PALEOCOMMUNITY TEMPORAL DYNAMICS: THE LONG-TERM DEVELOPMENT OF MULTISPECIES ASSEMBLIES

Edited by

William Miller, III

Consisting mostly of papers presented at the Paleontological Society Symposium, *Paleocommunity Temporal Dynamics*, held August [illegible] at the Society of Economic Paleontologists and Mineralogists Midyear Meeting at Columbus, Ohio

THE PALEONTOLOGICAL SOCIETY SPECIAL PUBLICATION NO. 5
1990

Randall S. Spencer
Series Editor

STABILITY OF RECENT UNIONID (MOLLUSCA: BIVALVIA) COMMUNITIES OVER THE PAST 6000 YEARS

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INTRODUCTION

Historically, the greatest freshwater bivalve species diversity in the world was in the Tennessee, Cumberland and Alabama River systems. The Tennessee River System had 94 and the Cumberland River System had 85 taxa reported (Starnes and Bogan, 1988). Ortmann (1918, 1924, 1925, 1926), Wilson and Clark (1914), Neel and Allen (1964), van der Schalie (1939, 1973) and van der Schalie and van der Schalie (1950) documented this diverse fauna. However, even in the early days of this century these authors noted the decline in the mussel populations and the loss of species from certain rivers (e.g. Ortmann, 1909a, 1918).

Diversity of the freshwater bivalve fauna has been reported usually by river system or for a particular river or creek. This information has appeared as either a published list or as part of an environmental survey. Only recently have attempts begun to appear that address the question of what constitutes a unionid community (Miller et al., 1986; Strayer, 1981).

Freshwater bivalves identified from archaeological deposits in the eastern United States provide an important supplement to the historic museum records of unionid distribution. Archaeological deposits by their nature are datable and by association, so are the non-cultural materials associated with the cultural remains. Evidence of human use of freshwater bivalves covers at least the last 10,000 years in eastern North America. The value of unionids from archaeological sites in reconstructing prehistoric faunas and the local ecology has been long recognized (e.g. Ortmann, 1909b; Baker, 1925; Parmalee, 1956; Matteson, 1960; van der Schalie and Parmalee, 1960). More than 30 archaeological sites have had the recovered unionid remains reported (see Bogan et al. 1987, for list of citations).

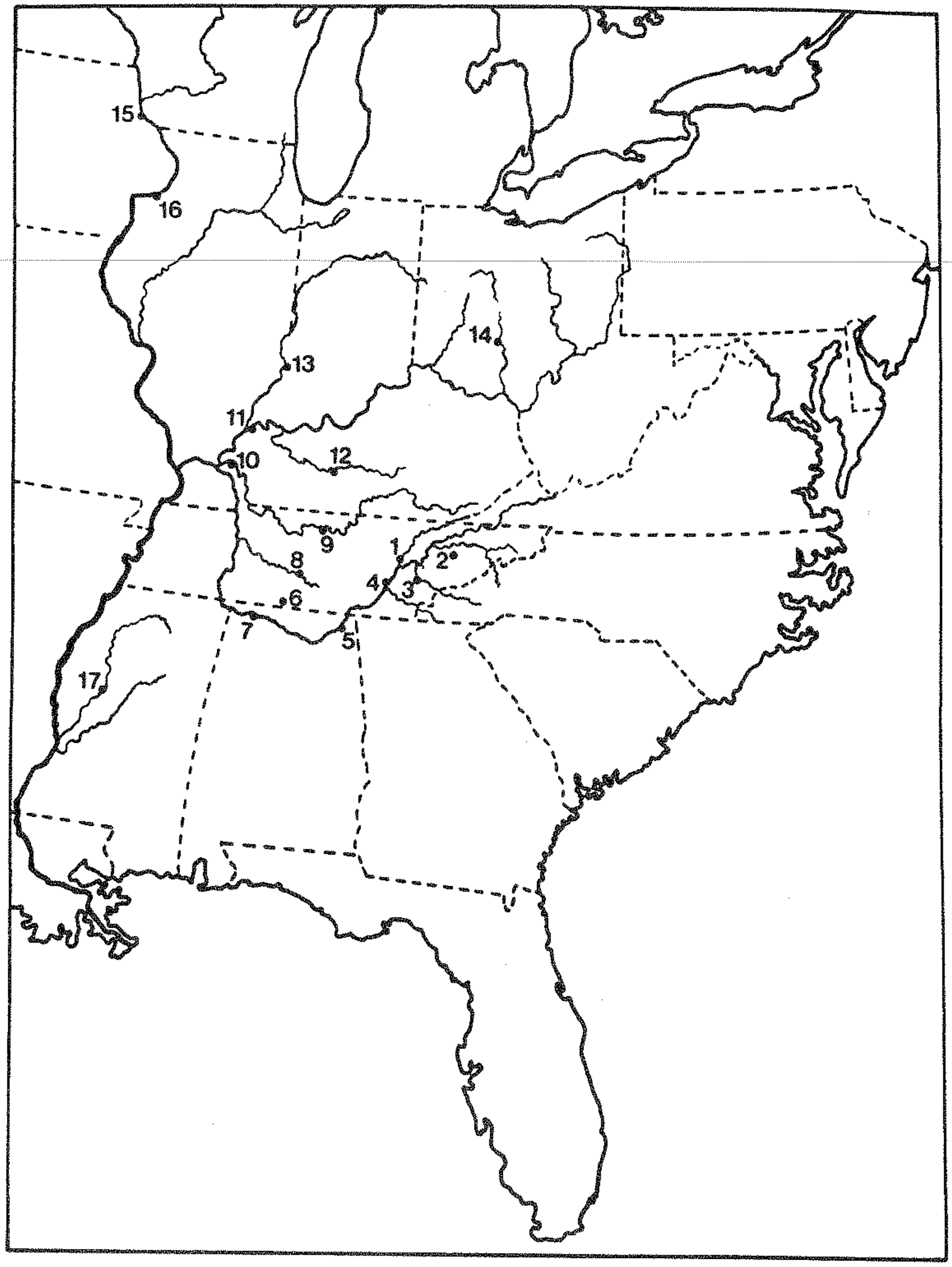

Figure 1. Location of archaeological samples discussed in this paper. Numbers correspond to those used in Table 1.

