Aboriginal and Modern Freshwater Mussel Assemblages (Pelecypoda: Unionidae) from the Chickamauga Reservoir, Tennessee

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ABSTRACT.— From December 1976 through March 1979, ca. 40,500 mussel valves were collected from 28 aboriginal shell middens in the Chickamauga Reservoir (TRM 495-528), Rhea and Meigs counties, Tennessee. Approximately 46 species were identified in 27,875 specimens from 14 of these Middle Woodland through Mississippian component sites. Valves of *Pleurobema* spp., *Elliptio* spp., *Actinonaias ligamentina*, and *Dromus dromas* comprised 75% of the total. About 28 species represented in the shell middens are now either extinct, or are extirpated from the reservoir. Five species have invaded and become established in the reservoir, and four others, rare in prehistoric times, have greatly increased their range and abundance since impoundment.

INTRODUCTION

Accumulations, often huge, of freshwater mussel valves and snail shells along the banks of the Tennessee and other major rivers in southeastern United States attest to the degree aboriginal man used this easily accessible food resource. Although Parmalee and Klippel (1974) showed that this subsistence resource is relatively low in food energy compared with most other meat animals, and that it was exploited as a supplement rather than a staple, mollusks were nevertheless taken in great quantities and did provide an abundant food supplement. The prehistoric naiad (freshwater mussel) fauna of the Tennessee and Cumberland River systems was one of the richest in the world and consisted of at least 90 species. Although the Indian harvested vast quantities of mussels over a period of thousands of years, there is no evidence to suggest that this activity brought about the extinction of even one species or was detrimental to naiad populations in general. However, the effect of dam construction, impoundment, siltation, and overharvesting by commercial shellers over the last 75 years is a different matter (Isom 1969).

Relatively few detailed ecological and taxonomic studies involving

shell assemblages from aboriginal middens that are so prevalent along the Tennessee River have been undertaken. One notable exception was the analysis of over 100,000 mussel valves studied by Morrison (1942) from Archaic and Woodland shell middens that were located in what is now the Pickwick Landing Dam reservoir in northwestern Alabama. The more recent study by Warren (1975) involving analysis of 60,350 naiad specimens recovered from the Widows Creek site in northeastern Alabama provided an effective account of the species assemblage, the limnological and other habitat conditions reflected by this assemblage, and the extent of use of the naiads by the Woodland inhabitants of the site. Although extensive archaeological field work was carried out during 1937-1939 at Hiwassee Island (Lewis and Kneberg 1946), now within the Chickamauga Reservoir, and extensive shell middens were encountered, no study of this material was made and samples of unmodified shell were not retained.

Our interest in sampling a series of aboriginal shell middens that still remain along the shores of the middle and upper Chickamauga Reservoir was based on several factors: (1) no previous studies of prehistoric shell middens located in this section of the Tennessee River had been undertaken to assess the naiad species formerly present and their relative abundance at these sites; (2) since impoundment, much of this nonrenewable archaeological resource has been inundated and that which remains is subject to continual destruction through wave action, erosion, digging activities of artifact collectors, and general weathering; (3) these shell middens provided an opportunity to evaluate similarities and dissimilarities among cultural groups who once lived along this section of the river as to how extensively they exploited this food resource; and (4) recent surveys of naiad populations in the Chickamauga Reservoir, compared with shell samples collected from aboriginal middens, could provide significant data relative to changes in species assemblages during the last 2000 years.

MATERIALS AND METHODS

A total of 28 shell middens located along an approximately 50 km stretch of the middle and upper Chickamauga Reservoir (TRM 495-528) was sampled over a 2½ year period from December 1976 to March 1979. Some middens were extensive (Fig. 1), and shell that had eroded from the banks covered the beach (observable only during winter low water levels) for a distance of 300 m or more at certain sites. Most of the middens reflect an occupation by Late Woodland (ca. AD 600-1000) cultural groups; however, at least one single component Middle Woodland (ca. AD 1-600) site and two Mississippian component sites (ca. AD 1000-1600) were encountered. Lithic and ceramic samples were collected

