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PALAEOECOLOGY OF A NORTHEAST INDIANA WETLAND HARBORING REMAINS OF THE PLEISTOCENE GIANT BEAVER (*CASTOROIDES OHIOENSIS*)

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ABSTRACT. Recovery of a femur of an adult Pleistocene giant beaver (*Castoroides ohioensis*) from a cornfield in Whitley County, Indiana, prompted an analysis of the palaeoecology of the site. Inspection of historic maps and more recent United States Geological Survey (USGS) topographic maps facilitated reconstruction of the pre-disturbance physiography of the site. What is currently a ditched agricultural area was once an extensive shallow lake associated with Spring Creek, which drains into the Eel River. The lake occurred on the interlobate Packerton Moraine created during Wisconsin glaciation. Analysis of subfossils taken from the deepest limnogenic sediments (170 cm) to the upper limit of the peat layer (60 cm) indicates that the lake was eutrophic, mineral-rich, and surrounded by boreal forest for much of its existence. A radiocarbon date of 11,240 ± 80 yr BP, taken within 10 cm of the upper limit of limnogenic sediments, suggests that the lake was extinguished at an early time, perhaps before the demise of the boreal forest. The lake was succeeded by an emergent marsh and finally a peat-forming wetland dominated by bulrushes (*Scirpus* spp.). Anthropogenic re-routing of Spring Creek and other ditching has desiccated the wetland, and only farmland remains. Thirteen plant species and 16 animal species (mostly mollusks) were recovered from the site. The gastropod assemblage was similar to other late-glacial and Holocene marls with only a few exceptions. One species recorded in the deposit, *Lymnaea haldemanni*, is no longer extant in Indiana. *Helicodiscus parellelus* and *Uniomerus tetralasmus* are reported as new subfossil records for the region. The giant beaver remains are presumed to have been deposited *circa* 10,000 yr BP, the same time that the species is thought to have gone extinct.

Keywords: *Castoroides*, Gastropoda, Indiana, lakes, macrofossil, paleoecology, peatland, Pleistocene

The giant beaver, the largest rodent of the North American Pleistocene, is surrounded by controversy. Much of this controversy involves whether or not the Pleistocene giant beaver (*Castoroides ohioensis*) shared feeding and behavioral characteristics with the modern beaver (*Castor*). *Castoroides ohioensis* attained lengths of 1.9–2.2 m (6.2–7.2 feet) and weights of 90–125 kg (200–275 lbs) (McDonald 1994). Early studies concluded that the giant beaver felled trees and built dams as does the modern beaver (e.g., Moore 1890; Hay 1912; Cahn 1932). Moreover, the medial "pinching" of the internal pterygoid plate of the skull, which constricts the posterior end of the nasal passage into upper and lower vents (Moore 1890; Hay 1912; Stirton 1965), was thought by Stirton (1965) to offer a greater air reserve for the extended underwater activity that is so common in *Castor*. Later studies suggest that the incisors were not efficient in cutting trees, and that the giant beaver did not, therefore, construct dams (Powell 1948; Stirton 1965; Holman 1975, 1995; Kurten & Anderson 1980; McDonald 1994). Furthermore, Hay (1912) had long before noted that the "pinching" of the internal pterygoid plate and other alterations of the skull had been an accommodation for the insertion of large internal pterygoid muscles into the pterygoid fossae, rather than a cavity for air reserves. Finally, Holman (1975, 1995) related that *Castoroides* had a smaller brain with a smoother outer surface than in *Castor*, suggesting that *Castoroides* had much less complex behavior patterns and social interactions than the latter.

There is a general agreement that *Castoroides* thrived in lakes and ponds that were bordered by swamps (Powell 1948; Stirton

1965; Saunders 1977; Kurten & Anderson 1980; Harington 1986; Holman 1995) as well as marsh habitats (Holman 1975, 1995). The giant beaver is thought to have co-existed alongside the American mastodont, *Mammut americanum* (Moore 1890; Powell 1948; Graham et al. 1983) and the modern beaver (Harington 1986; McDonald 1994). Most authors believe that *Castoroides* was a good swimmer, though was clumsy on land. Its habits have been envisioned more as those of the marsh-dwelling muskrat (Stirton 1965; Kurten & Anderson 1980), as a giant "swamp rat" moving along wide trails through the coarse vegetation of the marshy shores of a lake or across the swampy floodplain of a glacial river (Powell 1948), or as a "large, clumsy water hog," meandering about in marshes and ponds feeding upon aquatic vegetation (Holman 1975, 1995). It is thought to have fed upon coarse leaves, the roots of sedges, cattails, and other vegetation (Powell 1948; McDonald 1994). Many authors believe that a reduction or loss of its preferred habitat at the end of the Pleistocene and perhaps its overspecialization, including the inability to disperse readily and to build dams, contributed to its extinction (Stirton 1965; Kurten & Anderson 1980; Harington 1986; Holman 1995). Direct competition with the modern beaver may also have been involved (Powell 1948; Kurten & Anderson 1980; Holman 1995).

Although *Castoroides* remains are relatively frequent in Indiana, few of those remains have been recovered in a context that allowed detailed interpretation of the rodent's habitat. With the controversy regarding the animals' behavior, adaptations, and sudden extinction, the examination of the plant and animal subfossils found in association with the giant beaver becomes important. Additionally, the palaeoecology of marl deposits, such as the Wilkinson Locality (described herein), in general, has received less scientific attention than peat deposits. Although several studies have been conducted on marl deposits in North America (Baker 1918; Baker 1920; Whittaker 1921; Russell 1934; La Rocque 1952; Reynolds 1959; Zimmerman 1960; Swinehart 1995), the study of macroscopic subfossils in Indiana's marl deposits has been almost entirely neglected. Only a few studies have been conducted. (Baker 1920; Swinehart 1995; Swinehart & Parker 2000; and a note in Blatchley & Ashley's (1901) treatise on the lakes and marl deposits of the northern part of the State).

The present paper reports on macroscopic subfossils recovered from the Wilkinson Giant Beaver Locality in northeast Indiana. The objectives are to: 1) reconstruct the palaeoenvironment of the Wilkinson giant beaver using macroscopic subfossils as indicators, 2) document, using subfossils and stratigraphy, the biological and limnological changes of the wetland from time of creation to present, 3) compare the subfossils of the Wilkinson Site to other post-glacial wetland deposits in the southern Great Lakes region, and 4) discuss the presence or absence of modern analogues of the Wilkinson palaeoenvironment in the context of potential *Castoroides* habitat.

STUDY AREA

The Wilkinson Locality is located 2.7 miles SE of Larwill, Whitley County, Indiana (NWQ, SWQ, SWQ, NEQ, Sec. 14, T31N, R8E, Lorane Quad). The area is situated in an outwash channel associated with the interlobate Packerton Moraine of late-Wisconsin age. The outwash channel is filled with marls, mucks, and peats (Gray 1989); and these deposits are traversed by Spring Creek, which flows into the Eel River. The bedrock underneath the drift is composed of dolomite and limestone (Gray 1987), and the glacial drift is also limestone-rich. These qualities impart alkaline waters throughout the region except for a few rare cases where biological and other processes favor acidification.

The study site is dominated by limnic and wetland sediments created by an extinct, shallow lake associated with Spring Creek. The original course of Spring Creek was changed as early as the late 1800's by extensive ditching. Subsequent farming has resulted in an area that bears little resemblance to its aquatic origins. Figure 1 illustrates, based on historic maps, soil surveys, and local topography, what the site might have looked like during pre-settlement times.