The archaeological record of the unionids recovered from along the Tennessee, Cumberland, middle Green, lower Wabash, lower Ohio, and upper Mississippi rivers provides an excellent opportunity to examine the diversity and composition of the unionid fauna prior to Euro-American influences (Figure 1, Table 1). Unionids from an archaeological site are assumed to represent the results of collecting on a local shoal or riffle, not materials carried in from a distant source. Thus, such an assemblage is assumed to represent a sample of the local fauna at a given point in time. Archaeological unionids from the last 6000 years are used to document long term stability of the unionid species diversity and species richness that is contrasted with the modern fauna from these same areas.

METHODS

The first problem facing any use of the historic and archaeological literature on unionids is the constantly changing nomenclature. This has been a long standing problem. The standardized nomenclature of unionids of North America used here is that published in Turgeon et al. (1988). All of the records used in this report were first standardized against this list. This allowed a common list of taxa to be used for all reports, both archaeological and modern (see Appendix 1).

A unionid community is defined here as those species found in association in a restricted section of a river or stream. The important information describing the community is the species richness and the relative abundance of the species.

Initially, I had to establish that the unionid fauna from a particular site was internally consistent through time and there had not been any major faunal shifts. The subsamples from the Clinch River (Parmalee and Bogan, 1986) were compared as were the published data for the Chickamauga Reservoir (Parmalee et al., 1980), Pickwick Landing (Morrison, 1942), Carlson Annis Shellmound (Patch, in press) and the three sites on the Wabash River (Parmalee, 1969). Each of these samples will be discussed independently. The data from the subsamples were compared against each other using both the Jaccard Index and the Shannon-Weiner Index. Both of these programs were run on a PC using programs written by M. Brauning and R. Horwitz in BASIC. The cluster analysis was done using the statistical package SYSTAT. Single linkage and average linkage cluster analyses were performed using the values for the Jaccard's Index (Tables 1-8). The cluster patterns were all basically the same for the two clustering methods. Cluster analysis of the Jaccard's Indices was performed to test the idea that the unionid faunas of similar sized streams should have comparable faunal diversity. This would follow from the river continuum concept (Vannotte et al., 1980) and was suggested by Starnes and Bogan (1982). Four of the single linkage tree diagrams are presented here (Figures 2-5). Each set of comparisons was done with the samples reduced to the lowest set of species contained in the compared samples. The summary table of all species for the 16 localities is presented here as Appendix 1. The two indices were chosen because they are stable statistics I feel are applicable in this situation. Jaccard's index shows the similarity of the two samples based on the number of shared taxa divided by the total number of taxa in the two samples. The higher the percent similar, the greater the similarity of the two samples being compared. The Shannon-Weiner Index was chosen to examine the evenness of the representation of individuals across species. The value of the Shannon-Weiner Index ranges upward from a minimum of 0. The smaller the number the less evenly distributed the individuals across the taxa in the sample. While a higher value (e.g. 3.2 and above) would indicate increasing evenness in the distribution of individuals across the taxa in a sample.

Archaeological deposits have a potential bias not found in the paleontological record. Almost all materials recovered from an archaeological site have passed through human hands. The collecting and subsequent incorporation and inclusion in the archaeological record is culturally controlled. Samples from the Clinch River Breeder Reactor Plant Site and Chickamauga Reservoir were carefully screened for any evidence of cultural selection in the collection of the unionids. Multiple samples from the same site were analyzed for any evidence for selection in size or species composition. The size of the individuals in each sample ranged from juvenile specimens about 1-2 cm up to large adult specimens. The only bias observed was the habitats in which the native Americans collected. They collected from the areas with the greatest abundance - mainstream riffle/shoal areas. Thus species with restricted habitats such as deep water, mud bottom or other habitats adjacent to the shoals would either be under- or unrepresented in the samples. Anodonta spp. live in ponded, soft bottom areas and would not be expected. Also, Cumberlandia monodonta, which lives in a very specialized habitat (Stansbery, 1966), would not be expected. Theler (1987) provides further comments on the role of cultural bias in the archaeological record. He presents evidence for the interpretation of some samples reflecting initial colonization and bed development.

Sample size also greatly effects an analysis. A rarefaction analysis has not been performed on the archaeological samples but based on observation, a sample in excess of 2000 valves appears to be a minimum sample size required to recover all but the rarest species. This is based on a large series of samples usually containing 40-45 species. The origin of the sample may in some cases bias the diversity. All of the samples discussed were either the total sample recovered or were taken from all areas of the site excavated.

SAMPLES

Parmalee and Bogan (1986) reported the unionid fauna from the Clinch River Breeder Reactor Plant Site (CRBRP). Three samples were recovered from the site: an Early Woodland sample dated 785-345 B.C.; a Middle Woodland sample dated 65-625 A.D.; and a Mississippian culture period sample dated 1100 A.D. (Table 1).

Table 1. Summary data for all samples used in these analyses.

	LOCATION	NO. OF SAMPLES	TOTAL TAXA	TOTAL IDENTIFIED VALVES
1.	CLINCH RIVER	3	45	23,904
2.	LITTLE PIGEON RIVER	1	46	3,855
3.	LITTLE TENN. RIVER	3	40	2,854
4.	CHICKAMAUGA RES.	14	48	27,875
5.	WIDOW'S CREEK	1	50	59,809
6.	ELK RIVER	1	17	2,169
7.	PICKWICK RES.	4	49	31,349
8.	DUCK RIVER	1	33	2,538
9.	CUMBERLAND RIVER	3	40	23,073
10.	ANGEL SITE (OHIO R.)	1	31	5,549
11.	GREEN RIVER	3	33	21,871
12.	SCIOTO RIVER	1	25	1,977
13.	WABASH RIVER	3	38	32,208
14.	UPPER MISSISSIPPI R.	9	28	25,512
15.	E. MOLINE-MISS. RIVER	1	27	6,920
16.	YAZOO RIVER	2	32	7,510
	TOTAL	51	99	278,973

Table 2. Summary results for the three samples from the Clinch River Breeder Reactor Plant Site (Clinch River) (data from Parmalee and Bogan, 1986).

SHANNON-WEINER INDEX

	Sample No.	No. Taxa	Index	Sample Size (Valves)
Early Woodland	1	21	3.6570	93
Middle Woodland	2	43	4.0423	20,238
Mississippian Period	3	38	4.4319	2,713
Total of samples	4	45	4.1207	23,904

JACCARD'S INDEX

Early Woodland	1			
Middle Woodland	.4651	1		
Mississippian Period	.5263	.7555	1	
Total sample	.4444	.9111	.8	1

Table 3. Summary results from the comparison of the five samples and sample total from Chickamauga Reservoir (data from Parmalee et al., 1982).

