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Unionid Fauna of the Lower Cumberland River from Barkley Dam to the Ohio River, Kentucky (Mollusca: Bivalvia: Unionidae)

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ABSTRACT

Unionids of the lower Cumberland River, Kentucky, were surveyed by brail and SCUBA from Barkley Dam to the Ohio River. The only previous survey was conducted in 1910–1911 by Wilson and Clark. The two surveys are compared and show a significant decrease in the number of surviving species. Live individuals of 24 species were found in our surveys compared to 45 species found by Wilson and Clark in the region now inundated by Lake Barkley. Three species were found that had not been reported previously from the Cumberland River. Alteration of habitat resulting from impoundment, pollution, and rapid fluctuation of discharge from hydroelectric dams apparently are the major causes for the decline in native species, while impoundment probably has enhanced invasion by species from the Ohio River.

INTRODUCTION

In recent years the number of species of unionids on the federal endangered species list (USFWS 1993) has increased, and there is growing interest in the scientific community in conserving biodiversity and understanding its importance to a healthy environment (Wilson 1994). In contrast, there is an apparent waning interest in protecting rare, threatened, and endangered species and the environment by the current U.S. Congress. With the rapid spread of zebra mussels into the Ohio and Mississippi river systems, an already impoverished native unionid fauna is faced with greater threats, making it imperative that unique, rare, and endangered species be studied and documented. Documentation of species and recent changes in their abundance and distribution is critical for understanding the importance of complex ecosystems if biodiversity is to be preserved. With these issues in mind, the results of several surveys of the lower Cumberland River conducted by us in 1981 and 1988 are reported here and compared to a 1910–1911 survey by Wilson and Clark (1914).

STUDY AREA

The Cumberland River arises in the Cumberland Mountains in southeastern Kentucky. It flows westerly, arching southward into central Tennessee. From there it flows westerly, gradually arching northward into western Kentucky and northwesterly to its junction with the Ohio River at Smithland, Kentucky. The "official" U.S. Army Corps of Engineers junction, Cumberland River mile (CRM) 0.0, occurs at Ohio River mile (ORM) 922.7 (Anonymous 1994). The actual confluence of the two bodies of water where mixing begins is at the official Cumberland River mile 2.2 (Figure 1). The Cumberland River and the larger and nearly parallel Tennessee River are two of the most ancient rivers of North America. This in part is the reason for the great diversity of unionids that once populated the rivers (Wilson and Clark 1914). Documentation of the unionids of the middle and upper Cumberland River by numerous authors in recent years indicates major declines of the unionid fauna of those areas (Anderson, Layzer, and Gordon 1991; Blankenship and Crockett 1972; Call and Parmalee 1982; Clark 1981, 1985; Harker et al. 1980; Isom, Gooch, and Dennis 1979; Miller, Rhodes, and Tippit 1984; Neel and Allen 1964; Parmalee, Klippel and Bogan 1980; Schmidt 1982; Schuster, Butler, and Stansbery 1989; Starnes and Bogan 1982). Two important reviews providing gen-

