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PREHISTORIC AND MODERN FRESHWATER MUSSEL (MOLLUSCA: BIVALVIA: UNIONOIDEA) FAUNAS OF THE TENNESSEE RIVER: ALABAMA, KENTUCKY, AND TENNESSEE

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ABSTRACT

The Tennessee River, approximately 1050 km in length, originates with the confluence of the French Broad and Holston rivers at Knoxville, Knox County, Tennessee, USA. It flows southwest to about Huntsville, Alabama, where the mainstem changes to a north-westerly direction across northern Alabama, then flows north along the western edge of Middle Tennessee toward its confluence with the Ohio River in Kentucky. Approximately 159450 specimens of freshwater mussels recovered from 15 prehistoric aboriginal sites, reported in the literature and/or identified by the authors, represent at least 75 species. At least 24 of these species occurred throughout the entire length of the mainstem Tennessee River. Collections from the 1800s and throughout the major dam construction era (1920s–mid 1940s) showed a distinct reduction in the distribution and diversity of mussels from the prehistoric period. Today, the river, now a series of impounded reservoirs along its entire length, shows a further reduction in species diversity coupled with significant changes in assemblages from those of prehistoric and pre-impoundment periods. Several populations of indigenous mussel taxa, once abundant throughout the river, are now reduced to a few isolated and functionally extinct (non-reproducing) relict individuals. The majority of species adapted to shoal areas were extirpated or became extinct as a result of impoundment or other detrimental anthropogenic factors. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS: aboriginal sites; freshwater mussels; reservoirs; Tennessee River; eastern United States

INTRODUCTION

Freshwater mussels of the order Unionoidea occur on all of the continents except Antarctica, but they display their greatest species diversity in North America (Burch, 1975; Cummings and Mayer, 1992; Williams *et al.*, 1993). Stansbery (1970) determined that about half of the species of freshwater bivalves in the world are found in eastern North America. Unfortunately, this diversity is disappearing rapidly. According to Williams *et al.* (1993), a total of 281 valid species and 297 recognizable taxa of freshwater mussels have been described from specimens collected in the United States and Canada, and 42.2% of these taxa are considered by them to be extinct, endangered or threatened.

Bogan (1990) reported that paleocommunities of freshwater mussels in the eastern United States remained relatively stable for at least 6000 years prior to the harvesting and/or removal of the eastern forests by European settlers. A reduction in freshwater mussel species richness and diversity in Ohio was noted by Higgins (1858), who blamed the decline on deforestation and the resultant siltation. Also in Ohio between 1801 and 1850, the damming of rivers resulted in a decline in the abundance of migratory fish (Trautman, 1981). Trautman also blamed the dumping of sawdust, brewery waste and animal remains into the water for fish kills reported during this period. Rhoads (1899) observed an impoundment of the Monongahela River in Pennsylvania that concentrated pollutants and prolonged the exposure of freshwater mussels to both domestic and industrial wastes. Beginning in 1900, both treated and untreated waste from Chicago, Illinois, were dumped into the headwaters of the Illinois River and by 1912 the mussel fauna that formerly inhabited the upper stretches was destroyed and was still absent from the river

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in 1966 (Starrett, 1971). Ortmann (1918) reported the same decline of mussels for many of the tributaries of the Upper Tennessee River for which he attributed, among other activities, wood pulp and extracting plants, salt and plaster of Paris industries, and impoundments. In 1888, the Watauga River, a tributary of the Upper Tennessee River, was used for disposal of sawdust that smothered the bottoms of pools (Jordan, 1889).

Given the above history, it seems reasonable to assume that the reduction in mussel diversity seen today began in the 1800s as forests were cut and siltation from erosion began to smother some of the bivalves that had evolved in a previously stable, pristine habitat. Concurrently, from the early 1800s to the present, North American freshwater mussels were subjected to a steady increase in chemical and physical pollution that keeps pace with the expansion of the human population. In addition to these forms of pollution, deleterious effects of impoundment on freshwater mussel diversity is well known, and has been reported by various authors (Rhoads, 1899; Ortmann, 1909, 1925; van der Schalie, 1939; Bates, 1962; Isom, 1969; Fuller, 1974; Parmalee *et al.*, 1980, 1982; Williams *et al.*, 1992; Layzer *et al.*, 1993; Ahlstedt and McDonough, 1994).

Cause and effect in the study of biodiversity versus human activities is certainly speculative, particularly after more than 100 years have passed. The uncertain effects of human-induced changes on the aquatic habitats that exist today would be much easier to understand if a biological inventory of the original fauna of the North American wilderness was available to serve as a base line to gauge the effects of human activities on those indigenous biotic communities. Freshwater mussels, because of their durable shell structure composed of calcium carbonate, offer a glimpse into the past of the natural distribution of mussel communities inhabiting a pristine aquatic environment of the pre-Columbian North American continent. Fortunately, native aboriginal groups collected and utilized the soft parts of these freshwater bivalves as a food resource; discarded shells thrown into refuse dumps formed 'mounds' or lenses along the banks of rivers, especially in eastern North America. The state of preservation is such that specimens recovered from these sites can usually be identified to species level.

Zooarchaeologists have recorded and analyzed the subfossil remains of shells left by native Americans in middens or mounds along the Tennessee River several thousand years ago (Morrison, 1942; Warren, 1975; Parmalee *et al.*, 1982; Casey, 1986). Valves of nearly all species of mussels known to occur historically in the Tennessee River have been recovered in these prehistoric middens when sample sizes number in the thousands (Morrison, 1942; Warren, 1975; Parmalee *et al.*, 1982; Parmalee, 1994). Bogan (1990) analyzed mussel species diversity and evenness within archaeological sites along the Tennessee River, as well as stability among sites.

Historically and most recently, malacologists have been interested in the diverse unionid fauna found throughout the state of Tennessee (Lewis 1871; Pilsbry and Rhoads, 1897; Bickel, 1968; Starnes and Bogan, 1988; Parmalee and Bogan, 1998) and especially in the Tennessee River itself (Lewis, 1871; Hinkley, 1906; Ortmann, 1918, 1925; Scruggs, 1960; Pardue, 1981).

Purpose

The purpose of this study was twofold. First, to identity the species and the distribution of subfossil freshwater mussel shells occurring in aboriginal middens throughout the mainstem Tennessee River. Collection localities were chosen that were reasonably evenly spaced along the course of the river. This data set allowed an interpretation of the prehistoric baseline mussel communities that inhabited the prehistoric Tennessee River in its natural state prior to European expansion into North America. Second, utilizing published records, the authors attempted to define the pre- and post-impoundment mussel faunas to the extent that the available data allows. Compilation of these two data sets allowed a comparison between three temporal mussel faunas in the Tennessee River: 1) a prehistoric fauna inhabiting a pristine free-flowing habitat; 2) a stressed fauna exposed to various degrees of pollution and sedimentation; and 3) the fauna of a regulated river. This paper will show that since aboriginal peoples first began to harvest freshwater mussels from the Tennessee River *ca.* 6000–7000 years before the present, the abundance, distribution and diversity of these molluscs have undergone major changes in response to a changing environment.

Study area

The authors chose to study the mussel assemblages of the Tennessee River for two reasons. First, prehistoric shell middens occur along its entire course, and second, the river is completely regulated. The Tennessee River flows nearly 1050 km from its source, the confluence of the French Broad and Holston rivers at Knoxville, Tennessee (TN), south into Alabama (AL), northwest across northern Alabama, and then north to its confluence with the Ohio River at Paducah, Kentucky (KY) (Figure 1).