SHANNON-WEINER INDEX

	Sample No.	No. Taxa	Index	Sample Size
Middle Woodland	1	33	3.8612	953
Late Woodland	2	42	3.4652	11,437
Mississippian Period	3	29	3.3765	2,871
Mid./Late Woodland	4	46	3.8440	7,118
L. Woodland/Miss.	5	36	3.1700	5,496
Total	6	48	3.5991	27,875

JACCARD'S INDEX

Middle Woodland	1				
Late Woodland	.6444	1			
Mississippian Period	.7027	.5434	1		
Mid./Late Woodland	.6170	.7872	.5869	1	
L. Woodland/Miss.	.6136	.7173	.6190	.6875	1
Total	.6041	.8085	.5744	.8913	.7446

Table 4. Comparison of the four samples from Pickwick Landing and the combined sample total (data from Morrison, 1942).

SHANNON-WEINER INDEX

	Sample No.	No. Taxa	Index	Sample Size (Valves)
Lu 5	1	42	3.8009	4,307
Lu 67	2	39	3.6175	4,358
Lu 59	3	47	3.4927	19,099
Lu 70	4	36	3.5325	3,585
Total	5	49	3.6727	31,349

JACCARD'S INDEX

Lu 5	1				
Lu 67	.6666	1			
Lu 59	.8723	.75	1		
Lu 70	.6808	.5625	.6938	1	
Total	.8333	.8260	.8775	.7291	1

Table 5. Comparison of three samples from various parts of the middle and lower Cumberland River (data from Breitburg, 1983; Casey, 1986).

SHANNON-WEINER INDEX

	Sample No.	No. Taxa	Index	Sample Size (Valves)
Iuka	1	26	3.6974	4,913
Millikan	2	19	2.8635	1,552
Penitentiary Branch	3	34	3.6130	16,608
Total	4	40	4.0562	23,073

JACCARD'S INDEX

Iuka	1			
Millikan	.3428	1		
Penitentiary Branch	.6388	.4444	1	
Total	.675	.5	.8	1

Table 6. Comparison of three samples from the Carlson Annis Shell Mound, Green River, Kentucky(data from Patch,in press)

SHANNON-WEINER INDEX	Sample No.	No. Taxa	Index	Sample Size
A 1	1	37	3.3581	3,354
C 2	2	34	3.3696	16,279
D 14-2	3	34	3.2959	2,238

JACCARD'S INDEX				
A 1	1			
C 2	.6666	1		
D 14-2	.5757	.5806	1	
Total	.7878	.75	.7096	1

Table 7. Comparison of the three sites in the Riverton Culture, Wabash River (data from Parmalee, 1969).

SHANNON-WEINER INDEX	Sample No.	No Taxa	Index	Sample Size (Valves)
Riverton Site	1	37	3.3581	8135
Swan Island	2	34	3.3696	6557
Robeson Hills Site	3	34	3.2959	18,516

JACCARD'S INDEX			
Riverton Site	1		
Swan Island	.8918	1	
Robeson Site	.8947	.8378	1

Table 8. Comparison of ten archaeological sites from the Upper Mississippi River (data from Theler, 1987; Van Dyke et al., 1980).

SHANNON-WEINER INDEX

	Sample No.	No. Taxa	Index	Sample Size (Valves)
47CR186-1	1	26	2.7414	6657
47CR313	2	16	1.9240	837
47GT1	3	19	1.7825	1423
47CR100	4	23	2.6043	2285
47CR186-2	5	20	2.8536	608
47CR186-3	6	18	2.2809	1059
47CR185	7	21	2.1830	2710
47CR310	8	18	1.4130	7332
47CR350	9	17	1.9065	1601
East Moline	10	25	3.4923	6920

JACCARD'S INDEX

Sample No.										
1.	1									
2.	.5	1								
3.	.5172	.4782	1							
4.	.6551	.4615	.6	1						
5.	.714	.4615	.4814	.6296	1					
6.	.433	.4347	.4	.56	.625	1				
7.	.6	.3571	.4285	.5172	.5714	.625	1			
8.	.4642	.1923	.32	.3214	.48	.3913	.6086	1		
9.	.5517	.2962	.2758	.5185	.5185	.44	.5185	.5454	1	
10.	.5666	.3214	.3928	.5357	.4827	.52	.72	.5	.6	1

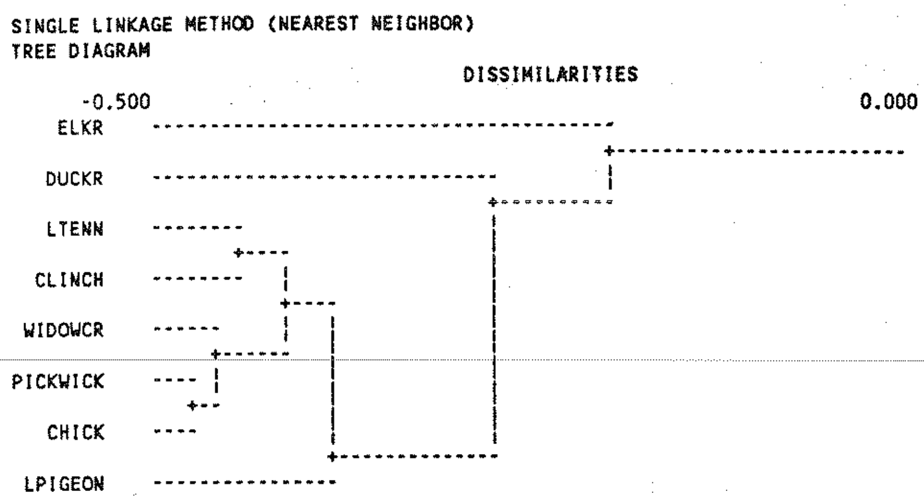

Figure 2. Analysis of samples from the Tennessee River System.

