula: also *P. obtusale* s.s. and its form *ventricosum*, and *P. lilljeborgi*.
- (b) Species of northern occurrence, absent only from the southern drainages of the Lower Peninsula: *P. insigne* (Fig. 3); also *P. lilljeborgi* form *cristatum* and *S. lacustre* form *ryckholti*.
- (c) Species restricted to the Lower Peninsula: *P. walkeri*, *S. fabale* and *P. obtusale* s.s. which are found generally throughout the Lower Peninsula, and *P. cruciatum* (Fig. 2), *S. transversum* (Fig. 4), *P. nitidum* form *contortum* and *S. lacustre* form *jayense* which occur only in the southern drainages of this peninsula, south of the Grand-Saginaw Valley.
- (d) Species occurring only in watersheds draining into Lake Michigan from both the Upper and Lower Peninsulas: *P. punctiferum* and its forms (Fig. 2).
- (e) Species common to the Great Lakes bordering the State: *P. amnicum*, *P. henslowanum* and *S. corneum*. *Pisidium conventus* and *S. nitidum* are also characteristic of the Great Lakes and in addition occur in certain lakes on Isle Royale in Lake Superior. *Pisidium idahoense* is typical of these habitats and also persists in highly localized relict populations in a few inland lakes and streams in the Lower Peninsula (see Fig. 4).

The observed distribution for both species and forms can, to a certain extent, be explained by habitat requirements and particularly by the post-glacial history of the territory and the paths of invasion that were used by these and other fresh water clams, as discussed below.





## ROUTES AND MEANS OF DISPERSAL

### General effect of former Drainage Confluences

Glaciation in the Great Lakes region not only created a large number of lentic and lotic habitats, but the subsequent formation of the present drainage basins played an instrumental role in the spread of numerous aquatic mollusks. When the peculiar distribution patterns of certain Michigan sphaeriids are considered, one can find in the patterns a reflection of the original drainage basins and evidences of some of the later changes in them. Fresh water clams were able to migrate from one drainage to another during periods of glacial confluence. Low water levels, following the retreat of the glaciers, interrupted many of these drainage systems so that (1) barriers to further migration were created and (2) some faunal elements were isolated.

The relation of the distribution of unionids or naiades to the post-glacial history of Michigan has been studied by several investigators. The major avenues of northward migration into this region from the Mississippi River drainages were outlined by Walker (1898, 1913), Ortmann (1924), van der Schalie (1938, 1945) and Goodrich and van der Schalie (1939). The three major routes that served for the dispersal of mussels were evidently also used by the sphaeriid clams. Briefly they are (Fig. 7): (a) the Illinois-Des Plaines outlet of glacial Lake Chicago (the present Lake Michigan), (b) the Maumee River, draining Lake Maumee (the present Lake Erie), which served for the colonization of the Lower Michigan Peninsula from the east, and (c) the Fox River Valley in eastern Wisconsin, which served as a path of entry into the Upper Peninsula. After these pelecypods successfully invaded Michigan waters, the confluences between the Mississippi and Great Lakes drainages were eventually broken and further dispersal of certain species was prevented by the formation of certain other barriers, such as the glacial Grand River, discussed below.

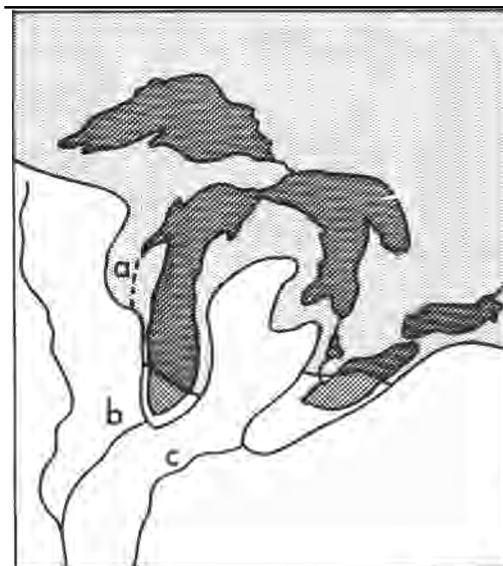


Fig. 7. Migratory routes of sphaeriid clams into Michigan. a: the Fox River Valley in eastern Wisconsin; b: the Illinois—Des Plaines drainage of glacial Lake Chicago; c: the Maumee River draining glacial Lake Maumee. The extent of glacial ice cover is indicated by stippling, and the present Great Lakes are shown by slanting lines.

The relationship between present day hydrographical patterns in the Great Lake area and those of post-glacial times can be seen by comparing Figs. 1 and 7, and, for greater detail in the Fox River Valley, Fig. 8.