Two recognizable geomorphic features marked the extralimitial distribution of numerous species of freshwater mussels found in the pre-impounded lotic Tennessee River. The first site was noted by Ortmann (1918): 'It appears that the Walden Gorge of the Tennessee River, below Chattanooga, forms some kind of barrier to Nayad distribution, at least for certain species; at any rate, it forms a natural division within the Tennessee system.' Later, Ortmann (1924) reiterated that the Tennessee River, based on his study of mussel forms, should be divided into two sections, '. . . that below Walden Gorge . . . down to Mussel [Ortmann's spelling] Shoals, and that above this point, . . . '. The second physical division comprised between 85 and 114 river kilometers of shoals and intermediate pools which were collectively termed Muscle Shoals. These stretches were referred to as Elk River, Big Mussel, Little Mussel, and Colbert Shoals. Muscle shoals extended between the towns of Riverton, TN, and Decatur, AL, from the lower end of Colbert Shoals at Tennessee River kilometer (TRK) 364 upstream to the upper end of Elk River Shoals (TRK 479) (Marian and Rumsey, 1995). These shoals divided the Tennessee River into its

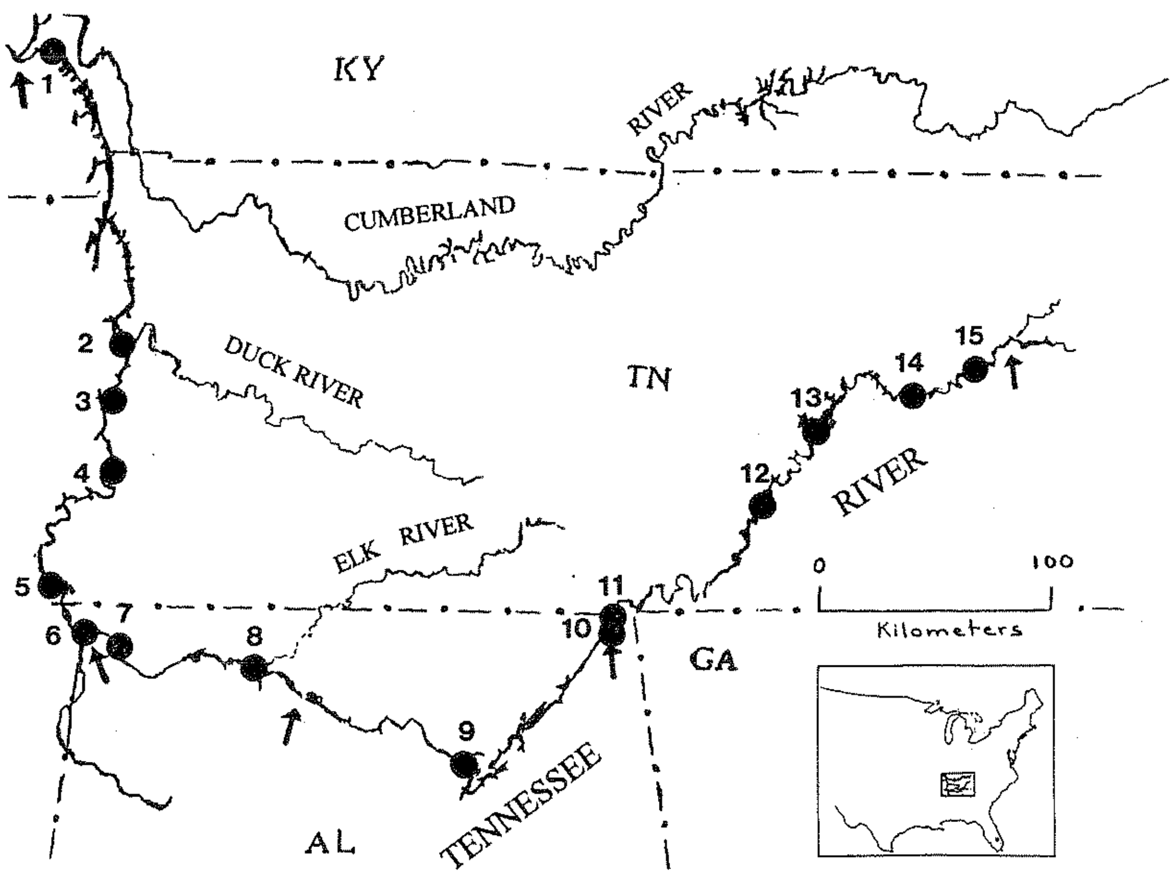

Figure 1. Location of 15 aboriginal sites (1, Dyke; 2, Eva; 3, Daniels Landing; 4, Site 40DR305; 5, Diamond Island; 6, Pickwick Basin; 7, Smith Bottom Cave; 8, Huston; 9, Hobbs Island; 10, Widows Creek; 11, Long Island; 12, Chickamauga Lake; 13, McDonald; 14, Site 40LD207; and 15, Knoxville) along the mainstem Tennessee River from which shell samples were recovered. The arrow (↑) shows the boundaries of the four nominal faunal zones within the Tennessee River

upper and lower reaches based on the impediment they imposed to commercial barge traffic. Ortmann (1925) contended that a change in the mussel fauna occurred '. . . in the region of Muscle Shoals (probably somewhat below)'. Barriers to mussel species in the Tennessee River will be addressed in the conclusion section of this paper.

Walden Gorge and Muscle Shoals were a hindrance to navigation, commerce and development along the Tennessee River, and therefore, damming the rapids was the progressive course of action undertaken in the early 1900s. The flood gates of Hales Bar Dam, located in the vicinity of Walden Gorge (TRK 694), were closed in 1913. In 1924, Wilson Dam was closed and began flooding the banks of the Tennessee River at Muscle Shoals (TRK 417). The formerly free-flowing Tennessee River proper is now a series of reservoirs throughout its entire length. The Tennessee Valley Authority (TVA) acquired Wilson Dam in 1933 and Hales Bar Dam in 1939. Today it operates a series of nine navigational dams that regulate the entire 1050 km of the Tennessee River. The present-day main stream dams operated by the TVA, their date of closure and their location on the Tennessee River, given in parenthesis, are as follows: Kentucky (1944) at TRK 36; Pickwick Landing (1938) at TRK 333; Wilson (1924) at TRK 417; Wheeler (1936) at TRK 442; Guntersville (1939) at TRK 562; Nickajack (replacing Hales Bar in 1967) at TRK 683; Hales Bar (1913) at 694; Chickamauga (1940) at TRK 758; Watts Bar (1942) at TRK 853; and Fort Loudoun (1943) at TRK 969.

Mussel communities of the Tennessee River

A hypothesis proposed by Ortmann in 1924 and expanded in 1925 suggests the presence of two communities of mussels in the pre-impounded Tennessee and Cumberland river systems that were segregated by their center of origin and historic range. One he termed the Cumberlandian, and the other the Ohioan, or Interior Basin fauna. According to Ortmann (1924, 1925), the Cumberlandian fauna consisted of at least 38 species that were confined to the Upper Cumberland River above Clarksville, TN, as well as the Upper Duck and Upper Tennessee rivers. Ortmann (1925) recognized that the Cumberlandian species extended downstream in the Tennessee River to Muscle Shoals, but not as far as Dixie, TN. The Interior Basin fauna supposedly originated in the Mississippi River Valley (i.e. the Interior Basin). Some of the Interior Basin mussel species barely extended their range into the Tennessee River, living only near its mouth. Other components of the Interior Basin fauna in the Tennessee River did not range upstream beyond Muscle Shoals (Ortmann, 1925; van der Schalie, 1939), while others, according to Ortmann (1925), extended upstream as far as Knoxville, TN. Some Tennessee River mussels could not be categorized with certainty as belonging to either the Cumberlandian or Interior Basin faunas, and they were therefore categorized as species of unknown origin (Ortmann, 1924). To facilitate discussion, species of unknown origin are grouped with the Interior Basin species.