METHODS

Field methods.—Three exploratory trenches were dug near the site of the recovery of a *Castoroides* femur discovered by Monte Wilkinsen, owner of the site. This was done initially by backhoe, then with shovel, and fi-

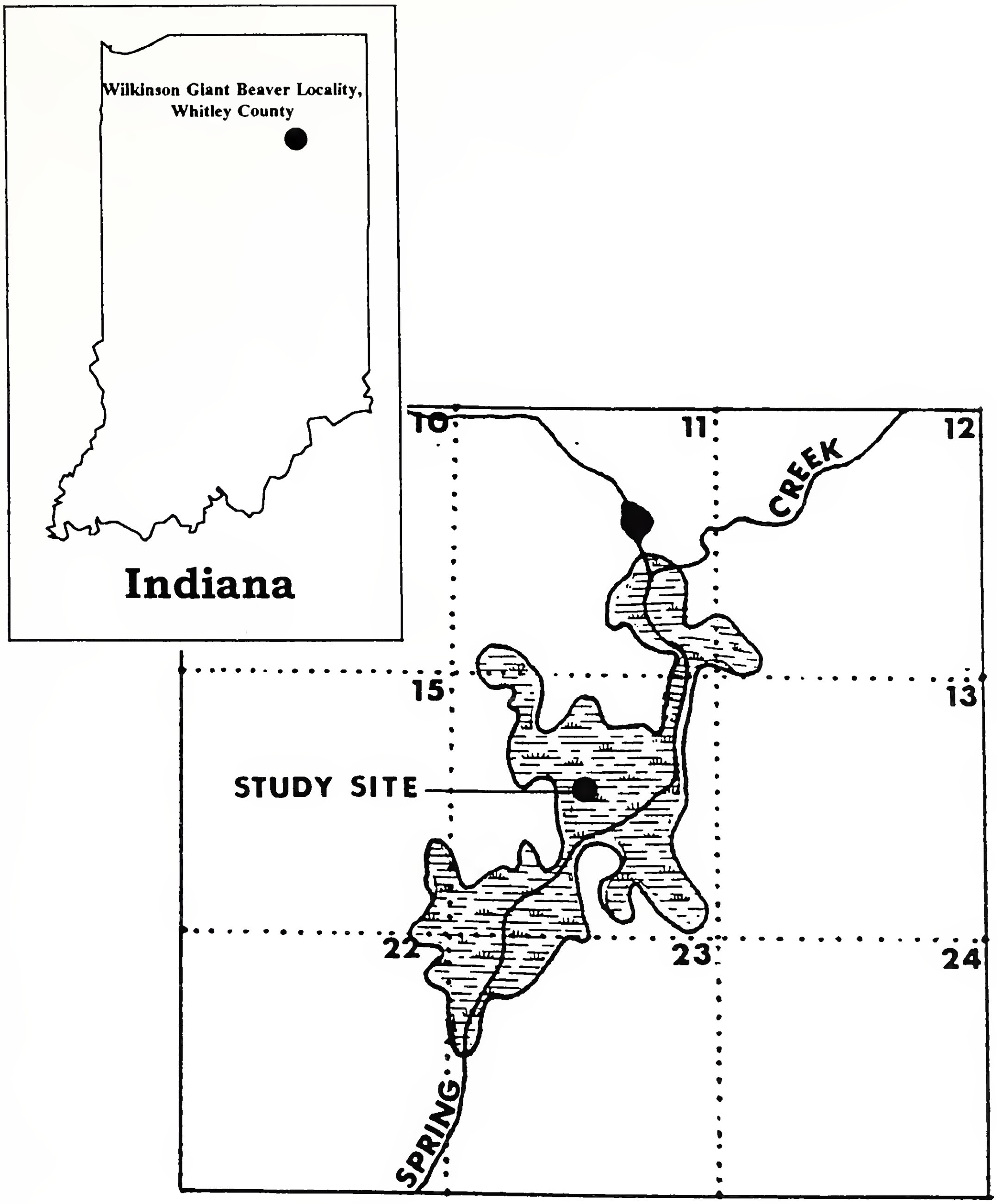

Figure 1.—Map showing the location and pre-settlement physiography of the Wilkinson Giant Beaver Locality, Whitley County, Indiana. Shaded area represents the known extent of lake deposits.

nally by trowel as the peat-marl interface (the level where the bone was recovered) was reached. Because no additional elements of the giant beaver were located during initial trenching, the trenches were then extended further outward, by backhoe, from the original spot of the find (Fig. 2). Water seepage was periodically pumped out of the trenches with a gasoline-powered pump. Initially, randomly selected bulk samples of sediment were washed through a 1.2 mm mesh screen for recovery of vertebrate, mollusk, and plant macrofossil materials. However, only plant macrofossils and mollusks, and no vertebrates, were recovered by this sampling, suggesting the *Castoroides* femur was a solitary bone not associated with the remainder of the skeleton. Therefore, a more systematic method was implemented to focus on the palaeonvironment (plant and invertebrate subfossils) of the site.

A one square-meter column of sediment was removed by trowel at 10 cm intervals from the surface down to the base of the deposit. The sediments were then transported to screening stations for washing, and the resulting concentrate was bagged for laboratory rewashing, sorting, and analysis. Water for screening was provided by pumps, drawing from groundwater seepage from a nearby sump. Additionally, bulk sediments were taken from each 10 cm depth interval and bagged for more detailed, quantitative sampling to be conducted in the laboratory.

Laboratory methods.—In the laboratory, all concentrate was re-washed to remove additional sand and clay. The resulting concentrate was dried and examined under a binocular microscope (10×), and the subfossils were hand sorted. Wood samples from the 70–80 and 90–100 cm depth intervals were submitted to Beta Analytic, Inc., for radiocarbon (^{14}C) dating. Swinehart undertook the study of plant macrofossils, mollusks, and the sediment samples, and Richards studied the few vertebrate remains.

Coarse, medium, and fine gravels, as well as woody and fibrous material from each depth interval were separated, oven-dried, and weighed with a Mettler PE 360 balance. Organic subfossil remains from the bulk-screening residues from all depths were identified and counted. This analysis was supplemental to that conducted on the bulk samples, and resulted in the documentation of infrequent macrofossils not encountered in the sub-sampling of bulk material.

Bulk sediment was sub-sampled in the laboratory for macrofossil analysis. Subsamples of 50 cm^3 volumes from each 10 cm depth interval were obtained by water displacement. Macrofossil subsamples were dispersed by gentle agitation in warm water. Some clasts of sediment required breakage by hand underwater. Dispersed sediments were then washed through a series of sieves, the smallest being 0.4 mm mesh. Sieve residue was placed into containers and analyzed immediately. All recognizable macrofossils were identified and counted. The resulting macrofossil diagrams represent the number of fragments per 50 cm^3 of bulk sediment (Fig. 2). Seeds and achenes were identified with the aid of Montgomery (1977), Martin & Barkely (1961), and Jessen (1955); mosses, Crum & Anderson (1981); bivalves, Cummings & Mayer (1992); and gastropods, Harmen & Berg (1971). Macrofossil diagrams were generated using Tilia© and Tilia●Graph© computer software (Grimm 1996). Voucher specimens of macrofossils were placed in vials containing 60% ethanol and are held by the first author and by the Indiana State Museum.

RESULTS

Age and stratigraphy.—The depth of limnic and wetland sediments at the Wilkinson Locality was 170 cm. The underlying material was composed of glacial outwash that was superseded by a layer of silt (10 cm). Most of the profile was composed of marl. The 70–80 cm and 90–100 cm depths had radiocarbon dates of 11,240 ± 80 yr BP and 11,990 ± 90 yr BP, respectively. The marl layer was probably produced between 14,000 and 10,500 yr BP. It is superseded by 20 cm of hemic sedge peat, sand and humus. The amount of coarse gravel (> 4 mm diameter) remained relatively constant throughout the profile but increased dramatically near the top of the marl stratum before disappearing at the initiation of the peat layer (Fig. 2). Smaller gravels and sands were present throughout the profile.