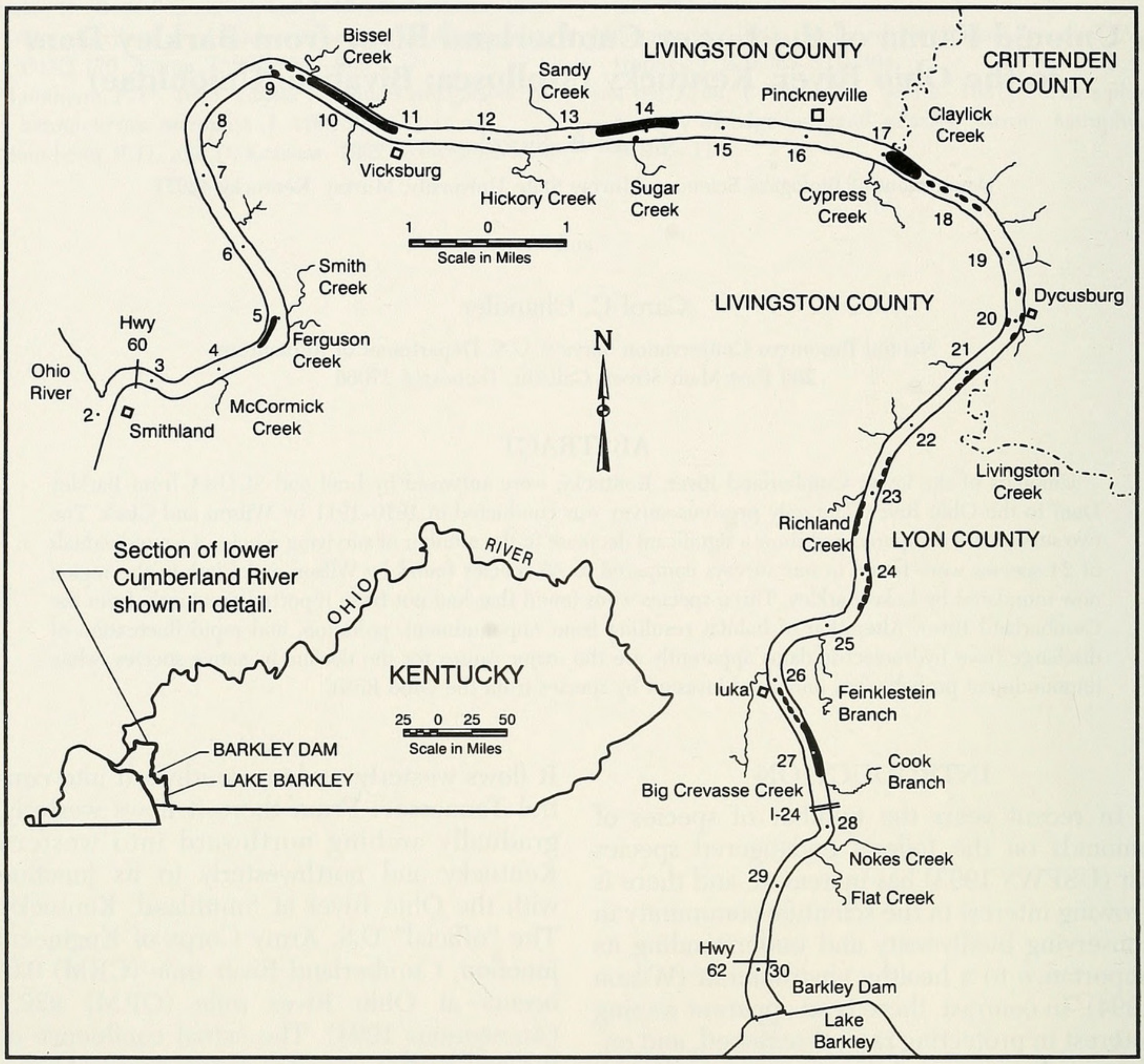

Figure 1. Map of lower Cumberland River, Kentucky, from Barkley Dam at Cumberland River mile 30.6 to the Ohio River showing major unionid beds as elongated, solid areas and river mile points as solid dots. Numbers 2 through 30 along the river represent miles from its confluence with the Ohio River. (Width of river is shown as twice actual scale.)

eral information about unionid distribution in the Cumberland River are those by Cicerello, Warren, and Schuster (1991) for Kentucky and Starnes and Bogan (1988) for Tennessee.

WILSON AND CLARK 1910–1911 SURVEY

Charles B. Wilson and H. Walton Clark (1914) published the results of a freshwater unionid survey of the Cumberland River conducted by them, John F. Boepple, and Ernest Danglade and supervised by Robert E. Coker. Their project involved several expeditions in summers of 1910 and 1911 to evaluate the shell resources then being utilized in the pearl button industry. By sampling with crowfoot brails, tongs, and rakes in deep water, wading in shallow water, and examining the catch of commercial shellers, they described the species composition and relative abundance of unionids from the headwaters above Cumberland Falls in eastern Kentucky to near the mouth where the Cumberland River enters the Ohio River. Their sample location farthest downstream was at Horse Ford near Kuttawa, Lyon County, Kentucky, at Cumberland River mile (CRM) 36.5 (58.7 km from the Ohio River at Smithland, Livingston County, Kentucky). They reported extensive beds from Cumberland Falls to Kuttawa. That study constitutes the only published report prior to our surveys of the unionids inhabiting the lower Cumberland River, including the region presently inundated by Lake Barkley. In their report, Wilson and Clark (1914) briefly discussed ecological requirements of some unionids and the influence of dams on this fauna.

The effect of dams on unionids living in once free-flowing rivers has been extensive (Bates 1962; Fuller 1974). When Wilson and Clark (1914) were conducting their survey, only one dam had been constructed on the lower Cumberland River below Nashville, Tennessee; eight had been completed upstream from Nashville. Lock and Dam A at CRM 150.6 were completed by the Army Corps of Engineers in 1904 near the present site of Cheatham Dam (CRM 148.7), Cheatham County, Tennessee, which was completed in 1957. Cheatham Dam forms the upstream boundary of Lake Barkley. Dam A formed a pool that backed up the Harpeth River entering at CRM 153. Wilson and Clark (1914) reported that siltation in the lower Harpeth River resulting from Dam A had eliminated a large unionid bed. Similar results were observed immediately upstream from other dams. However, Wilson and Clark reported rapid growth of unionids in the backwaters above the silt, and they believed that the dams would be more beneficial than harmful. They were referring to low dams, however, that did not raise the water above the original river banks. They had no experience with the high dams such as Barkley and Cheatham dams presently on the lower Cumberland River.

From near the present location of Cheatham Dam (CRM 148.7) to Barkley Dam (CRM 30.6), Lyon County, Kentucky, Wilson and Clark (1914) collected at 28 stations. From their descriptions many of their stations can be located on current maps or navigation charts. In the following discussion, locations given as approximate river miles could not be located precisely. Below mile 148, the upstream boundary of the present Lake Barkley, Wilson and Clark reported 47 species (Table 1). Eleven of the 47 species are listed on the federal endangered species list (USFWS 1993): *Cyprogenia stegaria, Dromus dromas, Epioblasma florentina, E. haysiana, E. obliquata, Hemistena lata, Lampsilis abrupta, Obovaria retusa, Plethobasus cooperianus, Pleurobema plenum,* and *Quadrula fragosa. Cyprogenia stegaria* was reported at Seven-mile Ferry (CRM 132.5), Owl Hollow Bar (ca. CRM 130), and Guisers [Geisers] bar (CRM 128.5). *Dromus dromas* occurred at Seven-mile Ferry and Red Rock Bar (ca. CRM 125) below Clarksville, Montgomery County, Tennessee. Only a shell of *Epioblasma florentina* was found at Half Pone Bar (CRM 145). *Epioblasma haysiana* was found at Clarksville (CRM 126) and above Ball [Bald] Island (CRM 97.6). *Epioblasma obliquata* was reported alive only from Half Pone Bar; a dead shell was found at Elk Creek Shoals (CRM 98.6). *Hemistena lata* was reported from Half Pone Bar. *Lampsilis abrupta* was reported from Seven-mile Ferry and Kuttawa, Kentucky (CRM 41). *Obovaria retusa* was reported from above Ball Island, foot of Dover Island (CRM 90.5), Canton, Kentucky (CRM 62), and Horse Ford (CRM 36.6). *Plethobasus cooperianus* was reported from Owl Hollow Bar, Guisers Bar, Clarksville, Red Rock Bar, Meeks Spring Bar (ca. CRM 118), Walters' Camp (ca. CRM 98), above and below Ball Island (CRM 97.4), Linton (CRM 73), Donelson [Donaldson] Creek (CRM 67), Canton (CRM 63), and Horse Ford below Kuttawa. At Walters' shell camp in 1911 Wilson and Clark noted a pile of ca. 150 tons of shells with *Plethobasus cooperianus* ranking second in abundance of the commercial species. *Pleurobema plenum* was found at Half Pone Bar, Seven-mile Ferry, and Jones Landing (ca. CRM 80) somewhere between Dover, Stewart County, Tennessee, and Linton, Trigg County, Kentucky. *Quadrula fragosa* was reported from Half Pone Bar, Seven-mile Ferry, Owl Hollow Bar, Clarksville, Red Rock Bar, Trices Landing (ca. CRM 124), above Meeks Spring Bar (ca. CRM 119), Meeks Spring Bar, foot of Dover Island, Jones Landing, Linton, below Canton, Eddyville Bar (CRM 44), above Kuttawa, below Money Cliff (CRM 39), and at Horse Ford. Wilson and Clark did not collect downstream from Horse Ford at CRM 36.5. Therefore, no records exist before our 1981 and 1988 surveys of the unionid fauna in the region now the tailwater of Barkley Dam from CRM 30.6 to the Ohio River.