Beneath the clear pristine rapids and pools at Muscle Shoals, the many components of the two faunas met and comingled. Not only did the two faunas overlap at Muscle Shoals, but species typically adapted to smaller tributary streams also found a suitable microhabitat there (shallow riffles and shoals) that satisfied their requirements to sustain populations in the mainstem Tennessee River. Because of the variety of habitat available to the mussel species at Muscle Shoals, the resultant assemblage found there was unsurpassed anywhere else in the world.

To malacologists, it became apparent that anthropogenic disturbance in the river system was destroying the Cumberlandian fauna and that there was a concurrent displacement by an Interior Basin mussel fauna (Ortmann, 1918, 1925; van der Schalie, 1939; Stansbery, 1964; Isom, 1969). Impoundment altered the character of the Tennessee River, converting an energetic hydrology into a deep, sluggish and turbid waterway. At present, the Tennessee River resembles the Mississippi River of the Interior Basin in North America more than it does its former condition with intermittent gravel shoals and rapids throughout much of its course. Many mussel species adapted to the Mississippi River Basin have now invaded the Tennessee River and replaced the once dominant Cumberlandian fauna that thrived there in prehistoric times.

METHODS

The present work compiles archaeological, early historical and recent molluscan data in an effort to define the extent and duration of unionid species distribution in the Tennessee River. Data were obtained both from published and unpublished studies.

Archaeological data represent mussel species identified from subfossil valves collected from 15 prehistoric (*ca.* 6000 BC–AD 1200) sites located between TRK 28 and 1035 (Table I). At least 159450 valves were identified from these 15 sites along the Tennessee River (Figure 1) as a means of determining the native assemblage of freshwater mussels that were once present. Previously published reports listed freshwater mussel valves collected and identified from only six of the 15 sites used in this study: Dyke Site at TRK 28 (Casey, 1986); Pickwick Basin at TRK 323 (Morrison, 1942); Smith Bottom Cave at TRK 407 (Parmalee, 1994); Widows Creek at TRK 656 (Warren, 1975); Chickamauga Lake at TRK 805 (Parmalee *et al.*, 1982); and Site 40LD207 at TRK 949 (Parmalee, 1990). Archaeological material obtained from three of the other sites, Eva Site at TRK 164 (Lewis and Lewis, 1961), Huston at TRK 453 (Webb, 1939) and McDonald Site at TRK 850 (Schroedl, 1978), were previously published, but the mussel specimens were not identified at the first two sites and were not completely reported at the third. Identification of valves collected from the six other sites (Daniels Landing at TRK 193, Site 40DR305 at TRK 230, Diamond Island at TRK 317, Hobbs Island at 539, Long Island at TRK 670 and Knoxville at TRK 1035) has not been published; these data supplement our molluscan records for additional stretches of the river in prehistoric times.

Pre-impoundment data were reported by Lewis (1871), Pilsbry and Rhoads (1897), Hinkley (1906), Ortmann (1918, 1925), van der Schalie (1939) and Bickel (1968). Post-impoundment records were taken from Scruggs (1960), Stansbery (1964), Isom (1969, 1971), Pardue (1981), Parmalee *et al.* (1982), Bates and Dennis (1985), Hubbs (1992, 1993, 1994, 1995) and Ahlstedt and McDonough (1994). Additional data were provided from original collections by M.H. Hughes and L.G. Hughes in Fort Loudoun and Watts Bar reservoirs from 1990 to 1995.

For the sake of stability, in this paper the unionid taxonomy of Turgeon *et al.* (1988) is recognized, with the following exceptions. Hoeh (1990) is followed in the resurrection of *Pyganodon* and *Utterbackia* for some species of *Anodonta*. *Quadrula tuberosa* is considered to be a form of *Q. metanevra*. Agreeing with Parmalee and Bogan (1998), *Pleurobema pyramidatum* (Lea, 1840) and *P. coccinium* (Conrad, 1834) are replaced by Rafinesque (1820) names: *P. rubrum* and *P. sintoxia*, respectively.

An absolute tally of species collected from the Tennessee River proper is difficult to make because several 'species' as presently conceived were considered to be 'forms' by earlier researchers, and *vice versa*. Today, many of these taxonomic discrepancies cannot be resolved from the data reported in earlier publications.

Based on the former aboriginal and pre-impoundment distribution of mussels and to facilitate discussion, we divide the Tennessee River into four nominal zones: 1) *Upper Tennessee Cumberlandian* from Knoxville, TN, to Bridgeport, AL (TRK 1049-665); *Lower Tennessee Cumberlandian* from Bridgeport, AL, to Elk River Shoals (TRK 665-479); *Muscle Shoals* from Elk River Shoals to Colbert Shoals (TRK 479-364); and *Lower Tennessee Interior* from Colbert Shoals to the Ohio River at Paducah, KY (TRK 364-0). Upper and lower limits to these four zones are indicated by arrows in Figure 1.

RESULTS

Upper Tennessee Cumberlandian

Of the 47 species of freshwater mussels inhabiting the upper Tennessee River above Walden Gorge in prehistoric times, 14 were Cumberlandian (Table I). The relative abundance of Cumberlandian species in those samples was 41%. *Dromus dromas*, *Epioblasma propinqua*, *Epioblasma arcaeformis* and *Lexingtonia dolabelloides* dominated the Cumberlandian fauna. More than 60% of all the valves identified were either the Cumberlandian, *D. dromas* (32%), or one of three Interior Basin species: *Elliptio dilatata* (14%), *Fusconaia subrotunda* (9%) and *Elliptio crassidens* (7%).

Table I. Number of valves identified for each of 75 freshwater mussel species that were collected at 15 aboriginal sites located along the Tennessee River in Alabama, Kentucky and Tennessee

