The Freshwater Mussels of Ohio
The true mystery of the world is the visible, not the invisible.
—Oscar Wilde
Contents

Preface ix
Acknowledgments xi
Abbreviations Used in Species Accounts xiii

Introduction 1
Species Accounts 27
  Family Margaritiferidae Henderson, 1929 27
  Family Unionidae Rafinesque, 1820 32
  Questionable and Potential Ohio Occurrences 338

Key to Species in This Book 363
Glossary 369
References 373
Index 397
The reasons for gathering together the material for a book of this kind are found in human needs. These needs may be current or anticipated, or they may rest in the conviction that all living organisms, including the human species, have relationships with and effects upon each other, regardless of how small or how large, how obvious or how obscure, and that these relationships are well worth knowing for reasons both pure and applied. We have, looking at our history, excellent reason to believe that more benefits to humankind remain to be discovered than we have anticipated in our wildest speculations. It is apparent that we have a growing need for knowledge and for the efficiencies necessary for its ease of ready access. This volume is one such accumulation of information and is arranged so as to be readily available for use.

There are those among us who have the conviction that all species of life have not only the right to exist but also the privilege to be understood and valued by human-kind. Our subject is the unionoid molluscs of our freshwater habitats, especially streams. Some species may be found in ponds, lakes, and impoundments, but by far the highest diversity of this life-form is in our flowing freshwater systems. While some future uses of these bivalves must necessarily remain speculative, an examination of our history (literature) reveals a number of ways these molluscs have been used in times past.

Native Americans found these animals not only easy to gather but also quite edible, with shells that could be fashioned into tools of several sorts. The occasional natural pearl was treasured as much then as in more recent times. Pearl buttons fashioned from discs cut from mother-of-pearl shell seem not to have appeared in the Ohio country until introduced about 1880 by immigrants along the Ohio River. By the early 1900’s, this art became an industry, and shortly the most common source of button material was mother-of-pearl from freshwater shell. Those collecting the raw material for the button factories were careful to search out the valuable natural pearls, which were then sold to itinerant buyers who resold them in Eastern and foreign markets for impressive sums.

The development of a technology to produce molded-glass and plastic buttons led to the replacement of pearl for all but the most expensive garments. The production of cultured pearls using pearl spheres brought strands of these near-natural gems within the price range of those other than the very wealthy.

And so since before the time of recorded history, these larger riverine bivalves, commonly called clams or mussels, less commonly naiads or unionids, have been used by humans in various ways. Over the same time span, the human population has been becoming ever more numerous and through its carelessness has been instrumental in the extirpation of many populations and the recent extinction of too many species. These extinctions and extirpations have come to pass largely through habitat degradation, although over-harvesting in some streams may have played a role. Major factors responsible for this relatively rapid decline have been the construction of impoundments, the dredging of streams for navigation and flood control, the addition to our streams of the sediments of agricultural and construction activities, and the addition of a wide spectrum of solid, semisolid, and liquid waste materials from the industries of a rapidly growing human population.

More recent observations by field malacologists have revealed that these animals are, with rare exception, sensitive to many of these pollutants. They are considered, in view of their rapidly decreasing numbers, to be the most endangered group of organisms in North America by the U.S. Fish and Wildlife Service. This very sensitivity may well lead to what could be their most valuable service yet to human society: they may indeed become our most efficient and effective indicators of pollution of riverine habitats that have been damaged in hazardous ways not visible to casual examination. Even now mussels are being used as the “miners’ canaries” of our waterways.
Ohio's streams are a valuable resource that we must protect and restore. As we move in the direction of wiser use of these resources, we should not forget the importance of protecting and restoring the faunas that have made these resources so rich. Just as many species of unionids have been eliminated from streams throughout the state, or their populations have been reduced, so too we must begin to work toward their restoration. Some species, given their remarkable means of distribution (as larvae on a more motile host), will become restored naturally because they will have access once again to improved streams. Others will need our assistance.

It would seem that the need for a book such as this one is eminently due, if not overdue. This volume identifies the various species, describes their geographic distribution, and relates the history these animals have had in the state. The authors sincerely hope and trust that the volume will help us focus our conservation efforts into the future.

— David H. Stansbery
Acknowledgments

We wish to thank Dr. Arthur Bogan, North Carolina Museum of Natural History, Raleigh, NC, for discussions of unionocean nomenclature; Kevin Cumming, Illinois Natural History Survey, Champaign, IL, for information on type depositories; and Richard Petit, South Myrtle Beach, SC, and Dr. Henk K. Mienis, Curator, National Mollusc Collection, Hebrew University of Jerusalem, Israel, for information on obscure literature.

The authors wish to particularly thank Mr. Randy Sanders, Mr. Joe Mion, and Mr. John Navarro of the Ohio Department of Natural Resources Division of Wildlife for keeping the project not only on track but also alive. The Ohio Division of Wildlife contributed all funds toward this book, and clearly it would not exist in any form without their support.

Dr. Watters thanks his immediate and extended family for support, badgering, and the occasional kick in the seat to complete this work. I thank my parents and my wife for indulging me in such an odd pursuit, and my grandfather for introducing me to the natural history of Ohio. I hope that mussels will still be around for my grandchildren (or even just my children!) to enjoy.

Dr. Hoggarth wishes to thank his parents, Robert Hoggarth and Helen Hoggarth. You helped me to see beauty and wonder in nature and encouraged the pursuit of my dream of becoming a biologist. My teachers helped me to put that dream into action. Four teachers I would especially like to acknowledge are Mr. Charles Randall, Upper Arlington High School; Dr. Ross F. Shaw, Seattle Pacific University; Dr. Paul Yokley, Jr., the University of North Alabama; and Dr. David H. Stansbery, The Ohio State University. The knowledge and enthusiasm each of you shared with me still seems unlimited. You have helped me fashion my own teaching and learning after your example. Many of my students at Otterbein College and Franz Theodore Stone Laboratory are to some small degree a product of your teaching. Students of mine who have made a special contribution to the knowledge of the mussels of Ohio are Diana (Lee) Dickson, Tara (Chinn) Grove, Jim Gates, Melissa Haltuch, Bill Rodman, Scott Ross, Erin (Stewart) Miller, Megan (Hysell) Michael, Leah Gillig, and Wayne Rossiter. Daniel L. Rice accompanied my students and me on many collecting trips, and his help and friendship are gratefully acknowledged. I am most grateful to my wife, Karen Cook-Hoggarth, and my sons, Mark Hoggarth and Kyle Hoggarth. You have helped me collect and process shells, and you have shared my excitement with each new species and each new discovery. Your continued support and encouragement made this volume possible.

Ms. Carol Myers Flaute prepared the original maps and labored long and hard to prepare the supporting ArcView files. Ms. Sarah Hazzard and Mr. Kody Kuehnl were invaluable in proofreading the final version and assisting with last-minute details; Mr. Kuehnl also was instrumental in filling in the sections on genetics and phylogeny. Dr. Robert Warren, Illinois State Museum, provided invaluable information on the use of mussels by prehistoric man. Mr. Fred Obhof organized the final specimens for photography. Photography for this book was the tortuous, accumulated efforts of Ms. Janna Thompson-Chordas, Mr. Tim Daniel, and G. T. Watters. Ms. Cynthia Bishop, then at the Ohio Division of Wildlife, made the pen-and-ink drawings in the Glossary.

Although the great majority of records used in this book were deposited at The Ohio State University Museum of Biological Diversity, we endeavored to include as many additional museums as possible to fill in gaps. To this end we are indebted to Dr. Tim Pearce, Carnegie Museum of Natural History; Dr. Diarmaid Ó Foighil and Dr. Jack Burch, University of Michigan Museum of Zoology; Dr. Robert Kennedy and Ms. Paula Work, Museum of Natural History and Science, Cincinnati; Dr. James Bissell, Cleveland Museum of Natural History; and Gary Coover, Boonshoft Museum of Discovery, Dayton.

We thank Dr. George Davis for permission to use previously published photos from Hoggarth, Malacologia (1999), and Roland Houart for permission to use previously published photos from Watters, Novapex (2008). And without
the gracious attention to detail of Jennifer Shoffey Forsythe, Juliet Williams, and Maggie Diehl, The Ohio State University Press, this book would never have become a reality.

Finally, we thank everyone who has ever deposited a mussel shell into the The Ohio State University Museum of Biological Diversity or has surveyed Ohio’s streams—a list of people numbering in the thousands. A book like this is the result of so many individual efforts by so many people that it would be impossible to thank everyone. So to anyone who has deposited a shell in the collection of the museum or has collected a shell in the state and deposited it in other collections, we say thank you. Many of the dots on the maps in this book are yours.
# Abbreviations Used in Species Accounts

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Full Name</th>
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<tbody>
<tr>
<td>ANSP</td>
<td>Academy of Natural Sciences, Philadelphia, PA</td>
</tr>
<tr>
<td>BMNH</td>
<td>Natural History Museum, London</td>
</tr>
<tr>
<td>CMNH</td>
<td>Carnegie Museum of Natural History, Pittsburgh, PA</td>
</tr>
<tr>
<td>MAH</td>
<td>Collection of Michael A. Hoggarth</td>
</tr>
<tr>
<td>ICZN</td>
<td>International Code of Zoological Nomenclature</td>
</tr>
<tr>
<td>MCZ</td>
<td>Museum of Comparative Zoology, Harvard University, Cambridge, MA</td>
</tr>
<tr>
<td>MNHN</td>
<td>Muséum national d’Histoire naturelle, Paris, France</td>
</tr>
<tr>
<td>OSUM</td>
<td>The Ohio State University Museum of Biological Diversity, Columbus, OH</td>
</tr>
<tr>
<td>SMF</td>
<td>Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany</td>
</tr>
<tr>
<td>UMMZ</td>
<td>University of Michigan Museum of Zoology, Ann Arbor, MI</td>
</tr>
<tr>
<td>USNM</td>
<td>Smithsonian National Museum of Natural History, Washington, DC</td>
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Ohio has an especially rich heritage of freshwater mussels, from both a biological and a historical perspective. Eighty species have been reported from the state. This number is 27% of all mussel species known to be from North America. More than 60 mussel taxa were described from specimens collected from Ohio, although many of them are now recognized as synonyms of other species.

This bounty of Ohio taxa is a result of the efforts of some of Ohio’s early naturalists. Isaac Lea (1792–1886), the undaunted Philadelphia describer of more than 800 mussel species, was sent specimens from his bother Thomas, a resident of the Cincinnati area. Their efforts alone accounted for numerous Ohio type localities. Samuel Hildreth (1783–1863), a Marietta physician, collected in the mussel-rich Muskingum River, documenting species that sadly no longer occur there today. Benjamin Tappan (1773–1857), Ohio senator, co-founder of the Smithsonian Institution, and founder of Ravenna, Ohio, was a patron of natural history and aided some of the best malacologists of his day, including Isaac Lea and Charles Adams. Jared Kirtland (1793–1877), legislator, physician, and naturalist, collected in eastern Ohio, while Victor Sterki (1846–1933), physician and malacologist, and Arnold Ortmann (1863–1927), Curator of Mollusks at the Carnegie Museum of Natural History in Pittsburgh, spent a great deal of time collecting mussels from the northeastern portions of the state. In particular, their collections from the Tuscarawas River at New Philadelphia represent one of the most comprehensive pictures of what occurred in a single Ohio stream prior to the mass extirpations that were soon to follow.

Today, Ohio is one of the best-surveyed states, thanks to the work of many dedicated collectors, the support of state and federal agencies, environmental regulations, the interest of conservation groups, and curious citizens. However, there are still discoveries to be made, as evidenced by the remarkable finding of the Purple Catspaw, Epioblasma obliquata obliquata, in Killbuck Creek (Hoggarth et al., 1995). It is because of the place Ohio has in the study of mussels and the interest that so many Ohioans have shown and continue to show in these animals—that we have written this book.

The Higher Classification of North American Freshwater Mussels

The recognition of higher taxa in North American mussels has been at best contentious. What constitutes a family or subfamily rank characteristic? To date, we still do not have a set of unifying characteristics that allows us to unite taxa at the family or subfamily level. Historically these differences were first based on shell characteristics, then anatomical characteristics, and most recently molecular DNA differences. Unfortunately, there has been a tendency to use one, and only one, of these types of data at a time while ignoring the larger picture. For example, no study has even considered the extensive fossil record of this group.

Linnaeus (1758) originally considered mussels as members of Mya, now reduced to a very small marine genus. The first division was made by Lamarck (1799) based solely on the presence or absence of hinge teeth—those without teeth were placed in Anodonta. Philipsson (1788) created Unio for those with teeth, thus removing all freshwater mussels from Mya. Lea added a further refinement by recognizing those with a wing as Symphynota. Further splitting based on shell characteristics continued with abandon.

Ortmann (1919) recognized the importance of anatomy and organized mussels into the Unionidae and Margaritiferidae based on gill morphology. His Unionidae was further divided into the Unioninae, Anodontinae, and Lampilinae, again based on gill morphology, particularly the structure of the marsupium. Heard & Guckert (1971) further refined the divisions but proposed three separate families: Margaritiferidae, Amblemidae, and Unionidae. However, few subsequent workers have used this scheme. Davis & Fuller (1981) reexamined the anatomical evidence as well as new immunoelectrophoretic data and essentially agreed with Ortmann except for making Margaritiferidae a subfamily of the Unionidae. Smith & Wall (1984) reinstated this group as a family. Hoeh et al. (1998), based on Cytochrome C Oxidase Subunit I DNA (COI) sequences, found evidence for separation of the Margaritiferidae from the Amblemidae and Anodontinae—suggesting either three families or three subfamilies.
Lydeard et al. (1996) used 16S rRNA DNA sequences and morphological data to construct a phylogenetic tree of unionoid relationships. This approach, the most comprehensive to date, maintained the separation of the Unionidae and Margaritiferidae. In their study, Lydeard et al. (1996) identified two subfamilies within the Unionidae: the Anodontinae and Ambileminae. Within the Ambileminae groups representing Quadrula, Megalonaias, Elliptio, and Amblema showed support, as did the Lampsilinae of other studies.

Graf & Ó Foighl (2000) performed a phylogenetic analysis using brooding and COI characteristics. Their results supported separation of Margaritiferidae, Unioninae, Anodontinae, Pleurobeminae, and Lampshelinae. Amblema was associated not with the pleurobemines, its usual place, but with the lampshelines.

The study of Graf (2000), using larval and adult characteristics, suggested that the Unionidae are paraphyletic and that all groups except for the Unionidae and Margaritiferidae represent a separate clade, the Etherioidea. We would like to see this controversial theory tested using molecular DNA data.

While the phylogeny of a group of organisms can never truly be known, our current level of understanding of the relationships between and among freshwater mussels, particularly those relationships dealing with the Unionidae, is elementary at best. The relationships that have been identified have not been thoroughly tested using multiple independent data sets and therefore may be inaccurate. Until such studies are undertaken, our current understanding of these relationships will be limited. However, based on the information currently available for unionoids, the consensus is that the Unionidae and Margaritiferidae represent a separate clade, the Etherioidea. Several DNA studies also suggest that the Anodontinae may be at least as distinct from other Unionidae as the Margaritiferidae (e.g., Hoeh et al., 1998). There also appears to be support for a lampsheline and a pleurobemine/amblime group. For the most current review of historical relationships among unionoids see Roe & Hoeh, 2003.

Recognition of lower level taxa including species and genera among freshwater mussels (Margaritiferidae and Unionidae) has been no less contentious among malacologists. As with higher level taxa, species and genera are delineated principally by shell characteristics, even though it has been extremely difficult to delineate mussel species based on these characteristics alone. This undoubtedly has led to the description and redescription of numerous taxa of freshwater mussels, while in the process complicating our ability to recognize accurate species, which in turn has hindered our conservation efforts in this imperiled group. However, the advent of molecular methods, particularly DNA sequencing, has provided a new way to assess species boundaries as well as address hypotheses of relationships between and among different mussel taxa. These studies have proved invaluable in identifying unique or cryptic species that require systematic changes as well as those requiring various conservation activities. Such studies have also helped identify morphological characters that set apart monophyletic groups of mussels from similar species (e.g., genus Hamiota; Roe et al., 2001) or have shown that certain morphological characters which we thought were good characters for uniting certain taxa actually may not be (e.g., genus Petamilius; Roe & Lydeard, 1998).

However, the majority of the studies utilizing molecular data to test current species and generic appellations have showed para- and polyphyletic relationships. To date, numerous molecular studies have provided important insights for the delineation of species as well as the relationships between species of freshwater mussels. Lydeard et al. (2000) used mtDNA sequences to show that several of the genera endemic to the Gulf Coast region were polyphyletic and not representative of natural groups. Other studies that found para- or polyphyletic genera include the genus Quadrula (Serb et al., 2003) and Lampshelia, Obovaria, Fusonaia, Pleurobema, and Quincuncina, among others (Campbell et al., 2005).

Still other studies utilizing molecular data have found that while our current understanding of what constitutes a single species may be accurate (i.e., molecular analyses identify all individuals sampled to comprise a monophyletic group), many of the populations that make up that species can and often do contain unique genetic variation (e.g., Mulvey et al., 1996; Jones et al., 2006; Serb, 2006; Burdick & White, 2007; Elderkin et al., 2007). In a few cases, morphological variability supporting unique species is not supported by molecular data (e.g., Mulvey et al., 1996; Buhay et al., 2002). Regardless the result, molecular data have proven invaluable in assisting researchers in generating a more realistic taxonomic scheme and assisting in generating meaningful and appropriate conservation activities (e.g., captive propagation, population augmentation, and reintroductions).

**Nomenclatorial and Systematic Concepts**

Every species that is described in this book has a unique, binomial scientific name. That name is composed of genus and species names (both in italics), the author of the description, and the year in which the name was first applied to that species. In some instances, the species name is followed by a subspecies name that is also printed in italics. The author and date are surrounded by parentheses if the species name has been moved from the genus in which
it was first placed by the author of the species; author and date are not enclosed in parentheses if the species remains in its original genus. Genera are organized into families, families into orders, orders into classes, classes into phyla, and phyla into kingdoms. North American freshwater mussels are members of the Kingdom Animalia, Phylum Mollusca, Class Bivalvia, Order Unionoida, and Families Unionidae and Margaritiferidae.

Five families of freshwater bivalve molluscs occur in Ohio: Margaritiferidae, Unionidae, Sphaeriidae, Corbiculidae, and Dreissenidae. Only the first three are native members of the Ohio molluscan fauna. The Margaritiferidae and Unionidae are commonly known as the pearly freshwater mussels (the subject of this book) while the Sphaeriidae are the fingernail or pea clams. The other two families are represented by Corbicula fluminea (Müller, 1774) and Dreisena polymorpha (Pallas, 1771) and Dreisena bugensis Andrusov, 1897, all exotics.

The specimens from which a species or subspecies were described are referred to as type specimens (holotype if so designated by the author of the name at the time of description or by monotypy). Other type specimens commonly encountered in the literature include paratype (all other specimens in the type series other than the holotype), lectotype (designated by a subsequent author from the type series when no holotype has been designated), paralectotype (all other specimens in the type series other than the lectotype), and syntypes (for which neither a holotype nor a lectotype has been designated). Topotypes are specimens that are not included in the type series but have been collected from the type locality. The type locality is the site from which the nominal species or subspecies was collected and described. Cotype, a term no longer used by the ICZN, may mean either a primary type (usually a syntype) or simply a specimen, not of the type lot, later identified by the author as a specimen of that species. In the synonymies given here, cotypes are listed because future study may reveal them to be primary types. Allo­types refer to specimens of a gender opposite that of the holotype.

Each name listed in the Species Accounts is followed by a list of synonyms in chronological order. Species names are listed in the synonymy if the specimens (or description or illustration in some cases where the type specimens have been lost) are clearly identical to another named species and that other named species has priority. Priority is established by date of publication and availability of the name. Some earlier names located in the synonymy for each species are unavailable for a number of reasons, the most common being that the name had already been used for another species (whether a valid species or not). Each species account following will therefore include the genus name, the species name, and the subspecies name (if appropriate); the author and date of publication (in parentheses if the species is no longer considered to be in the originally described genus); a citation to the original description; the type locality (if known); the location of the type material (if known); and a list of synonyms. The list of synonyms includes only novel combinations; it does not include every citation of a species (which would have doubled the length of this book). Vernacular names are also given. Those recognized by the American Fisheries Society (Turgeon et al., 1998) are shown first and in italics.

There is a tendency among today’s biologists, including some systematists, to be overly critical of the early descriptive authors. Convoluted synonymies, lack of type material, and vague type localities all seem to be the result of carelessness on the part of these scientists. This is an unfair assessment. We must remember that the naturalists of the 1700’s and 1800’s often worked in a near-vacuum. With Europe in a nearly constant state of war or revolution, workers in one country were often unaware of what their counterparts in another country had published. As a result, the same species was often described at least twice. Today we are spoiled by the ease with which we can access information from any point on Earth from our desks. We tend to forget the parochial nature of early scientific journals and books and the difficulty that even a simple literature search must have presented in those days. The lack of types arose not from carelessness but from the fact that the “type concept” as used today simply did not exist in those times. Our nomenclatorial rules have slowly evolved, and it is unfair to hold a worker in the 1700’s accountable for concepts that would not emerge for over one hundred years. These were years of great exploration, with scientists often relying on sailors or soldiers to bring back specimens from foreign lands. Given this source it is not surprising that some species were described with little or no locality data (or even with spurious data).

On the other hand, some early systematists clearly seemed to operate beyond the norm. Rafinesque is often vilified for his crude drawings and brief descriptions. Isaac Lea described species based on only the slightest of differences. He was an American unknowingly adherent to the contemporary French group of systematists known as the Nouvelle École (New School). Championed by Jules René Bourguignat (1828–92), they believed that if a mollusc specimen differed from any others by three characters or more, it was a different species. The characters could be quite minor, resulting in a “plethora of ill-conceived new species” (Dance, 1966). In more recent times De Gregorio (1914) has redescribed numerous Ohio species, apparently ignoring the work of previous workers.
Origin of the Ohio Fauna

Descendants of marine bivalves have invaded the freshwater environment several times during the past 400 million years. These were independent invasions, occurring at different times and comprising diverse groups. The result is a freshwater bivalve fauna composed of unrelated groups now found living side by side: zebra mussels, fingernail clams, freshwater mussels, Asian clams, marsh clams, etc. Several other freshwater groups, such as the Anthracosiacea and Archanodontacea, which flourished between 200 and 400 million years ago, resembled unionoids but seem to have been unrelated; these groups are now extinct.

Unionoid freshwater mussels, the subject of this book, may be traced back to at least the Triassic Period, 250 million years ago. At that time, all of the present-day continents were assembled into a single supercontinent, Pangaea. Freshwater mussel groups that today are found only on other continents apparently enjoyed a much wider distribution in Pangaea. Fossils very similar to those of the Hyriidae, a mussel group now occurring only in South America, Australia, and New Zealand, were found in the Triassic of Pennsylvania, Texas, and Arizona (Simpson, 1896; Richards, 1948). Mycetopodidae-like species, now found only in South America, were found in the Cretaceous of Colorado (White, 1878). An Iridinidae-like species, a group now found only in Africa, was found in the Cretaceous of Montana (Morris & Williamson, 1988). By the close of the Mesozoic Era, 65 million years ago, a diverse mussel fauna comparable to that found today occurred in North America. Ironically, this fauna is best known from western North America, an area that today is very depauperate in mussels. Climatic and orogenic changes drove most of these freshwater mussels to extinction. The extent of unionoid diversity in eastern North America is unknown due to the paucity of fossil material. The great radiation of species in the Cenozoic Era, culminating in our present fauna, may have been derived from the few survivors of the western fauna, migrations from Asia across the Bering land bridge and from Europe across Greenland, and whatever eastern fauna may have previously existed. The evolution of the North American unionoids is described in greater detail in Watters (2001).

No pre-Pleistocene mussel species are known from Ohio, but this does not necessarily mean that none occurred here. Ohio has no outcrops from the Mesozoic Era, that time during which fossil mussels reached their zenith. The Paleozoic Era outcrops that cover Ohio are too early for freshwater mussels to occur and, in any event, are predominately marine.

A series of glaciers scoured most of Ohio in the Pleistocene such that any earlier mussel faunas must have been eliminated. Most of Ohio’s mussels are derived from unglaciated rivers to the south, including the Ohio and Wabash rivers. Relatively few Ohio mussels owe their origin to the Lawrentian system, which includes the Great Lakes. Indeed, most of the Lake Erie fauna is of Wabash River origin. The Maumee River, now a Lake Erie tributary, was once part of the Wabash River. As the last glacier retreated, the river level fell below a divide at Fort Wayne, Indiana, and the Maumee River reversed direction and flowed not to the Wabash River but to Lake Erie. The river took its mussels with it, so that today western Lake Erie is populated by Ohio River mussels, not Lawrentian mussels.

Human Utilization of Freshwater Mussels

From at least the Archaic Period (ca. 8000–1500 b.c.), Native Americans employed freshwater mussels for a variety of uses: ornamental, ceremonial, and utilitarian, and as a food item. Having an iridescent nacre, or mother-of-pearl lining, mussels were valued as jewelry. Shells were carefully formed into beads and discs and were drilled for stringing. Especially cherished were pearls, which were occasionally placed in ceremonial mounds. Kunz (1898) reported a Hopewell mound in Ross County having more than 100,000 pearls. As tools, mussel shells were used as knives, tweezers, hoes, scrapers, and bowls. Some shells used for tools appear to have been brought from over 100 miles away (Theler, 1991). Mussel shells also were charred and crushed and then added to pottery clay to increase durability.

Some Native Americans consumed great quantities of mussels as food, as evidenced by the extensive shell middens still found along some rivers. The Aztalan Site in Wisconsin (ca. a.d. 1000–1150) had a midden composed of 8,500 shells comprising 23 species (Theler, 1991). Middens along the Green, Cumberland, and Tennessee rivers may cover up to 6 hectares each (Stansbery, 1966b). Some middens show few modified shells, suggesting that the mussels were gathered solely for food, and not for tools or ornamentation (Warren, 1995). In many middens these shells are charred, indicating that they were cooked before being eaten.

The importance of mussels in Native American diets, both as a source of calories and as a favored food, is the subject of debate. Mussel meat is relatively nutrient-poor. Theler (1991) showed that a one-hour harvest in a good-quality stream would produce one-half the daily caloric requirement of an individual, but required the ingestion of 200 mussels. Other studies suggest even less food value in mussels (Warren, pers. comm.), and thus mussels prob-
ably were harvested seasonally to supplement other food sources. Harvested areas included the deep channels of large rivers and muddy lakes, as well as the more accessible smaller streams (Warren, 1991). All sizes and species were harvested, indicating that Native Americans did not selectively gather the larger species for their greater food value but rather collected all mussels they encountered (Peacock, 2000). The impact of Native Americans on mussels through harvesting may have been localized and negligible, but this has not been adequately determined. Only people living close to the mussel beds utilized them for food—inland groups did not travel to gather them (Warren, 1983). However, there is some evidence that as Native American society became more agrarian, runoff began to impact mussels, just as it does today on a much larger scale (Peacock et al., 2005).