Historically, the Cumberland River contained at least 85 species of unionid bivalves

Table 1. Unionid clams of the lower Cumberland River, Kentucky, from the region now inundated by Barkley Lake to the Ohio River as reported by Wilson and Clark (1914) from CRM 36 - 148 and surveys in 1981 and 1988 from CRM 2.5 - 47.

Taxa[1]	Common Name	Nomenclature of Wilson and Clark (1914)	Reported in 1914	Present Surveys
Actinonaias ligamentina (Lamarck, 1819)	Mucket	*Lampsilis ligamentina gibba* (Simpson, 1900)	+	-
Amblema plicata perplicata (Conrad, 1841)	Roundlake	*Quadrula perplicata* (Conrad, 1841)	+	-
Amblema plicata plicata (Say, 1817)	Threeridge	*Quadrula undulata* (Barnes, 1823)	-	+
Anodonta suborbiculata Say, 1831	Flat floater		-	+
Arcidens confragosus (Say, 1829)	Rock pocketbook		-	+
Cumberlandia monodonta (Say, 1829)	Spectaclecase	*Margaritana monodonta* (Say, 1829)	+	-
Cyclonaias tuberculata (Rafinesque, 1820)	Purple wartyback	*Quadrula tuberculata* (Rafinesque, 1820)	+	shell
Cyclonaias tuberculata (Rafinesque, 1820)	Purple wartyback	*Quadrula granifera* (Lea, 1838)	+	-
Cyprogenia stegaria (Rafinesque, 1820)	Fanshell	*Cyprogenia irrorata* (Lea, 1828)	+	-
Dromus dromas (Lea, 1834)	Dromedary mussel	*Dromus dromas* (Lea, 1834)	+	-
Ellipsaria lineolata (Rafinesque, 1820)	Butterfly	*Plagiola securis* (Lea, 1829)	+	+
Elliptio crassidens (Lamarck, 1819)	Elephant-ear	*Unio crassidens crassidens* Lamarck, 1819	+	+
Elliptio dilatata (Rafinesque, 1820)	Spike	*Unio gibbosus* Barnes, 1823	+	+
Epioblasma flexuosa (Raf., 1820)	Leafshell		-	shell
Epioblasma florentina florentina (Lea, 1857)	Yellow blossom	*Truncilla florentina* (Lea, 1857)	shell	-
Epioblasma haysiana (Lea, 1833)	Acornshell	*Truncilla haysiana* (Lea, 1834)	+	-
Epioblasma obliquata (Rafinesque, 1820)	Catspaw	*Truncilla sulcata* (Lea, 1829)	+	-
Fusconaia ebena (Lea, 1831)	Ebonyshell	*Quadrula ebena* (Lea, 1831)	+	+
Fusconaia flava (Rafinesque, 1820)	Wabash pigtoe	*Quadrula undata* (Barnes, 1823)	+	+
Fusconaia subrotunda (Lea, 1831)	Long solid	*Quadrula subrotunda* (Lea, 1831)	+	-
Hemistena lata (Rafinesque, 1820)	Cracking pearly	*Lastena lata* (Rafinesque, 1820)	+	-
Lampsilis abrupta (Say, 1831)	Pink mucket	*Lampsilis orbiculata* (Hildreth, 1828)	+	shell
Lampsilis ovata (Say, 1817)	Pocketbook	*Lampsilis ovata* (Say, 1817)	+	-
Lampsilis ventricosa (Barnes, 1823)[2]	Pocketbook	*Lampsilis ventricosa* (Barnes, 1823)	+	-
Lampsilis anodontoides (Lea, 1831)[2]	Yellow sandshell	*Lampsilis anodontoides* (Lea, 1831)	+	-
Lampsilis teres (Rafinesque, 1820)	Yellow sandshell	*Lampsilis fallaciosa* (Smith, 1899)	+	-
Lasmigona complanata (Barnes, 1823)	White heelsplitter	*Symphynota complanata* (Barnes, 1823)	+	+
Leptodea fragilis (Rafinesque, 1820)	Fragile papershell	*Lampsilis gracilis* (Barnes, 1823)	+	+
Ligumia recta (Lamarck, 1819)	Black sandshell	*Lampsilis recta* (Lamarck, 1819)	+	+
Megalonaias nervosa (Rafinesque, 1820)	Washboard	*Quadrula heros* (Say, 1829)	+	+
Obliquaria reflexa Rafinesque, 1820	Threehorn wartyback	*Obliquaria reflexa* Rafinesque, 1820	+	+
Obovaria olivaria (Rafinesque, 1820)	Hickorynut	*Obovaria ellipsis* (Lea, 1828)	+	-
Obovaria retusa (Lamarck, 1819)	Ring pink	*Obovaria retusa* (Lamarck, 1819)	+	shell
Obovaria subrotunda (Rafinesque, 1820)	Round hickorynut	*Obovaria circulus* (Lea, 1829)	+	-
Plethobasus cicatricosus (Say, 1829)	White wartyback		-	shell
Plethobasus cooperianus (Lea, 1834)	Orangefoot pimpleback	*Quadrula cooperiana* (Lea, 1834)	+	shell
Plethobasus cyphyus (Rafinesque, 1820)	Sheepnose	*Pleurobema aesopus* (Green, 1827)	+	-
Pleurobema catillus (Conrad, 1836)[2]	Solid pigtoe	*Quadrula solida* (Lea, 1838)	+	-