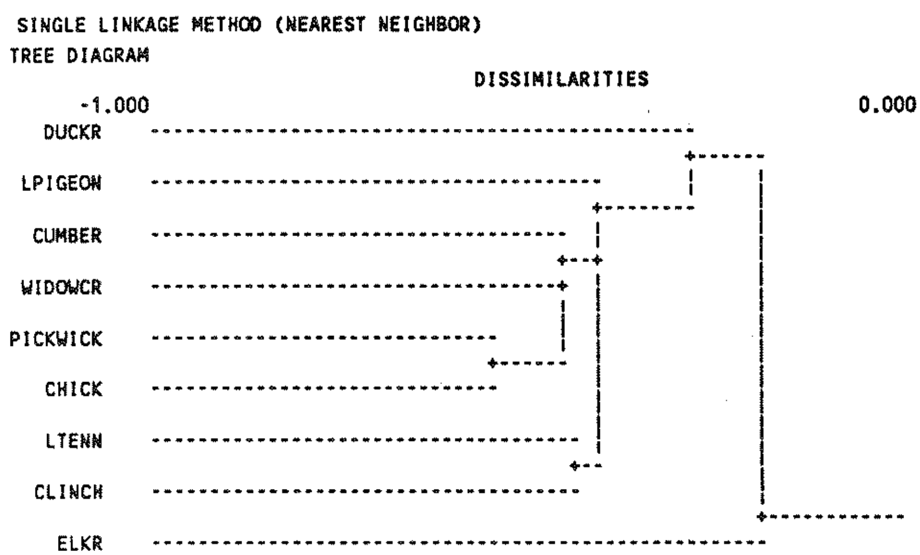

Figure 3. Analysis of Tennessee and Cumberland River samples.

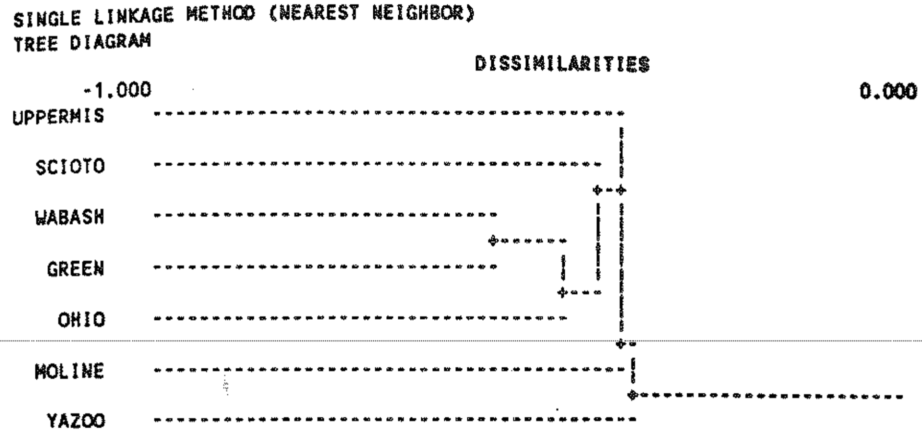

Figure 4. Analysis of upper Mississippi River, Ohio River samples and the Yazoo Sample totals.

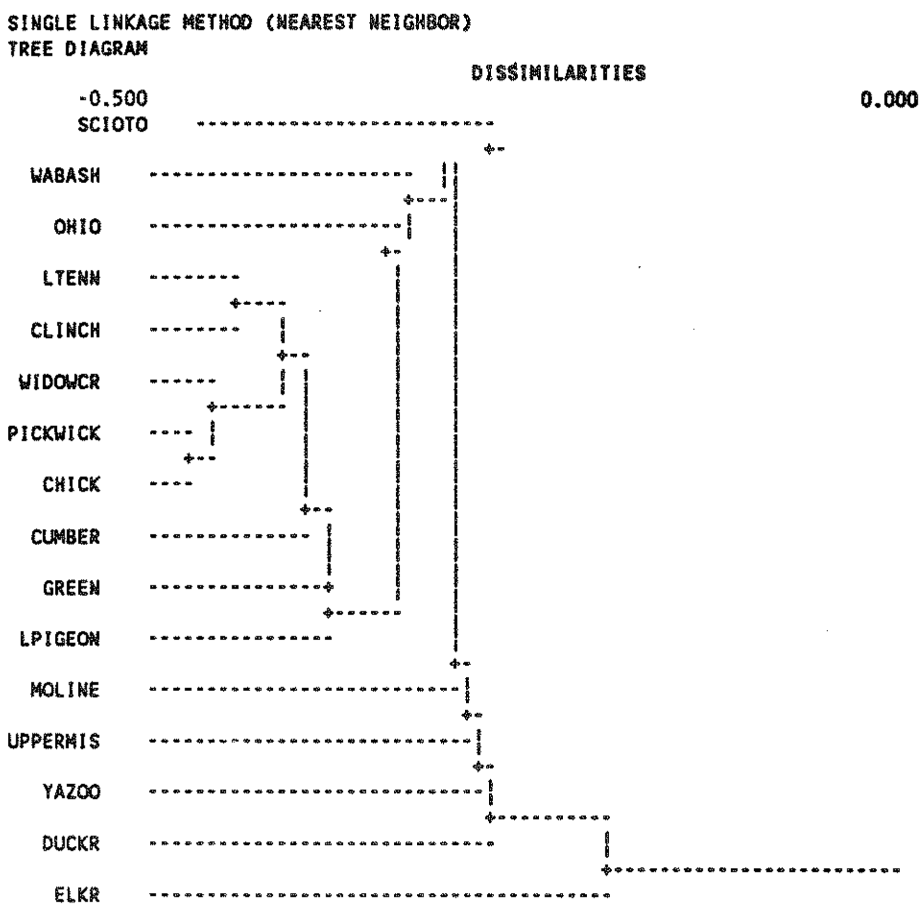

Figure 5. Analysis of summary data from all archaeological samples.

Parmalee (1988) reported the unionid valves recovered from a late prehistoric site (1300-1600 A.D.) on the lower Little Pigeon River (Table 1). This sample will serve to represent the prehistoric unionid fauna of another headwater tributary of the Tennessee River.

The Little Tennessee River is one of the major eastern tributaries of the Tennessee River in East Tennessee. Three small archaeological samples were combined to create a usable sample for this analysis. These were the Late Woodland sample (ca. 900-1000 A.D.) from Martin Farm (Bogan and Bogan, 1985), an early historic sample (ca. 1800 A.D.) from the Citico site (Bogan, 1983) and a late prehistoric sample from the Toqua site (Bogan, 1980; 1987a). These three archaeological samples are from the same section of the Little Tennessee River and cover the time span 1000 A.D to 1800 A.D. The sample sizes were too small to give reliable results in a comparison between samples. This combined sample will serve to represent this river with the noted possible biases (Table 1).