Species	Faunal zone and record of occurrence														
	Lower Tennessee Interior					Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian			
	Dyke Site	Eva Site	Daniels Landing	40DR305	Diamond Island	Pickwick Basin	Smith Bottom Cave	Huston Site	Hobbs Island	Widow's Creek	Long Island	Chickamauga Lake	McDonald Site	40LD207	Knoxville
1 *Actinonaias ligamentina* (Lamarck, 1819)	0	8	20	62	5	288	54	288	16	4802	12	2087	225	494	352
2 ***Actinonaias pectorosa* (Conrad, 1834)**	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
3 *Alasmidonta marginata* Say, 1818	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4 ***Alasmidonta viridis* (Rafinesque, 1820)**	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
5 *Amblema plicata* (Say, 1817)	0	8	7	16	1	97	3	126	1	146	0	92	12	63	24
6 *Cumberlandia monodonta* (Say, 1829)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
7 *Cyclonaias tuberculata* (Rafinesque, 1820)	49	10	175	352	42	6264	251	517	49	3723	2	889	160	467	35
8 *Cyprogenia stegaria* (Rafinesque, 1820)	2	12	2	207	1	658	19	38	32	187	1	55	2	28	6
9 ***Dromus dromas* (Lea, 1834)**	70	27	74	3508	156	3075	100	181	809	14142	60	9827	669	4001	187
10 *Ellipsaria lineolata* (Rafinesque, 1820)	3	5	1	19	0	5	0	0	0	1	0	0	0	0	0
11 *Elliptio crassidens* (Lamarck, 1819)	9	0	81	1004	46	85	11	5	32	827	12	1702	268	1114	99
12 *Elliptio dilatata* (Rafinesque, 1820)	245	9	53	1104	35	6435	1064	463	134	16962	25	3166	217	2956	14
13 ***Epioblasma arcaeformis* (Lea, 1831)**	8	3	14	239	2	1025	40	2	5	265	0	381	3	389	11
14 ***Epioblasma biemarginata* (Lea, 1857)**	0	0	0	0	0	21	15	0	0	2	0	0	0	0	0
15 ***Epioblasma brevidens* (Lea, 1831)**	0	1	3	33	0	110	7	20	2	95	1	9	2	2	0
16 ***Epioblasma capsaeformis* (Lea, 1834)**	0	0	0	0	0	594	*cf.*	72	0	110	0	*cf.*	0	*cf.*	*cf.*
17 *Epioblasma flexuosa* (Rafinesque, 1820)	14	1	10	13	0	0	*cf.*	3	8	471	0	26	0	*cf.*	0
18 ***Epioblasma florentina* (Lea, 1857)**	0	0	0	0	0	328	*cf.*	*cf.*	0	0	0	13	0	0	0
19 ***Epioblasma haysiana* (Lea, 1833)**	0	0	1	21	0	249	26	10	2	111	0	102	2	67	15
20 ***Epioblasma lewisii* (Walker, 1910)**	0	0	0	1	0	45	14	0	0	61	0	0	0	0	0
21 *Epioblasma obliquata* (Rafinesque, 1820)	0	24	0	5	0	1	0	0	0	0	0	1	0	0	0
22 *Epioblasma personata* (Say, 1829)	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0
23 ***Epioblasma propinqua* (Lea, 1857)**	0	1	10	354	3	2220	121	2	5	904	0	753	9	1644	46
24 ***Epioblasma stewardsoni* (Lea, 1857)**	0	0	0	*cf.*	0	345	24	0	0	116	0	124	0	*cf.*	5
25 *Epioblasma torulosa* (Rafinesque, 1820)	26	12	75	791	10	4875	341	29	266	949	18	658	9	51	24
26 *Epioblasma triquetra* (Rafinesque, 1820)	0	0	0	4	0	0	0	0	0	4	1	5	0	0	1
27 ***Epioblasma turgidula*** (Lea, 1858)	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0
28 ***Fusconaia barnesiana* (Lea, 1838)**	0	0	0	6	o	10	28	0	0	17	0	16	0	11	1
29 ***Fusconaia cor* (Conrad, 1834)**	0	0	0	0	0	245	0	*cf.*	0	317	0	0	0	0	0
30 ***Fusconaia cuneolus* (Lea, 1840)**	0	0	0	0	0	473	0	*cf.*	0	70	0	0	0	0	0
31 *Fusconaia ebena* (Lea, 1831)	4	0	0	0	0	0	0	0	0	0	?	0	0	0	0
32 *Fusconaia subrotunda* (Lea, 1831)	0	0	161	2488	47	78	1	1	27	1129	2	1386	73	2733	54
33 *Hemistena lata* (Rafinesque, 1820)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
34 *Lampsilis abrupta* (Say, 1831)	6	0	1	0	0	0	0	2	*cf.*	0	0	0	0	0	0
35 *Lampsilis fasciola* (Rafinesque, 1820)	0	0	0	7	0	0	17	5	0	39	0	3	0	7	2
36 *Lampsilis ovata* (Say, 1817)	0	2	4	21	0	238	44	14	0	357	0	56	0	4	2
37 *Lampsilis virescens* (Lea, 1858)	0	0	0	0	0	59	0	0	0	0	0	0	0	0	0
38 *Lasmigona costata* (Rafinesque, 1820)	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
39 ***Lemiox rimosus* (Rafinesque, 1831)**	0	0	0	8	1	143	57	34	1	61	0	24	0	29	1
40 *Leptodea fragilis* (Rafinesque, 1820)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
41 ***Lexingtonia dolabelloides* (Lea, 1840)**	0	*cf.*	7	15	1	373	53	69	7	1253	0	175	12	229	5
42 *Ligumia recta* (Lamarck, 1819)	0	0	2	3	0	0	1	6	0	8	1	8	0	1	0
43 ***Medionidus conradicus* (Lea, 1834)**	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
44 *Obliquaria reflexa* Rafinesque, 1820	0	0	0	2	0	0	0	1	0	3	0	0	0	0	0
45 *Obovaria olivaria* (Rafinesque, 1820)	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46 *Obovaria retusa* (Lamarck, 1819)	14	9	47	225	1	34	1	4	15	1617	4	458	41	89	
47 *Obovaria subrotunda* (Rafinesque, 1820)	1	13	0	89	0	66	8	3	8	483	0	178	10	38	0
48 *Plethobasus cicatracosus* (Say, 1829)	0	0	32	48	4	12	0	3	2	446	0	204	34	0	0
49 *Plethobasus cooperianus* (Lea, 1834)	0	4	3	231	6	0	0	1	8	845	*cf.*	246	54	405	10
50 *Plethobasus cyphyus* (Rafinesque, 1820)	0	0	2	17	1	0	1	0	2	73	7	27	5	39	20
51 *Pleurobema clava* (Lamarck, 1819)	47	*cf.*	10	71	2	1099	317	79	17	1114	0	196	21	*cf.*	0
52 *Pleurobema cordatum* (Rafinesque, 1820)	18	25	48	46	4	63	163	20	13	6455	24	1359	166	365	42
53 ***Pleurobema oviforme* (Conrad, 1834)**	0	0	0	0	0	257	0	0	0	60	0	0	0	*cf.*	0

Table I. (continued)

Species	Lower Tennessee Interior					Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian			
	Dyke Site	Eva Site	Daniels Landing	40DR305	Diamond Island	Pickwick Basin	Smith Bottom Cave	Huston Site	Hobbs Island	Widow's Creek	Long Island	Chickamauga Lake	McDonald Site	40LD207	Knoxville
54 *Pleurobema plenum* (Lea, 1840)	0	0	40	236	14	217	4	12	6	?	*cf.*	1555	114	335	81
55 *Pleurobema rubrum* (Rafinesque, 1820)	0	0	39	440	4	46	22	10	22	?	0	612	42	208	21
56 *Pleurobema sintoxia* (Rafinesque, 1820)	0	0	0	0	0	0	0	9	1	?	0	0	5	0	0
57 *Potamilus alatus* (Say, 1817)	0	0	0	1	0	2	0	0	0	0	0	3	0	0	0
58 *Ptychobranchus fasicolaris* (Rafinesque, 1820)	0	0	10	19	1	40	7	11	10	435	1	253	12	148	11
59 ***Ptychobranchus subtentum* (Say, 1825)**	0	0	0	1	0	288	67	14	0	78	0	16	0	5	7
60 *Pyganodon grandis* (Say, 1829)	0	0	0	0	0	16	1	0	0	1	0	0	0	0	0
61 *Quadrula cylindrica* (Say, 1817)	0	1	2	23	0	161	16	28	2	111	0	34	0	10	0
62 ***Quadrula intermedia* (Conrad, 1836)**	0	0	1	23	1	78	22	3	2	63	*cf.*	65	0	147	1
63 *Quadrula metanevra* (Rafinesque, 1820)	1	0	6	199	6	230	4	19	9	599	0	190	65	*cf.*	0
64 *Quadrula pustulosa* (Lea, 1831)	12	1	9	66	1	121	15	20	5	334	*cf.*	94	*cf.*	14	4
65 *Quadrula quadrula* (Rafinesque, 1820)	1	*cf.*	0	0	0	0	0	0	0	0	0	0	0	0	0
66 *Quadrula sparsa* (Lea, 1841)	0	0	0	0	0	0	17	*cf.*	3	0	*cf.*	0	0	*cf.*	1
67 *Strophitus undulatus* (Say, 1817)	0	0	0	0	0	1	0	0	0	0	0	*cf.*	0	2	0
69 ***Toxolasma lividus* (Rafinesque, 1831)**	0	0	0	0	0	94	18	2	0	38	0	0	0	0	0
70 *Truncilla truncata* (Rafinesque, 1820)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
71 *Villosa fabalis* (Lea, 1831)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
72 *Villosa iris* (Lea, 1829)	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
73 ***Villosa taeniata* (Conrad, 1834)**	0	0	1	0	0	758	119	35	0	24	0	0	0	0	0
74 ***Villosa trabalis* (Conrad, 1834)**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
75 ***Villosa vanuxemensis* (Lea, 1838)**	0	0	0	0	0	1	0	0	0	1	0	*cf.*	0	0	0
Total number of valves per column	534	176	951	12 018	395	31 950	3098	2166	1521	59 909	171	27 065	2232	16 095	1083
Total number of species per column	19	20	33	41	25	51	43	43	32	50	15	42	26	32	30
Total number of '*cf.*' entries per column	0	3	0	1	0	0	3	4	1	0	5	3	1	7	1

