A Distributional Atlas of the Freshwater Mussels of Kentucky

Wendell R. Haag and Ronald R. Cicerello

Part One (Dedication - page 151)
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Kentucky State Nature Preserves Commission
Scientific and Technical Series Number 8
A Distributional Atlas of the Freshwater Mussels of Kentucky
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Dedication

I would like to dedicate this book to two people who, during my days as a student in the 1980s, were instrumental in setting me on a very rewarding career path. Dr. Guenter Schuster, retired Professor of Biology at Eastern Kentucky University, took me under his wing when I was a highly motivated but terribly unfocused and immature undergraduate. His guidance and example were transformative, and we remain great friends today. Ronald Cicerello was my other great mentor during that time. His professionalism and integrity continue to inspire me, and the two summers I spent working for Ron at the Kentucky Nature Preserves Commission are among my most treasured and valuable experiences. The opportunity to collaborate with Ron on this book brought these seminal experiences full-circle.

Wendell R. Haag
Kentontown, Kentucky

I dedicate this book to three deceased mentors, conservationists, and friends, who positively influenced my life and career and Kentucky’s natural world. Drs. Branley A. Branson and John C. Williams, former Eastern Kentucky University Biology faculty, stimulated and motivated me, and many others, each in their often unconventional ways. Branley shared his love of fishes and contributed to their conservation through the careers of his students and by his efforts to protect eastern Kentucky’s Red River from destruction. John was a font of knowledge about field and lab techniques, and his mussel surveys of the Kentucky, Ohio, and other rivers are underappreciated contributions to our knowledge of the state’s fauna. Donald F. Harker, Jr., directed the Kentucky Nature Preserves Commission from 1977-1982. Don led a period of unprecedented growth in our knowledge of Kentucky’s biota, and the beginning of conservation efforts that now protect in KNPC-dedicated preserves many of the best remaining examples of Kentucky’s biological heritage. The legacy of these gentlemen is a generation of biologists who follow their lead to explore and protect Kentucky’s natural treasures.

Ronald R. Cicerello
Frankfort, Kentucky
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I. Introduction

Kentucky has a diverse natural environment, from the cool mountains of the Appalachians to the steamy lowlands along the Mississippi River. This landscape supports a correspondingly diverse flora and fauna. For example, the forests of eastern Kentucky and the fish fauna of streams throughout the state are among the richest in temperate regions of the world. The freshwater mussel fauna of Kentucky is even more remarkable from a global perspective because it is one of the richest, not just in temperate regions, but anywhere on Earth. Kentucky, along with Alabama, Georgia, and Tennessee, each have at least 100 native mussel species and subspecies, which exceeds by far even tropical areas such as the Amazon, Congo, and Mekong river basins (Haag 2012). Several of Kentucky’s rivers are home to more than 50 mussel species, and, in some places, one can find more species in one square meter of river bottom than occur on the entire continent of Europe. Each of Kentucky’s regions has a characteristic array of mussel species, which contributes to the diversity and distinctiveness of the natural landscape.

Mussels are important components of aquatic ecosystems (Vaughn et al. 2008). Like most bivalves, freshwater mussels are filter feeders that eat algae, bacteria, and other material suspended in the water. Material filtered from the water ultimately is deposited in the stream bottom where it is broken down further by other organisms. Mussels filter almost continuously, and, in streams with large populations, the combined feeding of thousands of mussels can improve water quality tremendously, which benefits fish and other aquatic organisms, as well as people who use the water. Mussels also are an important food source for a wide array of animals, including many fish species, turtles, and mammals such as muskrats and otters. In addition to contributing to ecosystem health, the health of mussel populations in turn depends on the health of other aspects of aquatic communities. The larvae (glochidia) of most mussel species require a brief period as parasites, usually on fishes, in order to develop into juvenile mussels. Most species are specialists whose glochidia can parasitize only certain types of fish: some mussels use only bass, some use minnows, others use only catfishes, and so on. Consequently, a diverse mussel fauna depends on the presence of a diverse fish fauna. These reciprocal benefits between mussels and other stream organisms are compelling examples of the close linkages on which the health of any ecosystem depends.

Mussels have been used in several ways by humans (Haag 2012). Prehistoric humans harvested large quantities of mussels primarily for food, and large shell middens can be found at archaeological sites along many of the larger rivers in the state. Prehistoric people also used mussel shells to temper pottery and they used shells and pearls for implements and decoration. More recently, mussels have been harvested commercially in Kentucky since at least the early 1900s. Mussels were harvested first for pearls, and later for the pearl button industry, and Kentucky was an important shelling ground for both of these endeavors. Pearling waned by the 1920s and the pearl button industry succumbed to the advent of plastic buttons by the 1960s. Even today, piles of drilled-out shells can be found at the site of old button factories along the Ohio and other large rivers in the state. In the 1980s and 1990s, Kentucky again became an important shelling ground for the cultured pearl industry, which used beads cut from mussel shells to implant into marine pearl oysters.

Like many other aspects of our natural environment, the mussel fauna of Kentucky is but a shadow of its former splendor. In the early 1900s, many streams in Kentucky were literally paved with mussels throughout much of their lengths, and mussel diversity in our larger rivers
was spectacular. Since that time, humans have altered the landscape and the rivers that drain it in many fundamental ways, and these impacts have severely degraded the mussel fauna. Although several Kentucky streams retain extraordinary mussel faunas, nearly all streams in the state have been negatively affected to some extent, and many streams have lost their mussel faunas almost entirely. In the last 100 years, 12 species in Kentucky have become extinct globally, about 10 others have been extirpated from the state, and another perhaps two dozen are in danger of disappearing from the state or becoming extinct. It is our hope that this book will assist conservation by more accurately describing the extent of these losses. We also hope this book will encourage others to become interested in mussels and to take an active role in saving these fascinating animals.

This book is intended to summarize all available information about the distribution of mussels in Kentucky, and to illustrate and describe changes in their distributions over the last 100 years or so. This period spans the time for which the majority of mussel distributional data are available. Furthermore, changes in mussel distributions over the last 100 years are almost entirely the result of the effects of modern society on streams and the natural world in general, and addressing these effects is the primary goal of conservation efforts. In some cases, we discuss apparent changes in mussel distributions over the last several thousand years based on archaeological data. Prehistoric humans also may have had effects on streams and mussel assemblages (e.g., Peacock et al. 2005), but archaeological data are unavailable for most streams and a comprehensive analysis of longer term changes in mussel distributions is beyond the scope of this book.

This book is not a guide to identification or a comprehensive treatment of mussel ecology. For a photographic guide to Kentucky mussels, see Cicerello and Schuster (2003). Illustrations and information on identification of mussels found in Kentucky also can be found in mussel books for nearby states (Cummings and Mayer 1992; Oesch 1995; Parmalee and Bogan 1998; Williams et al. 2008; Watters et al. 2009; McMurray et al. 2012). This book provides ecological information about each species, but this information is limited to characteristics that have the most direct bearing on distribution and conservation status (e.g., fish host use, apparent impoundment tolerance). For comprehensive treatments of general mussel ecology, see Strayer (2008); Cummings and Graf (2010); and Haag (2012). Additional ecological information about most Kentucky species can be found in Williams et al. (2008).
II. Physiography and geology of Kentucky

Kentucky is centrally located in the eastern U.S. (Figure 1) and consequently has elements of both northern and southern faunas. Kentucky comprises three major regions that differ fundamentally in their landscape, underlying geology, and ecological communities (Figure 2). These regions are described by three physiographic provinces: the Mississippi Embayment, the Interior Low Plateaus, and the Appalachian Plateaus. Each of these provinces is further subdivided into distinct sections and subsections. Physiography and underlying geology are among the primary factors that dictate the type of aquatic habitats that occur in any area. Below, we briefly describe each physiographic province and section and the type of aquatic habitats that occur in each. For more detailed information and a description of subsections, see Fenneman (1938); Quarterman and Powell (1978); Baer et al. (1982); and Powell (1983); our descriptions of physiography and geology are based on these sources. Descriptions of aquatic habitats in each province and section are based on Burr and Warren (1986) and our own observations.

II.A. Mississippi Embayment province

The Mississippi Embayment in Kentucky is alternately referred to as the Coastal Plain or the Jackson Purchase. This province consists of a low-lying basin extending from the Mississippi River delta on the Gulf Coast north to about the confluence of the Ohio and Mississippi rivers. The basin is filled with Cretaceous and Tertiary marine sediments deposited when the region was inundated by high sea levels during those periods, and by recent alluvial sediments from the Mississippi River and its tributaries. The province also is overlain by Pleistocene loess deposits (wind-blown silt), which range in Kentucky from nearly 20 meters (12 feet) deep at the steep bluffs along the Mississippi River to about 1.5 meters (5 feet) in the eastern portions of the province. The Mississippi Embayment encompasses all of extreme western Kentucky from the Mississippi River east to the Tennessee River and makes up about 5% of Kentucky’s land area (about 6,100 square kilometers or 2,300 square miles). The state’s lowest elevation of 79 meters (259 feet) occurs in the Mississippi Embayment.
along the Mississippi River in southwestern Fulton County, and the province’s highest elevation in Kentucky is 195 meters (640 feet) on the Tennessee River drainage divide in Calloway County.

Because of its lowland nature, the Mississippi Embayment harbors many plant and animal species found nowhere else in Kentucky and characteristic of extensive lowlands of the Deep South. In addition to the Mississippi River, major streams of the province are Clarks River, Mayfield Creek, Obion Creek, Bayou du Chien, and Running Slough. The Mississippi Embayment in Kentucky is made up of two sections,
the Mississippi Alluvial Plain and the Eastern Gulf Coast.

II.A.1. Mississippi Alluvial Plain section

The Mississippi Alluvial Plain is a nearly flat, low elevation floodplain (88–101 meters or 289–331 feet) bordering the Mississippi and lower Ohio rivers. Aquatic habitats consist of low-gradient bayous and sloughs and associated wetlands, and the Mississippi River. The Mississippi Alluvial Plain also contains many natural lakes, a habitat type that is rare or absent elsewhere in the state. Most are oxbow lakes or similar features that represent abandoned stream meanders. Streams and lakes historically were bordered mainly by bottomland hardwood or floodplain forest, often dominated by Bald Cypress or willows. Today, much of the natural vegetation of the Mississippi Alluvial Plain is replaced by intensive row crop agriculture, and many streams have been channelized (see section VI.B.3).

II.A.2. Eastern Gulf Coastal Plain section

The Eastern Gulf Coastal Plain is more varied topographically and geologically than the adjacent Mississippi Alluvial Plain. Much of this section is gently undulating with flat-topped ridges up to about 122 meters (400 feet). Extensive wetlands—similar to those in the Mississippi Alluvial Plain—occur in the valleys in association with major streams. All aquatic habitats in this section are essentially lowland in character. However, aquatic habitats range from small streams with upland characteristics flowing over Cretaceous gravels and sands to sluggish lowland streams with silt substrates; lowland streams also may have localized shoals formed by gravels transported from the uplands. The eastern portion of this section has been recognized as a distinct section within the Mississippi Embayment based on the distinctiveness of its fish fauna and is referred to as the Tennessee River Plain (Burr and Warren 1986).

II.B. Interior Low Plateaus province

The Interior Low Plateaus province extends from northern Alabama into central Tennessee and Kentucky, and north into southern Illinois, Indiana, and Ohio. This is a diverse province consisting of level plateaus, plains, dissected uplands, and rugged escarpments. In Kentucky, it spans the broad central region of the state from the Tennessee River east to the Appalachian Plateaus province, and makes up about 65% of Kentucky’s land area (about 68,000 square kilometers or 26,000 square miles). Elevations range from 92 meters (304 feet) to about 330 meters (1,090 feet). Most of the province is underlain by calcareous limestones of Mississippian or Ordovician age, but Pennsylvanian sandstones underlie much of the Shawnee Hills section. The predominance of limestone has resulted in numerous caves, springs, and other karst features throughout much of the province.

Upland streams make up most aquatic habitats in the Interior Low Plateaus, but the northwestern portion of the province (Shawnee Hills section) encompasses low gradient streams and extensive wetlands similar to those found in the Mississippi Embayment. At least portions of most major river systems in the state are found in this province. The Tradewater, Green, and Salt river systems are entirely within the Interior Low Plateaus, and large portions of the Cumberland, Kentucky, and Licking river systems flow through the province, as well as much of the Ohio River. In several areas, streams are highly influenced by subterranean springs, and some streams flow underground for short distances. The Interior Low Plateaus in Kentucky is made up of three sections: the Highland Rim, Shawnee Hills, and Bluegrass.
II.B.1. Highland Rim section

The Highland Rim section extends in a broad arc across southern Kentucky from the Tennessee River east to the Appalachian Plateaus, and north to the Ohio River between the Shawnee Hills and Bluegrass sections; this latter portion is disjunct and separated from the remainder of the section by a narrow band of the Shawnee Hills to the south. Maximum elevations gradually increase from about 122 meters (400 feet) in the western portion to 335 meters (1,099 feet) in the northeastern portion. This section is a broad upland plateau underlain mainly by Mississippian limestones and deeply dissected by surface streams. Karst topography and extensive subterranean drainage through sinkhole plains and caverns characterizes several areas in the section. All streams in the section are upland in character flowing mainly over gravel and sand substrates with localized bedrock. Small wetlands occur in the western portion of the section but are rare elsewhere and permanent natural lakes are absent. In Kentucky, the Highland Rim section is divided into six subsections: the Eastern Highland Rim, Western Highland Rim, Pennroyal Plain, Elizabethtown Plain, Greensburg Upland, and Cumberland Enclave.

II.B.2. Shawnee Hills section

The Shawnee Hills section occupies a large portion of northwestern Kentucky from near the mouth of the Cumberland River east to the Dripping Springs and Knobstone escarpments in west-central Kentucky. Elevations range from 92 meters (302 feet) to 329 meters (1,079 feet). This section is an undulating to hilly and deeply dissected plateau developed mainly on Pennsylvanian sandstones but with localized exposures of Mississippian limestones; the latter regions contain karst features. This section is also known as the Western Coal Field due to extensive coal deposits found in association with Pennsylvanian age strata. Valleys of major streams are filled with extensive and broad alluvial deposits. Streams on the plateau are generally upland in character and flow over gravel and sand substrates. Streams that flow through alluvial deposits are lowland in character and are associated with extensive wetlands and numerous oxbow lakes; these habitats are best developed in the Tradewater River and the lower portions of the Green, Pond, Rough, and Mud rivers and their tributaries. The Shawnee Hills section is divided into four subsections in Kentucky: the Mammoth Cave Plateau, Marion, Ohio River Hills, and Lowlands, and Brush Creek Hills.

II.B.3. Bluegrass section

The Bluegrass section is a large, roughly circular area encompassing the north-central part of the state. This section consists of a broad, uplifted dome of the center of which lies in Fayette County, near Lexington. The dome has been eroded such that distinct rock layers underlying the dome are exposed in a roughly concentric fashion with the oldest rocks found near the center. The central portion of the province (Inner Bluegrass subsection) is a gently undulating plain developed on Ordovician limestones with extensive karst features and deeply entrenched streams. Surrounding much of this region is a highly dissected region of rugged, steep hills on Ordovician shales and limestones (Eden Shale Belt subsection), followed by another undulating plain developed on Ordovician, Silurian, and Devonian age rocks (the Outer Bluegrass subsection). At the periphery of much of the section is a narrow band of steep, conical hills formed on Mississippian and Devonian shales, siltstones, and sandstones (the Knobstone Escarpment and Knobs subsection). Elevations range from about 305 meters (1,000 feet) at the center of the dome to about 140–349 meters (460–1,145 feet) in outlying regions. All streams in the section are upland in character flowing main-
ly over gravel, sand, and slabs rock substrates with extensive exposures of bedrock. Wetlands are rare and permanent natural lakes are absent. Streams tend to be well-buffered, due to the predominance of carbonate rocks (limestones), and highly productive due to the high phosphate content and natural fertility of soils in much of the section. In Kentucky, this section is divided into five subsections: the Knobstone Escarpment and Knobs, Northeastern Bluegrass, Outer Bluegrass, Eden Shale Belt, and Inner Bluegrass.

II.C. Appalachian Plateaus province

The Appalachian Plateaus province extends from New England south to northern Georgia and it encompasses the mountainous eastern region of Kentucky. The rugged and highly dissected Pottsville Escarpment that delimits the western boundary of the province in Kentucky runs diagonally from the Ohio River southwest to the Tennessee border. The province makes up about 30% of Kentucky’s land area (29,008 square kilometers or 11,200 square miles). The state’s highest elevation of 1,265 meters (4,145 feet) is on Big Black Mountain in Harlan County, and the lowest elevation in the province is about 366 meters (1,200 feet) on the western edge of the Pottsville Escarpment. Most of the province is underlain by Pennsylvanian sandstones, conglomerates, and shales, but larger, deeply entrenched rivers have exposed Mississippian limestones. Extensive coal deposits are associated with Pennsylvanian age strata.

Upland streams characterize all aquatic habitats in the province. Streams are often unproductive and poorly buffered due to the absence or scarcity of carbonate rocks in Pennsylvanian age strata. Wetlands are rare and natural lakes are absent. The Big Sandy River system, Little Sandy River, and Tygarts Creek are the larger streams that are entirely within the Appalachian Plateaus. In addition, three of Kentucky’s largest river systems, the Cumberland, Kentucky, and Licking, arise and flow through substantial portions of this province. The Appalachian Plateaus province in Kentucky is divided into three sections: the Unglaciated Allegheny Plateau, Cumberland Plateau, and Cumberland Mountains.

II.C.1. Unglaciated Allegheny Plateau section

The Unglaciated Allegheny Plateau encompasses the northern third of the Appalachian Plateaus province in Kentucky. The southern boundary of the section is approximately at the drainage divide between the Licking and Big Sandy river drainages to the north and the Kentucky and Cumberland river drainages to the south. This division is based on the prevalence of shales in the Unglaciated Allegheny Plateau and the prevalence of sandstones in the Cumberland Plateau section to the south, but the boundary is somewhat arbitrary and the two sections are similar in many ways. This section is mountainous and deeply dissected with steep, sharp-crested ridges. Streams occupy deep valleys with narrow floodplains and flow over cobble, gravel, and sand substrates.

II.C.2. Cumberland Plateau section

The Cumberland Plateau section encompasses most of the southern two-thirds of the Appalachian Plateaus province in Kentucky. In general, this section is less dissected than the Unglaciated Allegheny Plateau section because the overlying sandstone rocks are more resistant to erosion than the shales of the latter section; this results in flat-topped peaks that illustrate the former level plateau of the region. Nevertheless, the landscape is rugged and mountainous, and the Pottsville Escarpment in this section is deeply dissected by streams, which occupy spectacular gorges and canyons often with high waterfalls. For example, Cumberland Falls is located at the end of a 72 kilometer (45 miles) long
gorge eroded by the Cumberland River eastward and southward from the hypothesized original location of the Pottsville Escarpment at Burnside (see section V.D.). Elevations increase in a southeasterly direction as the Cumberland Mountains section is approached. Most streams occupy deep valleys with narrow floodplains and flow over cobble, gravel, and sand substrates.

II.C.3. Cumberland Mountains section

The Cumberland Mountains section is a long, narrow region running along Kentucky’s southeastern border with Virginia and Tennessee. This region consists of long, high ridges and is dominated by Pine Mountain (maximum elevation 998 meters or 3273 feet), which traverses most of the section. The highest point in Kentucky, Big Black Mountain, as well as several other peaks greater than 900 meters (2952 feet) occur in the Cumberland Mountains. The only major river in the section is the Poor Fork of the Cumberland River. The Poor Fork and its tributaries are deeply entrenched in narrow valleys, have moderate to high gradients, and flow over cobble, gravel, and sand substrates.
III. The river systems and aquatic habitats of Kentucky

The vast majority of streams in Kentucky ultimately flow into the Ohio River. The Ohio River basin encompasses all major river systems in the state including the Tennessee, Cumberland, Tradewater, Green, Salt, Kentucky, Licking, and Big Sandy rivers. The only exceptions are streams in the Mississippi Embayment that flow directly into the Mississippi River. Despite the common destination of most streams in the state, Kentucky provides a wide range of aquatic habitats.

At the coarsest level, streams can be divided into two types: upland and lowland. Most streams in Kentucky are generally upland in nature. Upland streams flow over continental rock strata and are characterized by coarse substrates (sand, gravel, cobble, or boulders), generally moderate to high gradient, turbulent flow, and consistently well-oxygenated water. Upland streams in Kentucky usually are not associated with wetlands or permanent natural lakes, but habitats similar to those found in lakes (e.g., slow current, fine substrates) can be found in pools and along stream margins, particularly in the lower reaches of streams. Despite the predominance of upland streams in the state, lowland stream habitats are well represented in portions of western Kentucky. Lowland streams flow over extensive alluvial deposits or marine sediments and are characterized by fine substrates (silt or sand), low gradient, less turbulent flow, and they may experience seasonally low oxygen levels. Lowland streams often are associated with extensive wetlands and other lentic habitats (e.g., oxbow lakes). Because they provide vastly different habitats, upland and lowland streams often support very different mussel faunas (Haag 2012).

Another major dichotomy in stream habitats is between large rivers and small streams, and these habitat types differ fundamentally in ways that have a large effect on mussel distributions (see Haag 2012 and sources therein). Small streams in general are less stable than larger streams. Flow in small streams responds quickly to rainfall, resulting in brief, highly turbulent and violent floods, which can radically reconfigure the streambed. Flood pulses in larger streams are attenuated and of longer duration and usually involve less turbulence due to the more uniform nature of the streambed. For example, the record flood of 1993 in the upper Mississippi River resulted in no detectable decrease in mussel abundance (Miller and Payne 1998); in contrast, major floods in smaller streams can cause massive mussel mortality (e.g., Hastie et al. 2001). Small streams also are more vulnerable to drought and may dry completely or be reduced to isolated pools, but larger streams usually maintain at least some flow even in severe droughts. In addition to stability, small and large streams differ in other ways that likely are important to mussels. Large streams may provide a greater diversity of habitats, ranging from swift, shallow riffles to extensive pools and backwater areas, while smaller streams provide a more limited array of habitats. Large streams have a greater diversity and abundance of fishes that can serve as hosts for larval mussels, as well as prey on mussels, and mussel food resources differ dramatically between small and large streams. As a consequence, mussel faunas of small and large streams are usually radically different, and the faunas of medium-sized streams are transitional between these two extremes.

Differences between upland and lowland streams are not always clear-cut, and, obviously, stream size represents a continuous gradient from headwater streams to the Mississippi River. Nevertheless, these broad classifications are useful for discussing mussel distributions, and we use them extensively in subsequent portions of this book. Many other factors influence mussel distributions and vary widely among Kentucky
streams. For example, water temperature can be much cooler in small, shaded mountain streams than in large, lowland rivers. Water hardness (the amount of calcium and magnesium in water) also influences mussel distributions because mussel shells are composed primarily of calcium carbonate. All of these factors vary greatly within and among river systems in Kentucky mainly according to physiography and underlying geology of the watershed.

For the purposes of this book, we divided Kentucky into 17 major drainage units (Figure 3). The Mississippi River and Ohio River mainstems each are considered a separate unit because they provide distinct habitats not found elsewhere in the state. Similarly, the Cumberland and Green river systems are subdivided further into three and two units, respectively, to reflect major differences in aquatic habitats and mussel faunas found in different parts of these river systems. In the following section, we describe each major drainage unit and the aquatic habitats present in each unit.

III.A. Mississippi River mainstem

The Mississippi River flows along Kentucky’s western border for approximately 157 kilometers (98 miles) from the mouth of the Ohio River in Ballard County, near Wickliffe, south to the Tennessee border. This section is classified as part of the lower Mississippi River and flows through the Mississippi Alluvial Plain section of the Mississippi Embayment physiographic province. The lower Mississippi River represents a much different type of aquatic habitat than found elsewhere in the Mississippi Embayment (see section III.B). The river is unimpaired, largely free-flowing, carries a high sediment load, and it is highly dynamic. The main channel is swift and deep with a sand and gravel bed that is scoured and redeposited regularly. Because of its dynamic nature, the main channel supports few mussels. Lowland habitats typically associated with the Mississippi Embayment (e.g., slow current, fine sediments) are found in backwater sloughs, side channels, oxbow lakes, and behind navigational wing dams. These habitats support substantial but localized mussel assemblages composed of a mixture of large river and lowland species.

III.B. Mississippi River tributaries

The major direct tributaries of the Mississippi River in Kentucky are Mayfield Creek, Obion Creek, and Bayou du Chien. In addition, Running Slough flows south into Reelfoot Lake in Tennessee, and Terrapin Creek flows south into the Obion River drainage of Tennessee. These streams flow through the Mississippi Alluvial Plain and Eastern Gulf Coastal Plain sections of the Mississippi Embayment province. Most are spring-fed lowland streams that historically were highly sinuous and associated with extensive riparian wetlands and bottomland hardwood and riparian forests. All of these streams and many of their tributaries have been channelized and straightened at least in part and many of the wetlands have been drained and converted to agriculture (see section VI.B.3.). Channelized sections of these streams have unstable sand bottoms and support few mussels. Remnant unchannelized sections of these streams and associated wetlands support mussel assemblages consisting of a mixture of lowland species and small to medium-sized stream species. Terrapin Creek and some headwater tributaries of the other streams are somewhat upland in character, flowing over shifting gravel substrates, and they support few or no mussels.

III.C. Ohio River and minor tributaries

The Ohio River forms the entire northern border of Kentucky from the mouth of the Big Sandy River at Catlettsburg, Boyd County, to the confluence with the Mississippi River, a dis-
tance of about 1,069 kilometers (664 miles). At its mouth, the Ohio River is larger than the Mississippi (as measured by discharge). The Ohio River flows through all three physiographic provinces of Kentucky, and the river’s character differs among these regions. The upper and middle sections of the river in the Appalachian Plateaus in Kentucky and the Bluegrass section of the Interior Low Plateaus are narrower, often bordered by high wooded hills or bluffs, have few islands, and have a relatively narrow floodplain with few wetlands. A remarkable feature of the middle section of the river is the Falls of the Ohio, a large complex of rapids and islands formed where the river flows over an erosion-resistant bed of Devonian limestone at Louisville. As the river enters the Shawnee Hills section of the Interior Low Plateaus, both the river and its floodplain begin to broaden considerably, hills are lower, islands become more frequent, and oxbow lakes, wetlands, and other floodplain features become increasingly common. These characteristics become more pronounced in a downstream direction, particularly in the Mississippi Embayment province, which has little topographic relief. Historically, the river was relatively shallow and had numerous sand and gravel bars and shoals. Today, the river is impounded throughout its length by a series of navigation dams (nine in Kentucky) that maintain a minimum depth of 3 meters (10 feet) in the channel at low flow; gravel and sand bars exist in some places, particularly along shore immediately downstream of dams and in the lower river, but shallow shoal habitats are largely non-existent. Despite impoundment and a history of water pollution, much of the river continues to support large and diverse mussel assemblages. These assemblages are dominated throughout by large river species, but lowland species become more prevalent in a downstream direction. Numerous small tributaries flow directly into the Ohio River. Many of these tributaries are too small to support mussels, but some support limited faunas characteristic of small upland or lowland streams; although they provide radically different habitats than the Ohio River itself, we included these streams in this unit for convenience. All species reported from minor tributaries also are reported from the mainstem Ohio River.

III.D. Tennessee River drainage

Only a small part of the Tennessee River drainage is located in Kentucky, where it drains portions of the Highland Rim section of the Interior Low Plateaus and the Eastern Gulf Coastal Plain section of the Mississippi Embayment. The river in Kentucky flows 79 kilometers (49 miles) north-northwest from the Tennessee state line to its confluence with the Ohio River at Paducah, McCracken County. The Tennessee is a large river and provides habitats similar to the lower Ohio River including a wide floodplain with wetland features. About half of its length in Kentucky (43 kilometers or 27 miles) is impounded by Kentucky Dam, which forms Kentucky Lake; this reservoir is relatively shallow and remains partially riverine in character. The 36 kilometer (22 mile) section downstream of Kentucky Dam is more riverine, but it is influenced by Lock and Dam 52 on the Ohio River. The major tributary of the Tennessee River in Kentucky is Clarks River, but other permanent tributaries include Cypress Creek, Jonathan Creek, and Blood River. Some tributary streams have upland features in their headwaters, but all are lowland in nature in their middle and lower reaches, and many have been channelized. The riverine section of the Tennessee River in Kentucky is Clarks River, but other permanent tributaries include Cypress Creek, Jonathan Creek, and Blood River. Some tributary streams have upland features in their headwaters, but all are lowland in nature in their middle and lower reaches, and many have been channelized. The riverine section of the Tennessee River in Kentucky supports a large river mussel fauna similar to the Ohio River. The Kentucky Lake section also continues to support some riverine species, but it also supports large populations of lentic species that have adapted to impoundment. Clarks River supports a diverse mixture of lowland species and small to medium-sized stream
species; other tributaries, particularly Cypress Creek, support a limited lowland fauna.

**Cumberland River drainage**

The Cumberland River originates in the Cumberland Mountains of southeastern Kentucky, flows west and north over Cumberland Falls, and then loops through southcentral Kentucky, turning south into Tennessee. The river reenters Kentucky in the western part of the state and flows north to its confluence with the Ohio River. The habitats and mussel fauna of the river and its tributaries differ substantially among each of the three following sections.
III.E. Lower Cumberland River drainage

The lower Cumberland River drainage is defined here as encompassing the Cumberland River and its tributaries from the Tennessee state line downstream to the mouth of the river, and the Red River, which flows into the Cumberland at Clarksville, Tennessee (not to be confused with the Red River of the Kentucky River drainage). This section of the Cumberland River flows 121 kilometers (75 miles) north-northwest from the Tennessee state line to its confluence with the Ohio River at Smithland, Livingston County. In this section, the Cumberland flows roughly parallel to the Tennessee River and its mouth is only 15 river kilometers (9 miles) upstream of the mouth of the Tennessee; at one point, the rivers flow within 3 kilometers (1.9...
miles) of each other. The lower Cumberland River drainage lies almost entirely within the Highland Rim section of the Interior Low Plateaus province; the extreme headwaters of some tributaries lie within the Shawnee Hills section. The Cumberland in this region is a large river and provides habitats similar to the Tennessee and lower Ohio rivers. Over half of the river’s length in Kentucky (72 kilometers or 45 miles) is impounded by Barkley Dam, which forms Lake Barkley; this reservoir is relatively shallow and remains partially riverine in character. The 49 kilometer (30 mile) section downstream of Barkley Dam is more riverine, but it is influenced by Lock and Dam 52 on the Ohio River. Major tributaries of the lower Cumberland River in Kentucky include Livingston Creek, Eddy Creek, Little River, and Red River. Despite close proximity to the lowlands of the Shawnee Hills section and the Mississippi Embayment province, all streams in the lower Cumberland River drainage are essentially upland in character and often have large springs and karst features. However, the floodplain of the Cumberland River has lowland features similar to the Tennessee River, and the lower portions of some tributaries are lowland in character. Much of this drainage is dominated by intensive row-crop agriculture. The riverine section of the lower Cumberland River supports a large river mussel fauna similar to the Tennessee and Ohio rivers. The Lake Barkley section continues to support some riverine species, but it also supports large populations of lentic species that have adapted to impoundment. The Little and Red rivers supported diverse mussel faunas composed of small to medium-sized upland stream species including several endemic species, but these faunas have largely been eliminated (see section VI). Small tributaries on the floodplain of the river downstream of Barkley Dam have limited faunas that may include lowland elements.

III.F. Middle Cumberland River drainage

The middle Cumberland River drainage is defined here as encompassing the watershed from the base of Cumberland Falls to the Tennessee state line; similar habitat and faunal characteristics extend into central Tennessee. Cumberland Falls represents the point at which the Cumberland River flows over the Pottsville Escarpment, which separates the Cumberland Plateau from the Highland Rim and Bluegrass sections of the Interior Low Plateaus physiographic province. The falls have eroded about 72 kilometers (45 miles) upstream from the hypothesized original location of the falls near Burnside, Pulaski County. Consequently, the river and its tributaries from the falls downstream to Burnside lie mostly within the Cumberland Plateau and occupy deep gorges. Major tributaries within the Cumberland Plateau are the Rockcastle and Laurel rivers and the upper section of the Big South Fork Cumberland River. Streams within the Cumberland Plateau flow primarily over sandstones, and as a result, they are characterized by relatively poorly buffered waters and low productivity similar to other streams in that section. The river and its tributaries downstream of and including Buck Creek lie mostly within the Highland Rim. Major tributaries in this section include Marrowbone, Crocus, Indian, Beaver, Fishing, Pitman, and Buck creeks, and the lower Big South Fork. In addition, portions of the Wolf River—a tributary of the Obey River, which enters the Cumberland River in Tennessee just downstream of the state line—lie within Kentucky. Streams in the Highland Rim flow over Mississippian limestones and hence are more productive and well-buffered than those on the Cumberland Plateau. The middle Cumberland River drainage has been completely transformed by Wolf Creek Dam, which created Lake Cumberland. Lake Cumberland inundated about 163 kilometers (101 miles) of the river from the dam to about 6 kilometers (3.7 miles) down-
stream of Cumberland Falls and substantial portions of most major tributaries. Downstream of Wolf Creek Dam, the remainder of river in Kentucky is cold year-round due to the great depth of Lake Cumberland, and natural river flows are highly altered by hydroelectric power generation and flood control schedules of the dam. The Laurel River also is impounded for much of its length or influenced by cold water dam release. The Cumberland River is a large river that historically supported an extremely diverse upland mussel fauna including many endemic species, but Wolf Creek Dam eliminated virtually all mussels in the river with the exception of the short, unimpounded reach immediately downstream of Cumberland Falls. Unimpounded portions of tributaries, especially the Rockcastle River, Buck Creek, and the Big South Fork support remnants of the middle Cumberland River drainage mussel fauna, but many of these streams also are affected by coal mining, oil drilling, and other factors.

III.G. Upper Cumberland River drainage

The upper Cumberland River drainage is defined here as encompassing the watershed from the headwaters downstream to Cumberland Falls. The Cumberland River proper begins at the confluence of the Poor Fork, Clover Fork, and Martins Fork near Harlan, Harlan County, and then runs generally west-southwest along the base of the southern flank of Pine Mountain to Pineville, Bell County. The watershed upstream of this point drains the Cumberland Mountains section of the Appalachian Plateaus physiographic province. At Pineville, the Cumberland River cuts through Pine Mountain to enter the Cumberland Plateau section, then meanders across the Plateau to Cumberland Falls. Cumberland Falls represents a natural barrier that separates the fauna of the upper and middle Cumberland River drainage (see section V.D.). In addition to Poor, Clover, and Martins forks, major tributaries of the upper Cumberland River include Marsh, Jellico, Yellow, Watts, Richland, Stinking, and Straight creeks, and Clear Fork. The upper Cumberland River is a medium-sized to large stream. In the Cumberland Mountains section, streams generally are high-gradient mountain streams that flow over coarse cobble and boulder substrates and have limited pool development. In the Cumberland Plateau section, streams have lower gradients with long pools and short riffles and a greater occurrence of fine sediments. Apart from a few small reservoirs on tributaries (e.g., Martins Fork Lake), there are no major impoundments in the drainage. The drainage is largely forested and water quality is high in several streams. However, coal mining and domestic and municipal pollution have degraded water quality throughout much of the drainage. Because of the dispersal barrier posed by Cumberland Falls, this drainage supports a depauperate mussel fauna composed primarily of a few small to medium-sized stream species.

III.H. Tradewater River drainage

The Tradewater River originates in Christian County north of Hopkinsville, Christian County, and flows northwest approximately 234 kilometers (145 miles) to its confluence with the Ohio River near Sturgis, Union County. The drainage lies entirely within the Shawnee Hills section of the Interior Low Plateaus physiographic province. The Tradewater is a medium-sized lowland stream throughout much of its length and is associated with some of the largest wetlands remaining in Kentucky. The upper section of the river and several tributaries are upland in nature. The largest tributary is Clear Creek. The Tradewater River is free-flowing throughout and is not channelized, but several tributaries are channelized. However, the entire watershed is seriously degraded by coal mining. Remaining mussel assemblages in the river are a mixture of low-
land species and small to medium-sized stream species, but some large river elements appear in the lower river; tributaries support a limited lowland fauna.

**Green River drainage**

The Green River drains a greater percentage of Kentucky’s land area than any other river system in the state. The watershed lies almost completely within Kentucky with the exception of a small portion of the headwaters of the Barren River in northcentral Tennessee. The Green River originates in Lincoln County in southcentral Kentucky and flows generally westward for 610 kilometers (379 miles) to its confluence with the Ohio River near Henderson, Henderson County. Because of the diverse landscape traversed by the river, aquatic habitats and mussel faunas differ substantially between the lower and upper parts of the watershed. The boundary between these two units is placed somewhat arbitrarily at the mouth of the Barren River (the river’s largest tributary) and does not correspond to a sharp physiographic divide or other abrupt changes in stream habitats. Nevertheless, the watershed is entirely upland in character upstream of this point, but lowland characteristics become increasingly prevalent downstream.