The arrival of Europeans eventually dispossessed Native Americans of their lands, including access to harvestable mussel beds. Initially Europeans made only limited use of mussels, primarily as a source of mother-of-pearl for inlay work and the serendipitous pearl. Europeans did not consume mussels on anywhere near the scale that had Native Americans, and mussels did not become a true commercial commodity until the last half of the 19th century. Beginning then, the commercial use of mussels occurred in three stages: the Pearl Rush; the Pearl Button Industry; and the Cultured Pearl Industry, the latter of which continues to this day.

The Pearl Rush began in 1857 when a pearl was found in a mussel from a New Jersey stream. Valued at $25,000, the discovery launched a whirlwind of mussel collecting that eventually swept all of the United States west to the Rocky Mountains and persisted until the early 1900’s. Although gem-quality pearls were quite rare, thousands of men, women, and children shucked every mussel they could find in hopes of easy riches (Kunz, 1908). How many millions of mussels were killed will never be known. To little avail, the U.S. Fish Commission called for legislation to curb the “reckless prodigality and waste of such resources by man” (Kunz, 1898). Eventually, a glutted market and over-harvested beds brought an end to the Pearl Rush, but the mussels had little respite before the next wave of over-exploitation arrived.

In 1887, Johanne Boepple, a German immigrant, brought his knowledge of pearl inlay artistry to America. He quickly realized the untapped potential of American mussels—as buttons. By a process of “punching” discs out of shells, mother-of-pearl could be tooled into buttons (fig. 1). In 1891, Boepple established his first factory in Muscatine, Iowa. The production of mother-of-pearl buttons was to become a multi-million-dollar business, with factories appearing over much of the eastern United States, employing tens of thousands of people. In Ohio, factories were established in Cincinnati, Marietta, and Manchester, where punched shells may occasionally be found to this day. Through the use of rakes, hooks, and particularly brails, deepwater beds previously untouched by the Pearl Rush were accessible (Claassen, 1994).

As with the Pearl Rush, the U.S. Fish Commission realized that this unregulated harvest was quickly leading to an economic disaster in the industry. But clammers refused to consider closed seasons: they wasted most of the shells they harvested; they harvested species they did not need; and they collected juveniles, too small to be of use (Smith, 1899; Coker, 1914). Failure to contain the commercial industry led to a bold measure by the Commission—the attempt to artificially grow and stock mussels, with the aim to rejuvenate the depleted resource. Established at the Fisheries Biological Station in Fairport, Iowa, a team of researchers engaged in the most in-depth study of mussels ever undertaken, the results of which still form the basis of our knowledge of these animals. Experiments were carried out to determine (a) if mussels could be raised in hatcheries and impoundments (Howard, 1914b; Isely, 1914; Howard, 1916; Corwin, 1920, 1921; Howard, 1922); (b) what mussels ate (Churchill & Lewis, 1924); and (c) how mussels infected hosts and what hosts were needed (Lefevre & Curtis, 1910a, b; Young, 1911; Surber, 1913; Howard, 1914a, 1914c, 1915). In addition, they made observations on morphology (Coker & Surber, 1911; Surber, 1912) and investigated the ingenious possibility of rearing glochidia in artificial media (Lefevre & Curtis, 1912a). From a practical point of view, the Fairport Station was a failure—no means were found to supply mussels to meet the demands of a wasteful and self-destructive industry. From a scientific point of view, the Station was a well-spring of knowledge about mussels. In 1917, the Station burned to the ground, taking many of the researchers’ invaluable notes with it.
By the turn of the century, the button industry was suffering. Over-harvesting had depleted most beds beyond the point of being profitable. The final blow came with the production of the plastic button. Cheaper and more durable, it signaled the end of the Pearl Button Industry founded some 70 years, and untold millions of mussels, ago.

The most recent wave of commercial use is by the Cultured Pearl Industry, centered largely in Japan, Australia, China, and other Pacific Rim countries. Cultured pearls are formed by inserting beads, or nuclei, cut from North American mussel shells into marine pearl oysters (Pinctada sp., family Pteriidae, the wing-oysters). The oyster lays down a veneer of nacre over the bead, forming a pearl. Whereas a non-cultured, natural pearl requires decades to reach a gem size, cultured pearls can be made in less than three years. Because the pearl is formed from a man-made implant, nearly any size and shape of pearl can be produced. Cultured pearls are significantly cheaper than natural pearls, allowing the general public to acquire them. Not surprisingly, the culture of pearls has become a multi-billion-dollar industry.

Beads originate from mussels in North America, particularly those in the Ohio and Mississippi river drainages. Shells are delivered to buyers, who then steam out the animals. Shells may be cut and tumbled into beads before shipment or shipped whole for bead production overseas. As of 1990, more than 26,000 tons of shells were harvested annually from North America. Buyers typically pay several dollars per pound of raw shells. Shells are turned into beads costing thousands of dollars per pound. In turn, the beads become gem-quality pearls worth millions of dollars. Kentucky, Alabama, Tennessee, and a few other states have an active industry supporting shellers, buyers, and others. Commercial claming is licensed and regulated in these states. Other states, including Ohio, Indiana, Pennsylvania, West Virginia, and Michigan, are closed to all commercial mussel harvest. Recently, mussel poaching has become a chronic problem in some of these closed states.

As with the Pearl Rush and the Pearl Button Industry, there is concern that the Cultured Pearl Industry will over-exploit the mussel resource. Mussels are slow growing, have little recruitment, and are already assailed by habitat destruction, pollution, and zebra mussels. At a 26,000-ton annual harvest, is this resource renewable? As evidence that it is not, some people believe that poaching is increasing because the legally harvested beds have been depleted. Others point to the fact that clammers may harvest, unwittingly or not, endangered species. Because of the difficulties of identifying some species, even by an expert under the best conditions, it is highly unlikely that clammers can distinguish all endangered species in the field. As zebra mussels eradicate the commercial beds, and as new methods and materials are devised to form pearls, the future of mussel harvesting in North America is far from clear. It remains to be seen if the mussel resource can continue to support this industry.

Anatomy, Life History, and Reproduction

Unionoid bivalves, the subject of this book, are commonly called freshwater mussels, naiads, clams, or even oysters, but they are only distantly related to those predominately marine groups. However, those names are entrenched in our vernacular (and those of other languages as well), and it would be useless to attempt to change them. Still, the reader should be aware that these animals are a group very distinct from true mussels (Mytilidae), clams (Veneridae), or oysters (Ostreiidae). Their closest living relatives may be an obscure marine group (the Trigonoideans), now found only off the coast of Australia, although this group had a long and diverse fossil history.

Freshwater mussels have two shells, or valves, arranged left and right. The earliest part of the shell is called the beak or umbo. The shell expands along the margins as the animal grows. Most freshwater mussels have a dorsal area called the hinge, which has interdigitating projections called teeth. These teeth serve to keep the shells aligned and prevent shearing during burrowing. The anterior-most teeth are called the cardinal (or pseudocardinal) teeth, whereas the posterior teeth are the lateral (or pseudolateral) teeth. Some mussels lack teeth altogether. The shells are held together in life by two adductor muscles which close the shells. These muscles counteract the ligament, a non-living proteinaceous structure which acts as a spring to open the shells. The muscular foot protrudes from the anterior half of the shells; the siphons, the openings through which water enters and exits the shells, are located posteriorly. On the inner surface of the shells are scars, sites of attachment for various muscles, including the adductors and the pallial line—the linear scar where the mantle tissue is anchored to the shell. The major landmarks of the freshwater mussel shell are illustrated in figures 2 and 3.

Freshwater mussels live by filter-feeding food from the surrounding water with their gills, or ctenidia. Because of their food-gathering function, these gills are much larger than is needed for respiration. North American species lack true siphons, or tubes for water intake and release, such that many species are confined to burrowing only to the posterior edge of the shell during much of the year. This renders them susceptible to predators, desiccation, and temperature and other environmental extremes. Never-
Fig. 2. Morphology of freshwater mussel shells. Also see the Glossary.
theless, many species live for 20–30 years, and some up to 200 years or more (Bauer & Wächtler, 2001). Other species, such as *Pleurobema clava*, may spend much of their life buried several centimeters beneath the surface, relying on water to percolate between the substrate particles for food and oxygen.

Unionoid food continues to be the subject of debate. Allen (1914, 1921), Churchill & Lewis (1924), and Fikes (1972) found the gut to contain mostly diatoms and other algae, although the diatoms passed through the digestive system intact. However, Imlay & Paige (1972) believed that mussels fed on bacteria and protozoans. Bisbee (1984) found different proportions of algal species in the guts of two mussel species, suggesting that not all unionids fed upon the same food. Recently, Nichols & Garling (1998) demonstrated that mussels were omnivores, feeding on detritus and zooplankton, as well as algae and bacteria. Newly metamorphosed juveniles do not filter-feed with their gills, but may feed on interstitial nutrients using cilia on their foot, gills, and mantle. This stage may last several years before changing to a filter-feeding mode (Tankersley et al., 1997). Yeager et al. (1993) believed that food for juveniles consisted of interstitial bacteria, yet an algal mix including silt was suggested as food by Humphrey & Simpson (1985) and Gatenby et al. (1993). Small amounts of silt have been found to enhance survivorship in cultured mussels, both adults and juveniles (Hudson & Isom, 1984; Humphrey, 1987b; Hove & Neves, 1991), probably by introducing bacteria and zooplankton.

Gametogenesis, the formation of eggs and sperm, is initiated by changes in water temperature and/or light levels. There appear to be threshold temperatures or light levels that cue reproductive events. For those species relying on some upper temperature threshold, constant low water temperatures, such as are found below some dams, may prevent reproduction from ever taking place. In such conditions, populations of adult mussels may live out their normal lives and die without ever producing offspring. For most Ohio mussels there is only one breeding season a year, although the extirpated *Cumberlandia monodonata* may breed twice a year (Howard, 1915; Gordon & Smith, 1990). Ortmann (1919) believed that *Lampsilis fasciola* and *Lampsilis cardium* had two broods per year and that *Potamilus alatus* and *Utterbackia imbecillis* breed year round.

Typically, sexes are separate, although small numbers of hermaphrodites have been found in many species (Poupart, 1706; Fischerstrom, 1761; van der Schalie, 1966, 1970; Heard, 1979). Some species, such as *Toxolasma patrum*, *Lasmigona compressa*, and *Utterbackia imbecillis*, are believed to be wholly hermaphroditic (Ortmann, 1912a, 1916; Utterback, 1916). The relative proportion of hermaphrodites may increase under low population densities, perhaps to bolster declining population numbers (Kat, 1983; Bauer, 1987c). Males liberate sperm into the water, sometimes as spherical (Utterback, 1931; Lynn, 1987; Barnhart & Roberts, 1997) or disc-shaped aggregates termed spermatozeugmata. Females downstream take up the sperm with incoming water. Fertilization success may be related to population density, with a threshold density required for any reproductive success to occur (Downing et al., 1993). For at least *Elliptio complanata*, there is evidence that mussels of both sexes may horizontally migrate to form aggregates during spawning, thus increasing fertilization success (Amyot & Downing, 1998). Eggs are fertilized in the suprabranchial chambers of the gills and then apparently are moved to the marsupia. The marsupia are regions of the gill that act as brood chambers for the glochidia. Their placement and structure vary from genus to genus and have been used as key taxonomic characteristics. The marsupium may change in shape and structure during the breeding season, particularly in lampshille mussels (Smith, 1979; Kays et al., 1990; Richard et al., 1991). During this time, the marsupium either does not function as a site of respiration (Richard et al., 1991) or operates at greatly reduced efficiency (Allen, 1921; Tankersley & Dimock, 1992). This region may remain non-respiratory during the non-breeding season as well (Richard et al., 1991).

The developing embryos are physiologically isolated in the marsupium from the outside water (Kays et al., 1990). Muscles associated with the water tubes may be responsible for maintaining this isolation (Gardiner et al., 1991). Larval shells are formed indirectly from mineral deposits in the gills that act as a source of calcium carbonate (Silverman et al., 1985). These minute bivalved larvae, or glochidia, develop over a period of days to months, depending on water temperature and species. Glochidia are a type of specialized veliger larvae. Freshwater mussels, and freshwater molluscs in general, lack the trochophore larvae so common to marine molluscs. When first discovered by Leeuwenhoek in 1697, glochidia were considered by some (but not by Leeuwenhoek) to be parasites living in the mussel’s gills, and they were given the scientific name *Glochidium parasiticum* by Rathke (1797). For nearly three-quarters of a century, a lively debate ensued as to whether these “agglomerations of animicules,” as Prévost called them (1826), were mussel parasites or mussel larvae. Houghton (1862) appears to have been the first to identify glochidia on fishes, and Forel (1866) experimentally demonstrated their parasitic role and their true identity as larval mussels.

North American freshwater mussels are historically divided into two behavioral groups based upon the duration that glochidia are held in the marsupia. Tachytotic or short-term breeders spawn in the spring or summer and release their glochidia later the same year, usually by July.
Fig. 3. Morphology of freshwater mussel shells (cont.). Also see the Glossary.
or August. Bradytictic or long-term breeders spawn in the summer or early autumn, form glochidia, and typically hold these larvae in the marsupium until the following spring or summer. There is evidence that glochidia that overwinter till spring in the marsupium experience less mortality once on the host than those glochidia of the same species that are released in the autumn and metamorphose that same year (Corwin, 1921; Higgins, 1930; Tedla & Fernando, 1969; Zale & Neves, 1982a). But some otherwise “bradytictic” individuals release glochidia in autumn or winter to overwinter on their hosts. They remain dormant on their host until a threshold temperature is reached the following spring, at which time they metamorphose and excyst (Watters & O’Dee, 1999). Some species, such as Pyganodon grandis and Leptodaea fragilis, apparently utilize host-overwintering glochidia as part of their normal life history. The ability to overwinter on hosts is related to the duration the glochidia spend attached to the host, with overwintering success declining with time (Watters & O’Dee, 1999). Overwintering of glochidia on hosts may aid in dispersal of the species and confer greater fitness on those glochidia capable of remaining attached till spring. Whether these glochidia overwinter in the marsupia or on their hosts, this prolonged developmental stage may be necessary for bradytictic species.

Nearly all freshwater mussels are obligate vertebrate parasites as larvae. Of the approximately 300 species in North America, only one, the Salamander Mussel, Simpsoniaiambigua, is believed to use exclusively a non-fish host, the Mudpuppy, Necturus maculosus (Howard, 1915, 1951). The remainder are believed to use fishes but may be capable of parasitizing amphibians as well (Watters, 1997a; Watters & O’Dee, 1998a). Although claims have been made that several species may complete their metamorphosis without a host (Leleve & Curtis, 1911: Howard, 1914b), evidence suggests that most North American mussels must parasitize a host to complete their life cycle. Two North American species, Lasmigona subviridis (Barfield & Watters, 1998; Lellis & King, 1998) and Utterbackia imbecillis (Dickinson & Sietman, 2008); an African irinid species (Kondo, 1990); and several South American mussels (Mansur & Campos-Velho, 1990) are known to bypass the parasitic stage completely.

Hosts are infested with glochidia when they come into contact with them in the water, or on the substrate, or by attempting to ingest them (fig. 4). Different mussel species have different methods of releasing these larvae. Some simply expel the glochidia along with water and waste products. Hosts take in suspended glochidia and pass them over their gills, where they attach (fig. 5), or they contact larvae on the substrate, where the parasites attach to the fins or skin (fig. 6). Some mussels, such as Anodonta suborbiculata, Anodontaoides fusussacianus, and Utterbackia imbecillis, release “webs” or “trot lines” of mucus containing glochidia that ensnare passing fishes (Hove et al., 1995a; Watters & O’Dee, 1997b). Other mussels bind glochidia into matrices called conglutinates (Chamberlain, 1934; Fuller, 1971). Several types of conglutinates have been identified (Watters, 2008). The simplest are formed entirely of glochidia, each enclosed in a fragile envelope. A more complex type is formed from eggs and glochidia. In these, the majority of the mass is composed of sterile eggs. In some species up to 85% of the total number of eggs have this structural, rather than reproductive, function and apparently are destined never to be fertilized (Barnhart, 1997). The eggs function to give shape and color to the entire mass, which has functional glochidia embedded in it or attached to it. Another type of conglutinate, found in Strophitus undulatus, is composed of a mucus rod containing the glochidia. When released by the female, the glochidia squeeze through pores in the conglutinate wall and move to the outside (Watters, 2002). Other conglutinates are even more complex, such as the fry lures of Ptychobranchus fasciolaris, which are multi-layer constructions complete with discrete pigmented areas and adhesive pads (Watters, 1999). Conglutinates also may resemble worms, insect larvae, or other food items (Barnhart & Roberts, 1997), or they may simply be fragile structures that rapidly disassociate into free glochidia. The latter probably act only to facilitate the movement of the glochidia out of the marsupia. Some mussels, such as Lampsilis, apparently can release either conglutinates or free glochidia (Watters, unpubl.), perhaps dependent on the time of year or the presence or absence of hosts. Glochidia or conglutinates may be moved to the supra-branchial chamber and expelled through the excurrent opening, but in many lampslines, the distal portion of the marsupia rupture and conglutinates are expelled directly to the outside. Recently, “superconglutinates” were discovered in several southern species (Haag et al., 1995; Hartfield & Butler, 1997). Superconglutinates are groups of individual conglutinates formed into a single lure. The lure is played out in the water on a strand of mucus up to
2.5 m long. No Ohio species has been found with superconglutinates.

Some lampshline species have modified the mantle into lures resembling fishes, insects, and other food items (fig. 7). These structures may undulate in swimming-like motions (Kraemer, 1970). Often the marsupial portion of the gills is protruded out of the shell between these flaps. When struck by a predatory fish, females snap their shells closed on the protruded marsupia, causing the marsupia to rupture and release clouds of glochidia which attach to the would-be predator. Radically different mantle lures have been found in the same “species,” such as *Lampsilis fasciola*, suggesting either the presence of sibling species or a startling polymorphism in mantle pigmentation and morphology within single species, even in a single population. There is some evidence that mussels and glochidia can detect nearby hosts and modify their behavior to increase their chances of attracting or attaching to them (Henley & Neves, 1997). Mantle tissue is sensitive to changes in light intensity and may react to the shadows of passing fishes (Hove & Anderson, 1997). In addition, it has been suggested that mantle tissue may release chemical attractants for hosts (Pepi & Hove, 1997).

Once shed by the female, glochidia must acquire a suitable host or die, usually within 24–48 hours. “Free” glochidia are preyed upon by numerous predators: insects, bottom-feeding fishes, flatworms, hydas, etc. Infective glochidia may travel some distance downstream in currents (Clark & Stein, 1921; Neves & Widlak, 1988). The estimated chances of a glochidium surviving to metamorphose and excyst range from 0.0001% (Jansen & Hanson, 1991) to 0.0000001% (Young & Williams, 1984). Although some species may compensate for this with high fecundity over many years (Bauer, 1987b), other species have been shown to develop late and then reach early senescence (Downing *et al.*, 1993). Species having lures and conglutinates generally produce fewer glochidia but are not able to parasitize as wide a range of hosts as those that broadcast large numbers of glochidia (Watters, 1997b, 2007). Because of the manner in which hosts acquire glochidia (lures, conglutinates, webs, etc.), it is not surprising to find that glochidia are over-dispersed, that is, most hosts either are unparasitized or carry only a few glochidia, whereas a very small number of hosts bear most of the parasite burden (Bangham, 1940, 1955; Weir, 1977; Dartnall & Walkey, 1979; Neves & Widlak, 1988). However, even heavily infected hosts show few ill effects, with few exceptions. Recently parasitized fishes may become lethargic and secretive but usually recover within 24 hours. Large, hooked glochidia, such as occur in *Strophitus undulatus*, may cause great agitation to hosts when attaching.

Glochidia clamp down on the host tissue, causing cells to rupture. This cellular fluid forms part of the food for the developing parasite (Arey, 1924b, 1932b; Blystad, 1924).

*Fig. 5.* Top—Glochidia encapsulated on gill filaments. Bottom—Newly attached, unencapsulated glochidia on gill filaments.

*Fig. 6.* Top—Glochidia encapsulated on the fin of a darter. Bottom—The same fin under scanning electron microscopy.
A host wound reaction forms a capsule by the movement of host cells over the glochidium (Faussek, 1895; Arey, 1921, 1932a). During growth, the larva will resorb much of its own tissue, including the adductor muscle and much of the mantle, as well as feeding on the host (Young, 1911; Blystad, 1924). The glochidia of most mussel species, except the margaritiferid species and the axe-head-shaped glochidia of Potamilus, do not appreciably change size during encystment. After a certain amount of time (from days to months, depending on water temperature and mussel species), the glochidium metamorphoses into a juvenile and excysts (Schierholz, 1889; Howard & Anson, 1923). Threshold temperatures necessary for completion of metamorphosis were identified for Lamellis cardium and undoubtedly exist for all species (Watters & O’Dee, 1999).

At temperatures below these thresholds, metamorphosis may be delayed indefinitely. The duration of metamorphosis decreases with increasing temperature until an upper threshold is reached. At this point, glochidia excyst, fail to metamorphose, and die (Dudgeon & Morton, 1984). Barnhart & Roberts (1997) found that although higher water temperatures greatly decreased the time to complete metamorphosis, metamorphosis occurred on more hosts species at lower temperatures.

Glochidia metamorphose into juvenile mussels. Whereas the glochidium lacks a foot and gills, and has a single adductor muscle and a larval thread, the juvenile has a functional foot, gill “buds,” and two adductor muscles. In many species (except anodontines), the glochidial shell is white but turns tan or brown after metamorphosis. Anodontione glochidia typically are tan. The glochidial shell is incorporated into the adult shell and may be visible in exceptionally well preserved specimens (Hoggarth, 1987).

Once metamorphosed, the juvenile drops from the host and burrows into the substrate (Bauer, 1986; Clarke, 1986; Buddensiek et al., 1993) or attaches to a larger object with a byssal thread. This buried juvenile stage may last several years and has been referred to as the mecoconch (Clarke, 1986). The thread is lost in most adults but persists for a year or more in some species (e.g., Truncilla donaciformis). The thread, which is formed by a gland within the foot, is very similar to the byssal threads of marine bivalves, such as Mytilus (Smith, 2000b).

Potential hosts may possess one of two types of immunity to attached glochidia. Natural immunity occurs in unsuitable hosts, which have tissue responses against the glochidia (Howard, 1914a; Bauer & Vogel, 1987). Acquired immunity occurs when a suitable host has been previously parasitized and has built up a temporary immunity. The number of exposures needed to achieve acquired immunity depends on the degree of prior infestations and the duration between them (Lefevre & Curtis, 1910a; Sbarber, 1913; Reuling, 1919; Arey, 1924a; Bauer, 1987a). Although acquired immunity may be demonstrated in the laboratory, acquired immunity in wild-caught fishes has been observed only once, and its overall prevalence in wild fishes is unknown (Watters & O’Dee, 1996). In both natural and acquired immunity, encysted glochidia are killed by the host and are either sloughed off or absorbed (Arey, 1932c; Fustish & Millemann, 1978; Zale & Neves, 1982b; Waller & Mitchell, 1989).

Host specificity varies greatly among mussels. Some species, usually widespread and abundant, are able to parasitize many species of fishes, including exotics (Trdan & Hoeh, 1982; Watters & O’Dee, 1997a; Watters & O’Dee, 1998a). Other mussel species, usually localized and rare, may use only a few fish species. Because this symbiosis is obligatory, plans to conserve and manage rare and endangered mussels must include management of the host as well. It is suspected that some mussel populations are not recruiting because their hosts no longer occur with them.

This host-parasite relationship apparently arose as a means of dispersal for the unionoids. Lacking internal fertilization and great motility as adults, mussel populations would be doomed to be carried back to the sea over many generations. By attaching themselves to a highly motile host, such as a fish, they are dispersed within and between drainages. Records of dispersal on the feet of waterfowl largely are apocryphal (Rees, 1965), and the idea that glochidia swim by clapping their shells, once the preferred theory, has been abandoned.

Natural predators of metamorphosed mussels consist of fishes, birds, muskrats, and raccoons (fig. 8). In Europe, the hooded crow has been shown to drop mussels from the air to crack them open (Berrow, 1991), and North American birds may have a similar behavior. Baker (1918) listed Freshwater Drum, Lake Sturgeon, Spotted Sucker, Common Redhorse, Pumpkinseed, and others as predators on freshwater mussels. Hanson et al. (1989) and Convey et al. (1989) reported muskrats eating up to 37,000 mussels a year in a Canadian lake. Muskrats are selective in the spe-
cies and sizes of mussels they consume, preferring smaller species and individuals (Watters, 1995b), and they may be an important source of predation on endangered species (Neves & Odom, 1989). Trapping of muskrats has been suggested in some areas as a means of protecting rare mussels. Juvenile mussels and small species are consumed by all of these predators, but large species are probably nearly immune to predation. Once a mussel has become an adult, most natural mortality arises as the result of catastrophes to habitat: scouring; droughts; beaver impoundments, etc.; or disease.

Unionids often are parasitized by unionicolid mites (Mitchell & Wilson, 1965; Davids, 1973; Vidrine, 1989) and monogenic trematodes (see review of Hendrix et al., 1985), which feed on gill and mantle tissue. Chironomid larvae may consume up to 50% of the mussel gill (Gordon et al., 1978), interfering with respiration and reproduction. Leeches also may infest unionids.

**Mussel-Host Associations**

Within the Species Accounts are lists of presumed mussel-host relationships. Each listing is followed by an abbreviation indicating how the relationship was determined: NS—not stated; NI—natural infestation; LI—laboratory infestation; NT—natural transformation; LT—laboratory transformation. These distinctions were first employed by Hoggarth (1992).

Natural infestations (NI) are based on wild-caught fishes parasitized with glochidia. Most studies reporting natural infestations were not continued to determine whether the glochidia metamorphose. Because glochidia may be difficult to identify to species, the determination of the juveniles is often inferred from what species co-occurred with the host. These studies may suffer from misidentified glochidia.

Laboratory transformations (LT) are the most common type of mussel-host association studies. Hosts are infested with glochidia and kept in captivity until metamorphosis occurs. This procedure identifies potential hosts. It suffers from identifying associations that may occur in an experimental setting but never occur in nature.

**Effects of Habitat on Shell Morphology**

Freshwater mussels are unusually plastic in their shell morphology—specimens of a species taken from different parts of its range may look completely unrelated. This great variation has led to the description of numerous superfluous names for some species, as evidenced by their tortuous synonyms. More so than nearly any other group of molluscs, freshwater mussel shells are the product of their immediate surroundings. Mussel shells vary in their degree of lateral compression or inflatedness, in the strength of their sculpture, and in their color patterns. By and large, these variations are not random.

