THE PEARLY MUSSELS OF NEW YORK STATE

David L. Strayer and Kurt J. Jirka

NEW YORK STATE MUSEUM

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NEW YORK STATE MUSEUM MEMOIR 26

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A Note about the Illustrations

Most of the color plates (Plates 1–25) and several of the figures (Figure 13) in this book were originally prepared for a large monograph, "Land and Fresh Water Mollusca of New York," by Henry A. Pilsbry of the Academy of Natural Sciences of Philadelphia. This monograph was begun about 1906 by Elizabeth J. Letson of the Buffalo Society of Natural Sciences, under the direction of John M. Clarke, then Director of the New York State Museum, and was to have been published by the New York State Museum. After Letson moved to Hawaii in 1909, the project was continued by Pilsbry, who finished the 1200-page work in 1925, in the same month in which Clarke died. The new Director of the New York State Museum, C.C. Adams, was unable to find the money to publish Pilsbry's monograph. A bill (number 562) introduced in the state senate in 1927 specially to provide funds to print the monograph failed to pass. The massive work was stored in Pilsbry's files from 1925 until his death in 1957, when it was transferred to the archives of the Academy of Natural Sciences of Philadelphia.

Three illustrators contributed to the original monograph. George S. Barkentin, an illustrator at the New York State Museum, prepared a few drawings under Clarke's direction in 1906–1908. However, Letson was not fully satisfied with Barkentin's work, so in 1908 she began to work with Wilfred P. Davison. When Pilsbry took over the work in 1909, he worked with Helen D. Winchester, an illustrator with the Academy of Natural Sciences of Philadelphia. Ms. Winchester prepared most of the artwork in Plates 1–25. The contribution of each of these talented illustrators is acknowledged in the legends to the color plates.

Today, these illustrations remain essentially unchanged. However, they were mounted upon paper that has become discolored and smudged over time. For this reason, we scanned the plates into electronic format to prepare them for publication. This allowed us to remove the smudged backgrounds, color correct the digitized illustrations, and recreate the annotations and numbering without altering the originals in any way. We then printed the plates at the same scale (life size) and in the same groupings as the original illustrations.

We are most grateful to the Academy of Natural Sciences of Philadelphia for granting permission to use these beautiful illustrations, and to Patricia Kernan and Magdalyn Sebastian of the New York State Museum and especially to Carol Spawn of the Academy of Natural Sciences of Philadelphia for their kind help in arranging for the loan of the original artwork. The historical information summarized above was taken mostly from correspondence held in the New York State Archives (New York State Museum Director's Correspondence Files-New York State Archives Series B0561, Boxes 9–42). James D. Folts of the state archives was most helpful in guiding our search of these materials.

Acknowledgments

Many people helped us with this project. The following curators kindly allowed us access to the collections under their charge and lent us specimens for illustration: William Emerson and Walter Sage (American Museum of Natural History); George Davis, Gary Rosenberg, and David Robinson (Academy of Natural Sciences at Philadelphia); Wayne Gall (Buffalo Science Museum); Kenneth Boss and Richard Johnson (Museum of Comparative Zoology at Harvard University); Ed Blakemore (New York State Museum); David Stansbery and Kathy Borror (Ohio State University Museum of Biological Diversity); John Burch and Fritz Paper (University of Michigan Museum of Zoology); and Robert Herschler (National Museum of Natural History, Smithsonian Institution). Kevin Cummings and George McIntosh kindly sent us lists of the holdings of their institutions (the Illinois Natural History Survey and the Rochester Museum and Science Center, respectively) and allowed us to examine several specimens. Kathryn Schneider let us examine the records held by the New York Natural Heritage Program. Douglas Carlson, J. Mark Erickson, Chris Fichtel, Mark Gretch, Willard Harman, Paul Novak, Jon Powell, and Barry Wicklow allowed us to quote some of their unpublished records or results, and Tom Watters sent us some hard-to-find literature. Carol Spawn, Patricia Kernan, Magdalyn Sebastian, and the Academy of Natural Sciences at Philadelphia helped arrange use of the color plates originally prepared for Henry Pilsbry's monograph on "Land and Fresh Water Mollusks of New York." John Yost photographed these plates and the shells shown in Plates 26 and 27, and Patricia Kernan redrew several figures. We thank Arthur Bogan, Jim Folts, Sharon Okada, Daniel Sass, Kathryn Schneider, Clifford Siegfried, Lisa Sievert, and Susanna von Oettingen for useful discussions and encouragement. The New York Natural Heritage Program provided funding for museum visits to Ohio State University and the University of Michigan. We thank Marjory Spoerri for typing an endless stream of manuscript, Arthur Bogan, Kevin Cummings, and Douglas Smith for reviewing the draft manuscript, and Robert Daniels for his help and support as editor for this project.

Introduction

The streams and rivers of eastern North America support an extraordinarily rich fauna of fish, shellfish, and other freshwater life. One of the richest of these groups, the pearly mussels of the order Unionoida, is the subject of this book. Eastern North America contains about 300 endemic species of pearly mussels (Bogan 1993; Williams et al. 1993). Their shells are beautiful and varied, ranging in size and form from tiny species scarcely 3 cm long as adults to huge, thick shells more than 25 cm long and weighing more than a kilogram, and from smooth, almost paper-thin shells to massive shells sculptured with knobs and spines. The parasitic life history of the unionoids is remarkable and has given rise to some amazing adaptations to find hosts. Unionoids inhabit a chronically unstable habitat, yet paradoxically they are among the longest-lived of freshwater invertebrates. Despite the economic importance and biological interest of unionoids, many interesting questions about their ecology and evolution remain unanswered.

In addition to their intellectual interest to biologists, pearly mussels are of direct economic and ecological importance. The thick, lustrous shells of pearly mussels have been used as a source of mother-of-pearl for pearl buttons (Carlander 1954; see also the fascinating account of Claassen, 1994), ornaments, and, more recently, nuclei for cultured pearls. Bits of unionoid shells are placed into an oyster, which then coats this nucleus with its own nacre. The fishery for unionoid shells is worth about $40 million per year in the United States (Bowen et al. 1994). Also, the pearls of unionoids themselves (especially those of *Margaritifera margaritifera*) have been collected since at least Roman times (Ziuganov et al. 1994).

Pearly mussels were an important source of food for many Native Americans (e.g., Bogan 1990; Parmalee and Klippel 1974). Some people still eat pearly mussels, although we find them too strong and fishy in flavor to be appealing, and it is illegal to collect living mussels in New York without a special permit.

Pearly mussels dominate the benthic communities of many unpolluted lakes, streams, and rivers, often reaching biomasses of 5–100 g dry mass m^{-2} (shell-free) (Strayer et al. 1994). The filtration capacity of such dense populations can be substantial (0.1–2 m^3 m^{-2} d^{-1}). Therefore, unionoids are probably of great importance in controlling the movement and fate of particles and particle-bound substances (e.g., some toxins and nutrients) in some freshwater ecosystems, although such functions have not been measured.

Finally, unionoids have been shown to be useful indicators of environmental quality. They are sensitive to many kinds of pollution (Fuller 1974), so the presence and diversity of pearly mussels provides a useful assessment of water quality. Furthermore, because pearly mussels are long-lived and accumulate many toxins, they can be used as biomonitors of environmental contamination (Carell et al. 1987; Pugsley et al. 1985, 1988).

Purpose of This Book

The purpose of this book is to summarize the distributions, past and present, of pearly mussels in New York, and to discuss the causes of those distributions. We also provide keys, illustrations, and descriptions of the shells of New York's pearly mussels as aids to their identification.

Over the past decade, there has been much interest in the distribution and current status of pearly mussel species (Allan and Flecker 1993; Neves 1993; Williams et al. 1993). As part of this upsurge in interest, recent surveys (especially those sponsored by the New York Natural Heritage Program) have added considerably to our knowledge of mussel distribution in New York. Although knowledge of mussel distribution in New York is far from complete, it is a good time to critically assess mussel distribution in the state.

Furthermore, 100 years have now passed since William B. Marshall (1895a) brought together what was then known about unionoid distribution in New York and discussed its causes. Marshall's paper was among the first of many works on the pearly mussel faunas of various states (Baker 1928a; Call 1895, 1900; Ortmann 1919) and has been cited widely, especially in studies of the Northeast (Clarke and Berg 1959; Ortmann 1919). Although Marshall's work is naturally now known to have errors and omissions, and much additional information is now available on New York unionoids, no more modern, statewide treatment of New York's unionoid fauna has appeared. The centenary of Marshall's (1895a) influential paper is an appropriate time to reconsider the questions that motivated Marshall.

Introduction to the Biology of Pearly Mussels

The life history of pearly mussels is highly unusual and probably determines their evolution, distribution, and abundance in ways that are not yet fully understood. In most unionoids, sexes are separate, but a few species (including *Lasmigona subviridis*, *Lasmigona compressa*, and *Utterbackia imbecillis* in New York) are normally simultaneous hermaphrodites, and in many other species hermaphroditic specimens are occasionally found (Kat 1983a; Ortmann 1919; van der Schalie 1970). Downing et al. (1989) suggested that *Elliptio complanata* is protandrous (i.e., changes sex from male to female as it grows), and Bauer (1987) found that females of *Margaritifera margaritifera* became hermaphrodites when experimentally transferred to low-density populations. It is not known whether other unionoids possess such remarkable sexual plasticity.

