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POST-GLACIAL FISHES FROM A LAKE MICHIGAN DRAINAGE IN MILWAUKEE, WISCONSIN

by Susan Teller-Marshall and David Bardack
University of Illinois at Chicago Circle

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in
Milwaukee, Wisconsin

by
Susan Teller - Marshall
and
David Bardack

Department of Biological Sciences
University of Illinois at Chicago Circle
Chicago, Illinois   60680

Abstract

A number of post-glacial fishes from Milwaukee, Wisconsin are identified and three post-glacial aquatic fossil assemblages from the Great Lakes Region are discussed. The Milwaukee fish are 7750 ± 125 radiocarbon years old and include *Umbra limi*, *Esox* sp., *Ictalurus melas*, *Micropterus dolomieui*, *Lepomis cyanellus*, *Lepomis gibbosus*, and a generically indeterminate catostomid. Geological and ecological evidence suggest that the fossils were deposited in a prairie stream that was probably the forerunner of the Kinnickinnic River. Analysis of the differences between the three known post-glacial aquatic fossil assemblages from the Great Lakes Region indicates that climate conditions during the post-glacial climatic optimum period were not significantly different from today.

Introduction

Until recently, few fossil fish were known from the post-glacial period of the Great Lakes Region (Baker, 1920; Uyeno and Miller, 1963; Wilson, 1967). Within the past few years, however, two vertebrate assemblages representing post-glacial aquatic communities in the vicinity of Lake Michigan have been studied. The first of these assemblages comes from a locality at the southern end of Lake Michigan near Michigan City, Indiana (Bland and Bardack, 1973; Teller and Bardack, 1975). The second, discussed here, is from a sewer excavation at Milwaukee, Wisconsin near the western shore of Lake Michigan. Both of these assemblages date back to the climatic optimum period [about 7000 - 5000 BP (Bryson *et al*, 1970).] A third locality at Fenton Lake in Genesee County, Michigan has yielded a post-glacial vertebrate assemblage roughly dated from 3000 - 1000 BP (Wilson, 1967), a period in post-glacial history that appears, on the basis of pollen data (Pearson, 1964; Sears, 1942; Smith, 1957, 1965), to have been cooler than the present.

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The fossil fish species recorded from these localities occur within these species' present ranges. Differences in the composition of the fish assemblage found at the Fenton Lake locality from that of the two sites near Lake Michigan appear to represent community variation rather than resulting from climate differences.

The Milwaukee assemblage includes several fish as well as invertebrate fossils. The fish are *Umbra limi*, *Esox sp.*, *Ictalurus melas*, *Micropterus dolumieui*, *Lepomis cyanellus*, *Lepomis gibbosus*, and a generically indeterminate catostomid. Most of the specimens are less that 5 cm. in length. The bone and scales are brown, and they are found in association with both adult and larval insects, snails and some small woody fragments.

Geography and Geology of the Fossil Site

Figure 1 shows these three post-glacial localities in relation to each other and to Lakes Michigan and Huron. Radiocarbon dates have been obtained for the Michigan City site (Winkler, 1962) and the Milwaukee site (Teledyne Isotopes). Each is based on fossil wood fragments. The Michigan City fishes occur in a bed situated between two strata radiocarbon dated at 5475 ± 250 years and 6350 ± 200 years BP. The Milwaukee fish, directly associated with the radiocarbon dated wood, are 7750 ± 125 years BP.
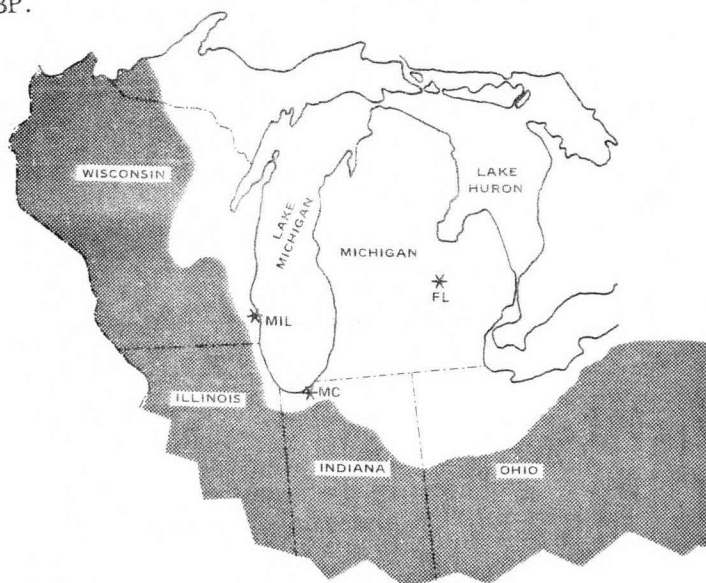

Figure 1. Approximate locations of the three postglacial aquatic fossil assemblages relative to Lakes Michigan and Huron. Shaded area pictured is outside of Great Lakes drainage. FL = Fenton Lake, MC = Michigan City, MIL = Milwaukee.