Parmalee et al. (1982) collected over 40,000 valves from 28 archaeological sites along the banks of the Tennessee River in the Chickamauga Reservoir in Rhea and Meigs counties. Fourteen sites could be confidently assigned to a cultural period and were reported by cultural period (Middle Woodland to Mississippian, 600-1500 A.D.). One site was sampled several times and the tabulation of each sample was compared. The relative abundances of species identified in the subsamples were essentially constant. The same is true of the various samples combined by cultural period as reported by Parmalee et al. (1982) (Tables 1, 3). The Shannon-Weiner values are all quite close, pointing to a relative constancy in the evenness of the abundance of the species. The values of the Jaccard's Index are all high documenting a high level of consistency in the species composition of the samples through time.

Warren (1975) examined a very large collection of unionids from a multicomponent shell midden, Widow's Creek, on the banks of the Tennessee River in Jackson County in northeast Alabama (Woodland-Mississippian periods, ca. 500-1500 A.D.). Unionid remains from this site represent materials collected from several distinct strata, and data are published only as a summary table (Table 1). Warren (1975) noted there are trends in the frequency of different species in two of the columns he examined (Warren, 1975, Fig. 6-8). He reported a decrease and then an increase in the incidence of *Dromus dromas* up the column while the incidence of *Elliptio dilatata* decreases.

Morrison (1942) reported on the analysis of the molluscan remains from a series of large Archaic Period (ca. 3000-5000 B.C.) shellmounds along the Tennessee River in North Alabama. These shellmounds were at and below Mussel Shoals. Samples from 4 sites were complete enough to be used in this analysis (Tables 1, 4). The values of the Jaccard's Index indicate a high level of similarity of the species composition of the samples while the Shannon-Weiner indices again illustrate a comparable evenness of distribution of the abundance of the species.

Robison (1986) identified faunal materials from eight Late Middle Woodland Sites (ca. 400-600 A.D.) along the upper Duck and Elk rivers. His unionid data from the Shofner Site, located on the lower part of Thompson Creek, a tributary of the Duck River and from the Owl Hollow Site, located close to the mouth of Town Creek, a tributary of the Elk River, are used. These two samples represent small river unionid faunas, similar to the sample from the Little Pigeon River, all to be compared directly with the big river unionid fauna of the Tennessee River. Robison (1986) presents the first evidence for Pegias fabula and Epioblasma lewisi from the upper Duck and Elk rivers.

Casey (1986) examined the archaeological evidence for freshwater bivalve use in the Lower Tennessee, Cumberland and Ohio River valleys. Two of her samples, Ikua (late prehistoric, ca. 1300 A.D.) and Millikan (ca 1000 A.D.), from the lower Cumberland River, are used here (Table 5). Her data are compared with the unionid data presented by Breitburg (1983) for the Late Archaic site (1650-1025 B.C.), the Penitentiary Branch Site on the Cumberland River in northern Jackson County, Tennessee. This is a sample from a Late Archaic site (1650 to 1025 B.C.).

Patch (in press) examined three unionid samples from a Late Archaic shellmound (ca. 1000-3000 B.C.) along the middle Green River in Kentucky (Tables 1, 6). These three samples are from different parts of the midden but the results presented in Table 6 show some differences between the samples but a comparable species diversity and evenness of species distribution.

Parmalee (1969) analyzed the unionid fauna from three late Archaic sites (1500 to 1000 B.C.) along the middle Wabash River (Tables 1,7). The Riverton Site is the upstream site, Swan Island Site is situated downstream from the Riverton Site and the Robeson Hills Site is located still farther down stream. The distance between the Riverton and Robeson sites is 26 miles.

Two other archaeological samples are included to broaden the coverage of the Ohio River System (Table 1). Parmalee (1960) reported the unionid fauna from the Angel Site (Mississippian Period, 1100 to 1500 A.D.) on the banks of the Ohio River in Vanderburgh County, Indiana. Stansbery (1965) analyzed the molluscan materials recovered from the McGraw Site, Ross County, Ohio, situated on the banks of the Scioto River.

Theler (1987) tabulated the unionid materials from 9 archaeological sites along the Mississippi River in southwestern Wisconsin. These samples span the time period 1 A.D. to 1000 A.D. This series of samples is supplemented by the unionid data from an early Middle Woodland shell midden in East Moline, Illinois, located on the bank of the Mississippi River (Van Dyke et al., 1980)(Tables 1, 8).

Two samples from the Lower Yazoo River in Mississippi (ca. 800 A.D.) are included for comparison. Bogan (1987b) identified a sample of unionid material from two archaeological sites on a small tributary of the Yazoo River, Yazoo County, Mississippi (Table 1). These samples were expanded by subsequent identification of additional material from the sites. This data was summarized by Bogan et al. (1987). This archaeological fauna is representative of a lower Mississippi River tributary. It contains some of the most southern distribution records of typical Interior Basin species, including the first record of an Ozarkian species east of the Mississippi River, as well as Gulf Coast species.

DISCUSSION

It has been shown that there is a consistency in the species diversity and evenness of the distribution of abundance of the species at a given site through time as well as a stability between samples of comparable age from different parts of the same river. Three samples from CRBRP and the total of all the samples were compared using Jaccard's Index and the Shannon-Weiner Index (Table 2). The small sample size of the Early Woodland sample was greatly overshadowed by the large Middle Woodland sample. However, the Jaccard's Index for the other two samples and the total are quite close. Both indices reflect the effects of various sample sizes. The Mississippian and Middle Woodland samples are similar and the greatest similarity is between the Total and the Middle Woodland sample based on the effects of sample size. Five species and the Pleurobema complex maintained the same relative frequencies in the Middle Woodland samples. Ortmann (1918) reported only 28 taxa from this area as compared with the 45 taxa reported in the archaeological record. The three samples from the Wabash River provide further evidence for the stability of the unionid community both within a river system smaller than the Tennessee River System and that rivers in the Interior Basin outside of the Tennessee River System exhibit long term community stability. The Shannon-Weiner indices for the three samples are very close, and the Jaccard's Index values show a very close similarity of the species composition. The species composition of these three samples are closer than any of the other sets of samples.

The upper Mississippi River samples provide a marked contrast to the Clinch River, Chickamauga Reservoir and Wabash River samples. The Shannon-Weiner Index values obtained for these 10 samples are the lowest of all of the samples compared. This can be interpreted in two ways. Some of the lack of evenness may be a result of sample size. However, the large samples from the Upper Mississippi River still have very low levels of evenness, the samples are dominated by one or two species, while the rest of the species are rare. The Jaccard's Index values for the upper Mississippi samples are lower than most of the other sets of samples. This may be due to the constantly shifting channels of the Mississippi River and the constantly changing ecology. Theler (1987) documented the progressive addition of species in a developing mussel bed. The figures in Table 8 support this interpretation of the archaeological data. There is no evidence for long term stability in the unionid communities in this active section of the upper Mississippi River.

