

Prehistoric Freshwater Mussel Assemblages of the Mississippi River in Southwestern Wisconsin

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ABSTRACT

Archaeological excavations at aboriginal sites adjacent to the Upper Mississippi River (UMR) in southwestern Wisconsin produced a series of freshwater mussel (naiad) assemblages that contained more than 29,000 valves of 28 mussel species. These subfossil mussel valves are the remains of mollusks harvested as a food source by prehistoric peoples between circa A.D. 1 and A.D. 1000. Taken together, the aboriginal assemblages provide an approximation of the regions' main stem UMR naiad communities during the latter part of the prehistoric era. A quantitative comparison of the subfossil collection with modern mussel survey data documents dramatic changes in the species composition of molluscan communities following habitat degradation of the UMR associated with EuroAmerican settlement.

INTRODUCTION

The navigation pools of the present-day Upper Mississippi River (UMR) were created by a series of locks and dams built by the U.S. Army Corps of Engineers during the 1930's and 1940's (Rasmussen, 1979:4). Although a number of recent studies have focused on freshwater mussels (naiades) in the UMR (*e.g.*, Havlik & Stansbery, 1978; Mathiak, 1979; Perry, 1979; Fuller, 1980; Thiel, 1981; Duncan & Thiel, 1983; Havlik, 1983), there are few pre-lock and dam, taxon specific reports of naiad distribution prior to significant habitat modification and the large scale commercial harvest that severely depleted mussel populations during the late 19th and early 20th century.

Some early reports on UMR freshwater mussels (Pratt, 1876; Witter, 1883; Marsh, 1887; Shimek, 1888) offer information on the presence and relative abundance of particular species, but lack quantitative data. Later studies undertaken by the U.S. Bureau of Fisheries and others during the period of intense mussel harvest for the pearl button industry (Smith, 1899; Baker, 1905; Coker, 1919; Coker *et al.*, 1921) provided detailed information on specific taxa, but lacked quantitative data on entire mussel assemblages. The survey by Ellis in 1930-31 (Van der Schalie & Van der Schalie, 1950) provided the only quantified pre-lock and dam information on mussels encompassing a large portion of the main stem UMR. This survey evaluated mussel resources after several decades

of unregulated harvest to supply shell for the button industry (Baker, 1903; Coker, 1919:66-69; Knott, 1980: 11-16) and regional outbreaks of 'pearl fever' when portions of the UMR were depleted of mussels in search of salable pearls (Kunz, 1898:395; Baker, 1905:250-251). Moreover, the UMR of Ellis' survey had undergone significant habitat changes due to construction of a hydroelectric dam at Keokuk, Iowa (Coker, 1914), modification of channel dynamics as a result of hundreds of wing and closing dams (Grier, 1926:92; Rasmussen, 1979:3-4), and heavy siltation (Ellis, 1936). The results of the Ellis survey reflect a stage in the degradation of the UMR, and are not representative of naiad communities prior to EuroAmerican settlement.

In 1978-80, archaeological excavations were conducted by personnel from the University of Wisconsin-Madison at a number of Woodland Tradition (A.D. 1 to A.D. 1000) prehistoric Indian habitation sites adjacent to the UMR in southwestern Wisconsin. Several of these sites contained food refuse deposits (middens) of freshwater mussel shells, each accurately dated by the radiocarbon method and/or through associated artifactual remains of known age. In the following report, nine prehistoric mussel assemblages are described. Eight of these subfossil assemblages from six sites were excavated during 1978-80 near the city of Prairie du Chien, adjacent to present-day Pool 10, in Crawford County, Wisconsin, and one assemblage was excavated in 1956 by David A. Baerreis at a site located in the Pool 11 area of Grant County, Wisconsin (see figure 1 and table 1). A detailed description of archaeological information for each site is presented in Theler (1983).