Figure 2 shows the occurrence of the fossil bearing sediments as well as the general sediment types deposited between the present ground surface and lake level, a distance of 90 feet. The sediment surrounding the fossils is a fine, crumbly gray clay with some gravel and sand, indicating a soft bottom of organic debris but probably a greater diversity of bottom type than indicated by the homogeneous fine clay surrounding the Michigan City fossils (Teller and Bardack, 1975).

The Milwaukee site lies just north of the Kinnickinnic River. At this point the river flows eastward along a winding course that ends in the Kinnickinnic Basin just south of Milwaukee Harbor.

During the period from 9000-4000 BP (Willman, 1971) the water in Lake Michigan reached its lowest level, the Lake Chippewa Stage (Hough, 1963 Fig. 6B) at 230 feet above sea level compared with 583 feet today. Water filled only the deepest parts of the Lake Michigan basin and both the Michigan City and Milwaukee fossil assemblages were deposited at sites well above the level of the water in Lake Chippewa.
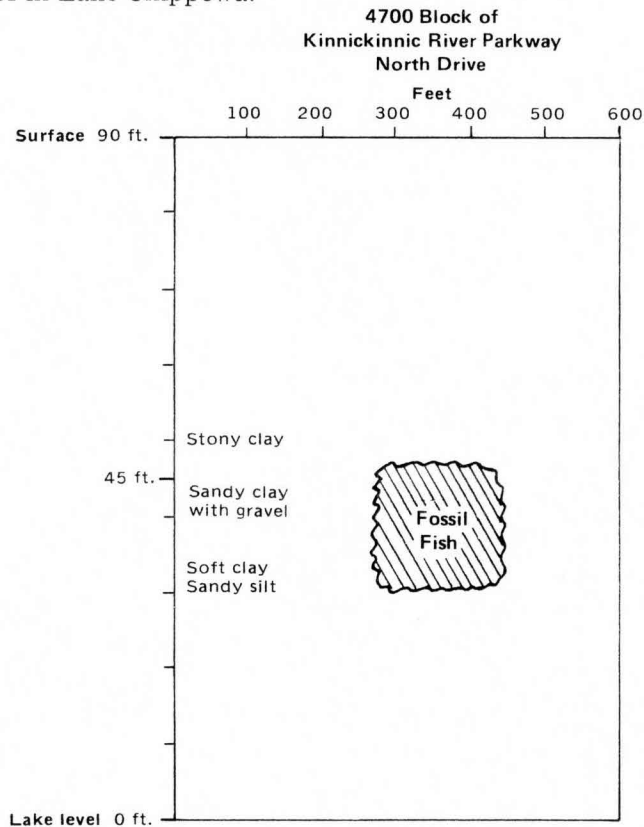
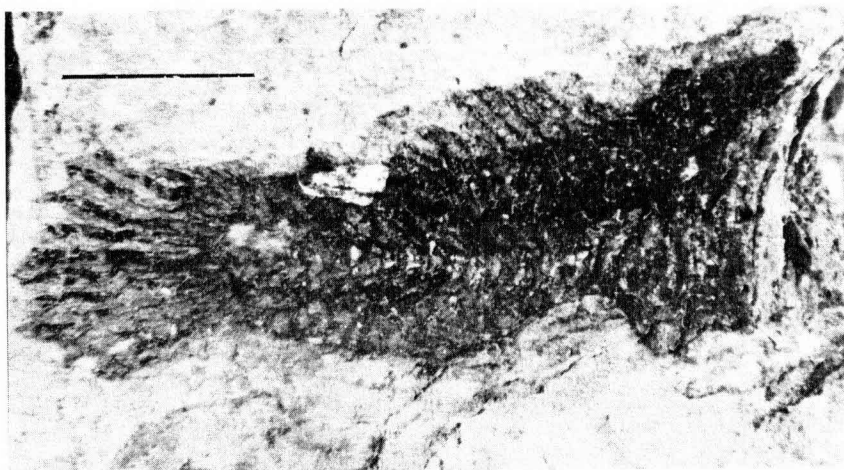**4700 Block of**
Kinnickinnic River Parkway
North Drive

Figure 2. Adaptation of Metropolitan Sewerage Commision of Milwaukee map 86-41 showing the location of fossil bearing sediments within the excavation site under Kinnickinnic River Parkway.

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Systematic Descriptions

Family Umbridae
Genus *Umbra*
Umbra limi (Kirtland)
Plate I

MPM VP 2689 *Umbra limi* posterior two thirds of fish. Scale bar - 1 cm.