### Routes of Penetration

*The role of the Illinois-Des Plaines outlet of Glacial Lake Chicago and the Maumee River draining glacial Lake Maumee.* The interpretation of the marked similarity of the Mississippi naiad fauna with that of the central Great Lakes is based on the direct connection, already referred to, of glacial Lake Chicago (the present Lake Michigan) and glacial Lake Maumee (the present Lake Erie) with the Mississippi drainage during the Pleistocene Epoch.

The same explanation may be used to interpret the distribution of certain

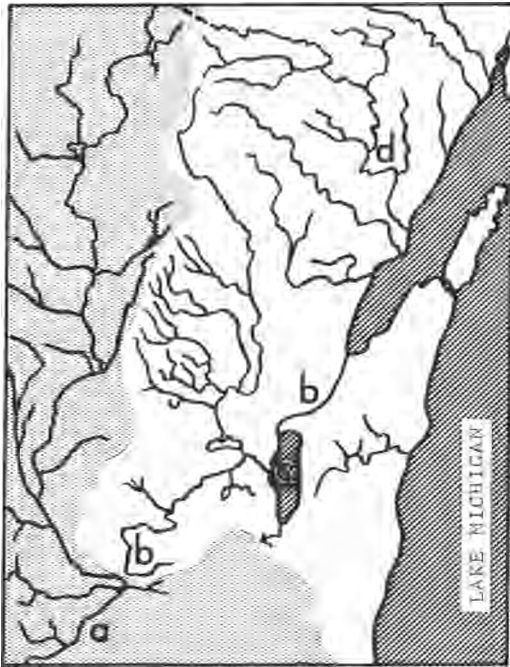


Fig. 8. The present drainage systems in the Fox River Valley in eastern Wisconsin. a: the Wisconsin River, still in the Mississippi River drainage; b: the Fox River, now in the Great Lakes drainage; c: Lake Winnebago; d: the Menominee River in the Upper Peninsula of Michigan. The Mississippi River drainage is indicated by stippling.

sphaeriids in Michigan, particularly that of the very localized species *Pisidium cruciatum*, *Sphaerium transversum*, as well as of *Pisidium punctiferum* s.s. and its form *armatum* Sterki, which are restricted to the southernmost drainages of the Lower Peninsula and whose further advance was quite evidently blocked by geographical changes.

Examination of museum specimens and of the literature (Sterki, 1895, 1916; Herrington, 1962) reveals that *Pisidium cruciatum* presently inhabits streams of the extensive Mississippi River drainage system and two Michigan streams, the Grand and Raisin Rivers (Fig. 2), which are tributaries of the Great Lakes - St. Lawrence River drainage. This pattern is similar to the discontinuous distribution

observed among several unionids.

*Pisidium cruciatum* reached the lower regions of the Grand River through the Illinois-Des Plaines drainage, and gained access to the River Raisin through the glacial Maumee River. The River Raisin evidently flowed directly into the Maumee at that time (van der Schalie, 1938).

*Sphaerium transversum* (Fig. 4) occurs in Michigan only in the Lower Peninsula south of the glacial Grand River Valley, but ranges a little farther north in Wisconsin (Baker, 1928) and much farther north in Canada (Great Slave Lake; Herrington, 1950). This species also reached Michigan through the Illinois-Des Plaines and Maumee River channels. Its northward spread in Michigan was blocked by the glacial Grand River barrier (see below), and in Wisconsin by the rupture of the glacial Fox River and subsequent stream-capture of part of this stream by the Great Lakes-St. Lawrence drainage system.

*Pisidium punctiferum* s. s. and *P. p.* form *armatum* Sterki (Fig. 3) are localized in Michigan in the lower reaches of the Grand River, a colonization which may again be interpreted as post-glacial invasion through the Illinois-Des Plaines drainage.

*Role of the Fox River Valley.* During the late Wisconsin stage of glaciation the Mississippi (Wisconsin River) and Great Lakes drainages (the present Fox River and Green Bay) were also connected through the Fox River channel in eastern Wisconsin (Goodrich and van der Schalie, 1939), and this route was employed by many of the species of sphaeriids presently inhabiting the Upper Peninsula of Michigan. The present drainages of this former confluence are shown in Fig. 8. The sphaeriids of Wisconsin (Baker, 1928; Morrison, 1932) and of the Lake Michigan Watershed of the Upper Peninsula are compared in Table 2. Most sphaeriids are found throughout the remnant drainages of the glacial Fox River confluence, although there are some significant exceptions.