METHODS AND MATERIALS

The mussel remains excavated during the 1978-80 fieldwork were bagged with their surrounding matrix and returned to the Department of Anthropology, University of Wisconsin-Madison. At the department's Laboratory of Archaeology, shells were cleaned, identified, and placed into storage. The mussel assemblage collected by Baerreis in 1956 is housed at the Laboratory of Archaeology, where it was studied by the author in 1981. A series of

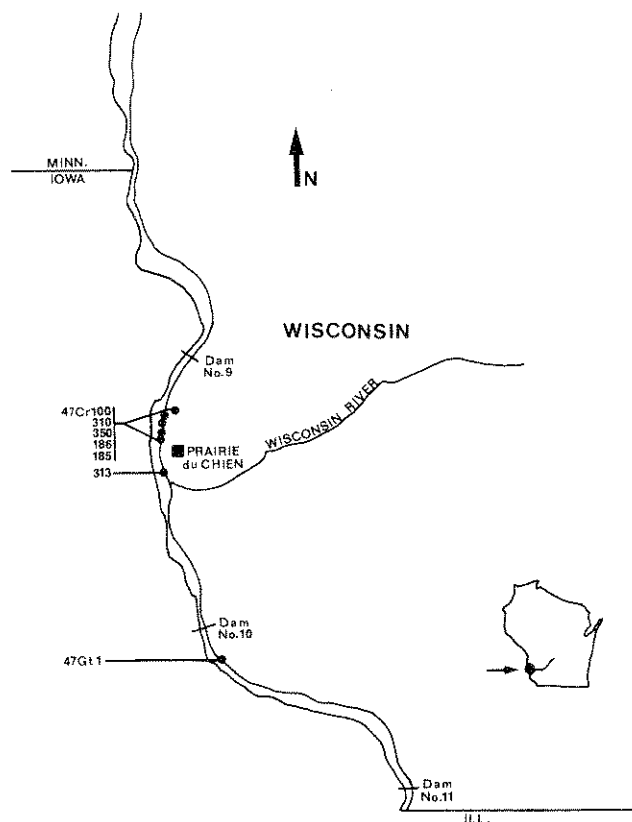


Figure 1. The location of described prehistoric shell middens in Pools 10 and 11 of the Upper Mississippi River.

voucher specimens for each of the taxa in the prehistoric assemblages is on deposit at the Ohio State University, Museum of Zoology (OSUM). The taxonomic nomenclature used in this report follows that presented by Stansbery (1982) and employed by Oesch (1984). The use of certain subspecific designations for subfossil material in this report is in keeping with the catalogued voucher series at OSUM.

RESULTS

The nine subfossil mussel assemblages from the navigational Pools 10 and 11 areas of UMR have a combined total of 29,198 valves, representing 13,384 individuals that could be identified as belonging to one of 28 species. The species represented, number of valves, minimum number of individuals (MNI), and the relative abundance (%) are presented for each assemblage in table 2. The MNI were determined by the maximum number of right or left valves of each species in each assemblage. These assemblages are combined in table 3 to facilitate comparisons with the historic surveys of Ellis (Van der Schalie & Van der Schalie, 1950), Thiel (1981) and Duncan and Thiel (1983). The quality of shell preservation varies between sites and is indicated to some degree by the number of unidentifiable valves listed for each assemblage (table 2). These valves were specifically unidentifiable due to damage or deterioration in virtually all cases.

The most abundant mussel species in the UMR subfossil material was the ebony shell, *Fusconaia ebena* (Lea, 1831) represented by 7,794 individuals comprising 58.23% of the combined assemblages. One of the most common UMR mussel species during the late 19th century, *F. ebena* occurred on a substrate of sand and/or gravel under a moderate to strong current velocity (Marsh, 1887: 47; Smith, 1899:290, 298; Coker, 1914:8, 1919:20, 22; Parmalee, 1967:31). The second most frequently encountered taxon was the monkey face mussel, *Quadrula metanevra* (Rafinesque, 1820) with 1,033 individuals totaling 7.72% of the prehistoric assemblages. *Q. metanevra* is reported to have occurred with the ebony shell in a similar habitat setting (Coker, 1919:42).