Systematic palaeobiology.—Thirteen plant taxa and sixteen animal taxa were recovered as macroscopic subfossils (Fig. 2). A brief discussion of each is presented below.

KINGDOM PLANTAE

Division Bryophyta
Family Amblystegiaceae

cf. *Campylium stellatum* (Hedw.) C. Jens.—*Subfossil Material:* Gametophyte fragments (INSM 71.12.2901.001–.002; Swinehart #4B.4.3.16). *Occurrence:* Occasional in marl between the depths of 120–140 cm. Habitat: In open, wet areas of highly alkaline marshes and fens (Crum & Anderson 1980). Also found in swamps and on wet banks (Welch 1957).

Division Spermatophyta
Family Pinaceae

Abies balsamea (L.) Mill.—*Subfossil material:* Leaf fragments (INSM 71.12.002901.003). *Occurrence:* Infrequent in marl, silt, and outwash between the depths of 100–165 cm. Habitat: Coniferous and mixed forests; occasionally in cedar swamps, fens, and bogs. Comments: Other macroscopic subfossil records from Indiana include Blueberry Bog, Elkhart County (Swinehart & Parker 2000) and Celery Bog, Tippecanoe County (Swinehart unpubl. data).

Larix laricina (DuRoi) K. Koch.—*Subfossil material:* Leaf scarred portions of twigs (INSM 71.12.002901.004–.005). *Occurrence:*

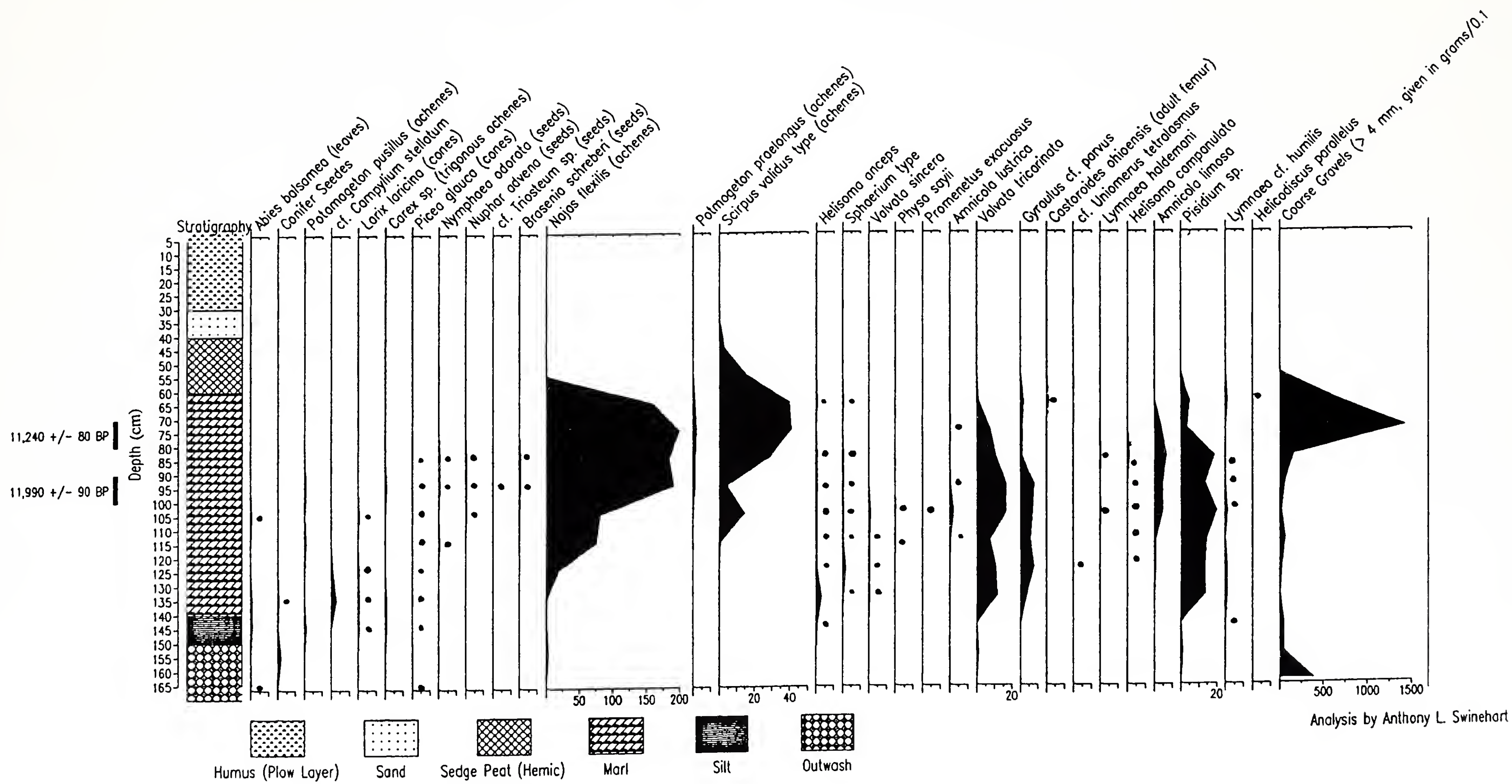

Figure 2.—Diagram of subfossil taxa from the Wilkinson Locality and their stratigraphic frequency and abundance. Histograms of individual taxa represent the number of subfossil fragments for 50 cm³ of bulk sediment. A dot indicates that the taxon was present, but in a quantity less than one fragment per 50 cm³. Coarse gravel is given as weight in grams per 0.1 m³ of bulk sediment.

Occasional in marl and silt between the depths of 100–150 cm. Habitat: Swamps, lakeshores and stream borders, fens, and bogs. Restricted to peatlands in the southern portions of its range. Pioneering opportunists, they prefer open areas where competition for light with other trees is minimal. Comments: Other macroscopic subfossil records from Indiana include Prairie Creek Site, Daviess County (Whitehead & Jackson n.d.); Blueberry Bog, Elkhart County (Swinehart & Parker 2000); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Little Arethusa Bog, Kosciusko County (Swinehart & Parker 2000); Binkley Fen and Ropchan Memorial Bog, Steuben County (Swinehart & Parker 2000); Celery Bog, Tippecanoe County (Swinehart unpubl.); Shafer Mastodont Site, Warren County (Swinehart 1996).

Picea glauca (Moensch) Voss.—*Subfossil material:* Leaves and cones (INSM 71.12. 002901.006; Swinehart #4B.4.14.15). *Occurrence:* Frequent in marl and silt between the depths of 80–150 cm. Also present in outwash at a depth of 165 cm. Habitat: Well-drained coniferous swamps, lakeshores and stream-borders, mixed forests (Voss 1972), and occasionally in peatlands; mostly in boreal climates. Extinct in Indiana. Comments: Other macroscopic subfossil records from Indiana include Prairie Creek Site, Daviess County (Whitehead & Jackson, n.d.); Bristol Fen, Elkhart County (Swinehart 1995); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Shafer Mastodont Site, Warren County (Swinehart 1996); Aker Mastodont Site, Marshall County (Swinehart unpubl. data).

Family Potamogetonaceae

Potamogeton praelongus Wulfen.—*Subfossil material:* Achenes (INSM 71.12.002901. 008–.011). *Occurrence:* Common in marl between the depths of 60–100 cm. Habitat: Lakes, in water up to 7 m (Voss 1972), in clear waters, often associated with *Ceratophyllum demersum, Najas flexilis, Potamogeton amplifolius, P. gramineus, P. natans, P. pectinatus,* and *P. robbinsii* (Swink & Wilhelm 1994).