Material: MPM VP 2689 fish body with scaled and proximal part
of dorsal and caudal fins
MPM VP 2690 fish body with centra and scales
MPM VP 2691 ventral half of fish body, scales, cleith-
rum, fragments of ribs

Osteological characters which define the Umbridae include a torpedo-shaped body, round to very slightly emarginate caudal fin, a few to most of the vertebral centra elongate and constricted anteriorly (Cavender, 1969). All of these characters are easily recognized in the Milwaukee specimens.

Among the three umbrid genera, both *Novumbra* and the young of *Dallia* show the characteristic vertebral column in which the centra are constricted anteriorly, but usually only in the mid-abdominal region. The other vertebral centra are symmetrical in lateral view (Cavender, 1969). The fossil specimens and *Umbra* exhibit anteriorly constricted centra throughout most of the vertebral column. These centra are characterized by a sharp, anterior constriction and thin sheets of bone which originate dorsolaterally on each centrum at right angles to the long axis

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of the centrum and extend caudad from the bases of the neural arches (Todd, 1973 Fig. 1 p. 587).

The scales of *Umbra* are large relative to scales of *Novumbra* and *Dallia* (Cavender, 1969). The fossil scales are identical with Lagler's (1947) figure of a scale from *Umbra limi* (Pl. III Fig. 14). These scales are distinguished as subquadrate cycloidal without primary radii and with mostly longitudinal ridges which do not parallel all margins of the scale (Lagler, 1947).
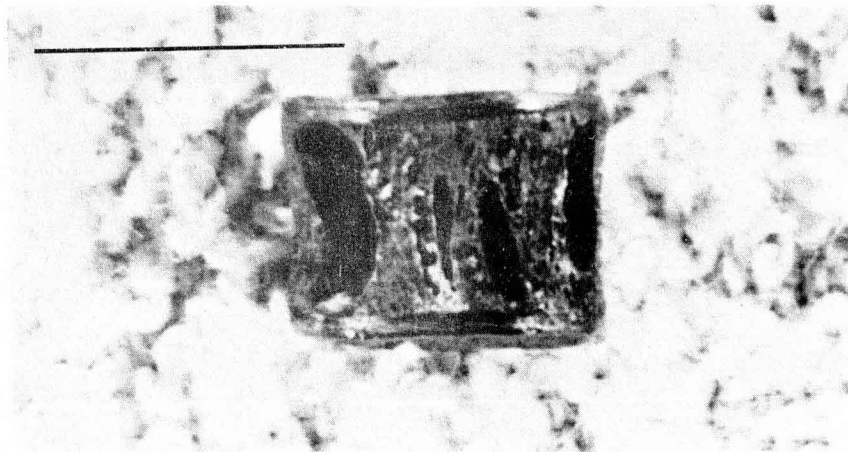
On the basis of these characters the fossil material is identified as *Umbra limi*, the central mudminnow.

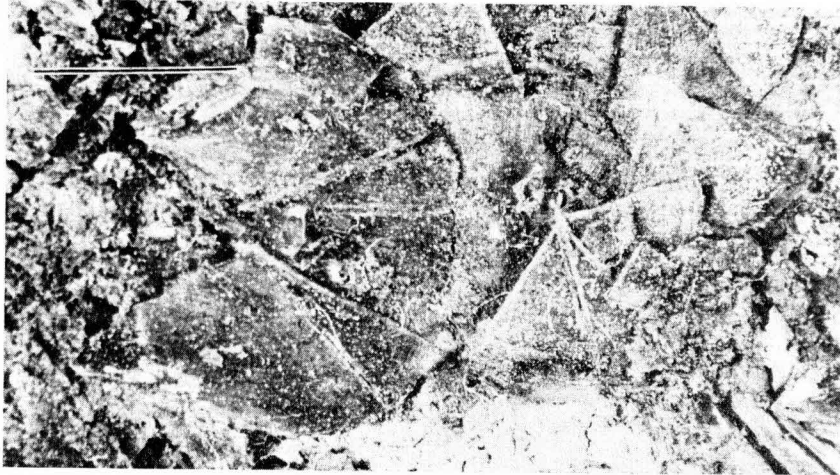Family Esocidae
Genus *Esox*
Esox sp.
Plate II

MPM VP 2693 *Esox* sp. centrum. Scale bar = 1 cm.

Material: MPM VP 2963 one abdominal centrum

Centra of fishes belonging to the genus *Esox* exhibit a number of characters which facilitate identification. The centra are deeper than long, with only a slight mesial constriction. Depressions for the neural arch bases and parapophyses extend nearly the entire length of the centrum; the remaining area around the periphery is nearly solid, consisting of many thin, longitudinal ridges crowded very close together so that the intervening grooves are slender. The fossil centrum exhibits this entire suite of characters. Judging from the size of this isolated centrum, the fish that possessed it was of considerable size, estimated at greater than 40 cm. in length.