Cumberlandian species are shown in bold type; *cf.*, valves are 'close to this species'.

Pre-impoundment mussel diversity compiled by Lewis (1871), Pilsbry and Rhoads (1897) and Ortmann (1918) indicated 55 species surviving in the river. Between 1868 and 1901, 21 Cumberlandian species were collected here, but in 1914 Ortmann (1918) collected only one—*D. dromas.* This suggests that prior to the construction of main channel dams, Cumberlandian species were already suffering a significant decline in the upper Tennessee River.

Based on post-impoundment mussel records obtained between 1957 and 1993 reported by Scruggs (1960), Isom (1969, 1971), Pardue (1981), Parmalee *et al.* (1982), Hubbs (1993) and Ahlstedt and McDonough (1994), the number of extant mussel species was reduced to just 39 in the new river–lake habitat created by impoundment in Fort Loudoun, Watts Bar, Chickamauga and Nickajack (i.e. Hales Bar) reservoirs. The only two Cumberlandian species encountered, *D. dromas* and *Pleurobema oviforme*, were both represented by old relict individuals. *Megalonaias nervosa* was absent from the Upper Tennessee River in archaeological and early historical collections, but in 1965 it dominated the mussel fauna of Nickajack Lake (Isom, 1969). In 1966, Isom was the first to report species that were previously unknown from the Upper Tennessee River; these included *Anodonta suborbiculata*, *Lasmigona complanata* and *Pyganodon grandis* from Chickamauga Lake, and *Utterbackia imbecillis* from Fort Loudoun reservoir (Isom, 1969, 1971). Parmalee *et al.* (1982) located two other recent invaders, *A. suborbiculata* and *Potamilus ohiensis* in Chickamauga Lake. In Chickamauga Lake, *Pleurobema cordatum* initially realized dominance at 74.6% (Scruggs, 1960). Subsequently, it nearly disappeared and was replaced in abundance by *E. crassidens* (Pardue, 1981; Ahlstedt and McDonough, 1994), a species also dominating the post-impoundment Watts Bar reservoir, where it comprised 85.2% of the sample (Pardue, 1981).

Lower Tennessee Cumberlandian

Fifty-four species of unionids, including 21 Cumberlandian species, were identified from subfossil prehistoric shells collected between Walden Gorge and Muscle Shoals. Cumberlandian species accounted for 30% of the total number of shells. Three species (*E. dilatata*, *D. dromas* and *P. cordatum*) accounted for more than 63% of the identified specimens.

Thirty-one mussel species were collected between 1899 and 1903 in the Lower Tennessee Cumberlandian zone (Hinkley, 1906; van der Schalie, 1939). In 1931, five Interior Basin species were reported from this zone for the first time. This section of the river was already straddled by two main channel dams, Wilson Dam downstream and Hales Bar upstream.

Only 23 unionid species were identified from combined collections in Guntersville and Wheeler reservoirs. Eighteen species were located in Guntersville Lake and 19 in Wheeler Lake (Scruggs, 1960; Isom, 1969). Species lists provide absolute diversity in these reservoirs, but they neglect species abundance. Therefore, a species represented by one individual is given the same weight as a species represented by millions of individuals. None of the species in either reservoir were Cumberlandian.

Muscle Shoals

A total of 65 species were identified from prehistoric collections made in the vicinity of Muscle Shoals. Twenty-four of these were Cumberlandian, comprising 32% of all the valves identified. *Cyclonaias tuberculata*, *D. dromas* and *E. dilatata* comprised over 54% of the archaeological samples.

Based on historical collections reported by Hinkley (1906), Ortmann (1925) and van der Schalie (1939), 62 species still inhabited Muscle Shoals in the early 1900s. In 1904, Hinkley collected 45 species at Florence, AL. Mussels that were dominant in archaeological material were last collected between 1904 and 1910 by either Hinkley (1906) or Smith (Ortmann, 1925) before the main channel dams were built. In 1904, Hinkley found nine species of *Epioblasma* at Muscle Shoals. On 26 August 1924, about 4 months after the closure of Wilson Dam, Ortmann (1925) found only two, *E. obliquata* and *E. personata*, which he considered to be Interior Basin species. Ortmann collected a total of 29 species from Muscle Shoals between Wilson Dam and the Florence Bridge. Although Ortmann located six Cumberlandian species at Muscle Shoals in 1924, another six were already gone. He also found four species (*Fusconaia ebena*, *M. nervosa*, *Obovaria olivaria* and *Tritogonia verrucosa*) that had not been reported, based on earlier records, from the vicinity of or upstream from Muscle Shoals in an archaeological or pre-impoundment context.

Only 36 species were collected in the vicinity of Muscle Shoals at Sevenmile Island in Pickwick Lake and the tailwaters of Wilson Dam in post-impoundment collections (Stansbery, 1964; Isom, 1969). Only two of these mussels, *L. dolabelloides* and *P. oviforme*, originated in the Cumberlandian region. The disappearance of the Cumberlandian fauna from Muscle Shoals is discussed by Ortmann (1925), van der Schalie (1939), Stansbery (1964), Isom (1969) and Pardue (1981).

Lower Tennessee Interior

Forty-four species of mussels lived in the prehistoric Tennessee River between the lower extent of Muscle Shoals and the river's mouth. Thirteen of these were considered to be Cumberlandian by Ortmann (1925), and they comprised 33% of the relative abundance of shells identified. *D. dromas*, *F. subrotunda* and *E. dilatata* comprised 56% of the valves collected here.

Ortmann (1925) collected 25 species at Dixie, TN (TRK 178) in 1924, and speculated, based on the known distribution of mussel species at that time, that a total of 51 species could be located there. From five sites along this section of the Lower Tennessee River, Ellis located a total of 21 species in 1931, while Goodrich found 12 species at another site (van der Schalie, 1939). Combined collections by Ellis, Goodrich and Ortmann totaled 31 species from the Tennessee River downstream from Muscle Shoals. After evaluating the effort of Ellis in 1931, van der Schalie (1939) concluded that this stretch of river probably did not contain as many as 51 species in 1924, as Ortmann (1925) had proposed.