Fusconaia ebena and *Q. metanevra* together total 65.95% of the UMR subfossil fauna with only eight of the remaining 26 species contributing more than 1.0% each. These eight are *Amblema plicata* (Say, 1817), with 920 individuals representing 6.87% of the combined assemblages, *Pleurobema sintoxia* (Rafinesque, 1820) 5.91%, *Quadrula pustulosa* (Lea, 1831) 4.56%, *Fusco-*

Table 1. UMR archaeological site locations.

Site number	Name	Location
47Cr350	Bullhead Slough Shell Midden	Mississippi River Mile (MRM) 639.0 adjacent to abandoned side channel trace, Bullhead Slough, in the SW ¼ of section 1, T7N, R7W, Crawford County, Wisconsin
47Cr310	Quarter Mile Shell Midden	MRM 638.9 adjacent to abandoned side channel trace, "Mud Slough" in SW ¼ of section 1, T7N, R7W, Crawford County, Wisconsin
47Cr100	Mill Coulee Shell Heap	At mouth of Mill Coulee, in the NE ¼, NW ¼ of section 6, T7N, R6W, Crawford County, Wisconsin
47Cr186	Mill Pond Site	MRM 636.9 adjacent to "Marais Lake" in the NW ¼, SW ¼ of section 13, T7N, R7W, Crawford County, Wisconsin: 47Cr186-1, Lower Shell Midden; 47Cr186-2, Upper Shell Midden; 47Cr186-3, refuse pit (Feature 26) filled with shell
47Cr185	Mill Run Site	MRM 636.2 adjacent to "Marais Lake" in the NE ¼, SE ¼ of section 23, T7N, R7W, Crawford County, Wisconsin
47Cr313	Hunter Channel Midden	MRM 632.3, on western shore of Schmidt Island, in the NW ¼ of section 12, T6N, R7W, Crawford County, Wisconsin
47Gt1	Stonefield Village	MRM 608.8 in section 13, T3N, R6W, Grant County, Wisconsin

naia flava (Rafinesque, 1820) 4.09%, *Actinonaias ligamentina carinata* (Barnes, 1823) 3.72%, *Obovaria olivaria* (Rafinesque, 1820) 2.56%, *Elliptio dilatata* (Rafinesque, 1820) 1.54%, and *Cyclonaias tuberculata* (Rafinesque, 1820) with 185 individuals representing 1.38% of the UMR subfossil material.

The remaining 18 species each contributed less than 1% to the prehistoric UMR assemblages and include in decreasing frequency of relative abundance, *Ellipsaria* (= *Plagiola*) *lineolata* (Rafinesque, 1820) with 83 individuals representing 0.62% of the combined subfossil material, *Plethobasus cyphyus* (Rafinesque, 1820), *Obliquaria reflexa* Rafinesque, 1820, *Quadrula quadrula* (Rafinesque, 1820), *Elliptio crassidens crassidens* (Lamarck, 1819), *Tritogonia verrucosa* (Rafinesque, 1820), *Truncilla truncata* Rafinesque, 1820, *Ligumia recta* (Lamarck, 1819), *Lampsilis higginsii* (Lea, 1857), *Quadrula nodulata* (Rafinesque, 1820), *Lampsilis ventricosa* (Barnes, 1823), *Lampsilis radiata luteola* (Lamarck, 1819) (= *L. r. siliquidea* (Barnes, 1823)), *Potamilus alatus* (Say, 1817), *Lasmigona costata* (Rafinesque, 1820), *Lasmigona complanata* (Barnes, 1823), *Lampsilis teres teres* (Rafinesque, 1820), *Strophitus undulatus undulatus* (Say, 1817), and *Arcidens confragosus* (Say, 1829) with one individual and representing 0.01% of the UMR subfossil material.