**III.I. Lower Green River drainage**

The lower Green River drainage is defined here as encompassing the watershed from, but not including the Barren River, to the confluence of the Green River with the Ohio River. Major tributaries include Panther Creek, and Pond, Rough, and Mud rivers. The drainage lies almost entirely within the Shawnee Hills section of the Interior Low Plateaus physiographic province, with the exception of the extreme headwaters of the Rough River, which lie on the Highland Rim. The lower Green is a large river and provides habitats similar to the Tennessee, lower Cumberland, and Ohio rivers. The river is impounded in this section by four navigation dams, and the lower Rough River has a single navigation dam. Although these dams largely eliminated shallow shoal habitats, they are small and allow these reaches to remain somewhat riverine in character. In addition, Lock and Dam 4, near Woodbury, was breached in 1965, returning a 32 kilometer (20 mile) section of the Green River to an unimpounded condition. The only large reservoir in the drainage is Rough River Lake, which inundates about 30 kilometers (18 miles) of the mainstem and portions of several tributaries. Streams in the lower Green River drainage provide a mixture of upland and lowland habitats, but the predominance of lowland habitats increases in a downstream direction. Panther Creek and other tributaries of the lower river are mainly lowland in character as are the lower reaches of the Pond, Rough, and Mud rivers. The upper reaches of the latter three streams are essentially upland in character, flowing over sand and gravel riffles. Wetlands, sloughs, and oxbow lakes also become increasingly common in a downstream direction. Many tributaries in the lower portion of the drainage have been channelized, and much of the watershed is seriously degraded by coal mining and oil drilling. Mussel assemblages in the lower Green River are dominated by large river species. Mussel faunas of tributaries are a mixture of lowland species and small to medium-sized stream species, but some large river elements appear in the lower reaches of the Rough, Pond, and Mud rivers. Smaller tributaries of the lower river support a limited lowland fauna.

**III.J. Upper Green River drainage**

The upper Green River drainage is defined here as encompassing the watershed from the headwaters to and including the Barren River. In addition to the Barren River, major tributaries of the upper Green River include Nolin River, Lit-
tle Barren River, Big Pitman Creek, and Russell Creek. Major tributaries of the Barren River include the Gasper River and Drakes Creek. The watershed lies mostly within the Highland Rim section of the Interior Low Plateaus physiographic province, but the lower sections of the Green, Barren, and Nolin rivers lie in the Shawnee Hills section. The Green and Barren rivers are medium-sized to large streams. The Green River in this unit is impounded by two navigation dams, and the lower Barren River has a single navigation dam. Although these dams largely eliminated shallow shoal habitats, they are small and allow these river reaches to remain somewhat riverine in character. In addition, Lock and Dam 4, on the lower Green River near Woodbury, was breached in 1965, returning a 32 kilometer (20 mile) section of the Green River and the lower Barren River to an unimpounded condition. The Green, Barren, and Nolin rivers are also impounded by large flood-control reservoirs (Green River Lake, Barren River Lake, and Nolin Lake). These reservoirs inundate substantial portions of these rivers and alter the natural temperature and flow of the rivers downstream. Oil drilling also has negatively impacted streams in portions of the watershed. All streams in this drainage are upland in character and flow over substrates of bedrock and slabrock with localized areas of gravel, sand, and silt. However, streams flow through wide floodplains, have relatively low gradients, and are generally shallow and may dry to isolated pools in the summer. In addition, streams are productive, warm, and turbid due in part to underlying geology (see section II.B.3). These features impart a somewhat lowland character to streams in some areas. Streams are enriched further by intensive agriculture present throughout much of the drainage and by municipal and domestic sewage. Mussel assemblages are composed mostly of small to medium-sized stream species, but large stream species occur in the lower reaches of some streams. In addition, some species more characteristic of lowland habitats in western Kentucky occur here.

III.K. Salt River drainage

The Salt River drainage is highly dendritic and is made up of three major branches: Salt River/Floyds Fork, Beech Fork, and Rolling Fork, each roughly equal in size. The watershed lies entirely within the Bluegrass section of the Interior Low Plateaus physiographic province. Although it is a large watershed, due to its dendritic nature large river habitats are limited to the lower Salt and Rolling Fork rivers; these reaches are influenced by backwaters from Cannelton Lock and Dam on the Ohio River. Only a single large reservoir, Taylorsville Lake, on the upper Salt River, exists in the watershed, but antiquated mill dams are present on several streams. All streams in the drainage are upland in nature and flow over substrates of bedrock and slabrock with localized areas of gravel, sand, and silt. However, streams flow through wide floodplains, have relatively low gradients, and are generally shallow and may dry to isolated pools in the summer. In addition, streams are productive, warm, and turbid due in part to underlying geology (see section II.B.3). These features impart a somewhat lowland character to streams in some areas. Streams are enriched further by intensive agriculture present throughout much of the drainage and by municipal and domestic sewage. Mussel assemblages are composed mostly of small to medium-sized stream species, but large stream species occur in the lower reaches of some streams. In addition, some species more characteristic of lowland habitats in western Kentucky occur here.

III.L. Kentucky River drainage

The Kentucky River drainage originates on the northern flank of Pine Mountain in southeastern Kentucky, and flows generally northwest to the confluence of the Kentucky and Ohio rivers at Carrollton, Carroll County. The Kentucky River proper begins at the confluence of the North Fork, Middle Fork, and South Fork near Beattyville, Lee County, and flows 411 kilometers (255 miles) to its mouth. In addition to the three forks, major tributaries of the Kentucky River include Eagle Creek, Elkhorn Creek, Dix River, and Red River (not to be confused with the Red River of the lower Cumberland River drainage). The upper portion of the drainage, including all three forks and the upper Red River system, lies within the Cumberland Plateau sec-
tion of the Appalachian Plateaus, and the remainder of the drainage lies within the Bluegrass section of the Interior Low Plateaus physiographic province. All streams in the drainage are upland in nature, but stream characteristics differ according to underlying geology. Streams on the Cumberland Plateau have relatively high gradient, low productivity and poorly buffered waters, and flow over sand, gravel, and cobble substrates. Streams in the Bluegrass generally are of lower gradient, have highly productive and well-buffered waters, and flow over substrates of bedrock and slabrock with localized areas of gravel, sand, and silt. In addition, streams in the lower portion of the drainage may have a somewhat lowland aspect similar to streams in the Salt River drainage. The Kentucky River downstream of the forks is a large stream. It is impounded throughout its length by fourteen navigation dams; these dams have eliminated most shallow shoal habitats, but they allow the river to remain somewhat riverine in character. Three major reservoirs exist in the drainage: Herrington Lake (Dix River), Buckhorn Lake (Middle Fork Kentucky River), and Carr Fork Lake (Carr Fork). Shorter reaches of some streams are impounded by antiquated mill dams; e.g., Elkhorn Creek. The upper drainage is largely forested, but coal mining has degraded water quality in many areas and several sizeable communities on the river or its tributaries further degrade water quality. The lower drainage is a mixture of agriculture, woodland, and urban areas associated with Lexington and Frankfort. Domestic and municipal pollution has degraded water quality throughout much of the lower drainage. The Kentucky River below the forks historically probably had a medium-sized to large stream mussel fauna, with an increasing representation of large river species in the lower river. Remnants of this fauna remain, but the river today has a high proportion of impoundment-tolerant or lentic species. Tributary streams throughout the drainage have mussel faunas typical of small to medium-sized upland streams, but streams in the lower watershed may have increased representation of lowland species similar to the Salt River drainage.

III. Licking River drainage

The Licking River originates in southern Magoffin County and flows northwest 496 kilometers (308 miles) to its confluence with the Ohio River at Covington, Kenton County. Major tributaries of the Licking River include the South Fork and North Fork Licking rivers, and Fleming, Fox, Slate, and Triplett creeks; major tributaries of the South Fork are Hinkston and Stoner creeks. The upper part of the drainage lies mainly on the Unglaciated Allegheny Plateau section of the Appalachian Plateaus, and the remainder of the drainage lies within the Bluegrass section of the Interior Low Plateaus physiographic province. Streams on the Unglaciated Allegheny Plateau have relatively high gradient, low productivity and poorly buffered waters, and flow over sand, gravel, and cobble substrates. Streams in the Bluegrass generally are of lower gradient, have highly productive and well-buffered waters, and flow over substrates of bedrock and slabrock with localized areas of gravel, sand, and silt; the South Fork and its tributaries have a greater predominance of gravel and sand with less bedrock. In addition, streams in the lower portion of the drainage may have a somewhat lowland aspect similar to streams in the Salt and Kentucky river drainages. The Licking River is impounded by a single large reservoir, Cave Run Lake, located on the upper river near the boundary between the Unglaciated Allegheny Plateau and the Bluegrass. This reservoir inundates about 61 kilometers (38 miles) of the mainstem and alters the natural temperature and flow downstream; otherwise, the remainder of the mainstem is free-flowing. The South Fork and its tributaries are impounded by a series of antiquated mill dams, but unimpounded reaches
remain between these dams. Water quality in the drainage upstream of Cave Run Lake is degraded by coal mining, oil drilling, and domestic and municipal pollution. The lower drainage is primarily agricultural, particularly in the South Fork and North Fork systems. Domestic and municipal pollution affect portions of the lower drainage, but the mainstem downstream of Cave Run Lake has few large communities. Mussel assemblages in the Licking River are a mixture of medium-sized to large stream species. Tributaries support small to medium-sized upland stream species, but streams in the lower drainage may have increased representation of lowland species similar to the Salt and Kentucky river drainages.

III.N. Kinniconick Creek

Kinniconick Creek originates in southern Lewis County and flows northeast about 82 kilometers (51 miles) to its confluence with the Ohio River near Garrison, Lewis County. The entire drainage is within the Bluegrass section of the Interior Low Plateaus physiographic province. However, the stream is unlike other Bluegrass streams and is more Appalachian in character due to its location in the mountainous Knobstone Escarpment and Northeastern Bluegrass subsections. The major tributary is Grassy Creek. Streams are upland in character with narrow, steep-sided valleys and flow over sand, gravel, cobble, and boulder substrates, and the water is less well-buffered than other Bluegrass streams due to the predominance of sandstones and shales. Kinniconick Creek has moderate gradient with long pools separated by short riffles. There are no major reservoirs in the drainage, but the lower portion of Kinniconick Creek is influenced by backwaters from Meldahl Lock and Dam on the Ohio River. The watershed is predominantly forested with agriculture in the valleys. Little coal is present in the watershed, but oil drilling occurs in some areas, and there are few large communities. Mussel assemblages are composed mostly of small to medium-sized stream species.

III.O. Tygarts Creek

Tygarts Creek originates in southwestern Carter County and flows northeast 185 kilometers (115 miles) to its confluence with the Ohio River near South Shore, Greenup County. The drainage lies entirely within the Unglaciated Allegheny Plateau section of the Appalachian Plateaus. The stream is upland in character, flows through a narrow valley, and has sand, gravel, and cobble substrates. The middle part of the stream has downcut through Pennsylvanian sandstones into Mississippian limestones where it flows through a gorge associated with karst features such as caves and large springs. There are no major reservoirs in the drainage, but the lower portion of Tygarts Creek is influenced by backwaters from Meldahl Lock and Dam on the Ohio River. The watershed is predominantly forested with agriculture in the valleys. Little coal is present in the watershed, but oil drilling occurs in some areas, and there are few large communities. Mussel assemblages are composed mostly of small to medium-sized stream species, but some large stream species occur in the lower creek near its confluence with the Ohio River.

III.P. Little Sandy River drainage

The Little Sandy River originates in southern Elliott County and flows northeast 140 kilometers (87 miles) to its confluence with the Ohio River near Greenup, Greenup County. The drainage lies entirely within the Unglaciated Allegheny Plateau section of the Appalachian Plateaus. Major tributaries are East Fork and Little Fork. All streams in the drainage are upland in character. Tributaries of the upper watershed are high gradient with sand, gravel, and bedrock substrates and low waterfalls. The mainstem and
East Fork have moderate gradients with gravel substrates and extensive sand deposits. The Little Sandy River is impounded by a single reservoir, Grayson Lake, and the lower portion of the river is influenced by backwaters from Greenup Lock and Dam on the Ohio River. A tributary, Claylick Creek, is impounded by Greenbo Lake. Water quality is degraded by coal mining, oil drilling, and domestic and municipal pollution. Mussel assemblages are composed mostly of small to medium-sized stream species.

III.Q. Big Sandy River drainage

The Big Sandy River drainage originates in the mountains of southwestern Virginia and flows generally north to the confluence of the Big Sandy and Ohio rivers at Catlettsburg, Boyd County. The Big Sandy River proper originates at the confluence of the Levisa and Tug forks near Louisa, Lawrence County, and flows 40 kilometers (25 miles) to its mouth. The Tug Fork and Big Sandy rivers form the state boundary with West Virginia. In addition to the Levisa and Tug forks, major tributaries in Kentucky include Blaine, Johns, and Beaver creeks, and Russell Fork. The headwaters in Virginia arise in the Cumberland Mountains section of the Appalachian Plateaus, but the drainage in Kentucky lies mainly within the Unglaciated Allegheny Plateau section. All streams in the drainage are upland in character with moderate to high gradients, flowing over sand, gravel, cobble, and boulder substrates. Like elsewhere in the Appalachian Plateaus, streams in the drainage are poorly buffered and low in productivity. The Big Sandy River and lower Levisa Fork are medium-sized to large streams with a greater predominance of sand and fine substrates. The Tug Fork flows primarily over a bed of shifting sand and coal particles. In the late 1800s and early 1900s, a series of navigation dams was built in the drainage including five on the Big Sandy River and one each on the Levisa and Tug forks. The only remaining dam in this system is Lock and Dam 3 on the Big Sandy River just downstream of the confluence of the Levisa Fork and Tug Fork. The lower portion of the Big Sandy River is impounded by backwaters from Greenup Lock and Dam on the Ohio River. The drainage has four major reservoirs in Kentucky and two in Virginia; reservoirs in Kentucky are Yatesville Lake (Blaine Creek), Paintsville Lake (Paint Creek), Dewey Lake (Johns Creek), and Fishtrap Lake (Levisa Fork). Water quality in nearly the entire watershed is seriously and profoundly degraded by coal mining. Water quality also is degraded by oil drilling, and domestic and municipal pollution. The Big Sandy River and lower Levisa Fork historically probably had a medium-sized to large stream mussel fauna, with an increasing representation of large river species in the lower river, but only remnants of this fauna remain. Remaining mussel faunas in other streams in the drainage are typical of small to medium-sized upland streams.
IV. Documenting the mussel fauna of Kentucky

IV.A. A brief history of mussel studies in Kentucky

Kentucky was one of the first regions west of the Appalachian Mountains to be explored and settled by people of European and African descent. It was here that much of the rich biodiversity of the interior of the North American continent was first encountered by scientists of the European tradition. Consequently, many plant and animal species were first described from specimens collected in Kentucky, and the state has a rich history of biological exploration. Biologists began making the trek over the mountains or down the Ohio River soon after the first explorers visited the region. The French naturalist, Francois André Michaux, visited Kentucky in 1802. Michaux was mainly a botanist, but he made some of the first recorded observations about the abundance of mussels in the Ohio River basin (Michaux 1805).

The first—and one of the most colorful—biologists to work extensively with mussels in Kentucky was Constantine Samuel Rafinesque. Rafinesque was a self-taught naturalist raised in France and Italy, and he immigrated to the United States in 1815 (Boewe 1988). In 1818, he made an extended trip by flatboat down the Ohio River from Pittsburgh nearly to the mouth of the river near Cairo, Illinois. He collected plants and animals, including mussels, at numerous locations, including the Falls of the Ohio at Louisville, and he visited John James Audubon at his home in Henderson, Kentucky. From 1819 to 1826, he was a professor of botany and natural science at Transylvania University in Lexington, from which he made many extended explorations throughout Kentucky and Tennessee (Call 1895). Many of the mussel species Rafinesque encountered were unknown to science, and he formally described a large number for the first time in his “Monograph of the Bivalve Shells of the River Ohio” (Rafinesque 1820a), and in a subsequent continuation (Rafinesque 1831). Despite his discoveries, Rafinesque was an eccentric and often erratic character who generated considerable enmity from his colleagues. His misadventures with Audubon are legendary (and perhaps partially apocryphal) and include Rafinesque smashing Audubon’s prized violin while attempting to capture a bat, after which Audubon took revenge by leading him on a tortuous trip through a canebrake and providing him with drawings of fictitious creatures, some of which Rafinesque described in print (Audubon 1899; Haag 2012). In addition, many of Rafinesque’s brief species descriptions and crude drawings are unrecognizable, he deposited few specimens in museum collections, and his collection localities are vague (e.g., “small creeks in Kentucky”). Despite these shortcomings, Rafinesque’s contributions to the study of mussels, particularly in Kentucky, are substantial. He described at least 33 currently recognized mussel species (about one-third of the state’s fauna) based on specimens he collected in Kentucky, and he was one of the few naturalists to see and report on the mussel fauna of the state’s streams prior to major alteration by humans. His legacy in Kentucky lives on in another way: when he was fired from Transylvania in 1826, he purportedly put a curse on the university, and students celebrate “Rafinesque Week” during Halloween to this day.

Thomas Say and Isaac Lea described about half of the currently recognized mussel species that occur in Kentucky (Say, 18 species; Lea, 27 species or subspecies). Thomas Say was one of the first American-born naturalists, and in 1826 he helped found an experimental utopian community on the lower Wabash River at New Harmony, in southern Indiana. Say documented the diverse mussel fauna of the Wabash River, and he described several mussel species from
specimens collected in the nearby Ohio River (e.g., Say 1829). Isaac Lea was a Philadelphia publisher who pursued natural history in his spare time, and it is unknown whether he ever visited Kentucky. He made most of his numerous species descriptions based on shells sent to him by others, including his brother, Thomas G. Lea. Thomas Lea lived in Cincinnati, Ohio, and was an ardent botanist and natural history enthusiast. He collected mussels extensively in the Ohio River at Cincinnati during the 1830s, and many of Isaac Lea’s mussel descriptions from the Ohio River were based on these specimens (e.g., Lea 1831). Another early naturalist in Cincinnati was John Gould Anthony, who lived there from 1835 to 1863. In addition to collecting mussels and snails extensively in the Ohio River and adjacent areas, Anthony made a walking trip in 1853 from Cincinnati through Kentucky, Tennessee, and Georgia to collect shells. Unfortunately, his records of this trip are scanty, and his collections became so disorganized that it was impossible to determine the site of origin for many specimens (Turner 1946). Nevertheless, Anthony later became a curator at the Museum of Comparative Zoology at Harvard University, and his collections were donated to the museum, providing information about the magnificent historical fauna of the Ohio River and other streams.

In the 1800s, the majority of scholarly work on mussels focused on describing and naming the rich array of North American species. DISTRIBUTIONAL INFORMATION FROM EARLY NATURALISTS SUCH AS RAFINESQUE, SAY, AND LEA IS LIMITED MOSTLY TO TYPE LOCALITIES FOR NEWLY DESCRIBED SPECIES AND SPECIMENS DEPOSITED IN MUSEUM COLLECTIONS, MANY OF WHICH HAVE VAGUE LOCALITY INFORMATION; COMPLETE LISTS OF SPECIES FOUND AT A PARTICULAR LOCATION ARE RARE, AND COMPREHENSIVE SURVEYS OF STREAMS OR RIVER SYSTEMS ARE VIRTUALLY NON-EXISTENT.

By the early twentieth century, most morphologically distinctive species had been described (but see section IV.D.3), and academics and newly formed government agencies began to study mussels in more detail. Many academics were interested in better determining the distribution of mussel species and in studying the extent of variation in shells throughout the range of a species. Government agencies were interested in large part in prospecting for and inventorying mussel stocks of value to the pearl button industry. Both of these goals were facilitated by vastly improved transportation in the early twentieth century, and, for the first time, a substantial body of information about mussel distributions began to accumulate.

One of the most important mussel researchers in academia at this time was Arnold E. Ortmann. Ortmann, who was born in Prussia, was curator of invertebrate zoology at the Carnegie Museum in Pittsburgh from 1903 until his death in 1927. Ortmann was one of the first scientists to synthesize mussel distributional patterns across large areas of North America, including Kentucky (e.g., Ortmann 1913; but see Simpson 1896, 1900). The distributional patterns he described were based on information from early naturalists, contemporaries, and his own collections. Ortmann travelled and collected mussels extensively and was one of the first to systematically survey entire river systems. Much of his work focused on the Ohio River basin in Kentucky, Tennessee, and Virginia. In Kentucky, he was the first to conduct a systematic mussel survey of the Green River system (Ortmann 1926a), and he visited other streams that had been largely ignored by previous naturalists (e.g., Licking and Big Sandy rivers, Reelfoot Lake drainage). The only currently recognized mussel species endemic to Kentucky, “Villosa” ortmanni (Kentucky Creekshell), was named in his honor (Walker 1925).

Other scientists of the first half of the twentieth century made important contributions to our knowledge of Kentucky mussel distributions. William J. Clench was a professor and curator of
mollusks at the Museum of Comparative Zoology at Harvard University from 1926 to 1966. In 1924, while a student at the University of Michigan, Clench and a colleague made an extended collecting trip through Kentucky, Tennessee, and Alabama, which was in part an effort to retrace the route of John Gould Anthony 70 years earlier (Remington and Clench 1925). Henry van der Schalie was a professor and curator of mollusks at the University of Michigan Museum of Zoology, and together with Clench, contributed to our knowledge of mussel distributions in the Tennessee, Tradewater, Green, and Salt river drainages (van der Schalie 1939; Clench and van der Schalie 1944). van der Schalie also assisted two Kentucky scientists, William Ray Allen (University of Kentucky) and Joe K. Neel (University of Louisville), in a comprehensive mussel survey of the Cumberland River in the late 1940s (Neel and Allen 1964). That survey is among the most important single studies on Kentucky mussel distributions because it documented in detail the fauna of the Cumberland River immediately prior to its near complete destruction by Wolf Creek Dam.

The primary government agency responsible for mussel studies in the first half of the twentieth century was the U.S. Bureau of Fisheries. The Bureau originated in 1871 as the U.S. Commission on Fish and Fisheries, reorganized as the Bureau of Fisheries in 1903, and ultimately evolved into the U.S. Fish and Wildlife Service in 1940. As mussels began to be exploited heavily by the pearl button industry in the early 1900s, the Bureau of Fisheries became the lead agency responsible for management of this resource. The Bureau sponsored extensive surveys of large rivers throughout the Mississippi River valley in an attempt to document the location and commercial potential of harvestable mussel stocks. These efforts included surveys of the Cumberland River and upper Kentucky River drainage, and observations on other streams including the Ohio River (e.g., Wilson and Clark 1914; Coker 1919; Danglade 1922).

The combined efforts of the early naturalists and scientists of the early 1900s provided a foundation for understanding mussel distributions in Kentucky. Despite the considerable knowledge gaps that remained, this information is invaluable because it provides a glimpse of the remarkable mussel fauna of the state prior to the major changes to rivers that occurred in the latter half of the twentieth century.

A leading figure in mussel research in Kentucky from the 1950s to the 1970s was David H. Stansbery of the Ohio State University. During this period, Stansbery collected North American mussels perhaps more widely than any individual scientist before or since, and he built one of the largest mussel research collections in the world. He visited streams across much of Kentucky, including many that had never before been surveyed for mussels. He also sampled some sites repeatedly, particularly in the Green and Rockcastle rivers (e.g., Stansbery 1965). His collections from the Green River at Munfordville and Lock and Dam 5 span more than 10 years and provide more comprehensive information about species richness than can be obtained from single visits to a site. Stansbery’s collections were among the first to document changes in mussel faunas brought about by widespread dam construction in the 1940s and 50s (e.g., Stansbery 1969), and they provide vital benchmarks for assessing other changes that occurred in the decades subsequent to his work (see section VI.A.). Another important contribution during this period was that of John C. Williams of Murray State University and Eastern Kentucky University, who conducted mussel surveys throughout the Ohio, Green, and Kentucky rivers (Williams 1969, 1975). Although these studies focused on commercially valuable mussel stocks, they were the most comprehensive surveys of the Ohio and Kentucky rivers at the time and virtually the first surveys of any kind in the lower Green River.
Passage of the U.S. Endangered Species Act and Clean Water Act in the 1970s provided impetus and funding for greatly expanded study of mussels across the nation. In Kentucky, this legislation was in part responsible for the first intensive, statewide surveys of mussels and other aquatic organisms, which were conducted by the Kentucky State Nature Preserves Commission (KNP; e.g., Harker et al. 1979, 1980, 1981; Hannan et al. 1984). These and subsequent surveys filled in many of the gaps in our knowledge of mussel distributions, and they discovered several species not previously known from the state (e.g., Warren and Call 1983). Since its formation in 1976, KNP has built and maintained a comprehensive database on mussel distributions in Kentucky, and that database is a primary source of information for this book (see section IV.C.1). Surveys for federally threatened or endangered species conducted by or at the behest of the U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, Tennessee Valley Authority, and other federal agencies also provided a wealth of information about mussel distributions (e.g., Tolin and Schettig 1984; USFWS 1985a; Miller et al. 1986; Cicerello and Hannan 1990).

Another important development in the late 1970s and 1980s was establishment of mussel research programs at universities within Kentucky. Apart from the small but important body of work conducted by William Allen, Joe Neel, and John Williams, little or no mussel research was conducted at Kentucky universities since the time of Rafinesque. In 1975, James B. Sickel established a research program at Murray State University that continued until his retirement in 2005. Sickel’s research was focused on the Tennessee and lower Cumberland rivers and provided important information on these poorly sampled areas including long-term changes in mussel assemblages (e.g., Pharris et al. 1984; Sickel 1985; Blalock and Sickel 1996). In 1979, Guenter A. Schuster established a mussel research program at Eastern Kentucky University that continued until his retirement in 2009. Schuster and his students conducted intensive mussel surveys in streams throughout much of central and eastern Kentucky (e.g., Schuster et al. 1989; Smathers 1990; McMurray et al. 1999; Akers 2000), including a reassessment of the Ohio River mussel fauna (Williams and Schuster 1989). He produced the first synthesis of mussel distributions in Kentucky (Schuster 1988) and coauthored the first comprehensive checklist of Kentucky mussels (Cicerello et al. 1991) and a photographic guide to mussels of the state (Cicerello and Schuster 2003). During his career, Schuster trained a large number of graduate and undergraduate students, many of whom went on to conduct additional studies of Kentucky mussels. During this same period, James B. Layzer led a research program at Tennessee Technological University beginning in 1987 that conducted extensive mussel studies in the Cumberland, Green, and Licking river drainages (e.g., Anderson et al. 1991; Cochran and Layzer 1993; Houslet and Layzer 1997).

Since the 1980s, mussel studies in Kentucky have continued to expand along with the increased awareness of the conservation plight of these animals. Mussel research has been conducted at most major universities in the state, and several now have active mussel research programs. Federal agencies such as the U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, Tennessee Valley Authority, and the National Park Service continue to be actively engaged in mussel conservation in Kentucky. Notably, the U.S. Fish and Wildlife Service established a Kentucky field office in 2001 in part due to the large number of endangered mussel species in the state. In addition to the KNP, state agencies such as the Kentucky Division of Water and Kentucky Department of Fish and Wildlife Resources have directed increasing focus on mussel conservation.
In 2002, the Kentucky Department of Fish and Wildlife Resources hired a full-time mussel biologist and established the Center for Mollusk Conservation (CMC) in Frankfort. The mission of the CMC is to restore and recover rare and imperiled mussels in Kentucky. Monte McGregor, State Mussel Biologist and Director of the CMC, and his staff have developed, refined, and in some cases, perfected, many methods for the culture and propagation of mussels in a hatchery environment. These methods allow production of large numbers of mussels, which can be used to restore the mussel fauna of depleted streams. In addition to their production efforts, the CMC has conducted mussel surveys across the state.

Interest in mussels has broadened beyond universities and government agencies to include private conservation organizations and other groups. The Nature Conservancy, the Kentucky Waterways Alliance, and the World Wildlife Fund all have been involved in mussel conservation initiatives in the state. Private environmental consulting firms also frequently conduct mussel surveys across the state mainly related to the Endangered Species Act; their efforts have contributed substantially to our knowledge of mussel distributions in Kentucky.

Because of the great proliferation of mussel studies in Kentucky since the 1980s, we will not attempt to list all of the individuals involved in this work or discuss their considerable contributions. However, many of these people and their work are referenced elsewhere in this book, particularly in the species accounts.

In addition to historical and contemporary mussel surveys, considerable study has been conducted of mussel shells found at archaeological sites in Kentucky. These studies focused mainly on large rivers, and they provide fascinating glimpses of the fauna of these streams over the past 10,000 years (e.g., Call and Robinson 1983; Casey 1987; Morey and Crothers 1998; see sections IV.B and IV.C.2).

IV.B. The state of our knowledge

As a result of the extensive mussel surveys and research conducted in Kentucky over the last 200 years, we have a reasonably good understanding of past and present mussel distributions throughout the state. Prior to 1970, about 328 sites in the state were surveyed for mussels (Figure 4). These surveys generally focused on larger streams, but they span most regions and drainages in Kentucky with the notable exception of the Mississippi Embayment. From 1970 to 1989, about 588 sites in the state were surveyed for mussels. A large percentage of surveys during this time period were conducted by the Kentucky State Nature Preserves Commission; these and other efforts filled in many gaps in our knowledge, particularly regarding the fauna of the Mississippi Embayment and smaller streams in the state. Surveys conducted from 1990 to 2015 were conducted by a broad array of people at about 842 sites, and combined with previous surveys they provide a relatively comprehensive database on Kentucky’s mussel fauna. All major drainages in the state have been surveyed to some extent, and many rivers have been surveyed multiple times (e.g., Licking, Green, Rockcastle).

Despite the considerable information available on Kentucky’s mussel fauna, many gaps remain in our understanding of past and present mussel distributions. Few collections were made in large rivers prior to their impoundment. Nearly all surveys in the Kentucky and lower Green rivers were conducted in the 1960s or later. These rivers were impounded for navigation as early as the 1830s, and, hence, we know virtually nothing about their original mussel fauna. The only information available for these streams prior to impoundment is a few vague records from unspecified localities by Rafinesque (1820a) and archaeological records of shells collected by prehistoric people (see subsequent). Similarly, most historical information for the Ohio River is
from surveys conducted in the 1960s, well after the river’s impoundment was completed in 1929. Information prior to this time is limited mainly to records from the vicinity of Cincinnati, unspecified localities from Call (1900), or archaeological sites. Considering all data sources, we
have a good estimate of historical species richness in the Ohio River as a whole (the river appears to have supported nearly all species of the Ohioan faunal region; see section V.B), but comprehensive information on the original fauna in specific sections or sites is largely absent. An exception is the Cumberland River, which was surveyed systematically in 1910–1911 and again in 1947–1949, shortly before its impoundment in 1950 (Wilson and Clark 1914; Neel and Allen 1964); these studies, along with other scattered records, provide invaluable information about the remarkable historical fauna of this river. Other streams have little historical information of any kind regardless of impoundment history. There are only a handful of pre-1960 records from the Licking and Big Sandy river drainages and virtually none from the Mississippi Embayment or smaller streams throughout the state.

Even in the absence of historical data, reconstructing the original mussel fauna of a stream can be aided by examining relic shells. Relic shells represent mussels that died at some time in the past. They are heavily weathered and often chalky and are easily distinguished from recently dead shells, which have lustrous mother-of-pearl in the interior of the shell and represent mussels that died within the last year or so. Recently dead shells provide evidence for the continued occurrence of a species in a stream but relic shells do not. In streams with well-buffered water (e.g., most of the Interior Low Plateaus province), relic shells may persist for decades after death of the animal. Even today, the Cumberland River downstream of Wolf Creek Dam yields relic shells representing individuals that lived in the river prior to dam construction 65 years ago, and these records augment historical surveys of the river. In streams from which mussels are now eliminated but were never surveyed historically, relic shells may be the only information about the stream’s original fauna. Similarly, relic shells can attest to the former abundance of species that are now rare or nearly extinct (e.g., *Pleurobema clava*). Relic shells erode quickly in streams with poorly buffered water (e.g., Appalachian Plateaus and Mississippi Embayment provinces), and this is a major factor in our limited knowledge of the historical fauna of poorly surveyed drainages such as the Big Sandy River. In addition, fragile, thin-shelled species (e.g., *Hemistena lata, Leptodea leptodon*) are poorly represented in relic shell assemblages even in well-buffered regions. Piles of discarded shells from former button factories from the early 1900s exist at several sites along the Ohio River, and these also provide information about historical assemblages. However, these records must be interpreted with caution because shells often were transported great distances by barge to button factories (Coker et al. 1919; see *Dromus dromas*).

Shells found in archeological excavations of prehistoric human habitation sites along rivers are another important resource for reconstructing the original fauna of a stream. These shells mainly represent mussels harvested for food 500–2,000 years ago. They were deposited over hundreds of years at some sites, resulting in huge shell middens containing millions of individuals (e.g., Morey and Crothers 1998; Haag 2009). Judging by the species composition in these middens, prehistoric people appear to have harvested mussels predominantly from main-channel mussel beds, where mussel densities usually are highest. Consequently, species characteristic of backwater and pool habitats usually are absent or underrepresented, and, similar to relic shell assemblages, species with thin, fragile shells are underrepresented probably due to poor preservation or destruction during excavation (see Haag 2009 and sources therein). Nevertheless, mussel assemblages from archeological sites are tremendously informative for two reasons. First, due to the sheer number of shells present in many of these middens, it is highly likely that they originated from the river immediately adjacent to the site (but see section
IV.C.2). This supposition is supported by the fact that, apart from the apparent sources of bias described previously, midden assemblages bear remarkable similarity to historical collections from the same rivers in most cases (Haag 2009). Second, because middens are the result of intensive collection over many years, they probably represent a large proportion of the species richness present in main-channel habitats at the site, and they also provide information about species relative abundance and assemblage composition in those habitats. Similar to relic shells, archeological records are the primary source of information about the original mussel fauna of several streams that were poorly surveyed historically (e.g., lower Green River). Information from prehistoric mussel assemblages is available for 34 sites in the state, including many of the state’s major drainages (Figure 5).

Information from 1970 to the present provides a relatively comprehensive picture of mussel distributions statewide in recent times. Two notable exceptions are the mainstem Kentucky River and the lower Salt River system. The Kentucky River remains poorly surveyed, and the mussel fauna of the lower Salt and Rolling Fork rivers is virtually unknown because these rivers flow through the Fort Knox military reservation and access to biologists is restricted due to the potential presence of unexploded ordnance in the stream beds. Otherwise, the main information gaps today regard species abundance and population demographics. The vast majority of mussel surveys report only species presence/absence or, at best, estimates of relative abundance, and quantitative estimates of absolute abundance exist for only a handful of sites in the state. Even fewer data are available about population size or age structure. These types of data are difficult and time-consuming to obtain, but they are necessary to accurately monitor and depict long-term trends in mussel populations. For example, in streams that have lost most of their mussel fauna, a few individuals of a particular species may survive even though its abundance has declined dramatically and the population may be nearing extinction. In other cases, a relatively large population may remain in a stream, but nearly all individuals are large and old, and the lack of recent recruitment portends a dramatic population decline in the near future as remaining individuals reach the end of their life span. In both of these examples, the severity of recent or future declines is not well represented by presence/absence data.

Figure 5. Location of archeological sites in Kentucky providing mussel distribution records.

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Taken as a whole, existing information about mussel distributions in Kentucky permits many strong conclusions about the nature and current state of the fauna despite these information gaps. Overall diversity statewide and in each river drainage is well documented, and in conjunction with distributional information from elsewhere in North America, these patterns provide inference about biogeographical factors that have shaped the mussel fauna of Kentucky. Furthermore, mussel declines have been so dramatic in many streams that they are evident even from patterns of species presence or absence over time.