Potamogeton pusillus L.—*Subfossil material:* Achenes (INSM 71.12.002901.035). *Occurrence:* Infrequent in marl and silt between the depths of 90–150 cm. Habitat: Lakes and ponds and occasionally quiet waters of streams, in shallow waters less than 2 m (Voss 1972), prefers calcareous waters, often associated with *Elodea canadensis, Myriophyllum exalbescens, Najas flexilis, Nuphar advena, Potamogeton natans, P. nodosus, P. pectinatus, P. zosteriformis,* and *Vallisneria americana* (Swink & Wilhelm 1994). Comments: Other macroscopic subfossil records of the genus *Potamogeton* from Indiana include Prairie Creek Site, Daviess County (Whitehead & Jackson, n.d.); Blueberry Bog and Bristol Fen, Elkhart County (Swinehart 1995; Swinehart & Parker 2000); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Burket Bog and Little Arethusa Bog, Kosciusko County (Swinehart & Parker 2000); Yost Bog, Lagrange County (Swinehart & Parker 2000); Aker Mastodont Site, Marshall County (Swinehart unpubl. data); Dutch Street Bog, Noble County (Swinehart & Parker 2000); Binkley Fen, Steuben County (Swinehart & Parker 2000); Shafer Mastodont Site, Warren County (Swinehart 1996).

Family Najadaceae

Najas flexilis (Willd.) Rostk. & F.W. Schmidt.—*Subfossil material:* Achenes (INSM 71.12.002901.012; Swinehart #4B.4. 16.18). *Occurrence:* Extremely abundant in marl throughout the 60–130 cm depths. Habitat: Extremely common in lakes, ponds, marshes, sloughs, rivers and streams. Also found on soft bottoms of open waters in peatlands. Commonly associated with *Ceratophyllum demersum, Elodea canadensis, Lemna minor, Myriophyllum exalbescens, Potamogeton foliosus, P. natans, P. nodosus, P. pectinatus,*, and *Vallisneria americana* (Swink & Wilhelm 1994). Fruits abundantly. Comments: Other macroscopic subfossil records of *Najas flexilis* from Indiana include Blueberry Bog and Bristol Fen in Elkhart County (Swinehart 1995; Swinehart & Parker 2000); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Burket Bog, Little Chapman Bog, and Kaiser Lake Fen in Kosciusko County (Swinehart & Parker 2000); Yost Bog, Lagrange County (Swinehart & Parker 2000); Aker Mastodont Site, Marshall County (Swinehart unpubl.); Dutch Street Bog, Tamarack Bog, and Svoboda Fen in Noble County (Swinehart 1994; Swinehart & Parker 2000); Binkley Fen and Ropchan

Memorial Bog in Steuben County (Swinehart & Parker 2000); and the Shafer Mastodont Site, Warren County (Swinehart 1996).

Family Cyperaceae

Carex sp.—*Subfossil material:* Achenes (INSM 71.12.002901.015). *Occurrence:* Infrequent in marl and silt in the 90–150 cm depths. Habitat: Variable. Comments: Other macroscopic subfossil records of *Carex* from Indiana include Prairie Creek Site, Daviess County (Whitehead & Jackson, n.d.); Blueberry Bog, Elkhart County (Swinehart & Parker 2000); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Burket Bog, Little Chapman Bog, and Kiser Lake Fen in Kosciusko County (Swinehart & Parker 2000); and Ropchan Memorial Bog, Steuben County (Swinehart & Parker 2000).

Scirpus acutus (Muhl.).—*Subfossil material:* Achenes (INSM 71.12.002901.016; Swinehart #4B.4.16.19). *Occurrence:* Extremely abundant in marl and sedge peat between the depths of 40–110 cm. Habitat: In shallow water or wet areas around lakes, ponds, marshes, and flowing waters; also found in fens and marl flats. *Scirpus validus* which has a similar achene grows in similar habitats. Comments: Other macroscopic subfossil records of *Scirpus* from Indiana include Blueberry Bog, Elkhart County (Swinehart & Parker 2000); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Burket Bog, Little Arethusa Bog, Little Chapman Bog, and Kiser Lake Fen in Kosciusko County (Swinehart & Parker 2000); Yost Bog, Lagrange County (Swinehart & Parker 2000); Aker Mastodont Site, Marshall County (Swinehart, unpubl. data); Dutch Street Bog, Noble County (Swinehart & Parker 2000); and Binkley Fen and Ropchan Memorial Bog in Steuben County (Swinehart & Parker 2000).

Family Nymphaeaceae

Brasenia schreberi Gmel.—*Subfossil material:* Seeds (INSM 71.12.002901.020–.021). *Occurrence:* Frequent in marl between the 80–100 cm depths. Habitat: Quiet ponds and lakes, usually in soft, acid waters (Voss 1972); commonly associated with *Elodea canadensis, Lemna minor, Myriophyllum exalbescens, Nuphar advena, Nymphaea odorata, Polygonom amphibium, Pontedaria cordata, Potamogeton pectinatus, Spirodela polyrhiza,* and *Utricularia vulgaris* (Swink & Wilhelm 1994). Comments: Other macroscopic subfossil records of *Brasenia schreberi* from Indiana include Blueberry Bog, Elkhart County (Swinehart & Parker 2000); Yost Bog, Lagrange County (Swinehart & Parker 2000); Burket Bog, Little Arethusa Bog, and Little Chapman Bog in Kosciusko County (Swinehart & Parker 2000); Dutch Street Bog and Tamarack Bog in Noble County (Swinehart 1994; Swinehart & Parker 2000); and Binkley Fen, Steuben County (Swinehart & Parker 2000).

Nymphaea tuberosa Paine.—*Subfossil material:* Seeds (INSM 71.12.002901.022–.024). *Occurrence:* Infrequent in marl between the 80–120 cm depths. Habitat: Emergent in quiet, shallow water of lakes, ponds, rivers and streams. Often associated with *Brasenia schreberi, Ceratophyllum demersum, Lemna minor, Najas flexilis, Nuphar advena,* and *Pontedaria cordata.* Comments: Other macroscopic subfossil records of *Nymphaea* from Indiana include Bristol Fen and Blueberry Bog in Elkhart County (Swinehart 1994; Swinehart & Parker 2000); Burket Bog and Little Chapman Bog in Kosciusko County (Swinehart & Parker 2000); and Yost Bog, Lagrange County (Swinehart & Parker 2000).

Nuphar advena Ait.—*Subfossil material:* Seeds (INSM 71.12.002901.025; Swinehart #4B.4.16.17). *Occurrence:* Frequent in marl between the 80–110 cm depths. Habitat: Emergent in quiet waters of lakes, ponds, rivers, and streams. Often associated with *Brasenia schreberi, Ceratophyllum demersum, Lemna minor, Nymphaea tuberosa* and *Pontedaria cordata.* Comments: Other macroscopic subfossil records of *Brasenia schreberi* from Indiana include Bristol Fen, Elkhart County (Swinehart 1994); Christensen Mastodont Site, Hancock County (Whitehead et al. 1982); Burket Bog, Little Arethusa Bog, and Little Chapman Bog in Kosciusko County (Swinehart & Parker 2000); Aker Mastodont Site, Marshall County (Swinehart unpubl. data); Dutch Street Bog and Svoboda Fen in Noble County (Swinehart & Parker 2000); and Ropchan Memorial Bog, Steuben County (Swinehart & Parker 2000).