DISCUSSION

The value of aboriginal shell deposits as a baseline to measure change in a stream's molluscan community since prehistoric times has been recognized by numerous researchers (e.g., Morrison, 1942; Stansbery, 1965; Parmalee *et al.*, 1980, 1982; Taylor & Spurlock, 1982; Parmalee & Bogan, 1986). The mussels recovered from the UMR aboriginal shell middens are considered to be an indicator of naiad distribution and relative abundance prior to EuroAmerican disruption of the main stem UMR aquatic ecosystem.

In the UMR subfossil assemblages, the ebony shell, *F. ebena* was the most abundant species in eight of nine discrete midden deposits and contributed nearly 60% of all individuals represented. During the late 19th century, *F. ebena* occurred in the main stem UMR in dense aggregates or "beds" containing millions of individuals (Smith, 1899:299; Coker, 1919:22). Marsh (1887:43) stated that *F. ebena* "is the most abundant species in the [Mississippi] river, equalling in numbers all other species of Uniones combined." Coker (1919:20, 24) describes *F. ebena* as comprising 75 to 80% of (commercial) species at Le Claire, Pleasant Valley, and at other points above Davenport, Iowa. In species counts made by Coker at commercial shell piles north of Keokuk, Iowa in 1912, he found 80% were *F. ebena*, 10% *Q. metanevra*, while seven other species (unspecified by Coker) accounted for the remaining 10%. It would appear that *F. ebena* comprised a major component of the UMR naiad fauna for at least two millennium before overharvest for the button industry, siltation, and the impediment of this species'

unique host fish (the skipjack herring, *Alosa chrysochloris*) with the construction of the hydroelectric dam at Keokuk, Iowa in 1913, spelled its demise in the UMR (Surber, 1913; Coker, 1914, 1930:165-169).

In modern surveys, *F. ebena* represented only 0.18% of Ellis' 1930-31 (Van der Schalie & Van der Schalie, 1950) survey efforts within the present-day Pool 10 area, while the recent work by Thiel (1981) and Duncan and Thiel (1983) failed to locate any living individuals. However, a small number of relict *F. ebena* were found living in Pool 10 near Prairie du Chien by Mathiak (1979) and more recently by David Heath (personal communication). *Quadrula metanevra* has also drastically declined relative to prehistoric numbers, with this species comprising 0.2% or less of the recent surveys in Pool 10 (see table 2).

The three ridge mussel, *Amblema plicata* contributes 6.87% of the combined subfossil assemblages, and accounted for more than 10.0% of an assemblage in only two instances (table 1). In the Ellis survey, *A. plicata* accounted for 7.46% of all species in the Pool 10 area region, while this taxon represented 72.1 and 52.9%, respectively, in systematic surveys by Thiel (1981) and Duncan and Thiel (1983). The three ridge mussel has become the most abundant UMR mussel species, thriving in the often turbid, reduced velocity waters of the present-day river.

Another species showing substantial population changes in the UMR is the washboard mussel, *Megalonaias nervosa* (Rafinesque, 1820). *Megalonaias nervosa* was not represented in the prehistoric material from Pools 10 and 11, but has been recovered in very small numbers with prehistoric UMR assemblages near Rock Island, Illinois (Van Dyke *et al.*, 1980). A single valve of this species was present at the Millville archaeological site (Theler, 1983) on the lower Wisconsin River 18 km above its junction with Pool 10 of the UMR. *Megalonaias nervosa* represented 1.33% of the Ellis survey in the Pool 10 area (Van der Schalie & Van der Schalie, 1950) and 2.8% and 6.8% of Thiel (1981) and Duncan and Thiel (1983) surveys, respectively, for Pool 10 (table 2). *Megalonaias nervosa*, like *A. plicata*, has shown a population increase under present-day habitat conditions.