IV.C. Sources of distributional data

IV.C.1. Historical and recent data

We compiled all available historical and recent data on mussel distributions in Kentucky through 2015. These data include published primary literature; government agency reports and other unpublished, gray literature sources; theses and dissertations; and collection reports from consulting firms. All of these sources are listed in the Appendix. We also retrieved all Kentucky distributional records represented by voucher specimens deposited in the following institutional or private collections: Academy of Natural Sciences of Drexel University (ANSDU; formerly Academy of Natural Sciences of Philadelphia); Carnegie Museum (CM); Cincinnati Museum of Natural History (CMNH); Copperhead Consulting, Paint Lick, KY; Daniel Boone National Forest (DBNF); East Kentucky Power (EKP); Eastern Kentucky University (EKU); Field Museum of Natural History (FMNH); Illinois Natural History Survey (INHS); Kentucky Division of Water (KDOW); Museum of Comparative Zoology, Harvard University (MCZ); Marshall University (MU); Murray State University (MSU); North Carolina Museum of Natural Science (NCMNS; including the Herbert D. Athearn collection); U.S. National Museum of Natural History, Smithsonian Institution (NMNH); The Ohio State University Museum of Biological Diversity (OSUM); Tennessee Technological University (TTU); University of Florida, Florida Museum of Natural History (UF); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ).

A major source for distributional records was the Kentucky Natural Heritage Program database maintained by the Kentucky State Nature Preserves Commission (KNP). This database includes most distributional records from the sources described above that pertain to 34 rare species monitored by KNP (KNP 2012). The database also includes collection records for all mussel species from extensive surveys conducted by KNP staff since its inception in 1976. Most voucher specimens collected by KNP are deposited at EKU, INHS, or OSUM.

We vetted records from museum collections by visiting those institutions and examining most specimens, or, in some cases, we relied on information from experts at those institutions. We also assessed the potential validity of unusual literature records not supported by museum voucher specimens. We paid particular attention to species with restricted distributions, unusual records beyond the normal range of a species, and species that are frequently misidentified. We categorized unusual records as follows. We considered a record that was not supported by museum voucher specimens unsubstantiated if it was plausible based on the general distribution of a species but would represent a substantial range extension, an unusual occurrence in a particular habitat type, or could represent misidentification of another similar species verifiably reported from the site. We considered a record doubtful if it was far beyond the known range of a species, represented a highly unlikely or otherwise unknown occurrence in a particular habitat type, or represented a species that is frequent-
ly misidentified. We considered a record *erroneous* if examination of voucher specimens confirmed the record was based on a misidentification or if other evidence suggested that the specimen was accompanied by inaccurate locality information or the record was otherwise in error. Records deemed to fall into any of these three categories are not plotted on distribution maps, but all are discussed in the species accounts. In some cases, a record was highly unusual or subject to doubt but we had no strong reason to discount it; for example, several of these records were supported by voucher specimens. We plotted these records but considered them *questionable*, and we discuss all of these records in the species accounts.

**IV.C.2. Archaeological data**

We compiled archeological records of prehistoric mussel distributions in Kentucky from published primary literature and unpublished sources as described in section IV.C.1. We also retrieved all archaeological records based on specimens deposited in the museum collections listed in section IV.C.1, but we did not visit museum collections that contain archeological material only; shell material in these collections often is unsorted and difficult to access. For similar reasons, we did not attempt to verify archeological records other than those represented by voucher specimens in the museums we visited.

In most cases, mussel assemblages from archeological sites are remarkably similar to historical collections from the same stream or to assemblages that would be expected in a stream based on present-day biogeographical patterns and the type of habitat present at the site (see section IV.B). In a few cases, archeological data indicate that certain species had substantially larger ranges than in historical times (e.g., *Dromus dromas* and *Epioblasma arcaeformis* in the lower Tennessee and Cumberland rivers), but the remainder of the fauna reported from these sites is congruent with historical or expected assemblage composition (e.g., Casey 1986, 1987). In Kentucky, there are only two archeological sites from which mussel species composition differs so radically from expectations that these sites warrant discussion and special consideration.

Shell middens from Wickliffe Mounds on the Mississippi River, Ballard County, contained a diverse mussel assemblage including many upland species characteristic of large rivers such as the Ohio, Tennessee, and Cumberland, and otherwise unknown from the lower Mississippi River (Wesler 2001). This assemblage is in stark contrast to the depauperate, mostly lowland fauna that currently inhabits the lower Mississippi River in Kentucky and elsewhere (see sections III.A and V.A). There are at least two possible explanations for the unexpected fauna found at Wickliffe. First, the Wickliffe site is less than 5 kilometers (3.1 miles) downstream of the mouth of the Ohio River, raising the possibility that mussels were transported from the lower Ohio River. Despite this proximity, the large number of shells present at the site (2350 specimens recovered) makes this explanation unlikely. The second and more likely explanation is that the Ohio River formerly may have entered the Mississippi River at a point downstream of its present confluence. The lower Mississippi River is highly dynamic, and, prior to levee construction, its course changed frequently. Brewer Lake is a large oxbow in Missouri adjacent the Mississippi River and opposite Wickliffe Mounds, and its southern terminus is about 6 kilometers (3.7 miles) downstream of Wickliffe (11 kilometers or 7 miles downstream of the present mouth of the Ohio River). Brewer Lake likely represents the former course of the Mississippi River at some time in the past. If so, Wickliffe Mounds would have been located on the lower Ohio River at that time, which would explain the presence of a mussel fauna that is similar in most respects to the fauna of the lower Ohio River in historical
and current times. We cannot confirm this hypothesis, and we have plotted all records from the Wickliffe site. However, readers should be aware that the species composition at Wickliffe Mounds strongly suggests that habitat conditions at the site in prehistory were very different than at any time in the recent past. For this reason, we do not include records from the Wickliffe site in our analysis of distributional patterns related to diversity, biogeography, and conservation status (sections V and VI).

The other exception is Watt’s Cave near the West Fork of the Red River, Todd County. Excavations in this cave revealed a diverse mussel assemblage including many obligate large river species (OSUM), but the West Fork is a small stream that likely supported only a limited headwater fauna, similar to its fauna today. The Cumberland River, near Clarksville, Tennessee, is about 22 kilometers (14 miles) south of Watt’s Cave. The close resemblance of the Watt’s Cave assemblage to prehistoric and historical assemblages in the mainstem Cumberland River suggests that this was the source for shell material found in the cave. Unlike the Wickliffe Mounds site, Watt’s Cave yielded only 35 shells, which makes transport a plausible explanation. Also unlike Wickliffe, there are no apparent alternative explanations that could account for the presence of so many species in a habitat type that is so incongruent with the habitat occupied by these species in recent times. For example, the narrow valley of the West Fork Red River shows no evidence of having carried a much larger stream in recent geological time (Kentucky Geological Survey 2016). For these reasons, we have not plotted or included in subsequent analyses species records from Watt’s Cave, but we discuss all of these records in the pertinent species accounts.

**IV.D. Problematic species and taxonomic issues**

For the majority of mussel species reported from Kentucky, their occurrence in the state is well documented based on vouchered museum specimens or substantiated literature records. However, the occurrence of several species reported from the state is less certain and open to question for various reasons. In the following sections, we discuss these problematic species whose occurrence or distribution in the state cannot be confirmed or for which previous reports are in error. We also discuss other taxonomic issues that have bearing on an accounting of the mussel fauna of the state.

**IV.D.1. Erroneous records**

The following five species are reported from Kentucky but we concluded that they cannot be reasonably considered members of the state’s mussel fauna. We exclude these species from our account of the state’s fauna either because previous reports were shown to be erroneous or because the occurrence of a species in the state is poorly documented or unlikely.

*Epioblasma obliquata perobliqua* (Conrad, 1836), White Catspaw.—*Epioblasma obliquata perobliqua* occurs mainly in tributaries of western Lake Erie, but a few historical records exist for northern tributaries of the Ohio River (Watters et al. 2009). The relationship of this taxon to *E. obliquata obliquata* is unknown. The only Kentucky record of *E. obliquata perobliqua* is a single specimen from the Ohio River, Union County (single valves of the same individual deposited at OSUM and UMMZ; see Cicerello and Schuster 2003); the specimen is undated, but it was probably collected in the 1800s. Hoggarth (1990) considered the locality for this specimen likely to be in error. We concur and consider this record erroneous.
**Glebula rotundata** (Lamarck, 1819), Round Pearlshell.—*Glebula rotundata* is widely distributed in Gulf Coast rivers from the Ocklockonee River, Florida, west to the Guadalupe River, Texas. This species is tolerant of brackish water and is most common in the lower reaches of coastal rivers (Williams et al. 2008). It occurs farther inland north to at least central Mississippi (Miller et al. 1992), but it is not reported from the Mississippi Embayment in Tennessee (Parmalee and Bogan 1998). The only Kentucky record of *Glebula rotundata* is a single, undated specimen from the Ohio River at Louisville, Jefferson County (OSUM). It is possible that this individual was a waif from populations to the south, but the distance to the nearest known population makes this unlikely. We regard this record as erroneous and suspect that the locality information for the specimen is in error.

**Lasmigona subviridis** (Conrad, 1835), Green Floater.—*Lasmigona subviridis* is primarily a species of the Atlantic Coast from the Hudson River drainage south to North Carolina, but disjunct populations are reported from the upper Kanawha River drainage, West Virginia, Virginia, and North Carolina; the Watauga River, Tennessee; and the Chattahoochee River, Alabama and Georgia (Parmalee and Bogan 1998; Williams et al. 2008). The only Kentucky record is a single individual collected from the Ohio River at Louisville, Jefferson County (OSUM). It is possible that this individual was a waif from populations to the south, but the distance to the nearest known population makes this unlikely. We regard this record as erroneous and suspect that the locality information for the specimen is in error.

**Quadrula sparsa** (Lea, 1841), Appalachian Monkeyface.—*Quadrula sparsa* is endemic to the Tennessee-Cumberland faunal province but it is generally considered to be restricted to the upper Tennessee River drainage in Tennessee and Virginia. Records of this species from the Cumberland River drainage are due to a confused taxonomic history in which the species has been placed variously within the synonymy of *Q. intermedia*, *Q. metanevra*, or *Q. tuberosa* (see discussion of *Q. tuberosa* in section IV.D.2 and Parmalee and Bogan 1998). There are at least three records of *Q. sparsa* from Kentucky, all from the mainstem Cumberland River. A specimen from Burnside, Pulaski County (UMMZ), was originally labelled “*Q. sparsa*” but later identified by David Stansbery as *Q. tuberosa*. Another specimen from Burnside (UIMNH) is labelled “*Q. tuberosa sparsa*”. Ortmann (1912) reported a record from Burnside (which may represent one of the previous specimens) and a record from Cumberland County, and he surmised that these records represented *Q. tuberosa*. We consider all of these records to represent *Q. tuberosa* (if a valid species) or *Q. metanevra*.

**Venustaconcha ellipsiformis** (Conrad, 1836), Ellipse.—*Venustaconcha ellipsiformis* is widely distributed in the upper Mississippi River drainage from Missouri north to Minnesota, west to Kansas, and east to Indiana; it is also widely distributed in tributaries of Lake Michigan (Cummings and Mayer 1992; Oesch 1995). The only substantiated records from the Ohio River basin are from the Wabash River drainage in Illinois (Cummings and Mayer 1997), but two historical records exist from the Ohio River. First, Call (1900) reports *V. ellipsiformis* (as *Unio spatulatus*) as common in the Ohio River adjacent Indiana. Second, the type localities of *Unio venusta* (Lea 1838), a synonym of *V. ellipsiformis*, are “Potosi, Missouri” and Cincinnati, Ohio” (see Watters et al. 2009). There are no other records of this species from the Ohio River or Kentucky, and we regard both records as erroneous. With regard to Call’s record, no specimens exist to support this occurrence, and it is unlikely that a common species in the Ohio River would have been undetected in the last 200 years and absent from archaeological samples. With regard to Lea’s record, we suspect that the locality infor-
mation for the specimen is in error (see Watters et al. 2009).

IV.D.2. Species of uncertain taxonomic status

The following mussel species are reported from Kentucky or potentially occur in the state, but taxonomic uncertainty precludes an assessment of their distribution at this time.

*Lampsilis hydiana* (Lea, 1838), Louisiana Fatmucket.—*Lampsilis hydiana* is widely reported in the lower Mississippi River basin in Louisiana, Mississippi, Arkansas, and Oklahoma, and in Gulf Coast rivers from the Mermentau River, Louisiana, west to the San Antonio River, Texas (Vidrine 1993; Howells et al. 1996). This species is genetically distinct from *L. siliquoidea* (Turner et al. 2000), but the two species are difficult to separate reliably based on shell morphology alone, and *L. hydiana* appears to represent a complex of several species (Harris et al. 2009). Consequently, the distribution of these taxa in the lower Mississippi River basin and elsewhere is unclear. *Lampsilis hydiana* is not reported from Tennessee (Parmalee and Bogan 1998), but it occurs in northeastern Arkansas and southeastern Missouri less than 80 kilometers (50 miles) from the Kentucky border and in southern and central Illinois (Harris et al. 2009; A. Stodola and K. Cummings, personal communication). This suggests that at least one taxon within the *L. hydiana* complex is more widely distributed than previously thought, particularly within the Mississippi Embayment. Individuals resembling *L. hydiana* are reported from Kentucky in Obion Creek, Hickman County (KDOw, KNP), and it is of potential occurrence elsewhere in the lowlands of western Kentucky. Confirming the presence and determination of the distribution of *L. hydiana* in Kentucky will require examination of genetic variation in populations currently regarded as *Lampsilis siliquoidea*.

*Quadrula apiculata* (Say, 1829), Southern Mapleleaf; and *Q. nobilis* (Conrad, 1853), Gulf Mapleleaf.—*Quadrula apiculata* and *Q. nobilis* are reported from Gulf Coast rivers from the Mobile Basin west to Texas, and in the lower Mississippi River basin primarily within the Mississippi Embayment (Williams et al. 2008). These taxa are closely related to *Q. quadrula* and *Q. rumphiana* of the Mobile Basin, but phylogenetic relationships within this group are unresolved and the species are difficult to separate reliably based on shell morphology. *Quadrula nobilis* appears to be a distinct species, but *Q. apiculata* and *Q. quadrula* were not resolved as monophyletic (Serb et al. 2003). Both *Q. apiculata* and *Q. nobilis* are reported from large streams in western Kentucky (e.g., Mississippi, lower Ohio, and Tennessee rivers; Parmalee and Bogan 1998; Cicerello and Schuster 2003), but the identity of most specimens has not been confirmed. Serb et al. (2003) included in their study three Kentucky specimens of putative *Q. quadrula*, but the specimens appeared at three different locations on their phylogenetic trees. A specimen from the Ohio River, Henderson County, was sister to *Q. nobilis* from the Neches River, Texas, and the Pascagoula River, Mississippi; a specimen from the Red River, Powell County, was sister to *Q. rumphiana* from the Mobile Basin; and the affinity of a specimen from the Ohio River adjacent Vanderburgh County, Indiana, was not resolved. These results support the occurrence of *Q. nobilis* in Kentucky, but overall they show that relationships within the *Q. quadrula* group are complex and in need of further study. Parmalee and Bogan (1998) and Williams et al. (2008) speculated that *Q. apiculata* and possibly *Q. nobilis* were introduced from the Mobile Basin into the Tennessee River by commercial shellers in the 1980s. The identity and origin of Tennessee River specimens has not been confirmed, but specimens resembling *Q. apiculata* and *Q. nobilis* were collected from the lower Ohio and Tennessee rivers in the early
1900s (NMNH, INHS). Because of the uncertainty that exists within the *Q. quadrula* group, the identity and distribution of these taxa cannot be specified with confidence at this time and we treat all Kentucky records of this group as *Q. quadrula*.

*Quadrula tuberosa* (Lea, 1840), Rough Rock-shell.—*Quadrula tuberosa* is considered endemic to the Tennessee-Cumberland faunal province and is reported from both the Tennessee and Cumberland river drainages, where it was restricted to large streams. Many authors have not recognized *Q. tuberosa* as a distinct species, but they differ in how the synonymy of this species is assigned. Ortmann (1918, 1925) considered *Q. tuberosa* a large stream variant of *Q. intermedia*, which is restricted to the Tennessee River drainage. Most recent sources treat *Q. tuberosa* as a synonym of *Q. metanevra* (Parmalee and Bogan 1998; Williams et al. 2008). This raises the possibility that *Q. tuberosa* included more than one taxon, one of which may have been endemic to the Cumberland River drainage. *Quadrula tuberosa* was included in the mussel fauna of Kentucky by Cicerello and Schuster (2003). It is reported historically from several localities in the middle Cumberland River from Burnside, Pulaski County, downstream to Cumberland County, and the lower Big South Fork (Wilson and Clark 1914; UMMZ; UIMNH); it is also reported from the Cumberland River drainage in Tennessee (Parmalee and Bogan 1998). The taxonomic status of *Q. tuberosa* may remain unknown because, if it is a valid taxon, impoundment of the Cumberland River has destroyed most habitat for the species, and it is generally considered extinct. However, unusual specimens of *Q. metanevra* resembling *Q. tuberosa* are still encountered rarely in a short reach of the middle Cumberland River in Tennessee (D. Hubbs, personal communication), which provides hope for resolution of this issue.

### IV.D.3. Cryptic species

The use of DNA sequence data has greatly improved our understanding of mussel phylogenetics and taxonomy at all levels. At the species level, DNA data have revealed several cryptic species that were not recognized previously based on examination of shell morphology or other characters (e.g., Turner et al. 2000; Jones et al. 2006; Serb 2006). Fine-scale examination of genetic diversity and other traits in mussels necessary to uncover cryptic species has only begun, and most currently recognized species have not been studied in this manner. The potential for cryptic taxa exists in many species but is most likely within small stream species that are rare or absent in large rivers. This is because species restricted to small streams are expected to show a higher degree of isolation and genetic divergence over time than species that occur throughout a drainage basin, including in large streams that serve as dispersal corridors. For example, the Orangethroat Darter (*Etheostoma spectabile*) is a small-stream fish with limited dispersal capability that formerly was considered a single, widely distributed species. DNA data show that this taxon is made up of more than seven distinct species, some with highly restricted ranges (Ceas and Page 1997). Similar patterns are likely to be found in small-stream mussel species. “*Villosa* iris” represents a complex of species, but the full extent of this variation and its geographical distribution are not yet known (Kuehnl 2009). Cryptic species are particularly likely in the Cumberland River drainage. Several small-stream mussel species endemic to the Tennessee-Cumberland faunal province are currently thought to occur in both the Tennessee and Cumberland river drainages (e.g., *Medionidus conradicus*, *Pleurobema ovi-forme*, *Ptychobranchus subtentum*, “*Villosa* taeniata”), but populations in each of these river drainages have been isolated from each other for millennia. In most cases, small-stream fishes for-
merely thought to occur in both the Tennessee and Cumberland river drainages have been shown to represent distinct species in each drainage (e.g., Kinziger et al. 2001; Powers et al. 2004; Blanton and Jenkins 2008), and similar patterns are supported for mussels (Epioblasma florentina walker, Venustaconcha troostensis, “Villosa” vanuxemensis; Kuehnl 2009; Jones and Neves 2010; Lane et al. in press). A better understanding of fine-scale genetic variation in mussels surely will increase considerably the number of species in Kentucky. Many of these cryptic species will be highly imperiled due to their restricted distribution (e.g., see “Villosa” vanuxemensis), and it is likely that several cryptic species already have been lost before their phylogenetic status could be studied.

IV.D.4. Higher-level classification

Modern genetic methods also have improved our understanding of mussel phylogenetics at the genus level. These refinements to earlier classification schemes do not have direct bearing on our estimate of species diversity in Kentucky, but they will increase the number of genera occurring in the state and provide a more accurate depiction of relationships among species. Recent research has clarified the generic status and phylogenetic position of Reginaia ebena (formerly Fusconaia ebena; Campbell and Lydeard 2012) and Pleuronaia dolabelloides (formerly Lexingtonia dolabelloides; Campbell et al. 2005; Williams et al. 2008) and has revealed other inaccuracies in traditional taxonomy. Many mussel genera in Kentucky, as currently depicted, are polyphyletic and include multiple evolutionary lineages; these include Actinonaias, Elliptio, Lampsilis, Pleurobema, and Villosa (Campbell et al. 2005). In addition, Obovaria olivaria appears not closely related to other Obovaria. Numerous new genera will need to be newly named or resurrected from synonymy to more accurately reflect these phylogenetic relationships. In most cases, these relationships remain incompletely understood and new genus names have not been proposed. Consequently, we follow traditional usage of genus names in this book with the exception of Villosa.

The genus Villosa as traditionally depicted contains at least seven species in Kentucky and about 18 species in North America. A comprehensive examination of genetic variation in this genus showed that it is polyphyletic and that members of Villosa (sensu lato) are found within eight major, often unrelated, lineages (Kuehnl 2009). The type species for the genus is Villosa villosa, which is restricted to Florida and adjacent states, and the only close relatives of V. villosa also are restricted to Gulf and southern Atlantic Slope drainages. Consequently, the name Villosa is not applicable to any species in Kentucky, but new generic names for this group have not yet been assigned in most cases. We refer to these species as “Villosa” to indicate the phylogenetically inaccurate use of this name. The only “Villosa” in Kentucky that has an available generic name at this time is “Villosa” troostensis (formerly “V.” trabalis), which is part of a monophyletic clade including Venustaconcha ellipsiformis and Ve. pleasii of the midwestern U.S. and Ozark Mountains, respectively (Kuehnl 2009). Based on this finding, we refer to that species as Venustaconcha troostensis.

IV.E. Hypothetical species

The occurrence of the following species in Kentucky is hypothetical based on their occurrence in adjacent states in habitats similar to those found in Kentucky. However, no available evidence supports their occurrence in the state.

Epioblasma lenior (Lea, 1842), Narrow Catspaw.—Epioblasma lenior is endemic to the Tennessee-Cumberland faunal province. It was widespread in the Tennessee River drainage in Alabama, Tennessee, and Virginia, but it is re-
ported in the Cumberland River drainage only from the Stones River, Tennessee (Parmalee and Bogan 1998; Williams et al. 2008). Its absence elsewhere in the Cumberland River drainage, including in Kentucky, is unexplained, but this is a small species that could have been overlooked. The Stones River supported the last known population on Earth, but this population was destroyed by construction of J. Percy Priest Dam in 1967 and the species is considered extinct (Haag 2012).

_Epioblasma turgidula_ (Lea, 1858), Turgid Blossom._—_Epioblasma turgidula_ may have been endemic to the Tennessee-Cumberland faunal province. It was widespread in the Tennessee River drainage in Alabama and Tennessee, but a disjunct population or a related species also occurred in Arkansas and Missouri (Parmalee and Bogan 1998; Williams et al. 2008; Harris et al. 2009). Only two museum specimens exist from the Cumberland River drainage, including the holotype for the original species description (USNM) and a specimen in the British Museum of Natural History; both are labelled “Cumberland River, Tennessee” (R.I. Johnson 1978). Parmalee and Bogan (1998) depict an additional record from the Cumberland River, Smith County, Tennessee, but the provenance of the latter record is not stated. Based on these records, it is possible that the species occurred in the Kentucky portion of the Cumberland River at one time. Alternatively, the paucity and vague nature of historical records from the Cumberland River suggests that the species was restricted to the Tennessee River drainage (see also _Epioblasma biemarginata_). The last known population of this species was in the Duck River, Tennessee, but this population was destroyed by construction of Normal Dam in 1976 (Haag 2012).

_Uniomerus declivis_ (Say, 1831), Tapered Pondhorn._—_Uniomerus declivis_ is a characteristic but uncommon species of lowland rivers in the Mississippi Embayment, and it also occurs in Gulf Coast rivers from the Mobile Basin west to southern Texas and possibly Mexico (Morrison 1976). This species occurs primarily in larger streams and is replaced in smaller streams by _U. tetralasmus_. However, the relationship between these two species is unknown and they are often synonymized under _U. tetralasmus_. The nearest reported populations of _U. declivis_ to Kentucky are in the Hatchie River, Tennessee, and northeastern Arkansas (Parmalee and Bogan 1998; Harris et al. 2009); the latter populations are about 80 kilometers (50 miles) from the Kentucky border. This species potentially occurs in Kentucky in the lower reaches of Obion and Mayfield creeks and Bayou du Chien in the Mississippi Embayment, and suitable habitat may exist in larger, lowland streams elsewhere in western Kentucky.
V. The mussel fauna of Kentucky: diversity and biogeography

Based on current taxonomic concepts and our accounting of the state’s fauna as described in section IV, Kentucky has 98 recognized native mussel species in 41 genera, plus two species that are each represented by two subspecies (Epioblasma florentina florentina and E. f. walkeri; E. torulosa torulosa and E. t. rangiana; Table 1). As discussed previously, the number of species and genera in the state will increase as better phylogenetic information becomes available. Our total of 100 species and subspecies differs from previous treatments of the Kentucky mussel fauna, which report up to 104 species and subspecies (e.g., Cicerello et al. 1991; Williams et al. 1993; Cicerello and Schuster 2003). These differences result from the inclusion in other treatments of records we conclude are erroneous (Epioblasma obliquata perobliqua, Glebula rotundata, Lasmigona subviridis) or species whose taxonomic validity or presence in the state cannot be confirmed at this time (Quadrula apiculata, Q. nobilis, Q. tuberosa).

All native mussel species in Kentucky are in the order Unionoida, and all are in the family Unionidae except Cumberlandia monodonta, which is in the family Margaritiferidae. In addition to unionid mussels, Kentucky has several native species of fingernail clams (order Veneroida, family Sphaeriidae) and at least three introduced species, all in the order Veneroida: the Asian Clam (Corbicula fluminea, family Corbiculidae) and the Zebra Mussel and Quagga Mussel (Dreissena polymorpha and D. rostriformis bugensis, family Dreissenidae; see section VI.B.4).

This total of 100 confirmed native mussel taxa is the fourth highest in the United States, exceeded only by Alabama (187), Tennessee (137), and Georgia (126; J. Williams, unpublished data). The higher mussel diversity of these states is explained largely by the fact that, states contain portions of Atlantic Coast or other Gulf Coast river systems (e.g., Mobile and Apalachicola river systems). These river systems have distinct evolutionary histories and harbor many mussel species not found in the Mississippi River basin (Haag 2012). For example, the Apalachicola River system of Alabama and Georgia shares only 11 of its 37 species with the Mississippi River basin. In contrast, the entirety of Kentucky is drained by the Mississippi River basin, and, as a consequence, the mussel fauna is more homogeneous than in those states.

The higher mussel diversity of Kentucky compared with most other states is explained by several factors. First, in part because of its large size, the Mississippi River basin harbors many more mussel and fish species than smaller river systems (e.g., Robison 1986). For example, states such as North and South Carolina, which are drained mainly by smaller Atlantic Coast river systems, have distinctive mussel faunas composed of many endemic species, but overall species richness is much lower than in many states drained by the Mississippi River basin. Second, Kentucky has a long and relatively stable geologic history. The vast majority of the state was not glaciated during the Pleistocene epoch nor was it inundated by sea level rises during that time. Consequently, development and evolution of the mussel fauna proceeded relatively uninterrupted for millions of years. In contrast, river systems in states north of the Ohio River were obliterated during glacial maxima, and many coastal rivers were inundated by high sea levels during glacial minima. Many species may have been driven to extinction in those areas, and their present mussel and fish faunas are composed mainly of species that have managed to recolonize those areas from former glacial refugia over the last 10,000 years (e.g., Burr and Page 1986; Wiley and Mayden 1985). Third, the Cumberland River drainage in Kentucky and
Tennessee contains many endemic species not found in other states (see section V.C).

Even though Kentucky is drained entirely by the Mississippi River basin, there are considerable differences among the mussel faunas of different parts of the state. No species are found in all 17 major drainages, and only 20 (20%) are found in 14–16 drainages (Table 1; Figure 6). Fifty species occur in 8 or fewer drainages, and 22 occur in only 1–2 drainages. Accordingly, river drainages differ widely in species richness (Table 2). In general, larger drainages have more species, but several notable exceptions from this pattern are informative regarding differences in the fauna among drainages and the factors that determine species richness and composition.

Among river drainages with similar biogeographical histories and environmental conditions, watershed size typically is a strong predictor of species richness (the species-area relationship); that is, larger watersheds have more species (Haag 2012; see also Rosenzweig 1995; Matthews 1998). Across all 17 major drainages of Kentucky, watershed size is not a good predictor of mussel species richness due to several conspicuous outliers with lower than expected richness, notably, the Mississippi River mainstem, Mississippi River tributaries, Tennessee River, upper Cumberland River, and the Big Sandy River (Figure 7). The poor explanatory power of this relationship suggests that these outlier drainages have different biogeographical histories or environmental conditions or differ in other ways from other drainages in the state, resulting in differences in their mussel faunas. Indeed, patterns of faunal similarity among all 17 drainages support the distinctiveness of most of these five outlier drainages (Figure 8).

The upper Cumberland River drainage has the most anomalous mussel fauna, showing little similarity to any other drainage (Figure 8). The low diversity and unusual species composition of this drainage are due to the biogeographical barrier posed by Cumberland Falls (see section V.D). The second major dichotomy on Figure 8 illustrates the fundamental differences between the fauna of lowland and upland drainages. Lowland drainages include the Mississippi River mainstem, Mississippi River tributaries, and one Ohio River drainage, the Tradewater River. These three drainages also show considerable dissimilarity to each other, and the Mississippi River mainstem is the most distinctive of the three. Among all other Ohio River basin drainages, the major split is between the upper Ohio River basin (Kinniconick and Tygarts creeks and the Little Sandy and Big Sandy river drainages) and all other drainages from the Licking River downstream to the lower Green River (and including the mainstem Ohio River). This split is reflective in part of the small size of most upper Ohio drainages (with the exception of the Big Sandy River drainage), but it also may be due to the generally lower diversity of upper Ohio drainages (see section V.B). The next major split is between the middle Cumberland River drainage and all other middle and lower Ohio River tributaries, which reflects the large number of endemic species present in the middle Cumberland (see section V.C). Despite the presence of endemic species in the lower Cumberland River drainage, it clustered most closely with the Tennessee River, probably because the mainstems of these two rivers have very similar faunas. The fauna of these two rivers is also very similar to the Ohio River, and their distinctiveness depicted on Figure 8 may be in part an artifact of the lack of historical sampling, particularly in the Tennessee River (see section V.B). Mussel faunas of Ohio River tributaries from the Licking River to the Green River show a high degree of similarity.

The clustering of drainages depicted on Figure 8 is largely concordant with and explained by major biogeographical patterns evident in the North American mussel fauna as a whole. North America comprises four mussel faunal regions, the Mississippian, Eastern Gulf, Atlantic,
Table 1. Mussel species occurrence in the 17 major river drainages of Kentucky. Letters correspond to drainages as follows: A, Mississippi River mainstem; B, Mississippi River tributaries; C, Ohio River and minor tributaries; D, Tennessee River; E, lower Cumberland River; F, middle Cumberland River; G, upper Cumberland River; H, Tradewater River; I, lower Green River; J, upper Green River; K, Salt River; L, Kentucky River; M, Licking River; N, Kinniconick Creek; O, Tygarts Creek; P, Little Sandy River; Q, Big Sandy River. Occurrence in each drainage is based on all accepted historical, recent, and archaeological records. See species accounts for discussion of specific records.

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</table>

(continued)
Table 1. (continued)

| Drainage       | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | Σ |
| Epitoblasma florentina florentina | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma florentina walkeri | X\textsuperscript{b} | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma haysiana | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma lewisi | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma obliquata obliquata | X | X | X | X | X | X |   |   |   |   |   |   |   |   |   |   | 6 |
| Epitoblasma propinqua | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma sampsoni | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 3 |
| Epitoblasma stewardsonii | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 |
| Epitoblasma torulosa rangiana | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 6 |
| Epitoblasma torulosa torulosa | X\textsuperscript{a} | X | X | X | X | X |   |   |   |   |   |   |   |   |   |   | 5 |
| Epitoblasma triqueta | X | X | X | X | X | X | X | X | X | X | X | X |   |   |   |   | 10 |
| Fusconaia flavia | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Fusconaia subrotunda | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 9 |
| Hemistena lata | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   | 5 |
| Lampsis abrupta | X\textsuperscript{a} | X | X | X | X | X | X | X | X | X | X | X |   |   |   |   | 9 |
| Lampsis cardium | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Lampsis fasciata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 12 |
| Lampsis ovata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 10 |
| Lampsis siliquidea | X\textsuperscript{a} | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Lampsis teres | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 11 |
| Lasigmonea complanata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Lasigmonea compressa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 3 |
| Lasigmonea costata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Leptoea fragilis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Leptoea leptodon | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 4 |
| Ligumia recta | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 13 |
| Ligumia subrostrata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 6 |
| Medioneidae conradius | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   | 2 |
| Megalonaiais nervosa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| Drainage          | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | Σ  |
| Obliquaria reflexa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 11 |
| Obovaria olivaria  | X | X | X | X | X | X | X | X | 8  |
| Obovaria retusa    | X | X | X | X | X | X | X | X | 8  |
| Obovaria subrotunda| X | X | X | X | X | X | X | X | X | 12 |
| Pegias fabula     | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 2  |
| Plectomerus dombeyanus | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 3  |
| Plethobasus cicatricosus | X | X | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   | 4  |
| Plethobasus cooperianus | X | X | X | X | X | X | X | X | 6  |
| Plethobasus cyphyus | X | X | X | X | X | X | X | X | 8  |
| Pleurobema clava   | X | X | X | X | X | X | X | X | X | 9  |
| Pleurobema cordatum | X | X | X | X | X | X | X | X | X | 11 |
| Pleurobema oviforme | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 2  |
| Pleurobema pientum | X | X | X | X | X | X | X | X | 6  |
| Pleurobema rubrum  | X | X | X | X | X | X | X | X | 9  |
| Pleurobema sintonia| X | X | X | X | X | X | X | X | X | 12 |
| Pleuronaia dolabelloides | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1  |
| Potamillas alatus  | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Potamillas capax   | X | X | X | X | X | X |   |   |   |   |   |   |   |   |   |   |   | 6  |
| Potamillas ohiensis| X | X | X | X | X | X | X | X | X | X | X | X |   |   |   |   |   | 12 |
| Potamillas purpuratus | X | X | X | X | X |   |   |   |   |   |   |   |   |   |   |   |   | 4  |
| Psychobranchus fasciolaris | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 13 |
| Psychobranchus subentum | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 1 |
| Pyganodon grandis  | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Quadrula cylindrica cylindrica | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Quadrula fragosa   | X | X |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 2  |
| Quadrula metanevra | X | X | X | X | X | X | X | X | X | X |   |   |   |   |   |   |   | 9  |
| Quadrula nodulea   | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 10 |
| Quadrula pustulosa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| Quadrula quadrula  | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| Quadrula verrucosa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |

(continued)
Table 1. (continued)

| Drainage | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | Σ |
| Reginaia ebena | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 9 |
| Simpsononas ambigua | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 9 |
| Sirophitus undulatus | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 13 |
| Toxolasma lividum | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 7 |
| Toxolasma parvum | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Toxolasma texanens | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 11 |
| Truncilla donaciformis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 14 |
| Truncilla truncata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 8 |
| Uniomerus tetralsmus | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| Uiterbackia imbecillis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| Venustaconcha troostensis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* fabalis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* iris | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* lenticosa | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* ornmanni | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* taenata | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| *Villosa* vanuxemensis | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |

Drainage totals: 24 21 76 58 73 73 12 31 71 67 58 60 56 23 31 26 29

*a* species reported from an archaeological site at Wickliffe Mounds are included in the table but are not included in row or column totals (see section IV.C.2).

*b* A specimen representing either *Epioblasma capsaeformis* or *E. florentina walkeri* is reported from the lower Cumberland River drainage in the Red River, Logan County; the total for this drainage reflects inclusion of one of these taxa, but row totals do not include these taxa.

*c* *Epioblasma flexuosus* is reported from an unspecified locality in the Green River and is attributed here to both the upper and lower Green River drainage.
Figure 6. Mussel species occupancy among river drainages of Kentucky. Totals include species and subspecies. Totals do not include archaeological records from the Wickliffe Mounds site on the Mississippi River (see section IV.C.2).

Figure 7. Mussel species-area relationships among river drainages in Kentucky. Letters correspond to drainages as follows: A, Mississippi River mainstem; B, Mississippi River tributaries; C, Ohio River and minor tributaries; D, Tennessee River; E, lower Cumberland River; F, middle Cumberland River; G, upper Cumberland River; H, Tradewater River; I, lower Green River; J, upper Green River; K, Salt River; L, Kentucky River; M, Licking River; N, Kinniconick Creek; O, Tygarts Creek; P, Little Sandy River; Q, Big Sandy River. (top) Species-area relationship for all 17 major drainages. (bottom) Species-area relationship for 11 major drainages excluding A, B, C, D, G, and Q (see text). Note the difference in the x-axis scale between panels. Species richness for the Mississippi River mainstem does not include archaeological records from the Wickliffe Mounds site (see section IV.C.2).
Pacific (Figure 9). Each region is further composed of distinct faunal provinces, which represent areas containing distinctive mussel assemblages as a result of their different biogeographical or environmental histories. Kentucky lies entirely within the Mississippian region, but it contains three of the eleven faunal provinces that make up that region: the Mississippi Embayment province, the Ohioan province, and the Tennessee-Cumberland province.