Family Caprifoliaceae

cf. *Triosteum* sp.—*Subfossil material:* Seed (INSM 71.12.002901.028). *Occurrence:* A single specimen from the 90–100 cm depth. Habitat: Dry or moist woods. Comments: No other records are known from Indiana.

KINGDOM ANIMALIA

Phylum Mollusca
Family Physidae

Physa sayii Tappan.—*Subfossil material:* Shells (INSM #71.10.2637.8–.9; Swinehart #4B.5.18.2). *Occurrence:* In marl; 100–120 cm. Habitat: This species is common to still, shallow waters (0.3–0.8 m) in open areas. It prefers moderate vegetation and well-aerated water (Zimmerman 1960). While Zimmerman (1960) reports that *P. sayii* prefers protected areas, Harmen & Berg (1971) found that it was most common in exposed areas. Goodrich et al. (1944) note that it can sometimes be found on wave-battered shores. Comments: Holocene subfossil records from the southern Great Lakes region include; Peoria County, Illinois (Baker 1918), Logan County, Ohio (Zimmerman 1960) and Kosciusko County, Indiana (Swinehart & Parker 2000). While Zimmerman (1960) and Swinehart & Parker (2000) found many individuals throughout the Ohio and Indiana marl deposits, respectively, Baker (1918) found only one juvenile in Illinois. The species was infrequent at the Wilkinson site and restricted to the 100–120 cm depths. *Physa sayii* is presently common in northern Indiana in lakes and occasionally in streams (Goodrich et al. 1944).

Family Lymnaeidae

Lymnaea cf. *L. humilis* Say.—*Subfossil material:* Shells (INSM #71.10.2637.1–.7; Swinehart #4B.5.18.1). Occurrence: In marl between 80–110 cm. Also in silt at 140–150 cm. Habitat: Harmen & Berg (1971) report this species as inhabiting exposed mud flats, where they forage between the gravels with their shells partially exposed to the air. Goodrich et al. (1944) also report this species as inhabiting mud flats. Comments: Subfossil reports for this species in the southern Great Lakes region come from Blatchley & Ashley (1901) from marls taken from North Mud Lake, Fulton County, Indiana; Baker (1920) from Flat Rock River, Bartholomew County, Indiana; Swinehart (1995) from Elkhart County, Indiana (misidentified as *L. palustris*); and Swinehart & Parker (2000) from Kosciusko County, Indiana. Blatchley & Ashley (1901) found the species occupying 12% of the total mollusks in the Fulton County deposit. Swinehart (1995) found it to be abundant in the Elkhart County deposit but infrequent in the Kosciusko County deposit. It was infrequent throughout the marl layer in the present study. Similar species under the generic synonyms of *Galba*, *Fossaria* and *Stagnicola* are common in Holocene marls of the region (see Baker 1918; La Rocque 1952; La Rocque & Forsythe 1957; Reynolds 1959; Zimmerman 1960). Goodrich et al. (1944) recognize two subspecies in Indiana's current mollusk fauna, *L. humilis modicella* and *L. humilis rustica*, but records of their current distribution in the State are incomplete.

Lymnaea haldemani Binney.—*Subfossil material:* Shells (INSM #71.10.2637.10; Swinehart #4B.5.18.9). *Occurrence:* In marl in the 80–90 cm and 100–110 cm depths. Habitat: Common in shallow waters (0.3–1 m) of larger lakes in abundant vegetation. It prefers sheltered bays, and is commonly found on floating vegetation and on the undersides of waterlilies (Zimmerman 1960). It has also been found on rotting *Typha* leaves (Harmen & Berg 1971). This species is always found in limited numbers (Zimmerman 1960). Comments: The only other known Holocene subfossil record for this species in the southern Great Lakes region is from Zimmerman (1960) from Logan County, Ohio. The fragile nature of the shell along with the fact that living specimens of this species are rarely found in large numbers limits palaeoecological inferences regarding post-glacial populations and distribution. Shells, always fragmentary, were rare in the Wilkinson deposit. *Lymnea haldemani* is not known to exist presently in Indiana.

Family Planorbidae

Helisoma anceps (Menke).—*Subfossil material:* Shells (INSM #71.10.2637.11–.16; Swinehart #4B.5.18.4). *Occurrence:* Frequent in marl and silt between the 60–150 cm depths. Habitat: Common in shallow waters (< 1 m) with abundant vegetation. While Reynolds (1959) reports that it prefers exposed habitats of open lakes, Harmen & Berg (1971) found it most commonly on inorganic substrates in protected areas of ponds as well as quiet pools of small streams. Comments: Holocene subfossil records for the southern

Great Lakes region include Mahomet, Illinois (Baker 1918), McLean County, Illinois (Baker 1930), Fulton County, Indiana (Blatchley & Ashley 1901), Bartholomew County, Indiana (Baker 1920), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), Ross County, Ohio (Reynolds 1959) and Logan County, Ohio (Baker 1920; Zimmerman 1960). The species is relatively abundant in the reported deposits. Probably common in the lake region of Indiana at present.

Helisoma campanulata (Say).—*Subfossil material:* Shells (INSM #71.10.2637.17–.19); Swinehart #4B.5.18.11). *Occurrence:* Frequent in marl between the 80–130 cm depths. Habitat: Occurs in shallow waters of varying substrates in both protected and wave battered areas (Zimmerman 1960). Harmen & Berg (1971) found it mostly on inorganic substrates of small marshy lakes. They rarely found it associated with other *Helisoma* spp., with the exception of *H. anceps* and *H. trivolvis*. Dexter (1950) found the species to be common in *Chara/Myriophyllum, Nymphaea/Pontedaria*, and *Decodon* zones of a basic bog lake in Ohio. Comments: Holocene subfossil records for *H. campanulata* in the southern Great Lakes region come from Mahomet, Illinois (Baker 1918), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), and Logan County, Ohio (Baker 1920; Zimmerman 1960). Although present throughout many marl deposits, this species is usually found in relatively low numbers at any given depth. Presently, *H. campanulata* is common in the lake area of Indiana (Goodrich et al. 1944).

Gyraulus cf. *G. parvus* (Say).—*Subfossil material:* Shells (INSM #71.10.2637.20–.26; Swinehart #4B.5.18.7). *Occurrence:* Abundant in marl between the depths of 60–140 cm. Rare between 140–165 cm. Habitat: Occurs in small, shallow, protected waters (Zimmerman 1960), especially in ponds and backwaters with dense aquatic vegetation (Harmen & Berg 1971). Dexter (1950) found it in all but the *Larix* and *Quercus-Fagus-Ulmus* zones of an Ohio peatland. Comments: Records of Holocene subfossils of *G. parvus/altissimus* in the southern Great Lakes region include McLean County, Illinois (Baker 1930), Fulton County, Indiana (Blatchley & Ashley 1901), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), Madison County, Ohio (La Rocque 1952), Ross County, Ohio (Reynolds 1959), and Logan County, Ohio (Zimmerman 1960). *Gyraulus parvus/altissimus* is usually very abundant in post-glacial marl deposits. Presently found throughout Indiana (Goodrich et al. 1944).