A number of mussel species that appear to have maintained or slightly increased from their prehistoric population densities include *Quadrula pustulosa*, *Fusconaia flava*, *Elliptio dilatata*, and *Lampsilis higginsii*. Two species, *Elliptio c. crassidens* and *Cyclonaias tuberculata* were present in small numbers in all the prehistoric assemblages, but appear to be extirpated from the present-day main stem UMR. *Plethobasus cyphyus* and *Tritogonia verrucosa* occurred in small numbers in seven of the nine subfossil assemblages, while *Pleurobema sinuata*, *Actinonaias ligamentina carinata*, and *Ellipsaria lineolata* occur in low to moderate numbers in all prehistoric assemblages. The four latter species have been reduced to small, relict populations and *P. cyphyus* is extirpated in the UMR Pools 10 and 11 region.

Havlik and Stansbery (1978:9) have documented ap-

Table 2. Freshwater mussels (Naiades) recovered from prehistoric shell middens in the Pool 10 and 11 area of the upper Mississippi River.

	47Cr186-1 A.D. 70		47Cr313 A.D. 160		47GT1 A.D. 170-430		47Cr100 A.D. 280-330		
	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%
Family Unionidae									
Subfamily Anodontinae									
<i>Strophitus u. undulatus</i> (Say, 1817)	3	2	0.06	0	0	0.00	0	0	0.00
<i>Arcidens confragosus</i> (Say, 1829)	0	0	0.00	0	0	0.00	1	1	0.08
<i>Lasmigona complanata</i> (Barnes, 1823)	4	4	0.12	0	0	0.00	0	0	0.00
<i>Lasmigona costata</i> (Rafinesque, 1820)	6	4	0.12	0	0	0.00	0	0	0.00
Subfamily Ambleminae									
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	26	15	0.43	2	2	0.42	1	1	0.13
<i>Quadrula quadrula</i> (Rafinesque, 1820)	19	10	0.29	0	0	0.00	0	0	0.00
<i>Quadrula metanevra</i> (Rafinesque, 1820)	399	202	5.82	20	13	2.71	177	90	12.02
<i>Quadrula nodulata</i> (Rafinesque, 1820)	6	3	0.09	0	0	0.00	0	0	0.00
<i>Quadrula pustulosa</i> (Lea, 1831)	310	163	4.70	17	10	2.08	55	31	4.14
<i>Amblema plicata</i> (Say, 1817)	476	242	6.97	10	6	1.25	20	14	1.87
<i>Fusconata ebena</i> (Lea, 1831)	3,253	1,700	48.99	573	312	65.00	987	510	68.09
<i>Fusconata flava</i> (Rafinesque, 1820)	432	220	6.34	50	32	6.67	20	11	1.47
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)	45	23	0.66	23	15	3.13	23	14	1.87
<i>Pleurobasus cyphus</i> (Rafinesque, 1820)	36	20	0.58	0	0	0.00	16	10	1.34
<i>Pleurobema sintoxia</i> (Rafinesque, 1820)	438	224	6.46	69	38	7.92	47	24	3.20
<i>Elliptio c. crassidens</i> (Lamarck, 1819)	15	9	0.26	5	4	0.83	5	3	0.40
<i>Elliptio dilatata</i> (Rafinesque, 1820)	287	145	4.18	5	4	0.83	3	2	0.27
Subfamily Lampsilinae									
<i>Obliquaria reflexa</i> Rafinesque, 1820	27	17	0.49	8	7	1.46	3	2	0.27
<i>Actinonaias ligamentina carinata</i> (Barnes, 1823)	580	308	8.88	23	14	2.92	33	17	2.27
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	64	34	0.98	10	7	1.46	2	1	0.13
<i>Obovaria olivaria</i> (Rafinesque, 1820)	188	96	2.77	19	13	2.71	25	13	1.74
<i>Truncilla truncata</i> Rafinesque, 1820	2	2	0.06	2	2	0.42	0	0	0.00
<i>Potamilus alatus</i> (Say, 1817)	3	2	0.06	0	0	0.00	0	0	0.00
<i>Ligumia recta</i> (Lamarck, 1819)	8	5	0.14	0	0	0.00	0	0	0.00
<i>Lampsilis teres teres</i> (Rafinesque, 1820)	0	0	0.00	0	0	0.00	2	2	0.27
<i>Lampsilis radiata luteola</i> (Lamarck, 1819)	13	7	0.20	0	0	0.00	1	1	0.13
<i>Lampsilis higginsii</i> (Lea, 1857)	11	7	0.20	0	0	0.00	2	2	0.27
<i>Lampsilis ventricosa</i> (Barnes, 1823)	6	6	0.17	1	1	0.21	1	1	0.13
Subtotal	6,657	3,470	100.02	837	480	100.02	1,423	749	100.01
Unidentifiable valves	1,082	—	—	190	—	—	26	—	—
Totals	7,739	3,470	100.02	1,027	480	100.02	1,449	749	100.01
							2,285	1,225	99.98
							152	—	—
							2,437	1,225	99.98