Table 1. (continued)

Taxa[1]	Common Name	Nomenclature of Wilson and Clark	Reported in 1914	Present Surveys
Pleurobema cordatum (Rafinesque, 1820)	Ohio pigtoe	*Quadrula obliqua* (Lamarck, 1819)	+	+
Pleurobema plenum (Lea, 1840)	Rough pigtoe	*Quadrula plena* (Lea, 1840)	+	-
Pleurobema rubrum (Rafinesque, 1820)	Pink pigtoe	*Quadrula pyramidatum* (Lea, 1831)	-	shell
Pleurobema sintoxia (Rafinseque, 1820)	Round pigtoe	*Quadrula coccinea* (Conrad, 1834)	-	shell
Potamilus alatus (Say, 1817)	Pink heelsplitter	*Lampsilis alata* (Say, 1817)	+	+
Potamilus ohiensis (Rafinesque, 1820)	Pink papershell	*Lampsilis laevissima* (Lea, 1829)	+	shell
Ptychobranchus fasciolaris (Rafinesque, 1820)	Kidneyshell	*Ptychobranchus phaseolus* (Hildreth, 1828)	+	-
Pyganodon grandis (Say, 1829)[3]	Giant floater	*Anodonta grandis* Say, 1829	-	+
Quadrula cylindrica cylindrica (Say, 1817)	Rabbitsfoot	*Quadrula cylindrica* (Say, 1817)	+	-
Quadrula fragosa (Conrad, 1835)	Winged mapleleaf	*Quadrula fragosa* (Rafinesque, 1820)	+	-
Quadrula metanevra (Rafinesque, 1820)	Monkeyface	*Quadrula metanevra* (Rafinesque, 1820)	+	+
Quadrula nodulata (Rafinesque, 1820)	Wartyback		-	+
Quadrula quadrula (Rafinesque, 1820)	Mapleleaf	*Quadrula lachrymosa* (Lea, 1828)	-	+
Quadrula pustulosa pustulosa (Lea, 1831)	Pimpleback	*Quadrula pustulosa* (Lea, 1831)	+	+
Strophitus undulatus undulatus (Say, 1817)	Squawfoot	*Strophitus edentulus shaefferiana* (Lea, 1852)	+	-
Tritogonia verrucosa (Rafinesque, 1820)	Pistolgrip	*Quadrula tritogonia* Ortmann, 1909	+	+
Truncilla donaciformis (Lea, 1828)	Fawnsfoot	*Plagiola donaciformis* (Lea, 1828)	+	+
Truncilla truncata Rafinesque, 1820	Deertoe	*Plagiola elegans* (Lea, 1831)	+	+
Utterbackia imbecillis (Say, 1829)[3]	Paper pondshell	*Anodonta imbecillis* Say, 1829	-	+
Villosa lienosa (Conrad, 1834)	Little spectaclecase	*Lampsilis lienosa* (Conrad, 1834)	+	-

(Hyphen indicates not found, plus indicates found alive, and "shell" indicates found only as a dead shell)
[1] Nomenclature agrees with that of Turgeon et al. (1988) except where noted otherwise
[2] Nomenclature of Ortmann and Walker (1922)
[3] Hoeh (1990)

(Starnes and Bogan 1988). This number is second only to the Tennessee River, which once had ca. 95 species (Starnes and Bogan 1988), the largest assemblage found anywhere (Johnson 1978). Many species once found in the middle and upper reaches of the Cumberland River belong to the Cumberlandian fauna, those unionids that apparently had their origin in the Cumberland and Tennessee river systems. Ortmann (1924) defined the Cumberlandian Region as extending from the headwaters of the Cumberland River down to near Clarksville, Tennessee, and the headwaters of the Tennessee River down to some point beyond Muscle Shoals, Alabama, including part of the Duck River, Tennessee.

Of the species reported by Wilson and Clark (1914) in the lower Cumberland River, only three were considered to be Cumberlandian forms (origin in Cumberlandian Region) by Ortmann (1925): *Dromus dromas, Epioblasma haysiana,* and *E. florentina.* Johnson (1980), however, added three more to the list, claiming that they had extended their range from the Cumberlandian Region into the Ohio drainage: *Epioblasma flexuosa, Lampsilis abrupta,* and *Plethobasus cicatricosus.* In the case of *Lampsilis abrupta,* Ortmann (1925) stated that it is a large river form and its "center of origin is in the Interior Basin."

With the demise of the pearl button industry, the lower Cumberland River saw few shellers. When the demand for shells for the cultured pearl industry sent shellers back to the rivers, the discovery that Cumberland River shells from below Nashville were too chalky or badly eroded and had a low value for the production of pearl nuclei kept shellers away.

Therefore, little was known about the recent unionid fauna until our surveys were conducted.

The purpose of our study was to determine the distribution and relative abundance of the unionid fauna of the lower Cumberland River from Barkley Dam to the Ohio River. The Nashville District Corps of Engineers had proposed channel maintenance operations that potentially could have an adverse impact on the mollusks. The Corps was required to ascertain whether any species on the federal endangered species list survived in the area of the river being considered for channel improvement. We present results of that survey and a comparison with the Wilson and Clark (1914) study along with a report on the range extension of three species into the Cumberland River and a comparison with archeological studies.