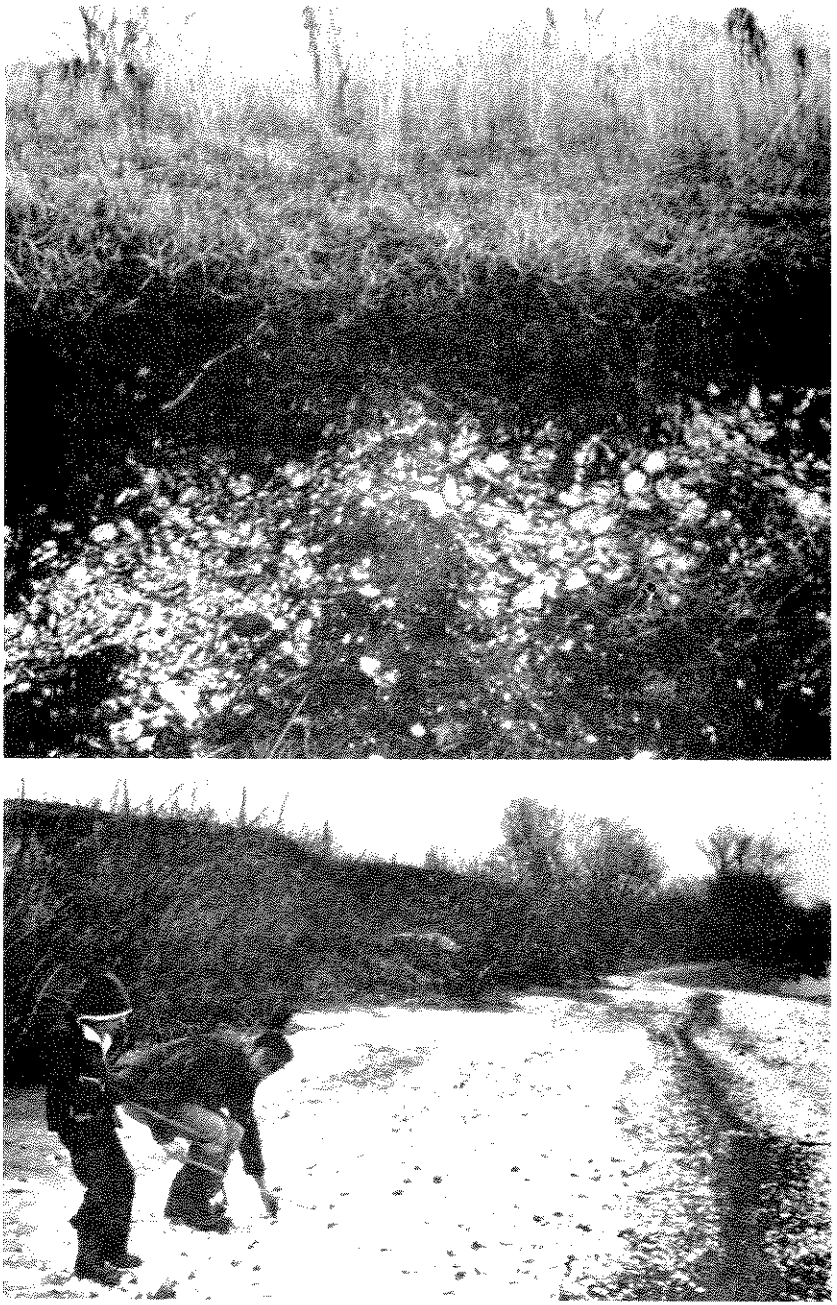

Fig. 1. Top: Aboriginal shell midden eroding from the bank of the Tennessee River (Chickamauga Reservoir). Bottom: Shell scattered by wave action along the beach below the same midden.

from the surface of the eroding shell banks and beaches, but a special effort was made to recover all such cultural material found within the portions of undisturbed shell lenses that were removed for this study. Since many of the deposits were comprised of residue from several cultural groups that spanned a considerable period of time, only those sherds and other artifacts found in direct association with the selected samples were used to define the temporal periods involved.

Considerable variation in midden size was apparent, with some containing only a few hundred valves and others literally hundreds of thousands. Most also contained shells of freshwater gastropods. Because of the typically compact nature of the shell lenses, we could remove only a small part of the shell comprising the midden and yet obtain a large but relatively unbiased sample of the species assemblage. All samples were returned to the Department of Anthropology, University of Tennessee, Knoxville, where the shell was washed and determinations of species were made by comparisons with fresh specimens in the Zooarchaeology Section mollusk collection. Approximately 40,500 freshwater mussel valves, representing about 50 species, were identified from the samples collected during this study. For this report we evaluated collections from 15 of the sites (Fig. 2) for which the temporal assessment was most exact; samples from these 14 sites consisted of 27,875 valves. All specimens recovered during this study are housed in the Zooarchaeology Section, Department of Anthropology, University of Tennessee, Knoxville.

RESULTS AND DISCUSSION

Present Status of Naiad Fauna in Middle and Upper Chickamauga Reservoir

During the past two decades several investigators attempted to determine the status of freshwater mussel populations inhabiting the middle and upper Chickamauga Reservoir from ca. TRM 495 to TRM 529 (Scruggs 1960; Isom 1969; Pardue 1981). The study by Scruggs (1960) was undertaken primarily to determine the abundance, effects of shelling operations, and potential for recovery of commercially valuable species, especially *Pleurobema cordatum* (Raf. 1820), on specific beds in the Tennessee River (Wheeler and Chickamauga reservoirs). Although also concerned with similar aspects of naiad ecology and economics, the comprehensive study by Isom (1969) provided a more complete assessment of the total mussel fauna assemblage and evaluated the factors that brought about changes in extant species and population abundance since impoundment.