During the breeding season, males release sperm into the water, which is filtered in by the female mussels. The fertilized eggs develop into peculiar larvae called glochidia, which are unique to the Unionoida. The glochidia are brooded in the female's gills for several weeks to several months (see below), and are then released into the water. Typically, 10^5–10^7 glochidia are produced per female (McMahon 1991). The glochidia cannot swim or crawl, and they can live freely for only a short time (e.g., 0.5–5 days in *Lampsilis radiata* [Tedla and Fernando 1969]), but during their brief lives, they must contact and attach to a fish host. And not just any fish will do—each species of pearly mussel requires fairly specific fish as its hosts. If the glochidia attach to the wrong kind of host, they are destroyed by the fish's immune system.

The odds against a glochidium finding an appropriate host must be extraordinarily long, so some kinds of pearly mussels have developed remarkable adaptations to improve these odds. In females of *Lampsilis* (a common genus in New York), the edge of the mantle is developed into a fish-shaped lure (pictured by Clarke 1981a, and Williams et al. 1993), which is prominently flapped. This mantle flap presumably increases the local density of curious fish available to serve as hosts. Indeed, we have seen groups of small fish gathered around displaying *Lampsilis* females. In other mussels, the glochidia are released in small packets called conglutinates. In some species, the conglutinates closely resemble small fish or insects, which are presumably attractive to potential hosts (Barnhart and Roberts 1996; Hartfield and Hartfield 1996). In another extraordinary adaptation, some southeastern species of *Lampsilis* release all their glochidia in a single packet called a superconglutinate, which bears an uncanny resemblance to a minnow and is dangled from the end of a meter-long clear mucous thread "fishing line" by the female (Haag et al. 1995). Given the strong selective pressure to find a fish host, it would not be surprising if additional morphological or chemical adaptations for host-finding remain to be discovered.

The glochidium attaches to the fins or gills of the fish. Typically, the glochidium spends several days to several months on the host, during which time juvenile organ systems begin to develop. Although glochidia do derive nutrition from their hosts, most species do not grow while attached to the fish. Presumably, the major functions of the parasitic—or perhaps more aptly, phoretic—phase are metamorphosis from larva to juvenile and dispersal into a habitat frequented by the fish host and the mussel species (Kat 1984).

Hoggarth (1992) and Watters (1994a) recently summarized what is known about host use by North American unionoids. Because Hoggarth (1992) distinguished among the different kinds of evidence used to infer unionoid–host relationships, we used his paper as our primary source of information for the hosts listed in our species accounts. Where host use was established from field observations of glochidial attachments on fish (or by unspecified means) instead of laboratory trials, we describe the unionoid–host relationship as tentative or probable rather than definitive. Watters' (1994a) more comprehensive compilation and recent original findings were used to supplement Hoggarth's (1992) paper.

One unionoid (*Simpsonaias ambigua*) uses a salamander (the mudpuppy, *Necturus maculosus*) as a host (Howard 1951). Further, it has been claimed that three species of unionoids (*Obliquaria reflexa*, *Strophitus undulatus*, and *Utterbackia imbecillis*) can develop without fish hosts, but these important claims have not been verified (Kat 1984).

The timing of this life cycle differs across species (Kat 1984). Tachytictic species spawn in spring and early summer and release glochidia in late summer.

Bradytictic species spawn in mid- to late summer and do not release their glochidia until the following spring.

The ecology of juvenile unionoids is poorly known (but see Neves and Widlak 1987). Apparently, juveniles typically live buried out of sight in the substratum (Amyot and Downing 1991; Yeager et al. 1994), although they sometimes are collected with adults at the sediment surface. Juveniles may be deposit-feeders as well as filter-feeders (Yeager et al. 1994).

After a juvenile period of 1–10 years, depending on the species (Coker et al. 1921; Jirka and Neves 1992), mussels reach sexual maturity. There is some indication (Downing et al. 1989) that unionoids may be protandrous; that is, change sex from male to female as they grow. Life spans differ widely across species, from fewer than ten years to more than a century (Bauer 1992; Coker et al. 1921).

Adult pearly mussels are filter-feeders, able to ingest a broad range of particle sizes (Allen 1914; Jorgensen et al. 1984). Both algae and detritus probably are important food sources (Allen 1914; James 1987). Mussels in turn are eaten by muskrats and raccoons (e.g., Hanson et al. 1989; Neves and Odom 1989) as well as fish (Coker et al. 1921) and birds (Berrow 1991). Additional information on the biology of pearly mussels is available in the fine reviews of Fuller (1974) and McMahon (1991).

Geography and Environmental Conditions in New York

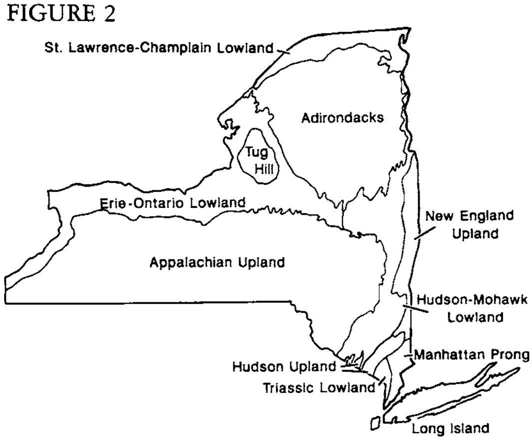
The political geography and major landform regions of New York are shown in Figures 1 and 2. The landforms, climate, and land use of New York are highly varied. The following account is summarized from Thompson (1977).

The Appalachian Uplands extend over southwestern and south-central New York. This region is underlain by sedimentary rocks and is rolling to rugged. Surface

FIGURE 1

Counties of New York

FIGURE 2



Major landforms of New York, modified from Isachsen et al. (1981)

waters are moderately soft (<5 ppm calcium in the Catskills, for example) to hard. Most of this region is forested or used for dairying.

North and east of the Appalachian Uplands lies a band of lowland regions: the Erie–Ontario Lowland and the Hudson–Mohawk Lowland. This is an area of low relief and hard waters. Much of this area is used for dairying and for some fruit and vegetable production. Several of New York's major cities (Buffalo, Niagara Falls, Rochester, Syracuse, Utica, and Albany–Schenectady–Troy) lie in the lowland regions, so some of the streams in this area have been badly polluted.

Long Island, a part of the Atlantic Coastal Plain, consists largely of a glacial end moraine and sandy outwash plains. With a mean annual temperature of more than 10°C, its climate is much milder than that of the rest of New York. The western end of Long Island is suburban and urban, but its eastern end still contains much agricultural land.

A small part of the Triassic Lowland, a rolling area underlain by sedimentary rock and lava, lies just north of New York City in the Hudson River Valley. The eastern edge of New York between New York City and Vermont is part of the New England Upland. This is a rugged area with relief of 300–600 m. It is underlain by crystalline rocks, and it is largely forested or used for dairying today. The waters of this area are moderately soft to moderately hard.

The Adirondack Upland forms most of northeastern New York. The Adirondacks are formed of Precambrian crystalline rocks. Local relief is 300 to 600 m, and surface waters are mostly soft to very soft. With a mean annual temperature of approximately 5°C, the climate is cold and wet; the southern Adirondacks receive about 125 cm of precipitation per year. Most of the Adirondacks is forested today, and much of the region (24,000 km^2) is included in the Adirondack Park.

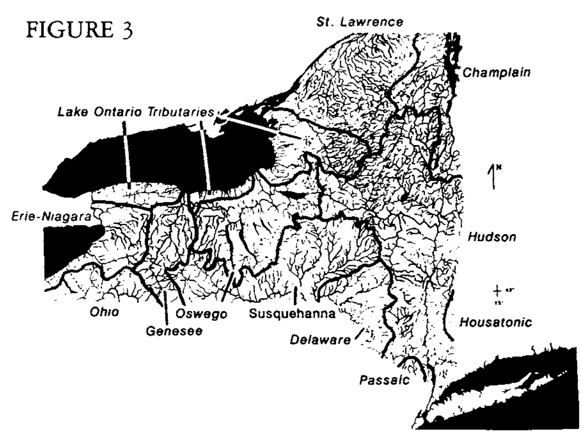
Another upland region, the Tug Hill Upland, lies southwest of the Adirondacks. Tug Hill is an extension of the Appalachian Upland and is similarly underlain by sedimentary rocks. It is cool and exceptionally snowy, receiving up to 500 cm of snow per year. This region is largely forested today.

Finally, north and east of the Adirondacks is the St. Lawrence–Champlain Lowland. With a mean annual temperature of 7°C, this is a cool, flat to rolling region that contains both forests and farms.

The major watersheds and streams of New York are shown in Figures 3 and 4. Southwestern New York drains to the Ohio River through the Allegheny River and its three important tributaries, French Creek, Cassadaga Creek, and Conewango Creek.