1981 AND 1988 SURVEYS

Methods

The 1981 survey was conducted using three commercial boats equipped with 4.9 m crowfoot brails and operated by commercial shellers. Brails have been used in the shell industry since the end of the 19th century (Coker 1919). Our brails consisted of a metal or wooden bar with 1 m lengths of line or light chain attached every 7.6 cm. Attached to the lines were bundles of four-pronged hooks made of heavy (10 to 14 gauge) wire. The ends of the wire were bent upward at various angles depending on the type of sediment in which the brail was used and on the method of hauling. The tips of the hooks were melted to form a bead to help hold the unionid, a modification invented by J. F. Boepple (Wilson and Clark 1914), one of the founders of the pearl button industry in the United States. One or two brails were towed slowly by a boat such that the bar was suspended just above the sediment surface and the hooks raked the bottom. A hook tip that enters the opening between the two valves of a unionid will cause the individual to clamp shut on the hook. If the hook is secure it will pull the individual from the sediment; the individual will remain attached until the brail is hauled to the surface. A jonboat equipped with a 2.4 m brail and operated by Murray State University personnel was also used. Three SCUBA divers sampled selected sites where brails were not effective, such as among large rocks and snags. Shorelines were searched for empty shells that may have washed ashore or piles of shells left by muskrats. Both conditions usually indicate that a bed is nearby. Beds discovered by brailing and areas in the vicinity of shell piles observed along the shoreline were also examined by divers. The commercial shellers brailed the middle, right, and left margins of the channel from river mile 30 to the Ohio River at CRM 2.2. Where unionids were encountered in numbers suggesting a bed, several brail hauls were made to more fully determine the location and extent of the bed and the species composition. SCUBA diving on beds was used to search for species not caught by the brails. Representative samples of brail catches and all SCUBA samples were counted to determine the relative abundance of species. Other brail samples were examined only for species composition. Empty shells found along shore were examined for species not encountered by other collecting methods. The 1988 survey was conducted by two SCUBA divers. One additional site was sampled by divers in Lake Barkley at Clay Bay, CRM 47.0. Names of species correspond to those given in Turgeon et al. (1988) except where otherwise noted.

Results and Discussion

The distribution of all species found during our 1981 and 1988 surveys is presented in Table 2. The sample locations are reported by river mile and position within the river as either left, middle, or right of the channel as viewed facing downstream.

Unionid beds. Unionid beds are considered to be locations of stable substrate, usually of gravel and sand stabilized by compact silt and clay, in which individuals of various age classes and species occur in significant densities, generally more than 1/m^2. The establishment of a bed requires many years since recruitment is generally a slow process. It is not uncommon to find beds composed of individuals ranging from 5 to 25 years in age with very few juveniles.

Figure 1 shows the Cumberland River from Barkley Dam to the Ohio River. Elongated solid areas indicate the major beds found in the surveys. The small, oval, solid areas indicate smaller concentrations. The only bed that several retired commercial shellers could recall as ever having produced commercial harvests was in the vicinity of mile 14 between Pinckneyville and Sandy Creek. Diving and brailing at the site revealed a bed with limits from mid-channel to the right bank from CRM 13.1–14.7. Nineteen species were found in the bed, which was the largest and most species rich in the Barkley Dam tailwater section of the river. The age composition of the bed indicated that some of the species in this section of the river may be on the verge of demise, most individuals being over 15 years old with no evidence of recruitment since the construction of Barkley Dam in 1965. The rapid rise and fall of water level caused by the intermittent discharge of water for power generation at Barkley Dam may be one cause for the lack of recruitment.

The surveys located other beds at CRM 4.5–5.0, middle; CRM 9.4–11.0, middle; CRM 17.0–17.3, right-middle-left; and CRM 26.5–27.2, middle-right. The bed at CRM 4.5–5.0, confined to a narrow mid-channel region, consisted mainly of *Megalonaias nervosa* with minor representatives of 13 other species. The bed at CRM 9.4–11.0 was rather spread out down the mid-channel. Fourteen species were represented with *Fusconaia ebena* being the most abundant and *Megalonaias nervosa, Elliptio crassidens,* and *Pleurobema cordatum* following in that order.

At CRM 17.0–17.3 a small bed was located in the vicinity of another old shell pile on the right bank at CRM 17.3. The bed was small but extended from bank to bank and contained 12 species.

The bed at CRM 26.5–27.1 was dense and extended from the bottom of the right bank out to mid-channel. Fifteen species were recovered alive along with empty shells of *Obovaria retusa* and *Pleurobema rubrum.* This bed is in danger of being destroyed by channel maintenance dredging.

Old shell piles along shore. Because of the steep river banks and bank slumping caused by the fluctuating discharge at Barkley Dam and wave action from passing vessels, there were few shoreline sites where empty shells were likely to wash ashore and few locations where old shell piles remained exposed. Only a few shells were found on gravel bars or clay banks; most of these were *Corbicula fluminea* (Müller), one of the Asiatic clams.

Three large shell piles were found mostly buried in the bank, which had apparently slumped over them. These were located on the right bank at miles 14.3, 17.3, and 19.5. Digging in the bank uncovered many shells, mostly "pinks," *Cyclonaias tuberculata, Elliptio crassidens,* and *Elliptio dilatata,* and "washboards," *Megalonaias nervosa.* "Pinks" are shells with a pink or purple nacre that were not used in the pearl button industry; they were usually culled by shellers along shore to remove them from the harvest and to prevent them from returning to the beds. Washboards in the Cumberland River were generally stained and of low value, so they too were frequently culled (Wilson and Clark 1914). Because of the species composition of the piles, it is assumed that they are old cull piles from pearl button days 40 to 90 years ago. Commercial shellers probably culled the unwanted shells along shore near the beds where they were working. Two of the three shell piles occurred adjacent to existing beds, which supports the idea that the beds are very old. Some of the living individuals in these beds could well be older than 30 years. It is difficult to determine accurately the age of a clam beyond about 15 years without thin sectioning the shell because the shell growth slows and the external rest lines tend to be poorly separated. The third pile was near a landing at Dycusburg, probably a location where commercial shellers processed their harvest.