Promenetus exacuosus (Say).—*Subfossil material:* One shell. *Occurrence:* In marl, 100–110 cm. Habitat: Found in quiet waters associated with many types of substrates (Zimmerman 1960), but mostly over sand and mud with thick vegetation (Reynolds 1959). La Rocque (1952) reports that it is most common in marshy areas or mud flats with pH's from 7–7.6. Similarly, Harmen & Berg (1971) found it most commonly in cattail marshes on the undersides of dead, floating *Typha* leaves. Dexter (1950) found it abundantly in the *Nymphaea/Pontedaria, Potamogeton*, and *Decodon* zones. It is locally associated with the algae *Cladophora* and *Oedogonium* (Reynolds 1959). Zimmerman (1960) reports that *P. exacuosus* is most common to cooler waters, and dense vegetation favors the lower temperatures that it seems to prefer. Comments: Holocene subfossil records for *P. exacuosus* in the southern Great Lakes region include Fulton County, Indiana (Blatchley & Ashley 1901), Madison County, Ohio (La Rocque 1952), Ross County, Ohio (Reynolds 1959), and Logan County, Ohio (Baker 1920, Zimmerman 1960). Although its presence is not uncommon in Holocene marls, it usually occurs in small numbers. Goodrich et al. (1944) assumed that it is currently found throughout Indiana.

Family Hydrobiidae

Amnicola limosa (Say).—*Subfossil material:* Shells (INSM #71.10.2637.27–.31; Swinehart #4B.5.18.13). *Occurrence:* Abundant in marl between 70–130 cm. Habitat: Common in protected areas of shallow lakes and muddy bays in 0–3 m of water (Zimmerman 1960). It is also found in marshes, ponds, temporary stream pools, creeks and rivers (Harmen & Berg 1971). Reynolds (1959) reports that it has been found in brackish water as well as freshwater and prefers sandy substrates with dense beds of *Chara, Potamogeton, Vallisneria*, and *Elodea*. Dexter (1950) reports it from the *Chara/Myriophyllum, Nymphaea/*

Pontedaria, and *Decodon* zones. Zimmerman (1960) states the most important limiting factor for this species is vegetation (preferably abundant) and protection from exposure. He also reports that this species can endure long periods of emergence as long as it remains moist, but unusually high water temperatures can rapidly exterminate it from a waterbody. Comments: Holocene subfossil records of *A. limosa/leightoni* in the southern Great Lakes region include Mahomet, Illinois (Baker 1918), McLean County, Ohio (Baker 1930), Fulton County, Indiana (Blatchley & Ashley 1901), Bartholomew County, Indiana (Baker 1920), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), Ross County, Ohio (Reynolds 1959), and Logan County, Ohio (Zimmerman 1960). This species is usually very abundant in Holocene marl deposits. Presently found throughout Indiana, especially in the lake area (Goodrich et al. 1944)

Amnicola lustrica Pilsbry.—*Subfossil material:* Shells (INSM #71.10.2637.32–.34; Swinehart #4B.5.18.10). *Occurrence:* Infrequent in marl between the depths of 70–120 cm. Habitat: This species is less common than *A. limosa,* although it occupies similar habitats (Harmen & Berg 1971). It prefers shallow (0–2 m), highly vegetated waters, where it often inhabits filamentous algae (Zimmerman 1960). Comments: Holocene records for *A. lustrica* include Fulton County, Indiana (Blatchley & Ashley 1901), Bartholomew County, Indiana (Baker 1920), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), and Logan County, Ohio (Baker 1920; Zimmerman 1960). It is presently found in the lake area of Indiana.

Family Valvatidae

Valvata sincera Say.—*Subfossil material:* Shells (INSM #71.10.2637.42–.44; Swinehart #4B.5.18.12). *Occurrence:* Frequent in marl; 110–140 cm. Habitat: This species is reported as being primarily from deep water (5–6 m), usually below 3 m in depth, of cold lakes with limited vegetation (Zimmerman 1960). Harmen & Berg (1971) found it at a depth of 5 m. Comments: Holocene subfossil records for *V. sincera* include Urbana, Illinois (Baker 1920), Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000) and Logan County, Ohio (Zimmerman 1960). A similar species *V. lewisi* was reported for Madison County, Ohio by La Rocque (1952). *Valvata sincera* is often found in association with *V. tricarinata* but in much fewer numbers. *Valvata sincera* is presently common in lakes in northern Indiana.

Valvata tricarinata (Say).—*Subfossil material:* Shells (INSM #71.10.2637.35–.41; Swinehart #4B.5.18.8). *Occurrence:* Abundant in marl between the 60–140 cm depths. Occasional in silt and outwash between 140–165 cm. Habitat: Inhabits a wide variety of conditions but is most common to lakes. Harmen & Berg (1971) report that most specimens from lotic conditions are depauperate. Dexter (1950) found it to be common in the *Chara/Myriophyllum, Potamogeton, Nymphaea/Pontedaria* and *Decodon* zones. Reynolds (1959) reports that the species is partial to firm bottoms and is usually associated with *Oedogonium, Cladophora* and *Vaucheria.* Comments: Holocene subfossils of *V. tricarinata* in the southern Great Lakes region have been reported for Urbana, Illinois (Baker 1920), Mahomet, Illinois (Baker 1920), McLean County, Illinois (Baker 1930), Bartholomew County, Indiana (Baker 1920) Elkhart County, Indiana (Swinehart 1995), Kosciusko County, Indiana (Swinehart & Parker 2000), Logan County, Ohio (Baker 1920; Zimmerman 1960), and Ross County, Ohio (Reynolds 1959). This is one of the most widely distributed and abundant mollusks of Holocene marls. Goodrich et al. (1944) speculate that this was one of the first aquatic mollusks to re-invade newly deglaciated areas. It presently occurs throughout Indiana (Goodrich et al. 1944).

Family Endodontidae

Helicodiscus parallelus (Say).—*Subfossil material:* One shell (Swinehart #4B.5.18.3). *Occurrence:* In marl, 60–70 cm. Habitat: Goodrich et al. (1944) report this species as being most common in flood plains. Comments: Accounts of this species in other Holocene marls are not known. Only a single specimen was recovered from the Wilkinson site. The species, presently, is distributed throughout Indiana.

Family Sphaeridae

Pisidium sp.—*Subfossil material:* Shells (INSM #71.10.2637.45.50; Swinehart #4B.5.

18.6). *Occurrence:* Abundant in marl between 60–140 cm. Occasional in silt and outwash between 140–165 cm. Habitat: Variable. Comments: Common in Holocene marls.

Sphaerium sp.—*Subfossil material:* Shells (INSM #71.10.2637.51–.54; Swinehart #4B.5.18.14). *Occurrence:* Frequent in marl and silt between 60–150 cm. Habitat: Variable. Comments: Common in Holocene marls.

Family Unionidae

cf. *Uniomerus tetralasmus* (Say).—*Subfossil material:* Single specimen (both valves) (INSM #71.10.2637.). *Occurrence:* In marl; 60–70 cm. Habitat: Common in ponds, small creeks, and headwaters of larger streams in mud or sand (Cummings & Mayer 1992). May withstand desiccation and, as a result, is often found where other mussels are absent (Cummings & Mayer 1992). Comments: There are no known Holocene subfossil records for this species in the Midwest.

Phylum Chordata (Subphylum Vertebrata)
Class Aves
Order Anseriformes
Family Anatidae

Branta canadensis, (Canada Goose).—*Subfossil material:* Left ulna, distal 2/5 (INSM #71.3.143.1). Habitat: Historically, the Canada goose was a common migrant and permanent resident of the state. It favors larger bodies of water adjacent to extensive marshland, but may be found on nearly any aquatic habitat (Mumford & Keller 1984).