Early on it was recognized that some mussel shells changed in a predictable way within a given river reach—the Law of Stream Distribution (Ortmann, 1920). Headwater forms often are compressed and thin-shelled, with low umbos, whereas big river forms are usually inflated and thick-shelled, with prominent umbos. This gradient in characteristics occurs across taxonomic lines but is most obvious in amblesines. Watters (1994) interpreted this as an adaptation to life in flashy headwaters, where streamlining is at a premium.

Sculpture also varies in strength but can usually be associated with habitat. Savazzi & Peiyi (1992) and Watters (1994) experimentally demonstrated that unionoid shell sculpture was used for anchoring and antiscouring. Thus, for any sculptured mussel species we should find the greatest sculpture in fast-moving water and the least in slow-moving water. This is born out by *Amblema plicata*, whose stream individuals are coarsely sculptured but lake specimens are nearly smooth.

Color patterns probably represent the sequestering of metabolic byproducts in the periostracum. freshwater
mussels differ from the great majority of molluscs in that the outward shell color and pattern are not present in the shell itself but reside only in the periostracum. Stripped of periostracum, mussel shells are uniformly white. The colors and patterns in freshwater mussel shells cannot be construed as camouflage, as most mussels live their lives buried in the substrate. What portion of the shell is exposed is often covered with algae, larval insect cases, and marl. The colors are probably non-adaptive.

For the same reason, nacre color cannot be considered to have any apparent value to the mussel. Variations in nacre color often occur within specific populations. For example, *Obovaria subrotunda* nearly always has white nacre, yet the population in Middle Fork Salt Creek of the Scioto River system often has purple nacre. *Elliptio dilata tata* is usually purple nacred but may have purple, white, or salmon nacre in individuals living side by side in some streams. *Pleurobema sintoxia* usually has white nacre except for those in the Maumee River system, where nearly half have pink nacre. Furthermore, whereas *Pleurobema sintoxia* may have white or pink nacre, its close cognate *Pleurobema cordatum* very rarely has pink nacre. It is difficult to ascribe an environmental cause that would allow three different nacre colors in some populations and only one in others or that would make some individuals strongly rayed and others unrayed. Clearly, color in mussels is the byproduct of genetics. Variations in patterns and colors probably represent polymorphisms and linked genes rather than environmental effects.

### Effects of Habitat Modifications and Pollutants

#### IMPOUNDMENTS

Rivers have been dammed by humans for millennia, for many purposes: to run mills and hydroelectric turbines; to irrigate otherwise inarable land; to control floods; to allow navigation of waterways; and to create bodies of water for recreation. But impoundments are not the same as naturally occurring pools in a river: impoundments have a hydrology different from those of natural pools, with different flow patterns, topographies, and temperatures. These differences often result in a change in the aquatic fauna, including mussels. For example, 15 mussel species were found in Lake Cooper, a man-made impoundment on the Mississippi River, but in adjacent Lake Pepin, a naturally formed pool, 30 species were encountered (van der Schalie, 1938).

The loss of these mussels is a result of habitat modifications caused by impoundment. A free-flowing river has riffles, runs, pools, shoals, water-willow stands, and meanders (fig. 9). But impoundment dramatically reduces this habitat heterogeneity (fig. 10) (Bates, 1962; Blalock & Sickel, 1996). The original channel remains but is often buried under deeper water and fine sediments. But most mussels do not occur in deep water, and those that do are often stunted (Hautkioja & Hakala, 1974; Lewandowski & Stanczykowska, 1975). This channel begins to accumulate sediments, smothering most mussels. Ellis (1936) showed that a silt accumulation of ¼-inch to 1-inch depth resulted in mortality approaching 90% in the mussels he tested.

If not smothered outright by accumulating sediments, mussels may be affected adversely in other ways. Reproduction may be reduced or stopped entirely, and growth may be slowed. Bates (1962) found no evidence of mussel reproduction in the channel of Kentucky Lake of the Tennessee River, even though adult mussels were present. Rivers having high levels of suspended solids result in slower mussel growth (Semenova et al., 1992). Juvenile mussels, which live buried for several years, may be killed by overlaying sediments (Bauer et al., 1980; Buddensiek et al., 1993). Silt results in the loss of light penetration, reducing algal food available to mussels, and leads to oxygen depletion. The bottom waters of the channel may become cold enough to stunt the growth of mussels (Harmen, 1974; Ghent et al., 1978; Semenova et al., 1992) and interfere with reproduction (Hruska, 1992; Heinricher & Layzer, 1999).

After impoundment, the original mussel fauna may be eliminated or greatly reduced (Holland-Bartels, 1990) or may be changed in favor of silt-tolerant species, such as anodontines and species of *Leptidea* and *Potamilus* (Clark & Gillette, 1911; Ellis, 1931; Bates, 1962; Isom, 1969; Klippel & Parmalee, 1979; Parmalee & Hughes, 1993; Blalock & Sickel, 1996). These species often occur in the now permanently inundated floodplains. Thus, while some impoundments may contain numerous mussels, they invariably are invading, soft-substrate-adapted species that have replaced the original fauna.

Dams may represent physical barriers to mussel hosts.

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*Fig. 9. The Elk River in West Virginia supports a high diversity of mussels and fishes because of numerous habitat types: riffles, runs, pools, meanders, canopy, gravel bars, water willow, etc.*
Some mussel populations may no longer be recruiting juveniles because their hosts are absent (Suloway et al., 1981; Jones, 1991; Burkhhead et al., 1992). Watters (1996c) showed that dams as low as 1 m in height affected host movements and restricted the range of some mussels. Tailwaters tend to accumulate mussels, another source of evidence that the dam is acting as a barrier.

Tailwaters are affected as well (Ligon et al., 1995). Fluctuating water levels may strand or otherwise expose mussels to extreme temperatures, resulting in mass mortalities (Riggs & Webb, 1956; Neck & Howells, 1994). Low temperatures associated with some tailwaters may adversely affect mussel reproduction and growth. High-volume water discharges and abrupt stoppages cause instability of substrate below dams (Miller & Payne, 1992; Nagel, 1992; Yeager, 1993). Sedimentation in tailwaters reduces fish diversity and abundance by altering necessary habitats, thereby removing necessary mussel hosts (Potts, 1984; Holland & Huston, 1985; Nelson et al., 1987). Mussels may be absent for miles below some dams because of these problems.

That impoundments are detrimental to aquatic life in general, and to most mussels in particular, has been demonstrated by many case studies. Perhaps several dozen mussel species in North America, and numerous more freshwater snails, were driven to extinction by the effects of impoundments (Stansbery, 1973a; Layzer et al., 1993; Lydeard & Mayden, 1995). Although mussel faunas change through time, with or without dams, and species become extinct as a matter of course, the interference of human activity has dramatically accelerated this process. For example, the Tennessee River’s mussel diversity decreased from 100 species to 44, owing mainly to impoundment (Isom, 1969). In the Fort Loudoun Reservoir alone on the Tennessee River, Isom (1971) found only four mussel species, while Ortman (1918) reported 64 species from the same general area before impoundment. The area of the Chickamauga Reservoir of the Tennessee River supported 46 species for perhaps 2,000 years prior to impoundment (Parmalee et al., 1982). After impoundment, 28 species were extirpated, and several are now extinct. Similar reductions in diversity after impoundment were documented for the Cumberland River (Layzer et al., 1993; Schmidt, 1986), where the construction of the Center Hill hydroelectric dam resulted in the loss of 78% of the original mussel species. In the Little Tennessee River, only 6 of the original 50 mussel species at Tellico Lake remained after impoundment (Parmalee & Hughes, 1993). The mussels of other rivers, such as the Kaskaskia River (Suloway et al., 1981) and the Tombigbee River (Williams et al., 1992), have met a similar fate.

**LAND USE PRACTICES**

Land use practices (fig. 11), such as logging, mining, construction, farming, livestock, etc., often impact mussel populations by releasing runoff of silt, salt, pesticides, fertilizers, and other pollutants. Proximity of streams to roads may increase the amounts of salt, heavy metals, and other pollutants that enter a stream (Van Hassel et al., 1980). Mussels are smothered or poisoned, and contaminants may remain in the sediments for years, precluding recolonization. Runoff also causes changes in fish composition, perhaps removing a necessary host from a mussel population. But detrimental effects are not confined to the physical destruction of the riparian corridor. Alterations in land cover and canopy are important as well. Morris and Cor- kum (1996) found greater temperature fluctuations, and higher ammonia and nitrogen concentrations, in a stream bordered by a grassy site than one bordered by a wooded one. The two sites had the same mussel diversity, but the grassy site was dominated by an anodontine.

**CHANNELIZATION, DREDGING, AND SNAGGING**

Channelization, dredging, and snagging reduce available host and mussel habitat (Nelson, 1993) and alter circulation patterns and substrate composition (Loar et al., 1980). Dredging and channelization affect mussels in many ways. Mussels caught in the dredge path are destroyed, and sediments churned into the water column may travel downstream and affect mussels outside the construction area. Mussels may be smothered by or exposed to resuspended contaminants (Engler, 1979). Valovirta (1990) showed that simply removing large rocks from a stream caused the substrate to become unstable, killing mussels. Channelization on a greater scale is catastrophic to mussels and has been implicated in the decline of some populations (Yokley & Gooch, 1976; Grace & Buchanan, 1981a; Schuster
Fig. 11. Land use in Ohio’s watersheds.
et al., 1989; Valovirta, 1990; Hartfield, 1993). Dredge spoil may reenter the river through upland runoff, and contaminants may reenter through groundwater. Although soft-substrate-adapted mussels may invade dredged areas, most affected reaches are not recolonized by mussels of any kind.

The snagging of fallen trees and debris is a common practice to ostensibly prevent a river from inundating its natural floodplains. Like channelization, snagging reduces the available habitat (Marzolf, 1978). It also increases bank erosion, creates unstable substrates as the stream recovers, and generally reduces aquatic diversity. Channelization and snagging actually may increase flood heights (Belt, 1975), creating additional runoff and the need for additional remediation. Thus the effects of channelization, dredging, and snagging may become chronic, affecting aquatic organisms long after the actual “improvement” has been completed.

POLLUTANTS

Havlik & Marking (1987) and Farris & Van Hassel (2007) gave reviews of the effects of contaminants on mussels. Readers are urged to consult these sources for more information on specific contaminants.

Although effects of pesticides are species-specific, in general, sub-lethal levels of PCBs, DDT, Malathion, Rotenone, and other compounds inhibit respiratory efficiency and accumulate in the tissues. Mussels are more sensitive to pesticides than many other animals tested.

Mussels are particularly sensitive to heavy metals (Keller & Zam, 1991), and responses may be species-specific (see the example for copper in Jacobson et al., 1993). Adult mussels may be able to survive short-term exposure through behavioral responses (Keller, 1993), but chronic exposure at lower levels may impact mussel populations. For example, low levels of metals may interfere with the ability of glochidia to attach to the host (Huebner & Pynnönen, 1992).

Glochidia are very sensitive to ammonia from wastewater treatment plants (Goudraeu et al., 1993). At sub-lethal exposures adult mussels exhibit decreased respiratory efficiency (Anderson et al., 1978). Ellis (1931) discovered that mussels found below sewage outfalls had dead glochidia in the marsupia contaminated with bacteria and fungi.

Acidic water from mine runoff and sandy soils may eliminate mussels and preclude recolonization (Simmons & Reed, 1973; Humphrey, 1987a). Mussels may be able to survive several weeks of exposure to relatively low pH because of buffering in the blood (Mäkelä & Oikari, 1992), but chronic exposures are lethal. Low pH also interferes with the glochidia’s ability to close its shells on a host (Huebner & Pynnönen, 1992). Houselet & Layzer (1997) found that mussels living below a coal strip mine were significantly smaller than those of the same age occurring above the influence of the mine.

Liquori & Insler (1985) and Anders & Wiese (1993) gave circumstantial evidence that salinity was lethal to some glochidia. This may be a problem in runoff from salt used for clearing roads in winter. Salinity also is a concern near oil and gas production areas.

Effects of Introduced Bivalves

ZEBRA AND QUAGGA MUSSELS

Zebra and quagga mussels are not true mussels (Mytilidae), but belong to the family Dreissenidae (fig. 12). Although there are native members of this group in North America, they are mainly estuarine species. The zebra mussel, Dreissena polymorpha (Pallas, 1771), is native to the Caspian and Black Sea region, and the Volga and Ural rivers. However, as canals were built westward across Europe in the 1700’s, zebra mussels followed, eventually colonizing most of Europe and even reaching the British Isles in the 1800’s. Zebra mussels probably reached North America in 1985 or 1986 in the ballast water of a cargo ship (Hebert et al., 1989). That ship had taken on freshwater in Europe for the transoceanic voyage that ended in Lake St. Clair. There it discharged its ballast water to take on cargo, releasing either larvae or juveniles of the mussels.

In 1991, a second species of exotic dreissenid mussel was found in North America and named the quagga mussel. It now occurs in Lake Erie, Lake Ontario, parts of Lake Huron, and the St. Lawrence Seaway. Eventually it was identified as Dreissena bugensis Andrusov, 1897, another eastern European species (Rosenberg & Ludzianskiy, 1994). Quagga mussels tolerate deeper water (to 107 m) and muddier substrates than do zebra mussels (Snyder et al., 1990). Despite these slightly different environmental tolerances, the two species are often found together.

Zebra mussels become sexually mature within their first year. Spawning takes place when spring water temperatures warm to 12°C and continues until water temperatures fall below this threshold. Depending on the weather in any given year, spawning may begin as early as May and last until October or December, but typically spawning is most concentrated in July and August. Females may produce 1 million eggs per year, which hatch into free-swimming veliger larvae. Unlike our native mussels, dreissenids do not have a parasitic larval stage. Their larvae may float in the water column for 3–4 weeks before transforming into a juvenile and settling to the bottom. Adults may live for 6 years (Snyder et al., 1990).

Zebra and quagga mussels produce fibers from the byssal gland in the base of the foot that are used to anchor
the mussels to the substrate. These fibers, called byssal threads, may be released by the mussel to allow movement. They are extremely strong. Native unionoid mussels also produce a single byssal thread as a juvenile, but it is usually lost in the first year’s growth.

Zebra and quagga mussels are highly detrimental to native mussels, sphaeriid clams, and snails (Strayer, 1999). They congregate on the shell around the native unionoid mussel siphons, removing both food and oxygen before these necessities can become available to the native species. Gametes released by male native mussels may be ingested by zebra mussels, thereby interfering with reproduction. The extremely strong byssal threads of the zebra mussels may “sew” the shells of native mussels shut. Clusters of zebra mussels attached to the ends of native mussels may create drag, pulling the native mussels out of the substrate where they are swept ashore to die. At sub-lethal levels of infestation, native mussels experience lowered glycogen levels and increased stress, resulting in decreased fitness (Haag et al., 1993).

Up to 10,000 zebra mussels have been found on a single native mussel. Lewandowski (1976) found that 85% of the native mussels in a Polish lake were infested with zebra mussels but the degree of infestation varied with season and year. He observed that zebra mussel spat preferred other zebra mussel shells and living unionids over dead shells or stones. In the Mississippi River, colonization rates of zebras on natives increased from 27% to 99.7% within a year (Tucker, 1994). Zebra mussels formed a pavement on the gravel substrate such that dislodged unionids were not able to rebury. Tucker also found that thick-shelled, sculptured species were more heavily infested than smooth, thin-shelled species. Conversely, Haag et al. (1993) reported that the heavy-shelled, sculptured Amblema was not as susceptible to infestation as the smooth-shelled species of anodontines and lampshells.

In Ohio, native mussels have been nearly extirpated from the western basin of Lake Erie (ESI, 2000), although a few refugia may still exist. Zebra mussels are present in the Ohio River all along Ohio’s shore and have invaded the lower Hocking and Muskingum rivers. They have colonized numerous reservoirs as the result of human introductions. In some cases, creeks below the outfalls of these reservoirs have been contaminated as well, sometimes for several miles (Tymochtee Creek, for example).

In retrospect this invasion seems to have been inevitable. The reason it did not occur earlier was likely the long sailing time between Europe and North America. But new technology, faster ships, and the opening of the St. Lawrence Seaway finally allowed these creatures to make the journey successfully. The U.S. EPA required ships to retain their ballast and to exchange old freshwater ballast for new freshwater ballast. This change, designed to protect inland waters of the United States, allowed for the introduction of zebra mussels and other non-native species. At least seven species of Dreissena are known from Europe and Asia, and it is possible that they may make their way to our shores as well.

**CORBICULA, THE ASIAN CLAM**

In North America, the veneroid Asian clam Corbicula (Corbiculidae) (fig. 13) first appeared in the Columbia River in Washington in 1938, probably the result of intentional introductions by Asian immigrants to propagate an exotic foodstuff (Mills et al., 1993). By 1958, it had reached Arizona; in 1959 it was found in the Tennessee River; and by 1963 it had appeared in the Ohio River at Cincinnati (Sinclair & Isom, 1963). Today, few water bodies are free of this exotic clam. Similar introductions of other corbiculid species have taken place in other countries (Darrigan & Pastorino, 1993).

The systematics of the genus Corbicula are not well-known. It is not clear which species, or how many species, currently occur in North America. Most recent literature refers to a single species, Corbicula fluminea (Müller, 1774), but recent studies suggest at least two lineages of Corbicula in North America (Siripattrawan et al., 2000). Older literature also lists species such as *C. manilensis* (Philippi, 1844) and *C. leana* (Prime, 1864).

Larvae are brooded as trochophores and early veligers in the gills and released as late veligers to the plankton.
There is no parasitic stage in their life cycle. Upon settling, they may attach to objects with a byssal thread, but this thread is soon lost. Unlike zebra mussels, adult Asian clams do not attach themselves to objects with byssal threads as adults. But like zebra mussels, the Asian clam may be present in enormous numbers, clogging water pipes, drains, and other structures.

At one time it was believed that Asian clams would eradicate native mussels wherever the two co-occurred. This has not happened, at least not to any great degree, and there is little evidence to support the idea that Asian clams are detrimental to native mussels (Strayer, 1999). It is possible that the two compete for food, and Asian clams may ingest the gametes of unionoids. But, superimposed on a general decline in native mussel populations due to habitat alteration, pollution, commercial use, and zebra mussels, the effects of the Asian clam are difficult to gauge.

Conservation of Species

The Unionidae are the most endangered of our aquatic animal species (Neves, 1993). Over one-half (54%) of Ohio’s native freshwater mussel species are now endangered, extirpated, or extinct. Whether as a result of habitat degradation, competition with non-native species, pollution, or any other of a long list of negative environmental impacts (reviewed above), the unionoids have steadily lost the ecological battle with abundance and distribution. It is because of these losses that conservation of freshwater mussels is even an issue. However, as others have pointed out, the battles these species are waging with survival should send us a message. All life is dependent on all other life, and so in a sense our survival depends on the survival of these often overlooked animals. This message might direct us to begin to understand the problem but must lead to habitat restoration, water quality improvements, biotic reconstruction, and conservation.

Conservation broadly defined is the act of setting aside for the future. It is not the identification of existing populations of mussels, the preservation of those populations, or the reintroduction of organisms now extirpated, although conservation efforts might include any one of these activities. Instead, conservation is acknowledging the importance of a resource to society and then working to protect and restore that resource. The following sections of this Introduction will discuss the activities that are currently being applied to identify the condition of freshwater mussels in Ohio and the methods that are being used to protect and restore this resource. However, none of these discussions is important if we do not value the resource to begin with.

THE VALUE OF A MUSSEL

Value is subjective. What one person finds valuable, another may not. Still, if we look closely at any resource, we should be able to identify the attributes that make it valuable, all of which may be important to one member of society, but only a few of which may be significant to someone else. The accumulated list of value statements describes the ultimate perceived value of a resource. However, any single item on that list, if important to any single member of society, brings value to that resource. In this case, it is the least of all of these that establishes the conceptual mandate to protect, restore, and conserve. So what are the values of freshwater mussels? They can be divided into ecological, economic, cultural, aesthetic, and intrinsic value categories.

Freshwater mussels play important roles in the ecology of the streams and lakes where they live. Not only are they among the largest of our freshwater invertebrates; they are also among the longest-lived. During their lifetimes, some of which may be as long as 40 to 50 years (for Ohio species), they serve as substrate for other organisms, remove silt and other pollutants from the water through their filtering activities, serve as food for other wildlife species, and stabilize the substrate (Vaughn & Hakenkamp, 2001). They contribute to the biodiversity of aquatic habitats by being members of that community and by the symbiotic relationships (commensal, trophic, parasitic, etc.) in which they engage. Every species adds to the complexity of an ecosystem, and that complexity results in what is often referred to as ecosystem service to that community and to us (Reaka-Kudla et al., 1997).

Generally when one speaks of the economic value of freshwater mussels, one speaks of the pearl industry or, historically, the Pearl Button Industry. These industries were (buttons), and continue to be (cultured pearl), dependent on the shells of North American freshwater mussels (Coker, 1919; DeVillez, 1991; Fassler, 1991; McGregor & Gordon, 1992). The North American mussel
supply was valued at $50 million in the 1980’s (Fassler, 1991). Other economic values associated with freshwater mussels include their use as water quality indicators, their use as food by humans (much more important historically than now), and their use in the shell trade industry. Naturally produced pearls have been a commodity bought and sold as well (Fassler, 1991).

Many scientists who work with these animals share a sense of fascination with their shells. Shell collecting may be where scientists first became interested in freshwater mussels, which ultimately led to questions about the ecology, life history, anatomy, and systematics of the group. Freshwater mussels are exciting to study. They are mostly big, long-lived, and fairly complex animals living their entire lives in freshwater habitats. The way they live their relatively mundane lives and the associations they make with other living things provide ample opportunity to study ecology and evolution. One might examine the behavior of these animals, or one might become fascinated by some aspect of their anatomy. Any aspect of biology that can be studied can be studied using freshwater mussels.

Still, for other people it is enough to know that these mussels are embedded in the substrate of a nearby stream or lake. For them the fact that mussels exist is enough to bring them a sense of joy or wonder. It is not easy to promote freshwater mussels as the poster organism for the conservation of freshwater habitats—perhaps because of their sedentary existence and the fact that many people have never seen one as a living animal. Yet many would say that these animals are worth preserving because they are native, they are natural, and they are a part of this world that is both very old (in a geologic sense) and unique (in a biological sense).

CONSERVATION ACTIONS

Just as there are threats to the continued existence of freshwater mussels in Ohio, so too are there actions we can take to protect, restore, and conserve this fauna. The simplest and most effective method is to become aware of this group of organisms. This book, then, is a means of freshwater mussel conservation. Other methods include the investigation of freshwater mussel biology, the preservation of water and riparian resources, and the control and/or elimination of threats to these animals.

The investigation of the biology of freshwater mussels has taken many forms. Some scientists are examining the distributions of species to attempt to reconstruct past distributions to determine, among other benefits, where else to look for rare and endangered species. Hoggarth et al. (1995) reported finding a species of mussel in Ohio long thought to be extirpated from the state. Other scientists are examining the host-parasite relationships between fish and mussel because we realize that it will be impossible to protect mussels without protecting their fish hosts. Still other scientists are involved in captive propagation programs and the storage of genetic material to be used someday in the artificial propagation of freshwater mussels. The examination of relocation techniques that may someday play an important role in mussel conservation, once threats such as water pollution or competition with non-native species has been eliminated, is ongoing as well (Cope & Waller, 1995).

Habitat protection and restoration play equal roles in freshwater mussel conservation. One effective way of setting aside mussels for future generations is by setting aside land near streams. Protecting wooded stream banks and wetlands helps to preserve streams by stabilizing their banks, removing sediment and other pollutants, and controlling fluctuations in stream flow. These wooded and wet streamside habitats provide food to the stream in the form of leaves and other vegetation; they moderate the temperature of the water; and they often provide for the subtle differences in habitat necessary to allow for greater biodiversity in an area. As much as possible, habitat restoration activities should attempt to mimic as closely as possible the natural habitat conditions found in a stream before it was altered. The elimination of dams (see Joseph, 1998), the natural recovery of a channelized stream, and the return of wooded habitats adjacent to a stream all contribute to habitat restoration.

The elimination and/or control of non-native species is a more difficult problem. Currently there are no effective means of eliminating a nuisance species such as zebra mussels other than protecting waterways from them to begin with. Ohio Sea Grant (1995) has compiled a booklet that will assist in understanding and controlling this threat, and the Ohio Department of Natural Resources Division of Wildlife has prepared a State Management Plan for Aquatic Nuisance Species (1997).

The conservation of mussels, then, boils down to just these three concepts: realizing that mussels have value, identifying the threats to their continued existence in the state, and working to protect and restore their populations in Ohio. If there is a take-home message here, it is that even with all of the declining species, even with all of the threats, even with all of the unknowns regarding the basic biology and distribution of these animals in the state—even with all of these—it is not too late. It is not too late to protect what dwindling mussel resources we currently have, and it is not too late to restore some of the rich bounty Ohio has known in the past.
Distribution of Mussels in Ohio

Much of Ohio’s mussel diversity is due to Ohio’s physiography (fig. 14). To the south lies the Ohio River and to the north Lake Erie. Three physiographic provinces extend into Ohio: the Central Lowland (Huron-Erie Lake Plains and Till Plains sections), the Appalachian Plateaus (Glaciated Allegheny Plateaus and Allegheny Plateaus sections), and the Interior Low Plateau (Bluegrass Section). While the great majority of Ohio’s mussels are derived from the Ohio River fauna, a few species, such as the Eastern Pond-mussel, *Ligumia nasuta*, are part of the Lawrentian fauna of the Eastern Seaboard. Most of our mussels occur in the glaciated portion of the state, within the Central Lowland and Interior Low Plateau provinces and within the Glaciated Allegheny Plateaus Section of the Appalachian Plateaus Province. There are notable exceptions, such as the Muskingum River system, most of which flows through the unglaciated portion of the state but which possesses a streambed composed of glacial outwash high in carbonates and high in mussel diversity. Ohio’s major watersheds are shown in figure 15.

Ohio is composed of two large regions, differing in their geological history, soil types, and vegetation. The southeast third of the state was never glaciated and consists of portions of the Appalachian Mountains Foothills. This area stretches roughly from Wheeling in the northeast to Brown County in the southwest and includes the Hocking Hills region and Wayne National Forest. The bedrock there is composed of sandstone and shale, largely of Permian and Pennsylvanian Period origin, with mostly aluminum- and iron-enriched soils (alfisol) and a mixture of very old, nutrient-depleted soils (ultisol) and very young, nutrient-poor soils (entisols and inceptisols). The original vegetation consisted mainly of mixed oak forests. Some of Ohio’s largest rivers cut through this region: the Muskingum, Hocking, and Scioto rivers. Streams leading to these rivers and to the Ohio River beyond often flow over exposed bedrock and have high gradients. They may be relatively poor in calcium—a mineral that mussels need to construct their shells. As a consequence, these streams often have a depauperate mussel fauna.