Southeastern New York drains to the Atlantic Ocean by several major rivers. The Susquehanna River basin covers much of south-central New York. The major rivers of the Susquehanna system include the Canisteo, Cohocton, Chemung, Tioughnioga, Otselic, Chenango, and Unadilla Rivers. The Delaware River basin,

FIGURE 3



Major watersheds of New York State, modified from C.L. Smith (1985) including the East and West Branches of the Delaware and the Neversink River, lies southeast of the Susquehanna basin. The third major drainage basin of the Atlantic Slope is the Hudson. The Mohawk River is the major tributary to the Hudson. In addition, small areas of southeastern New York drain to the Atlantic Ocean through the Passaic and Housatonic Rivers.

The remainder of New York lies in the St. Lawrence River basin. The St. Lawrence system contains several sub-basins: the Erie–Niagara, including Tonawanda Creek; the Genesee; the Oswego, which drains the Finger Lakes through the Seneca River; the Black; and the Champlain. Between the Black and the Champlain lies a large area that we will refer to as the St. Lawrence basin in northern New York. The important rivers of this latter area include the Indian, Oswegatchie, Grass, Raquette, and St. Regis Rivers.

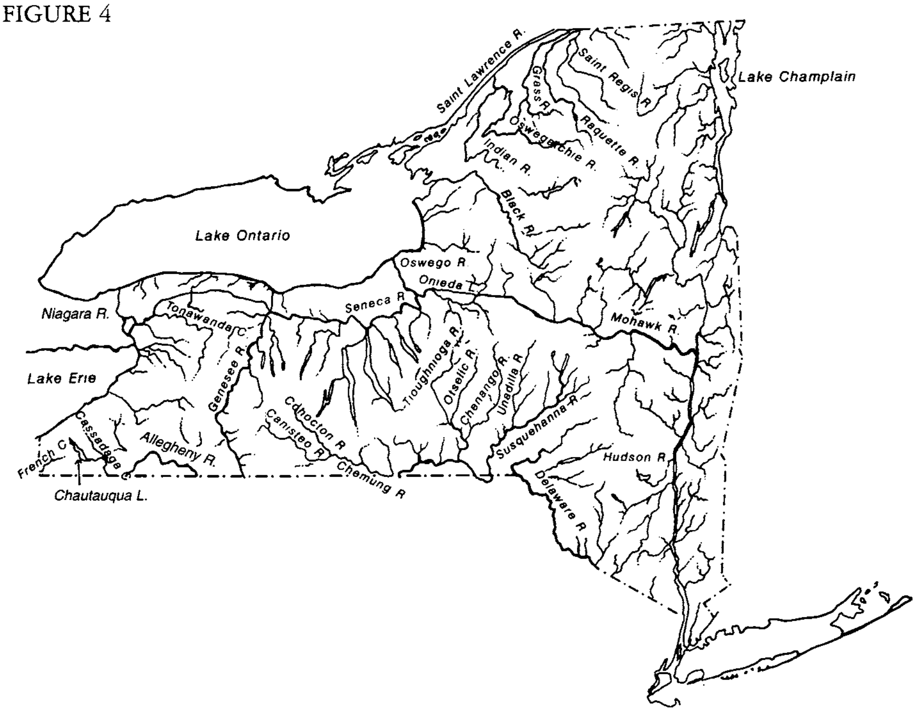
Between 1797 and 1857, navigational canals were built linking most of the major drainage systems of New York (Figure 5). These canals had the potential to allow pearly mussels to move across drainage divides, but as we discuss below (and as C.L. Smith [1985] discussed for fish), it is unclear how effective canals were as dispersal routes.

Almost all of New York has been greatly affected by the actions of humans. Very little old-growth forest remains in the state, and much of the state was cleared for agriculture by the mid-nineteenth century. Many of our larger streams were badly polluted by domestic and industrial effluents until the mid- to late twentieth century, and many have been changed greatly by large and small impoundments.

Historical Sources

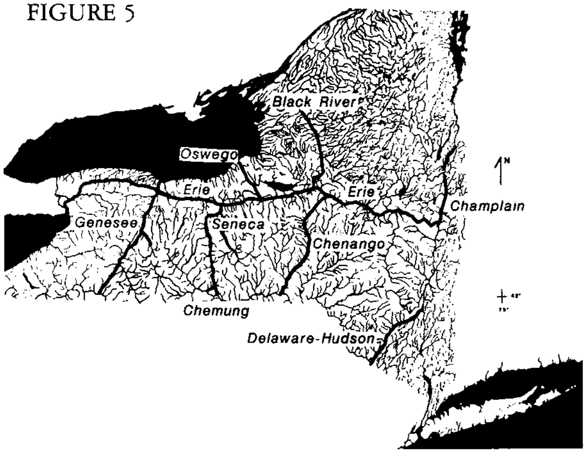
Many people have contributed to our knowledge of the distribution of pearly mussels in New York. The earliest contributors were naturalists trying to describe and catalogue the newly discovered fauna of North

FIGURE 4



Major streams, rivers, and lakes of New York

FIGURE 5



Major canals of New York,
modified from Thompson (1977)

America. Well-known figures such as Lamarck, Say, Rafinesque (Gordon 1987), and Lea all described material that they or their correspondents had collected from New York. These early reports are of limited value in a distributional sense, because collection data often were few, vague, or incorrect. The first comprehensive attempt to discuss New York's unionoid fauna was DeKay's (1844) monograph, which still was more concerned with cataloguing the fauna than with discussing the distribution of species within the state. DeKay listed only 21 of the approximately 50 species of pearly mussels now known from the state and provided only a few or vague localities for each species.

Several collectors working in the mid-nineteenth century added significantly to our knowledge of unionoid distribution in New York. The most important of these collectors was James Lewis, a dentist from Mohawk, who collected very thoroughly in parts of Herkimer and Otsego Counties between about 1850 and 1880. Lewis published several key papers on the fauna of the Mohawk area and the state as a whole (Lewis 1856, 1860, 1868a, 1868b, 1872, 1874). Lewis's list of 1874 included 39 valid species of pearly mussels from New York, although little distributional information was included. Many of Lewis's specimens are in the major museums of the United States. Other important workers of the mid-nineteenth century include C. Dewey (1856); Truman H. Aldrich, who made collections in the Troy area in 1867 (Aldrich 1869) and later became a congressman from Alabama; and R. Ellsworth Call, well known for his work on the mollusks of the American West and Midwest (Johnson 1975), who made scattered collections from New York in the late 1870s, when he was a young man.

Freshwater malacologists were very active in New York between 1880 and 1930. Marshall (1895a) reviewed pearly mussel distribution in New York, Letson (1905) catalogued the mollusks of the state, and Pilsbry (1925) wrote a large, unpublished monograph on the nonmarine mollusks of New York. Pilsbry also made large collections from Lake Champlain and surrounding regions, which are now held by the Academy of Natural Sciences at Philadelphia. Important workers of this period included Frank C. Baker, a noted malacologist who studied the mollusks of western and central New York (Baker 1898, 1901, 1928b); William M. Beauchamp, a minister and anthropologist who collected intensively in Onondaga County (Beauchamp 1886); Charles E. Beecher, who collected near Albany and in the Allegheny basin in New York and Pennsylvania; Elizabeth J. Letson, who led an active group of malacologists in the Buffalo area (Letson 1909; Robertson and Blakeslee 1948); Carlotta J. Maury, a paleontologist who collected living and fossil mollusks from western and central New York (Maury 1916); William S. Teator, a fruit grower who made very detailed, careful collections from northwestern Dutchess County (Garlinghouse 1976); and John Walton, who worked in and around Rochester (Walton 1891). By the end of this period, New York's fauna was fairly well known (Pilsbry listed 42 valid species from the state) and the broad outlines of distribution within New York were understood.

An important but unappreciated collector of this period was Jonathan Allen, president of Alfred University and best known for his interest in Devonian sponges (Lewis 1932). Allen collected widely in the upper Genesee and western Susquehanna basins, zoogeographically interesting areas that have otherwise received little attention from malacologists. Allen's collections are now in the Academy of Natural Sciences at Philadelphia and the University of Michigan Museum of Zoology.

A few major studies appeared between 1930 and 1970. Robertson and Blakeslee (1948), building on earlier work by Letson and others at the Buffalo Society of Natural Sciences, summarized what was known about molluscan distribution in the Buffalo area. Many of Blakeslee's specimens are in the Rochester Museum and Science Center. Morris K. Jacobson, a dedicated amateur, worked in mid-century in eastern New York, especially around New York City (Jacobson and Emerson 1971). Clifford O. Berg, whose research interests were in snail-killing flies (Sciomyzidae) (Clarke 1987), supervised two students who greatly increased our knowledge of the pearly mussels of central New York. Arthur H. Clarke's work (Clarke and Berg 1959) covered the area between the Genesee basin and Oneida Lake and is still widely cited as a standard reference on the unionoids of the Northeast. Willard N. Harman, a second student of Berg's who is better known for his work on the ecology of fresh-water snails (Harman 1972; Harman and Berg 1971), also wrote several important papers on the pearly mussels of central New York (Harman 1970a, 1970b, 1973, 1975, 1981; Harman and Forney 1970). Harman in turn supervised several students who worked on molluscan ecology, including Daniel E. Buckley, whose survey of the mollusk fauna of the Black River basin is the only detailed work on the unionoids of this section of New York.