On the basis of these studies approximately 20 species (synonymizing *Anodonta corpulenta* Cooper 1834 with *Anodonta grandis* Say

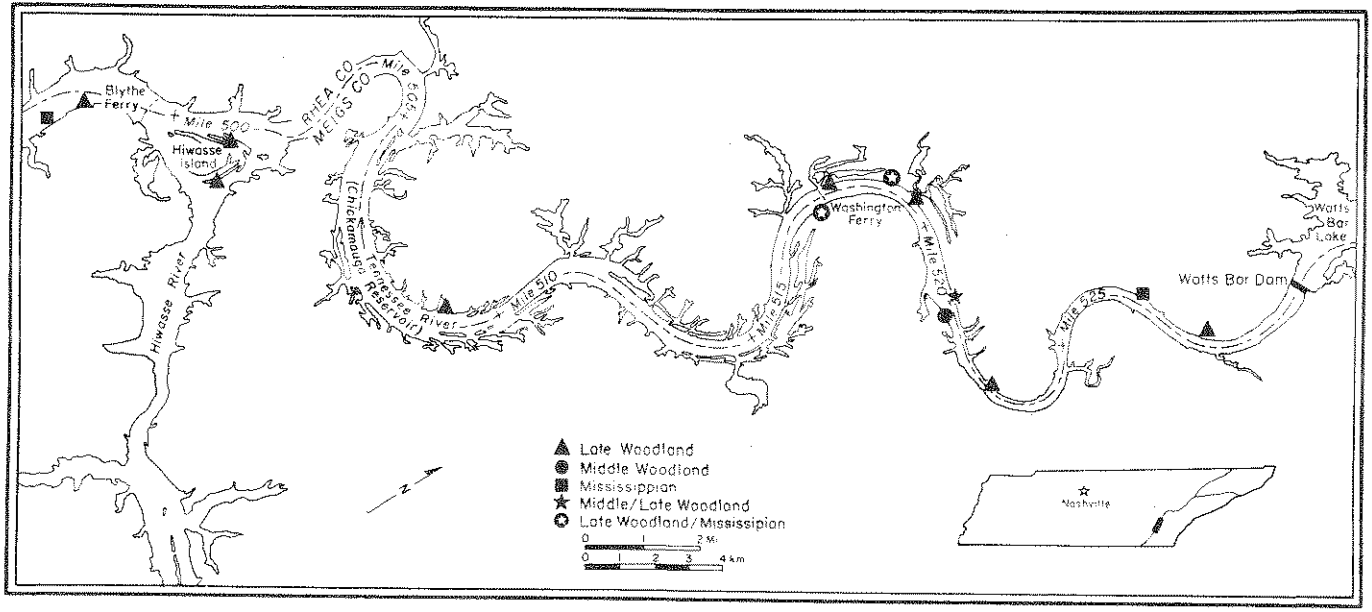

Fig 2. Upper Chickamauga Reservoir, showing locations of the 14 aboriginal shell middens sampled for this study.

1829) were found still inhabiting the middle and upper Chickamauga Reservoir (Pardue 1981). In addition, we collected specimens of three other species (*Anodonta suborbiculata* Say 1831, *Anodonta imbecillis* Say 1829, *Leptodea laevissima* Lea 1830) in the shallow mud-bottom bays at the mouth of the Hiwassee River. These results reflect the extirpation of approximately half of the naiad fauna known to have inhabited this part of the Tennessee River in prehistoric times (as evidenced from species represented in aboriginal shell middens) and in the early 20th century prior to impoundment (Ortmann 1918). Isom (1969) expressed the view that sedimentation, one of the consequences of impoundment resulting from a slowed current that prevents the substrate from being swept clean, and overharvesting by commercial shellers, are the two major factors in limiting mussel population growth and expansion in Tennessee River reservoirs.

Although populations of several species that are typical inhabitants of shallow mud-bottom bays and shorelines of the reservoir (e.g. *Anodonta* spp., *Leptodea* sp., *Potamilus* spp.) may become locally large, communities in the main river channel are composed primarily of *Elliptio crassidens* (Lamarck 1819), *Pleurobema cordatum*, *Quadrula pustulosa* (Lea 1831), and *Ellipsaria lineolata* (Raf. 1820). Several species still present in the reservoir are rare and their populations appear to consist of old nonbreeding adults: these are *Plethobasus cooperianus* (Lea 1834), *Cyprogenia irrorata* (Lea 1829), *Obovaria olivaria* (Raf. 1820), and *Dromus dromas* (Lea 1834). Until additional extensive sampling is carried out, the status of several other species, including *Lampsilis orbiculata* (Hildreth 1828), *Plethobasus cyphyus* (Raf. 1820), and *Actinonaias ligamentina* (Lamarck 1819), remains uncertain.