Baker's (1928) records of *P. punctiferum*

TABLE 2. Sphaeriids of the Fox River Valley in eastern Wisconsin and the Lake Michigan Watershed of the Upper Peninsula of Michigan. The records from the present Fox River drainage include those from Lake Winnebago (see Fig. 3)

SPECIES	MISSISSIPPI DRAINAGES		GREAT LAKES DRAINAGES	
	Misc. Drainages	Wisconsin River	Fox River	Lake Michigan Watershed
<i>Pisidium</i>				
<i>adamsi</i>				
<i>casertanum</i>				
<i>compressum</i>				
<i>cruciatum</i>				
<i>dubium</i>				
<i>fallax</i>				
<i>ferrugineum</i>				
<i>idahoense</i>				
<i>insigne</i>				
<i>lilljeborgi</i>			XX	
<i>nitidum</i>			XXXX	
<i>obtusale</i>			XXXX	
<i>punctiferum</i>			XXXX	
<i>variabile</i>			XXXX	
<i>walkeri</i>			XX	
<i>Sphaerium</i>				
<i>lacustre</i>	XX			XX
<i>occidentale</i>	XXXX			XXXX
<i>partumeium</i>	XXXX			XXXX
<i>rhomboideum</i>	XXXX			XXXX
<i>securis</i>	XXXX			XXXX
<i>striatum</i>	XXXX			XXXX
<i>sulcatum</i>	XXXX			XXXX
<i>transversum</i>				XX

form *simplex* Sterki in Lake Winnebago and the Fox River drainage lend supporting evidence for the former existence of a migratory route through eastern Wisconsin into the Upper Peninsula of Michigan. This form has a restricted range in Michigan (Fig. 2) occurring only in the Lake Michigan drainage of the western end of the Upper Peninsula (Baker 1922; UMMZ specimens), where it was isolated after rupture of the Fox River confluence. Conversely, the northward progress from Wisconsin into the Upper Peninsula of 3 other species was presumably arrested when the Fox River confluence was broken: *Pisidium cruciatum* failed to enter the present Great Lakes (Lake Michigan) drainage, while *P.walkeri* and *Sphaerium transversum* passed into the Fox River

of the Great Lake drainage, but as yet have failed to populate the Upper Peninsula. Two other species appear to have a discontinuous distribution in this hydrographical area: *Pisidium insigne*, which is found in the Upper Peninsula of Michigan, has not yet been recorded from Wisconsin, but will probably be found there after more intensive collecting. *Pisidium lilljeborgi*, although present in the Wisconsin and Fox drainages of Wisconsin and the Lake Superior Watershed of Michigan, is not known from the Lake Michigan Watershed of the Northern Peninsula, but is likely to be discovered in these drainages with further collecting.

The routes used by those species or forms that seem to have invaded Michi-

gan from the north are not accurately known. An extension of the Fox River Valley route would, however, explain the distribution of *Pisidium insigne*, *P. lilljeborgi* form *cristatum* and *Sphaerium lacustre* form *ryckholtii* which do not occur in the southern part of the Lower Peninsula. These species evidently did not penetrate the Lower Peninsula through the Illinois -Des Plaines or Maumee routes, but were presumably able to migrate through the Fox River Valley, colonize the Upper Peninsula, and pass southward into the northern area of the Lower Peninsula.

Barriers: Effect of the Glacial Grand River

During the Pleistocene Epoch, the lower peninsula of Michigan was transected by the glacial Grand River (Bretz, 1953) which channeled the waters of the Erie and Huron basins through the Grand-Saginaw Valley into glacial Lake Chicago (Hough, 1958). The present remnants of this glacial stream are the Grand River, flowing westward into Lake Michigan, and the Saginaw River, draining northeastward into Saginaw Bay of Lake Huron. Walker's (1898) zoogeographic study of the unionid clams of Michigan revealed that the great majority of species are essentially confined to the Grand-Saginaw Valley and to the streams south of it. In contrast, however, the Grand -Saginaw Valley was a barrier to only a few sphaeriids (3 species and 3 forms), as most species (18 species, including 6 forms) exhibit a general range throughout the state. The highly varied assemblage of sphaeriid clams occupying the Grand and Saginaw River drainages is presented in Table 3.

*Pisidium cruciatum*, *Sphaerium lacustre* form *jayense* and *S. transversum* do not extend north of the Grand-Saginaw drainages. *S. lacustre* s.s., has a general range in North America; in Michigan, however, the form *jayense* is not found north of the Grand-Saginaw Valley.