More recently, Douglas Smith (1982, 1983, 1985a) detailed pearly mussel distribution in eastern New York, and we have surveyed mussel communities in several parts of the state (Jirka 1991; Strayer 1987, 1992, 1994, 1995; Strayer and Ralley 1991; Strayer et al. 1991, 1994). J. Mark Erickson and his students (Erickson and Fetterman 1996) have made important collections of the pearly mussels of St. Lawrence County in northern New York, and Kathryn Schneider and others in the New York Natural Heritage Program have made useful collections from throughout the state. Eileen Jokinen's survey of the freshwater snails of New York (Jokinen 1992) resulted in some interesting unionoid collections, which are held in the New York State Museum. Clarence F. Clark (n.d.), David H. Stansbery and Kathy G. Borror (Stansbery, pers. comm.) have made limited but significant collections in the Allegheny basin of southwestern New York.

Of course, in addition to the major figures listed above, many other people—both professional malacologists and amateurs—have worked on the distribution and ecology of pearly mussels in New York. Where possible, we acknowledge their contributions in our text.

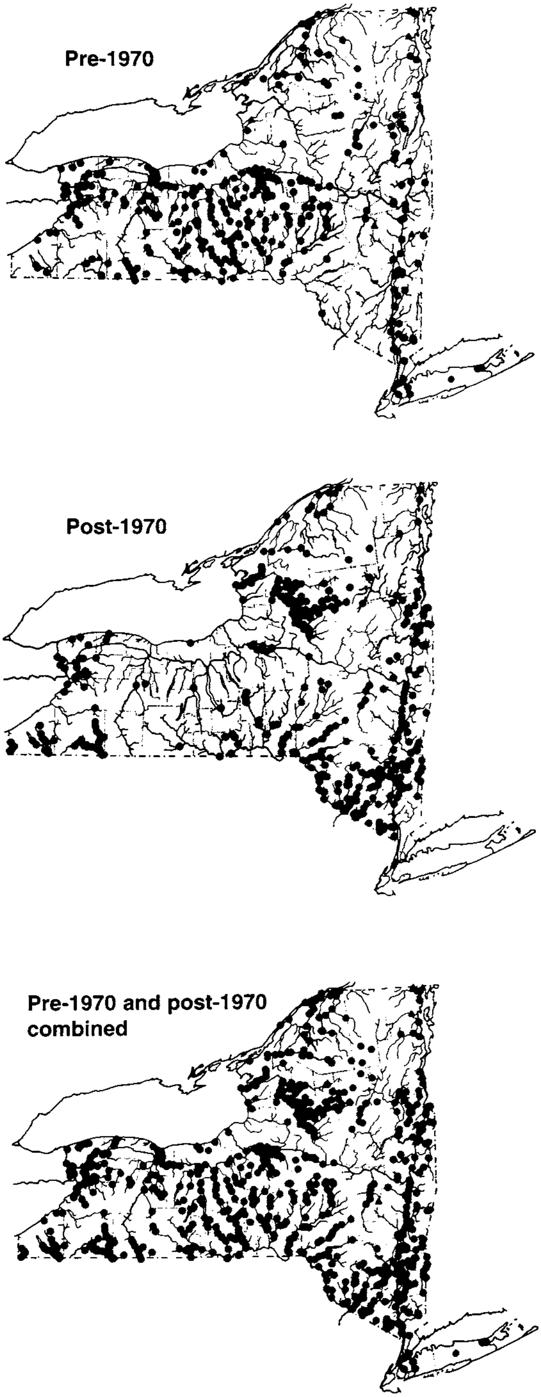
Figure 6 shows all the sites from which pearly mussels have been collected or sought in New York, both before and after 1970, based on our records. Although coverage of the state has generally been good, there are several obvious discontinuities in the distribution of collection effort. Cattaraugus Creek; the streams of Niagara and Orleans Counties; the mid-Mohawk basin, including Schoharie Creek; Long Island; and the St. Lawrence River and its tributaries in northern New York have never been thoroughly surveyed for pearly mussels. Much of central New York has not been surveyed since the work of Clarke and Berg (1959) and Harman (1970a) in the mid-1950s and mid-1960s, respectively. In view of the number of rare species in the region, the rich fauna of western New York needs closer attention than the old surveys of Letson (1909) and Robertson and Blakeslee (1948) and the quick overviews of Strayer et al. (1991) and Strayer (1995) have provided.

Overview of the Unionoid Fauna of New York

New York has a moderately rich unionoid fauna compared with surrounding states (Figure 7). In pre-Columbian times, New York probably held about 50 species of pearly mussels, many fewer than the very rich faunas of Alabama, Tennessee, and Kentucky, but many more than the faunas of states and provinces north and east of New York. Furthermore, although two species of pearly mussels (*Lasmigona compressa* and *Pyganodon lacustris*) were first described from New York, no species is confined to the state. At present, New York contains about 40 unionoid species (see below); probably only about a dozen states now contain more species.

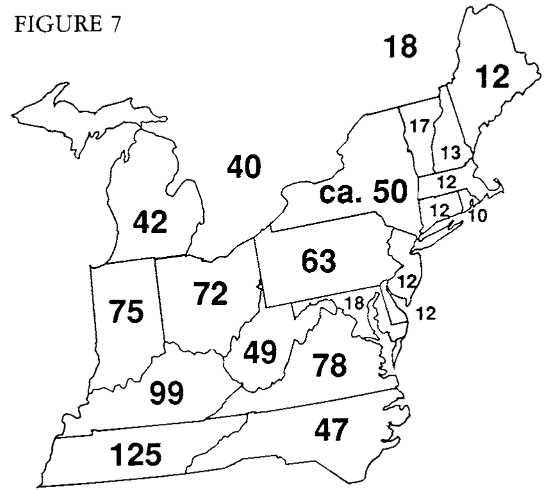
The gradient in species richness from the Southeast to the Northeast is accompanied by a shift in the composition of the pearly mussel fauna from members of the subfamily Ambleminae (in the sense of Davis and Fuller 1981) to members of the Anodontinae. Moving from Tennessee to New York to New England, the representation of amblemines falls from 86% to 63% to 43% of the unionoid fauna. Furthermore, in Tennessee, all three amblemine tribes (Lampsilini, Pleurobemini, and Amblemini) are well represented, but in New York and New England the Lampsilini become progressively more important. At the same time, anodontines constitute 13%, 35%, and 52% of unionoid species in Tennessee, New York, and New England, respectively.

FIGURE 6



Sites from which unionoids have been reported or searched for in New York

FIGURE 7



Species richness of unionoids in New York and some nearby states, modified from data of Williams et al. (1993).

Controls on Pearly Mussel Distribution in New York

Even a cursory examination of the maps showing the ranges of pearly mussels in New York reveals that species are distributed very unevenly across the state. No species is found in all or even most of the inland waters of New York, some species are found in many places and others in few, and the patterns of distribution differ considerably among species. Although the causes for these varied distributional patterns are imperfectly understood, several factors are thought to be of paramount importance. These are discussed briefly below.

Dispersal Routes

Almost all of New York was covered by ice during the last glaciation, and even the small part of southwestern New York that was ice-free was probably too cold to support mussels during the peak of glaciation (cf. Flint 1971; Pielou 1991). Thus, all mussels now present in New York must have arisen from dispersal over the last 18,000 years since the glaciers began to retreat. Van der Schalie (1945) showed convincingly that unionoids rarely are able to disperse across drainage divides and that postglacial dispersal of unionoids was controlled largely by the history of drainage connections. Thus, current patterns of distribution are readily interpreted as a result of the history of drainage connections. As we will see, New York has had a complicated history of drainage connections, both natural and artificial, but unionoid ranges are nevertheless largely consistent with this history.

The pearly mussels now living in New York arose from mussels that survived glaciation in two general regions: parts of the Ohio and Mississippi River basins south of the glacial border (so-called Interior Basin species) and parts of the Atlantic Slope that were either south or east of the glacial border (Atlantic Slope species). The eastern refugia are now submerged by the ocean (Schmidt 1986).

Interior Basin species reached New York through three routes. First, 20 species simply moved upstream through the Ohio River drainage, probably from Kentucky and West Virginia, into the Allegheny basin in southwestern New York. For several species restricted in New York to the Allegheny basin (e.g., *Obovaria subrotunda*, *Pleurobema clava*, *Villosa fabalis*), this was the only route of entry into the state. Other species that moved up the Ohio basin into New York (e.g., *Actinonaias ligamentina*, *Alasmidonta marginata*, *Pleurobema cordatum*) also entered the state through other routes.