The list of unionid species identified in the Pickwick Basin archaeological samples was compared with the list of species prepared for the same area by Ortmann (1925) and Stansbery (1964). The Jaccard's Index for the comparison of Morrison's data and the combined list of Ortmann and Stansbery was 0.5. There were 39 species from the archaeological list on the historic list. Also, ten species occurred in the archaeological sample, not collected by Ortmann (1925) or Stansbery (1964). This comparison illustrates two points. One, many of the more secretive species collected today may not be present in the archaeological record. Secondly, there has been a shift in the species composition of the communities with

Euro-American influences. This is even more strongly documented in the Chickamauga Reservoir samples (Parmalee et al., 1982).

Based on the evidence that the unionid community at a given place remains quite stable over a long period of time (documented here for ca. 6000 years), all samples from a particular area like the Clinch River Breeder Reactor Site and the Chickamauga Reservoir have been added together to form a composite total. It was assumed that if there was some sort of community stability within a particular section of a river, the Tennessee River, that the total samples, a total sample of the fauna over time at that locality, should cluster in a pattern reflecting the similarity of the communities. The communities of the smaller rivers should cluster and the big river communities should cluster together, and logically the samples from a given river should be expected to group together. The summary data for all 16 sites listed in Appendix 1 were run through the Jaccard's Index and the resulting matrix was submitted for cluster analysis. Four trees are presented here (Figures 2-5). The samples from the Tennessee River and tributaries, and the Elk and Duck rivers were clustered first (Figure 2). The samples from Pickwick Reservoir and Chickamauga Reservoir areas clustered combining next with the Widows Creek sample. These are the three big river samples from the Tennessee River. The lower Clinch River samples and the combined sample from the Little Tennessee River clustered together next as large tributary rivers followed by the sample from the Little Pigeon, followed lastly by the samples from the Duck and Elk Rivers. Figure 3 adds the data from the Cumberland River to the data for Figure 2. The Cumberland River fauna clusters in with the big river samples from the Tennessee River. Figure 4 compares the data for the Ohio River system, upper Mississippi River and the Yazoo River. The samples from the smaller rivers, the Green and Wabash rivers, cluster together next with the Angel Site on the lower main channel Ohio River, followed by the sample from the Scioto River. The Scioto River sample is a small sample that may account for its position in the cluster. The sample from Moline on the upper Mississippi and the Yazoo were closest. This is not as surprising as might be expected. The Yazoo unionid fauna is primarily a Ohio River fauna with some of the coastal plain species added. When all of the data are pulled together into a single tree many of the patterns remain but there is also some confusion (Figure 5). The clusters seen in Figures 2, 3, and 4 remain and tend to merge. The Green River sample clusters between the Cumberland and the Little Pigeon samples, not with the Wabash River as in Figure 4. The one odd point that remains is that the Duck and Elk River samples still cluster together but are off on the side of the tree.

The unionid communities discussed here are interpreted as exhibiting long term stability in terms of modern communities, not in terms of geologic time. Five to six thousand years of compositional stability and relative constancy of the species abundance, at least in the riffle/run areas, has not previously been documented in freshwater. The stability and consistency of the unionid fauna in the lower Clinch River, the Tennessee and Wabash rivers can be contrasted with the apparent rapidly colonizing and short-term transient communities of the upper Mississippi River as discussed by Theler (1987). This stability of a paleocommunity in freshwater continued until the early settlement of the eastern United States and its clearing by the European settlers. The changes were at first subtle, but cumulative. The disturbance and destruction of the freshwater fauna has been reported by Ortmann (1909a, 1918). He noted some streams were already dead from the effluents of paper mills, oil well brine and the results of coal mining. This was in the early part of the twentieth century. The fish, unionids and crawfish were either extirpated or the species diversity was severely depleted. The series of dams constructed by the Tennessee Valley Authority on the Tennessee River had a devastating effect on the once diverse fauna of the Tennessee River. Parmalee et al. (1982) document that 28 species represented in the Chickamauga Reservoir samples are now either extinct or extirpated from the impounded stretch of the Tennessee River. The genus Epioblasma was represented by 12 species in the archaeological record, six species are now extinct and six are rare with their ranges severely reduced. An additional five species have invaded and become established, while four other species rare in prehistoric times have greatly increased their range and abundance since impoundment. Those expanding their range are Anodonta grandis, A. suborbiculata, A. imbecillis, and Lasmigona complanata. Ellipsaria lineolata, Megalonaias nervosa, Tritigonia verrucosa, and Obliquaria reflexa were absent from the archaeological record above Mussel Shoals or represented a very minor part of the unionid community. Today, these species are well established in the upper Tennessee River (Parmalee et al., 1982). An examination of the archaeological samples used in this analysis quickly reveals that species which are common today, such as Megalonaias, Obliquaria, and Ellipsaria, are either very minor parts of the community or were absent. This is especially true of Megalonaias that was only identified in the sample from the Angel Site on the Ohio River, East Moline on the upper Mississippi River and from the Yazoo River in western Mississippi. This species has been abundant and commercially important in the pearl button industry from the early part of this century and is still important in the cultured pearl industry today.

The important ideas to be derived from this investigation for the study of paleocommunities are that freshwater molluscan communities can be stable in both species richness and relative abundance. These faunas are susceptible to rapid and dramatic changes. The documentation of long-term stability in freshwater communities points to a very old and well established unionid fauna in the rivers of the Interior Basin south of the glacial maximum. A community must survive a long time in the geological sense if it is to be preserved in the fossil record. However, the conditions for preservation have to be conducive to preservation of the hardparts of the animals in the community. Such a fossil assemblage from a high energy riverine environment has not been found to date in the southeastern United States.

ACKNOWLEDGEMENTS

This paper would not have been possible without the monumental amount of effort by all of those who have analyzed unionid samples used in this discussion. I extend my deepest appreciation to all of them. Paul W. Parmalee is especially acknowledged for sparking and fostering my interest in the archaeological unionid record. The Tennessee Valley Authority and National Park Service provided funds for the excavation and analysis of those archaeological samples from the Little Tennessee Duck and Elk rivers. Mrs. Terry Sloman and Mrs. Marsha Brauning kindly provided the software for the Jaccard's and Shannon-Weiner analyses and Terry executed the cluster analyses. Terry and Marsha are both thanked for their help and discussion of the techniques with me. Ms. Elizabeth Carrozza is thanked for preparing Figure 1. Mrs. Diana C. Patch is thanked for allowing me to use her Green River data and for our several long discussions about the importance of archaeological molluscan samples, the formation of shell middens, cultural biases and past ecological implications. Barry Miller is thanked for critically reviewing an earlier draft of this paper.