Glaciated Ohio was overlain to varying degrees by the Kansan, Illinoian, and Wisconsin glaciers, beginning approximately 600,000 years ago and ending (for now) about 10,000 years ago. Mussels were obviously absent in this region during the last glaciation. Mussels therefore did not colonize this area of Ohio until at least 10,000 years ago—the same time Ohio’s earliest humans, the Paleoindians, colonized the area. As the glacier retreated, meltwater flowed mainly south to the newly formed Ohio River, and the corridor for most of Ohio’s mussels was established.

Mussel distributions also have been influenced by the construction of canals (fig. 16). These structures linked disparate drainages and allowed mussels and their hosts to migrate to places outside their natural range. Two great canal systems were built in Ohio linking Lake Erie to the Ohio River. The Ohio and Erie Canal was completed in 1832, linking Cleveland and Portsmouth. The Miami and Erie Canal was completed in 1845, linking Toledo and Cincinnati. Spurs of the Ohio and Erie Canal connected to the Muskingum and Hocking rivers, and other spurs reached as far as Pennsylvania. A spur of the Miami and Erie Canal connected to the Wabash River. Mussels were apparently abundant in at least some canals. Of the Columbus feeder canal of the Ohio and Erie Canal, Higgins (1858) noted: “Many species have traversed the whole length of the canal, and many species there thrive and become abundant which are quite rare in the adjacent rivers.” Species living in the canals were not just soft-substrate taxa but also included riverine species, as evidenced by records at the Carnegie Museum of Natural History, Pittsburgh, of now-endangered species living in these canals. Several species were even described from canals. But Ohio’s canal system was out-competed by the railroad, and its demise was complete in 1913 when floods demolished canals state-wide. How these canals changed the distributions of mussels in Ohio is unknown, but we are certain that some genetic mixing must have occurred.

Regulation of Mussels in Ohio

No one denies that Ohio’s mussel fauna has experienced dramatic declines. Much effort and money has been spent to ensure that whatever remains will be protected for posterity. Federally endangered species are under the jurisdiction of the U.S. Fish and Wildlife Service and the Ohio Department of Natural Resources (ODNR) Division of Wildlife. All other species, regardless of rarity, are under the jurisdiction of the ODNR Division of Wildlife. No other state, local, or private agency has statutory authority over these animals.

Several laws are of importance to anyone wishing to work with mussels in Ohio. Early on, the ODNR Division of Wildlife recognized that the mussels that were being commercially harvested, mostly in the lower Muskingum River, were not a renewable resource given the current rate of harvest. All commercial collecting was stopped statewide in 1975. However, a limited number of mussels could still be used for bait purposes. Realizing that endangered species were occasionally being shucked for
bait prompted the Division to end that practice as well, and currently it is illegal to collect any live mussel or dead shell, including Asian clams, zebra mussels, and quagga mussels, regardless of rarity, without a Scientific Collecting Permit.

The state endangered status of Ohio mussels is based strictly upon their occurrence within the state’s borders. A species may be abundant just across the state line, but that does not affect its Ohio status. For this reason, some Ohio species considered endangered may be quite common globally. Some of these species occur in the lower Muskingum River, where they are considered endangered. Endangered status does not necessarily mean that a species exists in few numbers. *Pleurobema cordatum*, an Ohio endangered species, is abundant in the lower Muskingum River. It is considered endangered because that is one of the only places it occurs in the state, and, abundant or not, it could be extirpated by a single ecological catastrophe.

**Records Used in This Book**

The distributional maps figured in this book are based on 35,000+ records at The Ohio State University Museum of Biological Diversity (OSUM). Additional records were included from the Carnegie Museum of Natural History, Pittsburgh; the University of Michigan Museum of Zoology, Ann Arbor; the Cincinnati Museum of Natural History and Science; the Cleveland Museum of Natural History; and the Boonshoft Museum of Discovery (formerly the Dayton Museum of Natural History). Collection sites are shown in figure 17.
Fig. 14. Ohio's physiographic regions.
Fig. 15. Ohio’s principal drainages.
1—Tenmile Creek. 2—Maumee River. 3—Portage River. 4—Sandusky River. 5—Huron, Vermilion, and Black rivers. 6—Cuyahoga River. 7—Grand and Ashtabula rivers. 8—Mahoning River. 9—Pymatuning Creek. 10—Wabash River. 11—Miami River. 12—Scioto River. 13—Muskingum River. 14—Hocking River. 15—minor Ohio River creeks.
Black line—divide between Lake Erie and Ohio River drainages. Gray lines—eleven-digit hydrologic units.
Fig. 16. Ohio’s canal system: Miami and Erie Canal (left) and Ohio and Erie Canal (right).
Fig. 17. Collection sites used in this book.
Original description
Unio crassidens var. b Lamarck, 1819: 71, no figure given.

Type locality. “Habite l’Amerique septentionale, dans le Mississipi [sic], l’Ohio, et plusieurs lacs” [“Living in northeastern America, in the Mississippi, the Ohio, and several lakes”]. Two of Lamarck’s three unnamed varieties were listed as “du Mississipi [River]” and “du lac Erie.” This species does not occur in Lake Erie. The type locality was restricted by Johnson (1969) to “the Ohio River, Cincinnati, Ohio.”

Type material. The unnumbered specimen listed as variety (b) by Lamarck is in the Muséum national d’Histoire naturelle, Paris, and was selected as the lectotype by John son (1969).

Synonymy
Unio crassidens var. b Lamarck, 1819: 71.

Unio (Elliptio) nigra Rafinesque, 1820: 291, pl. 80, figs. 1–4 [Type locality: “l’Ohio [River].” Lectotype ANSP 20243 by designation of Johnson & Baker (1973: 163)].

Unio (Elliptio) nigra var. fusca Rafinesque, 1820: 291 [Type locality: none given. Type not located].

Unio (Elliptio) nigra var. maculata Rafinesque, 1820: 291 [Type locality: none given. Type not located].

Unio cuneatus Barnes, 1823: 263–264 [Type locality: “the Ohio [River].” Type lost fide Johnson (1970)].

Mya cuneata (Barnes, 1823). Eaton, 1826: 220.

Obliquaria (Aximedia) venus Rafinesque, 1831: 3 [Type locality: “in the Kentucky and Cumberland [rivers], very rare.” Type not located].


Margaria (Unio) crassidens (Lamarck, 1819). Lea, 1836: 19.

Margaron (Unio) crassidens (Lamarck, 1819). Lea, 1852b: 24.

Unio discus Lea, 1838. Sowerby, 1868: pl. 62, fig. 310 [misidentification].

Unio crassus Say, 1816. Sowerby, 1868: pl. 95, fig. 520 [misidentification].


Unio danielsii Wright, 1899a: 31 [Type locality: “Spring Creek, Decatur Co., Georgia.” Lectotype USNM 168967 by designation of Johnson (1967)].

Unio polymorphus Wright, 1899b: 42 [Type locality: “Spanish Creek, Okelenokee Swamp, Charleton Co., Georgia.” Lectotype USNM 152060 by designation of Johnson (1967)].


Unio (Elliptio) danielsii Wright, 1899. Simpson, 1900a: 708.

Elliptio crassidens (Lamarck, 1819). Ortmann, 1912a: 266.

Elliptio nigra [sic] (Rafinesque, 1820). Ortmann, 1919: 91, pl. 8, fig. 1.

Elliptio (Elliptio) nigra [sic] (Rafinesque, 1820). Frier son, 1927: 25.


Elliptio pachyodon Pil sbry, 1953: 447, pl. 65, fig. 8 [Type locality: “St. Petersburg, Florida. Pliocene.” Holotype ANSP 18586].

Elliptio (Elliptio) crassidens var. danielsii (Wright, 1899).


Elliptio (Elliptio) crassidens var. crassidens (Lamarck, 1819).


Status. Listed as Endangered (as Elliptio crassidens crassidens) by Ohio Division of Wildlife; not listed by U.S. Fish & Wildlife Service as of 2009.

ADULT SHELL
Shell. Medium to fairly large in size (to 150 mm), thick and massive, oval to rather elongate, often drawn to point posteriorly and having a “humped” appearance; moderately inflated.

Anterior margin. Short, straight to broadly rounded to the ventral border.

Ventral margin. Very broadly rounded, straight or concave towards the posterior.

Posterior margin. Long, rather straight to the dorsal margin; often merging imperceptibly with the dorsal margin.

Dorsal margin. Long, straight, joining posterior margin with obtuse angle or confluent with it.

Umbo. Very wide, very low; umbos nearly face each other but in some individuals may be twisted prominently forward; umbonal sculpture of 1–2 very weak diagonal ridges.

Ligament. Long and prominent, tan to dark brown, not concealed by shells.

Disc sculpture. Disc of shell smooth except for low angulations on posterior slope; posterior slope weakly corugated or wrinkled in juveniles; old individuals may become sulcate.

Periostracum. Juveniles may be shiny or have a velvety finish, but adults have a matte or shaggy finish; juveniles yellow or reddish brown with numerous fine green lines or rays; adults become reddish-brown or black and lack rays; posterior slope dark.

Nacre. Deep purple or salmon, very rarely white, often iridescent posteriorly; occasionally with gold or brown Tulberg spots.
Fig. 50. *Elliptio crassidens* (Lamarck, 1819)
Solid dots—live or fresh dead since 1980
Bullseye—all records, any condition
**Hinge plate.** Well-developed, massive, long, arched; right cardinal a single, massive, triangular denticle, often with small anterior accessory tooth; left cardinal bifid, the teeth well-separated; laterals well-developed, massive, fairly short, straight, one in right valve, two in left; interdental wide, thick, long.

**Muscle scars.** Anterior adductor small, oval, deeply impressed; posterior adductor nearly flush or impressed; small anterior adductor distinct from anterior pedal protractor scar, posterior adductor distinct from small posterior pedal retractor scar; dorsal suspensors located under interdental in an irregular line. Pallial line entire, located far from shell margin. Accessory line poorly developed, short.

**Umbonal cavity.** Very wide, shallow, open.

**Glochidia.** Subtriangular, dorsal margin long and evenly curved, lateral margins rounded, tapering to a pointed ventral terminus, hooks absent (Ortmann, 1911: 364, pl. 89, fig. 6; Surber, 1915: 9, pl. 1, fig. 13).

Literature records (Ortmann, 1912a: 268; Surber, 1915: 9, pl. 1, fig. 13; Utterback, 1915: 200) indicate glochidial dimensions for length (0.13 to 0.15 mm) and height (0.15 to 0.16 mm). Surber (1915: 9) noted, “In this species the glochidium seems to be intermediate in shape between examples of the Anodontia group on the one hand and certain species of the Lampsis-Quadrula group on the other, best represented in the former by Alasmidonta calceola [A. viridis], and in the latter by such species as Quadrula ebena, etc. Compared with Unio gibbosa [E. dilatata] it is more circular in outline, if we except the pointed margin, and has a shorter, more curved hinge line. It is an aberrant type related to Margaritana margaritifera.”

**Reproductive biology.** Tachytictic. Outer gills are marsupial. “Breeding season” reported as June and July (Baker, 1928a). Ortmann (1919) found both eggs and developing glochidia in June. Glochidia were released in leaf-shaped conglutinates (Ortmann, 1912a); these are of the simple nonelastic type (Watters, 2008).

**Reported potential hosts**

*Alosa chrysochloris* (Skipjack Herring)—Howard, 1914a (NI).

**Habitat.** In Ohio, in stable cobble and muddy sand in rivers. In southern North America it commonly is found in much smaller creeks.

**Range.** Mississippi River system, Mobile River system and other Gulf drainages (as *E. crassidens incrassata* Lea, 1840), and the Apalachicola River drainage. Brim Box & Williams (2000) synonymized *E. crassidens incrassata* Lea, 1840 with *E. crassidens*.

**Range in Ohio.** Ohio River, where it may be locally abundant, and historically from the Scioto River up to Columbus and the Tuscarawas River at New Philadelphia. Occasional specimens have been found as far upstream as Little Darby Creek, but these undoubtedly represent stray occurrences. Does not occur in the Lawrentian drainages—a record from the Grand River is suspect.

**Similar species.** The Elephant Ear may only be confused with the *Elliptio dilatata* (Rafinesque, 1820), the only other *Elliptio* currently found in Ohio. Other massive shells of similar shape, such as *Actinonaias* species, lack the purple nacre. *Elliptio crassidens* is heavier, larger, and less elongate than *Elliptio dilatata*. In Ohio *E. dilatata* uncommonly occurs in the Ohio River, where *E. crassidens* may be locally abundant. Conversely, *E. dilatata* is common in creeks whereas *E. crassidens* is extremely rare there.

**Comments.** Individuals gradually slow in growth during their entire life. Specimens reach ca. 150 mm and live over 30 years.

**Elliptio dilatata** (Rafinesque, 1820)

Figures 51, 52, 53

**Etymology.** *L. dilato*, spread out, dilate, enlarge, amplify. Rafinesque’s concept of width corresponds to the current concept of length. An elongate specimen in today’s terminology would be described as wide or dilated by Rafinesque in his time.

**Vernacular name(s).** Spike, Little Spike, Ladyfinger, Bluefinger Spike.

**Original description**

*Unio* *(Eurynia)* *dilatata* Rafinesque, 1820: 297, species no. 11, no figure.

**Type locality.** Rafinesque did not give a type locality, but the title of his paper was “Monographie des Coquilles Bivalves Fluviales de la Rivière Ohio, . . .” However, as Johnson & Baker (1973: 153) selected a specimen from the Kentucky River as lectotype, that becomes the type locality regardless of Rafinesque’s intentions, as clearly stated in ICZN Art. 76.2.

**Type material.** From the types mentioned by Vanatta (1915: 555), Johnson & Baker (1973: 153) selected ANSP 20248a as lectotype.

**Synonymy**

*Unio nasuta* Lamarck, 1819: 75 [non Say, 1817. Type locality: “le lac Erî.” Type: *Muséum national d’Histoire naturelle, Paris, France?*].

*Unio (Eurynia) dilatata* Rafinesque, 1820: 297.

*Obliquaria sinuata* Rafinesque, 1820: 320 [Type locality: “Dans le Kentuky [River].” Lectotype ANSP 20252 by
Fig. 51. *Elliptio dilatata* (Rafinesque, 1820).  
A. OSUM 6469.2, Olentangy River, Marion Co., OH. 92 mm.  
B. OSUM 38857, Lake Erie, Ottawa Co., OH. 68 mm.  
C, F, Hinge detail: OSUM 61320.1, Meigs Creek, Morgan Co., OH. 86 mm.  
D, H. OSUM 57626.4, Ohio River, [Co.?], OH. 77 mm.  
E. OSUM 55836.1, Little Darby Creek, Madison Co., OH. 61 mm.  
G. OSUM 62335.6, St. Joseph River, Williams Co., OH. 98 mm.  
Beak sculpture detail: OSUM 55836.4, Little Darby Creek, Madison Co., OH. 27 mm total length.


Elliptio dilatatus var. sterkii Grier, 1918: 9–10 [Type locality: “Big Bend, Presque Isle, Erie Co., Penn.” Holotype CMNH 61.4268].

Elliptio dilatatus sterkii Grier, 1918. Ortmann, 1919: 101, pl. 8, fig. 3.


Elliptio (Eurynia) dilatatus (Rafinesque, 1820). Frierson, 1927: 33.

Elliptio (Eurynia) dilatatus var. fulvus (Rafinesque, 1831). Frierson, 1927: 34.

Elliptio (Eurynia) dilatatus delicatus (Simpson, 1900). Frierson, 1927: 34.

Elliptio (Elliptio) dilatatus delicatus (Simpson, 1900). Baker, 1928a: 128, pl. 56, figs. 7, 8.

Elliptio (Elliptio) dilatatus sterkii Grier, 1918. Baker, 1928a: 130, pl. 56, figs. 3–6.

Elliptio (Eurynia) nasutus nasutus (Lamarck, 1819). Haas, 1969: 244.

Elliptio (Eurynia) nasutus fulvus (Lamarck, 1819). Haas, 1969: 244.

Elliptio (Eurynia) nasutus var. armathwaitensis (Wright, 1898). Haas, 1969: 245.

Elliptio (Eurynia) nasutus delicatus (Simpson, 1900). Haas, 1969: 245.

Elliptio dilatata form sterkii Grier, 1918. Strayer & Jirka, 1997: pl. 25, figs. 3, 3a, 4, 4a, 5.

Status. Not listed by either Ohio Division of Wildlife or U.S. Fish & Wildlife Service as of 2009.

ADULT SHELL

Shell. Medium to fairly large sized (to 130 mm), moderately thick, very elongate, usually pointed posteriorly; usually compressed.

Anterior margin. Long, straight to broadly rounded to the ventral border.

Ventral margin. Very broadly rounded to straight, rarely concave in very old adults.

Posterior margin. Long, rather straight to the dorsal margin.

Dorsal margin. Long, straight, joining posterior margin with obtuse angle.

Umbo. Wide, very low; umbo face slightly forward; umbonal sculpture of 2–4 angled or slightly undulating ridges.

Ligament. Long and prominent, tan to dark brown, not concealed by shells.
Fig. 52. *Elliptio dilatata* ( Rafinesque, 1820)
Solid dots—live or fresh dead since 1980
Bullseye—all records, any condition
**Disc sculpture.** Disc of shell smooth except for low angularizations on posterior slope.

**Periostracum.** Juveniles may be shiny, but adults have a matte finish; juveniles yellow or tan with fine green lines or rays; adults may become black; dorsal slope usually dark.

**Nacre.** Usually purple or purple bordered with white; some populations have purple, salmon, and white nacre individuals living sympatrically; often iridescent posteriorly; Tulberg layers rare.

**Hinge plate.** Well-developed, very long; right cardinal a single, massive, triangular denticle, often with small anterior accessory tooth; left cardinal bifid, the teeth widely separated; laterals well-developed, massive, long, straight, one in right valve, two in left; interdentum impressed, short.

**Muscle scars.** Anterior adductor medium-sized, oval, impressed; posterior adductor nearly flush to impressed; small anterior adductor distinct from anterior pedal protractor scar, posterior adductor narrowly joined to small posterior pedal retractor scar; dorsal suspensors located under interdentum in a cluster. Pallial line entire, located far from shell margin. Accessory line poorly developed, short.

**Umbonal cavity.** Very wide, shallow, open.

**Glochidia.** Subelliptical, dorsal margin straight, ventral margin semicircular, lateral margins about equal, the anterior margin slightly more produced than the posterior margin. Loose-looped sculpture covers the exterior surface of the valve, hooks absent (Lea, 1874b: 69, pl. 1, fig. 13; Ortmann, 1911: 364, pl. 89, fig. 7; Hoggarth, 1999: figs. 34a–f).

Literature records (Lefevre & Curtis, 1910a: 97, fig. n; Lefevre & Curtis, 1912: 146, fig. 1o; Surber, 1912: 10, pl. 2, fig. 38; Ortmann, 1912a: 271; Utterback, 1915: 201; Ortmann, 1919: 111; Hoggarth, 1999: figs. 34a–f) indicate glochidial dimensions for length (0.20 to 0.22 mm), height (0.19 to 0.23 mm), and hinge (0.14 to 0.15 mm). Lea (1863: 54) noted, “Embryonic shell short pouch-shape, white, has no hooks, very nearly the same as phaeolus [P. fasciolaris].” This glochidium has a much longer hinge line and a more depressed shell than P. fasciolaris. The glochidium is more similar to those of the genus Epioblasma than any other. However, it can be distinguished from them by the absence of supernumerary hooks in the glochidium of E. dilatata.

**Reproductive biology.** Tachytictic. Individuals reach maturity from 4 to 6 years of age (Jirka & Neves, 1992). The Spike spawns from March to July (Jirka & Neves, 1992), and eggs develop in May and apparently again in July and August (Ortmann, 1919). Although Ortmann (1919: 96) had reported a Spike with eggs in August, and dismissed it as “clearly an abnormal case,” there is evidence that the Spike has two breeding periods a year (Watters & O’Dee, 1998c). In their study glochidia were recovered in August and September, and again in November. Wisconsin individuals were found with glochidia from May through July (Heath et al., 1998). In Ohio, individuals overwinter buried in the substrate, but surface in April, presumably to spawn (Watters et al., 2001). Glochidia are discharged in white, lanceolate conglutinates (Utterback, 1915).

**Reported potential hosts**

- *Cottus carolinae* (Banded Sculpin)—Luo, 1993 (LT).
- *Dorosoma cepedianum* (Gizzard Shad)—Wilson, 1916 (NI).
- *Perca flavescens* (Yellow Perch)—Clarke, 1981b (NS).
- *Pomoxis nigromaculatus* (Black Crappie)—Clarke, 1981b (NS).
- *Pylodictis olivaris* (Flathead Catfish)—Howard, 1914a (LT).
- *Sander canadensis* (Sauger)—Howard, 1914a (NI).

**Habitat.** A widespread species, the Spike is most common in sand and cobble in creeks. It is rare in large rivers such as the Muskingum and Ohio rivers. Although it occurs in Lake Erie, it is usually not common in other lakes and ponds.

**Range.** Mississippi River drainage, including the Ohio, Cumberland, and Tennessee rivers. North to Minnesota.
and Wisconsin. East to Pennsylvania and New York. West
in the Missouri, Red, and White rivers. South to Missis-
sippi. Great Lakes drainages.

**Range in Ohio.** Widespread but declining, most common
in the Big Darby Creek system. Western basin of Lake Erie,
particularly around the Bass Islands.

**Similar species.** It is most similar to purple-nacred forms
of *Ligumia recta*. That species grows to a much larger size
than *E. dilatata* and has fine double-looped beak sculpture.
*Elliptio dilatata* has coarse single loops or parallel ribs. It is
more elongate and less massive than *Elliptio crassidens*.

**Comments.** Individuals gradually slow in growth during
their entire life. Specimens rarely reach ca. 130 mm and
25 years old.

**Epioblasma Rafinesque, 1831**

**Etymology.** Gr. *epi-*, upon, over, above + Gr. *ob-*, toward,
to + Gr. *elasma*, metal beaten out, metal plate. Rafinesque
(1831: 2) noted that the genus *Epioblasma* “Differs from
*Amblyea* and *Ellipsaria* by lamellar tooth obliqual, diver-
gent towards the back and straight.” In the left valve of *E.
flexuosa* (Rafinesque, 1820), the space between the lateral
teeth is slightly greater anteriorly than posteriorly; or, in
Rafinesque’s view, they appear divergent “towards” (*ob-*)
the “back” (*orumbo*) which is positioned upon or above
(*epi-*) the shell.

**Original description**
*Epioblasma* Rafinesque, 1831: 2.

**Type species.** *Epioblasma biloba* Rafinesque 1831, by
monotypy. Bogon (1998), based on the discovery of a
Rafinesque syntype in the Férussac collection, believed
that *Epioblasma biloba* Rafinesque, 1831, is the female of
what is known as *Epioblasma rangiana* (Lea, 1838).

**Synonymy**
*Epioblasma* Rafinesque, 1831: 2.

*Dysnomia* Agassiz, 1852: 43 [Type species: *Obliquaria
(Quadrula) flexuosa* Rafinesque, 1820, by original des-
ignation].

*Dysnomia* [sic] Bielz, 1869: 43.

*Dysnomia* [sic] Paetel, 1890: 143.

*Dysnomia* (Truncillopsis) Ortmann & Walker, 1922: 65
[Type species: *Truncilla triqueret* Rafinesque, 1820, by
original designation].

*Dysnomia* (Scalenilla) Ortmann & Walker, 1922: 68 [Type
species: *Unio sulcatus* Lea, 1829, by original designa-
tion].

**Geographic range.** Mississippi and Mobile river drain-
ages, Lake Erie and Lake Michigan and their drainages.

Absent from the Atlantic Coastal Plain, Florida, and the
Apalachicola River.

**Epioblasma flexuosa**
*(Rafinesque, 1820)*

**Figures 54, 55**

**Etymology.** *L. flexuosus*, full of turns or windings, tortu-
ous, flexuous. In his original description (1820: 306) Rafin-
esque used the word “flexuous” to describe the curvature
of both the annulae and the shell margin—appropriately
so for this species, and especially so for the female of this
species which he had not as yet seen.

**Vernacular name(s).** Leafshell, Northern Leafshell.

**Original description**
*Obliquaria* (Quadrula) *flexuosa* Rafinesque, 1820: 306–307,
species no. 33, no figure.

**Type locality.** Originally “Dans le Kentuky [River]. Salt-
river et Green-river.” The lectotype is from the Kentucky
River, which becomes the type locality.

**Type material.** The type mentioned by Vanatta (1915:
55) was selected as lectotype (ANSP 20249 from the Ken-

**Synonymy**

*Obliquaria* (Quadrula) *flexuosa* var. *bullata* Rafinesque,
1820: 307 [non *Quadrula bullata* Rafinesque, 1820
(see under *Quadrula pustulosa*). Type locality: none
given. Type not located].

*Unio foliatus* Hildreth, 1828: 284, fig. 16 [Type locality:
(1852: 43) considered this the female of the species.].

*Unio flexuosus* (Rafinesque, 1820). Conrad, 1835: 8, pl. 4,
fig. 2.


*Dysnomia flexuosa* (Rafinesque, 1820). Agassiz, 1852: 43.

*Truncilla (Dysnomia) foliata* (Hildreth, 1828). Simpson,
1900a: 521.

*Dysnomia* (Dysnomia) *flexuosa* (Rafinesque, 1820).

Ortmann & Walker, 1922: 70.

*Plagiola* (Epioblasma) *flexuosa* (Rafinesque, 1820). Johnson,
1978: 283–287 [in part], pl. 5 [in part], pl. 15, fig. 5.

**Status.** Listed as Extinct by both Ohio Division of Wildlife
and U.S. Fish & Wildlife Service as of 2009.

**ADULT SHELL**

**Shell.** Medium size (to 80 mm), rather thick and heavy,
bifurcate in profile, particularly in females, moderately in-
fated. Juveniles much more elongate than adults.