Prehistoric Mussel Assemblages Based on Midden Samples

Table 1 shows the mussel species represented by 27,875 valves collected from one Middle Woodland, eight Late Woodland, two Mississippian, one Middle/Late Woodland, and two Late Woodland/Mississippian sites along the middle and upper Chickamauga Reservoir, Meigs (MG) and Rhea (RH) counties, Tennessee. Although Archaic (8000-1000 BC) and Early Woodland (1000 BC-AD1) shell middens occur in considerable numbers and are often of great magnitude in the middle (Alabama) and lower (West Tennessee) reaches of the Tennessee, none have been located in the section of the river between Knoxville and Chattanooga. Shell middens left by peoples of the Early Woodland culture appear to be rare in the upper Tennessee River; we were unable to locate any Early Woodland sites, and found only one single component Middle Woodland site (40MG51) during our survey. For whatever reason(s), therefore, it appears that aboriginal man did not begin to harvest freshwater mussels as a food resource in any quantity in the upper Ten-

nessee River until ca. AD 100.

In evaluating similarities and differences among mussel species assemblages collected by people of various cultural groups, factors such as individual preference or selection (e.g. large vs. small specimens), location of the habitation site in relation to available mussel beds, season of the year collected, and probable differences in species comprising the beds along a section of river, must be taken into account. On the basis of samples collected during this study it is apparent that certain species, such as *A. ligamentina* and *D. dromas*, or an assemblage of closely related forms (e.g. *Pleurobema* spp.), were common and generally distributed throughout this section of the river during the past 2000 years. Considering the total sample from all cultural units, valves of *Pleurobema* spp., *A. ligamentina*, and *D. dromas* comprised 75% of all valves collected.

Valves of *D. dromas* varied from 24% in the Middle Woodland site sample to 45% in the multicomponent Middle Woodland/Mississippian sites, averaging 35% of the total sample. Of the 60,350 valves studied by Warren (1975) from the Widows Creek site shell midden (Tennessee River, northeastern Alabama: Early Woodland to Late Middle Woodland), *D. dromas* comprised 23% of all shells. Of the seven shell mounds sampled in the Pickwick Landing Basin (Tennessee River, northwestern Alabama: Archaic, Woodland), *D. dromas* was "One of the most abundant species in these shell deposits . . . and made up a major part of the total mussel fauna gathered for food" (Morrison 1942:359). Although a form of *D. dromas* is still fairly common in unimpounded reaches of the upper Powell and Clinch rivers in East Tennessee, the large river form appears to be surviving at only one restricted locality in the Tennessee River (Chickamauga Reservoir) (Pardue 1981).

Ortmann (1918:556) stated that *E. crassidens* is "In the Tennessee below Knoxville, and down to Chattanooga, it is extremely abundant"; it is reported to now be "by far the most abundant species in the upper Tennessee River" (Pardue 1981:44). Valves of this large, big-river mussel occurred in all middens sampled and accounted for about 6% of the total shell sample. Specimens of the related species, *Elliptio dilatatus* (Raf. 1820), also occurred at all sites but had been collected in greater numbers (ca. 12% of the total) than *E. crassidens*, possibly because it was more numerous in shallower riffles and shoals and consequently more accessible to the Indian. Today, populations of *E. dilatatus* have been greatly reduced in the Tennessee River, probably as a result of impoundment and its concomitant adverse factors. *Actinonaias ligamentina* is another species that occurred consistently in all middens; valves of this species varied from ca. 4.5% of the total from Late Woodland/Mississippian sites to nearly 9.5% at the Middle Woodland site (average for all sites, 7.5%). At the Widows Creek site (Warren 1975) its

Table 1. Freshwater mussel species from 14 prehistoric aboriginal sites along the Chickamauga Reservoir, Rhea and Meigs counties, Tennessee.