Comparison with Wilson and Clark survey. All of the unionids found in our study and those reported by Wilson and Clark (1914) for the lower Cumberland River are listed in Table 1. Wilson and Clark reported 45 species from between CRM 148–125 and 33 species from CRM 124–36. Our survey lists 33 species (24 found alive) from CRM 47–2.2. Of the 14 species Wilson and Clark reported from above CRM 124 that did not occur below that point, two are Cumberlandian forms (Ortmann 1925): *Dromus dromas* and *Epioblasma florentina.* One Cumberlandian species, *Epioblasma haysiana,* was reported by Wilson and Clark below CRM 124 from above Ball Island at CRM 98. It is unlikely that these species still exist in the lower Cumberland River. Ac-

Table 2. Abundance of live unionid clams collected by brailing or SCUBA diving left, middle, or right of the river channel in surveys conducted in 1981 (a) and 1988 (b) in the lower Cumberland River, Kentucky, from CRM 47 to the Ohio River. (The letter S indicates that only one or more dead shells were found.)

Taxa	CRM 2.5 Right, Dive (b)	CRM 4.3 Left, Dive (b)	CRM 4.7-5.0 Middle, Brail (a)	CRM 4.9 Left, Dive (b)	CRM 9.0-9.3 Middle, Brail (a)	CRM 9.4-11.0 Middle, Brail (a)	CRM 10.6-11.0 Middle, Brail (a)	CRM 11.0-12.4 Middle, Brail (a)	CRM 13.5-14.0 Right, Brail (a)	CRM 13.9 Right, Dive (a)	CRM 13.9 Left, Dive (a)	CRM 14.2 Right, Dive (a)
Amblema plicata	20	2	2	5	1	3		3	3	2		1
Anodonta suborbiculata												
Arcidens confragosus			3		1					1		
Cyclonaias tuberculata												
Ellipsaria lineolata			4			4			6			
Elliptio crassidens			5			14	1		8			
Elliptio dilatata										1		
Epioblasma flexuosa												
Fusconaia ebena	1		6			25		1	10	2		2
Fusconaia flava	4		1			1				1		
Lampsilis abrupta												
Lasmigona complanata	1	1							1			
Leptodea fragilis	6	3		2		1						
Ligumia recta										1		
Megalonaias nervosa	51	4	41	8	3	19		2	31	10	1	18
Obliquaria reflexa	5		3		4			5	5			2
Obovaria retusa												
Plethobasus cicatricosus												
Plethobasus cooperianus												
Pleurobema sintoxia												
Pleurobema cordatum			2			13			6	4		
Pleurobema rubrum												
Potamilus alatus	4	7	3	7	3	2		1			1	
Potamilus ohiensis												
Pyganodon grandis	1											
Quadrula metanevra	1		1			3		1	6			
Quadrula nodulata			1		1	2			4			
Quadrula p. pustulosa			1			1		1		1		
Quadrula quadrula	10		3		3	3		1	4		1	1
Tritogonia verrucosa	2					1			5			
Truncilla donaciformis									1			
Truncilla truncata												
Utterbackia imbecillis												
TOTAL LIVE UNIONIDS	106	17	76	22	16	92	1	15	90	23	3	24
TOTAL SPECIES LIVE	12	5	14	4	7	14	1	8	13	9	3	5

Table 2. (continued)

Taxa	CRM 17.0-17.5 Left, Brail (a)	CRM 17.3 Right, Dive (a)	CRM 17.5-19.6 Middle, Brail (a)	CRM 19.6 Left, Dive (a)	CRM 19.8 Right, Dive (b)	CRM 20.0 Left, Dive (a)	CRM 20.0 Right, Dive (b)	CRM 20.0-20.2 Right, Brail (a)	CRM 23.3 Right, Dive (a)	CRM 23.8-24.4 Middle, Brail (a)	CRM 24.2 Left, Dive (b)	CRM 24.5 Right, Dive (b)
Amblema plicata	3	2			11			1		1	17	8
Anodonta suborbiculata												
Arcidens confragosus												
Cyclonaias tuberculata												
Ellipsaria lineolata	3											
Elliptio crassidens	11		9		1							
Elliptio dilatata												
Epioblasma flexuosa												
Fusconaia ebena	10		2		1			1	1	1		
Fusconaia flava			1		1			1		1		
Lampsilis abrupta												
Lasmigona complanata												
Leptodea fragilis	1		1		2		3				1	4
Ligumia recta												
Megalonaias nervosa	13		3		21		1		3	2		4
Obliquaria reflexa	3		1		2				1		33	3
Obovaria retusa												
Plethobasus cicatricosus												
Plethobasus cooperianus		S										
Pleurobema sintoxia												
Pleurobema cordatum	8		1									
Pleurobema rubrum												
Potamilus alatus	3		1		3	3						2
Potamilus ohiensis												
Pyganodon grandis						1						
Quadrula metanevra			1								1	
Quadrula nodulata		1	1					1			3	1
Quadrula p. pustulosa												
Quadrula quadrula	1	4	1	1	2			2			3	2
Tritogonia verrucosa		1	1		1							
Truncilla donaciformis												
Truncilla truncata											1	
Utterbackia imbecillis											1	
TOTAL LVE UNIONIDS	56	8	23	1	45	4	4	6	5	5	59	24
TOTAL SPECIES LIVE	10	4	12	1	10	2	2	5	3	4	8	7

Table 2. (continued)