The Allegheny basin was connected to the Genesee and Susquehanna basins through a series of postglacial lakes in the headwaters of the Genesee (Clarke and Berg 1959), and then to the Genesee by the Genesee Canal, which ran from Olean to Rochester. Apparently, few if any mussels moved east along these routes; the fauna of the upper Genesee basin is poor, containing only three species (*Lampsilis siliquoidea*, *Lasmigona compressa*, and *Strophitus undulatus*) that are present in the Allegheny basin. All three of these species occur in the Erie–Niagara and lower Genesee basins as well, so they also could have entered the upper Genesee from the north. Only one Interior Basin species (*Alasmidonta marginata*) seems likely to have moved eastward from the Allegheny to the Susquehanna basin. Taken together with the evidence presented by C.L. Smith (1985) that few if any fish (possibly the tonguetied minnow and redside dace) moved east from the Allegheny basin, it appears that dispersal by way of postglacial connections (including the Genesee Canal) between the Allegheny and drainages to the east was minimal.

Many Interior Basin unionoids and fish (Bailey and Smith 1981) entered the Lake Erie basin from the Wabash River during an early postglacial stage when the lake drained to the southwest through the Maumee and Wabash Rivers. Such species were then able to move east through the Lake Erie drainage to New York, especially during a low-water stage when most of what is now Lake Erie was dry and a large river flowed across most of the lake bed (see "Erroneous and Questionable Records" for a more detailed discussion). Thirty-one Interior Basin species entered New York through Lake Erie. Again, although many of these species (e.g., *Actinonaias ligamentina*, *Ligumia recta*, *Pleurobema cordatum*) also came into the state through other routes, several species reached New York only through the Lake Erie basin and are found in New York only in the Erie–Niagara basin (e.g., *Epioblasma triquetra*, *Simpsonaias ambigua*, *Truncilla* spp.) or in areas that were hydrologically connected to the Erie–Niagara basin (e.g., *Alasmidonta viridis*, *Fusconaia flava*, *Quadrula pustulosa*).

The Erie–Niagara basin was hydrologically connected with central and eastern New York twice: first, about 13,000 years ago, when Lake Erie drained eastward through the Mohawk River; and second, since 1825, when the Erie Canal was built between Lake Erie and the Hudson River. Many Interior Basin species moved eastward to some extent along these routes. It is difficult to be sure to what extent species used each of the two connections. Interior Basin species that are widespread in central and eastern New York (e.g., *Anodontoides ferussacianus*, *Lasmigona costata*) or that were collected very early from eastern New York (e.g., *Lasmigona compressa*, taken near Albany in 1829) probably arrived in central and eastern New York through the Mohawk outlet. Other species (e.g., *Fusconaia flava*, *Toxolasma parvum*) probably owe at least part of their current ranges to the Erie Canal.

Finally, about ten Interior Basin species probably came into the Champlain and St. Lawrence basins in northern New York through the Ottawa River outlet of Lake Huron and the upper Great Lakes. During various low-water phases, the upper Great Lakes (Huron, Michigan, and Superior) emptied into Lake Ontario through the Trent Valley (in Ontario) and into the St. Lawrence River through the Ottawa River. During the last phase, Interior Basin species reached the Ottawa River, St. Lawrence River, and Champlain basins. All the species arriving by this route also reached New York through Lake Erie, so no Interior Basin species is now found in New York only in the St. Lawrence–Champlain region.

The ultimate origin of these Interior Basin colonists to northeastern New York is uncertain. They could have entered the upper Great Lakes from Lake Erie before Erie and Huron were separated during the low-water phases, or they could have invaded Lake Michigan when it drained southward through the Illinois River. Alternatively, these species might have arrived in the Lake Michigan basin through the confluence between the Fox and Wisconsin Rivers (Mathiak 1979; van der Schalie 1939). Although there is little information on which to base a decision, the last-named confluence is perhaps the most likely source of the Interior Basin species in northeastern New York. Several species widespread in the Lake Erie basin (*Epioblasma torulosa rangiana*, *Lampsilis fasciola*, *Obovaria subrotunda*, *Ptychobranchus fasciolaris*, *Villosa fabalis*), the Lake Michigan basin (e.g., *Lasmigona complanata*, *Venustaconcha ellipsiformis*), or both basins (*Cyclonaias tuberculata*, *Epioblasma triquetra*, *Obliquaria reflexa*, *Truncilla* spp.) are strikingly absent from the Ottawa and lower St. Lawrence basins. Because the glacial refuge that supplied the Illinois and Wisconsin Rivers may well have been in Missouri rather than in the Ohio River basin, there may be considerable genetic divergence between populations of Interior Basin species in northeastern New York and those of western and central New York. Only detailed genetic studies are likely to settle the origin of the Interior Basin species in northeastern New York. Whatever their ultimate origin, two of these Interior Basin species (*Lampsilis ovata* and *Pyganodon grandis*) appear to have moved south from Lake Champlain through the Champlain Canal into the Hudson basin.

Other species survived glaciation in refugia on the Atlantic Slope. Thirteen Atlantic Slope species reinvaded the Susquehanna, Delaware, and Hudson basins after deglaciation. The precise routes by which these species reached New York are not known. The lower parts of the Susquehanna and Delaware basins were not glaciated, and in fact, parts of the Hudson basin now below sea level were dry but not ice-covered during glaciation. Species may simply have moved upstream within these basins once they were open. Alternatively, fish hosts may have moved through former confluences on the coastal plain or through brackish coastal waters (cf. Schmidt 1986; Strayer 1987). The same drainage connections that allowed Interior Basin species to move east across New York also permitted unionoid species to move off the Atlantic Slope into central and northern New York. Thus, *Elliptio complanata*, *Lampsilis radiata*, *and Pyganodon cataracta* probably followed early postglacial confluences into the Oswego, Genesee, and Champlain basins. *Alasmidonta undulata*, *Lasmigona subviridis*, and perhaps *Lampsilis cariosa* appear to have followed the Erie Canal westward, as they have limited distributions in central New York. *Ligumia nasuta*, the only Atlantic Slope species that is widespread in the Erie–Niagara basin, apparently moved into Lake Huron through the Trent or Ottawa River outlets, from which it moved back into New York through Lake Erie, although it might also have moved west along the Erie Canal. *Margaritifera margaritifera* probably reached its inland localities (e.g., Lake Champlain, Oneida Lake) through movements of anadromous populations of its salmonid hosts, especially the Atlantic salmon (see Strayer 1987 for a speculative discussion).

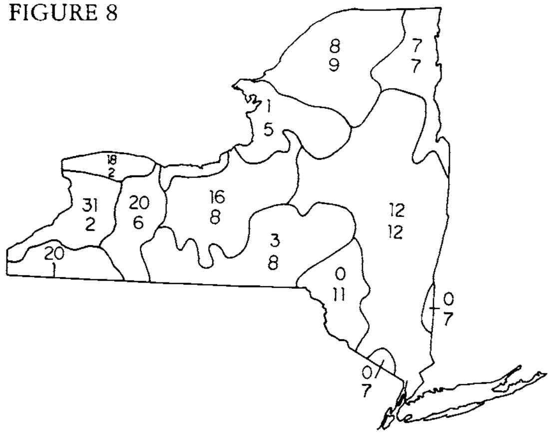
Finally, a few species probably were introduced by humans into parts of their ranges in New York, most likely through fish stocking. The best documented cases are *Ligumia nasuta* in the Allegheny basin and *Uniomerus tetralasmus*, but the occurrence of *Anodontoides ferussacianus*, *Lasmigona compressa*, and even *Alasmidonta marginata* in the Susquehanna basin and *Utterbackia imbecillis* in the Adirondacks all are suggestive of human introductions.

The dispersal history just outlined has had a strong influence on the composition of New York's unionoid communities (Figure 8). Samples taken from parts of New York have almost no species in common with samples taken from other parts of the state, and unionoid community composition can change sharply over short distances when drainage divides are crossed.

Fish Hosts

Because larval unionoids are obligate, more or less species-specific parasites of fish, it would be reasonable to expect the distribution and abundance of unionoids to be closely tied to that of their host fish. Surprisingly little information is available to test this expectation, and what is available does not provide a clear answer about the importance of host distribution as a control of unionoid distribution. Because a complete list of

FIGURE 8



Species richness of unionoids derived from the Interior Basin (upper number) and the Atlantic Slope (lower number) in the major watersheds of New York. *Strophitus undulatus* was assigned to the dominant group in each watershed.

hosts is not available for any North American unionoid species, and many unionoids have no known hosts, evidence bearing on this problem is fragmentary and largely indirect.

Some authors (e.g., Watters 1992) have suggested that concordant geographic patterns of fish diversity and mussel diversity are evidence that fish distribution controls unionoid distribution within a zoogeographic region. Streams that support diverse fish communities usually also contain diverse mussel communities (compare Figure 7 with maps of regional fish diversity [Hocutt and Wiley 1986]; Watters 1992; but see Clark 1977, for a counterexample). It is of course possible that this concordance is evidence that fish and mussels share common controlling factors (e.g., habitat diversity, history, pollution) rather than proof that fish control mussels. Watters (1992), after a careful analysis designed to minimize spurious correlations, concluded that the correlation between fish diversity and unionoid diversity was so strong that it suggested control of the mussel community by fish distribution.