**V.A. Mississippi Embayment faunal province**

The Mississippi Embayment faunal province in Kentucky overlays precisely the Mississippi Embayment physiographic province, and it includes two of the outlier drainages depicted on Figure 7: the Mississippi River mainstem and Mississippi River tributaries. This region is dominated by lowland aquatic habitats (sections III.A and III.B), and, accordingly, it supports a distinctive mussel fauna composed of numerous lowland species (e.g., *Anodonta suborbiculata*, *Ligumia subr ostrata*, *Potamilus purpuratus*, *Toxolasma texasiensis*, *Uniomerus tetralasmus*). These are characteristic species throughout the Mississippi Embayment faunal province (Haag 2012), and their presence largely is responsible for the distinctiveness of the Mississippi River and Mississippi River tributaries (Figure 8). The occurrence of these species elsewhere in the state is mostly limited to tributaries of the lower Ohio River (see section V.B), particularly the Tradewater River, which is reflected in the clustering of this drainage with Mississippi Embayment drainages (Figure 8).
The Mississippi Embayment fauna is further characterized by the absence of a large number of upland species that have not dispersed beyond the Ohio River basin (see subsequent) and other upland species that are otherwise widely distributed in the Mississippi River basin. The Mississippi Embayment physiographic province is thus important biogeographically because it acts as a barrier that has isolated upland aquatic faunas west, north, and east of the region (e.g., Robison 1986; Mayden 1988). Although the Mississippi Embayment faunal province has high mussel diversity from a global perspective (about 59 species throughout the province), species richness is lower than in other areas in part because lowland habitats may represent stressful environments that are inhospitable to many species (e.g., periodic low dissolved oxygen; see Haag 2012). Species richness is further limited in the Mississippi River mainstem by its dynamic and unstable nature (section III.A). These biogeographical and habitat factors largely explain the distinctiveness and lower than expected species richness of mussel faunas of the Mississippi River mainstem and Mississippi River tributaries.

V.B. Ohioan faunal province

Apart from those in the Mississippi Embayment, all other river drainages in Kentucky are within the Ohio River basin, and the mussel fau-
na of much of the basin represents the Ohioan faunal province. The Ohioan province encompasses the Ohio River and all of its tributaries except the upper two-thirds of the Tennessee and Cumberland river systems, which make up the Tennessee-Cumberland faunal province (Haag 2010; see section V.C). The downstream extent of the Tennessee-Cumberland province occurs in the Tennessee River approximately at Muscle Shoals, in northwestern Alabama, and in the Cumberland River in the vicinity of Clarksville, Tennessee. The entire Tennessee River drainage in Kentucky is therefore considered within the Ohioan province because in historical times it lacked endemic species characteristic of the Tennessee-Cumberland province (but see section IV.C.2). The lower Cumberland River drainage as defined here (section III.E) encompasses both the Ohioan and Tennessee-Cumberland provinces. The Red River contains a wide array of species endemic to the Tennessee-Cumberland province and is included in that faunal province. Although a few of these endemic species occur in the Little River, the fauna of the remainder of the lower Cumberland River drainage is characteristic of the Ohioan province. All other river drainages in the Ohio River basin have characteristic Ohioan mussel faunas.

The Ohioan province is the second-most diverse faunal province in North America and contains about 78 species, nearly all of which occur in Kentucky. The province shares a large proportion of its species with the Tennessee-Cumberland province, but it is distinguished from that province largely by the absence of Tennessee-Cumberland endemic species. The Ohioan province also is distinguished by the presence of several species that are absent in the Tennessee-Cumberland province (e.g., *Epiblasma sampsonii*, *E. torulosa rangiana*, *Lasmigona compressa*, *Quadrula nodulata*, “*Villosa* ortmanni”, and possibly *Pleurobema clava*). Most aquatic habitats in the province are upland in nature, but lowland habitats and several lowland species that are absent in the Tennessee-Cumberland province occur in the lower part of the Ohio River basin (see subsequent).

The mussel fauna of the Ohioan province is relatively homogeneous throughout, probably because the mainstem of the Ohio River provides a dispersal corridor throughout the basin (Haag 2012). Fish faunas among river drainages in the basin show considerably more heterogeneity. For example, the Green River contains several endemic fish species, and the fish fauna of this drainage overall differs substantially from other Ohio River tributaries (Burr and Warren 1986). These differences are related in part to the complex pre-Pleistocene history of the Ohio River basin. Notably, the Kentucky, Licking, and Big Sandy river drainages flowed north into the Teays River to ultimately join with the ancestral Mississippi River, while the Green, Cumberland, and Tennessee river flowed into the much smaller ancestral Ohio River, allowing these two regions to follow independent evolutionary trajectories for millions of years (Burr and Warren 1986). In contrast to fishes, the Green River has only one known endemic mussel species (“*Villosa* ortmanni”). Not accounting for differences in drainage size, mussel diversity generally increases somewhat in a downstream direction, with tributaries of the lower Ohio River having higher diversity than tributaries of the upper river (Table 2). This may be due to a mingling in lower Ohio River drainages of species originating in the Teays, ancestral Ohio, and Mississippi river basins, and a failure of many species to disperse farther upstream into upper Ohio River drainages. Nevertheless, all drainages from the Green to the Licking rivers show a high degree of faunal similarity (Figure 8). The potential presence of cryptic endemic species (see section IV.D.3) may increase heterogeneity among Ohioan river drainages to some extent.

The most notable differences among Ohioan river drainages in Kentucky is the increasing representation of lowland mussel species in a
Table 2. Mussel species richness (including subspecies) and watershed size for the 17 major river drainages of Kentucky. With the following exceptions, watershed size is for the entire watershed including sections in other states. Watershed area for the Mississippi River mainstem is for the watershed upstream of and including the Ohio River. Watershed area for Mississippi River tributaries is the combined area of all tributaries. Estimates of species richness are total richness including all historical, recent, and archaeological records with the exception of archaeological records from the Wickliffe Mounds site on the Mississippi River (see section IV.C.2). Drainages are ordered from greatest to least total species richness. River drainages are defined in section III.

<table>
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<th>Drainage</th>
<th>Watershed size (km²)</th>
<th>Total species richness</th>
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<tr>
<td>Ohio River and minor tributaries</td>
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<tr>
<td>Middle Cumberland River</td>
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<tr>
<td>Lower Cumberland River</td>
<td>46,430</td>
<td>73</td>
</tr>
<tr>
<td>Lower Green River</td>
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<td>13,996</td>
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<td>Salt River</td>
<td>7,560</td>
<td>58</td>
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<td>Licking River</td>
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<td>56</td>
</tr>
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<td>Tradewater River</td>
<td>2,442</td>
<td>31</td>
</tr>
<tr>
<td>Tygarts Creek</td>
<td>881</td>
<td>31</td>
</tr>
<tr>
<td>Big Sandy River</td>
<td>13,334</td>
<td>29</td>
</tr>
<tr>
<td>Little Sandy River</td>
<td>1,875</td>
<td>26</td>
</tr>
<tr>
<td>Mississippi River mainstem</td>
<td>1,018,510</td>
<td>24</td>
</tr>
<tr>
<td>Kinniconick Creek</td>
<td>655</td>
<td>23</td>
</tr>
<tr>
<td>Mississippi River tributaries</td>
<td>2,829</td>
<td>21</td>
</tr>
<tr>
<td>Upper Cumberland River</td>
<td>5,120</td>
<td>12</td>
</tr>
</tbody>
</table>

westerly direction as lowland habitats become more prevalent. Some lowland species begin to appear in the lower reaches of the Licking and Kentucky river drainages, and especially in the Salt River drainage. However, this trend is most apparent in the lower Green and Tradewater river drainages, which have several species more characteristic of the Mississippi Embayment faunal province (e.g., *Arcidens confragosus*, *Ligumia subrostrata*, *Potamilus capax*, *Toxolasma texasiensis*, *Uniomerus tetralasmus*). This increasing representation of lowland species is evident in the similarity between the Tradewater River and Mississippi Embayment streams (Figure 8). Because of its large number of upland species, the percentage of Mississippi Embayment species is much lower in the lower Green River drainage, which is responsible for its clustering with other Ohioan drainages.

Within the Ohioan province, the Tennessee and Big Sandy river drainages are the two major outliers in the species-area relationship. Neither of these streams was well surveyed prior to major human alterations, and this lack of sampling is probably a large part of the explanation for their lower than expected species richness. For example, many large river species that are widespread elsewhere in the Ohioan province or the
Tennessee River are not reported from the Kentucky portion of the Tennessee River but probably occurred there historically (e.g., *Epioblasma* spp., *Hemistena lata*, *Leptodea leptodon*, *Plethobasus cicatricosus*, *Pleurobema plenum*). Furthermore, the Tennessee River drainage in Kentucky includes few or no small, upland streams; consequently, many small-stream species characteristic of the drainage as a whole are absent or not reported (e.g., *Alasmidonta viridis*, *Strophitus undulatus*, “*Villosa*” *iris*). Species richness in the Big Sandy River drainage is particularly low for a large, Ohioan drainage. Reported richness in the Big Sandy (29 species) is less than half that in the comparably sized upper Green River drainage (67 species) and half that reported from the smaller Licking River drainage (56 species). Like the Tennessee River, the Big Sandy River was poorly surveyed historically. It is possible that the Big Sandy River has lost a greater proportion of its fauna due to the severity of insults that stream has received (see section VI.B.2); if so, historical species richness probably was considerably greater than available evidence indicates. Furthermore, the drainage may have naturally supported fewer species than other drainages because of its low productivity and the shifting sand substrate that characterizes much of the drainage (see section III.Q).

Omitting the Tennessee and Big Sandy rivers and another strong outlier, the upper Cumberland River drainage (see section V.D), results in a strong relationship between species richness and watershed size among all Ohio River tributaries in Kentucky, including the lower and middle Cumberland River drainages (Figure 7). This strong species-area relationship suggests that all these drainages share similar evolutionary histories and environmental conditions. However, even though watershed size alone predicts species richness remarkably well, this relationship belies the major differences in species composition between the Cumberland River drainage and all other drainages in the state (Figure 8).

**V.C. Tennessee-Cumberland faunal province**

The middle Cumberland River drainage and parts of the lower Cumberland River drainage lie within the Tennessee-Cumberland faunal province (see section V.B). The upper Cumberland River drainage as defined here (section III.G) was not considered separately from the middle Cumberland River drainage in the most recent effort to describe biogeographical relationships within the North American mussel fauna (Haag 2010). The biogeographical affinities of the upper Cumberland River drainage are poorly known (but see section V.D), and this discussion of the Tennessee-Cumberland province applies mainly to the lower and middle Cumberland river drainages except where otherwise noted.

The Tennessee-Cumberland province is the most diverse mussel faunal province in North America. It has a total of about 116 species and subspecies, at least 36 of which are endemic to the province. About 24 of these endemic taxa occur in the Cumberland River drainage, and all but three are reported from Kentucky (see section IV.E). The other endemic species in the province are restricted to the upper and middle Tennessee River system, but none are reported from the Tennessee River drainage in Kentucky (see section V.B). Endemic species largely characterize this province and are responsible for the distinctiveness of the fauna of the middle Cumberland River drainage compared with other drainages in Kentucky (see Figure 8). This province also has inordinately high fish diversity and endemism (e.g., Starnes and Etnier 1986).

The reasons for the high species richness and endemism of the Tennessee-Cumberland province are not completely understood, but several factors are proposed (see Starnes and Etnier 1986; Hollingsworth and Near 2009). First, similar to other southern tributaries of the Ohio River, the Tennessee and Cumberland river systems were not directly affected by Pleistocene glaciation, and hence, have been relatively stable
for millions of years. Second, these river systems have a complex history during which they have been isolated from the Ohio and Mississippi river systems but connected to each other for long periods. For example, both rivers may have flowed directly to the Gulf of Mexico at various times (Galloway et al. 2011). This history of isolation is doubtless responsible in large part for their high levels of endemism. Third, connectivity with the Ohio and Mississippi river systems recently and at other times in the past has allowed species exchange with those large systems.

In the lower Cumberland River drainage, Tennessee-Cumberland province endemic species are found primarily in the Red River system, but at least three of these species also occur in the Little River and other lower Cumberland tributaries (Actinonaias pectorosa, “Villosa” taeniata, “V.” vanuxemensis). The Red River system in Kentucky contains at least nine Tennessee-Cumberland endemic species, and two additional species are reported from that system in Tennessee (Epioblasma capsaeformis and E. florentina walker). Endemic species absent from the Red River are large river species (e.g., Epioblasma haysiana, E. lewisi, Dromus dromas) or those restricted to the middle Cumberland River drainage (e.g., Venustaconcha troostensis). The middle Cumberland River drainage contains all Tennessee-Cumberland endemic species reported from Kentucky, with the exception of Pleuronaia dolabelloides and possibly “Villosa” vanuxemensis, which in Kentucky are reported with certainty only from the lower Cumberland River drainage. The middle Cumberland River drainage shares two endemic species with the upper Cumberland River drainage (Alasmidonta atropurpurea and Anodontoides denigrata), but the biogeographic affinity of these species is unknown.

V.D. Upper Cumberland River drainage and Cumberland Falls

Along with the Mississippi River mainstem, the upper Cumberland River drainage is the strongest outlier among all drainages in the state with regard to the species-area relationship (Figure 7), and it has the most unusual mussel fauna of any drainage in Kentucky (Figure 8). Based on the species-area relationship among all Ohio River tributaries (but excluding outliers), species richness in the upper Cumberland River drainage (12 species) is 25% of that predicted for a drainage its size (48 species, 5120 kilometers²). Even using the full dataset including all drainages in the state, observed richness is only 30% of predicted (41 species). Furthermore, the upper Cumberland River drainage lacks nearly all of the endemic species that characterize the Tennessee-Cumberland faunal province, but it contains two species that are largely restricted to that drainage (Alasmidonta atropurpurea and Anodontoides denigrata). These unique aspects of the mussel fauna of the upper Cumberland River drainage appear to be due almost entirely to Cumberland Falls.

The Cumberland River drops 17 meters (55 feet) over Cumberland Falls, and this long-standing barrier has had a profound influence on the distribution of mussel and fish species in the region. The original location of Cumberland Falls is proposed to be near Burnside, Pulaski County, where the Cumberland River flowed over the Pottsville Escarpment at the boundary between the Cumberland Plateau and the Highland Rim. Subsequently, the falls have progressed upstream about 72 kilometers (45 miles) in the last 25–30 million years to their current location (McGrain 1966). As streambed erosion progressed upstream, it also resulted in large waterfalls on several Cumberland River tributaries (e.g., Eagle Falls), and the large rapids on the Big South Fork, Laurel River, and Rockcastle River are probably the remnants of ancient wa-
These waterfalls are insurmountable barriers to the movement of mussels and their host fishes, and large rapids (especially the Narrows on the Rockcastle River) also may be filters that restrict movement (Burr and Warren 1986).

The effectiveness of Cumberland Falls as a barrier is demonstrated by the historical occurrence of 22 mussel species in the river at the base of the falls but only 4 species immediately above the falls (Wilson and Clark 1914; Neel and Allen 1964; Cicerello and Laudermilk 1997). Overall, the 12 mussel species reported from the upper Cumberland River drainage stands in stark contrast to the 73 species reported from the middle Cumberland River drainage in Kentucky, and the fish fauna above and below the falls shows a similarly stark and abrupt discontinuity in species richness (Burr and Warren 1986). In addition to the falls themselves, the potential role of large rapids as barriers is demonstrated in the Rockcastle River, in which several mussel and fish species that are otherwise widespread in the middle Cumberland River drainage are either absent or occur mainly downstream of the Narrows (e.g., *Epioblasma brevidens*, *E. capsaeformis*, *E. triquetra*, *Fusconaia subrotunda*, *Obovaria subrotunda*; see Burr and Warren 1986 for fishes).

The barrier of Cumberland Falls appears to have allowed the aquatic faunas of the upper and middle Cumberland River drainages to follow largely independent evolutionary trajectories despite their proximity. The diverse fauna of the river downstream of the falls is a result of its complex history of exchange with the Tennessee River system, the former isolation of these two systems from other rivers, and past and present exchange with the Ohio and Mississippi river systems (see section V.C). In contrast, evidence from fishes suggests that the fauna of the upper Cumberland drainage is largely derived from exchange with the adjacent upper Kentucky River system via multiple headwater capture events (Kuehne and Bailey 1961). Headwater capture is the process by which natural erosion causes a stream to cut across a drainage divide, thereby diverting or capturing streams in an adjacent drainage. Populations of several fish species in the upper Cumberland are more closely related genetically to populations in the upper Kentucky River system than to populations elsewhere in the Cumberland River system (e.g., Strange and Burr 1997; Strange 1998; Berendzen et al. 2008; Heckman et al. 2009), and at least two, *Etheostoma sagitta sagitta* and *E. susanae*, have diverged as distinct taxa apparently because of their long history of isolation above the falls. The fish fauna also lacks endemic fishes that are widespread in the middle Cumberland and most big river species, which are not expected to disperse via headwater capture (Burr and Warren 1986).

Headwater capture and faunal exchange with the upper Kentucky River system also may explain the composition and unique nature of the mussel fauna upstream of Cumberland Falls. Similar to fishes, the mussel fauna of the upper Cumberland conspicuously lacks large river species that are present immediately below Cumberland Falls (e.g., *Cyclonaias tuberculata*, *Ellipsaria lineolata*, *Elliptio crassidens*, *Truncilla truncata*; Cicerello and Laudermilk 1997). Endemic mussel species characteristic of small streams throughout the middle Cumberland River drainage are similarly absent above the falls (e.g., *Medionidus conracicus*, *Pegias fabula*, *Psychobranchus subtendentum*, "Villosa" taeniata), even though several occurred in the pool at the base of the falls. Apart from *Alasmidonta atropurpurea* and *Anodontoides denigrata*, the only Tennessee-Cumberland endemic species present above the falls is *Actinonaias pectorosa*. However, this species apparently was absent above the falls in 1911 and may have been introduced about that time by pearlers along with *Lampsilis cardium* and *L. ovata* (Wilson and Clark 1914). The remainder of the fauna of the upper Cum-
berland River drainage is composed primarily of headwater species that are widespread in the upper Kentucky River drainage (e.g., Alasmidonta viridis, Elliptio dilatata, Lampsis fasciola, and potentially Strophitus undulatus). Unfortunately, genetic relationships between populations of these species in the upper Cumberland and those in the upper Kentucky and middle Cumberland river drainages are unknown.

The origin and biogeographical affinity of Alasmidonta atropurpurea and Anodontoides denigrata are unknown. These species are considered by default members of the Tennessee-Cumberland province fauna (e.g., Haag 2012), but they are largely restricted to the upper Cumberland River drainage and occur in the middle Cumberland River drainage only near or upstream of the proposed original location of the falls at Burnside (see subsequent). Similar to endemic fishes, these mussel species may have evolved in isolation from ancestors that colonized the upper Cumberland via headwater capture from the upper Kentucky River system (Alasmidonta marginata and Anodontoides ferussacianus). Alasmidonta marginata occurs in the upper Kentucky River system, but A. ferussacianus is not reported from that region in recent times; however, this is primarily a northern species that may have been more widely distributed during cooler periods of the Pleistocene or before. The restricted distribution of these species, as well as endemic fishes, may have been maintained by the downstream movement barrier posed by Cumberland Falls. These species also appear to have strict affinities for cool, poorly-buffered headwater streams typical of the Cumberland Plateau, and the main channel of the Cumberland River and the well-buffered streams of the Highland Rim may have been inhospitable habitats that further prevented dispersal or colonization (Starnes and Etnier 1986; Haag 2012).

The occurrence of these two mussel species between the original and current location of the falls (i.e., Rockcastle and Laurel rivers) suggests that dispersal and subsequent divergence occurred at an early date, when the falls were near their original location. The occurrence of these species in the upper Big South Fork is more difficult to explain because that stream enters the Cumberland River slightly downstream of the hypothesized original location of Cumberland Falls (McGrain 1966). However, several fishes that are largely restricted to the region above the proposed original location of the falls (e.g., Etheostoma kennicotti, E. sagitta sagitta, Chrosomus cumberlandensis) also occur sporadically in the upper Big South Fork (Burr and Warren 1986, Warren et al. 1991; Bivens et al. 2013). The occurrence of these species in the Big South Fork may be explained by uncertainty regarding the original location of Cumberland Falls. Alternatively, these small-stream species may have entered the Big South via headwater capture from the upper Cumberland River drainage, a portion of which lies in close proximity to the upper Big South Fork system.

The origin of the upper Cumberland River drainage mussel fauna, as presented here, is conjectural but is supported by strong evidence from the fish fauna of the region. Phylogeographic studies necessary to inform this question—similar to those conducted for fishes—are unavailable for mussels. Because of the rapid decline of mussel populations in the upper Cumberland River drainage (see section VIB.2), such studies must be conducted soon if we are to gain a better understanding of the unique and interesting biogeographical history of this region.
VI. Conservation status of the Kentucky mussel fauna

VI.A. Mussel declines

Sadly, the spectacular mussel fauna of Kentucky has been greatly diminished in the last 200 years. At one time, many, if not most, larger streams in the state were literally paved with mussels throughout much of their length (e.g., Wilson and Clark 1914; Clench 1925, 1926), and mussels probably occurred to some extent in all but the smallest headwater streams. Today, several streams continue to support impressively dense and diverse mussel faunas, but vast river reaches are practically devoid of mussels and most streams have experienced substantial changes in their mussel fauna. Some evidence suggests that substantial changes to the mussel fauna began even in prehistory, as Native Americans adopted large-scale maize agriculture (Peacock et al. 2005). However, no species extinctions are documented in Kentucky in prehistory, and the mussel fauna appears to have been largely intact when it was first seen by naturalists in the early 1800s (Haag 2009, 2012).

Since that time, nearly all river systems have experienced species losses (Table 3). Of the 17 major drainages in the state, only direct tributaries of the Mississippi River in far western Kentucky show no evidence of species loss. Many of the lowland species in this drainage appear to be tolerant of considerable disturbance (Haag 2012), which may in part explain the intact nature of the fauna. However, this drainage was largely unsurveyed prior to the 1980s, and its historical fauna is unknown. The Mississippi River mainstem also appears to have lost few species for the same reasons. The greatest declines in species richness occurred in the lower and middle Cumberland River drainages, both of which have lost nearly half of their mussel fauna. Most other drainages have suffered a 21–39% loss of species richness. The upper Green River drainage and Kinniconick Creek are notable exceptions that retain 88% and 91% of their known historical richness, respectively. In some cases, declines in particular streams are even greater than drainage-wide patterns (Table 4).

As troubling as these numbers are, most probably underestimate the extent of species loss. With the potential exceptions of the middle Cumberland River drainage and the Ohio River, historical species richness is not well documented in most drainages in the state (see section IV.B). Historical richness undoubtedly was higher in most drainages, and if so, species losses are underestimated. For example, the conspicuously low species richness of the Big Sandy River drainage is surely due in part to the lack of historical sampling (see section V), and this large stream undoubtedly has lost more than the 24% of its species indicated by available information. More seriously, our estimates of species loss do not depict the potential for additional losses in the near future. Many of the factors leading to declines in species richness are still in effect (see subsequent), and further declines are likely to occur in most drainages.

The abundance and distribution of most mussel species in Kentucky have declined to some extent, and many species have declined dramatically (Figure 10; Table 5). A total of 22 species (22% of the fauna) have disappeared from the state, and of these, 12 are extinct globally. All 12 extinct species are members of the genus *Epioblasma*. Another 16 species have disappeared from at least 50% of the drainages they occupied historically, and 35 species have disappeared from 10–49% of their historical drainages. Only 27 species (27% of the fauna) still occur in >90% of their historical drainages.

Similar to river drainage losses in species richness, drainage occupancy does not fully depict the dire situation of many mussel species or the great extent to which they have declined. Of the 27 species that continue to occupy most of
Table 3. Declines in mussel species richness in the 17 major river drainages of Kentucky. Total species richness includes all historical, recent, and archaeological records with the exception of archaeological records from the Wickliffe Mounds site on the Mississippi River mainstem (see section IV.C.2). 1990-2015 species richness totals include only records of live individuals or recently dead shells during that period, and they exclude recent, documented reintroductions or introductions (e.g., Cumberlandia monodonta, Dromus dromas, Epioblasma torulosa rangiana). Drainages are ordered from greatest to least declines in species richness. River drainages are defined in section III.

<table>
<thead>
<tr>
<th>Drainage</th>
<th>Total species richness</th>
<th>1990-2015 species richness</th>
<th>Percent decline in species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle Cumberland River</td>
<td>73</td>
<td>37</td>
<td>49</td>
</tr>
<tr>
<td>Lower Cumberland River</td>
<td>73</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td>Little Sandy River</td>
<td>26</td>
<td>16</td>
<td>39</td>
</tr>
<tr>
<td>Ohio River and minor tributaries</td>
<td>76</td>
<td>47</td>
<td>38</td>
</tr>
<tr>
<td>Tradewater River</td>
<td>31</td>
<td>20</td>
<td>35</td>
</tr>
<tr>
<td>Salt River</td>
<td>58</td>
<td>39</td>
<td>33</td>
</tr>
<tr>
<td>Upper Cumberland River</td>
<td>12</td>
<td>8</td>
<td>33</td>
</tr>
<tr>
<td>Kentucky River</td>
<td>60</td>
<td>41</td>
<td>32</td>
</tr>
<tr>
<td>Lower Green River</td>
<td>71</td>
<td>53</td>
<td>25</td>
</tr>
<tr>
<td>Tennessee River</td>
<td>58</td>
<td>44</td>
<td>24</td>
</tr>
<tr>
<td>Big Sandy River</td>
<td>29</td>
<td>22</td>
<td>24</td>
</tr>
<tr>
<td>Tygart's Creek</td>
<td>31</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>Licking River</td>
<td>56</td>
<td>44</td>
<td>21</td>
</tr>
<tr>
<td>Upper Green River</td>
<td>67</td>
<td>59</td>
<td>12</td>
</tr>
<tr>
<td>Kinniconick Creek</td>
<td>23</td>
<td>21</td>
<td>9</td>
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<td>Mississippi River mainstem</td>
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<td>23</td>
<td>4</td>
</tr>
<tr>
<td>Mississippi River tributaries</td>
<td>21</td>
<td>21</td>
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</tr>
</tbody>
</table>

Table 4. Declines in mussel species richness in four Kentucky streams. Total species richness includes all historical and recent records; archaeological records do not exist for these streams (but see section IV.C.2). 1990-2015 species richness totals include only records of live individuals or recently dead shells during that period. Current species richness for the Little South Fork is based on a recent survey (Ahlstedt et al. 2014) and does not include all 1990-2015 records. Recent, comprehensive surveys have not been conducted for the other three streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Total species richness</th>
<th>1990-2015 species richness</th>
<th>Percent decline in species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little River</td>
<td>28</td>
<td>5</td>
<td>82</td>
</tr>
<tr>
<td>Red River</td>
<td>32</td>
<td>9</td>
<td>72</td>
</tr>
<tr>
<td>Nolin River</td>
<td>31</td>
<td>11</td>
<td>65</td>
</tr>
<tr>
<td>Little South Fork Cumberland River</td>
<td>29</td>
<td>5</td>
<td>83</td>
</tr>
</tbody>
</table>
their historical drainages, several are widespread species that have adapted to some extent to stream alteration (e.g., *Amblema plicata*, *Elliptio dilatata*, *Lampsilis cardium*, *Leptodea fragilis*, *Potamilus alatus*, *Pyganodon grandis*, *Quadrula pustulosa*), and a few others even appear to have increased in abundance since historical times (e.g., *Anodonta suborbiculata*, *Plectomerus dombeyanus*, *Utterbackia imbecillis*). However, several of these 27 species were originally restricted to only one or two drainages, and even though they survive there, they occupy a fraction of their original range in those drainages and their abundance is greatly reduced (e.g., *Epioblasma florentina walkeri*, *Ptychobranchus subtentum*, *Venustaconcha troostensis*). Other species that have disappeared from a substantial number of drainages survive only tenuously in other drainages today. As one example among many, *Obovaria subrotunda* survives in 67% of drainages that it occupied historically, but nearly all surviving populations are small, isolated, and highly vulnerable to extinction. Even species that remain widespread today have disappeared from vast stream reaches they formerly occupied in great abundance (e.g., Cumberland River). About 78% of Kentucky’s mussel species survive in the state, but many face an uncertain future and may disappear from Kentucky or become extinct within a human generation.

**VI.B. Causes of mussel declines**

The streams of Kentucky have been altered by humans in numerous ways, and many have been utterly transformed from their natural condition. Overall, mussel declines in Kentucky and elsewhere are the combined result of these numerous impacts to streams, but these factors vary in severity and scope. However, the specific causes of many mussel declines remain poorly understood. Localized mussel declines or other changes in mussel faunas surely began at an early date (e.g., Peacock et al. 2005; Haag 2009), but the magnitude and pace of declines accelerated rapidly beginning in the early twentieth

Figure 10. Declines in the number of river drainages occupied by mussel species in Kentucky. Percent declines were calculated for each species as 1 - number of drainages occupied from 1990–2015/ total number of drainages occupied in all time periods. Total number of drainages occupied includes all historical, recent, and archaeological records with the exception of archaeological records from the Wickliffe Mounds site on the Mississippi River mainstem (see section IV.C.2). 1990–2015 records include only records of live individuals or recently dead shells during that period, and they exclude recent, documented reintroductions or introductions (e.g., *Cumberlandia monodonata*, *Dromus dromas*, *Epioblasma torulosa rangiana*).
Table 5. Mussel species that have been extirpated from substantial portions of their historical range in Kentucky. Species in bold are considered extinct. Note that these listings do not depict substantial declines that many species have experienced within drainages (see text). See Figure 10 for information about how range reductions were calculated.

<table>
<thead>
<tr>
<th>Species extirpated from Kentucky</th>
<th>Species extirpated from ≥50% of historically occupied drainages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dromus dromas</td>
<td>Cumberlandia monodonta</td>
</tr>
<tr>
<td>Epioblasma arcaeformis</td>
<td>Cyprogenia stegaria</td>
</tr>
<tr>
<td>Epioblasma biemarginata</td>
<td>Epioblasma brevidens</td>
</tr>
<tr>
<td>Epioblasma capsaeformis</td>
<td>Lampsilis abrupta</td>
</tr>
<tr>
<td>Epioblasma flexuosa</td>
<td>Lasmigona compressa</td>
</tr>
<tr>
<td>Epioblasma florentina florentina</td>
<td>Medionidus conradicus</td>
</tr>
<tr>
<td>Epioblasma haysiana</td>
<td>Obovaria olivaria</td>
</tr>
<tr>
<td>Epioblasma lewisi</td>
<td>Obovaria retusa</td>
</tr>
<tr>
<td>Epioblasma obliquata obliquata</td>
<td>Pegias fabula</td>
</tr>
<tr>
<td>Epioblasma personata</td>
<td>Plethobasus cooperianus</td>
</tr>
<tr>
<td>Epioblasma cincinnatiensis</td>
<td>Pleurobema clava</td>
</tr>
<tr>
<td>Epioblasma propinqua</td>
<td>Pleurobema oviforme</td>
</tr>
<tr>
<td>Epioblasma sampsonii</td>
<td>Pleurobema plenum</td>
</tr>
<tr>
<td>Epioblasma stewardsonii</td>
<td>Pleurobema rubrum</td>
</tr>
<tr>
<td>Epioblasma torulosa rangiana</td>
<td>“Villosa” lienosa</td>
</tr>
<tr>
<td>Epioblasma torulosa torulosa</td>
<td>“Villosa” vanuxemensis</td>
</tr>
<tr>
<td>Hemistena lata</td>
<td></td>
</tr>
<tr>
<td>Leptodea leptodon</td>
<td></td>
</tr>
<tr>
<td>Plethobasus cicatricosus</td>
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</tr>
<tr>
<td>Pleuronana dolabelloides</td>
<td></td>
</tr>
<tr>
<td>Quadrula fragosa</td>
<td></td>
</tr>
<tr>
<td>“Villosa” fabalis</td>
<td></td>
</tr>
</tbody>
</table>

century. In the following sections, we summarize the major factors that have shaped the current mussel fauna of Kentucky.

VI.B.1. Dam construction

Dam construction is the single largest factor in mussel declines (Haag 2012). Unlike most other potential factors, its effects are clear and unequivocal. Dams transform shallow, free-flowing streams into deep, still pools, which are unsuitable habitats for most stream species, and large dams have several negative downstream effects (see subsequent). Dam construction in Kentucky began in the late 1700s primarily to power grain mills and sawmills, and mill dams were ubiquitous across the state (Clark 1977; Parola et al. 2007). More than 600 Kentucky place names include “Mill”, attesting to the historic prevalence of these structures (USGS 2011). These dams doubtless caused localized mussel declines, but most were small and affected only short stream reaches, many were on small streams that supported limited mussel faunas, and many were demolished or collapsed, allowing streams to revert to a natural condition.
Large dams on larger streams have more far-reaching effects. First, because large streams typically have much higher species richness than small streams, large dams effect a greater proportion of the mussel fauna. Second, large dams impound long stream reaches often including the lower reaches of tributaries. Third, dams on large streams disrupt the connectivity within a drainage basin, leaving populations in tributaries isolated from others in the basin (see section VI.B.6). Finally, large, hydroelectric or flood-control dams radically transform the river downstream in addition to impounding the river upstream of the dam (see subsequent).

Large dam construction began in Kentucky as early as the 1830s to improve navigation on the Green and Kentucky rivers (Table 6). Even the largest streams in the state were relatively shallow originally. For example, the Ohio River had an average low-water depth of only about 3 feet and it had numerous shallow shoals and riffles (Rafinesque 1820b; Pearson and Krumholz 1984). These areas were ideal mussel habitat, but they restricted river traffic for much of the year. By the early 1900s, most large rivers in the state were impounded almost completely for navigation. By 1929, the Ohio River was almost completely impounded by a series of 50 navigation dams (23 in Kentucky), which raised the minimum low-water depth to 9 feet and eliminated all shoals and riffles. Subsequently, these dams on the Ohio River were replaced by a series of 20 larger, high-lift dams (9 in Kentucky), which further deepened the river. The lower 30 kilometers (19 miles) of the Ohio River remains unimpounded and largely free-flowing; year-round navigation is possible because of the large size of the river and periodic channel dredging. In addition, the 70 kilometer (44 mile) reach downstream of Smithland Lock and Dam and upstream of the impounded reach is influenced only by older, moveable dams (locks and dams 52 and 53; see subsequent), which allows this reach to remain largely riverine. However, these dams are scheduled to be replaced by Olmsted Lock and Dam, which is under construction about 3 kilometers downstream of Lock and Dam 53.

Many navigation dams allow rivers to remain partially riverine, especially immediately downstream of the dams, and these riverine habitats often continue to support large populations of mussel species that can adapt to such conditions (e.g., Garner and McGregor 2001). The first navigation dams on the Ohio River had moveable wicket gates that could be raised at low water and lowered at high water, which periodically returned the river to a free-flowing condition. The high-lift dams that replaced these earlier dams are in a fixed position, and, combined with their greater height, they permanently impound longer reaches of the river and further reduced remaining riverine habitat. Regardless of their configuration, navigation dams effectively eliminated shallow shoal habitats in large rivers throughout Kentucky and most of the U.S., and they appear to have eliminated many large river species that depended on these habitats.

Beginning in 1925, large hydroelectric and flood-control dams were constructed on most larger rivers not already impounded for navigation (Table 6). These dams are much higher than navigation dams, and they typically impound much longer river reaches, which are transformed completely from a riverine to a lentic environment. For example, Wolf Creek Dam on the Cumberland River is 79 meters (258 feet) high and impounds about 161 kilometers (100 miles) of the river, as well as substantial portions of tributaries. Because of the depth of these reservoirs, water released into the river downstream usually is cold year-round, and hydroelectric power generation and flood control schedules result in radical fluctuations in stream flow that do not resemble natural conditions. Wolf Creek Dam also renders the remainder of the 112 kilometers (70 miles) of the Cumberland River in Kentucky downstream of the dam unsuitable

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<td>Lock and Dam 27-53</td>
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<td>Taylorville Lake</td>
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<td>Olmsted Lock and Dam</td>
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<td>Lock and Dam E and F</td>
<td>1922-1923</td>
<td>Big Sandy River</td>
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<td>Green River Lake</td>
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<sup>a</sup> under construction; estimated date.