Taxa	CRM 25.5 Right, Dive (a)	CRM 26.3-27.0 Middle, Brail (a)	CRM 26.9 Right, Dive (a)	CRM 27.1 Right, Dive (a)	CRM 27.6 Left, Dive (a)	CRM 28.1 Right, Dive (b)	CRM 28.3 Right, Dive (b)	CRM 28.5 Right, Dive (a)	CRM 47.0 Left, Dive (b)	TOTAL LIVE	% TOTAL
Amblema plicata		5	6	6	1		13	1	6	123	13.23
Anodonta suborbiculata									2	2	0.22
Arcidens confragosus										5	0.54
Cyclonaias tuberculata			S							0	0.00
Ellipsaria lineolata			1							18	1.94
Elliptio crassidens		3	1	3						56	6.02
Elliptio dilatata										1	0.11
Epioblasma flexuosa					S					0	0.00
Fusconaia ebena		2	7	3						75	8.06
Fusconaia flava		1	1	2						15	1.61
Lampsilis abrupta					S					0	0.00
Lasmigona complanata			3	2						8	0.86
Leptodea fragilis	2		1				25			52	5.59
Ligumia recta		2								3	0.32
Megalonaias nervosa		3	10	7			1			256	27.53
Obliquaria reflexa		1					5			73	7.85
Obovaria retusa			S							0	0.00
Plethobasus cicatricosus					S					0	0.00
Plethobasus cooperianus										0	0.00
Pleurobema sintoxia					S					0	0.00
Pleurobema cordatum		3	3							40	4.30
Pleurobema rubrum			S							0	0.00
Potamilus alatus		1		1	1		2	1		46	4.95
Potamilus ohiensis								S		0	0.00
Pyganodon grandis							2			4	0.43
Quadrula metanevra		2								16	1.72
Quadrula nodulata	1									16	1.72
Quadrula p. pustulosa										4	0.43
Quadrula quadrula		7	4	4			7		31	95	10.22
Tritogonia verrucosa		3	2	2						18	1.94
Truncilla donaciformis										1	0.11
Truncilla truncata							1			2	0.22
Utterbackia imbecillis				S						1	0.11
TOTAL LIVE UNIONIDS	3	33	39	30	2	0	56	2	39	929	99.89
TOTAL SPECIES LIVE	2	12	11	9	1	0	8	2	3	24	

cording to Stansbery (1970) *Epioblasma florentina* is restricted to the South Fork Holston River, Virginia, while *Epioblasma florentina walkeri*, perhaps the same as *Epioblasma florentina* of Wilson and Clark, is "reduced to the lower Stones and Red Rivers of the Cumberland River system," and *Epioblasma haysiana* is restricted to a 16 km region of the Clinch River. *Dromus dromas* was recently found living in the Cumberland River 160 km upstream from Nashville at CRM 296.8 by Parmalee et al. (1980), and there is a possibility that it still exists in the upstream section of Lake Barkley above Clarksville within the original Cumberlandian Region where Lake Barkley still retains some of the characteristics of a free-flowing river.

Within the region now in Lake Barkley, the data from Wilson and Clark (1914) indicate a gradual change in species composition with the number of species declining downstream. This is to be expected because, as the river increases in size and decreases in gradient, the variability of habitats is reduced and fewer shoals occur, the shoals being a favored habitat for small river forms.

The 14 species Wilson and Clark (1914) reported only from above CRM 124 (CRM 124–148) were *Cyclonaias tuberculata, Cyprogenia stegaria, Dromus dromas, Epioblasma florentina, E. obliquata, Fusconaia subrotunda, Hemistena lata, Lasmigona complanata, Obovaria subrotunda, Pleurobema sintoxia, Ptychobranchus fasciolaris, Truncilla donaciformis, T. truncata,* and *Villosa lienosa.* With the exception of the two Cumberlandian species already mentioned (*Dromus dromas, Epioblasma florentina*) that were not reported below CRM 125, the other 12 species are widely distributed in other river systems, and three (*Lasmigona complanata, Truncilla donaciformis, T. truncata*) are present in the lower Cumberland today.

Several species were found in our study that were not reported by Wilson and Clark (1914) in the lower Cumberland River and several that have never been reported from the Cumberland River. Those not reported by Wilson and Clark are *Anodonta suborbiculata, Arcidens confragosus, Epioblasma flexuosa, Plethobasus cicatricosus, Pleurobema rubrum, Pyganodon grandis, Quadrula nodulata,* and *Utterbackia imbecillis.*

Epioblasma flexuosa was found in our survey at CRM 27.5 only as a single valve with part of the periostracum attached. Casey (1987) reported shells from archaeological sites at CRM 26L, 26.6R, and 27.3L that date between 1000 and 1300 A.D. Neel and Allen (1964) reported *Epioblasma lewisi* (Walker) from the upper Cumberland River where Wolf Creek Dam is now located. Both are assumed to be extinct (Stansbery 1970).

Plethobasus cicatricosus was recovered as a single, badly eroded valve at CRM 27.6. It has not been reported live from the Cumberland River but was previously reported from prehistoric rock shelters along the middle Cumberland River by Parmalee, Klippel, and Bogan (1980) and by Casey (1987) at CRM 26.6R and CRM 27.3L. Stansbery (1970) considered it restricted to a single population in the Tennessee River in northern Alabama below Wilson Dam.

Pleurobema rubrum was recovered only as a relic shell, both valves with most of the periostracum attached, at CRM 26.9. It was not reported by Wilson and Clark (1914) from the lower Cumberland, but they found a few in the upper Cumberland. It was found by Parmalee, Klippel, and Bogan (1980) in the prehistoric rock shelter deposits along the Cumberland River in Smith County, Tennessee.

Pyganodon grandis and *Utterbackia imbecillis* were not reported by Wilson and Clark from the main river, but they were found in a floodplain lake, Haynes Lake, a short distance downstream from Clarksville, Tennessee.