	Middle Woodland (1 site)		Late Woodland (8 sites)		Mississippian (2 sites)		Middle/Late Woodland (1 site)		Late Woodland/ Mississippian (2 sites)			
	VALVES											
SPECIES	No.	%	No.	%	No.	%	No.	%	No.	%	Total No.	Percent of Total
Amblema plicata	10	1.05	25	.22	36	1.25	8	.11	13	.24	92	.33
Fusconaia barnesiana			8	.07			4	.06	4	.07	16	.06
Fusconaia subrotunda	63	6.61	391	3.42	102	3.55	543	7.63	287	5.22	1,386	4.97
Quadrula cylindrica	1	.10	15	.13	1	.03	12	.17	5	.09	34	.12
Quadrula intermedia	2	.21	22	.19			7	.10	34	.62	65	.23
Quadrula metanevra	6	.63	101	.88	43	1.50	16	.22	24	.44	190	.68
Quadrula pustulosa	6	.63	32	.28	2	.07	32	.45	22	.40	94	.34
Quadrula spp.			5	.04							5	.02
Cyclonaias tuberculata	27	2.83	394	3.44	159	5.54	117	1.64	192	3.49	889	3.19
Elliptio crassidens	83	8.71	537	4.70	153	5.33	544	7.64	385	7.01	1,702	6.11
Elliptio dilatatus	79	8.29	1,496	13.08	239	8.32	936	13.15	416	7.57	3,166	11.36
Lexingtonia dolabelloides	2	.21	117	1.02	21	.73	24	.34	11	.20	175	.63
Plethobasus cicatricosus	7	.73	81	.71	47	1.64	16	.22	53	.96	204	.73
Plethobasus cooperianus	8	.84	74	.65	77	2.68	42	.59	45	.82	246	.88
Plethobasus cyphyus	2	.21	10	.09	7	.24	6	.08	2	.04	27	.10
Pleurobema clava	8	.84	104	.91	4	.14	55	.77	25	.45	196	.70
Pleurobema cordatum	45	4.72	445	3.89	399	13.90	212	2.98	258	4.69	1,359	4.88
Pleurobema plenum	61	6.40	641	5.60	219	7.63	291	4.09	343	6.24	1,555	5.58
Pleurobema pyramidatum	17	1.78	250	2.19	50	1.74	181	2.54	114	2.07	612	2.20
Pleurobema spp.	88	9.23	360	3.15	29	1.01	116	1.63	51	.93	629	2.26
Lasmigona costata							1	.01			1	T
cf. Strophitus undulatus							1	.01			1	T

Actinonaias ligamentina	90	9.44	921	8.05	250	8.71	568	7.98	258	4.69	2,087	7.49
Plagiola triquetra							5	.07			5	.02
Plagiola arcaeformis	8	.84	69	.60	2	.07	274	3.85	28	.51	381	1.37
Plagiola interrupta	1	.10	2	.02			5	.07	1	.02	9	.03
Plagiola torulosa	26	2.73	203	1.77	15	.52	256	3.60	158	2.87	658	2.36
Plagiola propinqua	18	1.89	256	2.24	11	.38	392	5.51	76	1.38	753	2.70
Plagiola torulosa/ propinqua			22	.19			10	.14			32	.11
Plagiola cf. capsaeformis	7	.73	49	.43			20	.28			76	.27
Plagiola florentina			1	.01			12	.17			13	.05
Plagiola turgidula			2	.02			14	.20			16	.06
Plagiola obliquata			1	.01							1	T
Plagiola haysiana	1	.10	37	.32	1	.03	52	.73	11	.20	102	.37
Plagiola flexuosa			11	.10			14	.20	1	.02	26	.09
Plagiola stewardsoni	2	.21	52	.45			61	.86	9	.16	124	.44
Lampsilis fasciola							3	.04			3	.01
Lampsilis ovata			2	.02	5	.17	44	.62	5	.09	56	.20
Lemoix rimosus	3	.31	6	.05			10	.14	5	.08	24	.09
Ligumia recta					6	.21	2	.03			8	.03
Obovaria retusa	23	2.41	162	1.42	34	1.18	148	2.08	91	1.66	458	1.64
Obovaria subrotunda	11	1.15	79	.70	2	.07	60	.84	26	.47	178	.64
Potamilus alatus	1	.10					2	.03			3	.01
Villosa cf. venuxemi			5	.04			11	.15	2	.04	18	.06
V. venuxemi/ P. capsaeformis/ P. florentina			8	.07			26	.37			34	.12
Cyprogenia irrorata	13	1.36	23	.20	4	.14	10	.14	5	.09	55	.20
Dromus dromas	230	24.13	4,301	37.61	932	32.46	1,878	26.38	2,486	45.23	9,827	35.25
Ptychobranchus fasciolare	4	.42	114	1.00	21	.93	67	.94	47	.86	253	.91
Ptychobranchus subtentum			3	.03			10	.14	3	.05	16	.06
TOTALS	953	99.94	11,437	100.01	2,871	99.97	7,118	99.99	5,496	99.98	27,875	100.00

valves comprised 8% of the total. Although Scruggs (1960) reported *A. ligamentina* as still present in Chickamauga and Kentucky reservoirs, Pardue (1981) failed to recover it during mussel surveys of Watts Bar, Chickamauga, and Nickajack reservoirs. With the possible exception of a few relic individuals, this species appears to have been extirpated from all stretches of the middle and upper Tennessee River.