**Anterior margin.** Flat before the umbo, then broadly
rounded to the ventral border.
acuminate. Sharply pointed; terminating acutely.
acute. Sharp, pointed.
adductor muscle (scar). Muscles connecting the two shells anteriorly and posteriorly, used to close the shells. The muscles leave characteristic scars on the shell where they attach.
alate. Having a wing-like projection of the two valves of the shell, extending dorsally beyond the hinge line. See wing.
alotype. Type material of a species of the opposite sex to the holotype. See cotype, holotype, lectotype, neotype, paralec-totype, paratype, syntype, topotype.
amphidetic. Having the ligament present on both sides of the umbo.
analogous character. One of two or more characters that are functionally similar but structurally and developmentally different.
annumlus (pl. annuli). Major growth lines on the outside of the shell, often considered annular in nature.
anterior. The front part of something.
anterior adductor muscle (scar). See adductor muscle.
anterior protractor muscle (scar). A muscle used to move the foot; it has a characteristic scar.
apomorphic character. In a pair of homologous characters, the inherited change of a previously existing character into a new character. See pleisiomorphic character.
apposed. Set opposite to one another.
arcuate. Curved like a bow, arched.
beck. See umbo.
beak cavity. See umbonal cavity.
bivalvia. A class of the phylum Mollusca characterized by an external, two-piece, calcareous shell, a muscular foot, and the lack of a head or radula.
bradytictic. Reproduction in which the glochidia are overwintered in the marsupial demibranch of the female unionid. Also called winter breeders.
branchiae. Gills; those organs of an aquatic organism that maximize the area of contact of living permeable tissue with the environment; comparable to the lungs of terrestrial forms; the site of exchange of those fluids used in metabolism with those produced by metabolism.
branchial aperture. An opening, formed by the mantle (pallial) margins, through which water passes into the branchial cavity. Same as incurrent aperture.
byssus (byssal thread). A filament or very few filaments of material by means of which the juvenile of some individuals of some species are attached to other, usually larger or heavier, objects; as a result, the juvenile remain tethered to a site on or in the stream substrate.
cardinal teeth. The anterior-most hinge teeth (when present). Often short and triangular. Also known as pseudocardinal teeth in the Unionacea.
clastra. Elongate ridges of the mesial-posterior hinge plate of anodontines which are neither parallel to nor homologous with the lateral or lamellar teeth.

clavate. Club-shaped.
compressed. Flattened from side to side; the opposite of inflated.
conglutinate. The packages of glochidia formed by the female; often resemble host prey items. See Watters (2008).
corrugated. Sculptured with undulating ribs or folds.
cotype. A specimen identified by the author of a species as an example of that species. May be part of the type series. See allo-type, holotype, lectotype, neotype, paralectotype, paratype, syntype, topotype.
depressed. Low, flattened.
diaphragm. In unionoid anatomy, a horizontal, transverse, perforate dividing wall of tissue between the branchial and supra-branchial cavities, frequently attached to the body mass mesially and to the mantle lobes laterally; consisting of the basal proximal parts of all four demibranches.
dimyarian. Having two adductor muscles.
disc. The central portion of the shell.
divaricate. Spreading out widely, "V"-shaped, forked.
dorsal. Pertainning to, or situated on or near, the back.
dorsal suspensor muscles (scars). Minute muscles arranged in bundles beneath the umbo.
ecophenotype. A form of a species caused by environmental rather than genetic factors.
edentulous. Without teeth.
elliptical. Having the shape of an ellipse.
emarginate. Having a margin or an edge something less than a straight line; slightly concave.
equivalve. Having valves equal or very nearly so in size.
excurrent aperture. The opening through which water is expelled from a bivalve mollusc. Same as suprabranchial aperture.
extinct. A species that has been globally lost.
extirpated. A species that has been lost from a particular area (such as a state) but still exists elsewhere.
gills. See branchiae.
glochidium (pl. glochidia). The parasitic larva of freshwater mussels.
growth lines. See annulus.
hinge plate. The dorsal portion of the shell that may have interdigitating teeth; may be absent in some species.
holotype. The original specimen or illustration upon which the author of a species bases his description. See allotype, cotype, lectotype, neotype, paralectotype, paratype, syntype, toptype.
holomologous character. One of a pair of characters in which one is derived directly from the other. Three or more characters are homologues if each gave rise to the next in linear sequence. Contrast with analogous character.
homonym. Taxonomic names that are spelled the same but were coined by different authors or at different times. The oldest name is the senior homonym and the valid name. Other names are junior homonyms. For example, Unio childreni Hanley, 1843 is a junior homonym of Unio childreni Gray, 1834. See synonym.
ICZN. International Code of Zoological Nomenclature, a collection of "rules" drafted by the International Commission of Zoological Nomenclature (1999), a paralegislative body that, in addition to writing the Code, rules on special cases.
impoundment. A portion of a river or stream that has been pooled by the presence of a dam.
icurrent aperture. The opening through which water is drawn into a bivalve mussel by ciliary action. Same as branchial aperture.
inflated. Swollen from side to side; the opposite of compressed.
interdentum. The portion of the hinge plate positioned between the cardinal and lateral teeth.
iridescent. Rainbow-like colors produced from crystalline interactions in the shell.
lamellate. In reference to hinge teeth, blade-like.
lateral teeth. The posterior-most hinge teeth (when present). Often long and bladelike. Also known as pseudolateral teeth.
lectotype. One of several syntypes, designated by an author after the original publication of a species name as the type specimen; designated only where there was no original holotype. See allotype, cotype, holotype, neotype, paralectotype, paratype, syntype, toptype.
ligament. The non-living connection between the shells on the dorsum; acts as a spring to open the shells.
marsupium. The portion of the female gills or brachiae that are used to contain the glochidia until release.
microfossa. Minute muscle scars within the pallial line; lateral attachments of the mantle to the nacre.
mollusca. A phylum of soft-bodied animals typically producing a shell of calcium carbonate and/or conchiolin by means of a mantle and moving by means of a muscular foot.
monotypy. A species that became the type of a genus if it was the only species an author originally listed for the genus. Later additions by other workers, or the original author himself, are invalid. See original designation, subsequent designation, subsequent monotypy, tautonomy.
nacre. The prismatic inner lining of the shell; also called mother-of-pearl.
neotype. The designation made if the type material is lost, destroyed, or deemed inadequate for identification. See allotype, cotype, holotype, lectotype, paralectotype, paratype, syntype, toptype.
nomen dubium. A taxonomic name that cannot be confidently matched with a species because of deficiencies in the original description and/or illustration. Although it may act as a synonym or a homonym, it does not become the valid name for any taxon.
nomen nudum. A taxonomic name that was not validly introduced according to the ICZN rules. It has no taxonomic value and cannot be a synonym or a homonym.

oblique. Slanting or inclined; neither perpendicular nor horizontal.
obtuse. Angles greater than 90° and less than 180°.
orbicular. Having the form of an orb; round, spherical.
original designation. A designation made if a genus was described and the original author specified a species to be the type of the genus. See monotypy, subsequent designation, subsequent monotypy, tautonomy.

ovate. Having the shape of a chicken egg or of a longitudinal section of one; ellipsoidal but not elliptical (which see).
pallial line. The linear muscle scar that marks where the mantle attaches to the shell.
pallial retractor. A muscle that withdraws the distal mantle margin within the shell.
paralectotype. A designation made if a species is described from a series of specimens or illustrations and the original author
of the species did not choose one to represent the holotype; a subsequent worker chooses one as the lectotype. The remaining specimens from the type series are paralectotypes. See allotype, cotype, holotype, lectotype, neotype, paratype, syntype, toptype.

paratype. A designation made from remaining specimens of a type series if a species is described from a series of specimens or illustrations and the original author of the species chose one to represent the holotype. See allotype, cotype, holotype, lectolectotype, neotype, syntype, toptype.

patronym. A name formed by the addition of a prefix or suffix indicating relationship to the name of one's father or paternal ancestor; a name coined in honor of a particular person.

pedal levitor. A muscle that functions in the lifting of the foot. The proximal terminus is in or near the umbonal cavity of the unionoid.

pedal retractor. A muscle that withdraws the foot within the shell.

periostracum. The non-living outer layer of the shell; may be eroded away in old individuals or completely lost in weathered or sub-fossil dead shells.

plesiomorphic character. The original, preexisting character in a pair of homologous characters. Contrast with apomorphic character.

plications. Parallel ridges or folds on the surface of the shell.

posterior. The back end of something.

posterior adductor muscle (scar). See adductor muscle.

posterior retractor muscle (scar). A muscle used to move the foot; it has a characteristic scar.

posterior ridge. A ridge extending from the umbo posteriorly across the dorsum to the posterior margin; may be prominent or barely perceptible.

proximal. Nearest to the point of origin or attachment.

pustule. A bead-like sculpture on the shell.

pyriform. Shaped like a pear.

quadrat. Square or approximately square.

rotund. Round or rounded out, spherical.

subsequent designation. A designation made if a genus was described with more than one species of that genus, and the original author did not specify which one was to be the type of the genus; the genus remains without a type until someone subsequently designates one. See monotypy, original designation, subsequent monotypy, tautonomy.

subsequent monotypy. A designation made if a genus was described with more than one species, but all but one are unidentifiable (nomen dubium); the remaining species becomes the type of the genus. See monotypy, original designation, subsequent designation, tautonomy.

sulcus. On the shell, a depression or groove extending from the umbo to the ventral margin.

suprabranchial aperture. Same as excurrent aperture (which see).

symplesiomorphic character. A homologous character shared by a group of taxa and having originated in an ancestor earlier than the common ancestor of the group.

synonym. Taxonomic names that apply to the same biological
entity. The oldest name is the senior synonym and usually is the valid name for the taxon. Other names are junior synonyms. For example, *Unio foliatus* Hildreth, 1828 is a junior synonym of *Obliquaria flexuosa* Rafinesque, 1820 because both names represent the same species. See *homonym*.

**syntype.** A specimen from the type series from which no holotype or lectotype has been chosen. See *allotype, cotype, holotype, paralectotype, lectotype, neotype, toptype*.

**tachytictic.** Reproduction in which the glochidia are not overwintered in the marsupial demibranch of the female unionoid. Fertilization, larval development, and parasitic period all occur within the same calendar year. Also called summer breeders.

**tautonomy (tautonymy).** A name applied if a list of species accompanies the original description of a genus, and one of those species names is an obvious variant of the genus name; that species becomes the type of the genus. For example, *Margaritifera margaritifera* and *Villosa villosa* are tautonomous names. See *monotypy, original designation, subsequent designation, subsequent monotypy*.

**tooth.** Interdigitating portions of the hinge of the two shells. Usually of two types: cardinal and lateral.

**topotype.** A specimen collected from the original type locality. See *allotype, cotype, holotype, paralectotype, lectotype, neotype, syntype*.

**triangulate.** Having the shape of a triangle.

**Tulberg layers.** Blemishes in the nacre, often brown, gold, or gray.

**type locality.** The source of a species as stated by the original author. If no type locality was given, one may be designated by a subsequent worker. Type localities also may be amplified or corrected.

**umbo.** A projecting point or knob on a surface; specifically, the swollen dorsal region of a shell valve; plural *umbos*. Also referred to as beaks. Umbos may face each other or face forward.

**umbonal cavity.** The depression on the dorsal aspect of the inside of the shell that is the inner aspect of the umbo; may be deep or shallow.

**valve.** A single piece, actually half, of a bivalve shell.

**ventral.** Pertaining to, or situated on or near, the underside.

**vernacular name.** A name in the common native speech, as distinguished from scientific nomenclature.

**wing.** A projection of the valves on the dorsum forming a triangular process; may be either anterior or posterior to the umbo, or both.
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Index

Page numbers and entries in **bold** refer to primary references, chapter titles, major section titles, and recognized common names.

A

aberti, Cypregeria, 68

Abbreviations Used in Species Accounts, xiii

abrupta, Lampsisis, 136–40, 145, 149, 207

abrupta, Lampsisis (Ortmanniana), 136 abrupta, Unio, 136

Acknowledgments, xi–xii

acquired immunity, 12

acrispatius, Unio ciliardias var., 266

Actinonaias, 32, 84

Actinonaias carinata, 32–36, 361

Actinonaias carinata orbis, 32

Actinonaias ellipsiformis, 361

Actinonaias ligamentina, 36, 140, 157, 177

Actinonaias ligamentina carinata, 32–36

Actinonaias ligamentina ligamentina, 36–40

Actinonaias pectorosa, 34, 38, 190

Actinonaias rafinesqueana, 36

Aeglia, 136

Aeglia ovata, 149

aesopus, Margarita (Unio), 218

aesopus, Margaron (Unio), 218

aesopus, Plethobasus, 218

aesopus, Pleurobema, 211, 218

aesopus, Pleurobema (Plethobasus), 218

eaesopus, Unio, 211, 218

aesopus, Unio cyphias var., 218

affinis, Unio, 153

alabamensis, Lasmigona complanata, 166

Alasmodon, 40, 162

Alasmodon arcuata, 338

Alasmodon complanata, 164

Alasmodon corrigata, 41

Alasmodon hisans, 172

Alasmodon margaritiferum, 338

Alasmodon marginatus, 338

Alasmodon margaritifer, 338

Alasmodon ponderosum, 162

Alasmodon rhombica, 294

Alasmodon rugosa, 172

Alasmodon (Decurambis) scriptum, 41

Alasmidonta, 40

Alasmidonta, 40

Alasmidonta, 40

Alasmidonta, 40, 341, 344

Alasmidonta calceola, 84

Alasmidonta calceola danielsii, 45

Alasmidonta calceola magnacostatus, 45

Alasmidonta complanata, 162

Alasmidonta costata, 162, 170

Alasmidonta deltoidea, 40

Alasmidonta edentula, 40

Alasmidonta heterodon, 40

Alasmidonta margaritifera, 338

Alasmidonta marginata, 40, 41–45, 153, 162, 170, 173

Alasmidonta marginata var. variabilis, 41

Alasmidonta monodonta, 27

Alasmidonta rugosa, 172

Alasmidonta scriptum, 40

Alasmidonta undulata, 40, 43

Alasmidonta viridis, 45–49, 84, 349

Alasmidonta (Bulliella), 40

Alasmidonta (Decurambis) marginata, 41

Alasmidonta (Decurambis) marginata susquehannae, 41, 43

Alasmidonta (Pressodonta), 40

Alasmidonta (Pressodonta) calceola, 45

Alasmidonta (Pressodonta) minor, 45

Alasmidonta (Pressodonta) viridis, 45

Alasmidonta (Ptygidera), 40

Alasmisodonta, 40

Alasmodon, 40

Alasmisodonta ambigua, 288

Alasmisodonta arcata, 338

Alasmisodonta convagrosa, 341

Alasmisodonta costata, 172

Alasmisodonta dubia, 288

Alasmisodonta edentula, 294

Alasmisodonta hisans, 172

Alasmisodonta lepitoron, 179

Alasmisodonta marginata, 41

Alasmisodonta pressa, 41

Alasmisodonta truncata, 41, 45

Alasmisodonta undulata, 294

alasmidinta, Complanaria, 168

alasmidonta, Unio, 166

alasmidontina, Unio, 166

alata, Lampsilis, 241

alata, Lampsilis (Proptera), 241

alata, Lymnadia, 241

alata, Metaptera, 241

alata, Mya, 241

alata, Mysca, 241

alata, Proptera, 241

alata, Symphynota, 241

alata, Unio, 241

alatus, Lampsilis, 241

alatus, Margarita (Unio), 241

alatus, Margaron (Unio), 241

alatus, Potamiulus, 8, 67, 166, 241–45

alatus, Unio, 241

alatus, Unio (Symphynota), 241

alatilis, Unio, 145

ambigua, Alasmodon, 288

ambigua, Hemilaustena, 288, 290

ambigua, Margariana, 290

ambigua, Simpsonaias, 10, 288–92

ambigua, Simpsonoiconcha, 290

Amblamodon, 162

Ambiasmodon, 162

Ambiasmodon hisans, 162

Amblemma, 2, 49, 72, 77, 233, 309, 344

Amblemma antrosa, 120, 122

Amblemma costata, 49

Amblemma gibba, 114

Amblemma gibba var. dixiformis, 114

Amblemma gibba var. olrievea, 114

Amblemma gibba var. raditula, 114

Amblemia gigantea, 193

Amblemia olivaria, 200

Amblemia perplivata quintardi, 51

Amblemia perplivata quintardi, 51

Amblemia persuviana, 51

Amblemia plicata, 13, 51

Amblemia plicata costata, 51

Amblemia plicata hippocopaca, 51

Amblemia plicata perplivata, 54

Amblemia plicata pilbyri, 51

Amblemia plicata plicata, 49–54, 195

Amblemia plicata quintardi, 51

Amblemia plicata southallii, 51

Amblemia rariplivata, 51

Amblemia rariplivata persuviana, 51

Amblemia torula, 114

Amblemia torula var. angulata, 114

Amblemia (Amblemma) plicata, 51

Amblemia (Megaloanaias) gigantea, 193

Amblemia (Megaloanaias) triumphant, 193

Amblemiace, 1

Amblemine, 2

Amphistoma, 265

Amygdalonias, 310

Amygdalonaias donaciformis, 310
Anodonta, Life History, and Reproduction, 6-13
Anodonta, 54, 61, 84, 292, 298
Anodonta argentea, 59
Anodonta arcularius, 292, 294
Anodonta arkansasensis, 294
Anodonta bealei, 260
Anodonta benedictensis, 260
Anodonta benedicti, 261
Anodonta buchanensis, 59
Anodonta corporalenta, 260
Anodonta cygnea, 56, 262
Anodonta dakota, 261
Anodonta dakotana, 261
Anodonta dallasianna, 260
Anodonta danielisii, 260
Anodonta declivus, 260
Anodonta decora, 260
Anodonta delissens, 132
Anodonta dufia, 288
Anodonta edentula, 294
Anodonta ferruginea, 59
Anodonta ferrusacacena, 59
Anodonta ferrusacacena var. incertopsis, 59
Anodonta ferrusacacena, 61, 294
Anodonta ferrusacacennus, 58, 59
Anodonta feliospis, 295
Anodonta fontiana, 260
Anodonta gessneri, 265
Anodonta giantae, 260
Anodonta globosa, 254
Anodonta grandis, 56, 258
Anodonta grandis bealei, 262
Anodonta grandis corporulenta, 262
Anodonta grandis decora, 261
Anodonta grandis foottiana, 261
Anodonta grandis gigantea, 261
Anodonta grandis grandis, 262
Anodonta grandis lugubris, 262
Anodonta grandis plana, 262
Anodonta grandis simpsoniana, 262
Anodonta grandis var. benedictensis, 261
Anodonta grandis var. foottiana, 261
Anodonta grandis var. gigantea, 261
Anodonta grandis var. leonensis, 261
Anodonta hallenbeckii, 265
Anodonta harpehensis, 260
Anodonta hockingenis, 261
Anodonta horda, 321
Anodonta hoyttenisenis, 261
Anodonta imbecilis, 321
Anodonta imbeciliss, 321
Anodonta imbricata, 261
Anodonta incerta, 321
Anodonta incertus, 321
Anodonta inornata, 261
Anodonta lacustris, 354
Anodonta lata, 260
Anodonta lewisii, 261
Anodonta linneana, 261
Anodonta linneana var. incertopsis, 59
Anodonta margaritatus, 256
Anodonta marvaytiana, 260
Anodonta marvaytiana, 261
Anodonta marvaytiana, 260
Anodonta micans, 261
Anodonta modesta, 59
Anodonta nilssonii, 260
Anodonta oblica, 59
Anodonta ohiensis, 132, 323
Anodonta opaca, 260
Anodonta ovata, 260
Anodonta palna, 258
Anodonta papyracea, 294
Anodonta pavonia, 294
Anodonta pensylvanica, 292, 295
Anodonta pensylvanica, 292
Anodonta pepiniana, 260
Anodonta plana, 258
Anodonta plumosus, 292, 294
Anodonta salmonia, 262
Anodonta salmonia, 260, 294
Anodonta sheffereiana, 294
Anodonta sheffereiana, 294
Anodonta simpsoniana, 260
Anodonta somersisi, 261
Anodonta stewartiana, 258
Anodonta subangulata, 261
Anodonta subellin Draco, 294
Anodonta suberculacena, 294
Anodonta suberculacena, 261
Anodonta suberculata, 294
Anodonta suberculata, 54, 58-58, 324, 326
Anodonta sulcata, 261
Anodonta tetracana, 294
Anodonta texaensis, 260
Anodontia undulata, 292
Anodontia undulata, 292
Anodontia virgata, 260
Anodontia wardiana, 294
Anodontia wardiana, 54
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 54
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Anodontia (Anodontia) grandis, 262
Arcidens, 341
Arcidens confroagous, 341–44
Arcidens confroagous, 341
Arcidens (Arcidens) confroagous, 341
archid, Margarita (Unio), 86
archid, Margarina (Unio), 86
arcuata, Alasmodont, 338
arcuata, Alasmodonta, 338
arcuata, Margaritana, 338
arcuata, Mya, 338
arcula, Margaritana, 40
arellatus, Anodonta, 292
arellatus, Anodon, 294
argentea, Anodonta, 59
argentea, Margaron (Anodonta), 59
argentea, Strophitus, 59
arkansasensis, Anodonta, 294
arkansasensis, Margaron (Anodonta), 294
Arkansas, 341
armathwaitei, Elliptio (Euryria) nasuta var., 86
armathwaitei, Venomus gibbosus var., 86
arquatum, Psychobranchnus (Psychobranchnus) fasciolare, 251
asperata, Quadrula, 280
asperata, Quadrula (Buellata) pustulosa, 282
asperatus, Quadrula pustulosa, 282
asperimis, Unio, 286
asperimis, Margaron (Unio), 286
asperimis, Margaron (Unio), 286
atrat, Unio (Niaia), 175
atrat, Unio, 175
atrococrassatus, Complanaria, 191
atrococrassatus, Margaron (Unio), 191
atrococrassatus, Unio, 191
attempt, Obliquaria, 183

B
badium, Sulcularia, 162
Banan Shell, 157
Bankclymbor, 157
Baphia calceola, 45
Baphia complanata, 164
Baphia confroagous, 343
Baphia dehiscens, 132
Baphia dehiscens, 132
Baphia hildrethiana, 290
Baphia marginifera, 340
Baphia marginata, 41
Baphia minor, 45
Baphia rufug, 172
Baphidae, 338
Baruta, 77
Baruta ponderosa, 77
Baruta sinuata, 86
Bastard, 341
bealei, Anodonta, 260
bealei, Anodonta grandis, 262
bealei, Anodonta (Pyganodon) grandis, 262
bealei, Margaron (Anodonta), 261
bealei, Anodonta, 262
Bean, Rayed, 326–29
benedictensis, Anodora, 260
benedictensis, Anodonta, 260
benedictensis, Anodonta grandis var., 261
benedictensis, Anodonta (Pyganodon) grandis, 262
benedictensis, Margaron (Anodonta), 260
benedictensis, Margaron (Anodonta), 260
benedictensis, Symphygota, 258, 261
benedictii, Anodonta, 261
benedictii, Margaron (Anodonta), 261
biangulata, Quadrula, 286
bicolor, Unio, 86
Big Black, 191
Big Floater, 258
Big River Pigtoe, 226
biloba, Epioblasma, 89, 108
biloba, Epioblasma torulosa, 110
biregi, Anodonta (Anodontoides), 59
biregi, Anodontoides, 59
biregi, Anodontoides ferussacianus, 61
biregi, Quadrula, 334
Black Creekshell, 334
Black Rock Shell, 191, 341
Black Sandshell, 186–91
blandus, Unio lanceolatus var., 251
blatchleyi, Lampsilis, 179
blatchleyi, Lampsilis (Proteria), 179
blatchleyi, Leptidea, 182
Blossum, Tubercled, 112–16
Bluefinger Spike, 84
Bluepoint, 49
Boepple, Johann, 5
Bourguignat, Jules René, 3
bournianum, Epioblasma, 225
bournianum, Unio, 222, 226
boykiniana, Megalanolaim, 195
bradytictic breeding, 10
brazosensis, Margaron (Unio), 51
brazosensis, Unio, 51
brevialis, Unio, 200
breviden, Epioblasma, 72
burchanensis, Anodonta, 59
burchanensis, Anodontoides ferussacianus, 61
burchanensis, Anodontoides ferussacianus var., 59
burchanensis, Margarita (Anodonta), 59
burchanensis, Margaron (Anodonta), 59
Buck Horn, 306
bugeysis, Dreissen, 3, 17–18
Bullata, 265
bullata, Obliquaria (Quadrula), 280
bullata, Obliquaria (Quadrula) flexuosa var., 89, 280
bullata, Quadrula, 89, 282
bullatus, Quadrula, 282
bullatus, Unio, 280
Bullella, 40
Bullhead, 5–6
Button Industry, 5–6