Class Mammalia
Order Rodentia
Family Castoridae

Castoroides ohioensis, (giant beaver).—*Subfossil Material:* Right femur, lacking medial condyle area; recovered in two pieces (INSM #71.3.128). *Occurrence:* Recovered on surface from soils dug from trench. Because trenching extended only down into the upper few inches of marl, and because the femur was impacted with mollusk-rich marl, it is likely that the femur originally occurred within the upper few inches of the marl level, likely within the 60–70 cm depth. Habitat: Because the species is extinct its habitat preference and habits are not known for sure. However, the functional morphology of skeletal elements (discussed above) and ecological associations (discussed below) do provide some insight. Comments: Including the present, there are 16 credible published records for Indiana: Boone County, Jamestown (Hay 1912); Cass County, Logansport (Martin 1912; Hay 1912); Daviess County, Prairie Creek Site (Tomak 1975); Dekalb County, unspecified locality (Cahn 1932); Grant County, Fairmount (Hay 1912, 1912b); Hancock County, Greenfield vicinity (Moore 1893); Hancock County, Christensen mastodont locality (Graham, Holman and Parmalee 1983); Madison County, Summitville (Hay 1912); Martin County, Shoals (Adams 1946); Miami County, Macy (Hay 1923); Newton County, Mount Ayr (Cahn 1932); Randolph County, Winchester/Union City (Moore 1890, 1893); St. Joseph County, unspecified locality (Engels 1931); Starke County, Grovertown (Hay 1923); Wayne County, Richmond (Moore 1893); Whitley, Wilkinson locality (present). Three additional early published records cannot be substantiated: Carroll County (Cope & Wortman 1884); Kosciusko County (Cope & Wortman 1884); and Vanderburgh County (Collett 1876). Remains from four additional localities (Madison, Pike, Wayne and Whitley Counties) have not yet been published upon, and will not be detailed here.

Castor canadensis, (Beaver).—*Subfossil material:* Anterior lumbar/posterior thoracic vertebra, neural arch only, lacking spine (INSM # 71.3.143.2). Habitat: In Indiana, the beaver is most abundant in the lakes, marshes, and streams of the northern part of the state (Mumford & Whitaker 1982). Comments: The vertebra was from the Thoracic T-11 through T-14, or lumbar L-1 or L-2 part of the series. A subadult was represented. It is interesting that remains of the modern beaver occurred stratigraphically earlier on the Wilkinson locality than those of the giant beaver.

Order Artiodactyla

Large Artiodactyla, *sp. indet.*—*Subfossil material:* Molariform enamel portion (INSM # 71.3.143.3). Comments: Crown enamel portion from hypsodont molariform tooth that includes one fossette. The enamel is relatively unworn.

DISCUSSION

Geologic history.—The Wilkinson Site, began as a raging meltwater river that deposited clean, sorted glacial drift in a channel on the Packerton Moraine. As the meltwaters slowed, a few organic remains indicative of the surrounding forest composition were left behind in the outwash. Finally, stagnation of the water resulted in settling of finer materials, primarily silts, which blanketed the outwash. A shallow lake remained, and an inlet and outlet were maintained by Spring Creek, which provided ample drainage and oxygen- and nutrient-rich water. It may also have been the source of occasional conifer remains, which indicate a surrounding forest of *Picea glauca*, *Abies balsamea* and *Larix laricina*. Infrequent remains of charred wood suggest occasional fires.

The waters feeding Wilkinson Lake were nearly saturated with bicarbonates brought into solution via contact with the characteristically lime-rich glacial till. Because the marl in the basin did not appear to be formed wholly or partially by the calcium carbonate tests of *Chara* thalli (none were recovered), it can be assumed that the primary source of the marl precipitate was the uptake of CO_2 by phytoplankton and littoral vegetation, or possibly the flow of sub-terranian aquifers into the lake. The shallow nature of the lake meant that the trophogenic zone extended to the substrate throughout, and carbon dioxide levels were probably low throughout the water column. This would hinder most marl precipitates from being brought back into solution as bicarbonate.

The *Castoroides* femur occurred at a level when coarse gravel had also been deposited, possibly accounting for the stream transport and/or scattering of unburied skeletal remains. (This was also a period when molluscan remains were becoming sparse, suggesting at least periodic drying of the habitat. A gradual increase in *Najas* and *Scirpus* remains coincides with the decrease in mollusks).

Vegetation.—The early submergent flora was composed of pondweeds such as *Potamogeton pusillus* and *Najas flexilis*. Both are characteristic of mineral-rich waters. The *Najas* eventually became extremely abundant, at least as evidenced by the abundant remains of its achenes in the sediment. While *Najas* and additional submergent vegetation, such as *Potamogeton praelongus*, became important members of the flora, emergent vegetation began to appear. *Nymphaea odorata*, *Nuphar advena* and *Brasenia schreberi*, because of the shallow depth, probably grew across the entire water body.

As vegetative remains and marl began to fill-in the shallower margins of Wilkinson Lake, bulrushes (*Scirpus validus* and *Scirpus acutus*) took hold and colonized. While most were probably restricted to the marginal wetlands, many probably invaded the shallow waters of the open lake. It is this marsh environment where the giant beaver lived, died, and was buried. Eventually, the open water filled-in entirely, and a sedge- and bulrush-dominated wetland remained. Spring Creek maintained its presence in the area, and probably changed course many times as it traversed the sedge meadow. The creek carried sediments, and sometimes gravels, that were deposited along its course. During spring snowmelt, fast moving waters would carry large gravels into the wetland. This may explain the curious abundance of coarse gravel in strictly limnic sediments below the marl/peat interface.

Mollusks.—Based on modern analogues, it is concluded that the molluscan fauna encountered in the marls of the Wilkinson site indicates the area was once a relatively small, shallow, wind-sheltered lake with moderate to heavy vegetation cover and the presence of muddy or marly flats. The mollusks give some indication of the water quality in Wilkinson Lake. Based on ecological amplitudes provided by Harmen & Berg (1971) the composition of the mollusk assemblage at Wilkinson Lake suggests that the water probably maintained pH values of 7–8.5, alkalinity values of 100–150 ppm, and dissolved oxygen values of 10–14 ppm.

The decline of mollusks at the end of marl production is attributed to the closure of open water habitat and the transition to a sedge meadow. Given the position and age of the radiocarbon dates, Wilkinson Lake and the subsequent sedge meadow probably extinguished long before the demise of the boreal forest.

By far the most abundant mollusks throughout the marls of the Wilkinson deposit were *Valvata tricarinata, Gyraulus parvus, Amnicola limosa* and *Pisidium* spp. Similarly, Swinehart (1995, unpubl. B.A. thesis, Goshen College) found these species to be the most abundant throughout the Bristol Fen deposit in Elkhart County, Indiana. Reynolds (1959)