At least four and possibly five species (or forms, depending upon the taxonomic approach) of *Pleurobema* were represented in the middens, and combined their valves comprised nearly 16% of the total. Of the *Pleurobema* complex, valves of *P. cordatum* and *P. plenum* (Lea 1840), both of which today are usually found inhabiting large rivers at depths of 3 to 6 m, were the most numerous. *Pleurobema pyramidatum* (Lea 1834), another medium-to-large river deep water species, ranked third in abundance within this complex. Of interest is the fact that combined, all species of *Pleurobema* comprised approximately 24% of the shells recovered at the two Mississippian sites, 16% of those at the Late Woodland sites, and 23% of those at the Middle Woodland site. At Widows Creek, valves of *Pleurobema* amounted to about 13% of the total (Warren 1975). Continued harvesting of these species by the Indian over a long period of time attests to their former abundance and probable habitation of the more shallow shoal areas of the river. *Pleurobema cordatum* appears to be the only species of this complex still inhabiting the upper Tennessee River.

Ortmann (1918, 1925) considered *Pleurobema clava* (Lamarck 1819) a species of the Ohio River drainage, replaced in the upper Tennessee River system by the form or species *Pleurobema oviforme* (Conrad 1834). The relationship between these two is still not clear, but they do not appear to intergrade; Warren (1975) recorded both from the Widows Creek site. Although specimens from the Chickamauga Reservoir middens should theoretically tend more toward *P. oviforme*, and admittedly some were questionable, shells of this complex more closely approached in appearance those of *P. clava* than those of *P. oviforme* from the Duck River and tributary streams of the Tennessee River in the northeastern part of the state. In any case, *P. clava* appears to have been a part of the upper Tennessee River mussel assemblage since at least Middle Woodland times, but it evidently was uncommon (valves amounted to $< 1\%$ of the total). *Lexingtonia dolabelloides* (Lea 1840), a "Cumberlandian" species once locally common in the middle and upper Tennessee River and its tributaries, has been extirpated throughout most of its range. Although valves of this species amounted to $< 1\%$ of the total, they occurred in all middens examined.

Shells of four species of *Quadrula* occurred in the middens, but combined they totaled only 388, less than 2% of all specimens collected. Valves of *Q. metanevra* (Raf. 1820) were the most numerous, followed

by those of *Q. pustulosa*; both species still occur as viable populations in the Chickamauga Reservoir, apparently having adapted to impoundment conditions. Both *Q. cylindrica* (1817) and *Q. intermedia* (Conrad 1836) are apparently now extirpated in the upper Tennessee River; judging by the relatively few specimens obtained in the middens, both were uncommon in prehistoric times. Today, limited populations of *Q. intermedia*, a "Cumberlandian" species that typically inhabits small-to-medium size rivers, occur in the upper Powell and Clinch rivers of northeast Tennesseee and in the Duck River of Middle Tennessee. In prehistoric times, however, the species occurred throughout the upper and middle Tennessee River; Morrison (1942) reported it present but not common in Pickwick Basin shell mounds, northwestern Alabama. *Amblema plicata* (Say 1817), a species now relatively common in the Chickamauga Reservoir (Pardue 1981), appears to have been uncommon to rare in prehistoric times (valves comprised $< 0.5\%$ of the total).

The combined number of valves (477) of the three species of *Plethobasus* constituted less than 2% of the total. However, valves occurred in all cultural components, but the low numbers apparently reflect their limited abundance in the upper Tennessee during the last 2000 years. At the Widows Creek site they comprised less than 3% of the total (Warren 1975), and Morrison (1942) reported only a few specimens of *P. cyphyus* and *P. cicatricosus* (Say 1829) and none of *P. cooperianus* from the Pickwick Basin middens. Ortmann (1925:338) commented that *P. cyphyus* occurred sparingly in the main river in the lower Tennessee drainage, while *P. cooperianus* "goes into the upper Tennessee up to the Knoxville region, but it is rare there." Although *P. cicatricosus* was recorded from below Wilson Dam by Stansbery (1964), it is now nearing extinction and is represented by a few old relic individuals. Based on a few valves recovered from sheller's cull piles (taken in the early 1970s), *P. cyphyus* appears to continue to survive in the Chickamauga Reservoir. One valve of *P. cooperianus* was also found in a cull pile. Although Scruggs (1960) recorded it from the Washington Ferry area (TRM 518), Pardue (1981) failed to find it anywhere in the middle or upper reaches of the Chickamauga Reservoir.