C
calni, Carunculina parva, 302
Calceola, 40
Calceola angulata, 40, 45
Calceola, Alasmidonta, 84
Calceola, Alasmidonta (Pressodonta), 45
Calceola, Baphia, 45
calculea, Margarita (Margaritana), 45
calculea, Margaritana, 45
calculea, Margaron (Margaritana), 45
calcula, Unio, 45
calculus, Stribhitus, 45
calculus, Unio, 40, 45
calculus, Uniois, 45
calgunsinos, Margaron (Unio), 334
calgunsinos, Unio, 334
camels, Margarita (Unio), 251
camels, Margaron (Unio), 251
camels, Ptychobranchus phaseolus var., 251
camelus, Unio, 251
camptodon, Elliptio (Unioemer) tetratalas-
ms, 319
camptodon, Unio, 317
camptodon, Unio (Uniomerus) tetratalasmus
var., 317
camptodon, Elliptio tetratalasmus, 319
canadenis, Lampisits ovata, 142
canadenis, Lampisits ventricosa, 140
canadenis, Margaron (Unio), 140
canadenis, Unio, 140
canals, 21
Canthyria collina, 222
capax, Lampisits, 352
capax, Lampisits (Lampisits), 352
capax, Potamius, 243, 352–54
capax, Prothera, 352
capax, Unio, 352
capparisa, Unio, 102
cappilus, Unio, 326
cardia, Lampisits, 140
cardiaea, Unio, 233, 238
cardium, Lampisits, 8, 140–45, 149, 151, 153, 157, 177, 354
cardium, Lampisits (Lampisits), 140
cardium, Unio, 140
carintata, Actinonaias, 32–36, 361
carintata, Actinonaias ligamentina, 32–36
farrinata, Lampisits (Ortmanniana), 32
carintata, Lampisits (Ortmanniana) carintata, 32
carintata, Mya, 32
carntatus, Unio, 32
Caronsolina, 299
Caronsolina glans, 299
Caronsolina glans glans, 299
Caronsolina glans moesta, 299
Caronsolina moesta, 299
Caronsolina parva, 302
Caronsolina parva caloni, 302
cataracta, Pygargodon, 256
cataracta, Pygargodon cataracta, 256, 356
cattaila, Pleurobema, 238
cattaila, Pleurobema cocinema var., 238
cattaila, Pleurobema cordatum, 238
cattaila, Pleurobema cordatum var., 238
cattaila, Pleurobema obliquum, 238
cattaila, Quadrula (Obliquula), 238
cattaila, Unio, 236
cattaila, Unio, 238
Catspaw, 95–99
Catspaw, Purple, 95–99
Catspaw, White, 99–102
Catholic, Pisconia, 128
chadwicki, Lampisits siliquidea, 154
Channelization, Dredging, and Snag-
ging, 15–16
chattanoogae, Pleurobema, 222
childrenri, Unio, 153
chloris, Lasigmorna viridis var., 45
claticroides, Unio, 213
ciatricoides, Plutobema, 213
ciatricoides, Pleurobema, 213
ciatricoides, Pleurobema, 213
ciatrico, Pleurobema, 213
ciatrico, Quadrula, 213
ciatricosum, Pleurobema (Plethobasus), 213
ciatricosum, Plethobasus, 211–15, 218,
221
claticosum, Unio, 213
claticosum, Unio, 213
claticosum, Dynomia torulosa, 105
claticosum, Dynomia (Pilea) torulosa, 105
claticosum, Dynomia (Torulosa), 105
claticosum, Margaron (Unio), 105
claticosum, Truncilla (Pilea) perplexa
var., 105
claticosum, Unio, 105
clinerescens, Tocolasma, 299
clira, Obvaria, 209
clira, Margarita (Unio), 207
clira, Margaron (Unio), 207
clira, Obvaria, 209, 337
clira, Unio, 136, 207
clira, Unio subrotundus var., 209
clavula, Plutobema, 6, 221, 222–26
clavula, Pleurobema clava, 225
clavula, Unio, 222
clavula, Margarita (Unio), 222
clavula, Margaron (Unio), 222
Clubsheil, 222–26
Clubsheil, Common, 222
Clubsheil, Northern, 222
Clubsheil, Ohio, 222
Clubsheil, Ohio River, 222
Cob Sheil, 266
cocinea, Pleurobema catilis var., 238
cocinea, Quadrula, 238
cocinea, Quadrula (Obliquula), 238
coconium, Pleurobema, 238
coconium, Pleurobema cordatum, 238
coconium, Pleurobema cordatum form, 238
coconium, Pleurobema cordatum var., 238
coconium, Pleurobema obtusum, 238
coconium, Margarita (Unio), 236
coconium, Margaron (Unio), 238
coconium, Unio, 236
cocinea, Quadrula, 238
cocodrinius, Unio, 350
cognata, Unio, 310
cohongronta, Lampisits ventricosa, 140
Cokeria, 49
Cokeria southalli, 49, 51
collina, Canghyria, 222
coloradoensis, Potamilis purpuratus, 32
Combsheil, Round, 102–5
Common Clubsheil, 222
Common Creep, 292
Common Pigtoc, 226
comperus, Plethobasus, 218
comperus, Plethobasus cyphus, 218
comperus, Pleurobema (Plethobasus), 218
comperus, Unio, 218
Complanaria, 162
Complanaria alasmodontina, 168
Complanaria atroscutatus, 191
Complanaria complanata, 164
Complanaria compressa, 168
Complanaria compressus, 168
Complanaria confragosus, 343
Complanaria costata, 172
Complanaria gigas, 162, 164
Complanaria heros, 191
Complanaria plicatus, 49
Complanaria rugosa, 172
complanata, Alasmobdodon, 164
complanata, Alasmidonta, 162
complanata, Baphia, 164
complanata, Complanaria, 164
complanata, Elliptio, 8, 77–80
complanata, Lasigmorna, 162–66, 170,
175, 179, 245
complanata, Lasigmorna complanata, 164
complanata, Margarita (Margaritana), 164
complanata, Margaritana, 164
complanata, Mya, 77, 164
complanata, Pierosyna, 164
complanata, Symphyota, 164
complanata, Symphyota (Pierosyna), 164
complanatus, Unio, 77
compressa, Complanaria, 168
compressa, Lasigmorna, 8, 166–70, 349
compressa, Lasigmorna (Platytnis), 168
compressa, Microcordylicia, 168
compressa, Symphyota, 162, 166
compressa, Symphyota (Symphyota), 168
compressissimus, Margaron (Unio), 251
compressissimus, Unio, 251
compressus, Complanaria, 168
compressus, Margarita (Unio), 73
compressus, Unio, 73, 166
comptodon, Uniomerus tetratalasmus, 319
concestator, Lampisits, 334
concestator, Margaron (Unio), 334
concestator, Unio, 334
confragosus, Baphia, 343
confragosus, Margarita (Margaritana), 343
confragosus, Margaritana, 343
confragosus, Margaron (Margaritana), 343
confragosus, Unio, 343
confragosus, Arcidens, 341–44
confragosus, Arcidens (Arcidens), 343
confragosus, Complanaria, 343
confrugosus, Unio, 343
conglutinates, 10–11
crassa, Pleurobema, 221
coriangus, Quadrula (Quadrula), 306
coriangus, Triaria, 306
coriangus, Unio, 306
coradi, Obliria reticulata var., 196
corsaquinus, Unio, 225
correction actions, 20
Conservation of Species, 19–20
toques, Margaron (Unio), 334
toques, Unio, 334
continus, Unio validus var., 126
contrayens, Quadrula quadridens, 286
contrayens, Quadrula quadrata, 286
cooperiana, Quadrula, 215
cooperiansus, Margarita (Unio), 215
cooperiansus, Margaron (Unio), 215
cooperiansus, Pleurobema, 215
cooperiansus, Quadrula, 215
cooperiansus, Unio, 215
Corbicula, the Asian clam, 18–19
Corbiculaceae, 3, 18–19
Corbicula, uncinata, 3, 18
Corbicula leana, 18
Corbicula maniliensis, 18
cordata, Quadrula, 230
cordata, Quadrula (Obliria), 226
cordata, Quadrula (Obliria) cordata, 226
cordatum, Obvaria, 226
cordata, Pleurobema, 226
cordatum, Pleurobema, 14, 22, 105, 124,
128, 213, 226–30, 233, 236, 240
cordatum, Pleurobema cordatum, 226
cordatum, Pleurobema obliquum, 226, 230
cordatus, Unio, 226
cornuta, Mya, 196
cornuta, Theliderma, 196
cornutus, Margarita (Unio), 196
cornutus, Margaron (Unio), 196
cornus, Unio, 196
corpurulentus, Anodonta, 260
corpurulentus, Anodonta, 260
corpurulentus, Anodonta grandis, 262
corpurulentus, Margaron (Anodonta), 261
corpurulentus, Pyganodon grandis, 265
curtina, Alasmidonta, 41
Corbiculina, 299
costa, Alasmidonta, 162, 170
costa, Alasmidonta, 172
costa, Ambelona, 49
costa, Ambelona plicata, 51
costa, Complaniaria, 172
costa, Crenodonta peruviana, 51
costa, Lasigmata, 170–75
costa, Symphyogia (Lasmigona), 172
costatus, Plecemeris, 49
costatus, Unio, 49
cochiana, Quadrula, 32
cochiana, Unio, 265
Cracking Pearl Mussel, 132–35
crassa, Margaritifera, 269
crassa, Mya, 36

Index
delhiscens, Anodonta, 132
delhiscens, Baphia, 132
delhiscens, Hemilastena, 132
delhiscens, Margaritana, 132
delhiscens, Margarita (Unio), 132
delhiscens, Margaron (Unio), 132
delhiscens, Unio, 132
delicate, Truncilla sulcata, 99
delicate, Truncilla (Scalenaria) sulcata var., 108
Delicate Floater, 354
delicatus, Elliptio (Elliptio) dilatatus, 86
delicatus, Elliptio (Eurynia) dilatatus, 86
delicatus, Elliptio (Eurynia) nasutus, 86
delicatus, Unio (Elliptio) gibbosus var., 86
deltoidea, Alasmidonta, 45
deltoidea, Baphia, 45
deltoidea, Margaritana, 45
deltoidea, Margaritana, 45
deltoidea, Margaron (Unio), 45
deltoidea, Margaron (Unio), 45
deltoidea, Strophitus, 45
deltoidea, Unio, 45
deltoideus, Unio, 45
depresa, Obliquaria (Plagiola), 72, 73
depygis, Obovaria lens var., 209
depygis, Obovaria subrotunda, 209
depygis, Unio, 209
detectus, Plethobasus cicatriciosus form, 213
detectus, Unio, 213
diaphana, Unio (Metaperta), 175
diformis, Amblema gibbosa var., 114
dilatata, Elliptio, 14, 77, 80, 84–89, 135, 186, 190, 358
dilatata, Unio (Eurynia), 84
dilatatus, Elliptio, 67
dilatatus, Elliptio (Elliptio), 67
dilatatus, Elliptio (Eurynia), 86
dilatatus, Unio, 77, 86
Diplasma vitrea, 200
discoides, Unio, 245
discus, Unio, 82
Dyomina, 89
diusans, Unio, 153
Distribution of Mussels in Ohio, 21
dolabraformis, Unio, 140
donaciformis, Amygdaloniae, 310
donaciformis, Margaritana, 310
donaciformis, Margaron (Unio), 310
donaciformis, Plagiola, 310
donaciformis, Plagiola (Amygdaloniae), 310
donaciformis, Truncilla, 12, 120, 310–13, 315, 317
donaciformis, Unio, 310
donacopis, Unio, 326
doncheilus, Margarita (Unio), 282
doncheilus, Margaron (Unio), 282
doncheilus, Unio, 282
Dreissenidae, 3, 17
Dreissenia bugensis, 3, 17–18
Dreissena polymorpha, 3, 17–18
Dromus, 70
dubia, Alasmidonta, 288
dubia, Anodonta, 288
duttonianus, Unio shepardianus forma, 182
Dysnomia, 89
Dysnomia flexuosa, 89
Dysnomia flexuosa levisi, 92
Dysnomia lewisii, 92
Dysnomia perobliqua, 99
Dysnomia perolatosa, 110
Dysnomia personata, 102
Dysnomia rangiana, 110
Dysnomia sulcata pectina, 95
Dysnomia sulcata perobliqua, 99
Dysnomia torulosa, 114
Dysnomia torulosa cincinnatiensis, 105
Dysnomia torulosa torulosa, 114
Dysnomia triquetra, 116
Dysnomia (Dysnomia flexuosa, 89
Dysnomia (Dysnomia lewisii, 92
Dysnomia (Plica) personata, 102
Dysnomia (Plica) torulosa, 110
Dysnomia (Plica) torulosa cincinnatiensis, 105
Dysnomia (Plica) torulosa rangiana, 110
Dysnomia (Scalenilla), 89
Dysnomia (Torulosa cincinnatiensis, 105
Dysnomia (Torulosa rangiana), 110
Dysnomia (Torulosa) torulosa, 110
Dysnomia (Truncillopsis), 89
Dysnomia (Truncillopsis) triquetra, 116
Dysnomia, 89
Effects of Habitat Modifications and Pollutants, 14–17
Effects of Introduced Bivalves, 17–18
Eggshell, 200
eighti, Unio, 191
eighti, Margaron (Unio), 191, 195
eighti, Unio, 191
Elasmogona, 162
Elasmogona, 162
electronis, Unio, 319
elegans, Amygdaloniae, 415
elegans, Margarita (Unio), 415
elegans, Margaron (Unio), 415
elegans, Plagiola, 415
elegans, Plagiola (Amygdaloniae), 415
elegans, Unio, 415
elegans, Unio truncatus var., 415
elegantopsis, Unio elegans var., 415
Elephantear, 80–84, 162
Elephantear, Pink, 80
Elktoe, 41–45
Elktoe, Northern, 41
eßiott, Unio, 54
Ellipsaria, 72
Ellipsaria fasciolaris, 251
Ellipsaria lineolata, 73–76, 284
ellipsaria, Obliquaria (Ellipsaria), 72, 73
Ellipse, 358–61
ellipsformis, Actinonaias, 361
ellipsformis, Lamelilus (Venusta), 359
ellipsformis, Liguonia, 359
ellipsformis, Unio, 358, 359
ellipsformis, Venustaconcha ellipsiformis, 358–61
eilips, Lamelilus, 200
ellips, Margarita (Unio), 200
ellips, Margaron (Unio), 200
ellips, Obovaria, 200
ellips, Obovaria (Pseudoon), 200
ellips, Unio, 200, 211
elliptia, Unio (Ammalalia), 222
Elliptia, 2, 76, 196
Elliptio complanata, 8, 77–80
Elliptio crassidens, 67, 80–84, 89
Elliptio crassidens incrassata, 84
Elliptio decivis, 358
Elliptio dilatata, 14, 77, 80, 84–89, 135, 186, 190, 358
Elliptio dilatata form sternii, 86
Elliptio dilatata var. sternii, 86
Elliptio dilatat var. subgibbosa, 86
Elliptio dilatatus, 67
Elliptio gibbosus, 86
Elliptio nigricans, 82
Elliptio pachyodon, 82
Elliptio (Elliptio) crassidens crassidens, 82
Elliptio (Elliptio) crassidens var. crassidens, 82
Elliptio (Elliptio) crassidens var. danielii, 82
Elliptio (Elliptio) dilatatus, 86
Fusconaia undata, 122
Fusconaia kirtlandiana, 130
Fusconaia rubiginosa, 126
Fusconaia subrotunda, 130
Fusconaia subrotunda kirtlandiana, 130
Fusconaia subrotunda leucorhina, 132
Fusconaia subrotunda var. leucogona, 130
Fusconaia solida, 238
Fusconaia undata, 126