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APPENDIX 1. Summary tabulaton of molluscan data by archaeological context

TAXA	CLINCH RIVER	LITTLE PIGEON RIVER	LITTLE TENN. RIVER	CHICKAMAUGA RESERVOIR	WIDOW CREEK	ELK RIVER	PICKWICK RESERVOIR	DUCK RIVER	CUMBERLAND RIVER	ANGEL SITE	GREEN RIVER	SCIOTO RIVER	WABASH RIVER	UPPER MISS. RIVER	EAST MOLINE	YAZOO RIVER
Actinonaias ligamentina (Lamarck, 1819)	3228	148	279	2087	4802	-	288	-	2752	2	374	100	8023	925	74	-
Actinonaias pectorosa (Conrad, 1836)	-	-	-	-	1	9	-	-	-	-	-	-	-	-	-	-
Alasmidonta marginata Say, 1818	-	1	-	-	-	-	1	-	-	-	-	6	-	-	8	-
Alasmidonta viridis (Rafinesque, 1820)	-	31	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Amblema plicata (Say, 1817)	523	22	23	92	146	-	98	4	164	55	138	78	346	1787	259	165
Anodonta grandis Say, 1829	-	1	-	-	1	-	16	-	-	-	-	-	-	-	-	-
Arcidens confragosus (Say, 1829)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3
Cyclonaias tuberculata (Rafinesque, 1820)	2042	74	23	889	3723	-	6264	1	601	424	384	41	631	330	1138	-
Cyprogenia aberti (Conrad, 1850)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	83
Cyprogenia stegaria (Rafinesque, 1820)	2463	5	1	55	185	-	658	-	326	29	1549	2	937	-	-	-
Dromus dromas (Lea, 1834)	974	32	211	9827	14,142	-	3075	-	3063	-	-	-	-	-	-	-
Ellipsaria lineolata (Rafinesque, 1820)	-	-	-	-	1	-	5	-	162	38	57	-	73	149	105	5
Elliptio crassidens (Lamarck, 1819)	18	23	53	1702	827	-	85	-	62	411	473	6	84	57	1	2
Elliptio dilatata (Rafinesque, 1820)	1428	70	377	3166	16,962	153	6435	56	2828	586	3302	232	5243	392	441	73
Epioblasma arcaeformis (Lea, 1831)	969	26	4	381	262	-	1025	-	1179	-	-	-	-	-	-	-
Epioblasma biemarginata (Lea, 1857)	-	-	-	-	2	-	20	-	-	-	-	-	-	-	-	-
Epioblasma brevidens (Lea, 1831)	188	1	2	9	95	-	110	-	206	-	-	-	-	-	-	-
Epioblasma capsaeformis (Lea, 1834)	84	42	12	76	110	14	594	7	-	-	-	-	-	-	-	-
Epioblasma flexuosa (Rafinesque, 1820)	-	-	-	26	371	-	-	-	330	12	-	-	-	-	-	-
Epioblasma florentina (Lea, 1857)	15	1	-	13	-	-	328	1	-	-	-	-	-	-	-	-
Epioblasma haysiana (Lea, 1833)	439	23	16	102	111	-	249	-	31	-	-	-	-	-	-	-
Epioblasma lewisi (Walker, 1910)	-	-	1	-	61	-	45	1	-	-	-	-	-	-	-	-
Epioblasma obliquata (Rafinesque, 1820)	3	-	-	1	-	-	1	-	-	3	6	1	6	-	-	-
Epioblasma personata (Say, 1829)	-	-	-	-	-	-	24	-	-	-	1	-	-	-	-	-
Epioblasma propinqua (Lea, 1857)	236	-	8	753	904	-	2217	-	1032	-	-	-	-	-	-	-
Epioblasma sampsoni (Lea, 1861)	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-
Epioblasma stewardsoni (Lea, 1852)	198	2	3	1224	116	-	345	-	-	-	-	-	-	-	-	-
Epioblasma torulosa (Rafinesque, 1820)	316	11	3	690	949	-	4762	-	638	60	8278	420	5950	-	-	-
Epioblasma t. cincinnatiensis (Lea, 1840)	-	-	-	-	-	-	-	-	13	-	7	-	-	-	-	-
Epioblasma triquetra (Rafinesque, 1820)	30	-	-	5	4	-	-	3	5	2	47	2	132	-	-	-
Epioblasma turgidula (Lea, 1858)	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	-
Fusconaia barnesiana (Lea, 1838)	80	347	337	16	17	319	-	599	-	-	-	-	-	-	-	-
Fusconaia cor (Conrad, 1834)	-	-	-	-	317	-	283	-	-	-	-	-	-	-	-	-
Fusconaia cuneolus (Lea, 1840)	-	-	-	-	70	-	-	-	-	-	-	-	-	-	-	-