Three species found in our surveys were not reported from the Cumberland River by Wilson and Clark (1914), Neel and Allen (1964), or Parmalee, Klippel, and Bogan (1980): *Anodonta suborbiculata, Arcidens confragosus,* and *Quadrula nodulata.* All three were listed by Johnson (1980) as having originated in the Mississippian Region. He suggested that *Arcidens confragosus* had a refugium in the Meramec River, Missouri, during the Pleistocene and that all three found a refuge in the Ozarkian Region below the Ozark Crest. Johnson (1980) presumed that their extension into the Ohioan Region occurred after the Pleistocene; however he did suggest that the Green River, Kentucky, may have been a refugium during the Pleistocene. These three species apparently have entered the lower Cumberland River since the Wilson and Clark survey, and the altered habitat caused by dams may have influenced the invasion. In 1929 the Army Corps of Engineers completed Lock and Dam 52 at Paducah, Kentucky. This dam maintained an upstream elevation of 92 m above mean sea level. This reduced the flow in the lower Cumberland River and may have encouraged the invasion by the three Mississippian species. The completion of Barkley Dam in 1965 may have contributed to the invasion as well. The impoundment conditions apparently have been favorable for their range extension. A similar event occurred in the Tennessee River following impoundment of Kentucky Lake in 1944. None of the three Mississippian species was reported from the Tennessee River by Ortmann (1918, 1924, 1925) or van der Schalie (1939) except for *Quadrula nodulata*, which van der Schalie (1939) listed from Paducah, Kentucky, at the junction of the Tennessee and Ohio rivers. Stansbery (1964) found *Anodonta suborbiculata* in the Tennessee River at Muscle Shoals, Alabama, in 1963; Isom (1969) found *Arcidens confragosus* in 1965; and Yokley (1972) reported *Quadrula nodulata, Arcidens confragosus*, and *A. suborbiculata* in Kentucky Lake in 1972.

To explain the previous absence of these three species—*Anodonta suborbiculata, Arcidens confragosus*, and *Quadrula nodulata*—in the Cumberland River, one must examine the geological history of the region. Ortmann (1925) pointed out that the Tennessee and Cumberland rivers were at one time joined and separated from the Ohio River, at least for some distance beyond the present confluence. Thornbury (1965) suggested that the two rivers had a pre-Pleistocene connection below Paducah, Kentucky, and continued westward through the Metropolis Lowland now occupied by the Ohio River, which at that time flowed through the Cache Lowland to the north. The junction with the Ohio River may have occurred near Cairo, Illinois, or perhaps as far south as Memphis, Tennessee. The isolation of the Tennessee River from the Cumberland River by the present Ohio River at the end of the Pleistocene in conjunction with reduced gradient in the lower sections of the rivers essentially isolated the Cumberlandian fauna in the upper reaches and allowed the invasion of the Ohioan and Mississippian faunas to proceed. But, apparently, the direct connection of the Cumberland River to the Ohio River during the Pleistocene was not sufficient to allow all of the Ohioan and Mississippian species to invade. If length of time alone were the factor limiting the invasion, then all of the common Interior Basin (Mississippian and Ohioan) fauna might have extended into the Cumberland River. Obviously barriers, both ecological and geological, prevented wholesale invasion just as they prevented most of the Cumberlandian fauna from extending beyond the Tennessee and Cumberland rivers. Before successful invasion can occur, the appropriate host fish must be present and a sufficient number of unionids (as larvae, juveniles, or adults) or a gravid female must be transported to a suitable habitat where a reproducing population can become established. Then habitat suitability and lack of competition are required.

In fact, the lower Cumberland River may have experienced fluctuations between Ohioan and Cumberlandian species composition since the Pleistocene. During the dry, hypsithermal (Franklin 1994) from 8700 to 5000 years ago, Cumberlandian species may have been more common in the lower Cumberland River, and species such as *Epioblasma flexuosa, E. obliquata*, and *Pleurobema clava*, which may have originated in the Cumberlandian Region, moved into the Ohioan Region. Between 700 and 1000 years ago at least two species, *Dromus dromas* and *Epioblasma arcaeformis*, were common in the region now the Barkley Dam tailwater (Casey 1987). The changing climate with increasing moisture may have restricted the Cumberlandian fauna upstream as Ohioan species invaded the lower reach of the river, which was becoming larger and deeper and more like their natural habitat in the Ohio River.

Another notable change from 1911 to the present is the replacement of *Quadrula fragosa* with *Q. quadrula*. It could be argued that Wilson and Clark (1914) were actually looking at *Quadrula quadrula* but identified it as *Q. fragosa*. However, the figures by Coker (1919) clearly distinguish the two and we assume they recognized the difference. We are presently observing a changing species composition from *Quadrula quadrula* to *Q. apiculata* (Say, 1829) in Kentucky Lake within the last 15 years, suggesting that these changes can occur rapidly as better-adapted species invade. This, of course, has major implications for attempts at preservation of endangered species.

Impoundment and pollution have resulted in a large reduction in the number of native species in the Cumberland River. However, altered habitat and reduction in native species have allowed more Interior Basin species, well adapted to impoundment conditions, to invade the lower Cumberland River.

There were 30 species reported by Wilson and Clark (1914) in the Cumberland River downstream from CRM 148 that we did not find alive (Table 1). Remnants of these species may survive in the upper regions of Lake Barkley where riverine conditions occur, but it is probably safe to say that they all have disappeared from lower sections of the Cumberland River from approximately Dover, Tennessee, CRM 89, to the Ohio River.

CONCLUSIONS

Twenty-four species of unionids in 18 genera still survive in the lower Cumberland River from mile 47 to mile 2.2. Nine additional species in seven genera were found only as relic shells. No live specimens listed on the federal endangered species list were encountered, although relic or subfossil shells of six endangered species were found: *Epioblasma flexuosa, Lampsilis abrupta, Obovaria retusa, Plethobasus cicatricosus, P. cooperianus,* and *Pleurobema rubrum.* Thirty species reported in 1914 were not found alive in our study. It is unlikely that very many of these survive in the Barkley Dam tailwater section of the Cumberland River. Impoundment, both on the Ohio and Cumberland rivers, appears to be the major cause for change in species composition. However, the changing climate since the Pleistocene, changes in availability of host fish, pollution, and successful invasions by species from other regions have played various roles in determining the present species composition. Unionid communities are in constant flux. Better knowledge regarding what controls the makeup of unionid communities is needed if their biodiversity is to be preserved.

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