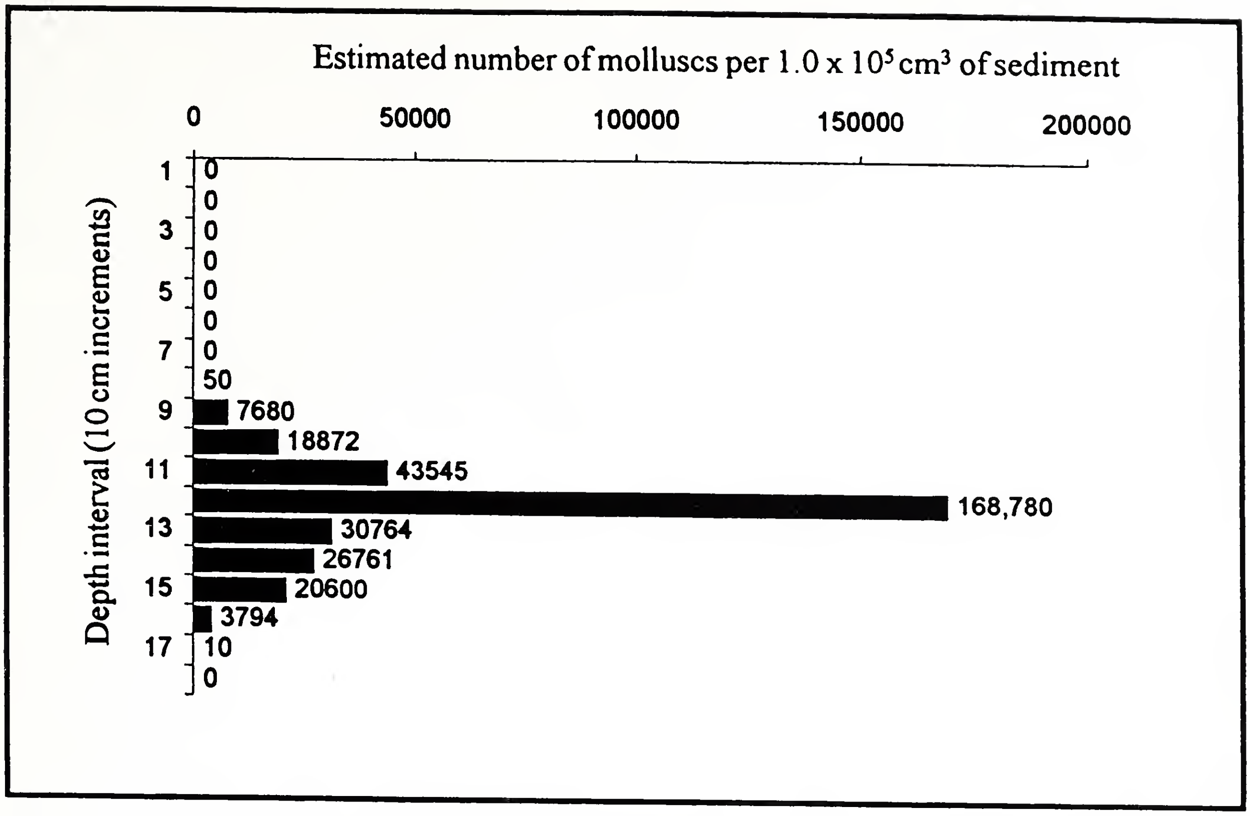

Figure 3.—Approximate number of mollusk shells per 0.1 m^3 of bulk sediment at 10 cm intervals throughout the Wilkinson sediment profile.

and Zimmerman (1960) also found *Valvata tricarinata*, *A. leightoni* (*cf. G. limosa*) and *Gyraulus altissimus* (*cf. G. parvus*) as being among the most abundant. All of these species indicate a shallow, weedy lake. The estimated number of mollusks for each 0.1 m^3 volume for each depth increased rapidly, then sharply at 120 cm to over 168,000 (Fig. 3) before decreasing again to zero near the 70 cm depth. The 120 cm depth also had the greatest richness of mollusks. It is assumed that the great abundance and richness of mollusk taxa at this level is a function of ample food and high habitat heterogeneity. As the water became shallower, aquatic vegetation, including algae (an important food source), probably increased, creating both a variety of food items as well as structure (e.g., submergent, floating, and emergent vegetation). Continued shallowing of the water and closing of open water probably reduced light and oxygen levels sufficiently to rob many species of suitable food and habitat.

A few conclusions can be made about conditions in the lake from some of the less abundant species. *Valvata sincera* dropped out of the assemblage early in the filling of Wilkinson Lake. Since this species has been noted as preferring deeper water, its demise may have been facilitated early by sediment in-filling. The appearance of *Helicodiscus parallelus* at the marl/peat interface is indicative of a transition from open water to wetland conditions. The near absence of unionid mussels from the deposit may indicate that few fishes were present, as unionids usually require fishes as hosts for their parasitic larvae. Correspondingly, no fish scales or fish bones were recovered from the deposit.

CONCLUSIONS

Early post-glacial lakes.—The discovery of limnic deposits from lakes and wetlands that have long ago extinguished (so long ago that their aquatic origins are often topographically obscured), not only emphasizes the reality of classic hydrarch succession (despite heated objections to it on the part of many ecologists), it also provides an invaluable archive for understanding the palaeoenvironments inhabited by extinct organisms. Moreover, such deposits help in reconstructing post-glacial biotic migrations and successions. Based on studies of the Wilkinson deposit and other similar deposits in the southern Great Lakes region, it appears that several species of organisms were ubiquitous pioneers to newly created, late-glacial lakes and ponds. With regard to plants, members of the genus *Potamogeton* as well as *Najas flexilis* are particularly common. In marls, the mollusks, *Valvata tricarinata*, *Gyraulus parvus*, *Amnicola limosa* and *Pisidium* spp. are almost always present. While these species may be indicative of general conditions in a given wetland, it is the infrequent or scattered taxa that may be of more ecological interest because they may indicate environmental thresholds or ecotones for their respective taxa. Descriptive and numerical investigations on the mollusk communities of the lakes and wetlands of Indiana are few and insufficient not only in terms of documenting extant taxa, but also as a resource for palaeoecological inference. Much research on the existing mollusk faunas and their relationship to vertebrate communities, predominating vegetation, wetland hydrology and morphometry, substrate type, and water chemistry is recommended. These data will not only add to our knowledge of extant communities, but it will also facilitate inferences about palaeoenvironments and their succession. Additionally, further research on the subfossils in the marl deposits of Indiana, and elsewhere, would provide more precise documentation and understanding of late-Pleistocene and Holocene biogeography.

The habitat of *Castoroides ohioensis*.— The Wilkinson beaver died near the time when its species went extinct, *circa* 10,000 years ago (see Cahn 1932). The Wilkinson site at the time the specimen died was a mineral-rich, wet meadow, dominated by bulrushes. Cattails, although not evidenced by subfossils, were probably also present in appreciable numbers. The surrounding forest was dominated by white spruce, balsam fir, and tamarack, with birch and aspen probably occupying disturbed sites and lakeshores.

Many authors believe that a reduction or loss of the preferred habitat of the giant beaver at the end of the Pleistocene and perhaps its overspecialization, including the inability to disperse readily and to build dams, contributed to its extinction (Stirton 1965; Kurten & Anderson 1980; Harington 1986; Holman 1995). The question of habitat loss can be addressed by studying palaeoenvironments and comparing the ancient habitats to potential modern analogues. Based on the subfossil analysis of the Wilkinson sight, functional analogues of the habitat of the giant beaver have existed from the time when it flourished to the present day. All of the taxa found at the Wilkinson site, are extant and common members of modern shallow-water wetlands. Only the boreal conifers have significantly changed their range and distribution, but even these are still found commonly in the northern Midwest. Moreover, suitable wetland habitats for giant beaver have increased, not decreased, since the retreat of the last glaciers, due in large part to colonization of barren outwash channels by emergent vegetation as well as ecological succession and consequent in-filling of deeper water bodies. At the time of settlement of Indiana, shallow wetlands were so plentiful that in the spring of the year one could put a canoe in at the area that is now Fort Wayne and travel all the way to Lake Michigan without having to portage more than a mile or two. It would seem then, that habitat and food loss are not likely factors in the extinction of the giant Beaver.

The exact reason for the extinction of the giant beaver and the other North American "ice age" megafauna is not known. However, there are two changes that occurred at about the time the megafauna began to go extinct; climate and the immigration of humans to North America. The changes associated with transitions from interglacial climates to glacial climates, and back again, do not seem to be a logical explanation for the extinctions, because such glaciation cycles have occurred many times during the Quaternary with apparently no major effect on the populations of the North American megafauna. Therefore, the only apparent, new variable that occurred during the last glaciation is the appearance of humans. Whether people negatively affected the megafauna via hunting, introduction of disease, or both, is still a subject of much controversy.

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