TABLE 3. Sphaeriidae of the Grand — Saginaw Valley, Michigan<sup>4</sup>

Species	Grand Saginaw River River
<i>Pisidium</i>	
<i>adamsi</i> Prime	X
f. <i>sargenti</i> Sterki	X
<i>casertanum</i> (Poli)	X
f. <i>roperi</i> Sterki	X
<i>compressum</i> Prime	X
<i>cruciatum</i> Sterki	X
<i>dubium</i> (Say)	X
<i>fallax</i> Sterki	X
<i>ferrugineum</i> Prime	X
f. <i>medianum</i> Sterki	X
<i>insigne</i> Gabb	X
<i>lilljeborgi</i> Clessin	X
<i>milium</i> Held	X
<i>nitidum</i> Jenyns	X
f. <i>contortum</i> Prime	
f. <i>pauperculum</i> Sterki	X
<i>obtusale</i> C. Pfeiffer	X
f. <i>rotundatum</i> Prime	X
f. <i>ventricosum</i> Prime	X
<i>punctiferum</i> (Guppy)	X
f. <i>armatum</i> Sterki	X
<i>variabile</i> Prime	X
<i>walkeri</i> Sterki	X
f. <i>mainense</i> Sterki	X
<i>Sphaerium</i>	
<i>fabale</i> Prime	
<i>lacustre</i> (Muller)	X
<i>occidentale</i> Prime	X
<i>partumeium</i> (Say)	X
<i>rhomboideum</i> (Say)	X
<i>securis</i> Prime	X
<i>striatinum</i> (Lamarck)	X
<i>sulcatum</i> (Lamarck)	X
<i>transversum</i> (Say)	X

The Grand-Saginaw Valley also forms the southern boundary of the distribution of *Pisidium insigne*, *P. lilljeborgi* form *cristatum* and *Sphaerium lacustre* form *ryckholtii*. Examination of broader range patterns reveals that *P. insigne* has a naturally northern occurrence. *P. lilljeborgi* s.s., also a northern species, occurs throughout Michigan except in the Lake Michigan watershed of the Upper

<sup>4</sup> *Pisidium lilljeborgi* f. *cristatum* Sterki and *Sphaerium lacustre* f. *ryckholtii* (Normand) are found only north of the Valley, and *Sphaerium lacustre* f. *jayense* Prime occurs only south of it.

Peninsula; only the form *cristatum* has a limited range in the Lower Peninsula.

From the material at hand, it would seem that several more species and forms inhabit the Grand River than occur in the Saginaw River. It is however suspected that further collecting in the Saginaw Valley might also reveal the presence of the more widespread species *Pisidium insigne* and *P. milium*; *P. cruciatum* and *P. punctiferum*, of limited range, probably do not occur there. Should their absence be confirmed, this distribution pattern would indicate that a rupture in a single drainage creates an effective barrier to dispersal; i.e., that glacial Grand River must have given rise to the easterly-flowing Saginaw River before *P. cruciatum* and *P. punctiferum* were able to populate this area from the west.

#### Means of Dispersal

It has often been suggested that various aquatic animals are responsible for the dispersal of sphaeriid clams. Among these are various aquatic insects (Kew, 1893; Fernando, 1954), crayfishes (Kew, 1893), fishes (Odhner, 1951), frogs, salamanders and aquatic birds (Kew, 1893). Published accounts of sphaeriids attached to the exterior of other aquatic and terrestrial animals indicate that the spread of these bivalves is linked to the movements and dispersal of their transport hosts, i.e., largely to the water connections. Odhner (1951) also mentioned the possibility of endozoic dispersal: unborn juveniles, protected in the gills within the shell of the parent, may occasionally be able to pass through the intestine of a fish without injury. Such a mode of dispersal is still dependent on the movements of the host animal in the waterways.

While overland carriage as a means of dispersal of sphaeriid clams is not altogether discounted, it is relegated to a secondary role. It seems reasonable to assume that the distribution of sphaeriids was originally accomplished by active

migration through confluent drainage patterns. Transportation by other animals has doubtlessly followed and in most cases has effectively masked the original distribution patterns. The original distribution patterns of *P. cruciatum*, *P. punctiferum*, *S. transversum* and *S. lacustre* form *jayense* in Michigan are still clearly discernible, those of *P. fallax*, *P. insigne*, *P. walkeri*, *P. liljeborgi* form *cristatum*, *P. obtusale* s.s. and its forms *rotundatum* and *ventricosum*, *S. fabale*, and *S. lacustre* form *ryckholti* are evident to a lesser degree, while passive dispersal has presumably disguised to varying extents the original ranges of the remaining species and forms.