Family Catostomidae
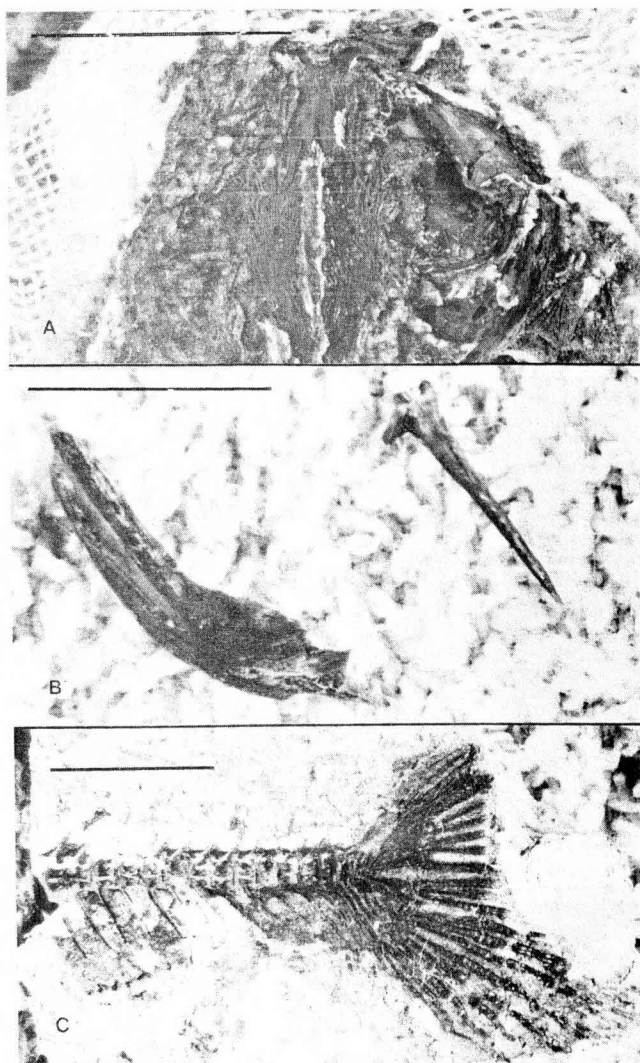Genus: Indeterminate
Plate III

MPM VP 2694 catostomid scales. Scale bar = 1 cm.

Material: MPM VP 2694 median fin rays and scales
MPM VP 2695 median fin rays and scales
MPM VP 2696 scales

Catostomid scales are cycloid with primary radii developed in both the anterior and posterior fields, and with a central or sub-central focus (Lagler, 1947). The fine circuli follow the shape of the scale, and are closely spaced.

The fossil scales are large, but nearly all of them are so fragmentary that measurements are not possible. MPM VP 2694 exhibits the most complete fragment of any specimen. The depth of this scale as measured through the focus is 16 mm. and the scale is longer than deep. It is likely that the scales do not belong to any of the smaller catostomid genera. The fossil scales were compared with catostomid scales in the Field Museum of Natural History fish collection in the hope that a generic identification would result, but among the remaining genera, scales alone cannot be satisfactorily used for a certain identification. The fossil material is thus assigned to the status of indeterminate catostomid.

Family Ictaluridae
Genus *Ictalurus*
Ictalurus melas Refinesque
Plate IV Figures A,B,C

Scale bar = 1 cm.