For most native aquatic species because water temperature is less than 21°C (70°F) year-round and streamflow fluctuates radically on a daily basis (Miller et al. 1984; Tippit et al. 1997). Most other large dams in the state have similar downstream effects to some extent. Mussel reproduction appears to have ceased in the upper Licking River in Bath County after construction of Cave Run Dam, and the once diverse and dense mussel assemblage in that portion of the...
river has now largely died out (Smathers 1990; W. R. Haag, observations). Similarly, construction of Green River Dam is implicated in mussel declines in the river downstream of the dam. Recent restoration of more natural flow regimes from Green River Dam may help alleviate this situation (Konrad et al. 2012), and similar flow improvements are planned for other dams in the state.

Of the 17 major river drainages in Kentucky, all but the Mississippi River, Mississippi River tributaries, Tradewater River, Kinniconick Creek, and Tygarts Creek are directly and extensively modified by dams. The effects of widespread dam construction on the mussel fauna are profound. All mussel species extinctions in Kentucky to date, and most in North America, are directly attributable to habitat destruction by dams (Haag 2012). Species that were restricted to shallow shoal habitats in the Ohio and other large rivers were among the first to become extinct (e.g., *Epioblasma flexuosa*, *E. personata*, *E. propinqua*). Along with impoundment of the Ohio River, the single most destructive dam in Kentucky was Wolf Creek Dam on the Cumberland River. This dam eliminated the last population of *Epioblasma lewisii* on Earth, it directly contributed to the extinction of *Epioblasma hayssiana*, and it resulted in the imperilment of at least a dozen other species. All other large dams in the state have directly contributed to mussel declines by direct habitat destruction. Furthermore, dams have fragmented stream habitats, leaving remnant mussel populations in free-flowing streams isolated and at increased risk of extinction (see section VI.B.6).

**VI.B.2. Coal mining and oil and gas extraction**

As a major coal producing state, the landscape and streams of Kentucky are highly altered by coal mining. Coal mining in Kentucky occurs primarily in the Appalachian Plateaus physiographic province in eastern Kentucky and in the Shawnee Hills section of the Interior Low Plateaus physiographic province in western Kentucky. Oil and natural gas extraction also take place in many areas of the state. These activities appear to have had substantial, negative effects on the mussel fauna, but in most cases their specific effects are poorly understood.

Coal is extracted from underground mines or surface mines, both of which can seriously degrade stream ecosystems. Both types of mines may produce acid mine drainage, which occurs when iron sulfide is exposed to oxygen and water, producing sulfuric acid and dissolved iron, and the low pH mobilizes other heavy metals such as lead, copper, and mercury. Underground mines often discharge large volumes of ground water and thus can be major, long-term sources of acid mine drainage pollution to streams. Acid mine drainage can eliminate many forms of aquatic life due to the combination of acidic conditions, metal toxicity, and ionic stress from high conductivity (e.g., Roback and Richardson 1969; Warner 1971; Soucek et al. 2000). Surface water or groundwater associated with surface mines may be acidic, alkaline, or circumneutral, but in most cases, leaching of newly exposed bedrock produces runoff with greatly elevated concentrations of metals and other ions. Surface mining also results in massive sediment inputs into streams, more rapid runoff and more intense floods, and in its most extreme manifestation, mountaintop removal, entire stream valleys are buried under tens to hundreds of feet of fill. In addition to mining itself, coal washing, processing, and transport can result in severe water pollution.

Water pollution from surface mines and associated activities can eliminate many stream organisms, and negative effects may continue for decades even after reclamation (e.g., Matter and Ney 1981; Pond et al. 2008; Lindberg et al. 2011). The negative effects of coal mining and related activities on water quality and stream ecosystems in general are well known, but their
specific effects on mussels are not well studied. The most comprehensive study to date found lower growth and survival in mussels exposed to coal mining contaminated sediments compared with sediments from non-contaminated reference streams (Wang et al. 2013). Exposure to coal fines in stream sediments also can result in tissue and organ abnormalities (Henley et al. 2015).

In Kentucky, the effects of coal mining on streams are perhaps most widespread and conspicuous in the Big Sandy River drainage. Streambeds in much of the watershed (particularly the Tug Fork) are composed of a large percentage of coal fines and larger coal particles. In 2000, a 72-acre retaining pond failed, releasing 300 million gallons of coal slurry into Coldwater Fork, Martin County, eliminating all aquatic life in at least 120 kilometers (75 miles) of the Tug Fork and Big Sandy River. Across sampling periods from 2002 to 2008, an average of only 22% of fixed water quality monitoring sites in the drainage fully supported aquatic life (based on USEPA criteria), and only 13% of randomly chosen sites met these criteria (KDOW 2004, 2010). Water quality degradation in the Big Sandy River drainage has many sources, but coal mining is a major factor, and these water quality values are the lowest of any major drainage in the state. However, many streams in the Little Sandy, upper Licking, upper Kentucky, middle and upper Cumberland, lower Green, and Tradewater river drainages are severely impaired by coal mining (e.g., Grubb and Ryder 1972; Harker et al. 1979, 1980, 1981).

Coal mining is implicated in mussel declines throughout the coal-bearing regions of Kentucky (e.g., Jones 1973; Harker et al. 1979, 1981). However, a lack of historical sampling in most streams makes it difficult to estimate the timing and extent of declines or to attribute potential declines specifically to coal mining. Elimination of mussels by acid mine drainage was noted by the early 1900s in the Monongahela River, Pennsylvania (Ortmann 1909). The earliest mention of the effects of acid mine drainage on mussels in Kentucky is in the lower Big South Fork Cumberland River and the Cumberland River upstream of Pineville, in which mussels had been nearly eliminated by acid mine drainage by the 1940s (Neel and Allen 1964). It is likely that acid mine drainage had similar effects on the mussel fauna in the Big Sandy River, upper Kentucky River, Tradewater River, and other drainages from an early date, but specific documentation of these effects is lacking. The effects of coal mining on mussels in Kentucky are best documented in the middle Cumberland River drainage. From the late 1970s to the present, an increase in coal mining and oil extraction is associated with the near total elimination of mussels from the Little South Fork and Horse Lick Creek, which formerly harbored among the most intact mussel assemblages remaining in the drainage after construction of Wolf Creek Dam (Anderson et al. 1991; Layzer and Anderson 1992; Haag and Warren 2004; Warren and Haag 2005; Ahlstedt et al. 2014).

The effects of oil and gas extraction on mussels are less well documented than the effects of coal mining. The elimination of mussels from the Little South Fork was associated with increased oil extraction in addition to coal mining, but the specific effects of oil extraction were unknown (Warren and Haag 2005). Water containing a high concentration of salts in solution is commonly produced along with oil extraction, and these brine wastes may contaminate streams. In the late 1950s, oil field brines raised the salinity of the upper Green River 100 times above natural levels of 0.01 parts per thousand (ppt) to over 1.0 ppt, which is in the range of brackish water, and this was coincident with a decline in mussel populations in that stream (Charles 1964; Williams 1969). Oil field brines are implicated in mussel declines in many other regions of Kentucky (e.g., Harker et al. 1981; KDOW 1989). In addition to its poorly understood ef-
fects, oil and gas extraction is of particular concern in mussel conservation because it occurs more widely in Kentucky than coal mining, it is expanding rapidly, and recent technological advances such as hydraulic fracturing (“fracking”) may pose additional threats.

**VI.B.3. Stream channelization**

Stream channelization primarily to drain wet, low-lying regions for agriculture has destroyed hundreds, if not thousands, of miles of streams in Kentucky. Channelization transforms shaded, meandering streams with heterogeneous substrate and depth profiles into shorter, straight ditches with little riparian vegetation, shifting sand and silt substrates, and uniformly shallow depth profiles. For example, the original 152 kilometer (94 mile) course of Mayfield Creek has been shortened by 57 kilometers (35 miles). Furthermore, by lowering the base level of a stream, channelization can initiate progressive upstream erosion, called headcutting, which can destabilize an entire watershed far beyond the channelized reach (Shields et al. 2000). In Kentucky, channelization has occurred at least since the early 1900s and is most widespread in western Kentucky, mainly in lowland areas of the Mississippi Embayment and Shawnee Hills. All major direct tributaries of the Mississippi River (Mayfield Creek, Obion Creek, and Bayou du Chien) have been channelized entirely or in part, and channelization is widespread in the lower Ohio, Tennessee, lower Cumberland, Tradewater, and lower Green river drainages. Stream channelization also has occurred to a lesser extent across most of the state. Channelization can result in the almost complete elimination of the mussel fauna of a stream, or, at best, reduction of the fauna to a subset of species tolerant of unstable habitats (Hartfield 1993; Haag 2012). In some cases, the original stream channel may remain intact (although with greatly reduced flow) adjacent to the dredged channel, and these remnant habitats generally support a larger percentage of the original mussel fauna than the channelized section (e.g., Mayfield Creek, Obion Creek, Bayou du Chien). These remnant sections of the original channel represent opportunities for restoration, which should benefit the aquatic faunas (Parola and Biebighauser 2011).

**VI.B.4. Invasive species**

Kentucky has several non-native invasive aquatic organisms, but the effects of most of these species on native mussels are unknown. The Common Carp (*Cyprinus carpio*) was introduced to North America from Europe in the last half of the 1800s and quickly became an abundant species across the continent; it is ubiquitous in nearly all streams in Kentucky (Burr and Warren 1986). Common carp feed by rooting in the bottom, which may increase turbidity, and they may feed heavily on small bivalves (Bartsch et al. 2005). However, the effects of carp on native mussels have not been studied.

Another conspicuous and well-established invasive species is the Asian Clam, *Corbicula fluminea*. *Corbicula* probably was introduced into the Pacific Northwest in the 1920s by Chinese immigrants (Britton and Morton 1979). By the 1950s, it had spread gradually as far east as the Colorado River system in Arizona, but in 1957 it suddenly appeared nearly 3200 kilometers (2000 miles) to the east in the Ohio River near Paducah, probably due to an unknown human vector (McMahon 1982). From this point, *Corbicula* spread quickly throughout the Ohio and Mississippi River basins probably by a combination of natural dispersal and human vectors. For example, in 1961, it was abundant in the lower Green River, Muhlenberg County, but had not reached the section of the river in the vicinity of Mammoth Cave (Bates 1962). By the 1970s, it occurred across Kentucky and is now a dominant member of the bivalve fauna in most streams. The appearance and rapid proliferation
of *Corbicula* in Kentucky in the 1960s and 1970s is coincident with enigmatic mussel declines in many streams (see section VI.B.5). However, evidence for strong competition with native mussels or other negative effects is equivocal at this time (reviewed in Strayer 1999 and Haag 2012), and diverse, dense mussel assemblages coexist with large populations of *Corbicula* in many streams.

More recent invasive bivalves are the Zebra Mussel and the Quagga Mussel (*Dreissena* spp.). *Dreissena* appeared in Lake Erie or Lake St. Clair in about 1986 probably in ballast water from transoceanic shipping (Hebert et al. 1989). By 1991, it escaped into the Mississippi River basin and first appeared in Kentucky in the lower Ohio and Tennessee rivers. By 1995, dense populations existed throughout the Ohio River and the lower Kentucky River; populations in the Ohio River reached densities as high as 50,000/m² (Vittor 1996). Since that time, *Dreissena* populations in the Ohio River have crashed, but isolated occurrences have been reported in the lower Green River, Lake Cumberland, and the Big Sandy River (USGS 2015).

Unlike *Corbicula*, the effects of *Dreissena* on native mussels are well-documented and devastating. *Dreissena* attaches to hard substrates including native mussels; a single native mussel may be infested with as many as 10,000 *Dreissena* (Hebert et al. 1991). Primarily by competing with native mussels for food, *Dreissena* virtually eliminated native mussels from the Great Lakes within a few years after their arrival, and they had similar effects in the upper Mississippi River, Hudson River, and other areas in the upper Midwest and Northeast (Ricciardi et al. 1998; Strayer 1999). Despite the dramatic effects of *Dreissena* in other areas, the mussel fauna of Kentucky to date largely has been spared a similar fate. Apart from the Ohio and lower Kentucky rivers, *Dreissena* has not become well established in Kentucky perhaps because of its intolerance to warm temperatures, its relatively poor ability to colonize flowing streams, or other factors. In the Ohio River, *Dreissena* populations are highly variable temporally and spatially, which may buffer their effects (Payne and Miller 2002). During peak *Dreissena* abundance in the mid-1990s, native mussel mortality in response to fouling by *Dreissena* at three sites in the lower Ohio River was less than 40% compared with the 90–100% mortality typically seen in more northern regions (Morrison 1998).

VI.B.5. Enigmatic mussel declines

Mussel populations throughout Kentucky doubtless have been negatively affected by general water quality and habitat degradation in the last 100 years or more. Throughout much of the twentieth century, water quality in the Ohio River and other streams was exceptionally poor due to a wide variety of domestic and industrial pollution (ORSANCO 1962; Pearson and Krumholz 1984). The effects of this type of water quality degradation on mussels are not well studied, but it is expected to result in a gradual erosion of mussel abundance and diversity, the extent of which is variable depending on the severity of pollution. It is likely that mussel populations did decline gradually in many streams as expected during the last 100 years. However, many populations have declined abruptly in recent decades in a manner that is inconsistent with the chronology of insults to streams. For example, general water quality in many streams has improved in the decades since passage of the U.S. Clean Water Act and similar legislation, and streams such as the Ohio River continue to support large mussel populations despite a history of chronic water pollution.

Beginning in about the 1970s, free-flowing streams across North America began to experience dramatic and rapid declines in mussel populations (Haag 2012). These declines often occur in streams that largely lack obvious sources of
severe pollution and that continue to support diverse fish, snail, and aquatic insect communities. Most or all mussel species appear to be affected similarly, primarily through an abrupt cessation or reduction in reproduction or recruitment. Consequently, mussel populations disappear as adults reach the end of their life span; short-lived species disappear first and long-lived species persist for a longer period. This type of enigmatic decline has occurred in streams across Kentucky. Notably, the Little and Red rivers (both lower Cumberland River drainage) and the Nolin River (upper Green River drainage) have lost nearly their entire mussel fauna since the 1960s (Table 4). The numbers reported on Table 4 do not fully depict the severity of these declines. Remaining mussel populations in these streams occur at extremely low abundance and are primarily represented by old individuals of long-lived species (e.g., *Amblema plicata*, *Actinonaias ligamentina*, *Cyclonaias tuberculata*). These characteristics suggest that the mussel fauna of these streams soon will be lost almost completely. In addition to these three streams, enigmatic declines appear to be occurring in several other streams including Drakes Creek (upper Green River drainage), the Dix and Red rivers (Kentucky River drainage), Kinniconick Creek, and Tygarts Creek.

The cause of these declines is unknown but their rapid and broad mode of action suggests that one or a few widespread, pervasive factors are responsible. Increased sedimentation in streams is widely invoked as a cause of mussel declines (e.g., Brim Box and Mossa 1999), but it is unlikely that sedimentation increased abruptly in the 1970s, coincident with enigmatic mussel declines (Haag 2012); however, their role in mussel declines remains incompletely understood. Other potential factors such as disease and the appearance of the invasive bivalve, *Corbicula fluminea* (see section VI.B.4), are not well studied (Haag 2012). Apart from dams and the effects of coal mining, these enigmatic declines are one of the greatest contributors to loss of mussel diversity in Kentucky. Until their causes are understood, we have little ability to prescribe preventative or remedial actions.

**VI.B.6. Habitat fragmentation and isolation**

Habitat fragmentation and isolation of populations are insidious factors potentially related to mussel declines in many areas. Large dams or other severe impacts to large streams have effectively eliminated the interconnectivity that existed within river systems historically. For example, all remnant mussel populations in unimpounded streams in the middle Cumberland River drainage (e.g., Big South Fork, Buck Creek, Rockcastle River) are now isolated from each other because Wolf Creek Dam destroyed the dispersal corridor between them (i.e., the Cumberland River). Population isolation occurs in any stream system that is fragmented by dams or other severe impacts to the mainstem stream that previously served as a dispersal corridor.

Habitat fragmentation eliminates the potential for immigration into an isolated population from other populations, and this can have several negative effects. First, immigration is important in allowing populations to recover from drought, localized human impacts (e.g., a chemical spill), or other factors that result in sharp reductions in population size. Second, small populations may not be self-sustaining and may
depend on immigration from larger populations, even in the absence of severe impacts. Third, in very small populations, inbreeding can reduce the vigor of remaining individuals over time.

The extent to which these factors may be causes of mussel declines varies greatly depending on the extent of habitat fragmentation, the size of isolated populations, and life history characteristics of species (Haag 2012). For example, in the middle Cumberland River drainage, populations of large river species that survive only in the lower reaches of unimpounded tributaries are at particular risk of extinction because they likely depended on immigration from larger populations in the Cumberland River, which are now destroyed (e.g., see *Truncilla truncata*). In contrast, small-stream species that were widely distributed and abundant in tributary streams and rare in the mainstem (e.g., *Villosa* "taeniata") ostensibly have a greater chance of long-term survival in the absence of severe human impacts.

Habitat fragmentation results in an extinction debt, in which population size and diversity in surviving mussel assemblages continue to be eroded long after the direct effects of habitat destruction have been manifested. Despite differences among species, all isolated populations are vulnerable to these effects to some extent. Other severe human impacts such as coal mining compound the extinction debt and hasten its payment by further reducing population size. Although its effects are subtle and difficult to quantify, habitat fragmentation is one of the most serious and intractable threats facing the mussel fauna, and it can be expected to result in additional species losses in the future.
VII. Interpreting species accounts

We prepared species accounts for all 98 mussel species reported from Kentucky. We also prepared separate accounts for two subspecies: *Epioblasma torulosa torulosa* and *E. t. rangiana*. We did not prepare separate accounts for *Epioblasma florentina florentina* and *E. f. walkeri* because of uncertainty about the taxonomic status of these subspecies and their historical distribution; all information for these two subspecies appears in the account for *E. f. walkeri*. Each species account includes distribution maps and the text is organized into four sections: general distribution, Kentucky distribution, habitat and larval hosts, and conservation status. Below, we describe our methods for preparing each section and provide guidance about their interpretation.

VII.A. General distribution

We provide a description of the overall distribution of each species for context in understanding the distribution of a species in Kentucky. We determined the general distribution of each species based on a large number of sources, primarily: Ortmann (1919); Isely (1924); Murray and Leonard (1962); R.I. Johnson (1978); Matthiak (1979); Clarke (1981a, b; 1985); Cummings and Mayer (1992); Vidrine (1993); Oesch (1995); Howells et al. (1996); Strayer and Jirka (1997); Parmalee and Bogan (1998); Backlund (2000); Nedeau et al. (2000); Sietman (2003); Jones et al. (2005); Williams et al. (2008); Harris et al. (2009); Watters et al. (2009); and Williams et al. (2014). Other sources are given in Haag (2010). Sources for general distribution are not cited in species accounts except for specific instances related to discussion of species introductions, uncertain records, or other issues.

VII.B. Kentucky distribution

We plotted all verified or accepted records for each species on dot distribution maps. Sources for the vast majority of records are not specified in the species accounts due to obvious space limitations. Unusual or noteworthy records discussed in the accounts are referenced either by a literature citation or institutional abbreviation as identified in section IV.C.1. Records attributed to KNP are those originating from KNP surveys but not otherwise reported in the literature or represented by catalogued museum voucher specimens. Other records not represented by literature or museum sources are based on personnel communications from colleagues and are referenced as such.

Each species has two separate maps corresponding to two time periods: pre-1990 and 1990–2015. We provided an additional depiction of temporal patterns in species occurrence in the following way. For the pre-1990 maps, records of living individuals or recently dead shells collected from 1970 to 1989 are plotted as solid circles (●). Records of relic shells from 1970 to 1989 and all records prior to 1970 are plotted as open circles (○). For 1990–2015 maps, all records of living individuals or recently dead shells collected during this period are plotted as solid circles and all records of relic shells are plotted as open circles.

Collection records from archaeology sites are plotted as triangles (▲), and these records appear exclusively on pre-1990 maps. Records of recent, documented species introductions or reintroductions from conservation activities are plotted as inverted triangles (▼). Significant records with imprecise locality information (e.g., Kentucky River) are plotted as solid squares (■) approximately in the midpoint of the stated stream; imprecise records are not plotted for species that had an abundance of records with
precise localities. On both maps, each symbol represents one or more collections; separate records in close proximity were plotted as one locality.

The Kentucky Distribution section provides a verbal description of the distribution of each species in the state in historical and recent times based on the distribution maps. For species first described from Kentucky, we begin this section by providing the type locality. Descriptions of species distributions generally proceed from west to east based on the major drainages defined in Section III and are followed by more specific discussion of unusual, problematic, or other noteworthy records. We use the terminology of Jenkins et al. (1972) to describe the hierarchical organization of streams: a basin is a group of interconnected drainage basins (e.g., Ohio River basin); a drainage is a group of interconnected streams or systems entering a basin (e.g., middle Cumberland River drainage; see Section III); and a system is a group of interconnected streams within a drainage (e.g., Rockcastle River system). We also describe species occurrence based on physiography or other geographical boundaries if these boundaries are germane to the species’ distribution. When we refer to ‘lowland habitats in western Kentucky,’ we are referring to habitats found in the Mississippi Embayment province and the Shawnee Hills section of the Interior Low Plateaus province (see Section II). We describe species distribution and relative abundance statewide or in specific drainages following Smith (1965), as follows: generally distributed implies that any suitable habitat within the prescribed area should be expected to yield individuals with a reasonably thorough search; occasional implies that suitable habitat may or may not yield individuals even after prolonged search; sporadic implies that encountering individuals even after a prolonged search cannot be predicted. We based these descriptions primarily on our own field experience in Kentucky and, in some cases, on literature reports. This scheme is an attempt to provide some level of objectivity and consistency to inherently subjective assessments of species occurrence in the absence of comparable quantitative data. Nevertheless, readers are cautioned that even these descriptions have a high level of subjectivity.

VII.C. Habitat and larval hosts

We provide general information about the habitat occupied by each species and its abundance relative to other species with which it co-occurs. This information is based primarily on our own observations but is supplemented by literature sources. We provide general information on host use for each species as relevant to the species’ distribution and habitat use in the state. This information is based on a large number of sources summarized in Cummings and Watters (2010); readers desiring more specific information should consult those sources.

VII.D. Conservation status

We provide a description of trends in the distribution and abundance of each species in Kentucky over the last 100 years or so and a discussion of factors potentially related to these trends. These assessments were made based on changes in distributions illustrated on the distribution maps, literature sources, and our own experience. We emphasize that these assessments are subjective to a large degree and quantitative data to support these assessments are rarely available. Furthermore, it is often difficult to assess changes in species distributions because of differences in sampling effort between time periods. For example, the Ohio River has not been surveyed systematically since the early 1980s survey of Williams and Schuster (1989), and it is difficult to determine whether the relative dearth of occurrences for many species in 1990–2015 relative to pre-1990 reflects a lack of sampling or a
decline in distribution or abundance (e.g., *Truncilla donaciformis*). This section closes with the formal conservation status assigned to each species in Kentucky by the Kentucky State Nature Preserves Commission (KNP 2012) and range-wide by the American Fisheries Society (AFS; Williams et al. 1993) and the U.S. Fish and Wildlife Service (USFWS 2016; only for species listed as Threatened or Endangered under the U.S. Endangered Species Act). For some species, we make recommendations about revision of current conservation status in Kentucky.
VIII. Species accounts
**Actinonaias ligamentina** (Lamarck, 1819)

**Mucket**

**General Distribution**
Mississippi River basin from Louisiana and Mississippi north to Minnesota, and west to Kansas and Nebraska. Throughout the Ohio River basin from the mouth upstream to New York. Great Lakes basin from Lake Michigan to the Niagara River.

**Kentucky Distribution**
Type locality: Ohio River. Generally distributed nearly statewide, but absent from the Mississippi River and direct tributaries, and sporadic and rare in oth-
er lowland habitats in western Kentucky; absent in the upper Cumberland River drainage above Cumberland Falls.

**Habitat & Larval Hosts** Generally restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates, but can occur in the lower reaches of smaller tributaries. Most abundant in medium-sized streams such as the upper Green, Licking, and Rockcastle rivers, and in larger tributaries of the upper Kentucky River drainage; in these rivers, it is often the dominant species in main-channel mussel beds. Usually a minor component of mussel beds in the largest rivers, such as the Ohio, Tennessee, and lower Green, where it is only sporadic to occasional. Larvae metamorphose robustly on black basses (*Micropterus*), but the extent to which it uses other host species is poorly known.

**Conservation Status** *Actinonaias ligamentina* was historically a common and often dominant species in many Kentucky rivers (Danglade 1922; Ortmann 1926a; Neel and Allen 1964) and it remains so today. However, several local populations have been extirpated by severe impacts such as coal mining (e.g., Horse Lick Creek; Haag and Warren 2004), and others may be reduced or may be experiencing long-term declines. For example, *A. ligamentina* continues to dominate mussel beds in much of the upper Green River, but evidence of recruitment is rare in many places. Because this species can live for nearly 50 years (Moles and Layzer 2008), reduced recruitment may not result in measurable declines in population size for many years; improvements in water release from Green River Dam and other conservation measures in the watershed may help to correct this situation (Konrad et al. 2012). Most large-scale declines of this species in Kentucky are directly associated with dams. It appears minimally tolerant of impoundment, and it persists in impounded streams only in sections that retain considerable riverine influence, such as the lower Ohio River. It formerly was abundant in the middle Cumberland River (Neel and Allen 1964), but was extirpated from that stream by Wolf Creek Dam, with the exception of a small population immediately below Cumberland Falls (Cicerello and Laudermilk 1997). Although now apparently absent in the impounded Kentucky River, it was the second most abundant species in an archaeological assemblage from the river in Woodford County (Call and Robinson 1983), and a specimen was found in excavations at the original site of Fort Boonesborough (ca. 1780) in Madison County (N. O’Malley, personal communication). It is unclear the extent to which the current rarity of this species in large rivers is a natural feature of these assemblages or a result of impoundment. It was rare in the lower Tennessee River prior to impoundment, and was rare or absent in archaeological assemblages from the lower Cumberland and Green rivers (Ortmann 1925; Casey 1987; Morey and Crothers 1998). Even if *A. ligamentina* never was a dominant member of mussel beds in the largest rivers, impoundment likely has further reduced its abundance and distribution in these habitats. AFS: currently stable.
**Actinonaias pectorosa (Conrad, 1834)**

Pheasantshell

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**General Distribution**
Endemic to the Tennessee-Cumberland faunal province, occurring in northern Alabama, southern Kentucky, Tennessee, and southwestern Virginia.

**Kentucky Distribution**
Sporadic to occasional in the lower Cumberland River drainage, mainly in the Red River system, Logan County; one record exists from the Little River,
Trigg County (KNP). Generally distributed to occasional in tributaries throughout the middle Cumberland River drainage but rare in the mainstem. Generally distributed in the upper Cumberland River drainage, including the mainstem upstream to Bell County.

**Habitat & Larval Hosts**

Most common in small to medium-sized streams in gravel and sand substrates, and rare even historically in the middle Cumberland River except for the area immediately below Cumberland Falls (Neel and Allen 1964). Larvae metamorphose robustly on black basses (*Micropterus*), but the extent to which it uses other host species is poorly known.

**Conservation Status**

*Actinonaias pectorosa* is a characteristic and locally common member of mussel assemblages throughout much of the Cumberland River system. Due to its occurrence mainly in smaller streams, *A. pectorosa* was affected to a lesser extent than other Tennessee-Cumberland endemic species by impoundment of the Cumberland River. Nevertheless, this species has declined substantially in Kentucky and its future is in jeopardy. It is now apparently extirpated from the lower Cumberland River drainage (Little and Red rivers) and Pitman Creek, and it is rare or nearly extirpated in Buck Creek, Horse Lick Creek, and the Little South Fork Cumberland River. It was abundant formerly in the Cumberland River immediately below Cumberland Falls (Neel and Allen 1964; Stansbery 1969) but has declined substantially at that location (Cicerello and Laudermilk 1997). It remains relatively common only in the Big South Fork Cumberland River, Rockcastle River, and the upper Cumberland River above Cumberland Falls, but the long-term status of these populations is unknown. Interestingly, *A. pectorosa* appears to have become more common in the upper Cumberland River in recent times and may even have been absent there historically. It is now the most common mussel species above the falls (Cicerello and Laudermilk 2001), but it was not reported there in 1911, and only one individual was collected in the late 1940s (Wilson and Clark 1914; Neel and Allen 1964). The reasons for this increase are unknown, but it is possible that the species was introduced above the falls by pearlers in the early 1900s (see Wilson and Clark 1914). KNP: none, but this species warrants listing as threatened; AFS: special concern.
**Alasmidonta atropurpurea** (Rafinesque, 1831)

Cumberland Elktoe

Endemic to the middle and upper Cumberland River drainages, Kentucky and Tennessee, but restricted to streams above the hypothesized original location of Cumberland Falls near Burnside, Kentucky, and the upper Big South Fork system. The record from Collins River, Tennessee (Parmalee and Bogan 1998), likely represents a misidentification of *A. marginata* or an undescribed taxon (Butler and Biggins 2004). Historical records of *A. marginata* in the upper Cumberland River drainage are misidentifications of *A. atropurpurea*. The restricted range of *A. atropurpurea* may be a result of divergence from ancestral species in isolation above Cumberland Falls, perhaps involving headwater exchange with the upper Kentucky River system (see section V.D).
Type locality: Cumberland River. Even within its restricted range, the distribution of *A. atropurpurea* is quite localized. Upstream of the present location of Cumberland Falls, it is reported from only two sites in the Cumberland River, McCreary/Whitley counties (UMMZ), and Williamsburg, Whitley County (Clarke 1981b; MCZ; all as *A. marginata*), and from only three tributaries: Marsh and Jellico creeks, McCreary County, and Laurel Fork, Whitley County; not reported from the drainage upstream of Williamsburg. Between the present and original location of the falls, it is reported from a single stream in the Rockcastle River system (Sinking Creek, Laurel County; KNP), and from two sites in the Laurel River system: Laurel River, Laurel County (as *Strophitus undulatus*; Neel and Allen 1964; UMMZ), and Lynn Camp Creek, Whitley County (as *A. raveneliana*; UMMZ). The record from Horse Lick Creek, Jackson County (Rockcastle River system; Ahlstedt 1986), is considered a misidentification of *A. marginata*. Downstream of the original location of the falls, it is reported only from the Big South Fork system upstream of and including Rock Creek, McCreary County. It does not appear to co-occur with *A. marginata*, even in the Big South Fork and Rockcastle River systems, which contain both species.

This species is restricted to poorly buffered streams on the Cumberland Plateau and is largely restricted to small streams. This species appears to be a host specialist on suckers (Catastomidae), especially Northern Hog Sucker (*Hypentelium nigricans*).

The historical range of *Alasmidonta atropurpurea* is unclear because small streams in its range were not well surveyed prior to degradation by coal mining and other impacts (e.g., Harker et al. 1980). Its apparent absence upstream of Williamsburg may be due to these factors. Regardless, *A. atropurpurea* is highly vulnerable to extinction because its restricted distribution lies mostly within coal-bearing regions. It appears extirpated from the Laurel River system due to coal mining, impoundment by Laurel River Reservoir, and stream channelization and urbanization associated with Corbin (Lynn Camp Creek). It survives in Jellico and Sinking creeks, but these populations are small and isolated (Cicerello and Laudermilk 2001; KNP; J. Kiser, personal communication). The small population present in Laurel Fork as recently as 1996 was not found in 2008 (R. Evans, personal communication). A large population existed throughout Marsh Creek until at least the mid-1990s (Cicerello 1995), but this population has declined dramatically probably due to coal mining and oil drilling (KDOW; M. Compton, personal communication). A large population persists in Rock Creek, a tributary to the Big South Fork, but it is isolated from other populations by coal mine pollution in the lower portion of the creek and the adjacent section of the Big South Fork (Cicerello 1996). The upper Big South Fork watershed now likely supports the largest remaining population on Earth. Although *A. atropurpurea* occurs only sporadically in the Kentucky section of the Big South Fork, it is widespread and abundant in several smaller tributaries in Tennessee, and connectivity among these streams suggests that the upper Big South Fork may harbor a single, large metapopulation (Ahlstedt et al. 2003–2004; Butler and Biggins 2004). Long-term survival of the species depends not only on maintenance of high water and habitat quality in the Big South Fork, but on identification and remediation of factors responsible for declines in other streams. Because of the complex biogeographical history of the upper Cumberland River drainage (see section V.D), it is imperative to assess genetic relationships among remaining populations. KNP: endangered; AFS: endangered; USFWS: endangered.
Alasmidonta marginata Say, 1818

Elktoe

**General Distribution**  Mississippi River basin from the Ouachita and Ozark highlands in Arkansas north to Minnesota, and west to eastern Kansas and South Dakota. Ohio River basin upstream to New York, but absent in lowland regions of the lower basin. Great Lakes basin from Lake Michigan to the St. Lawrence River system, and the Hudson and Susquehanna river drainages on the Atlantic Coast.
Sporadic to occasional in upland streams in the lower and middle Cumberland, upper Green, Kentucky, and Licking river drainages. Absent in lowland habitats in western Kentucky including the Tradewater River, and reported from the lower Green River drainage only in the Rough River, Hardin County (KNP). Reported from the Ohio River and the Salt River drainage by only two historical records each: Ohio River, adjacent Indiana (Call 1900); Ohio River, Kenton County (Watters et al. 2009); Floyds Fork, Jefferson County (OSUM); Rolling Fork, Marion County (MCZ; Clarke 1981b). Reported in the Little Sandy River drainage from only one stream, Laurel Creek, Elliott County (KNP). Not reported from Kinniconick Creek, Tygarts Creek, or the Big Sandy and upper Cumberland river drainages; records from the latter (UMMZ; MCZ; Clarke 1981b) are *A. atropurpurea*. This species is widely distributed and often common in the northern portion of its range, but it is sporadic and typically rare south of the Ohio River (e.g., Ortmann 1924; Neel and Allen 1964; Williams et al. 2008). In Kentucky, it is common locally only in the Red River, Menifee and Wolfe counties (Houp 1993; Cicerello 1997), and in the lower Licking and South Fork Licking rivers upstream to Harrison and Robertson counties (KNP; W.R. Haag, personal observations).

Restricted to upland regions, but can occur in nearly any size stream from the largest rivers to small streams. This species appears to be a host generalist to some extent, able to use a wide range of fish species, but its larvae metamorphose most robustly on suckers (Catostomidae; M. Hove, personal communication).

*Alasmidonta marginata* appears to have been sporadically distributed in Kentucky even historically, but its range in the state has thinned considerably and only seven remaining populations are known. This species appears intolerant of impoundment, and it has not been reported from the Ohio River in over 100 years. It probably was present at least locally in the lower Green and Kentucky rivers, but these rivers were not surveyed prior to impoundment. It appears extirpated in the lower Cumberland River drainage and the Rough, Barren, Nolin, Salt, and South Fork Kentucky river systems. It was rare but widely distributed in the middle Cumberland River (Neel and Allen 1964), but this population was eliminated by Wolf Creek Dam, and the population in the Little South Fork apparently was extirpated by coal mining and oil drilling (Warren and Haag 2005). It now appears extirpated throughout the Cumberland River drainage, except perhaps in the Rockcastle River system, where it is sporadic and rare at best (Cicerello 1993; Layzer and Madison 1994; Haag and Warren 2004). It remains widespread but rare in the upper Green River, Edmonson, Hart, and Green counties (Cicerello 1999; McGregor et al. 2007, 2009; KNP). The large population present in the Red River (Kentucky River drainage) until the 1990s appears to have declined dramatically (M. McGregor, personal communication). Apart from these populations and the large population in the lower Licking River drainage, only three other populations are known, and each is small and isolated: Elkhorn Creek, Franklin County; Ball’s Fork Troublesome Creek, Knott County; Laurel Creek, Elliott County (all KNP). KNP: threatened; AFS: special concern.
**Alasmidonta viridis** (Rafinesque, 1820)

Slippershell Mussel

**General Distribution**  
Mississippi River basin from the Ouachita and Ozark highlands in Arkansas north to southern Wisconsin, and west to eastern Kansas and Iowa. Ohio River basin upstream to West Virginia, but absent in lowland regions of the lower basin. Great Lakes basin from Lake Michigan to the Niagara River.

**Kentucky Distribution**  
Type locality: Ohio River. Generally distributed throughout the central portion of the state from the Salt to the Licking River drainage. Also widespread in the
upper Rough River system (lower Green River drainage), the upper Green River drainage, and the Cumberland River drainage from the Red River system upstream; one of the few species present above Cumberland Falls. Apart from the type locality, only a single record is available for the Ohio River (Kenton County, NMNH). Absent from lowland habitats in western Kentucky, but two records exist for the upper Mud River system, Logan County (KDOW, KNP). Not reported from Ohio River tributaries upstream of the Licking River.