Furthermore, there have been a few striking cases in which human-induced changes in fish distribution caused large changes in mussel distribution. A dam was built across the Mississippi River at Keokuk, Iowa, preventing the upstream movement of the skipjack herring, which is the host of *Fusconaia ebena*. Subsequently, *F. ebena*, formerly an abundant species in the Mississippi River in Wisconsin and Minnesota, nearly disappeared from the upper river (Mathiak 1979). Conversely, as part of a shad restoration program in the Connecticut River, fish "elevators" and ladders were built to allow shad passage over dams. *Anodonta implicata*, which is thought to use *Alosa* spp. as hosts, rapidly followed the shad upstream, extending its range about 200 km (D. Smith 1985b). Thus, in a few cases, we have direct evidence of control of unionoid distribution by fish hosts.

Although these cases are compelling, a large body of distributional evidence exists showing that host ranges are not generally the primary controls of unionoid ranges. Specifically, several papers (e.g., Gordon et al. 1993, 1994; Strayer 1983; Strayer and Ralley 1991) have pointed out that unionoid species occur at only a small proportion of sites where their hosts occur. Indeed, for almost every species included in this book for which any hosts are known (and remember that the lists of hosts given here are incomplete), the range of the hosts in New York (C.L. Smith 1985) is very much greater than the range of the unionoid. The only exceptions are *Leptodea fragilis* and *Potamilus alatus*, whose ranges in New York actually are similar to that of their only known host, the freshwater drum. Nevertheless, the life history of neither of these unionoids has been carefully studied, so it is possible that even they use additional, more widely distributed hosts.

Up to this point, this discussion has assumed that the presence or numbers of a suitable host might determine the presence or numbers of a unionoid species. More subtle interactions are possible. For example, early studies (Arey 1923, 1932; Reuling 1919) showed that even suitable host fish might build up immunity to glochidial infections following exposure to glochidia, and that this immunity might extend to unionoids other than the species involved in the original infection (cf. Weaver et al. 1991). Thus, it is possible that the immune status of the host community, perhaps itself determined by interspecific competition for hosts (see below), rather than simply the presence of a host, might determine unionoid distribution and abundance. In conclusion, we doubt that fish distribution is generally the primary determinant of unionoid distribution, but further work in this area is clearly needed.

Environmental Conditions

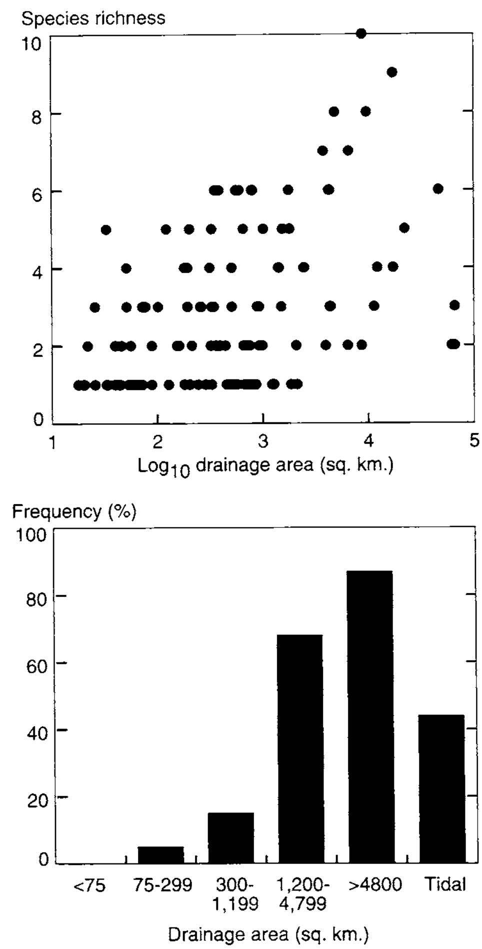
Of course, a mussel species will not be present at a particular site, even if dispersal routes are available and host fish are present, unless environmental conditions are suitable. In fact, mussel species are found at only a small proportion of sites where dispersal routes and hosts are present, suggesting that ecological restrictions of some kind are of paramount importance in determining mussel distribution. Much has been written about the environmental requirements of various mussel species, based on the conditions observed at collection sites, but little of this information is precise, quantitative, or rigorously tested. Consequently, the environmental requirements of most mussel species have not been clearly defined.

No mussel species in our area is found commonly in temporary waters (but see *Uniomerus tetralasmus*), and many more species are found in running waters than in standing waters. Although large, shallow, productive lakes such as Chautauqua and Oneida may support moderately rich mussel assemblages of eight to ten species, most lakes support fewer than five species. Ponds and small lakes often lack unionoids altogether, or contain one or two common species. *Elliptio complanata*, *Pyganodon* spp., *Lampsilis radiata*, and *Lampsilis siliquoidea* are especially frequent in lakes, but no species is restricted to standing waters. Mussels living in lakes often are morphologically distinctive (stunted, inflated, and light colored), apparently in response to ecological conditions in lakes (Baker 1928b; Ortmann 1919; van der Schalie 1941).

Most mussel species are found more frequently in running waters than in standing waters. The size of a stream clearly exerts a strong influence on the composition of the mussel fauna (e.g., Ortmann 1919; Strayer 1983; van der Schalie 1938). Large streams usually contain more mussel species than small streams, and many species are present only in streams above a certain minimum size (Figure 9; see also Strayer 1983; van der Schalie 1938). It is not known which of the many ecological factors that vary with stream size are responsible for determining mussel distribution. Nevertheless, in New York, these patterns are expressed only weakly (Figure 9; see also Strayer 1993), suggesting that other ecological factors are important as well.

The identity, importance, domain, and mode of operation of these other ecological factors are far from clear at present. Many authors have suggested that current velocity and substratum particle size are important determinants of mussel distribution, but several studies (Holland–Bartels 1990; Strayer 1981; Strayer and Ralley 1993; Strayer et al. 1994; see Kat 1982, for a counterexample) have failed to find a strong link between current or substratum and mussel distribution. This area clearly needs further attention. Other ecological factors that seem to be important in some situations include the stability of the substratum

FIGURE 9



Upper: species richness of unionoids as a function of stream size; Lower: frequency of occurrence of *Lampsilis cariosa* in streams of different sizes. Both based on data from the Susquehanna, Delaware, and Hudson River basins of New York and Pennsylvania, after Strayer (1993).

(Vannote and Minshall 1982; Young and Williams 1983a), shear stress on the stream bottom (Layzer and Madison 1995), the hydrology of the stream (Di Maio and Corkum 1995; Strayer 1983, 1993), and water chemistry, especially nutrient concentrations (Bauer 1988; Strayer 1993). These factors deserve careful study to determine the conditions under which they are important. It is remarkable and disappointing that the influence of ecological conditions, apparently of great importance to mussel distribution and the subject of much attention, is still so poorly understood.

Biological Interactions

Of course, it is possible that mussel distribution is determined in part by interactions with other members of the stream biota. The only biological interactions that have received much attention are parasitism on hosts (see section above) and predation by vertebrates, especially mammals. Muskrats, which may take large numbers of mussels, are both species- and size-selective (e.g., Bovbjerg 1956; Hanson et al. 1989; Neves and Odom 1989). Muskrat predation is sometimes so intense (e.g., Neves and Odom 1989) that it probably affects species distributions, at least locally. Raccoons, otters, various birds, and some fish (e.g., sturgeon, freshwater drum, catfish) also take unionoids, although we doubt that they often significantly affect mussel distribution. Studies of predation have focused on adult mussels, but the possibility that predators, whether vertebrate or invertebrate, might consume significant numbers of post-larval or juvenile mussels has not yet been investigated. Mussels also harbor a wide range of parasites and commensals (e.g., Coker et al. 1921; Davids 1973; Gordon et al. 1978; Mitchell 1957; Neves 1987), but none is known to affect mussel distribution.

Competition for food or space among mussel species, or between mussels and other organisms, although dismissed by some authors (e.g., Strayer 1981), has scarcely been investigated (but see Kat 1982). Because mussel species may share hosts and because hosts may, at least in some circumstances, become immune to further glochidial infections after repeated infections, it also is possible that mussels may compete within or among species for hosts. Whether any sort of competition affects distributional patterns remains to be determined.