Figure A MPM VP 2704 *Ictalurus melas* dorsal view of ethmoid and frontals

Figure B MPM VP 2697 *Ictalurus melas* left cleithrum and right pectoral spine

Figure C MPM VP 2797 *Ictalurus melas* caudal region

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Material: MPM VP 2697 fish body, pectoral girdle and spines, caudal skeleton
MPM VP 2698 posterior of skull roof plus fragments of Weberian apparatus
MPM VP 2699 posterior neurocranium and part of Weberian apparatus
MPM VP 2700 caudal skeleton and right pectoral spine
MPM VP 2701 left pectoral girdle
MPM VP 2703 pectoral girdle and spines
MPM VP 2704 cranial roof
MPM VP 2705 right cleithrum and pectoral spine; left lower jaw
MPM VP 2706 right cleithrum and pectoral spine
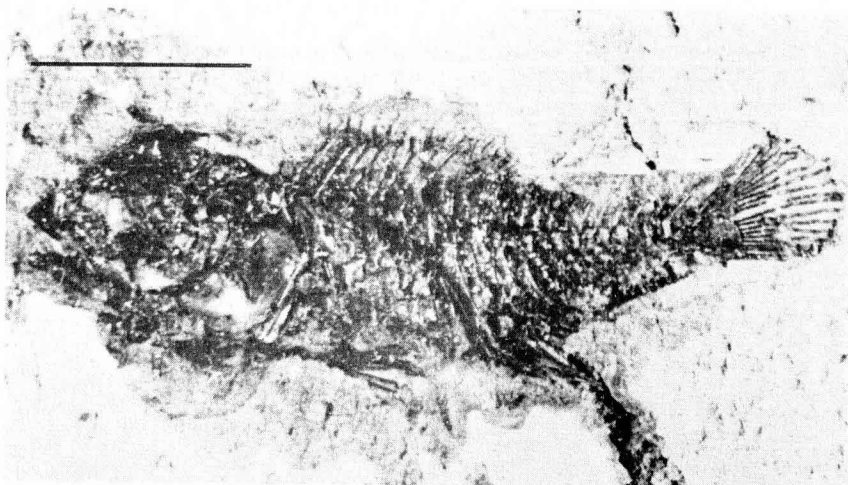MPM VP 2707 fragments of lower jaws and branchiostegals; right pectoral spine

Lundberg (1970) lists the following advanced characters possessed by *Ictalurus melas* which are also evident in the fossil specimens: the medial processes of the supraethmoid cornua are absent; the ornamentation on the posterior portion of the cleithrum is lost; the posterior process of the cleithrum is reduced; and the anterior distal serrae, anterior dentations and posterior dentations on the pectoral spine are absent or weakly developed.

Plate IV shows the ethmoid region (Figure A), pectoral elements (Figure B) and caudal fin (Figure C) of the fossil ictalurid. *I. melas* and MPM VP 2704 exhibit a broad, central triangular notch at the anterior edge of the ethmoid ossification. In other species of *Ictalurus*, there are medial processes of the supraethmoid cornua which form a more circular enclosure at the anterior edge of the ethmoid (Lundberg, 1970; Paloumpis, 1964).

In other species of *Ictalurus* the posteroventral process of the cleithrum is ornamented with distinct ridges, but in *I. melas* and MPM VP 2697, 2701, 2703, 2705, and 2706 the posterior process of the cleithrum lacks any ornamentation except for a few faint ridges. Species of *Ictalurus*, with the exception of *I. melas*, exhibit strong posterior dentations on the pectoral spine. These dentations are absent or only weakly developed in the fossil specimens.

Some caution should be used in basing a specific identification on pectoral spine material alone, as there is considerable intraspecific variation with respect to the degree of serrations present (Dennison, pers. comm.). The reduction of pectoral spine serrations and even the complete absence of serrations in some specimens is, nonetheless, a characteristic of *I. melas*. This character, in combination with those mentioned above, indicates that the Milwaukee material should be assigned to *Ictalurus melas*.

Family Centrarchidae
Genus *Micropterus*
Micropterus dolomieui Lacepede
Plate V

MPM VP 2714 *Micropterus dolomieui* whole fish. Scale bar = 1 cm.

Material: MPM VP 2708 head and anterior end of body
MPM VP 2709 head fragments
MPM VP 2710 whole fish, impression only except for a
few skull fragments
MPM VP 2711 peel of whole fish
MPM VP 2712 peel of head fragments
MPM VP 2713 whole fish
MPM VP 2714 whole fish
MPM VP 2715 preoperculum

Scales of these specimens show the typical centrarchid pattern (cf. Lagler, 1947 Figs. 32-40). There are ten dorsal spines and three anal spines preserved in most specimens. As in *Micropterus* the bodies are slender, with the greatest depth contained more than three times in the standard length, and the scales are smaller than in *Lepomis*. The cleft of the mouth extends to the middle of the orbit and the smooth preoperculum is boomerang-shaped, its vertical and horizontal limbs forming an angle of 100° or more.

The fossil specimens are not *M. salmoides*, which has both a larger mouth cleft and the lower jaw articulation occurring far back behind the eye.

Also, in *M. salmoides* the shortest dorsal spine is less than half the length of the longest dorsal spine (Pflieger, 1975). In fossil specimens MPM VP 2710, 2711, 2713 and 2714 in which these