Habitat & Larval Hosts
Largely restricted to small or medium-sized streams, and can penetrate far into headwaters where it may be the only species present; this species is particularly characteristic of small streams in the Bluegrass physiographic section. A few records exist from larger streams including the Ohio, Green, and lower Licking rivers. This species is a host specialist mainly on sculpins (Cottus), but some populations also may use darters (Percidae) (A. Shepard, personal communication).

Conservation Status
*Alasmidonta viridis* remains a characteristic and locally common species in small, upland streams, particularly in central Kentucky. Because it occurs predominantly in small streams, it has been affected by large impoundments to a lesser extent than most other mussel species in the state. Nevertheless, this species does not adapt to impounded streams, and many local populations likely have been extirpated or isolated by numerous small watershed lakes and mill dams. A variety of other, mostly unknown, factors have contributed to a thinning of its range. This species is nearly extirpated from the Cumberland River drainage. Only one surviving population is known in the lower Cumberland River drainage (Pleasant Run, Logan County, KNP). In the middle Cumberland River drainage, it appears extirpated from the Little South Fork by coal mining and oil drilling (Warren and Haag 2005), and only two remaining populations are known, both of which are small: upper Rockcastle river system, Jackson County (Cicerello 1992; Haag and Warren 2004), and Beaver Creek, Wayne County (KNP). In the upper Cumberland River drainage, it was locally common in Marsh Creek, McCreary County, and uncommon in Laurel Fork, Whitley County, until at least the mid-1990s (Cicerello 1995; Cicerello and Laudermilk 2001), but both of these populations have declined dramatically or are extirpated probably due to coal mining and oil drilling (M. Compton and R. Evans, personal communication); no other populations are known above Cumberland Falls. In the Green River drainage, it occurs only sporadically in the upper Rough, Barren, and Nolin river systems, and is otherwise known to persist in only two streams: Russell Creek, Adair County, and the Green River, Casey County (KNP). It remains generally distributed and locally common in the Salt, Kentucky, and Licking river drainages, especially in the Bluegrass physiographic section, but recent collections at some sites have yielded only relic shells (e.g., Dix River system). AFS: special concern.
Amblema plicata (Say, 1817)

General Distribution

One of the most widely distributed North American mussel species, occurring throughout eastern North America with the exception of Atlantic Coast and most eastern Gulf Coast drainages. Mississippi River basin from Louisiana north to Minnesota, and west to Kansas and South Dakota. Throughout the Ohio River basin from the mouth upstream to New York. Great Lakes basin from Lake Michigan to the Niagara River, the southern Hudson Bay basin west to Saskatchewan, and in Gulf Coast drainages from the Choctawhatchee River, Florida, to the Nueces River, Texas.
Kentucky Distribution

Generally distributed statewide with the exception of the upper Cumberland River drainage above Cumberland Falls. Widespread but rare historically in the middle Cumberland River, and reported elsewhere in the middle Cumberland River drainage only in Beaver Creek, Russell County, and the Rockcastle River system (Neel and Allen 1964); a single archaeological record exists for the Big South Fork, McCreary County (J. Kiser and P. Parmalee, personal communication).

Habitat & Larval Hosts

Occurs in a wide variety of habitats from the Mississippi River to small streams, in uplands and lowlands, but typically does not penetrate far into the headwaters, and generally uncommon in smaller streams. This species achieves its maximum abundance in main-channel mussel beds, but it also thrives in depositional areas. It adapts readily to riverine impoundments such as Kentucky and Barkley lakes, but is absent in most other lentic habitats. It is a dominant component of mussel beds in some parts of the Ohio River and in the Tennessee and lower Cumberland rivers. Host use of this species is not well studied, but available information and information for a close relative, A. neislerii, suggests that it is a generalist, able to use a wide variety of fish species as hosts.

Conservation Status

*Amblema plicata* remains common in a variety of habitats statewide, and its overall distribution appears to have changed little in the last 100 years. The distribution of the species appears much reduced in the Tradewater River, which has been heavily affected by coal mining. It was extirpated from the middle Cumberland River by Wolf Creek Dam, and appears to persist in the middle Cumberland River drainage only in the Rockcastle River system, where it remains common (Cicerello 1993, 1994). Several populations in the state show evidence of vigorous recent recruitment (e.g., Ohio, Tennessee, Green, and Licking rivers), but the health of most populations is unknown. Because *A. plicata* can live >50 years (Haag and Rypel 2011), long-term declines may not be evident for some time. Populations in the impounded Tennessee and lower Cumberland rivers may have increased due to the inundation of former river floodplains, which this species has colonized extensively (Blalock and Sickel 1996; Garner and McGregor 2001). AFS: currently stable.
Anodonta suborbiculata Say, 1831

Flat Floater

Probable historical distribution included the Mississippi River basin from Louisiana north to southern Minnesota, and west to Kansas and South Dakota, and the Ohio River basin upstream to about the Green and Wabash river drainages, including the lowermost portions of the Tennessee and Cumberland rivers. This species thrives in depositional environments in lakes and reservoirs; consequently, it has greatly increased its range in the last 50 years following widespread stream impoundment. It now occurs in the Ohio River basin upstream to Ohio and West Virginia (Watters et al. 2009). Its historical distribution in Gulf Coast drainages is unclear. It was not reported in the Mobile River basin prior to 1976 but is now widespread there in large, impounded rivers (Williams et al.)
Similarly, it was not reported in Texas in the 1930s but now occurs west to at least the Brazos River (Howells et al. 1996).

**Kentucky Distribution**

Historically, this species was probably confined to the western third of Kentucky from the Mississippi River east to the lower Green River drainage. It now occurs sporadically or occasionally throughout the Ohio River, Kentucky and Barkley lakes, and in other Ohio River tributaries east to at least the lower Kentucky River drainage. It has expanded its range in reservoirs of the Tennessee River drainage as far upstream as Knoxville (Parmalee and Bogan 1998), but apparently has not yet colonized similar habitats in the middle Cumberland River drainage.

**Habitat & Larval Hosts**

In its original Kentucky range, this species occurs in lowland streams, wetlands, oxbow lakes, and depositional backwaters of larger rivers. It now may be found in reservoirs or other lentic habitats beyond its historical range. This species is a host generalist, able to use a wide range of fish species.

**Conservation Status**

*Anodonta suborbiculata* doubtless has experienced localized declines or extirpation in response to widespread wetland drainage and stream channelization in western Kentucky. However, this is a highly adaptable species because of its fast growth, early maturity, and generalist host use; these traits allow it to tolerate considerable disturbance and to colonize habitats that are unsuitable for most other mussel species (Haag 2012). It remains a conspicuous and locally abundant member of mussel assemblages in lowland habitats of western Kentucky, where it can persist even in highly modified, channelized streams or transient, floodplain lakes. It is one of the few mussel species whose distribution in Kentucky has increased substantially in recent decades. The impoundment of large rivers such as the Ohio, Tennessee, lower Cumberland, and lower Green has greatly increased the extent of suitable habitat for this species and has allowed natural dispersal throughout those drainages. Increased sedimentation in free-flowing streams also may have increased habitat availability for the species. Recent occurrences of this species in isolated habitats such as Green River Reservoir, and a pond and a small reservoir (Benjy Kinman Lake) in the lower Kentucky River drainage (Carroll and Henry counties, respectively) are likely the result of stocking of fishes infected with glochidia of *A. suborbiculata*. Stocking of infected fishes may have aided in its expansion in other areas (e.g., Williams et al. 2008) and can be expected to result in establishment of additional populations in reservoirs or other lentic habitats nearly anywhere in the state. AFS: currently stable.
Anodontoides denigrata (Lea, 1852)

Cumberland Papershell

Endemic to the middle and upper Cumberland River drainages, Kentucky and Tennessee, but most of the range of this species is in Kentucky. Mainly restricted to streams above the hypothesized original location of Cumberland Falls near Burnside, Pulaski County. Occurs in a few small streams in the upper Big South Fork Cumberland River system, Tennessee, but not reported from that system in Kentucky (T. Hern, personal communication). The only other Tennessee record is from the Clear Fork Cumberland River, Campbell County (Wilson and Clark 1914), which likely is the type locality (Ortmann 1918). This species formerly was synonymized with the widespread A. ferussacianus (e.g., Williams et al. 1993), but the two taxa are genetically distinct sister species (Bogan and Raley...
The historical distribution of *A. denigrata* elsewhere in the Cumberland River drainage is unclear. The only other reports of *Anodontoides* from this drainage are from the Little and Red river systems in western Kentucky (see *A. ferussacianus*), and the Stones and Roaring rivers, Tennessee (Wilson and Clark 1914; Bogan and Raley 2013). Specimens from the Little and Stones rivers were identified as *A. denigrata* by Bogan and Raley (2013). However, genetic analysis showed that a specimen from the Little River is *A. ferussacianus* (M. Compton, personal communication); tissue samples from the Stones River were not available. If the Stones River population is conspecific with *A. denigrata*, the name *A. argenteus* (Lea, 1840; described from the Stones River) has priority over *A. denigrata*. We cannot rule out the possibility that *A. denigrata* (= *A. argenteus*) had a wider distribution in the Cumberland River drainage, but such a distribution is at odds with that of all other fishes and mussels thought to have evolved in isolation above Cumberland Falls (see *Alasmidonta atropurpurea* and section V.D). Until additional information becomes available, we follow traditional usage of *A. denigrata* and the conclusion that this species is restricted to streams near or upstream of the original location of Cumberland Falls.

### Kentucky Distribution
The distribution of *Anodontoides denigrata* is similar to that of *Alasmidonta atropurpurea*, but *A. denigrata* is more widely distributed above Cumberland Falls. Reported as far upstream as the Cumberland River, Bell County (Wilson and Clark 1914; Ortmann 1918; UMMZ; all as *A. ferussacianus*), and widely but sporadically distributed in tributaries in Bell, Knox, McCreary, and Whitley counties (UMMZ, as *Strophitus undulatus*; Cicerello and Laudermilk 2001). Below the falls, reported only from a few sites in the Laurel and Rockcastle river systems (Neel and Allen 1964, as *Strophitus undulatus*; UMMZ, as *A. ferussacianus*; KNP). Not reported from the Big South Fork system in Kentucky.

### Habitat & Larval Hosts
Like *Alasmidonta atropurpurea*, this species usually is restricted to small, poorly buffered streams, and the two species often occur together; however, *A. denigrata* can occur in smaller streams than *A. atropurpurea*. The Bell County collections are the only reports of the species from the Cumberland River proper, and it was not found elsewhere in the river in subsequent surveys (Neel and Allen 1964; Cicerello and Laudermilk 2001). Glochidia of this species metamorphose robustly on minnows (Cyprinidae), but it may be a host generalist, able to use a wide variety of host fishes.

### Conservation Status
The historical range of *Anodontoides denigrata* is unclear because small streams in its range were not well surveyed prior to degradation by coal mining and other impacts (e.g., Harker et al. 1980). Its apparent absence upstream of Bell County may be due to these factors. Regardless, *A. denigrata* is highly vulnerable to extinction because its restricted distribution lies mostly within coal-bearing regions. Above Cumberland Falls, a large population existed throughout Marsh Creek, where it was the most abundant species, until at least the mid-1990s (Cicerello 1995), and it was sporadic but locally common in several other tributaries (Cicerello and Laudermilk 2001). Many of these populations, including the one in Marsh Creek, have declined dramatically or are possibly extirpated probably due to coal mining and oil drilling (M. Compton and R. Evans, personal communication). Below the falls, it appears extirpated from the Laurel River system due to coal mining, impoundment by Laurel River Reservoir, and stream channelization and urbanization associated with Corbin (Lynn Camp Creek). Below the falls, only three small remaining populations are known, all in the Rockcastle River system: Sinking Creek, Laurel County (KNP); South Fork Rockcastle River, Clay/Laurel counties (E. Hartowicz, personal communication); and Laurel Fork, Jackson County (KNP). KNP: endangered; AFS: not recognized; USFWS: petitioned for listing.
Anodontoides ferussacianus (Lea, 1834)

Cylindrical Papershell

Mississippi River basin from Arkansas north to Minnesota, and west to Colorado and Wyoming. Ohio River basin upstream to New York, but generally absent in lowland regions of the lower basin, and absent in most of the Tennessee and Cumberland river drainages; the only Tennessee River drainage record is from the Powell River, Virginia (Ortmann 1918). Throughout the Great Lakes basin from Lake Superior to the St. Lawrence River, the southern Hudson Bay basin west to Saskatchewan, and the Hudson River basin on the Atlantic Coast.
Type locality: Ohio River, Cincinnati, Ohio. Occasional in the northern third of
the state, especially in the Bluegrass physiographic section, from the Salt to the
Licking river drainages, and in several small, direct tributaries to the Ohio River (e.g., Boone, Oldham
counties). Absent from the Appalachian Plateaus, with the exception of one record from Tygart’s Creek,
Greenup County (Zeto 1979), and an archeological record from the Red River, Menifee/Powell counties
(D. Dourson, personal communication). Sporadic in the Green River drainage, with isolated records from
the Pond, Rough, Mud, and Barren river systems; a record for the upper Green River (Williams 1969) is
unsubstantiated. Reported from the Cumberland River drainage only in the Little River system, Christian
County (KNP); Red River system (Dry Fork), Logan County (KNP); and from single historical collections
in the Roaring and Stones rivers, Tennessee (Wilson and Clark 1914; Bogan and Raley 2013); other reports
of this species in the middle and upper Cumberland River drainages are referable to A. denigrata. Historical
specimens from the Little River were identified as A. denigrata (=A. argenteus) by Bogan and Raley
(2013), but genetic analysis of a recent specimen from the Little River confirmed its identification as
A. ferussacianus (M. Compton, personal communication). Not reported from the Tennessee River drainage in
Kentucky or from lowland habitats in western Kentucky, but a single record exists from the upper Trade-
water River, Christian County (KNP).

Characteristic of small streams, but several records exist from the Ohio and
lower Licking rivers (Call 1900; Laudermilk 1993; CM; OSUM), and a single
archaeological record exists from the lower Green River, Butler County (Claassen 2005). This species is
widespread and often abundant north of the Ohio River and in the Great Plains (e.g., Cummings and Mayer
1992; Watters et al. 2009), but it is highly localized in Kentucky and elsewhere in the southern portion its
range (Oesch 1995; Harris et al. 2009). In Kentucky, it is typically uncommon or rare but may be locally
common in a few places (e.g., Eagle Creek, Gallatin/Grant/Owen counties). This species is a host general-
ist, able to use a wide range of fish species.

The localized distribution of Anodontoides ferussacianus in Kentucky appears to
be relatively unchanged in the last 100 years. Because of its fast growth, early
maturity, and generalist host use, this species may be tolerant of disturbed or stressful habitats, such as
those in Great Plains streams (Haag 2012), and these traits likely allow it to weather a moderate degree of
human impacts. Nevertheless, some local populations appear to have declined or been extirpated. It has not
been found in the Ohio River for over 100 years, and the species was considered extirpated in the Little
River system until a single live individual was found in 2014 (Muddy Fork Little River, Christian County,
M. Compton, personal communication). Because Kentucky is at the southern limit of this species’ range
and many populations are small and isolated, its persistence in the state is vulnerable to localized, severe
impacts or long-term impacts such as global climate change. KNP: none, but this species warrants listing as
a species of special concern; AFS: currently stable.
**Arcidens confragosus** (Say, 1829)

Rock Pocketbook

**General Distribution** Mississippi River basin from Louisiana north to southern Minnesota, and west to eastern Kansas and South Dakota. Ohio River basin from the mouth upstream to at least Daviess County, Kentucky, but a single unsubstantiated historical record exists from the Ohio River at Cincinnati (Watters et al. 2009); absent in the upper half of the Tennessee and Cumberland river drainages. Gulf Coast drainages from the Mobile River basin, Alabama, west to the Guadalupe River, Texas.
Kentucky Distribution

Generally distributed to occasional in the western third of the state from the Mississippi River to the lower Barren River, Warren County, and the Green River upstream to Edmonson County. A historical record from the Big South Fork Cumberland River, Pulaski County (MCZ), is considered erroneous and probably based on inaccurate locality information.

Habitat & Larval Hosts

This species is found in depositional environments mainly in large, lowland rivers, but it also occurs sporadically in smaller lowland streams (e.g., Clarks River, McCracken County; Obion Creek, Hickman County). It adapts readily to riverine impoundments such as Kentucky and Barkley lakes, but despite its affinity for depositional habitats, it is strongly associated with rivers and absent in most lentic environments. This species is never abundant, but most lowland river mussel assemblages contain at least a few individuals. Host use of this species is poorly known, but it appears to be a generalist, able to use a wide variety of fish species.

Conservation Status

The distribution of *Arcidens confragosus* in Kentucky appears to have changed little in the last 100 years. Although typically uncommon in the state today, it is uncommon throughout its range, even in historical collections (e.g., Coker 1919). Like many lowland species, it seems somewhat resilient and adaptable to disturbance. It adapts to some extent to impounded rivers such as the Ohio, lower Tennessee, lower Cumberland, and lower Green that retain riverine characteristics. The species has increased its range in the Tennessee River upstream to Alabama subsequent to impoundment (Williams et al. 2008), and it also appears to have extended its range somewhat in the Ohio River in recent decades. Despite its apparent resilience and adaptability to impoundment, this species is likely vulnerable to severe human impacts to streams. It has not been found recently in the Tradewater River, which has been heavily impacted by coal mining. Likewise, it was probably more widespread in lowland streams such as Bayou du Chien and Obion and Mayfield creeks prior to channelization of those streams. AFS: currently stable.
Cumberlandia monodonta (Say, 1829)

Spectaclecase

General Distribution
Mississippi River basin from Arkansas upstream to Minnesota and Wisconsin, and west to eastern Kansas. Ohio River basin from the mouth upstream to West Virginia.

Kentucky Distribution
Type locality: Falls of the Ohio and Wabash River. Probably widely distributed historically in the Ohio River and in the lower reaches of large tributaries. Documented from five sites in the Ohio River; formerly of regular occurrence at the Falls of the Ohio, Jef-
ferson County (Call 1900). Also reported from the Tennessee, Cumberland, and Green rivers; generally
distributed in the middle Cumberland River prior to impoundment (Neel and Allen 1964). Not reported
from the Salt, Kentucky, or Licking rivers, but potentially occurred in those rivers historically. Introduced
in the upper Big South Fork Cumberland River in 2008, apparently upstream of the species’ historical
range (see subsequent).

**Habitat & Larval Hosts**

Restricted to large streams, where it occurs primarily under slab rocks and
bedrock shelves or among boulders, often in deep water. The rarity of this
species in historical collections is probably due to its specialized habitat, which is often overlooked by con-
ventional survey methods. In these habitats, the species can be abundant; in the Tennessee River in Ala-
bama prior to impoundment, as many as 200 were found under a single slab rock (Hinkley 1906), and simi-
larly high local densities are reported elsewhere (Stansbery 1966; Baird 2000). The host for this species is
unknown despite considerable research effort; over 50 fish species have been tested but none have proven
suitable.

**Conservation Status**

*Cumberlandia monodonta* apparently has disappeared from most of its historical
range in Kentucky. The population in the middle Cumberland River was largely
eliminated by Wolf Creek Dam in 1950, but a single live individual was found in the river in 1982 (Miller
et al. 1984). Because this species can live >50 years (Haag and Rypel 2011), this individual probably re-
cruited prior to dam construction and the population is considered extirpated. In 2008, 43 individuals from
the Tennessee River drainage (Clinch River) were released in the Big South Fork Cumberland River,
McCreary County (McGregor et al. 2008), but the success of this introduction is not known. The species
now seems absent in most other rivers that may have supported populations historically, including most of
the Ohio River. However, it was recently discovered in the lower Ohio River, McCracken County (INHS),
and the lower Cumberland River, Livingston County (Fortenbery 2008), where it is sporadic and rare. The
Green River in Butler/Warren, Edmonson, and Hart counties appears to support the largest remaining popu-
lation in the state. Recent surveys in this section of the river revealed a large population with evidence of
recent recruitment (L. Koch, personal communication). Concerted sampling efforts in the specialized habi-
tat for this species may reveal additional populations elsewhere in the state. KNP: endangered; AFS: threat-
ened; USFWS: endangered.
Cyclonaias tuberculata (Rafinesque, 1820)

Purple Wartyback

Mississippi River basin from Arkansas north to Minnesota, and west to Missouri. Ohio River basin from the mouth upstream to Pennsylvania. Great Lakes basin from Lake Michigan to western Lake Erie.

Kentucky Distribution

Type locality: Ohio River and its tributaries. Generally distributed to occasional throughout the Ohio River and in larger streams from the Tennessee to the Licking river drainage. Absent in lowland habitats in western Kentucky including the Mississippi River and
direct tributaries, the Tradewater River, and much of the lower Green River drainage. An archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). Occasional in the lower Cumberland River drainage, and formerly generally distributed in the middle Cumberland River drainage upstream to the base of Cumberland Falls, but absent above the falls. Only a handful of records are available for the Kentucky River drainage including sites on the mainstem and a few larger tributaries, and Danglade (1922) reported it as occasional in the upper Kentucky River drainage (from unspecified locations but probably including the North Fork Kentucky River). Not reported from Ohio River tributaries upstream of the Licking River with the exception of a single historical record from the Big Sandy River, Lawrence County (UF). The occurrence of this species in the Big Sandy River is plausible, but we regard this particular record as doubtful because it came from a private shell collection known for locality errors (J. Williams, personal communication), and that collection contains other species from the same site whose occurrence there is unlikely (see *Dromus dromas*).

### Habitat & Larval Hosts
Generally restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates, but can occur in the lower reaches of smaller tributaries. Although common in main-channel mussel beds, this species is rarely a dominant member of those assemblages. This species is a host specialist on catfishes (Ictaluridae).

### Conservation Status
The distribution of *Cyclonaias tuberculata* in Kentucky has been reduced considerably in the last 100 years, and it remains common in only a few rivers in the state. This species is minimally tolerant of impoundment, and dams have reduced or extirpated many populations. It is now sporadically distributed in the Ohio River and remains common only in sections that retain considerable riverine influence, particularly the extreme lower section of the river. It remains common in the lower Tennessee River, but it is apparently extirpated from Kentucky and Barkley lakes, and no recent records exist from the lower Cumberland River. It was extirpated throughout the middle Cumberland River by Wolf Creek Dam (Neel and Allen 1964); a single live individual that apparently recruited prior to dam construction was found in 1982 (Miller et al. 1984). There are few or no historical records from the lower Green, lower Salt, and Kentucky rivers, but it probably occurred throughout those rivers prior to impoundment. Populations in smaller tributaries were likely dependent on immigration from larger rivers; consequently, small populations in streams isolated by downstream impoundments are now highly vulnerable to extinction (e.g., upper Barren River, Nolin River, Buck Creek). Other populations have declined or been extirpated for other reasons. A small population in the Little South Fork Cumberland River appears extirpated by coal mining and oil drilling (Warren and Haag 2005). It has declined for unknown reasons in the Salt River drainage and now persists there only as small populations in the Beech Fork and Rolling Fork. It seems to have disappeared from the entire Kentucky River drainage, likely due to a combination of direct and indirect effects of impoundment and general degradation of the upper watershed by coal mining and other factors. A small population remains in the Red River, Logan County, and it remains common in the Rockcastle River; however, there is little evidence of recent recruitment in either stream. Along with the lower Ohio and Tennessee rivers, the best populations remaining in the state are in the upper Green and Licking rivers; both of these rivers continue to support large and apparently healthy populations. AFS: special concern.
**Cyprogenia stegaria** (Rafinesque, 1820)

Fanshell

**General Distribution**
Ohio River basin from the mouth upstream to Pennsylvania. Populations in the St. Francis and Black rivers, Arkansas, formerly regarded as *Cyprogenia aberti*, now are assigned to this species (Harris et al. 2009).

**Kentucky Distribution**
Type locality: Ohio [River]. Formerly generally distributed to occasional throughout the Ohio River and in most larger tributaries. Absent in lowland habitats in western Kentucky including the Mississippi River and the Tradewater River. An archaeological
record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). Reported from one site in the Tennessee River (Gooch et al. 1979), and not reported historically from the lower Cumberland River; probably widely distributed in both rivers prior to impoundment, and archeological records are available for both streams (Casey 1986, 1987). An archaeological record from the West Fork Red River, Todd County (OSUM), is considered doubtful (see Section IV.C.2). Formerly generally distributed in the middle Cumberland River upstream to Russell County, but absent above the falls. Sporadic in the lower Green River but probably generally distributed prior to impoundment. Occasional in the Barren River and generally distributed in the Green River upstream to Green County. Sporadic but widely distributed in the Salt River drainage. Only two specific records are available for the Kentucky River drainage: an archaeological record from the Kentucky River, Woodford County (Call and Robinson 1983), and the lower Red River, Clark/Estill County (EKU). In addition, Danglade (1922) reported it as rare in the upper Kentucky River system (from unspecified locations but probably including the North Fork Kentucky River). Generally distributed in the Licking River upstream to Fleming County. Sporadic in Tygarts Creek, Carter County (OSUM). A single historical record exists from the Big Sandy River, Lawrence County (UF). The occurrence of this species in the Big Sandy River is plausible, but we regard this particular record as doubtful because it came from a private shell collection known for locality errors (J. Williams, personal communication; see Dromus dromas).

**Habitat & Larval Hosts**

 Generally restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates. Typically a minor component of main-channel mussel beds, but occasionally may be a dominant member of those assemblages. This species is a host specialist on darters (Percidae).

**Conservation Status**

*Cyprogenia stegaria* does not adapt well to impoundment, and its distribution has been drastically reduced by the loss of free-flowing large river habitat. Based on low genetic variation among surviving populations, populations throughout much of the Ohio River basin appear to have been interconnected historically (Grobler et al. 2011), but these populations are now fragmented and isolated by dams. It now appears absent from the Ohio River in Kentucky, but a small population survives farther upstream in the river in Ohio and West Virginia (P. Morrison, personal communication). It persisted in the lower Tennessee River, Livingston/Marshall counties, until the 1970s (Gooch et al. 1979), but has not been found recently; however, the species was reintroduced there in 2012 (M. McGregor, personal communication). It was extirpated from the middle Cumberland River by Wolf Creek Dam, and was likely extirpated from the lower Green and Kentucky rivers by navigation dams. The small populations in the Red River and Tygarts Creek persisted until the 1960s and 1980s, respectively. The cause of the disappearance of these populations is unknown, but their long-term survival may have been dependent on immigration from populations in larger rivers, which were eliminated by impoundment. It was widespread in the Salt River drainage, but most of these populations have disappeared from unknown causes. Apart from the reintroduced population in the Tennessee River, only three populations survive in Kentucky. A population remains in a short stretch of the Rolling Fork in Larue/Nelson counties, but the species is locally common there and is recruiting (Akers 2000; McGregor et al. 2007; KNP). The largest populations of this species on Earth are probably in the Green and Licking rivers. It is generally distributed and locally common in the lower Licking River and the upper Green River, and both populations show evidence of vigorous, recent recruitment. However, populations in the Barren and lower Green rivers are small and isolated from the upper Green River population by navigation dams. Other large populations survive in Arkansas and in the Clinch River, Tennessee and Virginia; elsewhere in its range, the species persists only in a handful of small, isolated, and possibly relict populations. KNP: endangered; AFS: endangered; USFWS: endangered.
**Dromus dromas** (Lea, 1834)

Dromedary Pearlymussel

Endemic to the Tennessee-Cumberland faunal province, occurring in northern Alabama, southern Kentucky, Tennessee, and southwestern Virginia.

Generally distributed throughout the middle Cumberland River prior to construction of Wolf Creek Dam, but not reported upstream of Burnside, Pulaski County; also present formerly in the lower Big South Fork Cumberland River, but not reported from other tributaries (Wilson and Clark 1914; Neel and Allen 1964). In 2008, 19 individuals from the Clinch River
(Tennessee River drainage), Tennessee, were released in the upper Big South Fork Cumberland River, McCreary County (McGregor et al. 2008), apparently upstream of the species’ historical range. Historically, the species occurred in the Cumberland River downstream only to about Clarksville, Tennessee, and in the Tennessee River downstream to the vicinity of Muscle Shoals, Alabama (Wilson and Clark 1914; Ornmann 1925); accordingly, there are no historical records of *D. dromas* in the lower portion of these rivers in Kentucky. However, archaeological records are available from the lower Tennessee River, Livingston County, and the lower Cumberland River, Livingston/Lyon counties (Casey 1986, 1987), and a relic specimen from the Cumberland River, Lyon County (MSU), could have originated from an archaeological site. These records indicate that *D. dromas* occurred nearly to the mouths of both rivers in prehistoric times. Furthermore, an archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site once were suitable for the species (Wesler 2001; see Section IV.C.2); by extension, these records suggest that *D. dromas* also occurred in the lower Ohio River at one time. Three historical records exist from the Ohio River, but none provide firm evidence of the species’ recent occurrence there. Relic specimens were collected from the site of an old button factory (ca. early 1900s) on the Ohio River, Daviess County (KNP), but these probably were transported there by barge with shells from the Tennessee or Cumberland rivers. Parmalee (1967) reported *D. dromas* as “a fairly common shell in the upper Ohio River in Indiana and Ohio”, and Baker (1906) reported the species from an unspecified locality in the Ohio River. We regard these records as erroneous because no specimens exist, and it is unlikely that a common species would have escaped detection by the intensive button fishery and associated scientific investigations on this section of the river in the early 1900s (e.g., Coker 1919). A single historical record exists from the Big Sandy River, Lawrence County (UF). The former occurrence of this species in the Big Sandy River is doubtful and we regard this record as erroneous because it came from a private shell collection known for locality errors (J. Williams, personal communication).

### Habitat & Larval Hosts

Restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates. This species was a dominant component of mussel assemblages in the middle Cumberland River prior to construction of Wolf Creek Dam (Neel and Allen 1964). This species is a host specialist on darters (Percidae).

### Conservation Status

*Dromus dromas* was extirpated from the Big South Fork Cumberland River by coal mining by the 1940s (Neel and Allen 1964), and Wolf Creek Dam on the Cumberland River eliminated the species from Kentucky shortly thereafter. No suitable habitat currently exists within the species’ known historical range in Kentucky. Elsewhere in its range, destruction of large-river habitat by dams has eliminated most other populations. Relict populations persisted in impounded portions of the middle Cumberland River, Tennessee, and the Tennessee River, Tennessee, until at least the 1980s (Parmalee et al. 1980; Ahlstedt and McDonough 1995–1996), but the only remaining reproducing populations are in the Clinch and Powell rivers, Tennessee and Virginia. Translocation of individuals from the Clinch River into the upper Big South Fork and the Tennessee River at Muscle Shoals, Alabama (J. Garner, personal communication), represent efforts to create additional populations of this species to safeguard it from extinction in the event of loss of the Clinch and Powell river populations. The success of these translocations is unknown. KNP: endangered; AFS: endangered; USFWS: endangered.
Ellipsaria lineolata (Rafinesque, 1820)

Butterfly

General Distribution  Mississippi River basin from Louisiana upstream to Minnesota, and west to eastern Kansas and Oklahoma. Ohio River basin from the mouth upstream to Pennsylvania. Occurs in Gulf Coast drainages only in the Mobile River basin.

Kentucky Distribution  Type locality: Falls of the Ohio River, Louisville, Kentucky. Generally distributed to occasional throughout the Ohio River and present in large tributaries from the Tennessee to the Licking river drainages. Not reported from the Mississippi River, but an archaeo-
logical record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). A single record exists for the Trade-water River, Caldwell/Hopkins counties (KNP). Generally distributed in the lower Tennessee and lower Cumberland Rivers. Formerly generally distributed in the Cumberland River from the mouth upstream to the base of Cumberland Falls, but absent above the falls. Sporadic in the lower Green River, and occasional in the lower Barren River and the upper Green River upstream to Green County. Only two records are available for the Salt River drainage: Beech Fork, Nelson County (R. Cicerello, personal observation), and Salt River, Anderson County (S. Pursifull, personal communication). Sporadic in the Kentucky River and occasional in the lower Licking River upstream to Fleming County. Not reported from Ohio River tributaries upstream of the Licking River, but may have occurred historically in the Big Sandy River.

**Habitat & Larval Hosts**

Generally restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates. Although characteristic of and locally common in main-channel mussel beds, this species is rarely a dominant member of those assemblages. This species is a host specialist on Freshwater Drum (*Aplodinotus grunniens*).

**Conservation Status**

*Ellipsaria lineolata* shows some tolerance of impoundment, but its distribution in Kentucky has been reduced by dams. It persists mainly in riverine sections of impounded rivers and in the few unimpounded large streams in the state (Green and Licking rivers). It remains locally common in riverine sections of the Ohio, lower Tennessee, and lower Cumberland rivers, but it is rare in Kentucky Lake (Lewis Environmental Consulting 2010) and apparently absent in Lake Barkley. It was formerly “very abundant” in the middle Cumberland River (Neel and Allen 1964), but this population was extirpated by Wolf Creek Dam. It remains common in unimpounded sections of the Barren and Green rivers, but it is sporadic and rare in the lower Green River probably because of the influence of navigation dams. Similarly, its rarity in the Salt River system likely is due to impoundment of most large stream habitat in that system, and it remains in the Kentucky River only at a few riverine sites downstream of navigation dams. AFS: special concern.
**Elliptio crassidens** (Lamarck, 1819)

Elephantear

**General Distribution**
Mississippi River basin from Louisiana upstream to Minnesota, and west to central Missouri. Ohio River basin from the mouth upstream to Pennsylvania. Gulf Coast drainages from the Ochlockonee River, Florida, west to the Amite River, Louisiana.

**Kentucky Distribution**
Generally distributed to occasional throughout the Ohio River and present in medium-sized to large streams from the Tennessee to the Big Sandy river drainages. Not reported from the Mississippi River, but an archaeological record from the Mississippi Riv-
er, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). A single record is available from the Tradewater River, Crittenden/Webster counties (Clench and van der Schalie 1944). Generally distributed formerly throughout the Tennessee and lower Cumberland rivers, but now rare in Kentucky Lake and apparently absent in Lake Barkley; also reported from the Red River, Logan County (lower Cumberland River drainage; OSUM). Formerly generally distributed in the middle Cumberland River upstream to the base of Cumberland Falls, and sporadic in tributaries including the Big South Fork, Rockcastle River system, and Laurel River; absent above Cumberland Falls (Wilson and Clark 1914; Neel and Allen 1964). Generally distributed to occasional in the Green River upstream to Green County, and occasional in the lower Rough and Barren rivers; an archaeological record is available for the Pond River, Hopkins County (Kreisa 1991). Sporadic in the Salt River drainage. Only one confirmed record is available for the Kentucky River drainage, a single shell found in archaeological excavations at the original site of Fort Boonesborough (ca. 1780) in Madison County (N. O’Malley, personal communication); probably widely distributed in the Kentucky River prior to impoundment. A record for the Middle Fork Kentucky River (Williams 1975) is plausible but unsubstantiated. Occasional to sporadic in the lower reaches of Ohio River tributaries from the Licking to the Big Sandy river drainages.

**Habitat & Larval Hosts**

Generally restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates where it may be a dominant component of mussel beds. Occurs rarely in smaller streams and usually only in their lower reaches near the confluence with large rivers (e.g., Kinniconick Creek, Tygarts Creek, Little Sandy River). This species is a host specialist on Skipjack Herring (*Alosa chrysochloris*) and Alabama Shad (*A. alabamae*).

**Conservation Status**

*Elliptio crassidens* has declined or disappeared in many streams apparently because dams block migrations of its host fishes. Alabama Shad is considered extirpated in Kentucky, and Skipjack Herring has declined across its range following widespread stream impoundment (Burr and Warren 1986; Boschung and Mayden 2004). *Elliptio crassidens* remains common or even locally abundant in several streams, but this species lives >50 years (Haag and Rypel 2011), and many populations appear to be non-recruiting relics that predate impoundment. It remains generally distributed throughout the Ohio River, but high-lift navigation dams constructed since the 1960s may block skipjack migrations, and evidence of recent recruitment is rare in most parts of the river (C. Lewis and R. Butler, personal communication). Navigation dams on the Kentucky River constructed in the 1800s appear to have eliminated skipjacks and *E. crassidens* from that system (see Burr and Warren 1986). Wolf Creek Dam on the Cumberland River directly destroyed most main-channel mussel habitat and likely eliminated skipjack runs throughout the drainage. *Elliptio crassidens* was once so abundant in the middle Cumberland River that it was an impediment to commercial harvest of more valuable species (Wilson and Clark 1914), but it is now apparently restricted to the short free-flowing reach below Cumberland Falls, where it is rare (Ciccerello and Laudermilk 1997). Individuals surviving below the falls and potentially in tributaries likely recruited prior to dam construction and the population in the middle Cumberland River drainage can be expected to disappear as these individuals reach the end of their life span. Evidence of recent recruitment is apparent in the lower Tennessee River and possibly in the lower Ohio River (C. Lewis, personal communication). The viability of other populations is unknown, but the preponderance of older individuals in most rivers in Kentucky and elsewhere suggests that interruption of skipjack spawning runs by dams has limited host availability for *E. crassidens* and ultimately will result in the disappearance of many populations (Haag 2012). KNP: none, but this species warrants listing as a species of special concern; AFS: currently stable.
Elliptio dilatata (Rafinesque, 1820)

Spike

Mississippi River basin from Louisiana and Mississippi north to Minnesota, and west to eastern Kansas. Throughout the Ohio River basin from the mouth upstream to New York. Great Lakes basin from Lake Michigan to the Niagara River and possibly downstream to the St. Lawrence River.