One of the most interesting naiad assemblages represented in the Chickamauga Reservoir middens consists of 12 species belonging to the genus *Plagiola (=Dysnomia=Epioblasma)* (Johnson 1978). Six of these *(arcaeformis* Lea 1834, *flexuosa* Raf. 1820, *haysiana* Lea 1834, *propinqua* Lea 1857, *stewardsoni* Lea 1852, *turgidula* Lea 1858) are now extinct. Five others *(capsaeformis* Lea 1834, *florentina* Lea 1834, *torulosa* Raf. 1820, *interrupta* Lea 1831, *obliquata* Raf. 1820) are either extremely rare, or their former ranges have been reduced to a few localized habitats, or both. All of those species inhabit (or did inhabit) small-to-medium size rivers, or the shallow riffle and shoal areas of large riv-

ers such as the Tennessee having a sandy-gravel substrate with rapid currents (Stansbery 1971). Although a few individuals of some of these species (e.g. *interrupta, obliquata*) may continue to survive after impoundment (Parmalee et al. 1980), they do not or cannot propagate, and the species within the affected sections of the river eventually die out. Only *P. triquetra* still occurs in viable populations in upper East Tennessee and locally in the Midwest and Great Lakes states.

All shells of the 12 species of *Plagiola* represented in the middens amounted to approximately 8% of the total sample; valves of *arcaeformis, propinqua,* and *torulosa* comprised 6.5% of this total. Two distinct forms of *P. torulosa* have been recognized (Ortmann 1918): *P. t. torulosa,* with the more inflated shell with a radial row of prominent knobs across the middle, occurred from about Knoxville downstream; the form *P. t. gubernaculum*, with a more compressed shell and poorly developed or wanting knobs, occurred in streams above Knoxville. Although valves of the form *torulosa* predominate in the Chickamauga Reservoir middens, a few approach the typical upstream form *gubernaculum.*

In a recent taxonomic revision of this complex, Johnson (1978) synonymized the species *P. lewisi* with *P. flexuosa,* although not all malacologists (e.g. Stansbery 1971) agree with this approach. Valves of these two species, or the species *P. flexuosa,* occurred only sparingly in the middens, which may reflect the former rarity of *P. flexuosa* in the Tennessee. Except for *arcaeformis, propinqua,* and *torulosa,* the same may be said of the other species of *Plagiola.* Of interest is the fact that only five valves of *P. triquetra,* the one species still locally common and widespread in streams of eastern Tennessee and the Great Lakes area, were recovered in the middens. Warren (1975) listed only four valves of this species in a sample of 60,350 valves from the Widows Creek site; Morrison (1942) reported it absent from the Pickwick Basin mounds. This rather ubiquitous inhabitant of numerous smaller streams and tributaries of the Tennessee apparently did not become well established in the shoals and riffles of the main river. This also seems to have been the case with *capsaeformis, turgidula, interrupta,* and *florentina,* all species of small-to-medium size rivers. It is of further interest that all shells of *Plagiola* spp. comprised 1% of the valves from the Mississippian component sites, but averaged about 6% of the totals from the Middle and Late Woodland sites.

Fusconaia subrotunda (Lea 1831) occurred in all middens and varied from about 3.5% of all valves in the Late Woodland and Mississippian sites to 7.5% in the multicomponent Middle/Late Woodland sites. Pardue (1981) found very few specimens of this mussel in the Chickamauga and Watts Bar reservoirs and we doubt that it will ever return to a semblance of its former abundance. *Cyclonaias tuberculata* (Raf. 1820), however, another ubiquitous although slightly less common shell

than *F. subrotunda* in the middens, is presently a common component of the Chickamauga Reservoir naiad fauna. With reference to *Obovaria retusa* (Lamarck 1819), Ortmann (1925:348) commented that "In the upper Tennessee it goes to Knoxville region, but is very rare." With the exception of one Late Woodland site, valves of this distinct species were recovered from all sites, but totaled < 2% for all samples. As a species it appears on the verge of extinction; a few old relic specimens are occasionally taken below Pickwick Dam and in the middle Cumberland River, Tennessee (Parmalee and Klippel 1982). It is now extirpated in the middle and upper Tennessee River.

Valves of a few species typical of small-to-medium size rivers, such as *Fusconaia barnesiana* (Lea 1838), *Lampsilis fasciola* (Raf. 1820), *Lemiox rimosus* (Raf. 1831), *Obovaria subrotunda* (Raf. 1820), and *Ptychobranchus subtentum* (Say 1825), occurred sparingly in some of the middens. Combined shells of these species comprised < 1% of all samples. Only eight valves of *Ligumia recta* (Lamarck 1819) were recovered (six in 40MG50, a Mississippian site). Although fairly common and widespread throughout the Tennessee River and its major tributaries today, this species was apparently a rare shell in the middle and upper Tennessee during aboriginal times. *Cyprogenia irrorata* (Lea 1829) is another species once widely distributed throughout the Ohio, Cumberland, and upper Tennessee River drainages. It occurred in most of the Chickamauga Reservoir middens, but sparingly. Warren (1975) identified 127 valves of this species (only 0.39% of the total) form the Widows Creek site. *Cyprogenia irrorata*, like most species adapted to riffle and shoal habitats in the Tennessee River, has been extirpated or reduced to relic populations of old individuals in river sections affected by impoundment.