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spines are preserved, the shortest dorsal spine is more than half the length of the longest dorsal spine. In MPM VP 2714 there are 15-16 caudal centra.
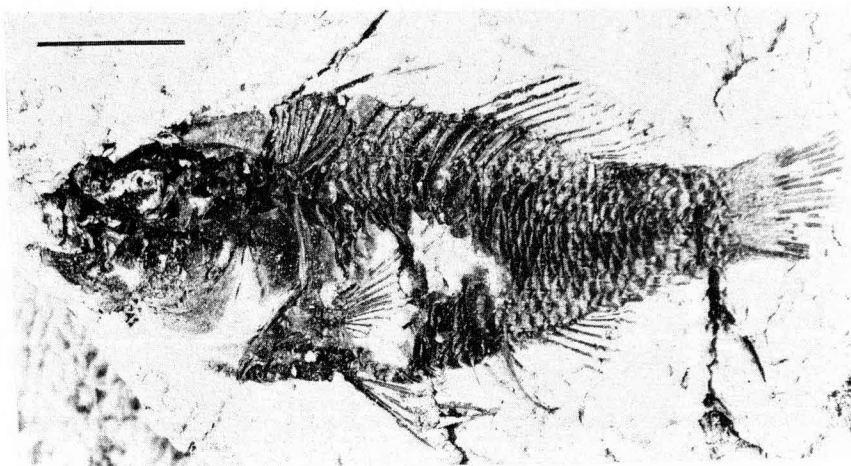
Of the two remaining species of *Micropterus*, found in cooler latitudes, *M. dolomieui* is differentiated from *M. punctulatus* by the number of lateral line scales and the number of dorsal fin rays (Pflieger, 1975). In *M. dolomieui* and MPM VP 2710 there are more than 65 lateral line scales; the soft dorsal rays are in completely preserved or absent from all of the fossil specimens. Based upon the characters available, the fossil material is assigned to *Micropterus dolomieui*.

Family Centrarchidae
Genus *Lepomis*
Lepomis cyanellus Rafinesque
Plate VI

MPM VP 2718 *Lepomis cyanellus* whole fish. Scale bar = 1 cm.

Material: MPM VP 2717 whole fish except caudal region
MPM VP 2718 whole fish
MPM VP 2719 whole fish except caudal region

The fossil specimens exhibit ten dorsal and three anal spines, and the scales exhibit the typical centrarchid pattern (cf. Lagler, 1947 Figs. 32-40). As in *Lepomis* the greatest depth is contained less than three times in the standard length and the scales are large.

Characters which differentiate *Lepomis cyanellus* include a body less deep than in other species of the genus; the greatest depth is usually less than the snout to dorsal fin distance (Pflieger,

1975). In both MPM VP 2717 and 2718, in which the dorsal fin is preserved, this is the case. In *L. cyanellus* and the fossil specimens the mouth cleft is deep, but it does not reach the middle of the eye. The dentary is more gently curved at its posterior edge then in other species of *Lepomis* (Branson and Moore, 1962 Fig. 60).

In *L. cyanellus* the preopercle angle is between 90-95° and there are serrations at the preopercle angle along the posterior border of that bone (Branson and Moore, 1962 Fig. 76). Scales of *L. cyanellus* possess a very narrow ctenoid patch. All of the fossil specimens exhibit these characters. Finally, in *L. cyanellus* the pharyngeal teeth are conical and the gill rakers are long and thin (Trautman, 1957). MPM VP 2719 exhibits a few conical pharyngeal teeth as well as long, thin gill rakers. On the basis of these characters the fossil specimens are assigned to *Lepomis cyanellus*.

Family Centrarchidae
Genus *Lepomis*
Lepomis gibbosus Linnaeus
Plate VII

MPM VP 2720 *Lepomis gibbosus* anterior half of fish. Scale bar = 1 cm.

Material: MPM VP 2720 whole fish except caudal fin
　　　　　MPM VP 2721 whole fish

The fossil specimens exhibit ten dorsal and three anal spines as well as scales with the typical centrarchid pattern (cf. Lagler, 1947 Figs. 32-40). As in *Lepomis* the greatest depth is contained less than three times in the standard length and the scales are large.

In *Lepomis gibbosus* the body is deep, with large scales (cf.

Bland and Bardack, 1973 Fig. 3). The mouth is very small, the jaw articulation being anterior to or reaching only the anterior border of the orbit (Trautman, 1957). The preoperculum is sharply angled and serrated along the posterior margin of its curve. The edge of the opercle is minutely serrated, and is not extended back as an ear flap (Ossian, 1973). Both fossil specimens exhibit these characters.

Branson and Moore (1962 Figs. 45-93) have shown that the lacrimal and jaw elements differ among the species of *Lepomis*. A comparison of skeletonized specimens of *L. gibbosus* and the fossil specimens shows that the lacrimal and jaw elements are similar. MPM VP 2720 includes one large pharyngeal tooth identical with those found just adjacent to the broad pavement teeth at the center of the pharyngeal mill of skeletonized specimens of *L. gibbosus*. On the basis of these characters the fossil specimens are assigned to *Lepomis gibbosus*.

In addition, there are nine specimens only identifiable as *Lepomis* sp. (MPM VP 2722-2730) and thirteen specimens identifiable only as generically indeterminate centrarchids (MPM VP 3262-3275).