There are hints from the distributions of several pairs of closely related species in New York that interspecific interactions of some sort may control distributions. Six pairs of such closely related species (one from the Interior Basin, the other from the Atlantic Slope) occur in New York (*Alasmidonta marginata* and *A. varicosa*, *Elliptio dilatata* and *E. complanata*, *Lampsilis ovata* and *L. cariosa*, *Lampsilis siliquoidea* and *L. radiata*, *Lasmigona compressa* and *L. subviridis*, and *Pyganodon grandis* and *P. cataracta*). When the Alleghenian Divide was breached by postglacial outlets to the Great Lakes and later by the Erie Canal, these species were able to expand into each others' ranges and came into contact. In at least two cases (*Lampsilis siliquoidea* and *L. radiata* and the *Pyganodon* species), the species apparently hybridized (Clarke and Berg 1959; Kat 1985, 1986; see also Bianchi et al. 1994, for a parallel case among aquatic snails). Although neither the prevalence nor geographic extent of hybridization is well known, these topics clearly merit further work. What is most striking about the distributions of these six species pairs (and suggestive of interspecific interactions) is the incomplete penetration and overlap of species ranges, even when apparently suitable ecological conditions exist. For example, the two species of *Elliptio* scarcely overlap in New York, although each is widespread and abundant within its range (Figures 23 and 24). Why has *E. dilatata* not moved into the Oswego or Champlain basins? Why did *E. complanata* fail to move west into the Erie–Niagara basin? Both *Elliptio* species thrive under a wide range of ecological conditions, use fish hosts that are present beyond their range boundaries, and have dispersal routes available to them. Likewise, the ranges of *Lampsilis ovata* and *L. cariosa* are most striking (Figures 28 and 30): *L. ovata* is found east and west of the Mohawk basin but never in the Mohawk, while *L. cariosa* is widespread both north and south of the Champlain basin but never in the Champlain basin itself. In fact, it is possible that *L. cariosa* passed through the Champlain basin to reach the St. Lawrence, and later disappeared from the basin. Other intriguing aspects of the distributions of species pairs in New York include the near or complete absence of the extremely eurytopic *Lampsilis siliquoidea* from the St. Lawrence, Champlain, and most of the Hudson basins (Figure 32), the failure of the similarly eurytopic *Lampsilis radiata* to move west beyond the Genesee (Figure 31), and the absence of *Pyganodon grandis* from the St. Lawrence basin (Figure 51). In all these apparently anomalous cases, the other species in the species pair occurs in the area in question. Of course, the distributional evidence we cite is weak and circumstantial and might have arisen by chance, not by species interactions. Nevertheless, we believe that the distributional anomalies are numerous and striking enough to suggest the possibility of strong interspecific interactions between the members of a species pair. Conceivably, these interactions could be genetic (e.g., hybridization and genetic swamping) or ecological (e.g., competition for fish hosts). The nature and strength of interactions between closely related mussel species recently brought into contact might repay close investigation.

A parallel case occurs in the Potomac River, where *Lampsilis ovata* was introduced into the native range of *Lampsilis cariosa* (Ortmann 1919). As *L. ovata* spread through the Potomac system, mussels with shell characters intermediate between *L. ovata* and *L. cariosa* appeared, and pure *L. cariosa* populations seem to have become scarce. The genetic and ecological details of this case are currently under investigation (R. Vilella, pers. comm.).

Human Influences

Post-Columbian human activities have caused large changes in freshwater mussel distribution in New York. We do not know precisely how large these changes have been because we do not have a good historical or archeological record (cf. Bogan 1990) of the pre-Columbian fauna, but as a minimum estimate of human-induced changes, we can compare our current fauna with that observed by nineteenth-century malacologists.

If we simply consider how many species of pearly mussels have been eliminated from New York, human effects look modest. Of the 49 to 52 species that probably once occurred in New York, perhaps six to 12 no longer live in the state, and most of these are peripheral species whose ranges barely reached New York (e.g., *Cyclonaias tuberculata*, *Pleurobema clava*). In view of the enormous environmental changes in New York caused by industry, agriculture, forestry, and urbanization, and the well-known sensitivity of unionoids to environmental degradation (e.g., Ortmann 1909; Fuller 1974; McMahon 1991), this faunal loss seems surprisingly small.

The relatively small statewide species loss may be due in part to the geographic separation between the richest mussel faunas (in largely rural western New York) and the areas of most severe human impacts in eastern and downstate New York. Nevertheless, if we look at metrics other than statewide species loss, we see that human impacts have been more severe than suggested by our initial assessment. About/of the 150 sites we have surveyed recently that once supported unionoids no longer support any unionoids at all; the entire fauna has been destroyed. Most of these defaunated sites are within or downstream from urban or suburban areas. Furthermore, even where some unionoids remain, the fauna may be greatly diminished in richness. Thus, the Delaware River now contains only one or two species, although it probably once held six to 10 (Strayer and Ralley 1991), and the Buffalo River drainage, which used to support at least seventeen species, now contains only six (Strayer et al. 1991). Likewise, the ranges of some species have contracted greatly since 1900, almost certainly as a result of human activities. Good examples include *Alasmidonta varicosa* and *Lasmigona subviridis* (Figures 18 and 37). Thus, we can see that human activities have eliminated several species from New York, modestly to greatly reduced the ranges of many others, completely eliminated the unionoid community from many streams (especially in urban areas), and thinned the community in many other streams.

Several human activities have been especially destructive. Before current pollution regulations were instituted, many streams received large loads of toxic or organic pollutants. The latter reduce or eliminate dissolved oxygen from the water. Such gross pollution killed most or all the aquatic animals, including the pearly mussels. Although many aquatic animals, including fish, returned to these formerly polluted streams when water quality improved, mussels seem to have been slow at recolonizing these streams. The absence of mussels from such streams even after pollution has ceased may reflect the inability of mussels to disperse across drainage divides or over dams, or may indicate that residual pollution (e.g., toxic metals) remains in the stream sediments decades after the streamwater quality has improved. Alternatively, Goudreau et al. (1993) have shown that even trace amounts of pollutants (in their case, a product of wastewater chlorination) can kill mussels in otherwise clean streams.

Physical alteration of the stream channel itself has damaged unionoid communities in many places in New York. Probably the most important of these alterations is stream impoundment, which has several important effects on the stream. Most obviously, the area above the dam, once a running-water habitat, is converted to a slack-water zone, usually with soft sediments, and often subject to large daily or seasonal fluctuations in water level, depending on the purpose of the reservoir. As most unionoid species cannot tolerate such conditions, the unionoid community is usually diminished in richness or eliminated altogether in the reservoir upstream of a dam (Bates 1962; Fuller 1974; Williams et al. 1992). The dam itself often blocks upstream movement of fish and so can reduce the range of any unionoid parasitic on a migratory fish (see discussion of *Fusconaia ebena* above). Furthermore, even if mussels are able to survive both upstream and downstream of a dam, the dam may prevent gene flow between these two populations. Finally, the dam may cause severe effects on unionoids downstream as well (Layzer et al. 1993). Just as the streambed above the dam is raised and filled by fine sediments, the streambed below the dam is robbed of fine sediments, resulting in a streambed that is lower and coarser than the original. By removing the fine particles in which mussels burrow, such scouring, which may extend to tens of kilometers downstream of the dam (Leopold et al. 1964), may have eliminated or impoverished mussel communities at many places in New York (cf. Donnelly 1993; Strayer and Ralley 1993). Also depending on the purpose of the reservoir, the hydrology and water temperature downstream from the dam may be enormously changed by impoundment, with consequent effects on the mussel community. Other physical alterations of the streambed (especially channelization) have had severe effects on mussel communities in parts of New York (e.g., the upper Wallkill [Strayer 1987]).

Urban and suburban developments have destroyed many mussel communities in New York. Other than gross pollution, the exact pathways by which development affects mussels are not well known. Probably the combined effects of increased sedimentation, nutrient enrichment, increased stream temperatures, altered hydrology, and inputs of toxins are involved.

Siltation and nutrient inputs from intensive agriculture are often cited as having negative effects on mussels and other stream-dwelling animals (e.g., Fuller 1974; Trautman 1981; USFWS 1990, 1994; Waters 1995). Agriculture has undoubtedly degraded the stream biota in many parts of the country, but New York's mussels do not show a clear pattern of impacts. The richest mussel communities remaining in the state (excluding the Niagara River) are in Tonawanda Creek and Cassadaga Creek, which support local communities of 13 to 16 species (Strayer 1995). Both streams run through agricultural watersheds and, according to a conventional assessment, both are strongly affected by agriculture. They are always turbid, have high nutrient concentrations, and, at least Cassadaga Creek, have livestock allowed directly in the stream. The impacts of agriculture on pearly mussels must vary considerably, depending on the agricultural practices used, the nature of the watershed, including soils, and the geomorphology of the stream, and in any case have been less damaging to New York's pearly mussels than urban, suburban, and industrial impacts (cf. Strayer 1980).

Finally, there is some evidence that humans have introduced mussels to areas in New York where they would otherwise not occur (see *Ligumia nasuta*, *Lasmigona compressa*, and *Uniomerus tetralasmus* as possible examples). Related to this are human impacts caused by canal building (see "Dispersal Routes") and the introduction of the zebra mussel (see below).

Continuing and Future Threats

We expect many unionoid populations in New York to continue to decline as a result of human activities. Perhaps the most serious threat is the ongoing invasion of the zebra mussel (*Dreissena polymorpha*), a European bivalve which arrived in North America in 1985 (Hebert et al. 1989) and is already widespread in New York (O'Neill and Dextrase 1994). Large numbers of zebra mussels—often hundreds to thousands per unionoid (Ricciardi et al. 1995)—attach to the exposed parts of unionoid shells, interfering with the normal activities of the unionoid and eventually killing the unionoid (Haag et al. 1993; Ricciardi et al. 1995). Within a few decades, zebra mussels will probably occupy most of New York, excluding only calcium-poor (<approximately 15 mg/L Ca) waters (Mellina and Rasmussen 1994; Ramcharan et al. 1992; Sprung

1987), small (<30 m wide) streams (Strayer 1991), and bodies of water with uniformly soft sediments (Mellina and Rasmussen 1994). If impacts on unionoids are as severe in New York as has been seen in the Great Lakes (Haag et al. 1993; Ricciardi et al. 1995), we can expect to lose many of our unionoid populations. Although unionoid populations in the Hudson River have been exposed to zebra mussels for four years, they have not yet been heavily colonized by zebra mussels (Strayer and Smith 1996). Nevertheless, the unionoid populations now appear to be declining sharply (Strayer and Smith 1996).