In the Lower Tennessee River, no Cumberlandian taxa were reported in pre-impoundment collections. In 1931, *F. ebena* dominated one sample near the mouth of the Tennessee River and *P. cordatum* dominated another sample taken upstream near Muscle Shoals (van der Schalie, 1939). Ellis also discovered three species (*Fusconaia flava*, *Quadrula nodulata* and *U. imbecillis*) that were previously unknown from the Tennessee River.

From post-impoundment collections, 46 species of mussels were accurately reported (in the present authors' opinion) from the Tennessee River downstream from Pickwick Landing Dam to the mouth of the Tennessee River (Scruggs, 1960; Isom, 1969; Bates and Dennis, 1985; Hubbs, 1992, 1993, 1994, 1995). Initially, *P. cordatum* was reported as the dominant species in Kentucky Lake (Scruggs, 1960), but eventually *F. ebena* achieved dominance there (Isom, 1969; Hubbs, 1992, 1993, 1994, 1995). *Amblema plicata* and *F. ebena* were codominant in the Kentucky Dam tailwaters (Miller *et al.*, 1992).

SUMMARY

A total of 92 mussel species were reported from archaeological, historical and/or recent collections from the Tennessee River (Table II). The composition and dominance of the mussel community that had remained stable for nearly 6000 years according to Bogan (1990) has changed dramatically based on historical and recent collections. Some of this change occurred prior to impoundment and some afterwards.

Based on positive identifications, the prehistoric mussel assemblages comprised a total of 75 species: 46 species in the Upper Tennessee Cumberlandian; 54 species in the Lower Tennessee Cumberlandian; 65 species at Muscle Shoals; and 46 species in the Lower Tennessee Interior. *D. dromas* (23%), *E. dilatata* (21%) and *C. tuberculata* (8%) comprised nearly 52% of all shells identified from the entire length of the river.

Approximately 78 species are known from historical collections prior to 1918 from the pre-impounded Tennessee River, but as many as 28 of these (*Actinonaias pectorosa*, *Alasmidonta marginata*, *E. arcaeformis*, *E. biemarginata*, *E. brevidens*, *E. capsaeformis*, *E. florentina*, *E. haysiana*, *E. lenoir*, *E. lewisii*, *E. propinqua*, *E. stewardsoni*, *E. turgidula*, *Fusconaia cor*, *F. cuneolus*, *Lampsilis virescens*, *Lemiox rimosus*, *Leptodea leptodon*, *Medionidus conradicus*, *Obovaria subrotunda*, *Pleurobema clava*, *Ptychobranchus subtentum*, *Quadrula intermedia*, *Toxolasma lividus*, *Villosa fabalis*, *V. iris*, *V. taeniata* and *V. vanuxemensis*) were not collected after 1910. A further seven species (*Epioblasma lenoir*, *Lampsilis teres*, *Leptodea*

Table II. Composibon of freshwater mussel species obtained from the Tennessee River proper in archaeological (before A.D. 1200), pre-impoundment (1831–1931), or post-impoundment (1956–1997) contexts

Species	Faunal zone and record of occurrence											
	Lower Tennessee Interior			Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian		
	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment
1 *Actinonaias ligamentina* (Lamarck, 1819)	x	x	x	x	x		x	x	x	x	x	x
2 ***Actinonaias pectorosa*** **(Conrad, 1834)**					x		x				x	
3 *Alasmidonta marginata* Say, 1818				x							x	
4 ***Alasmidonta viridis*** **(Rafinesque, 1820)**				x								
5 *Amblema plicata* (Say, 1817)	x	x	x	x	x	x	x	x	x	x	x	x
6 *Anodonta suborbiculata* Say, 1831			x			x						x
7 *Arcidens confragosus* (Say, 1829)			x									
8 *Cumberlandia monodonta* (Say, 1829)			x	x	x	x		x			x	
9 *Cyclonaias tuberculata* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
10 *Cyprogenia stegaria* (Rafinesque, 1820)	x		x	x	x	x	x	x	x	x	x	x
11 ***Dromus dromas*** **(Lea, 1834)**	x			x	x		x	x		x	x	x
12 *Ellipsaria lineolata* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
13 *Elliptio crassidens* (Lamarck, 1819)	x	x	x	x	x	x	x	x	x	x	x	x
14 *Elliptio dilatata* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
15 ***Epioblasma arcaeformis*** **(Lea, 1831)**	x			x			x			x	x	
16 ***Epioblasma biemarginata*** **(Lea, 1857)**				x	x		x					
17 ***Epioblasma brevidens*** **(Lea, 1831)**	x			x	x		x			x	x	
18 ***Epioblasma capsaeformis*** **(Lea, 1834)**				x			x			*cf.*	x	
19 *Epioblasma flexuosa* (Rafinesque, 1820)	x			x			x			x		
20 ***Epioblasma florentina*** **(Lea, 1857)**				x	x					x		
21 ***Epioblasma haysiana*** **(Lea, 1833)**	x			x	x		x			x	x	
22 ***Epioblasma lenoir*** **(Lea, 1843)**											x	
23 ***Epioblasma lewisii*** **(Walker, 1910)**	x			x			x				x	
24 *Epioblasma obliquata* (Rafinesque, 1820)	x			x	x					x		
25 *Epioblasma personata* (Say, 1829)				x	x							

Table II. (continued)

Species	Faunal zone and record of occurrence											
	Lower Tennessee Interior			Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian		
	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment
26 ***Epioblasma propinqua* (Lea, 1857)**	x			x	x		x			x	x	
27 ***Epioblasma stewardsoni* (Lea, 1857)**	*cf.*			x			x			x	x	
28 *Epioblasma torulosa* (Rafinesque, 1820)	x			x	x		x	x		x	x	
29 *Epioblasma triquetra* (Rafinesque, 1820)	x			x	x		x	x		x	x	
30 ***Epioblasma turgidula* (Lea, 1858)**					x					x		
31 ***Fusconaia barnesiana* (Lea, 1838)**	x			x	x		x			x	x	
32 ***Fusconaia cor* (Conrad, 1834)**				x	x		x				x	
33 ***Fusconaia cuneolus* (Lea, 1840)**				x	x		x				x	
34 *Fusconaia ebena* (Lea, 1831)		x	x		x	x		x	x			x
35 *Fusconaia flava* (Rafinesque, 1820)		x	x									
36 *Fusconaia subrotunda* (Lea, 1831)	x	x	x	x	x	x	x	x		x	x	x
37 *Hemistena lata* (Rafinesque, 1820)				x	x					x	x	
38 *Lampsilis abrupta* (Say, 1831)	x	x	x	x	x	x		x			x	x
39 *Lampsilis cardium* Rafinesque, 1820			x									
40 *Lampsilis fasciola* Rafinesque, 1820	x			x	x	x	x	x		x	x	
41 *Lampsilis ovata* (Say, 1817)	x	x	x	x	x	x	x	x	x	x	x	x
42 *Lampsilis teres* (Rafinesque, 1820)		x	x		x	x		x				
43 ***Lampsilis virescens* (Lea, 1858)**				x	x							
44 *Lasmigona complanata* (Barnes, 1823)			x									x
45 *Lasmigona costata* (Rafinesque, 1820)				x	x					x	x	x
46 ***Lemiox rimosus* (Rafinesque, 1831)**	x			x	x		x			x	x	
47 *Leptodea fragilis* (Rafinesque, 1820)			x		x	x	x	x			x	x
48 *Leptodea leptodon* (Rafinesque, 1820)					x							
49 ***Lexingtonia dolabelloides* (Lea, 1840)**	x		x	x	x	x	x	x		x	x	
50 *Ligumia recta* (Lamarck, 1819)	x	x	x	x	x	x	x	x	x	x	x	x
51 ***Medionidus conradicus* (Lea, 1834)**				x	x						x	