#### DISCUSSION

It must be understood that not all species disperse at the same time or at the same rate. The same obstacles may not exist at all times and the same obstacle may be overcome by some species but not by others in a given period of time. While *Pisidium obtusale* s.s., *P. walkeri* and *Sphaerium fabale*, for example, presently extend throughout the Lower Peninsula of Michigan, *P. cruciatum*, *P. punctiferum* and *S. transversum* have not as yet been able to spread north of the Grand-Saginaw Valley (either by active migration or through adventitious transport by other animals), and *P. insigne*, present in the north, is still absent from the region of Michigan south of that Valley.

The geographical range of a species is also confined by the limitations imposed by the ecological tolerances of the animals. Thus, dispersal takes place not only through time but also through an ecological continuum in space. *Pisidium idahoense* is infrequently found south of the North American Great Lakes and is only rarely found "inland" from the Great Lakes in that area. The disjunct inland localities of *P. idahoense* in Michigan may represent suitable habitats which have persisted locally, enabling relict populations to survive.

*Pisidium fallax* presumably migrated



through the glacial Fox River Valley (see Routes of Dispersal) into the Lake Michigan Watershed of the Upper Peninsula which is easiest of access from the Fox River, but it was apparently unable to invade and populate the Lake Superior Watershed. The apparent absence of *P. walkeri* from the entire Upper Peninsula is unexpected, for Baker (1928) reports this species to inhabit the Fox River drainage and other localities in eastern Wisconsin. Comparing the distribution of other pisidia, one would expect that *P. walkeri* also migrated from the Mississippi River drainage through the Fox River Valley into the Upper Peninsula (see Role of Fox River Valley). Further collecting in the Lake Michigan Watershed, may reveal the presence of the species in that area.

A surprisingly extensive sphaeriid fauna is localized in the waters of the Isle Royale, and island in northern Lake Superior (Walker, 1909; UMMZ specimens) which is much larger than that found in the Lake itself (Heard, 1962):

*Pisidium adamsi*  
*P. case rtanum*  
*P. conventus*  
*P. ferrugineum*  
*P. idahoense*  
*P. lilljeborgi*  
*P. milium*  
*P. nitidum*  
*P. obtusale*  
*P. punctiferum?*  
*P. subtruncatum*  
*P. variabile*  
*Sphaerium nitidum*  
*S. securis*  
*S. sulcatum*

This assemblage represents an isolated segment of the fauna of the "mainland" of Ontario, Canada. The routes by which these sphaeriids colonized Isle Royale are not accurately known. Presumably they migrated to the island from western Ontario after having passed northward up the Mississippi River, bypassing the Fox River Valley outlet, and around the basin of the present Lake Superior.

On the whole, the Michigan sphaeriid

fauna cannot yet be adequately correlated with that of surrounding territories because records for these areas are only fragmentary.

The apparent absence of species and forms from individual watersheds may be due to the lack of sufficient collecting in those areas. This is expected to apply to *P. lilljeborgi* s.s., a species presently unknown in Michigan only from the Lake Michigan Watershed of the Upper Peninsula, yet common throughout eastern Wisconsin. It is anticipated that with more intensive collecting it will be found in the Lake Michigan Watershed of the Upper Peninsula because this drainage system must have been utilized in populating the Lake Superior Watershed from the Fox River. *Pisidium insigne* is widespread in both watersheds of Michigan's Upper Peninsula but has not been recorded from Wisconsin at all. It, too, will probably be discovered in eastern Wisconsin throughout the Wisconsin and Fox drainages of the Fox River Valley migratory route.

The peculiar distribution of "forms" of certain species (see Distribution Patterns) is difficult to interpret. It is frequently found that the typical species has a different distribution than its forms as shown below for *P. lilljeborgi* and *P. obtusale*.

*Pisidium lilljeborgi* s.s. is more common in eastern Wisconsin (the Fox River Valley migratory route) and occurs throughout Michigan's Upper and Lower Peninsulas (being expected in the Lake Michigan Watershed of the Upper Peninsula, as previously mentioned). The form *P. l. cristatum* is widely distributed in Wisconsin, occurs over the Upper Peninsula, and penetrates only into the northern portions of the Lower Peninsula of Michigan.

The typical *P. obtusale* has not been recorded for either Wisconsin or the Upper Peninsula of Michigan but is common in the Lower Peninsula and is present on Isle Royale (Lake Superior). Baker (1928) reports two widely separate localities for the form *P. o. rotundatum* in Wisconsin,

whose hydrographical connections cannot be determined. In Michigan the form *P. (P.)* is found over the Lower Peninsula and replaces the typical *P. (P.)* in the Lake Michigan Watershed of the Upper Peninsula. The form *P. (P.)* is not listed for Wisconsin but occurs throughout the Lower Peninsula and the Lake Superior Watershed of the Upper Peninsula of Michigan. The common Wisconsin form is *P. (P.)* which Baker (1928) states to occur in the eastern part of the State.