Type locality: Kentucky River (see Johnson and Baker 1973). Generally distributed nearly statewide, including the upper Cumberland River drainage...
above Cumberland Falls. Absent from the Mississippi River and direct tributaries and the Tradewater River; sporadic and rare in other lowland habitats in western Kentucky. An archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2).

**Habitat & Larval Hosts**

Occurs in a wide variety of upland riverine habitats from large rivers to small streams, but does not penetrate far into the headwaters. Generally restricted to main-channel habitats in gravel and sand substrates, and typically absent from depositional habitats or lentic environments. Typically rare in the largest rivers (e.g., Ohio, Tennessee), and reaches maximum abundance in medium-sized streams where it can be the dominant species or may share dominance with *Actinonaias ligamentina* or *Quadrula pustulosa* (e.g., Green, Rockcastle, Licking rivers). This species is a host specialist on darters (Percidae).

**Conservation Status**

*Elliptio dilatata* remains one of the most widespread and common riverine mussel species in Kentucky. Nevertheless, this species does not adapt well to impoundment, and dams have eliminated many populations. Other populations have disappeared from a variety of mostly unknown causes. It was the most widespread and abundant mussel species in the middle Cumberland River drainage prior to construction of Wolf Creek Dam (Neel and Allen 1964), but the dam eliminated the species from the mainstem, with the exception of a small population remaining immediately below Cumberland Falls (Cicerello and Laudermilk 1997). Similarly, it was the most abundant species in a prehistoric mussel assemblage from the Kentucky River (Call and Robinson 1983), but the species is now nearly extirpated from the river after more than 100 years of impoundment. The species persists in the Ohio, Tennessee, lower Cumberland, and lower Green rivers, but it is rare in those streams and most individuals are old, suggesting that recruitment is limited (Williams and Schuster 1989; Miller and Payne 1993; Sickel and Chandler 1996; KNP). It is unclear to what extent the current rarity of this species in large rivers is a natural feature of these assemblages, or a result of impoundment. It was uncommon to rare in the lower Cumberland River in prehistoric times and in the early 1900s (Wilson and Clark 1914; Casey 1987), but its abundance varied among prehistoric sites on the Ohio River where it composed from 0–32% of assemblages (Call 1992, 1993; Casey 1986). Because of its host specialization on darters, its abundance in large rivers probably varied locally in accordance with the availability of shoal and riffle habitats required by most darter species. Impoundment and loss of shoal habitats doubtless has greatly reduced darter populations and may explain the current rarity and lack of recruitment of *E. dilatata* and other darter specialists in large rivers (Haag 2012). Although many large and reproducing populations persist in free-flowing streams across the state, other populations appear to have declined precipitously or are extirpated judging by the dearth of living individuals observed in recent years (e.g., Little River, Buck Creek, Little South Fork Cumberland River, upper Cumberland River drainage, Drakes Creek, Nolin River, Dix River system). AFS: currently stable.
Epioblasma arcaeformis (Lea, 1831)

Sugarspoon

General Distribution
Endemic to the Tennessee-Cumberland faunal province, but now extinct. Occurred in northern Alabama, southern Kentucky, and Tennessee. Formerly generally distributed and locally abundant in the upper Tennessee River drainage but sporadic and rare in the Cumberland River drainage (Ortmann 1918, 1925; R.I. Johnson 1978).

Kentucky Distribution
Only one specific record exists for this species in Kentucky in historical times: a single individual collected from the Big South Fork Cumberland River, 2
miles upstream of Burnside, Pulaski County, in 1911 (Wilson and Clark 1914). One other record exists from an unspecified location and date in the Cumberland River, Kentucky (R.I. Johnson 1978). In the Tennessee portion of the Cumberland River drainage, it is reported historically only from Nashville (R.I. Johnson 1978). Because of the paucity of collections from the Cumberland River drainage, its historical distribution there is unknown. Like many Tennessee-Cumberland endemic species, it probably occurred historically in the Cumberland River drainage from near Burnside, Kentucky, downstream to the vicinity of Clarksville, Tennessee, and in the Tennessee River drainage from eastern Tennessee downstream to the vicinity of Muscle Shoals, Alabama (e.g., see Dromus dromas, Epioblasma haysiana). However, like D. dromas, archaeological records of E. arcaeformis are available from the lower Tennessee River, Livingston County, and the lower Cumberland River, Livingston/Lyon counties (Casey 1986, 1987), and a relic specimen from the Cumberland River, Lyon County (MSU), could have originated from an archaeological site. Furthermore, an archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site once were suitable for the species (Wesler 2001; see Section IV.C.2); by extension, these records suggest that E. arcaeformis also occurred in the lower Ohio River at one time. An archaeological record from the West Fork Red River, Todd County (OSUM), is considered doubtful (see Section IV.C.2).

**Habitat & Larval Hosts**

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**

The paucity of historical records for this species indicates that it was rare in Kentucky even prior to recent human alteration of streams. The population in the lower Big South Fork likely was eliminated by coal mining by the 1940s (Neel and Allen 1964), and Wolf Creek Dam eliminated all potential remaining habitat for the species in the state. The entire historical range of this species is now impounded or affected by cold water dam discharge; the last known population was eliminated by Cherokee Dam on the Holston River, Tennessee, in 1941 (Stansbery 1970; Haag 2012). KNP: presumed extinct; AFS: endangered, possibly extinct.
Epioblasma biemarginata (Lea, 1857)

Angled Riffleshell

General Distribution

Endemic to the Tennessee-Cumberland faunal province, but now extinct. Occurred in the upper two-thirds of the Tennessee and possibly Cumberland rivers, and in the lower reaches of larger tributaries in northern Alabama, southern Kentucky, and Tennessee. Abundant historically in the middle Tennessee River drainage, particularly in the vicinity of Muscle Shoals, Alabama, but apparently rare in the Cumberland River drainage, where it is known from only two collections, both in Kentucky.
Reported only from the Cumberland River and the Big South Fork Cumberland River, both at Burnside, Pulaski County (Ortmann 1924, 1925; R.I. Johnson 1978).

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other Epioblasma.

The two records of *Epioblasma biemarginata* from Kentucky are not dated, but these collections probably were made in the 1800s. The species was not found in extensive surveys of the Cumberland River drainage conducted in 1911 and the late 1940s (Wilson and Clark 1914; Neel and Allen 1964), suggesting that the species disappeared from the state at an early date for unknown reasons. Alternatively, the absence of records from elsewhere in the Cumberland River drainage raises the possibility that these two records are erroneous and perhaps based on mislabeled specimens or incorrect locality information, and the species may have been restricted to the Tennessee River drainage.

At best, this species appears to have been extremely rare in Kentucky even prior to major human alteration of streams. Most of the historical range of this species is now impounded or affected by cold water dam discharge. A population persisted in a free flowing section of the Elk River, Tennessee, until 1967 when quarry washing operations in the vicinity eliminated most mussels (Stansbery 1970). A single individual was reported from the Tennessee River near Muscle Shoals, Alabama, in 1970 (Garner and McGregor 2001), but the species has not been seen since at either location or elsewhere. KNP: presumed extinct; AFS: endangered, possibly extinct.
**Epioblasma brevidens** (Lea, 1831)

Cumberlandian Combshell

**General Distribution**
Endemic to the Tennessee-Cumberland faunal province, occurring in northern Alabama, southern Kentucky, northeastern Mississippi, Tennessee, and southwestern Virginia.

**Kentucky Distribution**
Reported from the Red River (lower Cumberland River drainage) only from two relic specimens from one site just upstream of the state line (KNP); more widespread historically in the Tennessee portion of the Red River (OSUM). Formerly generally distributed
in the middle Cumberland River drainage upstream to at least the lower Rockcastle River, including Beaver Creek, Wayne County; Big South Fork Cumberland River, Pulaski and McCreary counties; and Buck Creek, Pulaski County. Apparently absent or rare in the middle and upper Rockcastle system.

**Habitat & Larval Hosting**

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Common to abundant in the Cumberland River, lower Big South Fork, and lower Rockcastle River prior to construction of Wolf Creek Dam (Wilson and Clark 1914; Neel and Allen 1964). This species is a host specialist on darters (Percidae) and sculpins (Cottidae).

**Conservation Status**

*Epioblasma brevidens* was extirpated from the lower Big South Fork by acid mine drainage by the 1940s (Neel and Allen 1964). Shortly thereafter, Wolf Creek Dam destroyed most habitat for the species in the state, resulting in elimination of the large population in the Cumberland and Rockcastle rivers. A large population remained in Buck Creek until the late 1960s (Eku), but this population declined in subsequent decades and is now very small (Schuster et al. 1989; McGregor 2003, 2005). The largest remaining population in Kentucky is in the upper Big South Fork where the species is occasional and uncommon but shows evidence of recent recruitment. The extent of habitat occupied in the Big South Fork in Kentucky is limited to about 6 stream miles, but this population extends upstream about 12 more miles into Tennessee (Ahlstedt et al. 2003–2004; McGregor et al. 2007). The Red River population persisted until at least the 1960s (OSUM), but living individuals have not been seen since in either Tennessee or Kentucky, and the population is considered extirpated. *Epioblasma brevidens* survives elsewhere only in the Clinch and Powell rivers in Tennessee and Virginia, and in the Bear Creek system, Alabama and Mississippi (all Tennessee River drainage; USFWS 2007). KNP: endangered; AFS: endangered; USFWS: endangered.
Epioblasma capsaeformis (Lea, 1834)

Oyster Mussel

General Distribution

Endemic to the Tennessee-Cumberland faunal province, occurring in northern Alabama, northwestern Georgia, southern Kentucky, Tennessee, and southwestern Virginia. The distribution and taxonomic status of this species are unclear. Individuals from the Duck River, Tennessee, are morphologically and genetically distinct from populations elsewhere in the Tennessee River drainage and recently were described as a separate species, E. ahlstedti (Jones and Neves 2010). This raises the possibility that other cryptic taxa exist within E. capsaeformis, particularly with regard to differences between Cumberland and Tennessee river drainage populations (see section IV.D.3 and accounts for E. florentina walkeri and “Villosa” vanuxemensis). However, because E. capsaeformis appears
to be extirpated from the Cumberland River drainage, a full understanding of the phylogenetic relationships within this taxon likely is unobtainable at this time. Determination of this species’ range also is complicated by confusion with *E. florentina* (see subsequent).

**Kentucky Distribution**

Apparently generally distributed in larger streams of the middle Cumberland River drainage prior to construction of Wolf Creek Dam, but the historical abundance and distribution of this species is unclear. Reported from the Cumberland River from Cumberland County upstream to Burnside, Pulaski County; Beaver Creek, Wayne County; the Big South Fork, Pulaski and McCreary counties; Buck Creek, Pulaski County; and the lower Rockcastle River, Laurel/Pulaski counties (Neel and Allen 1964; Schuster et al. 1989; UMMZ; EKU; OSUM). Some of these records may represent misidentifications of *E. florentina walkerii*. For example, a historical specimen from the Big South Fork labeled *E. capsaeformis* (UMMZ) was later identified as *E. florentina walkerii*, and other reports of the former species in that stream and elsewhere may be based on misidentifications (Ahlstedt et al. 2003–2004). Many historical records of *Epioblasma capsaeformis* were accompanied by descriptions of shell characteristics consistent with this species (Wilson and Clark 1914; Neel and Allen 1964), but specimens were not illustrated and few voucher specimens exist. Despite these uncertainties, substantiated records of *E. capsaeformis* (based on shell morphology only) exist throughout the middle Cumberland River drainage, and it appears to have occurred sympatrically with *E. florentina* in several streams (Jones 2004). In 2008, 97 individuals of *E. capsaeformis* from the Clinch River (Tennessee River drainage), Tennessee, were released in the Big South Fork, McCreary County (McGregor et al. 2008). Reported from the Red River (lower Cumberland River drainage) in Tennessee (OSUM) but not reported conclusively from the Kentucky portion of that system; one relic shell representing either this species or *E. florentina walkerii* was collected in 1988 from the Red River, Logan County, just upstream of the state line (KNP).

**Habitat & Larval Hosts**

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. This species was locally common in the Cumberland River prior to construction of Wolf Creek Dam (Wilson and Clark 1914; Neel and Allen 1964). This species is a host specialist on darters (Percidae) and sculpins (Cottidae).

**Conservation Status**

*Epioblasma capsaeformis* was extirpated from the lower Big South Fork by coal mining by the 1940s, and Wolf Creek dam on the Cumberland River destroyed most other habitat for the species in the state shortly thereafter. A population persisted in Buck Creek until at least the 1980s (Schuster et al. 1989; EKU; KNP), but this population has disappeared for unknown reasons. Because of the potential for confusion with *E. florentina walkerii*, the former occurrence of *E. capsaeformis* in the upper Big South Fork is unclear, but it has not been reported there in over 25 years (Ahlstedt et al. 2003–2004). This species appears to be extirpated from Kentucky and throughout the Cumberland River drainage with the exception of individuals from the Tennessee River drainage that were introduced into the Big South Fork (see previous). If Cumberland River drainage populations represented a separate species, that species appears to be extinct. KNP: endangered; AFS: endangered; USFWS: endangered.
Epioblasma cincinnatiensis (Lea, 1840)

Ohio Riffleshell

General Distribution

Endemic to the Ohio River basin, but now extinct. The taxonomic status and historical distribution of this species are poorly known. *Epioblasma cincinnatiensis* has been placed in the synonymy of *E. torulosa* (R.I. Johnson 1978) and was not recognized by subsequent treatments of the North American fauna (e.g., Williams et al. 1993; Turgeon et al. 1998). However, recent authors have considered *E. cincinnatiensis* a distinct species based on shell characters (Cicerello and Schuster 2003; Williams et al. 2008; Watters et al. 2009, as *E. phillipsii*). Specimens referable to *E. cincinnatiensis* are reported from the Ohio, Tennessee, Cumberland, Wabash, and Green rivers (Williams et al. 2008; Watters et al. 2009).
Type locality: Ohio River, Cincinnati. Known from only five localities in Kentucky. Reported from the Ohio River at Cincinnati, Kenton County (R.I. Johnson 1978; MCZ), and from archeological sites in Boone and Campbell counties (Call 1993; NMNH; OSUM). One relic shell was collected from the Barren River, Warren County, in 1987 (OSUM), and the species is reported from archaeological sites along the lower Green River, Butler County (Morey and Crothers 1998; Claassen 2005; Patch 2005). A record from the Nolin River, Grayson/Hart counties (Taylor 1983), is *E. torulosa rangiana*.

Probably restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

This species appears to have been rare even historically, and it has not been seen since the late 1800s. All known locations for this species throughout its range now are impounded or otherwise highly altered. KNP: presumed extinct; AFS: not recognized.
**Epioblasma flexuosa** (Rafinesque, 1820)

Leafshell

*Probably endemic to the Ohioan faunal province, but now extinct. Occurred in the Ohio River from near the mouth upstream to Ohio and West Virginia, and in the lower reaches of larger tributaries from at least the Wabash River upstream to the Muskingum River, Ohio. The occurrence of this species in the Tennessee-Cumberland faunal province is unclear. Most reports of *E. flexuosa* in that region are based on archaeological specimens, but separation of this species from the similar *E. lewisii* is based in large part on the color of the periostracum, and identification of these subfossil specimens should be considered tentative at best. There are few historical specimens of *E. flexuosa* from the Tennessee-Cumberland province, and it is likely that the species was restricted to the Ohioan province.*
in historical times, occurring in the lower portion of the Tennessee and Cumberland rivers, but being replaced by *E. lewisii* in the upper two-thirds of these drainages. However, the phylogenetic relationship between *E. flexuosa* and *E. lewisii* is unknown.

**Kentucky Distribution**

Type locality: Kentucky, Salt, and Green rivers. This species appears to have been widely distributed but sporadic in larger streams in Kentucky, and few specific collection localities exist. Most specific historical records are from the Ohio River in the vicinity of Cincinnati (Campbell and Kenton counties, Kentucky; MCZ; NMNH; OSUM; UMMZ). The apparent rarity of the species elsewhere in the river may simply reflect the much lower collecting effort expended prior to impoundment at less readily accessible sites. Call (1900) reported the species in the Ohio River from an unspecified location adjacent Indiana, and relic shells have been found in the lower river in McCracken and Livingston counties (INHS; MSU). Archaeological records of this species occur throughout the Ohio River, from Henderson County upstream to Greenup County (Parmalee 1960; Call 1992; Peacock 2008). An archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). A single relic valve was collected from the lower Cumberland River, Livingston/Lyon counties (Sickel and Chandler 1996). In addition, specimens lumped within a group of similar species (*E. flexuosa/lewisii/stewardsonii*) were reported from archaeological sites along the lower Tennessee River, Livingston County, and the lower Cumberland River, Livingston and Lyon counties (Casey 1986, 1987); these specimens are likely referable in part to *E. flexuosa* (see Ciceroello et al. 1991). An archaeological record from the West Fork Red River, Todd County (OSUM), may be referable to either *E. flexuosa* or *E. lewisii*, but this record is considered doubtful (see Section IV.C.2). The unspecified locations in the Green, Salt, and Kentucky rivers given as type localities are the only reports of the species in those drainages.

**Habitat & Larval Hosts**

Probably restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Little is known about the former abundance of this species, but the relatively large number of specimens from the Ohio River at Cincinnati in museum collections suggests that the species must have been reasonably common there. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**

*Epioblasma flexuosa* appears to have been one of the first mussel species to disappear in response to human alteration of rivers. The last substantiated occurrence of this species is from the Ohio River in 1900 (Stansbery 1976a). However, because little scientific collecting occurred on much of the river in the early 1900s, especially on the lower river, the species probably persisted at least until impoundment of the river was completed in 1929. Regardless, the species has not been seen alive in over 100 years and little or no free-flowing, large river habitat remains within its range. KNP: presumed extinct; AFS: endangered, possibly extinct.
**Epioblasma florentina walkeri** (Wilson and Clark, 1914)

Tan Riffleshell

Epioblasma florentina traditionally included three subspecies, but this concept has changed and other aspects of its phylogeny and distribution are unknown. *Epioblasma f. florentina* (Lea, 1857) was considered endemic to large streams throughout the Tennessee-Cumberland faunal province, and it was thought to be replaced by *E. f. walkeri* in smaller streams in that region. A third subspecies, *E. f. curtisi*, was endemic to Arkansas and Missouri. *Epioblasma f. florentina* and *E. f. curtisi* are considered extinct. Recent studies show that *E. f. walkeri* is composed of two sister taxa, *E. f. walkeri* in the Cumberland River drainage, and *E. f. aureola* in the Tennessee River drainage (Jones et al. 2006; Jones and Neves 2010). This suggests that *E. f. walkeri* was endemic to the Cumberland...
River drainage and widely distributed from the Red River upstream to the Big South Fork. However, because only one population of each taxon survives (see subsequent) and genetic material for *E. f. florentina* and *E. f. curtisi* is unavailable, a full understanding of the phylogenetic relationships within *E. florentina* is unobtainable at this time. Both *E. f. florentina* and *E. f. walkerii* are reported from the Cumberland River drainage, but uncertainties about these taxa preclude firm conclusions about their historical distribution. Some authors considered these taxa to represent ecophenotypic variation within a single species (Ortmann 1918, 1924; R.I. Johnson 1978). Furthermore, specimens of *E. f. florentina* from the Cumberland River illustrated in Neel and Allen (1964) were later identified tentatively as *E. f. walkerii* (Stansbery 1976b). Because of this uncertainty, we plot all records of the *E. florentina* group in Kentucky as *E. f. walkerii* to distinguish it from *E. f. aureola* of the Tennessee River drainage.

**Kentucky Distribution**  
The large river form, *E. f. florentina*, is reported in Kentucky only from the Cumberland River, Cumberland and Russell counties (Wilson and Clark 1914; Neel and Allen 1964; R.I. Johnson 1978), but at least some of these specimens may represent *E. f. walkerii* (see previous). *Epioblasma f. walkerii* is reported from the Cumberland River, Pulaski County; Beaver Creek, Russell County; and the Big South Fork, McCreary County (Ortmann 1925; Neel and Allen 1964; Jones et al. 2006). In addition, some or all of the reports of *E. capsaeformis* from the upper Big South Fork in the 1970s and 80s (e.g., Harker et al. 1979; Richardson 1989) may be *E. f. walkerii* (Ahlstedt et al. 2003–2004). Records of *E. florentina* from Buck Creek, Pulaski County; Cumberland River at Burnside, Pulaski County; and Beaver Creek, Russell County (UMMZ; MCZ; R.I. Johnson 1978), are *E. capsaeformis* (Schuster 1988; S. Ahlstedt, G. Schuster, D. Stansbery, personal communication). *Epioblasma f. walkerii* is reported from the Red River (lower Cumberland River drainage) in Tennessee (OSUM) but is not reported conclusively from the Kentucky portion of that system; one relic shell representing either this species or *E. capsaeformis* was collected in 1988 from the Red River, Logan County, just upstream of the state line (KNP). An archaeological record from the West Fork Red River, Todd County (OSUM, as *E. florentina*), is considered doubtful (see Section IV.C.2).

**Habitat & Larval Hosts**  
Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. It was locally abundant in the Cumberland River prior to construction of Wolf Creek Dam (Wilson and Clark 1914; Neel and Allen 1964). This species is a host specialist on darters (Percidae) and sculpins (Cottidae).

**Conservation Status**  
The big river form, *E. f. florentina*, has not been seen anywhere for over 60 years and is considered extinct. The Tennessee River subspecies, *E. f. aureola*, survives in only about 2 stream miles of a single tributary of the Clinch River in Virginia (R. Butler, personal communication). Wolf Creek Dam on the Cumberland River destroyed most habitat for *Epioblasma florentina* in Kentucky. The only remaining population of *E. f. walkerii* on Earth is in the upper Big South Fork in Kentucky and Tennessee (Jones 2004). Additional populations survived until at least the late 1960s in the Red and Stones rivers, Tennessee (Stansbery 1976b), but these populations have disappeared due to impoundment and other, unknown factors. The Big South Fork population appears to be recruiting, but it occupies only about 12 miles of river and may be declining due to coal mining and other impacts in the upper watershed (Ahlstedt et al. 2003–2004; McGregor et al. 2007). Improvement of water quality in the Big South Fork watershed is crucial to the survival of this species. KNP: *E. f. florentina* presumed extinct, *E. f. walkerii* endangered; AFS: *E. f. florentina* endangered, possibly extinct; *E. f. walkerii* endangered; USFWS: both subspecies endangered.
Epioblasma haysiana (Lea, 1834)

Acornshell

Endemic to the Tennessee-Cumberland faunal province, but now extinct. Occurred in the upper two-thirds of the Tennessee and Cumberland rivers, and in the lower reaches of larger tributaries in northern Alabama, southern Kentucky, Tennessee, and southwestern Virginia.

Formerly occasional in the middle Cumberland River from Cumberland County upstream to Burnside, Pulaski County, and the lower Big South Fork, Pu-
laski and McCreary/Wayne counties (Wilson and Clark 1914; Neel and Allen 1964; UMMZ; J. Kiser and P. Parmalee, personal communication). Not reported historically in other Cumberland River tributaries or in the mainstem upstream of Burnside, but specimens were reported from archaeological sites adjacent the lower Rockcastle River, Pulaski County (KNP), and the lower Laurel River, Laurel County (Dourson 1998).

**Habitat & Larval Hosts** Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Apparently uncommon in the Cumberland River, but locally abundant in the lower Big South Fork (Wilson and Clark 1914; Neel and Allen 1964). Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status** *Epioblasma haysiana* survived in the lower Big South Fork until the late 1940s despite severe acid mine pollution in that stream (Neel and Allen 1964). It was collected in the Cumberland River in 1911, but not in the late 1940s (Wilson and Clark 1914; Neel and Allen 1964), but it may have persisted in the mainstem until construction of Wolf Creek Dam in 1950. Regardless, Wolf Creek Dam eliminated all habitat for this species in Kentucky. By the late 1960s, all remaining habitat for this species throughout its range was destroyed by dams with the exception of a short stretch of the upper Clinch River, Virginia, which continued to support a small population. Massive industrial chemical spills in this section of the Clinch River in 1967 and 1970 appear to have eliminated this population, resulting in extinction of the species (Jenkins and Burkhead 1993; Haag 2012). KNP: presumed extinct; AFS: endangered, possibly extinct.
Epioblasma lewisii (Walker, 1910)

Forkshell

**General Distribution**

Probably endemic to the Tennessee-Cumberland faunal province, but now extinct. Occurred in the upper two-thirds of the Tennessee and Cumberland rivers and in the lower reaches of larger tributaries in northern Alabama, southern Kentucky, and Tennessee. Only two historical records of *E. lewisii* exist for the Ohio River (R.I. Johnson 1978; Watters et al. 2009), casting doubt on its recent occurrence beyond the Tennessee-Cumberland province. It is reported from archaeological sites on the lower Tennessee River in Tennessee (Hughes and Parmalee 1999). The veracity of archaeological records is difficult to assess because of the similarity of *E. lewisii* to *E. flexuosa* and the phylogenetic relationship between these two species is unknown (see *E. flexuosa*). However, it is possible that the dis-
distribution of this species extended farther downstream in the Tennessee and Cumberland rivers in prehistoric times (see *Dromus dromas* and *E. arcaeformis*).

**Kentucky Distribution**

Reported in Kentucky from only three sites in the middle Cumberland River from Russell County upstream to Burnside, Pulaski County (Walker 1910; Neel and Allen 1964; R.I. Johnson 1978).

**Habitat & Larval Hosts**

Restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**

*Epioblasma lewisii* appears to have been rare throughout its range even prior to human alteration of rivers (e.g., Ortmann 1918). It was not found in a survey of the entire Cumberland River drainage in 1911 (Wilson and Clark 1914), and only two individuals were found in the Cumberland River in Kentucky in the late 1940s (Neel and Allen 1964). This species was driven extinct in a short period by large-scale dam construction in the Cumberland and Tennessee River drainages from the 1920s to 1950 (Haag 2009). All streams in the Tennessee River drainage that supported the species were impounded by the early 1940s, but the species survived slightly longer in the Cumberland. A population remained in the Caney Fork River, Tennessee, until construction of Center Hill Dam in 1948. The population in the Cumberland River in Russell County, Kentucky, reported by Neel and Allen (1964) likely was the last on Earth, but it was eliminated by Wolf Creek Dam in 1950. KNP: presumed extinct; AFS: endangered, possibly extinct.
Epioblasma obliquata obliquata (Rafinesque, 1820)

Catspaw

Endemic to the Ohio River basin, occurring in the Ohio River and larger tributaries from the Tennessee River drainage upstream to the Muskingum River drainage, Ohio. The subspecies, *E. obliquata perobliqua* occurs in smaller streams in the western Lake Erie basin and possibly in northern tributaries of the Ohio River (Watters et al. 2009). A record of *E. obliquata perobliqua* is available for the Ohio River, Union County (OSUM, UMMZ; see Cicerello and Schuster 2003), but we consider this record erroneous (see section IV.D.1).
Type locality: Kentucky River. Widely distributed in larger streams throughout the state, but specific localities are few. Reported from the Ohio River historically at only one site (Kenton County; Lea 1870; MCZ), but other collections from unspecified localities exist (OSUM); also reported from archaeological sites in Henderson (Parmalee 1960) and Greenup (OSUM) counties. No records are available for the lower Tennessee or lower Cumberland rivers in Kentucky, but the species is reported from both streams just upstream in Tennessee (Parmalee and Bogan 1998), and it likely occurred throughout these rivers historically. Formerly sporadically distributed in the middle Cumberland River upstream to at least Burnside, Pulaski County (Neel and Allen 1964; R.I. Johnson 1978; NCMNS; EKU; UMMZ), and reported from the lower and upper Green River drainages from Muhlenberg County upstream to Hart County (Clench and van der Schalie 1944; R.I. Johnson 1978; OSUM; EKU). Not reported from the Salt River drainage but possibly occurred in the lower Salt River. Apart from the unspecified type locality, the only record from the Kentucky River is from an archaeological site in Clark County (KNP). One relic shell was collected in 1963 from the Licking River, Pendleton County (OSUM), but a historical collection of 11 specimens from an unspecified location in the Licking River also exists (R.I. Johnson 1978; MCZ).

Restricted to main-channel shoal habitats mostly of large streams in gravel and sand substrates. This species appears to be a host specialist on darters (Percidae) and sculpins (Cottidae).

Restricted to main-channel shoal habitats mostly of large streams in gravel and sand substrates. This species appears to be a host specialist on darters (Percidae) and sculpins (Cottidae).

Conservation Status

_Epioblasma obliquata obliquata_ was probably more common and widespread historically than the scarcity of records suggests. The large rivers that were home to this species were not sampled extensively prior to major modification by humans in the twentieth century. Wilson and Clark (1914) found only occasional individuals during their survey of the Cumberland River but stated “it can probably be procured in larger numbers during low water,” and they reported that the species was common enough to be well known to commercial mussel fisherman. It was relatively common in the Cumberland River, Tennessee (Parmalee et al. 1980; see subsequent), and several large historical collections of this species exist from the Ohio River (OSUM). Regardless, this species likely is extirpated from Kentucky and is now nearly extinct. It is clearly intolerant of impoundment, and dams have destroyed or radically altered streams throughout nearly all of its original range. It has not been seen in the Ohio River in about 100 years, since impoundment of that stream, and the last observation of living individuals in the Kentucky portion of the Cumberland River was in the late 1940s, immediately prior to construction of Wolf Creek Dam. Only three populations are known to have survived the era of intensive dam construction. A large, but apparently non-reproducing population persisted in an impounded section of the middle Cumberland River in Tennessee until at least the 1980s (Parmalee et al. 1980). A small population persisted in the Green River, Butler/Warren counties, until at least 1988 when a single, recently dead individual was found (OSUM); both of these remnant populations likely have died out. The only known remaining population is in Killbuck Creek, a relatively small stream in Ohio, but this population has declined rapidly since its discovery in 1994 (Hoggarth et al. 1995; USFWS 2010a). An effort is underway to propagate juveniles in captivity from Killbuck Creek broodstock. If successful, these individuals will be used to reestablish additional populations of this species in an attempt to prevent its extinction (L. Koch and M. McGregor, personal communication). In addition, the atypical occurrence of this species in a relatively small stream such as Killbuck Creek gives hope that other populations may survive elsewhere in similar habitats. KNP: endangered; AFS: endangered; USFWS: endangered.
*Epioblasma personata* (Say, 1829)

Round Combshell

**General Distribution**
Endemic to the Ohio River basin, but now extinct. Occurred in the Ohio River upstream to at least Cincinnati, and in the lower reaches of larger tributaries from the Tennessee River upstream to the Scioto River.

**Kentucky Distribution**
The only specific historical record of this species in Kentucky is from the Ohio River, Kenton County (Stansbery 1971; R.I. Johnson 1978), but it was also reported from an unspecified location in the Ohio River adjacent Indiana (Call 1900). It was reported from
an archaeological site on the Ohio River, Carroll County (Peacock 2008), and two adjacent archeological sites on the lower Green River, Butler County (Morey and Crothers 1998; Patch 2005). The species was reported historically from the Tennessee River drainage in Alabama and Tennessee, and the Cumberland River in Tennessee (R.I. Johnson 1978), but no records exist from portions of those rivers in Kentucky.

**Habitat & Larval Hosts**

Probably restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**

*Epioblasma personata* appears to have been rare throughout its range even prior to human alteration of rivers. Few specimens of this species exist in museum collections, and it composed only 3% and <1% of specimens at two archaeological sites on the lower Green River (Morey and Crothers 1998; Patch 2005). All of its historical range is now impounded or otherwise highly altered. The last substantiated record from the Ohio River is from the 1800s (Stansbery 1970), but it likely persisted in that stream at least until impoundment of the river was completed in 1929 (see *Epioblasma flexuosa*). The last report of this species anywhere was from the Tennessee River in 1924 (Ortmann 1925; Haag 2012). KNP: presumed extinct; AFS: endangered, possibly extinct.
Epioblasma propinqua (Lea, 1857)

Tennessee Riffleshell

Endemic to the Ohio River basin, but now extinct. Occurred in the Ohio River from near the mouth upstream to at least Cincinnati, and in the lower reaches of larger tributaries from the Tennessee River upstream at least to the Wabash River. The historical distribution of this species is difficult to assess because of its similarity and unknown phylogenetic relationship to Epioblasma torulosa. Most historical specimens are from the Tennessee River drainage; Ortmann (1918) originally considered this species endemic to that river system, but later considered it merely a variant of E. torulosa (Ortmann 1925). Specimens possibly representing E. propinqua are widespread and occasionally abundant in archeological assemblages from the Tennessee, Cumberland, Green, and Ohio rivers, but une-
quivocal identification of these specimens often is difficult or impossible (Parmalee et al. 1980; Casey 1987; Morey and Crothers 1998).

**Kentucky Distribution**
Reported in Kentucky specifically from only three sites in the Ohio River. Historical or relic specimens exist from Kenton (R.I. Johnson 1978; MCZ) and McCracken (INHS) counties, and archaeological specimens were reported from Carroll County (Peacock 2008). In addition, it was reported historically from an unspecified location in the Ohio River adjacent Illinois (Baker 1906). Archaeological specimens potentially referable to *E. propinqua* were reported from the Ohio River, Oldham County (OSUM), the Tennessee and lower Cumberland rivers, Livingston and Lyon counties (Casey 1986, 1987), and the lower Green River, Butler and Ohio counties (Morey and Crothers 1998; Morey et al. 2002); these records are not plotted here because of the uncertainty of these identifications.

**Habitat & Larval Hosts**
Probably restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**
*Epioblasma propinqua* appears to have been widespread and perhaps locally abundant in the largest rivers in Kentucky and elsewhere in its range, but all habitat for the species has been impounded for nearly 75 years. The last report of this species was from the lower Clinch River, Tennessee, in 1914 (Ortmann 1918), but it may have persisted there until construction of Norris Dam in 1936. KNP: presumed extinct; AFS: endangered, possibly extinct.
**Epioblasma sampsonii** (Lea, 1861)

Wabash Riffleshell

Apparently endemic to the Ohioan faunal province, but now extinct. Occurred in the Ohio River upstream to at least Greenup County, and in the lower reaches of larger tributaries from the Wabash River to the Kentucky River. Not reported from the Tennessee or Cumberland river drainages. The historical distribution of this species is difficult to assess because of its similarity and unknown phylogenetic relationship to *Epioblasma torulosa*; some authors have considered *E. sampsonii* a variant or ecophenotype of *E. torulosa* (Goodrich and van der Schalie 1944; Stansbery 1970).

General Distribution
The only historical report of this species in Kentucky is from the Ohio River, Kenton County (R.I. Johnson 1978; MCZ). Archaeological specimens were reported from the Ohio River, Henderson (Parmalee 1960), Bracken (Call 1992), and Greenup (Call 1992) counties; Rough River, McLean County (D. Stansbery, personal communication); and the Kentucky River, Woodford County (Call and Robinson 1983).

Probably restricted to main-channel shoal habitats of large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

*Epioblasma sampsonii* reportedly was common in the lower Wabash River in the 1800s (Clarke 1981c), but it appears to have been rare elsewhere in its range. All of its historical range is now impounded or otherwise highly altered. Most historical collections of this species do not have a specific date, but it has not been seen in at least 70 years (Clarke 1981c). KNP: presumed extinct; AFS: endangered, possibly extinct.
**Epioblasma stewardsonii** (Lea, 1852)

**Cumberland Leafshell**

Endemic to the Tennessee-Cumberland faunal province, but now extinct. Occurred in the upper two-thirds of the Tennessee and possibly Cumberland rivers, and in the lower reaches of larger tributaries in northern Alabama, southern Kentucky, and Tennessee. This species was most widespread historically in the Tennessee River drainage, and there are only two historical records from the Cumberland River drainage, one in Kentucky and one in Tennessee (R.I. Johnson 1978). Archaeological records specifically or potentially referring to *E. stewardsonii* are more widely distributed in the Cumberland River in Tennessee and in the lower Cumberland and Tennessee rivers (beyond the current-day boundaries of the Tennessee-Cumberland province), but these specimens are difficult to identify.
unequivocally because of poor preservation and similarity to *Epioblasma flexuosa* and *E. lewisii* (Parmalee et al. 1980; Casey 1986, 1987; Parmalee and Bogan 1998; Hughes and Parmalee 1999).