Table II. (continued)

Species	Faunal zone and record of occurrence											
	Lower Tennessee Interior			Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian		
	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment
52 *Megalonaias nervosa* (Rafinesque, 1820)		x	x		x	x		x	x			x
53 *Obliquaria reflexa* Rafinesque, 1820	x	x	x	x	x	x	x	x	x		x	x
54 *Obovaria olivaria* (Rafinesque, 1820)	x	x	x		x	x		x	x			x
55 *Obovaria retusa* (Lamarck, 1819)	x	x	x	x	x		x	x		x	x	
56 *Obovaria subrotunda* (Rafinesque, 1820)	x			x			x			x	x	
57 *Plectomerus dombeyanus* (Valenciennes, 1827)			x									
58 *Plethobasus cicatracosus* (Say, 1829)	x			x		x	x			x		
59 *Plethobasus cooperianus* (Lea, 1834)	x	x	x	x		x	x	x	x	x	x	x
60 *Plethobasus cyphyus* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
61 *Pleurobema clava* (Lamarck, 1819)	x			x	x		x			x		
62 *Pleurobema cordatum* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
63 ***Pleurobema oviforme* (Conrad, 1834)**				x	x	x	x				x	x
64 *Pleurobema plenum* (Lea, 1840)	x			x	x		x	x		x		x
65 *Pleurobema rubrum* (Rafinesque, 1820)	x	x		x	x	x	x	x		x	x	x
66 *Pleurobema sintoxia* (Rafinesque, 1820)		x	x	x			x			x		x
67 *Potamilus alatus* (Say, 1817)	x	x	x	x	x	x		x	x	x	x	x
68 *Potamilus ohiensis* (Rafinesque, 1820)			x			x						x
69 *Ptychobranchus fasciolaris* (Rafinesque, 1820)	x	x	x	x	x	x	x	x		x	x	x
70 ***Ptychobranchus subtentum* (Say, 1825)**	x	x		x			x	x		x		
71 *Pyganodon grandis* (Say, 1829)			x	x		x	x					x
72 *Quadrula apiculata* (Say, 1829)			x									
73 *Quadrula cylindrica* (Say, 1817)	x		x	x	x		x	x		x	x	
74 *Quadrula fragosa* (Conrad, 1835)			x		x				x			
75 ***Quadrula intermedia* (Conrad, 1836)**	x			x	x		x	x		x	x	
76 *Quadrula metanevra* (Rafinesque, 1820)	x	x	x	x	x	x	x	x	x	x	x	x
77 *Quadrula nodulata* (Rafinesque, 1820)		x	x									

Table II. (continued)

Species	Faunal zone and record of occurrence											
	Lower Tennessee Interior			Muscle Shoals			Lower Tennessee Cumberlandian			Upper Tennessee Cumberlandian		
	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment	Archae-ological	Pre-impoundment	Post-impoundment
78 *Quadrula pustulosa* (Lea, 1831)	x	x	x	x	x	x	x	x	x	x	x	x
79 *Quadrula quadrula* (Rafinesque, 1820)	*cf.*	x	x	x	x	x			x			
80 *Quadrula sparsa* (Lea, 1841)				x			*cf.*					
81 *Strophitus undulatus* (Say, 1817)				x	x					x	x	
82 ***Toxolasma lividus*** **(Rafinesque, 1831)**				x			x				x	
83 *Toxolasma parvus* (Barnes, 1823)			x		x			x				x
84 *Tritogonia verrucosa* (Rafinesque, 1820)		x	x		x	x		x	x			x
85 *Truncilla donaciformis* (Lea, 1828)		x	x			x		x	x			x
86 *Truncilla truncata* (Rafinesque, 1820)		x	x	x	x			x			x	x
87 *Utterbackia imbecillis* (Say, 1829)		x	x			x						x
88 *Villosa fabalis* (Lea, 1831)							x				x	
89 *Villosa iris* (Lea, 1829)				x	x						x	
90 ***Villosa taeniata*** **(Conrad, 1834)**	x			x	x		x					
91 ***Villosa trabalis*** **(Conrad, 1834)**				x	x							
92 ***Villosa vanuxemensis*** **(Lea, 1838)**				x			x			x	x	
Total number of species per column	44	33	46	68	63	36	53	40	23	47	55	38
Total number of '*cf.*' entries per column	2	0	0	0	0	0	1	0	0	1	0	0
Total number of entries per column	46	33	46	68	63	36	54	40	23	48	55	38

Cumberlandian species are shown in bold type; x, live or fresh dead mussel shells collected; *cf.*, valves are 'close to this species'.

leptodon, *M. nervosa*, *Quadrula fragosa*, *Toxolasma parvus* and *T. verrucosa*) were not recorded from archaeological samples but appeared in historical collections prior to 1910. *E. lenoir*, rare in historical collections, is considered here to be a cryptic endemic Cumberlandian species and may have been overlooked in archaeological samples. The other six species may also have occurred in the Tennessee River in prehistoric times, but were overlooked.

Sixteen nominal species of *Epioblasma* inhabited the prehistoric Tennessee River for at least 6000 years (Bogan, 1990), where they comprised nearly 13% of all the specimens collected from 15 aboriginal midden samples studied. Six of these species inhabited all four faunal zones discussed here. However, since the early 1900s, nearly all species in the genus have been eliminated from the entire river. From prehistoric to historic collections, the range of *Epioblasma* has diminished. All species were confined to either the Upper Tennessee Cumberlandian zone or Muscle Shoals. Fifteen species of *Epioblasma* were collected in the upper Tennessee Cumberlandian and/or at Muscle Shoals in pre-impoundment collections since the 1800s. Eight *Epioblasma* were reported from the upper Tennessee Cumberlandian before 1918, but have not been reported from there since that itme; five of the eight were last collected between 1889 and 1895. Another species, *Epioblasma capsaeformis*, was abundant throughout the upper Tennessee Cumberlandian until 1915, but was not reported by subsequent collectors in the mainstem river; two others were last collected before 1918 (Lewis, 1871; Pilsbry and Rhoads, 1897; Ortmann, 1918). The ten species of *Epioblasma* collected in historic times from Muscle Shoals were gone by 1924: one in the early 1800s, another six by 1904, one more between 1904 and 1910, and two in 1924 (Hinkley, 1906; Ortmann, 1925). All five species of *Villosa* found in the mainstem Tennessee River followed a similar pattern of extirpation. They were confined in historical collections to the same two zones: Upper Tennessee Cumberlandian (all *Villosa* were gone by 1901) and Muscle Shoals. All *Villosa* species were gone from the mainstem collections by 1924.

Only 53 species remain throughout the entire post-impoundment Tennessee River, based on recent publications (Scruggs, 1960; Bates, 1962; Isom, 1969, 1971; Pardue, 1981; Parmalee *et al.*, 1982; Dennis, 1984; Bates and Dennis, 1985; Hubbs, 1992, 1993, 1994, 1995; Way *et al.*, 1989; Miller *et al.*, 1992; Ahlstedt and McDonough, 1994). Based on the records utilized in this report, 11 species (*A. suborbiculata*, *Arcidens confragosus*, *F. flava*, *Lampsilis cardium*, *L. complanata*, *Plectomerus dombeyanus*, *P. ohiensis*, *Quadrula apiculata*, *Q. nodulata*, *Truncilla donaciformis* and *U. imbecillis*) were not identified from the Tennessee River before 1931, and are considered here as recent opportunistic invaders into the impounded river. Only 37 of the indigenous mussel species represented in prehistoric shell samples occur in the mainstem Tennessee River reservoirs today. At least 16 of these species are represented only by relict individuals and, based on valid evidence, do not represent reproductive populations. The most diverse reservoir fauna, as many as 46 species, may be found today in Kentucky Lake, while 35 species occur in both Pickwick Landing and Chickamauga reservoirs. The other reservoirs each contain 25 or fewer species.