The number of so-called "forms" with limited range in a distribution pattern parallel to the geological history of the area raises the question of whether these forms are not really true subspecies (i.e., geographical varieties) which arose in the present distribution of their parent species was determined or which have appeared in the formation of the present drainage systems and subsequent establishment of a restricted range for the parent species (or in the formation of the present drainage systems and subsequent establishment of a restricted range for the parent species). Unfortunately, too little is known concerning the overall distribution and general biology of sphaeriid clams (both species and "forms") to permit further conjecture at the present time. It is hoped, however, that this report will serve to stimulate other attempts to define the distribution and zoogeographical relationships of the Sphaeriidae.

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## ZUSAMMENFASSUNG

## DIE VERBREITUNG DER SPHAERIIDEN (PELECYPODA) IN MICHIGAN

Ungefähr 31 gegenwärtig im Staate Michigan, Vereinigten Staaten vorkommenden Arten sphaeriiden Muscheln ihren "Formen" sind diesem Staate allgemein verbreitet während übrigen geomorphologisch ökologisch beschränkter Verbreitung sind. Während Pleistozäns besiedelten vermutlich jene Sphaeriiden sich im Mississippibecken befanden (ebenso wie Unioniden Muscheln) Gegend vom Süden indem sie stromaufwärts in den post-glazialen Flüssen wanderten welche ungeheuren S entwässerten Raum heutigen Grossen S einnahmen. D Haupteinwanderungswege vom Mississippibecken (1) Michigans obere nördliche Halbinsel das Tal Foxflusses im östlichen W und (2) fr untere sadliche Halbinsel - D P Wasserweg glazialen Chicagosee (das heutige südliche Becken Michigansees) entwässerte und eiszeitliche Maumeefluss, damaligen Maumeeesee (das Becken jetzigen E) entleerte. D darauffolgende Bildung heutigen Seenkette ihren neuen Wasserscheiden und östlichem Abfluss unterbrach vorherigen Konfluenzen und schuf ein diskontinuierliches Verbreitungsbild indem einige Arten isoliert wurden und Ausbreitung anderer, zu verschiedenen Zeiten und mindermem grösserem Erfolge, Grenzen gesetzt wurden. Ein schlagendes Beispiel ein solches Hindernis stellt eiszeitliche Grandfluss dar, das Gebiet unteren Halbinsel durchquerte. N südliche Teil Halbinsel Sphaeriiden besiedelt worden, versperrte das weitere Vordringen dreier Arten: *Pisidium cruciatum*, *P. punctiferum* und *Sphaerium transversum* nach N. Gleicherweise bildete er südliche Grenze für P. welche nicht unmittelbar vom Süden sondern auf Umwegen vom N Halbinsel eingedrungen. Später teilte sich Grandfluss 2 nach entgegengesetzte Seiten fliessende, nach O verlaufenden heutigen Saginawfluss und nach Westen strömenden heutigen Grandfluss, und zwar noch bevor *P. cruciatum* und *P. punctiferum* vom Westen S eingedrungen. Das grösstentells ausschliesslich auf Staat umgebenden Grossen S beschränkte Vorkommen von *P. conventus*, *P. idahoense* und *S. nitidum*, welche Bewohner tiefer und kalter Gewässer sind, lässt sich auf ökologischer Grundlage erklären; das gleichfalls auf Grossen S sowie deren Abflussgebiet beschränkte *P. henslowanum*, *P. amnicum* und *S. corneum* durch wahrscheinlich erst Gegenwart erfolgte Einschleppung aus E. unmittelbaren Ursachen für örtliche Begrenzung verschiedener anderer Arten Formen jedoch weniger klar erkenntlich.

Im allgemeinen lässt sich sagen, dass einerseits durch aktive Wanderung Zeiten abwechselnder Überschwemmungen und niederer Wasserstände welche schliesslich ehemaligen Zusammenhänge zerstörten und andererseits durch Verschleppung, teils innerhalb Wasserwege mittels anderer Wassertiere wie Krebse, Frösche F, teils überlands durch Wasservogel, das ursprüngliche Verbreitungsbild vieler Sphaeriiden Binnengewässern Michigans verdunkelt wurde. Ein solches nur noch bei *P. cruciatum*, *P. punctiferum* und *S. transversum* klar erkenntlich während bei *P. fallax*, *P. obtusale*, *P. walkeri* und *S. fabale* teilweise verschleiert.