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Fusconaia ebena (Lea, 1831)	-	-	-	-	-	-	-	-	178	1466	-	-	11	15,053	160	3888
Fusconaia flava (Rafinesque, 1820)	-	-	-	-	-	-	-	-	-	-	2	2	361	1020	202	439
Fusconaia subrotunda (Lea, 1831)	1746	409	986	1386	1129	-	78	-	-	-	574	-	-	-	-	-
Hemistena lata (Rafinesque, 1820)	-	1	-	-	-	-	-	-	-	-	-	-	8	-	-	-
Lampsilis abrupta (Say, 1831)	1	-	-	-	-	-	-	-	43	-	-	-	2	-	-	-
Lampsilis cardium (Rafinesque, 1820)	-	-	-	-	-	-	-	-	-	-	-	-	-	12	20	-
Lampsilis fasciola Rafinesque, 1820	21	385	9	3	39	52	-	41	-	-	-	22	-	-	-	-
Lampsilis higginsi (Lea, 1857)	-	-	-	-	-	-	-	-	-	14	-	-	-	19	1	-
Lampsilis ovata (Say, 1817)	38	79	81	56	357	6	238	8	95	51	56	143	388	-	-	15
Lampsilis siliquoidea (Barnes, 1823)	-	-	-	-	-	-	-	-	-	-	1	46	-	16	18	127
Lampsilis teres (Rafinesque, 1820)	-	-	-	-	-	-	-	-	-	-	-	-	-	4	46	18
Lampsilis virescens (Lea, 1858)	-	-	-	-	-	-	59	-	-	-	-	-	-	-	-	-
Lasmigona complanata (Barnes, 1823)	-	-	-	-	-	-	-	-	-	-	-	-	2	6	9	-
Lasmigona costata (Rafinesque, 1820)	-	8	-	1	-	-	1	-	4	2	-	37	74	8	-	-
Lasmigona holstonia (Lea, 1838)	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemiox rimosus (Rafinesque, 1820)	623	8	2	24	61	-	155	51	-	-	-	-	-	-	-	-
Leptodea fragilis (Rafinesque, 1820)	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Lexingtonia dolabelloides (Lea, 1840)	438	96	50	175	1253	96	373	436	-	-	-	-	-	-	-	-
Ligumia recta (Lamarck, 1819)	5	2	5	8	8	-	-	-	69	82	45	114	122	22	49	1
cf Ligumia subrostrata (Say, 1831)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Medionidus conradicus (Lea, 1834)	-	172	12	-	-	306	-	249	-	-	-	-	-	-	-	-
Megalonaias nervosa (Rafinesque, 1820)	-	-	-	-	-	-	-	-	-	12	-	-	-	-	4	26
Obliquaria reflexa Rafinesque, 1820	-	-	-	-	3	-	-	-	20	2	51	-	44	116	1070	215
Obovaria jacksoniana (Frierson, 1912)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33
Obovaria olivaria (Rafinesque, 1820)	-	-	-	-	-	-	-	-	43	16	56	-	75	645	477	-
Obovaria retusa (Lamarck, 1819)	-	-	1	458	1617	-	34	-	892	160	1328	1	544	-	-	-
Obovaria subrotunda (Rafinesque, 1820)	20	9	2	178	483	-	63	1	531	40	69	59	1042	-	-	9
Pegias fabula (Lea, 1838)	-	-	-	-	-	34	-	43	-	-	-	-	-	-	-	-
Plectomerus dombyanus (Valenciennes, 1827)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	253
Plethobasus cicatricosus (Say, 1829)	1	-	-	204	446	-	12	-	45	105	-	-	848	-	-	-
Plethobasus cooperianus (Lea, 1834)	24	11	15	246	845	-	-	-	-	-	1	-	-	-	-	-
Plethobasus cyphyus (Rafinesque, 1820)	3	46	1	27	73	-	-	-	51	38	12	-	83	124	141	10
Pleurobema clava (Lamarck, 1819)	127	-	-	196	1114	-	1099	-	1440	-	-	5	-	-	-	-
Pleurobema coccineum (Conrad, 1834)	-	-	-	-	-	-	-	-	-	-	-	-	-	1517	1097	-

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Pleurobema cordatum (Rafinesque, 1820)	17	33	25	1359	-	-	63	-	2416	2782	-	58	5310	-	-	-
Pleurobema oviforme (Conrad, 1834)	-	24	49	-	60	6	-	10	-	-	-	-	-	-	-	-
Pleurobema plenum (Lea, 1840)	3466	21	28	1555	-	-	217	-	-	-	-	-	-	-	-	-
Pleurobema rubrum (Rafinesque, 1820)	634	1	7	612	-	-	46	-	2003	-	-	-	-	-	-	1203
Pleurobema spp.	1049	-	6	629	6455	-	-	-	171	-	2584	-	-	-	-	-
Potamilus alatus (Say, 1817)	-	9	7	3	-	-	2	-	-	6	2	-	52	12	3	-
Potamilus purpuratus (Lamarck, 1819)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ptychobranchus fasciolaris (Rafinesque, 1820)	791	124	34	253	435	4	51	-	597	-	1676	590	1304	-	-	-
Ptychobranchus subtentum (Say, 1825)	159	508	151	16	78	517	442	469	-	-	-	-	-	-	-	-
Quadrula biangulata Morrison, 1942	-	-	-	-	-	-	160	-	-	-	-	-	-	-	-	-
Quadrula cylindrica (Say, 1817)	103	6	3	34	111	1	161	8	91	5	175	5	214	-	-	10
Quadrula intermedia (Conrad, 1836)	303	-	-	65	63	-	177	-	-	-	-	-	-	-	-	-
Quadrula metanevra (Rafinesque, 1820)	2	-	6	190	599	-	56	-	120	113	21	-	87	1995	604	36
Quadrula nodulata (Rafinesque, 1820)	-	-	-	-	-	-	-	-	1	-	-	-	15	19	5	84
Quadrula pustulosa (Lea, 1831)	48	5	2	94	334	-	121	-	431	3	587	1	891	1117	846	456
Quadrula quadrula (Rafinesque, 1820)	-	-	-	-	-	-	-	-	2	13	1	-	8	88	6	282
Quadrula sparsa (Lea, 1841)	113	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula spp.	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	15
Strophitus undulatus (Say, 1817)	-	-	-	1	-	4	1	2	-	-	-	1	16	3	-	1
Toxolasma lividus (Rafinesque, 1831)	-	131	-	-	38	-	-	-	-	-	-	-	-	-	-	-
Toxolasma lividus glans (Lea, 1830)	-	-	-	-	-	-	52	-	-	-	-	-	74	-	-	-
Toxolasma parva (Barnes, 1823)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Tritigonia verrucosa (Rafinesque, 1820)	-	-	-	-	-	-	-	-	30	-	12	-	75	47	18	32
Truncilla truncata Rafinesque, 1820	-	-	-	-	-	-	-	-	7	4	1	3	132	25	120	4
Villosa fabalis (Lea, 1831)	-	-	-	-	1	-	-	-	-	-	2	-	1	-	-	-
Villosa iris (Lea, 1829)	-	167	-	-	-	-	-	7	-	-	-	-	-	-	-	-
Villosa lienosa (Conrad, 1834)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa spp.	6	200	1	-	-	564	-	470	-	-	-	-	-	-	-	-
Villosa taeniata (Conrad, 1834)	4	-	-	-	24	67	758	49	3	-	-	-	-	-	-	-
Villosa trabilis (Conrad, 1834)	1	183	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Villosa vanuxemensis (Lea, 1838)	28	302	18	52	1	17	-	22	-	-	-	-	-	-	-	-
Total	23,904	3855	2854	27,875	59,809	2169	31,349	2538	23,073	5549	21,871	1977	33,208	25,512	6928	7510
Total Taxa	45	46	40	48	50	17	49	23	40	31	33	25	38	28	27	32