Table 3. A comparison of some prehistoric and modern freshwater mussel (naiad) assemblages from the upper Mississippi River.

	Data source:	Pool 10			
		This report; subfossil	Ellis, 1930-31	Thiel, 1981	Duncan and Thiel, 1983
Number of individuals:	13,384 %	1,126 %	4,516 %	12,150 %	
Family Unionidae					
Subfamily Anodontinae					
<i>Anodonta imbecillis</i> Say, 1829	0.00	0.89	<0.1	1.6	
<i>Anodonta suborbiculata</i> Say, 1831	0.00	0.00	0.0	<0.1	
<i>Anodonta grandis</i> subsp.	0.00	7.19	0.3	0.8	
<i>Strophitus undulatus undulatus</i> (Say, 1817)	0.01	0.09	0.3	0.4	
<i>Arcidens confragosus</i> (Say, 1829)	0.01	0.27	0.2	0.3	
<i>Simpsonaias ambigua</i> (Say, 1825)	0.00	0.09	0.0	0.0	
<i>Lasmigona complanata</i> (Barnes, 1823)	0.04	0.00	<0.1	0.1	
<i>Lasmigona costata</i> (Rafinesque, 1820)	0.04	0.00	0.0	0.0	
Subfamily Ambleminae					
<i>Megalonaias nervosa</i> (Rafinesque, 1820)	0.00	1.33	2.8	6.8	
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	0.24	2.04	0.0	<0.1	
<i>Quadrula quadrula</i> (Rafinesque, 1820)	0.37	0.09	3.1	1.8	
<i>Quadrula metanevra</i> (Rafinesque, 1820)	7.72	0.09	0.2	0.1	
<i>Quadrula nodulata</i> (Rafinesque, 1820)	0.09	0.71	3.2	0.9	
<i>Quadrula pustulosa</i> (Lea, 1831)	4.56	2.93	6.7	3.5	
<i>Amblema plicata</i> (Say, 1817)	6.87	7.46	72.1	52.9	
<i>Fusconaia ebena</i> (Lea, 1831)	58.23	0.18	0.0	0.0	
<i>Fusconaia flava</i> (Rafinesque, 1820)	4.09	1.24	5.9	3.5	
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)	1.38	0.09	0.0	0.0	
<i>Plethobasus cyphus</i> (Rafinesque, 1820)	0.58	0.00	0.0	0.0	
<i>Pleurobema sintoxia</i> (Rafinesque, 1820)	5.91	0.00	0.0	<0.1	
<i>Elliptio crassidens crassidens</i> (Lamarck, 1819)	0.28	0.00	0.0	0.0	
<i>Elliptio dilatata</i> (Rafinesque, 1820)	1.54	3.20	0.8	2.2	
Subfamily Lampsilinae					
<i>Obliquaria reflexa</i> Rafinesque, 1820	0.55	3.02	1.2	2.1	
<i>Actinonaias ligamentina carinata</i> (Barnes, 1823)	3.72	0.53	<0.1	<0.1	
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	0.62	0.36	0.0	0.1	
<i>Obovaria olivaria</i> (Rafinesque, 1820)	2.56	0.36	1.4	0.9	
<i>Truncilla truncata</i> Rafinesque, 1820	0.13	2.04	1.0	5.3	
<i>Truncilla donaciformis</i> (Lea, 1827)	0.00	0.09	0.9	6.7	
<i>Leptodea fragilis</i> (Rafinesque, 1820)	0.00	4.44	<0.1	4.8	
<i>Potamilus alatus</i> (Say, 1817)	0.05	6.39	0.4	2.4	
<i>Potamilus ohioensis</i> (Rafinesque, 1820)	0.00	0.00	0.0	0.1	
<i>Potamilus capax</i> (Green, 1832)	0.00	0.09	0.0	0.0	
<i>Toxolasma parvus</i> (Barnes, 1823)	0.00	0.00	0.0	<0.1	
<i>Ligumia recta</i> (Lamarck, 1819)	0.11	0.53	0.1	0.6	
<i>Lampsilis teres teres</i> (Rafinesque, 1820)	0.02	47.51	0.0	0.0	
<i>Lampsilis teres anodontoides</i> (Lea, 1831)	0.00	0.27	0.0	<0.1	
<i>Lampsilis radiata luteola</i> (Lamarck, 1819)	0.07	5.68	0.0	0.4	
<i>Lampsilis higginsii</i> (Lea, 1857)	0.10	0.09	0.1	0.3	
<i>Lampsilis ventricosa</i> (Barnes, 1823)	0.08	0.71	0.3	1.6	
	99.97	100.00	101.0	100.2	