Invertebrates found with the fishes include a stonefly (Order Plecoptera), a dragonfly nymph (Order Odonata), a pair of water beetle elytra (Order Coleoptera, Family Dytiscidae), and the snail *Helisoma anceps*.

Discussion

There are presently three post-glacial vertebrate assemblages from the Great Lakes Region, with a total of nineteen fish species represented. Together these nineteen species significantly expand the knowledge of fish fossils from the region (see Teller and Bardack, 1975). The Milwaukee site has yielded the first Pleistocene mudminnow to be reported from the Great Lakes drainage (for other records see Cavender, 1969; Todd, 1973).

All of the fossil vertebrates from these sites have living conspecifics with known geographical distributions and habitat preferences. Once the fossils have been reliably identified, information about the natural history of their living relatives can be used to elucidate the habitat occupied by the fossils. This procedure is not without risk, especially with isolated fossils, because their living relatives can be found in more than one habitat. But when a locality yields many species whose modern counterparts share one preferred habitat, then interpretations of the fossil habitat are more firmly based.

The two previously studied fossil localities show differences in habitat based upon the species represented. The Fenton Lake locality was probably a deep, cool post-glacial lake while the

Michigan City locality appears to have been a warm, shallow marsh (Teller and Bardack, 1975).

Of the fish species found at Milwaukee, *Umbra limi* and *Ictalurus melas* (central mudminnow and black bullhead) prefer a soft bottom of organic debris. *Micropterus dolomieui* (smallmouth bass) and most catostomids are intolerant of turbidity (Pflieger, 1975; Scott and Crossman, 1973; Trautman, 1957) so that these fish likely inhabited a clear body of water with a bottom composed at least partially of organic debris as indicated by sediments surrounding the fossils.

The smallmouth bass is usually characteristic of a prairie stream or river. The smallmouth is less often associated with marsh vegetation and prefers cooler water than the largemouth (Scott and Crossman, 1973). The central mudminnow also prefers cooler water (Trautman, 1957) and is characteristic of low gradient clear rivers or streams (Pflieger, 1975). The black bullhead is the most abundant bullhead in many prairie streams (Pflieger, 1975). The favored habitat of all three of these species is stream pools in small, intermittent creeks and the oxbows and backwaters of large streams in the prairie region (Pflieger, 1975; Scott and Crossman, 1973; Trautman, 1957).

The pike and muskellunge (genus *Esox*) frequent a variety of habitats, but the muskellunge prefers low gradient streams with plentiful vegetation (Trautman, 1957). Both *Lepomis cyanellus* (green sunfish) and *L. gibbosus* (pumpkinseed) are found in prairie streams; the green sunfish is the most abundant sunfish in many streams of the prairie region (Pflieger, 1975). The pumpkinseed prefers the quiet water of slow moving streams with a good vegetational cover.

Snails associated with the Milwaukee fishes include *Helisoma anceps*, a species common to rivers and streams, but not usually associated with lakes. 'Water tiger' beetles are found either in standing or very slowly moving fresh water, and stoneflies and dragonflies are usually associated with several types of aquatic environment.

Woody fragments associated with the Milwaukee fishes consist of small diameter (less than 2 cm.) twigs and a few more sizeable chunky pieces; other than these fragments there is no evidence of aquatic, submerged or shoreline vegetation. However, only the matrix immediately surrounding each fossil specimen was available for study. It is possible that had a greater amount of matrix been examined more evidence of vegetation might have appeared.

The fossil evidence thus indicates that the Milwaukee locality was probably a slow moving prairie stream, possibly the forerunner of the Kinnickinnic River, which drained eastward into Lake Chippewa. West (1961) has shown that sediments as well as pollen profiles indicate a period of dessication in Wisconsin subsequent to the lowered water levels of the Lake Chippewa stage.

This would explain the existence of a prairie stream in the Milwaukee area which is now characterized by a natural vegetation that consists of basswood-maple forest according to USGS sheet 90 of the National Atlas series.

Fishes, like other organisms, have limited tolerance for environmental variables, so information about fishes that lived at a particular time and place should provide insight into the nature of the environment at that time and place (Cross, 1970). A comparison of fish species represented in each of the post-glacial localities shows that they reflect different communities (Teller and Bardack, 1975).

The Milwaukee and Michigan City fossils were both deposited during the post-glacial period most frequently referred to as the climatic optimum, a warm, humid phase in post-glacial history reflected by pollen profiles which include oak, beech, hemlock and other mesic deciduous elements. A more arid and then cooler period separate the climatic optimum from the present climate phase, and the present distributional patterns of a number of lower vertebrates can be explained by assuming that they expanded their distributional ranges either during the climatic optimum or during the warm, dry period which followed. However, some workers consider that the post-glacial climate following the changes initiated by ice retreat was not significantly different from the present (see Smith, 1965 and Pearson, 1964 for review; see also Willman, 1971).