G

gametogenesis, 8

generii, Anodonta, 265

Gaspé Floater, 254

geometricus, Unio, 317

geometricus, Unio declivis, 319

Giant Floater, 258–65

gibba, Lampris limatimenta, 36

gibba, Nephronaias limatimenta, 36

gibbosa, Ambloina, 114

gibbosa, Mya, 86

gibbosus, Elliptio, 86

gibbosus, Margarita (Unio), 86

gibbosus, Margaron (Unio), 86

gibbosus, Unio, 86

gibbus, Lampris limatimenta var., 36, 38, 40

gigantea, Ambloina, 193

gigantea, Ambloina (Melanoides), 193

gigantea, Anodon, 261

gigantea, Anodonta, 260

gigantea, Anodonta grandis, 261

gigantea, Anodonta grandis var., 261

gigantea, Margarita (Anodonta), 260

gigantea, Margaron (Anodonta), 260

gigantea, Melanoides, 193

gigantea, Melanoides gigantea, 193

gigantea, Anodon, 261

gigantea, Unio, 49, 191

gigas, Complanatia, 162, 164

gigas, Megadon, 162, 164

gigas, Unio, 162, 306

glaciator, 4, 21

glans, Carunculina, 299

glans, Carunculina glans, 299

glans, Euryinia (Carunculina), 299

glans, Lampris, 299

glans, Lampris (Carunculina), 299

glans, Margarita (Unio), 299

glans, Margaron (Unio), 299

glans, Toxolasma, 299

glans, Toxolasma glans, 299

glans, Toxolasma livida, 299

glans, Unio, 299

glassyback, 200

Glebula, 344

Glebula rotundata, 344–46

Glebula suborbiculata, 346

glebula, Unio, 344

globosa, Anodonta, 254

globosa, Symphynota, 352

globula, Obvaria subrotunda, 209

globula, Quadrula subrotunda, 209

glocidia, 8, 10–12

Glocidium, 8, 54

Glocidium parasiticum, 8, 54

Glossary, 369–72

Golf Stick, 204

Gonambus, 162

gouldia, Anodonta, 238

gouldia, Lampris, 334

gouldia, Margaron (Unio), 334

gouldia, Unio, 334

gracilis, Lampris, 175

gracilis, Lampris (Proteria), 175

gracilis, Margarita (Unio), 175

gracilis, Metaptera, 175

gracilis, Mya, 175

gracilis, Paraperta, 175

gracilis, Paraperta, 175

gracilis, Symphynota, 175

gracilis, Unio, 175

gracilis, Unio fragilis var., 175

grandensis, Anodonta, 346

grandis, Anodon, 260

grandis, Anodonta, 56, 258

grandis, Anodonta grandis, 262

grandis, Anodonta (Anodonta), 262

grandis, Anodonta (Pyganodon), 262

grandis, Margarita (Anodonta), 260

grandis, Pyganodon grandis, 10, 58, 61, 256, 258–65, 321, 346, 356

granifera, Cyclonaias, 65

granifera, Cyclonaias tuberculata, 65

granifera, Quadrula (Cyclonaias) tuberculata, 65

granifera, Quadrula (Rotundaria), 65

granifera, Rotundaria, 58, 65

grenferus, Margarita (Unio), 65

grenferus, Margaron (Unio), 65

grenferus, Unio, 65

Green Creek Shell, 43

Green Floater, 347–49

H

Hackle-back, 170

hallenbeckii, Anodonta, 265

Hamista, 2

harptethensis, Anodonta, 261

harptethensis, Anodonta, 260

harptethensis, Margaron (Anodonta), 260

Heelsplitter, Creek, 166–70

Heelsplitter, Fragile, 245

Heelsplitter, Pink, 241–45

Heelsplitter, White, 162–66

Hemilastona, 132, 288

Hemilastona ampullata, 288, 290

Hemilastona delhiscens, 132

Hemilastona latas, 132

Hemilastona oriens, 132

Hemionotus, 40
Hickorynut, 200–203

Hickorynut, Round, 207–11

Higher Classification of North American Freshwater Mussels, 1

Hildreth, Samuel, 1

hildrethi, Unio, 132

hildrethianus, Baphia, 290

hildrethianus, Margarita (Unio), 288

hildrethianus, Margarone (Unio), 288

hildrethianus, Strophitus, 288

hildrethianus, Unio, 288

hippopaeta, Ambelma plicata, 51

hippopaeta, Unio plicata var., 51

hippopaeta, Margarone (Unio), 49

hippopaeta, Unio, 51

hippopoea, Quadrula plicata, 51

hippopoea, Quadrula undulata, 51

hippopoea, Quadrula undulata form, 51

hippopoea, Unio, 49

hockingensis, Anodonta, 261

Holarctic Pearlshell, 338

holstonia, Unio, 162

horda, Anodan, 321

horda, Anodone (Lastena) ohiensis, 323

hordaeus, Anodan, 323

Horny-back, 196

host specificity, 12

hoightedensis, Anodan, 261

hoightedensis, Anodonta, 261

Human Utilization of Freshwater Mussels, 4

hyalins, Margarone (Unio), 347

hyalins, Unio, 347

hydians, Unio, 153

I

illius, Unio zigzag var., 310

imbecillus, Anodan, 321

imbecillus, Anodane (Utterbackia), 323

imbecillus, Anodan, 323

imbecillus, Anodonta, 321

imbecillus, Margarone (Anodonta), 321

imbecillus, Utterbackia, 8, 10, 58, 61, 321–26, 349

imbricata, Anodan, 261

imbricata, Anodone, 261

immunity, acquired, 12

immunity, natural, 12

imperitus, Unio, 251

impoundments, 14–15

incerta, Anodan, 321

incerta, Margarone (Anodonta), 321

incertopsis, Anodonta ferrugacuana var., 59

incertus, Anodan, 323

increasata, Elliptio crassidens, 84

inflata, Mya, 153

inflata, Symphynota, 153

inflatus, Lampslis, 153

inflatus, Unio, 153

inornata, Anodan, 261

intercedens, Margarone (Unio), 334

intercedens, Unio, 334

interduus, Unio plenus var., 233

interrupta, Obliquaria (Ellipsaria) fasciolaris var., 249

interrupta, Obliquaria (Plagiola), 72, 249

Introduction, 1

iris, Eurytia, 330

iris, Eurytia (Micromya), 330

iris, Lampslis, 330

iris, Margarone (Unio), 330

iris, Margarone (Unio), 330

iris, Micromya, 330

iris, Unio, 330

iris, Villosa, 153, 305, 329, 330–33, 337, 361

irrorata, Unio, 68

irrorata, Unio (Theliderma), 68

irroratus, Cyprogeta, 68

irroratus, Margarone (Unio), 68

irroratus, Maragone (Unio), 68

irroratus, Unio, 68

irroratus, Unio stegarius var., 68

J

jacintoensis, Arcidens confragosa, 343

jamesianus, Margarone (Unio), 319

jamesianus, Unio, 164

jugosus, 40

K

katherinae, Symphynota (Pterosyna), 164

katherinae, Unio, 164

kennicottii, Anodonta, 261

Key to Species in This Book, 363–68

Kidneyshell, 249–54

Kirtland, Jared, 1

kirklandiana, Unio, 130

kirklandiana, Fuscoaia, 130

kirklandiana, Fuscoaia subrotunda, 130

kirklandiana, Fuscoaia, 130

kirklandiana, Margarone (Unio), 130

kirklandiana, Margarone (Unio), 130

kirklandiana, Quadrula, 130

kirklandiana, Quadrula (Fuscoaia), 130

kirklandiana, Unio, 130

Knobbed Rifleshelle, 112

Knobbed Rockshell, 273

L

lachrymosa, Quadrula, 286

lachrymosa, Quadrula (Theliderma), 286

lachrymosa, Unio, 265

lacrymosus, Margarone (Unio), 286

lacrymosus, Margarone (Unio), 286

lacustris, Anodan, 354

lacustris, Anodanta, 354

lacustris, Leptodea fragilis, 175

lacustris, Margarone (Anodonta), 354

lacustris, Paraptera gracilis, 175

lacustris, Ptychobranchus (Ptychobranchus) fasciolaris, 251

lacustris, Pygannon, 258, 354–56

lacustris, Strophitus rugosus, 295

lacustris, Truncilla truncata var., 295

laevigatus, Unio, 207

laevissima, Lampslis (Proptera), 245

laevissima, Leptoea, 245

laevissima, Proptera, 245

laevissima, Symphynota, 245

laevissima, Unio, 245

laevissimus, Margarone (Unio), 245

laevissimus, Margarone (Unio), 245

laevissimus, Unio, 245

Ladyfingers, 84

Ladyfingers, Eastern, 77

Ladyfingers, Flat, 77

Lake Floater, 354–56

Lamarck, 1

Lamp Mussel, Wavy-rayed, 145

Lampslis, 2, 10, 84, 136, 182

Lampslis abruptus, 136–40, 145, 149, 207

Lampslis alata, 241

Lampslis alatius, 241

Lampslis amygdalum, 326

Lampslis anodontoides, 159, 305

Lampslis anodontoides anodontoides, 159

Lampslis anodontoides fallaciosa, 159

Lampslis anodontoides floridensis, 159

Lampslis anodontoides form anodontoides, 159

Lampslis anodontoides form fallaciosa, 159

Lampslis anodontoides var. floridensis, 159

Lampslis apicitus, 334

Lampslis batchleyi, 179

Lampslis capax, 352

Lampslis cardia, 140

Lampslis cardium, 8, 140–45, 149, 151, 153, 157, 177, 354

Lampslis concestrator, 334

Lampslis ellipsis, 200

Lampslis fallaciosa, 159

Lampslis fasciata opalina, 330

Lampslis fasciola, 8, 11, 138, 145–49, 157

Lampslis glans, 299

Lampslis gouldii, 334

Lampslis gracilis, 175
margaron (unio) glans, 299
margaron (unio) gouldii, 334
margaron (unio) gracilis, 175
margaron (unio) graniferus, 65
margaron (unio) hildrethianus, 288
margaron (unio) hippocrepis, 45
margaron (unio) iylealis, 347
margaron (unio) intercedens, 334
margaron (unio) iris, 330
margaron (unio) irroratus, 68
margaron (unio) jamesianus, 319
margaron (unio) kirtlandianus, 130
margaron (unio) lacrymosus, 286
margaron (unio) lacvissimus, 245
margaron (unio) leibi, 209
margaron (unio) lens, 207
margaron (unio) lensosus, 334
margaron (unio) ligamentinus, 36
margaron (unio) linecumii, 51
margaron (unio) luteolus, 153
margaron (unio) manubius, 319
margaron (unio) metaneurus, 273
margaron (unio) mississippiensis, 350
margaron (unio) moestus, 299
margaron (unio) monodonta, 27
margaron (unio) multiplicatus, 191
margaron (unio) multiradiatus, 145
margaron (unio) mytiloides, 222
margaron (unio) nashvillensis, 350
margaron (unio) nashvillianus, 350
margaron (unio) nasutus, 183
margaron (unio) nigerrimus, 334
margaron (unio) novi‑eboraci, 330
margaron (unio) obliquus, 226
margaron (unio) occidentis, 140
margaron (unio) ovatus, 149
margaron (unio) parvus, 302
margaron (unio) patula, 222
margaron (unio) periradiatus, 145
margaron (unio) pertenuis, 347
margaron (unio) phaseolus, 251
margaron (unio) pilatus, 102
margaron (unio) plenus, 230
margaron (unio) plicatus, 45
margaron (unio) pratti, 334
margaron (unio) pressus, 168
margaron (unio) pustulatus, 278
margaron (unio) pustuloseus, 282
margaron (unio) pyramidatus, 233
margaron (unio) rangianus, 108
margaron (unio) rectus, 186
margaron (unio) retusus, 204
margaron (unio) rotundatus, 344
margaron (unio) rubiginosus, 126
margaron (unio) rutersvillensis, 350
margaron (unio) saxus, 334
margaron (unio) schoolcraftensis, 282
margaron (unio) schoolcraftii, 282
margaron (unio) securis, 73
margaron (unio) solidus, 238
margaron (unio) stonensis, 86
margaron (unio) subtenuis, 140
margaron (unio) subutundus, 130
margaron (unio) symmetricus, 356
margaron (unio) tappanianus, 347
margaron (unio) tenuissimus, 179
margaron (unio) tetralasmus, 317
margaron (unio) topekaensis, 350
margaron (unio) triangularis, 116
margaron (unio) trignus, 126
margaron (unio) tuberculatus, 306
margaron (unio) undulatus, 191
margaron (unio) varicosus, 213
margaron (unio) ventricosus, 140
margaron (unio) venustus, 359
margaron (unio) wardii, 273
margaron (unio) zigzag, 310
marginata, alasmidonta, 40, 41–45, 153, 162, 170, 173
marginata, alasmidonta (decurambis), 41
marginata, alasmodon, 41
marginat, alasmodon, 41
marginat, Anodonta, 256
marginat, Anodonta, 41
marrattiana, Anodonta, 261
marrattiana, Anodonta, 260
marrattiana, Margaron (anodontata), 260
marrattiana, Anodonta, 261
maccarthyana, Anodonta, 260
marginata, marginata, 350
marginata, Marginata (marginata), 41
marginata, Marginata, 41
marginata, Pyganodon cataracta, 254–58, 356
marginat, Unio, 41
marginat, Unio, 41
marginat, Anodonta, 256
marginat, Anodonta, 41
marrattiana, Anodonta, 261
marrattiana, Anodonta, 260
marrattiana, Margaron (anodontata), 260
marrattiana, Anodonta, 261
marrattiana, Anodonta, 260
marginata, Marginata (marginata), 41
marginata, Marginata, 41
meadus, 162
meadus gigas, 162, 164
Megalodonias, 2, 191, 309, 344
Megalodonias beykineana, 195
Megalodonias gigantea, 193
Megalodonias gigantea gigantea, 193
Megalodonias hero, 193
Megalodonias nusa, 53, 191–96
Megalodonias triangularis, 193
Megaperta megaperta, 241
megaperta, Megaperta, 241
metamorphosis, 12
metanoea, Unio, 273
metanoea, Margarita (unio), 273
metanoea, Quadraula, 273
metanoea, Unio, 273
metanoea, Unio, 273
metanoea, Obliquaria (Quadraula), 273
metanoea, Quadraula, 265, 269, 273–76, 288, 305
metanoea, Quadraula (orthonymus), 273
metanoea, Quadraula (Quadraula), 273
metanoea, Unio (Theilderma), 273
metanoea, orthonymus metanoea, 273
Metaperta, 241
Metaperta alata, 241
Metaperta fragilis, 175
Metaperta gracilis, 175
Metaperta leptodon, 179
Metaperta obtusus, 245
Metaperta obovata, 245
meteniver, Unio, 273
micans, Anodonta, 261
micans, Anodonta, 261
micans, Margaron (anodontata), 261
micans, Anodonta, 261
micans, Anodonta, 261
micans, Margaron (anodontata), 261
Microconchylea compressa, 168
Micromya, 326
Micromya fabale, 326
Micromya fabalis, 326
Micromya iris, 330
Micromya lapillus, 326
minor, Alasmidonta (pressodonta), 45
minor, Baphia, 45
minor, Margaritana, 45
minor, Margaron (Margaritana), 45
minor, Strophitus, 45
minor, Unio margaritifer var., 338
miurus, Unio castus, 299
mussissippiensis, Pleurobema cocinea var., 238
mussissippiensis, Margaron (unio), 350
mussissippiensis, Unio, 350
mussourniensis, Pleurobema, 238
mussourniensis, Quadraula (obliquaria), 238
modesta, Anodon, 59
modesta, Anodonta, 59
modesta, Anodonta (anodontoides), 59
modesta, Margaron (anodontata), 59
modestus, Anodonta (anodontoides), 59
modestus, Anodonta (anodontoides), 61
modestus, Anodonta (anodontoides), 61
moesta, Carunculina, 299
moesta, Carunculina glans, 299
moesta, Lampsilis, 299
moesta, Lampsilis (carunculina), 299
moesta, Margaron (unio), 299
moesta, Unio, 299
monkey face, 273–76
monodonta, 40
monodonta undulata, 40
monodonta, Alasmidonta, 27
monodonta, Cumberlandia, 8, 27–31, 341
monodonta, Margaritana, 27
monodonta, Margaritana, 28
monodonta, Margaritifera, 27
monodonta, Margaron (unio), 27
monodonta, Unio, 27
monodonta, Margaritana (unio), 27
morocana, Margaritifera, 338
mountain creek shell, 347
mucket, 32–36, 36–40
mucket, Ohio, 136
mucket, Pink, 136–40
mucket, Square, 136
mucket, Yellow, 153
mucronatus, Mya, 86
mucronatus, Unio, 86
Mudpuppy, 10
Mule’s Ear, 27
multiplicatus, Margarita (Unio), 191
mutliciplicatus, Margaron (Unio), 191
multicliplicatus, Unio, 191
multicliplicatus, Unio heros var., 191
multiradiata, Lampsislis, 145
multiradiata, Lampsislis (Lampsislis), 145
multiradiatius, Lampsislis (Lampsislis), 145
multiradiatius, Margarita (Unio), 145
multiradiatius, Margaron (Unio), 145
multi-radiatius, Unio, 145
muskrats, 12–13
mussels as human food, 4–5
Mussel-Host Associations, 13
Mya, 1
Mya alata, 32
Mya arcuata, 338
Mya carinata, 32
Mya complanata, 77, 164
Mya cornuta, 196
Mya crassa, 36
Mya cuneata, 82
Mya cylindricus, 266
Mya gibbosa, 86
Mya gracilis, 86
Mya inflata, 153
Mya margaritifera, 338
Mya mucronatus, 86
Mya nasuta, 185
Mya nodosus, 273
Mya ovata, 149
Mya parva, 302
Mya pensylvanica, 292
Mya plana, 175
Mya plicata, 49
Mya praecoxa, 186
Mya rotunda, 207
Mya rugosa, 172
Mya rufilosa, 41
Mya sinuoides, 153
Mya triangularis, 116
Mya tuberculata, 306
Mya undulatula, 191
Mya ventricosa, 140
Mya verrucosa, 65
Myoeca alata, 241
Mytilidae, 6
mytilopsis, Margarita (Unio), 222
mytilopsis, Margaron (Unio), 222
mytiloideis, Pleurobema, 221, 222
mytiloideis, Unio, 122, 222, 226
mytiloideis, Unio, 122, 222, 233
Mytilus cygneus, 54
n
N
Naidea, 241
Narrow Pondshell, 349
nashvillianus, Margarita (Unio), 350
nashvillianus, Margaron (Unio), 350
nashvillensis, Margaron (Unio), 350
nasuta, Euryaia, 183
nasuta, Lampsislis, 183
nasuta, Ligumia, 183–86, 190, 352
nasuta, Mya, 183
nasuta, Unio, 84, 183
nasutus, Elliptio (Euryaia) nasutus, 86
nasutus, Margarita (Unio), 183
nasutus, Margaron (Unio), 183
nasutus, Unio, 86, 183
natural immunity, 12
naviformis, Unio, 266
Nayadina venusta, 262
Nectaris maculosus, 10
Nephroneiias, 32
Nephroneiias ligamentina, 32, 36
Nephroneiias ligamentina gibba, 36
Nephroneiias perax, 32
Nephroneiias sapotolensis, 32
nervosa, Lampsislis, 330
nervosa, Ligumia, 330
nervosa, Megalotates, 53, 191–96
nervosa, Plagiola, 310
nervosa, Unio, 310
nervosus, Unio (Leptodea), 191
nervosus, Unio, 310
niger, Elliptio, 82
niger, Elliptio (Elliptio), 82
niger, Unio, 82
nigerrima, Lampsislis, 334
nigerrimus, Lampsislis, 334
nigerrimus, Margarita (Unio), 334
nigerrimus, Unio, 334
nigrica, Unio, 76
nigra, Unio (Elliptio), 76, 82
nilssonii, Anodonta, 260
nodosus, Mya, 273
nodosus, Quadrula, 273
nodusus, Unio, 273
nudulata, Obligaria (Quadrule), 276, 278
nodulata, Quadrula, 276–80, 284
nodulata, Quadrula (Bullata), 278
nodulata, Quadrula (Pustulosa), 278
nodulata, Unio, 278
nodulosus, Unio, 280
Notea, 241
Nomenclatorial and Systematic Concepts, 2–3
Northern Arc Shell, 116
Northern Clubshell, 222
Northern Elk toe, 41
Northern Leafshell, 89
Northern Riflesheb, 108–12
Nouvelle école, 3
novi-eboraci, Euryaia (Microsynia) iris, 330
novi-eboraci, Lampsislis, 330
novi-eboraci, Ligumia iris, 330
novi-eboraci, Margarita (Unio), 330
novi-eboraci, Margaron (Unio), 330
novi-eboraci, Micromya iris, 330
nuda, Lasmigona costata, 172
O
obesa, Quadrula, 306
obesa, Trigonia verrucosa var., 306
Oblicaria, 196
obliqua, Margarita (Unio), 226
obliqua, Quadrula, 226, 230
obliqua, Quadrula (Fusconaia), 126
obliqua, Unio, 122, 124, 226, 233
Obligaria, 72, 196, 233
Obligaria attenuata, 183
Obligaria cyphya, 211
Obligaria flavia, 120
Obligaria obovata, 200
Obligaria reflexa, 108, 196–200, 276, 280
Obligaria reflexa var. conradi, 196
Obligaria rubra, 233
Obligaria sintoxia, 130
Obligaria simuta, 77, 84
Obligaria violacea, 86
Obligaria (Aximedia) venus, 82
Obligaria (Ellipsaria), 72
Obligaria (Ellipsaria) ellipsaria, 72, 73
Obligaria (Ellipsaria) fasciolaris, 249
Obligaria (Ellipsaria) fasciolaris var. fusata, 249
Obligaria (Ellipsaria) fasciolaris var. interrupta, 249
Obligaria (Ellipsaria) fasciolaris var. longa, 249
Obligaria (Ellipsaria) fasciolaris var. obliterata, 249
Obligaria (Ellipsaria) verrucosa, 306
Obligaria (Plagiola) depressa, 72, 73
Obligaria (Plagiola) interrupta, 72, 249
Obligaria (Plagiola) lineolata, 72, 73
Obligaria (Quadrule), 265
Obligaria (Quadrule) bullata, 280
Obligaria (Quadrule) cyphya, 218
Obligaria (Quadrule) flavia, 124
Obligaria (Quadrule) flexuosa, 63, 89
Obligaria (Quadrule) flexuosa var. bullata, 89, 280
Obligaria (Quadrule) metanevra, 273
Obligaria (Quadrule) nodulata, 276, 278
Obligaria (Quadrule) quadrula, 284, 286
Obligaria (Quadrule) reflexa, 196
Obligaria (Quadrule) reussa, 280
Obligaria (Rotundaria), 200
Obligaria (Rotundaria) obliquata, 63
Obligaria (Rotundaria) subrotunda, 200, 207
Obligaria (Rotundaria) subrotunda var. maculata, 128
Obligaria (Rotundaria) tuberculata, 65
Obligaria (Scalenaaria), 222
Obligaria (Scalenaaria) obliquata, 95
Obligaria (Scalenaaria) scalenia, 222
Obligaria (Sintoxia), 222
pavonia, Anodonta, 294
pavonia, Margarita (Anodonta), 294
pavonia, Margarita (Anodonta), 294
pavonius, Spathobasus, 294
pavonius, Spathobasus edentulus var., 294
pavonius, Spathobasus ragusus, 295
pealei, Unio, 200
Pearl Button Industry, 5–6
Pearl Rush, 5
pears, 4
Pearlshell, Cumberland, 27
Pearlshell, Eastern, 338–41
Pearlshell, Holartic, 338
Pearlshell, Old World, 338
Pearlshell, Round, 344–46
pearleins, Unio, 49
pearlii, Unio, 200
Pearlymussel, Cracking, 132–35
pectitus, Dostonia sulcata, 95
pectitus, Unio, 95
pectora, Actinonaias, 34, 38, 190
peggyae, Utterbackia, 321
pellurica, Lampsilis, 326
pentinsularis, Utterbackia, 321
pennsylvanica, Anodonta, 292, 295
pennsylvanica, Spathobasus undulatus, 295
pennsylvanica, Spathobasus (Spathobasus) undulatus, 295
pennsylvanica, Anodonta, 292
pennsylvanica, Mya, 292
pepiniensis, Lampsilis siliquoidea, 154
pepiniensis, Lasigmia costata, 172
pepiniensis, Spathobasus ragosus, 295
pepiniana, Anodonta, 261
pepiniana, Anodonta, 260
pepiniana, Anodonta (Pyganodon) grandis, 262
pepiniana, Margarita (Anodonta), 260
pepiniana, Margarita (Anodonta), 260
pepiniapus, Anodonta, 260
peridix, Neophreinaias, 32
performans, Unio compressissimus var., 251
perigobius, Unio triangularis var., 116
perigobius, Lampsilis venricosa var., 140
perlensis, Unio, 51
pernodosus, Quadrula pustulosa, 282
pernodosus, Quadrula (Pustulosa) pustulosa, 282
pernodosus, Quadrula (Quadrula) pustulosa var., 282
pernodosus, Unio, 282
perobliqua, Dostonia, 99
perobliqua, Epioblasma obliquata, 99–102
perobliquus, Dostonia sulcata, 99
perobliquus, Unio, 99, 108
perobliquus, Unio gibbosus, 99
peroalas, Unio, 145
perplexus, Unio, 110, 124
perplicata, Amblyema plicata, 54
perradiatus, Margarita (Unio), 145
perradiatus, Unio, 145
personata, Dostonia, 102
personata, Dostonia (Pilea), 102
personata, Epioblasma, 102–5
personata, Plagiola (Pilea), 102
personata, Scalenaaria, 102
personata, Truncilla (Pilea), 102
personatus, Margarita (Unio), 102
personatus, Margarita (Unio), 102
personatus, Unio, 102, 128
pertenuis, Unio, 347
pertenuis, Margarita (Unio), 347
pertenuis, Unio, 302, 347
perviviana, Cremodonta perviviana, 51
perviviana, Quadrula, 51
pervivianus, Ambloea, 51
pervivianus, Amblema rariplacata, 51
pervivianus, Unio, 49
phalena, Anodonta, 323
phaseolus, Margarita (Unio), 251
phaseolus, Margarita (Unio), 251
phaseolus, Psychobranus, 251
phaseolus, Unio, 88, 98, 249, 252
Philipsson, 1
phillipsii, Epioblasma, 106
phillipsii, Epioblasma, 105–8
phillipsii, Unio, 105
Pigtoe, 124
Pigtoe, Big River, 226
Pigtoe, Common, 226
Pigtoe, Flats, 236
Pigtoe, Full, 230
Pigtoe, Ohio, 226–30
Pigtoe, Ohio River, 226
Pigtoe, Pink, 233
Pigtoe, Pyramid, 233–36
Pigtoe, Ridged, 230
Pigtoe, River, 226
Pigtoe, Rough, 230–33
Pigtoe, Round, 236–41
Pigtoe, Solid, 236
Pigtoe, Spotted, 128
Pigtoe, Wabash, 124–28
Pigtoe, Warty, 280
Pigtoe, Welled, 211
pilaris, Unio, 126
pilaeus, Margarita (Unio), 102
pilaeus, Margarita (Unio), 102
pilaeus, Unio, 102
plieshy, Amblema plicata, 51
plieshy, Quadrula undulata var., 51
plieshy, Unio, 51
Pimpleback, 280–84
Pimpleback, Orangefoot, 215–18
Pimpleback, Purple, 63
Pimpleback, Round, 280
Pimpleback, Smooth, 280
Pimpleback, White, 280
Pimpleback, Winged, 276
Pink Elephantear, 80
Pink Heelsplitter, 241–45
Pink Mucket, 136–40
Pink Papershell, 245–49
Pink Pigtoe, 233
Pistolgrip, 306–10
Plagiola, 72, 249
Plagiola donaciformis, 310
Plagiola elegans, 315
Plagiola fasciolaris, 249
Plagiola lineolata, 73
Plagiola nervosa, 310
Plagiola secaris, 73, 284
Plagiola torulosa, 102
Plagiola triqueta, 116
Plagiola truncata, 315
Plagiola (Amygdalinae) donaciformis, 310
Plagiola (Amygdalinae) elegans, 315
Plagiola (Epioblasma) flexuosa, 89, 92
Plagiola (Pilea) obliquata, 95, 99
Plagiola (Pilea) personata, 102
Plagiola (Torulosa) torulosa, 105, 110, 114
Plagiola (Truncillopsis) triqueta, 116
Plagioplevis, 72
Plagioplevis secaris, 73
Plain Pocketbook, 140–45
plana, Anodonta, 260
plana, Anodonta grandis, 262
plana, Margarita (Anodonta), 260
plana, Margarita (Anodonta), 260
plana, Mya, 175
planulata, Unio, 251
planulatus, Unio, 249
planus, Unio, 175
planus, Unio leptodon var., 175
Plateiinae, 162
pleasi, Venustochona elliptiformis, 361
plebius, Symphysotis (Symphysotis) compressa var., 168
plebius, Unio compressus var., 166
Plectomerus costatus, 49
Plectomerus plicatus, 49
plena, Fascionaias, 230
plena, Quadrula, 230
plena, Quadrula (Obliquata) cordata, 230
plena, Quadrula (Obliquata) cordata var., 230
plenum, Pleuroboma, 226, 230–33
plenum, Pleuroboma cordatum var., 230
plenum, Pleuroboma obliquum var., 230
plenus, Margarita (Unio), 230
plenus, Unio, 230
Plethobasus, 72, 211
Plethobasus aescopus, 218
Plethobasus cicatrioides, 213
Plethobasus cicatricina, 213
Plethobasus cicatriosus, 211–15, 218, 221
Plethobasus cicatriosus form detectus, 213
Plethobasus compactus, 218
Plethobasus cooperianus, 65, 67, 215–18, 284
Plethobasus cyphus, 218
Plethobasus cyphus, 108, 211, 215, 218–221
Plethobasus cyphus compertus, 218
Plethobasus pachysteus, 213
Plethobasus striatus, 215
Pleuroboma, 2, 221
Pleuroboma aescopus, 211, 218
Pleurobema bournianum, 225
Pleurobema catillus, 238
Pleurobema catillus var. occinea, 238
Pleurobema catillus var. solida, 238
Pleurobema chattanoogense, 222
Pleurobema cicatricium, 213
Pleurobema cicatrioxis, 213
Pleurobema clava, 8, 221, 222-26
Pleurobema clava clava, 225
Pleurobema clava patulum, 225
Pleurobema coccineum, 238
Pleurobema coccineum forma solida, 238
Pleurobema coccineum pauperulum, 238
Pleurobema coccineum solida, 238
Pleurobema coccineum var. catillus, 238
Pleurobema coccineum var. mississippiensis, 238
Pleurobema conica, 211
Pleurobema cooperianus, 215
Pleurobema cordata, 226
Pleurobema cordatum, 14, 22, 105, 124, 128, 213, 226-30, 233, 236, 240
Pleurobema cordatum catillus, 238
Pleurobema cordatum coccineum, 238
Pleurobema cordatum cordatum, 226
Pleurobema cordatum form coccineum, 238
Pleurobema cordatum form pauperulum, 238
Pleurobema cordatum pauperula, 238
Pleurobema cordatum pauperulum, 238
Pleurobema cordatum pyramidalatum, 233
Pleurobema cordatum var. catillus, 238
Pleurobema cordatum var. coccineum, 238
Pleurobema cordatum var. plenum, 230
Pleurobema cordatum var. pyramidalatum, 233
Pleurobema conica, 82, 221, 222
Pleurobema dectisum, 222
Pleurobema flavus, 126
Pleurobema missouriensis, 238
Pleurobema mytiloides, 221, 222
Pleurobema mytiloides patulum, 222
Pleurobema obliquum, 226, 230
Pleurobema obliquum catillus, 238
Pleurobema obliquum coccineum, 238
Pleurobema obliquum cordatum, 226, 230
Pleurobema obliquum pauperulum, 238
Pleurobema obliquum rubrum, 233
Pleurobema obliquum var. plenum, 230
Pleurobema obvallis, 122
Pleurobema plenum, 226, 230-33
Pleurobema politus, 130
Pleurobema premorsa, 230
Pleurobema pyramidalatum, 233
Pleurobema ruber, 233
Pleurobema rubiginosus, 126
Pleurobema rubrum, 230, 233-36
Pleurobema sintoxia, 14, 128, 226, 230, 236-41
Pleurobema taitianum, 226
Pleurobema undatus, 126
Pleurobema (Plethobasus), 211
Pleurobema (Plethobasus) aequorus, 218
Pleurobema (Plethobasus) cicatriciosum, 213
Pleurobema (Plethobasus) compactus, 218
Pleurobema (Plethobasus) cyphium, 218
Pleurobeminae, 2
plicata, Amblooma, 13, 51
plicata, Amblooma plicata, 49-54, 195
plicata, Amblooma (Amblooma), 51
plicata, Anodonta, 59
plicata, Crenodonta, 51
plicata, Margaron (Anodonta), 59
plicata, Mya, 49
plicata, Quadrula, 51
plicata, Unio, 72, 240
plicata, Unio crassus, 49
plicata, Unio (Theliderma), 49
plicatus, Complanarius, 49
plicatus, Margaron (Unio), 49
plicatus, Margaron (Unio), 49
plicatus, Plectomerus, 49
plicatus, Unio, 49
Pocketbook, 149-53
Pocketbook, Fat, 352-54
Pocketbook, Fine-rayed, 145
Pocketbook, Plain, 140-45
Pocketbook, Rigid, 149
Pocketbook, Rock, 341-44
Pocketbook, Wavy-rayed, 145-49
politus, Pleurobema, 130
politus, Unio, 128
pollutants, 17
polyomphora, Dreisena, 3, 17-18
polyomphora, Unio, 82
ponderosa, Baristoa, 77
ponderosum, Alasmodon, 162
Pondhorn, 317-21
Pondhorn, Tapered, 356-58
Pondmussel, 349-52
Pondmussel, Eastern, 183-86
Pondshell, Long, 349
Pondshell, Narrow, 349
Pondshell, Paper, 321-26
Pondshell, Western, 349
porphyreus, Unio, 334
porrae, Unio, 319
Potamillus, 2, 12, 14, 179, 241, 284, 352
Potamillus alatus, 8, 67, 166, 241-45
Potamillus capax, 243, 352-54
Potamillus fasciolaris, 249
Potamillus olenisis, 132, 166, 175, 245-49
Potamillus purpuratus coloradoensis, 32
praelongia, Eulocynea, 186
praelonga, Mya, 186
praelongus, Unio, 186
Prairie Horn Shell, 317
Prairie Shell, 349
prasa, Quadrula pustulosa, 282
prasa, Quadrula (Bullata) pustulosa, 282
prasa, Quadrula (Pustulosa) pustulosa, 282
prasinus, Unio, 280, 281
prasinus, Unio bullatus var., 282
pratti, Unio, 334
pratti, Lampsilis, 334
pratti, Margaron (Unio), 334
pratti, Unio, 334
Prelimation, 12-13
Preface, ix
premorsa, Pleurobema, 230
premorsa, Unio, 280
pressa, Alasmodon, 168
Pressodonta, 40
pressus, Margaron (Unio), 168
pressus, Unio, 166
Prelasmodonta, 40
propeculatus, Unio, 95
propeculatus, Unio, 95
propeticus, Unio cylindricus var., 266
propeverutus, Unio, 86
Protera, 241, 247
Protera alata, 241
Protera capax, 352
Protera gracilis, 175
Protera laevissima, 245
Protera leptodon, 179
Pterosyna, 162
Pterosyna complanata, 164
Ptychobranchus, 249
Ptychobranchus fasciiculare, 251
Ptychobranchus fasciolare, 251
Ptychobranchus fasciolaris, 10, 72, 88, 98, 135, 249-54, 333
Ptychobranchus phaseolus, 251
Ptychobranchus phaseolus var. camelus, 251
Ptychobranchus (Ptychobranchus) fasciiculare, 251
Ptychobranchus (Ptychobranchus) fasciolare arquetum, 251
Ptychobranchus (Ptychobranchus) fasciolare longum, 251
Ptychobranchus (Ptychobranchus) fasciolaris lacustris, 251
Ptychobranchus (Subtentus), 249
Purple Catspaw, 95-99
Purple Lilliput, 299-302
Purple Pimpleback, 63
Purple Wartyback, 63-67
Purple, Little, 299
purpureus, Anodonta, 179
purpureus, Unio, 77
pusilla, Cyclonaias tuberculata, 65
pusilla, Quadrula granifera var., 65
pusilla, Quadrula (Cyclonaias) tuberculata, 65
pustulata, Quadrula, 278
pustulata, Quadrula (Quadrula), 278
pustulata, Unio (Theliderma), 306
pustulatus, Margaron (Unio), 278
pustulatus, Unio, 278
pustulatus, Unio nodulatus var., 278
pustulosa, Quadrula, 89, 105, 147, 215, 218, 265, 276, 278, 282
pustulosa, Quadrula (Bullata), 282
pustulosa, Quadrula (Pustulosa) pustulosa, 282
Index | 413
Quadrula fragosa, Quadrula (Quadrula), 282
Quadrula pustulosa, Unio, 265
Quadrula pustulosa, Margarita (Unio), 280
Quadrula pustulosa, Margaron (Unio), 280
Quadrula pustulosa, Unio, 280
Pyganodon, 54, 254, 292, 296, 354
Pyganodon catharacta, 256
Pyganodon catharacta catharacta, 256, 356
Pyganodon catharacta marginata, 254–58, 265, 356
Pyganodon grandis corpubenta, 265
Pyganodon grandis grandis, 10, 58, 61, 256, 258–65, 321, 324, 356
Pyganodon lacustris, 258, 354–56
Pyramid Pigtoe, 233–36
pyramidatum, Pleuroboma, 233
pyramidatum, Pleuroboma cordatum, 233
pyramidatum, Pleuroboma chordatum var., 233
pyramidatum, Quadrula, 233
pyramidatus, Margarita (Unio), 233
pyramidatus, Margaron (Unio), 233
pyramidatus, Unio, 233
pyramidatus, Unio mytiloides var., 233
Quadrula, 2, 84, 265, 306, 344
Quadrula asperata, 280
Quadrula biangulata, 286
Quadrula bullata, 89, 282
Quadrula bullata, 282
Quadrula cactiascos, 213
Quadrula coccinea, 238
Quadrula coccinea var. pampelula, 238
Quadrula coccinea var. pampelula, 238
Quadrula coccinea, 238
Quadrula cooperiana, 215
Quadrula cooperianus, 215
Quadrula cordata, 230
Quadrula coustiana, 32
Quadrula cylindrica, 266, 276, 309
Quadrula cylindrica cylindrica, 266–69
Quadrula cylindrica striigilata, 269
Quadrula cyphius, 218
Quadrula ehena, 84, 122, 128
Quadrula fragosa, 269–73, 276, 280, 288
Quadrula fragosa, 271
Quadrula granifera var. pustula, 65
Quadrula heros, 191
Quadrula kirtlandiana, 130
Quadrula lachrymosa, 286
Quadrula metanever, 273
Quadrula metanevra, 265, 269, 273–76, 288, 305
Quadrula metanevra wardii, 273
Quadrula obliqua, 226, 230
Quadrula obvolata, 122
Quadrula nodusus, 273
Quadrula nodulata, 276–80, 284
Quadrula nodulatus, 278
Quadrula osea, 306
Quadrula parkeri, 306
Quadrula pereviana, 51
Quadrula plena, 230
Quadrula plicata, 51
Quadrula plicata hippocpea, 51
Quadrula pustulata, 278
Quadrula pustulosa, 89, 105, 147, 215, 218, 265, 276, 278, 282
Quadrula pustulosa asperata, 282
Quadrula pustulosa pernodosa, 282
Quadrula pustulosa prasina, 282
Quadrula pustulosa pustulosa, 67, 72, 280–84
Quadrula pustulosa schoolcraftensis, 282
Quadrula pustulosa var. schoolcraftensis, 282
Quadrula pyramidatum, 233
Quadrula quadrula, 265, 271, 276, 280, 284–88
Quadrula quadrula contraryensis, 286
Quadrula quadrula contraryensis, 286
Quadrula quadrula fragosa, 271
Quadrula rariplicata, 51
Quadrula reflexa, 196
Quadrula rubiginosa, 126
Quadrula rubra, 233
Quadrula rugosa, 271
Quadrula solida, 124, 128, 238
Quadrula striata, 211
Quadrula striata striata, 215
Quadrula subrotunda, 130
Quadrula subrotunda globula, 209
Quadrula trigema, 124, 126, 229
Quadrula trigonosa, 306
Quadrula triumphans, 191
Quadrula tuberculata, 230
Quadrula undulata, 191
Quadrula undulata form hippocpea, 51
Quadrula undulata hippocpea, 51
Quadrula undulata var. pilshyri, 51
Quadrula undulata var. quintiaratii, 51
Quadrula verrucosa, 306
Quadrula verrucosus, 65
Quadrula obliquaria (Quadrula), 284, 286
Quadrula, Quadrula, 265, 271, 276, 280, 284–88
Quadrula, Quadrula (Quadrula), 286
Quadrula, Quadrula (Quadrula) quadrula, 286
Quadrula (Bullata), 265
Quadrula (Bullata) nodulata, 278
Quadrula (Bullata) pustulosa, 282
Quadrula (Bullata) pustulosa asperata, 282
Quadrula (Bullata) pustulosa prasina, 282
Quadrula (Cyclonaias) tuberculata, 65
Quadrula (Cyclonaias) tuberculata granifera, 65
Quadrula (Cyclonaias) tuberculata pusilla, 65
Quadrula (Cyclonaias) tuberculata utterbackiana, 65
Quadrula (Fusconaia), 120
Quadrula (Fusconaia) coccinea var. magnalacustris, 238
Quadrula (Fusconaia) kirtlandiana, 130
Quadrula (Fusconaia) obliqua, 126
Quadrula (Fusconaia) rubiginosa, 126
Quadrula (Fusconaia) solidia, 238
Quadrula (Fusconaia) subrotunda, 130
Quadrula (Fusconaia) trigona, 126
Quadrula (Fusconaia) undata, 126
Quadrula (Fusconaia), 120
Quadrula (Fusconaia) antrosa, 120
Quadrula (Fusconaia) flava, 126
Quadrula (Fusconaia) undata, 126
Quadrula (Fusconaia) undata selecta, 126
Quadrula (Fusconaia) undata trigona, 126
Quadrula (Fusconaia) undata trigonoides, 126
Quadrula (Luteacarna), 211
Quadrula (Luteacarna) striata, 215
Quadrula (Obliquata) catillius, 238
Quadrula (Obliquata) coccinea, 238
Quadrula (Obliquata) coccinea magnalacustris, 238
Quadrula (Obliquata) coccinea var. cuneus, 238
Quadrula (Obliquata) cordata, 226
Quadrula (Obliquata) cordata cordata, 226
Quadrula (Obliquata) cordata plena, 230
Quadrula (Obliquata) cordata var. plena, 230
Quadrula (Obliquata) missouriensis, 238
Quadrula (Obliquata) obliqua, 233
Quadrula (Orthonymus) metanevra, 273
Quadrula (Orthonymus) metanevra wardii, 273
Quadrula (Pustulosa) nodulata, 278
Quadrula (Pustulosa) pustulosa pernodosa, 282
Quadrula (Pustulosa) pustulosa prasina, 282
Quadrula (Pustulosa) pustulosa pustulosa, 282
Quadrula (Quadrula) clyndrica, 266
Quadrula (Quadrula) fragosa, 271
Quadrula (Quadrula) metanevra, 273
Quadrula (Quadrula) metaneva var. wardii, 273
Quadrula (Quadrula) pustulata, 278
Quadrula (Quadrula) pustulosa, 282
Quadrula (Quadrula) pustulosa var. pernodosa, 282
Quadrula (Quadrula) quadrula, 286
Quadrula (Quadrula) quadrula, 286
Quadrula (Quadrula) quadrula conjugans, 306
Quadrula (Quadrula) quadrula fragosa, 271
Quadrula (Quadrula) quadrula quadrula, 286
Quadrula (Quadrula) quadrula var. bull- ecki, 286
Quadraula (Rotundaria) granifera, 65
Quadraula (Rotundaria) tuberculata, 65
Quadraula (Sintexia) sintexia, 236
Quadraula (Striata), 211
Quadraula (Theidlerma) lachrymosa, 286
Quadraula (Theidlerma) lachrymosa var. lunulatus, 286
Quadraula (Trigonia) verrucosa, 306
quadruitis, Unio, 286
Queen, 341
Questionable and Potential Ohio Occurrences, 338–61
Quincuncina, 2
quintardi, Amblema perplicata, 51
quintardi, Amblema plicata, 51
quintardi, Amblema perplicata, 51
quintardi, Amblema undulata var., 51
quintardi, Unio, 51