## RÉSUMÉ

## LA DISTRIBUTION DES SPHAERIIDES (PÉLÉCYPODES) AU MICHIGAN

À peu près la moitié des 31 espèces de bivalves sphaeriides et de leurs "formes" habitant présentement l'état de Michigan aux États Unis d'Amérique y ont une distribution généralisée, tandis que la repartition du reste des espèces est géomorphologiquement ou écologiquement restreinte. Pendant l'époque pleistocène les sphaeriides présents dans le bassin du Mississippi ont vraisemblablement colonisé la région du Michigan de par le sud (tout comme les bivalves unionides) en remontant le cours des rivières post-glaciales par lesquelles s'évadaient les immenses pièces d'eau occupant la région des grands lacs présents. Les routes principales d'immigration du bassin du Mississippi étaient: (1) pour la péninsule supérieure ou septentrionale, la vallée du Fox, dans le Wisconsin oriental et (2) pour la péninsule inférieure ou méridionale, la voie Illinois - Des Plaines, par laquelle s'effectuait le drainage du lac Chicago glacial (correspondant au bassin méridional du présent Lac Michigan) et le fleuve glacial Maumee par lequel s'écoulaient les eaux du lac Maumee glacial (le bassin du Lac Erie présent). La formation subséquente des Grands Lacs actuels, avec les nouvelles lignes de partage des eaux, et leur écoulement vers l'est, rompit les confluences antérieures et créa une distribution sphaeriide discontinue, isolant certaines espèces et entravant plus ou moins efficacement en diverses périodes le progrès de certaines autres. La rivière Grand glaciale, traversant la région de la péninsule inférieure, fournit un exemple frappant d'un tel obstacle: suivant la colonisation de l'extrême sud de cette péninsule par les sphaeriides, elle limita effectivement la diffusion vers le nord des espèces *Pisidium cruciatum*, *P. punctiferum* et *Sphaerium transversum*. De même, cette rivière constitua la limite sud pour le *P. insigne* qui n'a pas pénétré dans la péninsule directement par les voies méridionales, mais l'a envahie du nord par des routes plus indirectes. La rupture du Grand glacial, donnant naissance à deux fleuves courant en sens opposé, le présent Saginaw prenant cours vers l'est et le présent Grand s'écoulant vers ouest, eut lieu avant que les espèces *P. cruciatum* et *P. punctiferum* eussent pu parvenir de l'ouest dans le bassin du Saginaw. La repartition, restreinte largement ou exclusivement aux Grands Lacs bordant l'état, de *P. conventus*, *P. idahoense* et *S. nitidum*, espèces d'eau froide et profonde, explique la base écologique; celle de *P. henlowanum*, *P. amnicum* et *S. corneum*, espèces d'origine européenne, qui sont localisées dans les Grands Lacs et leur ligne de drainage, par leur invasion probablement récente. Les causes immédiates de la distribution limitée de certaines autres espèces sont moins apparentes.

En général l'on peut dire que la distribution originale de beaucoup de sphaeriides dans les bassins riverains du Michigan a été obscurcie d'une part par une migration active pendant les périodes alternantes d'inondations et de niveaux bas qui finalement rompirent les confluences antérieures et, d'autre part, par un transport passif, soit à l'intérieur de ces mêmes voies d'eau au moyen d'autres animaux aquatiques tels qu'écrevisses, grenouilles ou poissons, soit à travers la région par Pentremise d'oiseaux aquatiques. Le trace de la distribution originale n'est encore clairement visible que pour les espèces *P. cruciatum*, *P. punctiferum* et *S. transversum*, tandis qu'il est partiellement masqué pour les espèces *P. fallax*, *P. insigne*, *P. walkeri* et *S. fabale*.

## RESEÑA

## LA DISTRIBUCION DE SPHAERIIDAE (PELECYPODA) EN MICHIGAN, E.E.U.U.

Como la mitad de las 31 especies y sus formas de esféridos que habitan hoy en Michigan son ms o menos de distribución general en el estado, aunque el resto tienen un area geomorfológicamente y ecológicamente restricta. Durante el Pleistoceno, estos esféridos presumiblemente repoblaron la region, desde el sur, por migración activa remontando las aguas a través de las confluencias de los cursos posglaciales. Las rutas mayores de migración desde el río Mississippi hacia el interior de Michigan fueron: (1) Hacia la Alta Península de Michigan, el Valle del Río Fox en Wisconsin oriental, y (2) Hacia la Baja Península el canal Illinois--Des Plaines que drenaba el lago glacial Chicago (la cuenca sur del presente Lago Michigan) y el Río glacial Maumee que drenaba el Lago Maumee (cuenca del presente Lago Erie).