LOCALITY	SPECIES NAME	GREAT LAKES	OHIO RIVER	GULF/ FLA
MC	L. osseus	▬	▬	▬
MC	I. nebulosus	▬	▬	▬
MC	M. salmoides	▬	▬	▬
MC	L. macrochirus	▬	▬	
MC	E. lucius	▬	▬	
MC	S. canadense	▬	▬	
MIL	I. melas	▬	▬	▬
MIL	L. cyanellus	▬	▬	▬
MIL	U. limi	▬	▬	
MIL	Esox sp.	▬	▬	
MIL	M. dolomieui	▬	▬	
MIL	L. gibbosus	▬	▬	
FL	E. masquinongy	▬	▬	
FL	S. vitreum	▬	▬	
FL	M. anisurum	▬	▬	
FL	C. cyprinus	▬	▬	
FL	C. catostomus	▬		
FL	S. namaycush	▬		
FL	C. clupeaformis	▬		

Table 1. Present southern extent of the distributions of fish species known from the Late Pleistocene of the Great Lakes Region. Distributions taken from Trautman, 1957; Scott and Crossman, 1973; Pflieger, 1975. MC = Michigan City, MIL = Milwaukee, FL = Fenton Lake.

Table 1 lists the fish species from all three post-glacial localities and compares the present southern distributional limits of these species. The Michigan City locality has the largest proportion of species whose distributional ranges extend as far south as the Gulf of Mexico or Florida while the Fenton Lake locality has no species which presently extend this far south. The Milwaukee locality appears to be intermediate in this respect.

All of the fish species from Michigan City and Milwaukee and four of the species from Fenton Lake have present distributions which extend as far south as the Ohio River, but three of the Fenton Lake species have present distributional ranges that do not extend further south than the Great Lakes.

Differences between the Michigan City and Milwaukee fish fossils suggest differences in the type of aquatic habitat. Since both fossil assemblages were deposited during the same climatic interval, they likely do not reflect climate differences. The Michigan City fish appear to have been deposited in a marshy pond which would tend to reach 70-80° F [21-27° C], at least in summer. The Milwaukee fishes include species such as the mudminnow, smallmouth bass and a catostomid. These fishes prefer cooler, flowing waters and are rarely found in marsh environments today. The differences between these two species groups as shown in Table 1 thus reflect components of two different aquatic communities rather than differences in temperature alone.

The Fenton Lake fishes were deposited during a later period which was decidedly cooler according to pollen data. Of the cold water species from Fenton Lake, those whose present distribution extend south only as far as the Great Lakes are not restricted to cooler climates per se, but rather to lakes that are large and deep enough to remain cooler during variable air temperature regimes. Finally, all of the nineteen species discussed here have present distributional ranges which extend north into cooler latitudes today.

So while the species composition of these fossil localities reveals differences in the aquatic environment and community type, it does not appear to indicate much change in climate during the post-glacial period.

It is more difficult when dealing with isolated fossils to reasonably assess the effect of post-glacial climate changes upon the species represented. A fossil assemblage, provided it is part of a contemporaneous fauna, yields information about parameters in addition to climate, such as habitat. The data from these three fossil localities indicate that some caution should be used in attempting to explain a fossil relict in terms of post-glacial climate changes.

Wilson and Zug (1966) attempt to explain a post-glacial fossil *Graptemys pseudogeographica* (false map turtle) in Michigan, outside that species' present range, by postulating a northward

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migration of this species during the climatic optimum, and its retreat to more southerly latitudes with the onset of a drier, cooler climate. However, Ernst and Barbour (1972 p. 126) show the present distribution of *G. pseudogeographica* extending as far north as North Dakota, indicating that this species is quite cold tolerant. Temperature, at least, does not seem to be limiting this species in the western part of its range.

There are a number of lower vertebrates with present distributional ranges that are reasonably explained by glacial and postglacial climate changes (Cross, 1970; Estes, 1970; Smith, 1957, 1965; VanDevender and King, 1975). However, Underhill (1957) noted an earlier study by Radforth (1944) who interpreted northern populations of five fish species in western Ontario as relicts of a post-glacial northern expansion of these species during the climatic optimum. Underhill disagreed, stating that a warmer climate certainly may have allowed greater northward expansion of those species requiring warmer waters, but only if the species under consideration had already extended their ranges beyond any geographical barriers. Since the climatic optimum period was also a period of low water at least in the Lake Michigan and Lake Huron basins (Teller and Bardack, 1975) physical barriers to fish migration may have been greater during this time.

The concept of a single, long term post-glacial climatic optimum period is being replaced by more sophisticated analyses of local climate events (Bryson *et al*, 1970) and presumably the interpretation of post-glacial history will be facilitated as more information on fossil assemblages becomes available.

Acknowledgements

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