From all the samples combined in this study throughout the prehistoric Tennessee River, a composite of 16 Cumberlandian and Interior Basin species accounted for over 90% of the shells collected in archaeological samples. Seven of these 16 species (*D. dromas*, *F. subrotunda*, *Pleurobema plenum*, *Obovaria retusa*, *L. dolabelloides*, *Plethobasus cooperianus* and *P. rubrum*) are still present in the Tennessee River, but in reduced numbers, and show little or no signs of recruitment. A further two species are extirpated (*Epioblasma torulosa*, *P. clava*) and two more are extinct (*E. arcaeformis* and *E. propinqua*). *Pleurobema cordatum* and *E. crassidens* were among the 16 most-abundant species prehistorically, and attained dominance, at least temporarily, in some reservoirs, while recent arrivals such as *M. nervosa* and *F. ebena* have become important species in the impounded Tennessee River. In addition, species that were uncommon to rare in prehistoric times, such as *Obliquaria reflexa* and *P. grandis*, are relatively common in reservoir habitats throughout the length of the Tennessee River today.

CONCLUSIONS

In the prehistoric Tennessee River, the unique Cumberlandian fauna thrived. Beginning in the 1800s, even before impoundment, the Cumberlandian fauna began to disappear from the Tennessee River proper. By the early 1900s, many of the Cumberlandian species inhabiting the prehistoric Tennessee River suffered a serious decline. After impoundment, the remnants of this extraordinary endemic fauna consist of only two species, represented by a few non-reproducing individuals.

The early loss of species from the river was difficult for researchers to assess. For example, Ortmann (1925) was not convinced that the sugarspoon (*E. arcaeformis*) even occurred in the Tennessee River below Walden Gorge. However, the sugarspoon was widespread throughout the length of the Tennessee River in prehistoric times. Ortmann (1925), van der Schalie (1939) and Isom (1969) postulated that the downstream limit to many of the Cumberlandian species was in the vicinity of Muscle Shoals or possibly a little further downstream at Bear Creek. The archaeological data suggest that 13 Cumberlandian species extended several hundred kilometers below Muscle Shoals, while at least two (*D. dromas* and *E. arcaeformis*) were located within 27 km of the mouth of the Tennessee River. At least 13 of the 38 Cumberlandian species recognized by Ortmann (1925) extended 133–334 km downstream from Muscle Shoals in the prehistoric river.

Recognition of faunal barriers at both Muscle Shoals and Walden Gorge is supported by the archaeological data reported in Table I. The concept of a barrier as perceived here is not a geological barrier, a physical impediment to movement or dispersal of a species across it; rather, it is an ecological barrier that serves as a boundary line or border between two different habitats. The lower end of Muscle Shoals approximates the boundary between the East Gulf Coastal Plain and the Highland Rim physiographic sections (the fall line). Coincidentally, Walden Gorge is cut through the face of the Cumberland Plateau as the Tennessee River leaves the Tennessee Valley and Ridge physiographic section. In prehistoric times, these boundaries may have marked the distributional limits of species adapted to the habitats found on either side of them. At least ten mussel species identified from prehistoric sites were located at, or upstream from, Muscle Shoals (Table I), but were not identified downstream from there in the main channel Tennessee River (e.g. *E. biemarginata, E. capsaeformis and E. florentina*). These ten species do not include either the small stream species found only in the mainstem river at Muscle Shoals (e.g. *L. virescens* and *V. iris*), or species that actually do occur downstream from Muscle Shoals in the Interior Basin, although they were not located in the Tennessee River below Muscle Shoals in the archaeological component of this study (e.g. *P. grandis* and *Strophitus undulatus*). Another three species (*F. ebena, O. olivaria* and *Quadrula quadrula*) were only found downstream from Muscle Shoals in the archaeological context (Table I) and for some unknown ecological reason(s) could not establish populations upstream from that point. This ecological barrier is of importance within the Tennessee River because it delimits the pre-impoundment distribution of mussel species found there. However, mussels and their offspring could and probably did traverse Muscle Shoals, because Cumberlandian mussel species limited in distribution by this barrier in the Tennessee River are also found upstream in the Cumberland and Duck river systems within similar ecological niches. In addition, a barrier at Walden Gorge apparently also existed in prehistoric times. Based on our archaeological data, seven species of mussels (*Ellipsaria lineolata, E, biemarginata, E. lewisii, F. cor, F. cuneolus, O. reflexa* and *P. grandis*) were not identified from the 46475 valves collected from sites on the Tennessee River proper above Walden Gorge, but all seven were collected about 8 km below Walden Gorge at the Widow's Creek Site.

The loss of mussel taxa from the Tennessee River prior to impoundment is evident, and the invasion of reservoir-adapted species that followed is certainly attributable to impoundment. This has caused a dramatic shift in the species composition and diversity when comparing today's deep sluggish reservoirs with the prehistoric free-flowing energetic Tennessee River. This is due to the loss of the more complex environment that existed in the former Tennessee River upstream from Muscle Shoals and the concurrent loss of mussel diversity associated with it. The habitat throughout the river is now homogenous and microhabitats that once existed in the river no-longer exist. The species that were adapted to a life above Muscle Shoals are the species that have vanished. Conversely, species that were adapted to life in the

Interior Basin have moved into the new habitat and now live in a geographical area that was extralimital in prehistoric times. Individuals of some riverine or lotic species that initially survived impoundment now appear to be growing old without any recruitment and will eventually become extirpated through attrition. Although they can survive in the new environment, they cannot reproduce there. Other riverine species have responded more slowly to the adversity of the altered habitat. They have survived in greater numbers and even dominated the early stages of impoundment (e.g. *E. crassidens*, *P. cordatum*), but without adequate recruitment their numbers will also continue to diminish.

Aboriginal nomadic peoples camped along the banks of the Tennessee River utilized its resources and moved on. Their use of the pristine river resources was sustainable. When descendants of European explorers began settling eastern North America over 400 years ago, they rediscovered the Tennessee River. Having cut the primordial forest, they proceeded about 100 years ago with an effort to 'improve' the river by impounding it. The river's power was harnessed and its character was destroyed within a 50-year period, but this did make for dependable transportation and profitable commerce for the new stewards of the land. Subsequently, a fauna that had struggled for existence since the Cretaceous and thrived in 1049 km of river for at least 6000 years, was gone in less than 150 years.

The damage done by poorly designed dams has destroyed millions of years of evolution which cannot be undone. It must be emphasized that the destruction of the mussel fauna in the Tennessee River was not caused solely by impoundment, but many of the mussel species in the river might have survived if some attention had been given to their physical requirements during the construction of these dams. Water taken from the bottom of a large dam generally provides an environment in the tailwaters that is inadequate for the needs of a healthy aquatic community. Some sort of mixing within the water column should be a priority in water releases so that the tailwaters of dams might remain a suitable habitat for the native aquatic communities. The loss of many native freshwater mussel communities in the Tennessee River is permanent, but the mistakes made there need not be repeated in the regulation of other rivers.

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