Después que la parte sur de la Baja Península de Michigan fué repoblada, su dispersión fué diversamente obstaculizada. El Río Grande glacial limitó la dispersión hacia el norte de *Pisidium cruciatum*, *P. punctiferum*, y *Sphaerium transversum*, y más tarde se dividió en el presente Río Saginaw de curso oriental y el Río Grande que corre hacia el oeste antes que *P. cruciatum* y *P. punctiferum* pudieran entrar en la corriente del Saginaw desde el oeste. La distribución, restricta mayormente a los Grandes Lagos fronterizos del estado, de *P. conventus*, *P. idahoense*, y *S. nitidum*, las cuales son especies de aguas profundas y frías, puede explicarse ecológicamente; la de *P. henslowanum*, *P. amnicum* and *S. corneum*, que son restrictas a los Grandes Lagos y sus drenajes, puede explicarse por su reciente importación de Europa. Las causas inmediatas de las ocurrencias locales de muchas otras especies y formas, sin embargo son menos aparente.

La migración activa durante periodos que alternaban entre inundaciones y aguas bajas, que terminó en la desunión de las confluencias, el transporte pasivo mediante otros animales acuáticos como langostas de agua dulce, ranas y peces, y el transporte aéreo por aves acuáticas, alteraron la distribución original de los esféridos en Michigan. El tipo original es todavía evidente en la distribución de *P. cruciatum*, *P. punctiferum*, y *S. transversum*, pero está parcialmente disimulado en *P. fallax*, *P. insigne*, *P. obtusale*, *P. walkeri*, y *S. fabale*.

## КОНСПЕКТ

## РАСПРОСТРАНЕНИЕ СПHAЕРИИДАЕ (BIVALVIA) В МУМ, СМА.

Василий X. ХхрА

Около половины всех 31 вида и форм двустворчатых моллюсков семейства Сфериидэ, живущих в штате Мичиган, равномерно рассеимо по территории штата, в то время как остальная часть их резко разграничена геоморфологически и экологически. Во время плейстоценовой тохм, виды NmHe населяющие штат, вероятно, колонизировали его двигаясь с Бра, как это делали перловицы и беззубки, мигрируя на север вверх по течению последних ручьев, которые питались из громадных водных скоплений теперешних Больших Озер. Главными путями миграции из

бассейна . Миссиссиппи были: 1) в верхние полуострова то - то , в долину Фокс Ривэр в восточной стн штата висконсин и 2) в нижние полуострова штата, в о н о Иллиной-Дэс Плэйнс, который питался из ледникового Озера Чикаго (южная база сов- Озера Мичиган) из ледниковой реки Мауми, вытекавшей из то же названия (60 30 современного) Последовавшее формирование современных Больших Озер, с их новыми притоками и истоками на восток, прервало прежние стени и создало оторванные зантн вод, изолируя виды мозмосков и останавливая развитие других видов в разное время различными результатами. Показательный пример такого препятствия была ледниковая Гранд Ривэр, курс которой а площадь Нижнего Полуострова; то , но часть этого полуострова 60 30 снова заселена семейством Сфериидэ, но остановила продвижение то видов: Р. и S. . Таким 60 30 эта образовала то границу для вида Р. , который не проник на полуостров прямо с юга, но - с более сложными путями. Ледниковая река Гранд Ривэр позже разделилась на два рукава, текшие в противоположных направлениях, то Сагино сегодняшнего дня, то в восточном направлении и современная на Ривэр, текшая на запад, а чем Р. , и Р. могли проникнуть в Сагино с запада.

Распространение ограниченное главным образом Большими Озерами по линии штатной границы для *P. conventum*, *P.* и *S.* - видам более глубокой и холодной воды, можно на основании экологии. Распространение же видов *P.* , *P.* *S. cornutus*, видам ограниченным Большими Озерами и их истоками, можно объяснить, вероятно, их недавним появлением из Европы. Непосредственные причины ограничения некоторых других видов или форм менее ясны.

Возможно, что активная миграция в периоды перемежающихся половодий и обмельчаний, которые в конечном результате разорвали прежнее слияние вод, то как и пассивное их перемещение, отчасти в этих водах другими пресноводными животными как раки, лягушки и рыбы, отчасти водными птицами, прежнее распространение семейства Сфериидэ во внутренних водах то Мичиган. Структура прежнего распространения все еще ясна только для видов *P.* , *P. punctiferum* и *S.* , в то время как она отчасти скрыта для видов *P.* , *P.* , *P.* и *S.* .