R
Rabbitsfoot, 266–69
radiata, Amblema gibbosa var., 114
radiata, Lampsilis radiata, 154
radiata, Lasmigona viridis var., 45
radiata, Odetella, 132
radiatus, Unionpis, 40
rafnisquescanus, Actinonaias, 36
Rainbow, 330–33
Rainbow Shell, 330
rangiana, Dynomia, 110
rangiana, Dynomia perplicia, 110
rangiana, Dynomia (Pilea) torulosa, 110
rangiana, Dynomia (Torusula), 110
rangiana, Dynomia (Torulus) 110
rangiana, Epiploasma, 110
rangiana, Epioblastus torulosa, 98, 99, 108–12, 114, 116, 124
rangiana, Truncilla, 110
rangiana, Trunricula perplicia, 110
rangiana, Truncilla (Pilea) perplicia var., 108
rangiana, Unio, 110
rangiansus, Margaron (Unio), 108
rangiansus, Margaronia (Unio), 108
rangiansus, Unio, 108
rarplicita, Amblema, 51
rarplicita, Quadruula, 51
rari-plicata, Unio, 49
Rayed Bean, 326–29
Records Used in This Book, 22
recta, Eurytina, 186, 188, 252
recta, Eurytina (Eurytina), 186
recta, Lampsilis, 186
recta, Lampsilis (Ligumia), 188
recta, Ligumia, 89, 186–91, 251, 252, 302
recta, Ligiunia recta, 188
recta, Ligumia (Ligumia), 188
recta, Unio, 182, 186
recta, Unio (Ligumia), 186
rectus, Lampsilis, 186
rectus, Margaronia (Unio), 186
rectus, Margaron (Unio), 186
rectus, Unio, 186

References, 373–97
reflexa, Obliquaria, 108, 196–200, 276, 280
reflexa, Obliquaria (Quadraula), 196
reflexa, Quadraula, 196
reflexa, Unio, 196
Regulation of Mussels in Ohio, 21–22
retna, Obliquaria (Quadraula), 280
retna, Obvovaria, 67, 136, 203, 204–7, 211
retna, Obvovaria (Obvovaria), 204
retna, Unio, 200, 204, 211, 280
retnas, Margaron (Unio), 204
retnus, Margaron (Unio), 204
rhombica, Alasmidonta, 294
rhombica, Margaronia, 294
Ribbed Creek Shell, 170
Ribbed Riffleshell, 170
Ridged Pocketbook, 149
Ridged Pigtoe, 230
ridibundus, Unio, 95
Riffleshell, Fluted, 170
Riffleshell, Knobbed, 112
Riffleshell, Northern, 108–12
Riffleshell, Ribbed, 170
Riffleshell, Tan, 108
Riffleshell, Tubercled, 105–8
Ring Pink, 204–7
Ringed Wartyback, 68
River Pigtoe, 226
rivularia, Unio, 317
Rock Pocketbook, 341–44
Rock Shell, 341
Rock Shell, Black, 191, 341
Rock Shell, Fine-rigged, 191
Rock Shell, Knobbed, 273
Rock Shell, Rough, 341
reissyi, Margaronia, 340
reissyi, Unio, 338
roesia, Obovaria cordatum var., 226
rostra, Unio, 183
rotunda, Mya, 207
Rotundaria, 63, 200
Rotundaria granifera, 65, 67
Rotundaria tuberculata, 63, 65
rotundata, Glebula, 344–46
rotundata, Unio, 344
rotundatus, Margaronia (Unio), 344
rotundatus, Margaron (Unio), 344
rotundatus, Unio, 344
Rough Pigtoe, 230–33
Rough Rocks, 341
Round Combshell, 102–5
Round Floater, 54
Round Hickorynut, 207–11
Round Pearlshell, 344–46
Round Pigtoe, 236
Round Pimbleback, 280
rubens, Unio, 236
rubra, Pleurobema, 233
rubra, Unio, 233
rubiginosa, Fusconaia, 124
rubiginosa, Fusconaia, 126
rubiginosa, Quadraula (Fusconaia), 126
rubiginosa, Unio, 126
rubiginusus, Margaronia (Unio), 126
rubiginusus, Margaron (Unio), 126
rubiginusus, Pleurobema, 126
rubiginusus, Quadraula, 126
rubiginusus, Unio, 124
rubiginusus, Unio trigones var., 124
rubra, Obliquaria, 233
rubra, Quadraula, 233
rubrum, Pleurobema, 230, 233–36
rubrum, Pleurobema obliquus, 233
rufa, Unio (Eurytina) fulvus var., 86
rugifera, 40
rugosa, Alasmidonta, 172
rugosa, Alasmidonta, 172
rugosa, Bapheia, 172
rugosa, Complanaria, 172
rugosa, Margaronia (Margaronia), 172
rugosa, Margaronia (Margaronia), 172
rugosa, Mya, 172
rugosa, Unio, 172
rugosum, Lasmigona, 172
rugosus, Anodon, 292
rugosus, Anodonta, 294
rugosus, Quadrula, 271
rugosus, Strophitus, 295
rugosus, Strophitus undulatus, 295
rugosus, Strophitus obliquus, 295
rugosus, Unio, 172, 266, 269
rugulosa, Mya, 41
ruttersvilensis, Margaron (Unio), 350
ruttersvilensis, Unio, 350
S
sageri, Lampsilis radiata var., 186
sageri, Unio, 186
Salamaneder Mussel, 288–92
Salamander Shell, 288
salmonia, Anodonta, 262
salmonia, Anodonta, 260, 294
salmonia, Margaronia (Anodonta), 260
salmonia, Margaron (Anodonta), 260
Sandshell, 170
Sandshell, Black, 186–91
Sandshell, Slough, 157
Sandshell, Yellow, 157–62
sapotalesis, Nephrosia, 32
sapatalesis, Unio, 32
satura, Lampsilis, 151
saxeus, Margaron (Unio), 334
saxeus, Unio, 334
sayanus, Unio, 356
sayi, Elliptio (Unio) tetralasmus, 319
sayi, Unio, 317, 321
sayi, Unio tetralasmus, 319
sayi, Unio (Unio) tetralasmus var., 317

Index | 415
Tubercled riffleshell, undata, undata, undilla, undilla, 
Turkey Wing, 306
Tubercled blossom, Truncilla, 306
Truncilla donaciformis, 12, 120, 310–13, 315, 317
Truncilla levisi, 92
Truncilla perplexa rangiana, 110
Truncilla rangiana, 110
Truncilla sulcata delicata, 99
Truncilla torulosai, 114
Truncilla triqueter, 89, 116
Truncilla triqueta, 116
Truncilla truncata, 120, 310, 313–17
Truncilla truncata var. fusca, 313
Truncilla truncata var. lacustris, 315
Truncilla truncata var. vermiculata, 313
Truncilla truncata var. vermiculata, 315
Truncilla (Dysnomia) foliata, 89
Truncilla (Pilea) perlexa var. cincinatien-
sis, 102
Truncilla (Pilea) perlexa var. rangiana, 108
Truncilla (Pilea) personata, 102
Truncilla (Plagioila), 249
Truncilla (Scalenaria) sulcata var. delicata, 108
Truncilla (Truncilla) triqueta, 116
Tubercled Blossom, 112–16
Tubercled Riffleshell, 105–8
Tuberculata, Obliquaria (Rotundaria), 65
Tuberculata, Obovaria stearia var., 68
Tuberculata, Quadrula, 306
Tuberculata, Quadrula (Cyclonaias), 65
Tuberculata, Quadrula (Rotundaria), 65
Tuberculata, Rotundaria, 63, 65
Tuberculata, Tritonina, 288, 306
Tuberculata, Cyclonaias, 63–67, 72, 122, 
218, 284
Tuberculata, Cyclonaias tuberculata, 65
Tuberculata, Margarita (Unio), 306
Tuberculata, Margarita (Unio), 306
Tuberculata, Mysa, 306
Tuberculata, Unio, 65, 306
Tuberculosa, Unio, 65
Turkey Wing, 306
Undata, Anodon, 294
Undata, Strophitus, 294
Undata, Fusconaia, 126
Undata, Fusconaia undata, 126
Undata, Fusconaia, 126
Undata, Quadrula (Fusconaia), 126
Undata, Quadrula (Fusconaia), 126
Undatus, Pleurobema, 126
Undatus, Unio, 120, 124, 126
Undulata, Alasmodonta, 40
Undulata, Anodon, 294
Undulata, Anodontia, 294
Undulata, Crenodonta, 191
Undulata, Margarita (Anodontia), 294
Undulata, Margarita (Anodontia), 294
Undulata, Monodonta, 40
Undulata, Mya, 191
Undulata, Quadrula, 191
Undulata, Unio, 40, 191, 294
Undulatus, Alasmodonta, 294
Undulatus, Anodontia, 294
Undulatus, Margarita (Unio), 191
Undulatus, Strophitus, 10, 11, 43, 61, 
265, 292–98
Undulatus, Strophitus undulatus, 295
Undulatus, Strophitus (Strophitus) undula-
tus, 295
Undulatus, Unio, 191
Undulatus, Lampisilis lienosa var., 334
Undulatus, Lampisilis lienosa var., 334
Undulatus, Unio, 334
Unio, 1
Unio abrupta, 136
Unio aesopus, 211, 218
Unio affinis, 153
Unio alasmodontina, 166
Unio alasmodontina, 168
Unio alata, 241
Unio altatus, 241
Unio altinis, 145
Unio anaticulus var. ohiensis, 225
Unio angustatus var. cuculius, 188
Unio anodontoides, 159
Unio apercus, 334
Unio arcior, 86
Unio arquatus, 186, 251
Unio asperimus, 286
Unio asperimus, 286
Unio atratus, 175
Unio atrorostatus, 191
Unio bicolor, 86
Unio bi-caelatus, 334
Unio bourrianus, 222, 226
Unio braziosensis, 51
Unio brevisalis, 200
Unio bullatus, 280
Unio bullatus var. prasinus, 282
Unio bullatus var. schoolcraftensis, 282
Unio calcicola, 45
Unio calcicola, 40, 45
Unio calcicola forma scitinincola, 41
Unio caliginous, 334
Unio camels, 251
Unio camptodon, 317
Unio canadensis, 140
Unio capax, 352
Unio capillaris, 102
Unio capillos, 326
Unio cardacea, 233, 238
Unio cardium, 140
Unio cardium var. occidens, 140
Unio cardium var. ventritosus, 140
Unio carinatus, 32
Unio castus mirus, 299
Unio catillus, 236
Unio catius, 238
Unio childreni, 153
Unio ciliatricoides, 213
Unio ciliaticous, 213
Unio ciliatricous var. varicosus, 213
Unio cilindricus var. acrispatus, 266
Unio cilindricus var. propetipica, 266
Unio cinchimatisis, 105
Unio circulos, 136, 207
Unio clavis, 222
Unio clavus, 222
Unio coecinus, 236
Unio coecoduensis, 350
Unio cognata, 310
Unio compterus, 218
Unio complanatus, 77
Unio compressa var. lindus, 168
Unio compressissimus, 251
Unio compressissimus var. performus, 251
Unio compressus, 73, 166
Unio compressus var. plebius, 166
Unio conversator, 334
Unio confrajosa, 343
Unio confrajosa, 343
Unio conjugans, 306
Unio consanquineus, 225
Unio contius, 334
Unio cooperius, 215
Unio cordatus, 226
Unio cornutus, 196
Unio costatus, 49
Unio couchiana, 265
Unio crassidens, 76, 82
Unio crassus, 36, 38, 49, 82, 136
Unio crassus var. plicata, 49
Unio cunecatus, 82, 116, 222
Unio cuneus, 236
Unio cyphias, 136
Unio cyphias, 265, 266
Unio cyphias var. aesopus, 218
Unio cyphias, 218
Unio danielei, 82
Unio declivis, 317, 356
Unio declivis geometricus, 319
Unio deitschens, 132
Unio deitschens orientopsis, 135
Unio deltoidea, 45
Unio deltoidea, 45
Unio depogis, 209
Unio detectus, 213
Unio dilatatus, 77, 86
Unio disoideus, 245
Unio discus, 82
Unio distans, 153
Unio dolabraformis, 140
Unio donaciiformis, 310
Index
Unio pustulosa, 265
Unio pustulosus, 280
Unio pyramidatus, 233
Unio quadratus, 286
Unio quadrulis, 286
Unio quintardii, 51
Unio ravius, 108
Unio vari-plicata, 49
Unio recta, 182, 186
Unio rector, 186
Unio reflexa, 196
Unio retius, 200, 204, 211, 280
Unio retius, 204
Unio riibundus, 95
Unio riva, 317
Unio roisyi, 338
Unio rostrata, 183
Unio rotundata, 344
Unio rotundatus, 344
Unio rubens, 236
Unio ruber, 233
Unio rubiginosa, 126
Unio rubiginosus, 124
Unio rugosa, 172
Unio rugosus, 172, 266, 269
Unio rutesulitensis, 350
Unio sagri, 186
Unio sapstalensis, 32
Unio saxius, 334
Unio sayant, 356
Unio sayi, 317, 321
Unio schoolcraftensis, 280, 281
Unio schoolcraftii, 282
Unio sphyrius, 218
Unio securia, 72
Unio securis, 72, 73
Unio shepardianus forma duttonianus, 182
Unio siliquoides, 153
Unio siliquoides, 153
Unio sinitoxa, 130
Unio solenifrons, 27
Unio solida, 240
Unio solidus, 236
Unio spatulatus, 359
Unio stegarius, 68
Unio stewardsonii stewardsoni, 95
Unio stonensis, 86
Unio striatus, 215
Unio subbrocaceus, 319
Unio subglobosus, 344
Unio suborbiculata, 344
Unio suborbiculatates, 344
Unio subovatus, 140
Unio subostratus, 330, 350
Unio subrotunda, 128
Unio subrotundus var. circularis, 209
Unio subtensus, 249
Unio subviridis, 347
Unio sulcatus, 89
Unio superiorensis, 153
Unio symmetricus, 356
Unio taiteianus, 200
Unio tappanianus, 347
Unio tappianus, 347
Unio teconensis, 36
Unio tenassimus, 179
Unio tetralasmus, 317
Unio tetralasmus camptodon, 319
Unio tetralasmus sayi, 319
Unio texensis, 299
Unio toepeaensis, 350
Unio torsus, 204
Unio torulosis, 196
Unio tragous, 271
Unio triangularis, 116, 126
Unio triangularis var. longiasculus, 116
Unio triangularis var. pergibusus, 116
Unio trigonus, 120, 124
Unio trigonus var. rubiginosus, 126
Unio triqueter, 116
Unio tristis, 338
Unio truncatus, 315
Unio truncatus var. elegantus, 315
Unio tuberculatus, 65, 306
Unio tuberculosa, 65
Unio unulatus, 286
Unio undatus, 120, 124, 126
Unio undulata, 40, 191, 294
Unio undulatus, 191
Unio unicus, 334
Unio validus var. continuus, 126
Unio variuscosus, 213
Unio vanghanianus, 183
Unio velum, 179
Unio ventricosus, 140, 177
Unio venustus, 358, 359, 361
Unio verrucosus purpureus, 65
Unio verrucosus, 65, 280, 306
Unio villosus, 326
Unio viridis, 347
Unio wardii, 273
Unio zigzag, 310
Unio zigzag var. illius, 310
Unio (Aximedia) elliptica, 222
Unio (Aximedia) levigata, 207
Unio (Elliptio), 76
Unio (Elliptio) cassa, 76
Unio (Elliptio) crassids, 82
Unio (Elliptio) danielsii, 82
Unio (Elliptio) fasciatus, 76
Unio (Elliptio) gibbusus, 86
Unio (Elliptio) gibbusus var. delicatus, 86
Unio (Elliptio) nigra, 76, 82
Unio (Elliptio) nigra var. fusca, 82
Unio (Elliptio) nigra var. maculata, 82
Unio (Elliptio) viridis, 45, 76
Unio (Eurynia), 77
Unio (Eurynia) dilatata, 84
Unio (Eurynia) fulves, 86
Unio (Eurynia) fulves var. fusata, 86
Unio (Eurynia) fulves var. rafa, 86
Unio (Eurynia) latissima, 186
Unio (Eurynia) solenoides, 266
Unio (Eurynia) teres, 157
Unio (Leptodea), 77
Unio (Leptodea) fragilis, 175
Unio (Leptodea) nervosa, 191
Unio (Leptodea) leptodon, 179
Unio (Liguimia) recta, 186
Unio (Margaretina) margaritifer, 340
Unio (Metaperta) diaphana, 175
Unio (Metaperta) diaphana var. lineolata, 175
Unio (Niaa) atrata, 175
Unio (Sayunio) dehiscens var. orienspovis, 132, 135
Unio (Symphynota) alatus, 241
Unio (Symphynota) tenuissimus, 179
Unio (Theliderma) cylindrica, 266
Unio (Theliderma) irrorata, 68
Unio (Theliderma) metanevra, 273
Unio (Theliderma) plicata, 49
Unio (Theliderma) puntalata, 306
Unio (Toxolasma) lividus, 299
Unio (Uniomirus) tetralasmus, 319
Unio (Uniomirus) tetralasmus var. camptodon, 319
Unio (Uniomirus) tetralasmus var. declivis, 356
Unio (Uniomirus) tetralasmus var. manubius, 319
Unio (Uniomirus) tetralasmus var. manubius, 319
Unio (Uniomirus) tetralasmus var. sayi, 319
Uniomirus, 317, 356
Uniomirus declivis, 321, 356–58
Uniomirus tetralasmus, 319, 356
Uniomirus tetralasmus, 317–21, 358
Uniomirus tetralasmus camptodon, 319
Uniomirus tetralasmus declivis, 358
Unionidae, 1, 2, 3, 32
Unioniinae, 1
Uniospis, 40, 292
Uniospis calcicola, 45
Uniospis edentula, 294
Uniospis mytiloides, 40
Uniospis radiata, 40
Unulatus, Unio, 286
U.S. Fish Commission, 5
Uterbachia, 321
Utterbachia, 54, 321
Utterbachia imbecillis, 8, 10, 58, 61, 321–26, 349
Utterbachia imbecillis fusca, 323
Utterbachia peggyae, 321
Utterbachia peninsulae, 321
Utterbachiana, 54
utterbachiana, Cyclonaias tuberculata, 65
utterbachiana, Quadrula (Cyclonaias) tuberculata, 65

V
value of a mussel, 19–20
variabilis, Alasmidonta marginata var., 41
varicosus, Margarita (Unio), 213
varicosus, Margaron (Unio), 213
varicosus, Unio, 213
varicosus, Unio cicatricosus var., 213
vaughanianus, Unio, 183
velum, Symphynota, 179
Veneridae, 6
ventricosus, Lampsis, 140
ventricosus, Lampsis ovata, 140
ventricosus, Lampsis (Lampsilis), 140
ventricosus, Margarita (Unio), 140
ventricosus, Margaron (Unio), 140
ventricosus, Mya, 140
ventricosus, Unio, 140, 177
ventricosus, Unio cardium var., 140
venus, Obliquaria (Aximedia), 82
Venusta, 358
venusta, Anodonta (Nayadina), 254, 261
venusta, Nayadina, 262
Venustaconcha, 333, 358
Venustaconcha ellipsiformis ellipsiformis, 358–61
Venustaconcha ellipsiformis pleasi, 361
venustus, Margarita (Unio), 359
venustus, Margaron (Unio), 359
venustus, Unio, 359, 361
vermiculata, Truncilla truncata, 315
vermiculata, Truncilla truncata var., 313
verrucosa, Mya, 65
verrucosa, Obliquaria (Ellipsaria), 306
verrucosa, Quadrula, 306
verrucosa, Quadrula (Triogonia), 306
verrucosa, Triogonia, 306
verrucosa, Triogonia, 265, 269, 288, 306–10
verrucosus, Margarita (Unio), 65
verrucosus, Quadrula, 65
verrucosus, Triogonia, 306
verrucosus, Unio, 65, 280, 306
vesiculatir, Lampsilis, 326
Villosa, 292, 326
Villosa fabalis, 305, 326–29, 333
Villosa irvis, 153, 305, 329, 330–33, 337, 361
Villosa irvis irvis, 330
Villosa lienos, 302, 333, 334–38
Villosa lienosa lienosa, 337
Villosa (Micromya) lienos, 334
villosus, Lampsilis, 326
villosus, Unio, 326
violacea, Obliquaria, 86
vires, Anodonta, 261
vires, Anodonta, 260
virgata, Anodonta, 294
virgatus, Strophitus, 294
virgatus, Strophitus undulatus, 295
virgatus, Strophitus (Strophitus) undulatus, 295
viridis, Alasmidonta, 45–49, 84, 349
viridis, Alasmidonta (Pressodonta), 45
viridis, Lasmigona, 45
viridis, Symphynota (Symphynota), 347
viridis, Unio, 347
viridis, Unio (Elliptio), 45
vitrea, Diplisma, 200
W
Wabash Pigtoe, 124–28
wagnerei, Fusconaia undata, 126
wardiana, Anodon, 294
wardiana, Anodonta, 294
wardiana, Margaron (Anodonta), 294
wardii, Margaron (Unio), 273
wardii, Orthonymus metanevra, 273
wardii, Quadrula metanevra, 273
wardii, Quadrula (Orthonymus) metanevra var., 273
wardii, Unio, 273
Warty Pigtoe, 280
Wartyback, 276–80, 280
Wartyback, Purple, 63–67
Wartyback, Ringed, 68
Wartyback, Threethorn, 196–200
Wartyback, White, 211–15
Washboard, 191–96
Wavy-rayed Pigtoe, 124–28
Wavy-rayed Pocketbook, 145–49
Welted Pigtoe, 211
Weltwing Mapleleaf, 269
Western Pondshell, 349
White Catspaw, 99–102
White Heelsplitter, 162–166
White Pimpleback, 280
White Wartyback, 211–15
Winged Mapleleaf, 269–73
Winged Orb Shell, 276
Winged Pimpleback, 276
Winnbagoensis, Lampsis ventricosa var., 142
Winnbagoensis, Strophitus rugosus, 295
wrightianus, Strophitus, 40
Y
Yellow Knob Shell, 218
Yellow Mucket, 133
Yellow Sandshell, 157–62
Z
zebra and quagga mussels, 17–18
zigzag, Margarita (Unio), 310
zigzag, Margaron (Unio), 310
zigzag, Unio, 310