**Kentucky Distribution**

Known in Kentucky only from one undated specimen from the middle Cumberland River, Pulaski County (R.I. Johnson 1978; UMMZ). Specimens from archaeological sites in the Tennessee River, Livingston County, and the lower Cumberland River, Livingston and Lyon counties, possibly representing this species were reported as members of a group of similar species (*E. flexuosa/lewisii/stewardsonii*; Casey 1986, 1987).

**Habitat & Larval Hosts**

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

**Conservation Status**

The single record of *Epioblasma stewardsonii* from Kentucky is not dated, but this collection probably was made in the 1800s. The species was not found in extensive surveys of the Cumberland River drainage conducted in 1911 and the late 1940s (Wilson and Clark 1914; Neel and Allen 1964), suggesting that the species disappeared from the state at an early date for unknown reasons. Alternatively, the presence of only a single record elsewhere in the Cumberland River drainage raises the possibility that these two records are erroneous and perhaps based on mislabeled specimens or incorrect locality information, and the species may have been restricted to the Tennessee River drainage. At best, this species appears to have been extremely rare in Kentucky even prior to major human alteration of streams. All habitat for this species has been impounded for over 60 years. The last reports of this species were from several sites in the lower Holston River, Tennessee, from 1913–1915 (Ortmann 1918), but it may have persisted there until construction of Cherokee Dam in 1941. KNP: presumed extinct; AFS: endangered, possibly extinct.
**Epioblasma torulosa rangiana** (Lea, 1838)

Northern Riffleshell

**General Distribution** Ohio River basin from the Wabash River upstream to Pennsylvania; not reported from the Tennessee or Cumberland river drainages. Great Lakes Basin in western Lake Erie and Lake St. Clair and their tributaries. The historical distribution of this taxon is difficult to assess because of its unknown relationship to *E. torulosa torulosa* and confusion between these taxa. Several authors have considered *E. t. rangiana* a small to medium-sized stream ecophenotype that gradates into *E. t. torulosa* in larger streams (e.g., R.I. Johnson 1978).
Widely distributed historically in the Green, Salt, Kentucky, and Licking river drainages. Reported from only two sites in the Ohio River, including historical collections from Kenton County (MCZ; OSUM) and archaeological specimens from Carroll County (Peacock 2008). Reported from the lower Green River drainage only at archaeological sites on the Green River, Ohio and Butler counties (Patch 1976; Morey and Crothers 1998; Morey et al. 2002; Claassen 2005). Generally distributed to occasional in the upper Green River drainage including the Green, Barren, and Nolin rivers, and Russell Creek. Sporadic in the Salt and Licking river drainages and reported only as relic shells or from archeological sites (Licking River, Morgan County; DBNF). The only specific locality records in the Kentucky River drainage are archaeological specimens from the Kentucky River, Woodford County (Call and Robinson 1983), and the Red River, Menifee/Powell counties (D. Dourson, personal communication); however, Danglade (1922) reported it as occasional in the upper Kentucky River drainage (from unspecified locations but probably including the North Fork Kentucky River).

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. This species is a host specialist on darters (Percidae) and sculpins (Cottidae).

_Epioblasma torulosa rangiana_ has declined dramatically throughout its range, and all natural populations in Kentucky appear to be extirpated. Populations in the Ohio, Kentucky, and lower Green rivers likely were eliminated by impoundment, and the population in the upper Green River may have been reduced to critically low levels by oil brine pollution in the late 1950s followed by altered flow from Green River Dam (see Williams 1969; Konrad et al. 2012). The causes of its disappearance elsewhere in the state are unknown. Physical stream habitat remains intact at many sites where _E. torulosa rangiana_ occurred formerly, and many of these sites continue to support diverse mussel assemblages. The absence of historical records of live individuals and the scarcity of relic shells in the Salt and Licking river drainages suggests that the species was rare in those drainages even historically and disappeared at an early date. There are numerous historical records of live or recently dead individuals from the upper Green River drainage (e.g., Ortmann 1926a; OSUM) and it was locally abundant at some sites (e.g., Nolin River, Grayson/Hart counties; Taylor 1983; KNP). The last report of a surviving population in Kentucky was the collection of 1–2 recently dead individuals in the Green River, Edmonson and Hart counties, in 1989 and 1987, respectively (OSUM; KNP); it is possible the species continues to occur at very low levels in the Green River. The species was reintroduced in 2013 and 2014 at four sites in the Licking River, Campbell, Pendleton, and Nicholas/Fleming counties, using source stock from the Allegheny River, Pennsylvania (KDFWR 2013; M. McGregor, personal communication); the success of these reintroductions is unknown. KNP: endangered; AFS: endangered; USFWS: endangered.
Endemic to the Ohio River basin, but now extinct. Occurred in the Ohio River from near the mouth upstream to Ohio and West Virginia, and in the lower reaches of larger tributaries from the Tennessee River upstream to the Muskingum River, Ohio. The historical distribution of this taxon is difficult to assess because of its unknown relationship to *E. torulosa rangiana* and confusion between these taxa. Several authors have considered *E. t. torulosa* a large stream eco-phenotype that gradates into *E. t. rangiana* in smaller streams in most of the Ohio River basin or *E. t. gubernaculum* in the upper Tennessee River drainage (e.g., R.I. Johnson 1978).
Kentucky Distribution

Type locality: Ohio and Kentucky rivers. Reported only sporadically from large rivers nearly statewide, but probably generally distributed in those habitats historically. Historical and archaeological records exist throughout the Ohio River from McCracken to Greenup counties. An archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the species in prehistoric times (Wesler 2001; see Section IV.C.2). Not reported specifically from the Tennessee or lower Cumberland rivers in Kentucky, but probably widely distributed in both rivers historically. Specimens referred to as *E. propinquata/torulosa/obliquata* are reported from several sites on both rivers (Livingston and Lyon counties, Casey 1986, 1987) and likely represent *E. t. torulosa* in part. A relic specimen of *E. torulosa* from the lower Cumberland River, Livingston County (MSU), cannot be identified unequivocally to subspecies (J. Sickel, personal communication), but it was reported as *E. t. torulosa* by Ciccerello et al. (1991). *Epioblasma torulosa torulosa* was widespread and abundant in the Tennessee River in Alabama and Tennessee, in prehistoric and historical times (Ortmann 1918; Hughes and Parmalee 1999), and it is widespread in archaeological assemblages from the lower Cumberland River in Tennessee (Parmalee and Bogan 1998). Reported from the Green River system only in the upper Green River, Hart County (OSUM), and the Barren River, Warren County (R.I. Johnson 1978; MCZ; OSUM); records for the Green River, Edmonson, Green, and Taylor counties, and Drakes Creek, Warren County (R.I. Johnson 1978), are *E. t. rangiana* (D. Stansbery and G. Schuster, personal communication). Not reported from the lower Green River drainage, but probably widespread historically in the lower mainstem. Specimens referred to as *E. rangiana/propinquata/obliquata* dominated archaeological assemblages from the lower Green River, Butler County (Morey and Crothers 1998); some of these specimens probably are referable to *E. torulosa torulosa*, but unequivocal identification is difficult because of the similarity of this taxon to *E. torulosa rangiana* and *E. propinquata* (see accounts for these taxa). Represented by a single record from the Salt River drainage (Beech Fork, Nelson County; OSUM) and two records from the Licking River (Campbell/Kenton and Pendleton counties; INHS, OSUM). The unspecified type locality is the only record of the species in the Kentucky River drainage (see R.I. Johnson 1978).

Habitat & Larval Hosts

Restricted to main-channel shoal habitats of medium-sized to large streams in gravel and sand substrates. Host use of this species is unknown, but it was probably a specialist on darters (Percidae) and possibly sculpins (Cottidae), similar to other *Epioblasma*.

Conservation Status

The relative scarcity of historical reports of this species in Kentucky probably is an artifact of the lack of collecting in large rivers prior to impoundment. Call (1900) reported this species as abundant in the Ohio River. Some museum collections from the Ohio River contain dozens of individuals, and archaeological assemblages often are dominated by this species. Based on these observations, *Epioblasma torulosa torulosa* appears to have been a widespread and locally dominant species in much of the Ohio River and possibly also in the Tennessee, lower Cumberland, and Green rivers, and it likely occurred at least sporadically in the lower reaches of most other larger streams in the state. Like other *Epioblasma* and other species that use darters as hosts, *E. torulosa torulosa* did not adapt to loss of shoal habitats after impoundment of large rivers. Nevertheless, it persisted in the lower Ohio River, McCracken County, into the late 1950s or 1960s (Parmalee 1967). The last reports of this species are from the Nolichucky River, Tennessee, in 1968, and the Kanawha River, West Virginia, in 1969 (USFWS 1985a). KNP: presumed extinct; AFS: endangered, possibly extinct; USFWS: endangered.
Epioblasma triquetra (Rafinesque, 1820)

Snuffbox

General Distribution
Mississippi River basin from the White River system, Arkansas, north to Minnesota, and west to eastern Kansas. Ohio River basin upstream at least to Pennsylvania, but generally absent in lowland regions of the lower basin. Great Lakes basin from Lake Michigan to the Niagara River.

Kentucky Distribution
Type locality: Falls of the Ohio River (at Louisville, Jefferson County, Kentucky. Widespread historically in the Ohio River and in all major drainages
from the Cumberland River to Tygarts Creek. Absent from lowland habitats in western Kentucky including most of the lower Green River drainage; archaeological records are available for the Pond River, Hopkins County (Kreisa 1991), and the lower Green River, Butler County (Morey and Crothers 1998; Claassen 2005; Patch 2005). Not reported from the Tennessee River drainage in Kentucky, but widespread in that drainage from Alabama to Virginia. Reported from the lower Cumberland River drainage only in the Red River, Logan County (KNP). Formerly generally distributed in the middle Cumberland River drainage upstream to Buck Creek, but only one record exists from the Big South Fork system (Little South Fork, Wayne County; E. Hartowicz, personal communication) and apparently absent from the Rockcastle River system; absent above Cumberland Falls (Neel and Allen 1964). Generally distributed in the upper Green River drainage upstream to Casey County. Sporadic to occasional in the Salt, Kentucky, and Licking river drainages but apparently largely absent in sections of those drainages in the Bluegrass physiographic section. Not reported from the Little Sandy or Big Sandy river drainages.

**Habitat & Larval Hosts**

Occurs in gravel and sand substrates in a wide variety of upland stream habitats from large rivers to small streams, but does not penetrate far into the headwaters. This species may be locally common, at least formerly, but it is rarely or never a dominant component of mussel assemblages. This species is a host specialist on darters (Percidae) and sculpins (Cottidae).

**Conservation Status**

Because it occurs in habitats ranging from the largest rivers to small streams, *E. triquetra* was the most widely distributed *Epioblasma* historically and it remains so today. Nevertheless, it has disappeared or declined across much of its range, and only about eight surviving populations are known in Kentucky, all of which are small and appear to be declining. Like other *Epioblasma*, it is dependent on darters as hosts and therefore did not adapt to the loss of shoal habitats after impoundment of large rivers. Live or recently dead individuals have not been found in the Kentucky portion of the Ohio River for over 100 years, but a small population may survive in the upper river in West Virginia (Butler 2007). It is now absent in other large rivers where it likely occurred at least sporadically prior to impoundment (e.g., Tennessee, lower Cumberland, lower Green, Kentucky). The large population in the middle Cumberland River (Neel and Allen 1964) was eliminated by Wolf Creek Dam. Other populations in the state have declined for largely unknown reasons. Live or recently dead individuals have not been seen in the Red River system (lower Cumberland River drainage) since the 1960s (OSUM). After construction of Wolf Creek Dam, a single population remained in the middle Cumberland River drainage until the late 1980s (Buck Creek, Pulaski County; Schuster et al. 1989; Layzer and Anderson 1992), but this population appears to be extirpated, and the species now may be extirpated throughout the Cumberland River drainage. It has declined dramatically in the upper Green River, likely in response to oil brine pollution in the 1950s and altered flow from Green River Dam (see Williams 1969; Konrad et al. 2012), and it is now extremely rare in that river (KNP; Butler 2007). Only one population is known in the Salt River drainage (Rolling Fork, Larue/Nelson counties), but this population has declined since the 1980s (McGregor et al. 2007; KNP). Three populations remain in the Kentucky River drainage (Red River, South Fork/Redbird River, and Middle Fork), but all are relatively small. The formerly large population in Slate Creek, Bath County, has declined dramatically since the 1980s and may now be extirpated (Butler 2007), and recruitment in the adjacent Licking River appears to be limited by cold water discharge from Cave Run Dam (Laudermilk 1993; McGregor 2002, 2003, 2006; KNP; KDOW; OSUM). Large populations existed in Kinniconick Creek, Lewis County, and Tygarts Creek, Carter and Greenup counties, into the late 1980s, but the species is now rare in these streams (Zeto 1979; Taylor 1980; Butler 2007; OSUM; KNP). KNP: endangered. AFS: threatened; USFWS: endangered.
**Fusconaia flava** (Rafinesque, 1820)

Wabash Pigtoe

**General Distribution**  
Mississippi River basin from Louisiana upstream to Minnesota, and west to eastern Kansas and South Dakota. Ohio River basin from the mouth upstream to Pennsylvania, including the lower Tennessee River drainage and much of the Cumberland River drainage. Great Lakes basin from Lake Michigan to the Niagara River, from which it appears to have colonized parts of the Lake Ontario and upper Hudson river basins via the Erie Canal (Strayer and Jirka 1997). Southern Hudson Bay basin in North Dakota and Manitoba. Populations in Gulf Coast drainages west of the Mississippi River may represent this or closely related species (Howells et al. 1996).
Type locality: Small tributaries of the Kentucky, Salt, and Green rivers. Generally distributed nearly statewide. Not reported from the Mississippi River and direct tributaries, but to be expected there; the species is reported from Reelfoot Lake and the Obion River drainage in Tennessee (Ortmann 1926b; Parmalee and Bogan 1998). Sporadic in other lowland habitats in western Kentucky; scattered records exist from the Clarks, Tradewater, and Pond rivers. Widespread in the lower Cumberland River drainage upstream to the Stones River, Tennessee (Parmalee and Bogan 1998), but not reported from the Kentucky portion of the Red River system (see Ray 1999). Sporadic and rare historically in the middle Cumberland River drainage upstream to Pulaski County (Neel and Allen 1964), and absent above Cumberland Falls.

Occurs in wide variety of habitats from the Ohio River to small streams, but does not penetrate far into the headwaters. This species is a characteristic member of large river mussel beds but it also may be a locally dominant member of mussel assemblages in smaller streams. This species is tolerant of impoundment to an appreciable extent and has adapted to some riverine impoundments such as Kentucky Lake, but it is absent in truly lentic environments. This species is a host specialist on a wide variety of minnows (Cyprinidae).

Fusconaia flava remains common in a variety of habitats statewide, but several local populations have been extirpated. It appears extirpated from the Tradewater River, which has been degraded by coal mining, and is nearly extirpated from the Little River system (lower Cumberland River drainage) from unknown causes. Wolf Creek Dam destroyed most habitat for the species in the middle Cumberland River drainage in Kentucky, and it now appears absent throughout that drainage. The population in the impounded Tennessee River may have increased due to the inundation of former river floodplains, which this species has colonized, but its rarity in similar habitats in Lake Barkley is puzzling. Elsewhere in the state, the distribution of this species appears to have changed relatively little, and many populations are robust and show evidence of recent recruitment (e.g., Ohio, Tennessee, upper Green, and Licking rivers). AFS: currently stable.
**Fusconaia subrotunda** (Lea, 1831)

Longsolid

Largely endemic to the Ohio River basin, occurring throughout the Ohio River and in larger tributaries from the Tennessee River upstream to Pennsylvania. Potentially occurred historically in the Maumee River system of western Lake Erie (Watters et al. 2009).

**Kentucky Distribution**

Formerly generally distributed to occasional throughout the Ohio River and in most larger tributaries, but usually absent in smaller streams. Absent in lowland habitats in western Kentucky including the Mississippi River and direct tributaries and the Tradewater...
River. Occasional in the lower Tennessee River, but probably present historically throughout the mainstem. Not reported from the lower Cumberland River drainage in Kentucky, but reported from the Cumberland River in adjacent Stewart County, Tennessee (Parmalee and Bogan 1998), and probably present historically throughout the mainstem. A record for the lower Cumberland River, Lyon County (UMMZ), is Reginaia ebena (J. Sickel, personal communication). Formerly generally distributed in the middle Cumberland River upstream to the lower Rockcastle River, and in the lower Big South Fork, but absent above Cumberland Falls (Neel and Allen 1964). A record for the upper Rockcastle River (Ahlstedt 1986) is erroneous (S. Ahlstedt, personal communication), and a record for the Little South Fork (Ahlstedt et al. 2014) is Pleurobema oviforme (Starnes and Bogan 1982). A single record is available for the Salt River drainage (Beech Fork, Nelson County, OSUM). Generally distributed to occasional in the Green, Kentucky, Licking, and Big Sandy river drainages. A record for Blaine Creek, Lawrence County (Bay and Winford 1984), is F. flava (G. Fallo, personal communication).

**Habitat & Larval Hosts**

Restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates. Typically a minor component of main-channel mussel beds. Host use of this species is unknown, but it is probably a host specialist on minnows (Cyprinidae), similar to other *Fusconaia*.

**Conservation Status**

*Fusconaia subrotunda* does not adapt well to impoundment, and because it occurs primarily in large streams, its distribution in Kentucky and across its range has been drastically reduced by the loss of free-flowing, large river habitat. It is now extremely rare in the Ohio River, and only a small population persists in the lower Tennessee River (Lewis and Sickel 2003; B. McClane, personal communication; OSUM). It was extirpated from the middle Cumberland River drainage in Kentucky by Wolf Creek Dam, and appears to persist in the entire Cumberland drainage only as a small, relict population in the Cumberland River below Cordell Hull Dam, Tennessee (Hubbs 2013). It appears extirpated from the Salt River drainage and the Rough and Nolin rivers (Green River drainage), and populations in the lower Green, Kentucky, and Big Sandy river drainages are small (KNP). The largest remaining populations in the state are in the upper Green and Licking rivers, where the species is locally common and shows evidence of recruitment. KNP: none, but this species warrants listing as threatened; AFS: special concern; USFWS: petitioned for listing.
**Hemistena lata** (Rafinesque, 1820)

Cracking Pearlymussel

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**General Distribution**

Endemic to the Ohio River basin, formerly occurring in the Ohio River upstream at least to Ohio and West Virginia, and in larger tributaries from the Tennessee River upstream to the Muskingum River, Ohio.

**Kentucky Distribution**

Type locality: Kentucky River. Probably widely distributed historically in the Ohio River and in larger tributaries, but specific localities are few. Reported from the Ohio River in Jefferson, Carroll, and Kenton counties (NMNH; OSUM), and from an unspecified...
location adjacent Indiana (Call 1900). No records are available for the lower Tennessee or lower Cumberland rivers in Kentucky, but the species is reported from both streams upstream in Tennessee (Parmalee and Bogan 1998), and it likely occurred throughout these rivers historically. Formerly generally distributed in the middle Cumberland River upstream to at least Burnside, Pulaski County (Neel and Allen 1964), and in the lower Big South Fork (Wilson and Clark 1914; Neel and Allen 1964; UMMZ). Reported from the lower Green River only from an archaeological site in Butler County (Morey and Crothers 1998), and occasional formerly in the upper Green River from Edmonson to Hart counties (Clench 1926; Stansbery 1965; NMNH). The unspecified type locality is the only record from the Kentucky River drainage. Not reported from the Salt, Licking, or Big Sandy river drainages but possibly occurred in the lower portions of those rivers.

**Habitat & Larval Hosts** Restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates, in which it burrows deeply. Typically a minor component of main-channel mussel beds. This species is a host specialist on minnows (Cyprinidae).

**Conservation Status** *Hemistena lata* is extirpated from Kentucky and from most of its historical range. This is a rare species in most historical collections, but its burrowing habits may have caused it to be overlooked. It was present “in fair numbers” in the middle Cumberland River in the 1940s (Neel and Allen 1964), and it may have been more common than records indicate in other streams. It is clearly intolerant of impoundment, and dams have destroyed or radically altered most habitat for the species. It has not been seen in the Ohio River in about 100 years, since impoundment of that stream for navigation (Watters et al. 2009), and navigation dams on the lower Green and Kentucky rivers were probably responsible for its early disappearance in those streams. The population in the middle Cumberland River was eliminated by Wolf Creek Dam in 1950. The species was last seen in Kentucky in the upper Green River, Hart County, in 1965, but this population appears to have been extirpated by oil brine pollution and altered flows from Green River Dam (see Williams 1969; Konrad et al. 2012). Only two remaining populations are known, one in the Elk River, Alabama and Tennessee, and the other in the Clinch River, Tennessee. These populations may one day provide source stock for reintroduction of the species into other parts of its historical range, such as the Green River. KNP: presumed extirpated; AFS: endangered; USFWS: endangered.
Lampsilis abrupta (Say, 1831)

Pink Mucket

**General Distribution**
Western tributaries of the Mississippi River from Louisiana to the lower Missouri River drainage, Missouri. Ohio River basin throughout the Ohio River and in and larger tributaries upstream to Pennsylvania.

**Kentucky Distribution**
Formerly occasional to sporadic throughout the Ohio River and in most larger tributaries, but usually absent in smaller streams. An archaeological record from the Mississippi River, Ballard County, suggests that conditions at that site were suitable for the spe-
cies in prehistoric times (Wesler 2001; see Section IV.C.2). Occasional throughout the Tennessee and Cumberland rivers prior to impoundment (Wilson and Clark 1914; Ortmann 1925; Neel and Allen 1964). Sporadic in the Green River upstream to Hart County and the lower Barren River (OSUM; MSU; KNP; TTU; Lewis Environmental Consulting 2011). A single record is available for the Salt River drainage (Salt River, Spencer County; KNP), and only two records are available from the Licking River (Bath and Campbell counties; TTU; INHS). Not reported from the Kentucky River system, but likely occurred in the mainstem historically. A single record exists for the Big Sandy River drainage (Levisa Fork, Floyd County; ANSDU).

**Habitat & Larval Hosts**

Restricted to main-channel habitats of medium-sized to large streams in gravel and sand substrates. Typically a minor component of main-channel mussel beds. This species is a host specialist on black bass (*Micropterus*) and other large predators such as Wall-eye and Sauger (*Sander*).

**Conservation Status**

*Lampsilis abrupta* was never abundant, even historically, but it was probably a regular component of large river mussel assemblages throughout Kentucky. For example, in the Cumberland River prior to impoundment, 1–3 individuals were found on each mussel bed (Wilson and Clark 1914). Today, the species remains in only a fraction of its original range and it is extremely rare. This species appears only marginally tolerant of impoundment, and the almost complete loss of free-flowing, large river habitat is probably largely responsible for its decline. The only recent records from the Ohio River are in the relatively free-flowing reach below Lock and Dam 52, McCracken County (J. Schwegman and B. McClane, personal communication); this population may be threatened by completion of Olmsted Lock and Dam, which will replace locks and dams 52 and 53. It was found in the lower Tennessee River as late as the 1980s, but has not been found there recently (Gooch et al. 1979; Sickel 1985; USFWS 1985b). The population in the middle Cumberland River in Kentucky was eliminated by Wolf Creek Dam in 1950, but the species still inhabits a short stretch of the river in Tennessee (Hubbs 2013). Small, isolated populations survive in free-flowing sections of the Barren and Green rivers below antiquated navigation dams and in the longer, unimpounded section of the upper Green River in Hart County. A single living individual has been found in the Licking River (TTU). One of the largest remaining populations is in the Tennessee River downstream of Pickwick Dam in Tennessee (R. Butler, personal communication). Juvenile individuals propagated from adults from this population have been released in Kentucky in the lower Tennessee River, Marshall County; the Green River, Edmonson and Hart counties; and at four sites in the Licking River, Campbell, Pendleton, and Nicholas/Fleming counties, in an attempt to reestablish or augment these populations (McGregor et al. 2007; M. McGregor and J. Layzer, personal communication); the success of these releases is unknown. KNP: endangered; AFS: endangered; USFWS: endangered.

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**Lampsilis cardium** Rafinesque, 1820

Plain Pocketbook

**General Distribution**  Mississippi River basin from Louisiana and Mississippi north to Minnesota, and west to Kansas and South Dakota. Throughout the Ohio River basin from the mouth upstream to New York. Great Lakes basin from Lake Superior to the St. Lawrence River system, and southern Hudson Bay basin south to North Dakota and west to Saskatchewan. Occurs in the upper Hudson River basin, which it may have entered via the Champlain Canal, and introduced in the Potomac River (Strayer and Jirka 1997). Populations west of the Mississippi River in Arkansas, Louisiana, Oklahoma, and Texas may represent *L. satura* in part, but phylogenetic relationships between these taxa are poorly known.
Type locality: Ohio River (see Johnson and Baker 1973). Generally distributed nearly statewide, but sporadic and rare in lowland habitats of western Kentucky. One record exists from the Mississippi River, Carlisle County (EKT), and scattered records exist from Clarks and Tradewater rivers; not reported from direct tributaries of the Mississippi River or the Pond River, but to be expected in those streams. Elsewhere in the state, this species is nearly ubiquitous, and it is one of the few species present in the upper Cumberland River drainage above Cumberland Falls.

Occurs in a wide variety of riverine habitats from large rivers to small streams, but does not penetrate far into the headwaters. This species is present in main-channel mussel beds, where it is a minor component, but it also occurs frequently in depositional areas along shore or in backwater pools. It is tolerant of impoundment to an extent and can adapt to some riverine reservoirs, but it is absent in truly lentic environments. Despite its wide distribution, *L. cardium* is probably not among the most numerically abundant species in the state because it does not form dense beds but occurs only as scattered individuals. This characteristic is likely due to the specialization of its glochidia on top predators such as black basses (*Micropterus*) rather than more numerically abundant fishes such as minnows, darters, and catfishes (Haag 2012).

*Lampsilis cardium* remains one of the most widespread mussel species in Kentucky and, with the exception of lowland or headwater streams, it may be found in nearly any stream that supports mussel life. Its tolerance of impoundment has allowed it to persist in some rivers impounded for navigation such as the Ohio and Kentucky, but it apparently did not adapt to impoundment in Kentucky and Barkley lakes and the lower Green River. It was extirpated from the middle Cumberland River by Wolf Creek Dam. Other local populations have been eliminated by water pollution or other factors. For example, coal mining and oil drilling appear to have eliminated the species from the Tradewater and Little South Fork Cumberland rivers, and it appears extirpated in the Little River system (lower Cumberland River drainage) from unknown causes. AFS: special concern.
Lampsilis fasciola Rafinesque, 1820

Wavyrayed Lampmussel

**General Distribution**
Ohio River basin upstream to Pennsylvania, but generally absent in lowland regions of the lower basin. Great Lakes basin from Lake Michigan to the Niagara River system.

**Kentucky Distribution**
Type locality: Kentucky River. Reported historically from two sites in the Ohio River, Kenton and Bracken counties (NMNH; OSUM), and from one unspecified locality adjacent Indiana (Call 1900). Generally distributed to occasional in Ohio River tributaries from
the Cumberland River drainage upstream to Tygarts Creek, but absent in the Tradewater River and other lowland habitats in western Kentucky. Not reported from the Tennessee River drainage downstream of the Duck River, Tennessee (Parmalee and Bogan 1998), with the exception of a single individual from the lower Tennessee River, Marshall/Livingston counties (C. Lewis, personal communication). Occasional in the lower Cumberland River drainage in the Little and Red river systems; not reported from the lower mainstem Cumberland River, but probably occurred there at least sporadically prior to impoundment. Generally distributed in the middle Cumberland River drainage. One of the few species present above Cumberland Falls, occurring upstream to Harlan County. Largely absent from the lower Green River drainage, with the exception of the upper Rough River system, but generally distributed in the upper Green River drainage. Occasional but locally common in Ohio River tributaries from the Salt River drainage to Tygarts Creek; not reported from the Little Sandy or Big Sandy drainages.

**Habitat & Larval Hosts**

Restricted to upland regions where it can occur in nearly any size stream. It is most common in small to medium-sized streams but usually is a minor component of mussel assemblages. This species is a host specialist on black basses (*Micropterus*) and Rock Bass (*Ambloplites rupestris*).

**Conservation Status**

*Lampsilis fasciola* remains widespread in upland regions of Kentucky, but it has disappeared or declined in much of its historical range and remains common in only a few streams. This species is intolerant of impoundment and has been largely extirpated from large rivers such as the Ohio, Cumberland, and Kentucky; only a single, recent record is available for the latter stream (USFWS). It appears extirpated from the Little and Red river systems (Lower Cumberland drainage) and the Nolin River system (upper Green River drainage) for unknown reasons. The species remains widespread and locally common in the middle Cumberland River drainage, particularly in the Big South Fork, Buck Creek, and Rockcastle River, but it has declined dramatically or is extirpated in the Little South Fork, Horse Lick Creek, the upper Cumberland River drainage, and other streams due to coal mining and oil drilling (Cicerello and Laudermilk 2001; Warren and Haag 2005). Populations occupy long reaches of free-flowing habitat in the upper Green River drainage, and the species is locally common in the Rolling Fork Salt River, Red River (Kentucky River drainage), South Fork Kentucky River system, and the South Fork Licking River. Most other populations in the state are small and isolated. AFS: currently stable.
Lampsilis ovata (Say, 1817)

Pocketbook

Endemic to the Ohio River basin, occurring throughout the Ohio River and in larger tributaries from the Tennessee River drainage upstream to Pennsylvania. The relationship of *L. ovata* to *L. cardium* is poorly known, and the two species can be difficult to differentiate. These species have been either synonymized or treated as subspecies (*L. cardium = L. ovata ventricosa*) based on the supposition that the two taxa represent ecophenotypic variation in which the *ovata* form was expressed in large rivers but gradates into the *cardium* form in smaller streams (e.g., Ortmann 1911; Cvancara 1963). However, the two forms co-occur in large rivers within the range of *L. ovata*, and the
ovata form is absent elsewhere in the Mississippi River basin, lending credence to the distinctiveness of the two species.

**Kentucky Distribution**
Type locality: Ohio River and its tributary streams. Generally distributed to occasional historically throughout the Ohio, Tennessee, Cumberland, Green, and Barren rivers, and sporadic in larger streams in the Salt, Kentucky, and Licking river drainages. The historical range of this species in the state is difficult to ascertain because of confusion with *L. cardium* and the lack of voucher specimens for many records. Neel and Allen (1964) reported it as restricted to the mainstem Cumberland River below the Cumberland Falls, but Wilson and Clark (1914) reported it from above the falls and in tributaries such as the Rockcastle River. However, Wilson and Clark (1914) also reported that *L. ovata* was introduced above the falls by pearlers and that specimens from the Rockcastle River were atypical. Rockcastle River specimens most closely resemble *L. cardium* (W. Haag, personal observation), and some previous reports of *L. ovata* from that stream (Ahlstedt 1986) are based on *L. cardium* (S. Ahlstedt, personal communication). Other reports of *L. ovata* from the Rockcastle River and Buck Creek (e.g., Layzer and Anderson 1992; Houp and Smathers 1995; McGregor 2005) are plotted here but viewed as questionable and likely representing *L. cardium*. Apparently valid records exist for Clarks River, McCracken County (Lewis 2006); Beech Fork and Rolling Fork (Salt River drainage, KDOF, KNP) and the Licking River, Pendleton County (OSUM). A record for the Red River (Kentucky River drainage; Houp 1980) is *L. cardium* (S. Call, personal communication). Other recent or archaeological records from smaller streams (i.e., Pond River, Nolin River, West Fork Drakes Creek, Rough River, Dix River, North Fork Licking River) are plotted here but viewed as questionable and likely representing *L. cardium*.

Unlike *L. cardium*, *L. ovata* typically is restricted to main-channel habitats of medium-sized to large rivers in gravel and sand substrates and does not occur in depositional areas. It is a minor component of main-channel mussel assemblages. Glochidia of *L. ovata* can metamorphose on black basses (*Micropterus*), similar to *L. cardium*, but metamorphosis is most robust on Saugeen (*Sander canadensis*), which may explain its occurrence mainly in large rivers. Populations in the Tennessee River drainage in Alabama, Tennessee, and Virginia differ from those elsewhere in the Ohio River basin by occurring in a wider range of stream sizes, suggesting that bass may be more suitable hosts for those populations.

**Conservation Status**
*Lampsilis ovata* was probably a regular member of large river mussel assemblages throughout the state, but its range is now drastically reduced. This species appears less tolerant of impoundment than *L. cardium*, and it persists in impounded rivers only in sections that retain considerable riverine influence. It is now rare in the Ohio River, remaining primarily in riverine reaches such as the lower river and below Cannelton Dam (Payne et al. 1994; Ecological Specialists 2000; McGregor 2005; J. Schwegman, personal communication). The large population in the middle Cumberland River (Neel and Allen 1964) was eliminated by Wolf Creek Dam, and the species may be extirpated throughout that drainage depending on the identity of individuals from the Rockcastle River. Other small populations survive in the Tennessee River, McCracken, Marshall, and Livingston counties (Sickel and Burnett 2001; McGregor 2005; Lewis 2006; Lewis et al. 2006); Beech Fork, Nelson County; and the Rolling Fork, Nelson/Larue counties. The species appears extirpated from the Kentucky and Licking river drainages. The largest population in the state is in the upper Green River, where the species remains generally distributed and locally common. Apart from these populations and several in the middle and upper Tennessee River drainage, *L. ovata* is nearly extirpated elsewhere in its range (Cummings and Mayer 1992; Watters et al. 2009). KNP: endangered; AFS: special concern.
Lampsilis siliquoidea (Barnes, 1823)

Fatmucket

General Distribution
Mississippi River basin from Mississippi north to Minnesota, and west to Colorado and Montana. Ohio River basin from the mouth upstream to New York, but absent from most of the Tennessee and Cumberland river drainages. Great Lakes basin from Lake Superior to the Niagara River (possibly also in the Lake Ontario basin; Strayer and Jirka 1997). Southern Hudson Bay basin and southern portions of the McKenzie River basin. The distribution of this species in the lower Mississippi River basin, including western Kentucky, is unclear because of similarity to the closely related Lampsilis hydiana, which occurs from Louisiana north to southern Illinois and west to Texas (see section IV.D.2).
Kentucky Distribution

Generally distributed nearly statewide, but absent from most of the Tennessee and Cumberland river drainages. Not reported from the Mississippi River except for an archaeological record from Ballard County (Wesler 2001; see Section IV.C.2), but sporadic to occasional in smaller lowland streams in western Kentucky; some of these populations may represent *L. hydiana*, but phylogenetic relationships of Kentucky populations remain uninvestigated (see section IV.D.2). Reported from the Tennessee River drainage only in the Clarks River system, and in the Cumberland River drainage only downstream of and including the Little River; a record for Buck Creek, Pulaski County (McGregor 2003), is considered erroneous.

Habitat & Larval Hosts

This species can be found in all but the smallest streams, and in habitats ranging from lowland streams of the Mississippi Embayment to mountain streams. It is characteristic of small to medium-sized streams where it is often the most abundant species, but like other *Lampsilis*, it typically does not occur in dense beds (see *L. cardium*). It is conspicuously rare in larger rivers where it is usually confined to depositional areas along shore or in backwater pools. For example, *L. siliquoidea* is rare in the Green and Licking rivers, but is ubiquitous in tributaries of these streams. This species adapts to impoundment to an extent but typically is absent from truly lentic habitats in Kentucky; in contrast, large populations often occur in natural lakes in the upper Midwest and Great Lakes regions. This species is a specialist on black basses (*Micropterus*) and potentially sunfishes (*Lepomis*).

Conservation Status

*Lampsilis siliquoidea* is one of the most widely distributed species in the state and remains abundant in many areas. The ubiquity of this species may give the impression that it is tolerant to a wide variety of human impacts. More likely, it may be one of the last species to disappear from a degraded stream simply because it was initially one of the most abundant species. Many local populations doubtless have been greatly reduced or extirpated by severe point-source pollution, channelization, or other impacts. For example, this species has not been found in the Little or Tradewater river systems in over 25 years and may be extirpated from those systems. Because it tolerates impoundment to some extent, it persists in streams such as the Kentucky River that are impounded for navigation, but it has been extirpated from streams impounded by larger dams for flood control and hydroelectric power generation. AFS: currently stable.