proximately 44 species of freshwater mussels that are known to have occurred in the Pool 10 area of the UMR, in contrast to the 28 taxa represented in the described prehistoric assemblages. This disparity of 16 species appears to be due in part to a bias by prehistoric harvestors against mussel taxa having a small adult shell size which were uncommon in all assemblages. In the subfossil assemblages, no individuals of *Toxolasma parvus* (Barnes, 1823) or *Truncilla donaciformis* (Lea, 1827) were re-

covered, while both species are presently widespread and locally common in the Pool 10 area. Mussel species having a slightly larger shell size, e.g., *Truncilla truncata* and *Obliquaria reflexa* are rare, but persistent in the subfossil assemblages. Juveniles of any taxon were rare or absent in the assemblages. It is assumed that small shelled individuals were not harvested as a food source at the sites considered, indicating a cultural bias towards large shelled species or individuals.

Other factors possibly influencing the species composition of the subfossil assemblages include water depth, which may have restricted prehistoric mussel harvesting to depths suitable for hand collecting. Any species that were preferentially deep water forms, may be disproportionately rare. Additionally, species characteristic of a low velocity current or backwater habitats with soft substrates (e.g., some Anodontinae) are rare or absent in the described assemblages.

Finally, it is probable that a number of species, in addition to the previously discussed *A. plicata* and *M. nervosa*, have dramatically increased in number or expanded their range northward in the UMR under the influence of the large scale habitat modifications of recent decades. This appears to be the case for *Anodonta suborbiculata*, Say, 1831 (Havlik, 1981), and is perhaps true for *T. parvus* and *T. donaciformis*. Other species recorded historically have always been rare and have a sharply circumscribed habitat preference (e.g., *Cumberlandia monodonta* (Say, 1829) and *Simpsoniata ambigua* (Say, 1825)), or are extralimital when encountered in the main stem UMR (e.g., *Alasmidonta marginata*, Say, 1818). These taxa are not unexpectedly absent from the prehistoric assemblages.

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