Recent Adaptations to Impoundment

Impoundment generally produces a reduced rate of current flow, increased water depth with often daily or seasonal extremes in water level and temperature fluctuations, and siltation. The adverse effects these conditions can exert in extirpating a species or reducing it to a few nonpropagating individuals have been discussed. The fate of at least a dozen species within the genus *Plagiola* provides ample documentation. On the other hand, changes in the aquatic habitat brought about by impoundment and the establishment of a "river-lake" has proved favorable to several species. Bates (1962) discussed this phenomenon for the lower Tennessee River (Kentucky Reservoir). Three species of *Anodonta* — *A. grandis* (Say 1829), *A. imbecillus* (Say 1829), and *A. suborbiculata* (Say 1831) — have now become well established locally in the shallow mud-bottom bays and/or shorelines throughout most of the reservoirs. No valves of *Anodonta* were recovered in the Chickamauga

Reservoir middens or at Widows Creek (Warren 1975), and Morrison (1942:359) listed *A. grandis* along with a few other species as being "present in small numbers only, if represented by more than one specimen each." *Leptodea fragilis* (Raf. 1820) often reaches its greatest abundance in habitat similar to that preferred by *Anodonta*. It now occurs locally throughout the Tennessee River although, as evidenced by recovery of only one valve of 60,350 collected at Widows Creek (Warren 1975) and none from the Pickwick Basin and Chickamauga Reservoir middens, it was extremely rare in prehistoric times. A single valve of *Potamilus alatus* (Say 1817) occurred in the Middle Woodland site midden and two shells in the multicomponent Middle/Late Woodland site. It was not present at the Widows Creek site (Warren 1975), and Morrison (1942) identified only "a few individuals" from the Pickwick Basin mounds. *Potamilus alatus* is another species that has adapted to and flourishes in Tennessee River reservoirs.

Viable populations of four other species now inhabiting the middle and upper Tennessee River provide an interesting contrast with their apparent prehistoric abundance and distribution. They are *Ellipsaria lineolata* (Raf. 1820), *Tritogonia verrucosa* (Raf. 1820), *Obliquaria reflexa* (Raf. 1820), and *Megalonaias gigantea* (Barnes 1823). All four appear to have their center of origin in the Interior Basin or Mississippi River drainages. *Ellipsaria lineolata* is presently relatively common in the Chickamauga and Nickajack reservoirs (Pardue 1981). Ortmann (1925) commented that it was rare in the upper Tennessee, and the paucity of shells from Pickwick Basin ("found only as scattered individuals in two of the mounds"; Morrison 1942:361) and Widows Creek (one valve), and no specimens from the Chickamauga Reservoir middens, attest to its rarity in prehistoric times. *Tritogonia verrucosa* is another species that has become established in the Chickamauga Reservoir, apparently in modern times, as no shells of this mussel were found in the midden samples we examined and it was not encountered by Warren (1975) at the Widows Creek site or by Morrison (1942) in Pickwick Basin mounds.

Pardue (1981) reported taking *M. gigantea* at one station in the Nickajack Reservoir at Chattanooga and from three localities in the Chickamauga Reservoir. Like *T. verrucosa*, *M. gigantea* has become established in the middle and upper reservoirs of the Tennessee River in recent times. No specimens were encountered in the Pickwick Basin mounds, at Widows Creek, or in the Chickamauga Reservoir middens. *Megalonaias gigantea* may well continue to extend its range and increase in abundance, since it seems to adapt well to a river-lake habitat. For example, *M. gigantea* is the most abundant species in the impounded stretches of the middle Cumberland River, Tennessee (Parmalee et al. 1980). The last of these four river species that has thrived and

increased in abundance as a result of impoundment of the Tennessee River is *O. reflexa*. Although Morrison (1942) did not encounter *O. reflexa* in the Pickwick Basin mounds, it was present during prehistoric times in the upper Tennessee River as evidenced by three valves from the Widows Creek site (Warren 1975) and two shells from the Chickamauga Reservoir middens (one valve from each of two multicomponent sites, 40RH18 and 40RH39, not included in this study). It is a typical river species that can adapt to a lake environment (Klippel and Parmalee 1979).

Data recovered from archaeological sites along the banks of the Chickamauga Reservoir have provided information that greatly enhances our understanding of the diachronic variability in the mussel fauna of the Upper Tennessee River. Pardue (1981), by considering presence /absence of species recovered from the upper Tennessee between 1918 and 1980, has clearly delineated the magnitude of change that has taken place in less than a century. Our data, recovered from archaeological contexts, suggests that comparatively little change took place over as much as two millennia preceding EuroAmerican settlement along this section of the river. Although the invasion and establishment of "new" species in the impounded stretches of the Tennessee River is noteworthy and may provide a potentially valuable commerical resource, these latecomers fail to equal the loss of so many of the river's endemic species that were once a part of one of the richest naiad faunas in the world.

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