Suburbanization of watersheds will probably continue to affect mussel populations in New York, as will non-point-source pollution from other land uses. Of particular concern is Bauer's (1988) observation that excessive nitrate appears to cause mussel populations to decline. Inputs of nitrate to streams in New York have been rising over the past few decades from increasing atmospheric inputs (Ollinger et al. 1993) and increasing use of nitrogenous fertilizers (Vitousek 1994). Of course, continued impacts from the human activities listed in the previous section will continue to destroy mussel populations in New York.

Methods

Sources of Information

We examined the following papers for records of pearly mussels from New York: Aldrich (1869), Bailey (1891), Baker (1898, 1901, 1916, 1928b), Beauchamp (1886), Buckley (1977), Call (1878, 1895), Clark (n.d.), Clarke (1981b, 1985), Clarke and Berg (1959), DeKay (1844), Dewey (1856), Grier (1923), Harman (1970a, 1970b, 1973, 1975, 1981, 1982), Harman and Forney (1970), Hoeh and Burch (1989), Jacobson (1945), Jacobson and Emerson (1971), Johnson (1946, 1947), LaRocque and Oughton (1937), Letson (1905, 1909), Lewis (1856, 1860, 1868a, 1868b, 1872, 1874), Marshall (1890, 1892, 1895a, 1895b), Maury (1916), Mearns (1898), Ortmann (1919), Robertson and Blakeslee (1948), D. Smith (1982, 1983, 1985a), Smith and Prime (1870), Strayer (1987), Strayer and Ralley (1991), Strayer et al. (1991, 1994), Townes (1937), Walker (1910), Walton (1891), and Weir (1977). The important paper of Erickson and Fetterman (1996) arrived too late for full consideration. We did not plot their records on the distribution maps, but we discuss them in the text.

We also examined specimens from New York in several museum collections (Table 1). Although we did not visit the Illinois Natural History Survey (INHS), Kevin Cummings was kind enough to send us a complete listing of their small but important collection of material from New York and send us several key lots for examination. As this book was in press, we examined the list of specimens held by the Rochester Museum and Science Center (RMSC), and examined several key lots, but we did not plot these distributional records on the maps. Significant records from the RMSC are discussed in the text. Because of time limitations and because not all of our museum visits were made with this book specifically in mind, we did not check all the specimens of all species. As a rule, our museum visits focused on the rarer species. Thus, museums contain additional distributional records for the common species, although it is unlikely that adding these records would substantially change the distributional patterns plotted on our maps.

Finally, we have included records from several recent, unpublished surveys as follows: Jirka's (1991) survey of 19 sites in the Susquehanna basin in New York; Strayer's (1992) survey of 20 sites in the Housatonic and Rondout basins in southeastern New York; Strayer's (1994) survey of 21 sites in the Passaic basin in southeastern New York; Strayer's (1995) survey of 15 sites in the Allegheny, Schoharie, and Tonawanda Creek basins; and Kathryn Schneider's survey of 30 sites in the Susquehanna basin and elsewhere in 1995. Brief reports of these surveys were submitted to the New York Natural Heritage Program, and significant vouchers are deposited in the New York State Museum. In addition, Doug Carlson of the New York State Department of Environmental Conservation kindly sent us several important records from northern New York as a byproduct of his fisheries surveys. Carlson's vouchers also are in the New York State Museum.

Erroneous and Questionable Records

In the distribution maps that follow, we have plotted records that we think are reliable and excluded those that we think are erroneous. If there is substantial doubt about the reliability of a record, whether plotted or not, we discuss the record and the evidence for its reliability in the text.

A record can be doubtful for two reasons: incorrect or uncertain identification of the species and incorrect or uncertain attribution of the collection locality. The strongest evidence for a correct species identification is personal examination of the specimen in question. For literature records unsupported by museum specimens, we were most likely to accept an identification if (1) the species is distinctive and not likely to be confused with other species; (2) the author was an experienced malacologist; and (3) the record is recent. As species concepts and range limits have become better understood, misidentifications have become less likely. For example, the range and diagnostic characters of *Anodonta implicata* were not widely understood until the early to middle twentieth century, which resulted in a large number of erroneous records of this species from central and western New York even by respected malacologists. Now that the morphological and geographical limits of this species are well understood (Johnson 1946), erroneous records are few.

TABLE 1

Museum Collections Examined for Specimens from New York

Species	AMNH	ANSP	BSM	MCZ	NYSM	OSUM	UMMZ	USNM
Actinonaias ligamentina	●	●	●	●	●	●	●	●
Alasmidonta heterodon	●	●	●	●	●	●	●	●
Alasmidonta marginata	●	●	●	H	●	●	●	D,H
Alasmidonta undulata	●	●	●	H	●	●	H	D,H
Alasmidonta varicosa	●		●	H	●	●	●	●
Alasmidonta viridis	●	●	●	●	●	●	●	●
Amblema plicata	●	●	●	●	●	●	●	H
Anodonta implicata	●	●	●	H	●	●	●	D,H
Anodontoides ferussacianus	●	●		H	●	●	●	H
Cyclonaias tuberculata	●	●	●	H	●	●	●	H
Elliptio complanata		■	●	H		■	■	D,H
Elliptio dilatata	●	●	●	H	●	●	■	H
Epioblasma obliquata	●	●	●	●	●	●	●	●
Epioblasma torulosa rangiana	●	●	●	●	●	●	●	●
Epioblasma triquetra	●	●	●	●	●	●	●	●
Fusconaia flava	●	●	●	●	●	●	●	H
Lampsilis abrupta	●	●	●	●	●	●	●	●
Lampsilis cariosa	●	●	●	H	●	●	●	D,H
Lampsilis fasciola	●	●	●	●	●	●	●	●
Lampsilis ovata	●	●	●	H	●	●	■	H
Lampsilis radiata	●	●	●	H	●	■	H	D,H
Lampsilis siliquoidea	●	●	●	H	●	■	H	H
Lampsilis teres	●	●	●		●	●	●	
Lasmigona complanata	●	●	●		●	●	●	
Lasmigona compressa	●	●	●	●	●	●	●	H
Lasmigona costata	●	●	●	H	●	●	■	H
Lasmigona subviridis	●	●	●	H	●	●	●	●
Leptodea fragilis	●	●	●	●	●	●	●	●

Key to symbols: ● = all specimens examined and all records included in this book; ■ = all specimens examined but only significant records included in this book; H = all specimens from the Hudson River basin examined and included in this book; D = all specimens from the Delaware River basin examined and included in this book.

Museum abbreviations as follows: AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences at Philadelphia; BSM = Buffalo Science Museum; MCZ = Musuem of Comparative Zoology (Harvard University); NYSM = New York State Museum; OSUM = Ohio State University Museum of Biological Diversity; UMMZ= University of Michigan Museum of Zoology, USNM = National Museum of Natural History, Smithsonian Institution.

TABLE 1, *continued*
Museum Collections Examined for Specimens from New York

Species	AMNH	ANSP	BSM	MCZ	NYSM	OSUM	UMMZ	USNM
Leptodea leptodon	●	●	●		●	●	●	●
Leptodea ochracea	●	●	●	H	●	●	●	●
Ligumia nasuta	●	●	●	■	●	●	●	●
Ligumia recta	●	●	●	●	●	●	●	●
Margaritifera margaritifera	●	●	●	H	●	●	●	●
Obliquaria reflexa	●	●	●	●	●	●	●	●
Obovaria olivaria	●	●	●	●	●	●	●	●
Obovaria subrotunda	●	●	●		●	●	●	●
Pleurobema clava	●	●	●	●	●	●	●	
Pleurobema cordatum	●	●	●	●	●	●	●	●
Potamilus alatus	●	●	●	●	●	●	●	H
Potamilus capax	●	●	●	●	●	●	●	
Potamilus ohiensis	●	●	●		●	●	●	
Ptychobranchus fasciolaris	●	●	●	●	●	●	●	●
Pyganodon cataracta	D,H	●		H	●		H	D,H
Pyganodon grandis	H	●		H	●		H	H
Pyganodon lacustris		●			●			
Quadrula pustulosa	●	●	●		●	●	●	
Quadrula quadrula	●	●	●		●	●	●	
Simpsonaias ambigua	●	●	●		●	●	●	
Strophitus undulatus	D,H	●		●	H		H	D,H
Toxolasma parvum	●	●	●	H	●	●	●	●
Truncilla donaciformis	●	●	●		●	●	●	●
Truncilla truncata	●	●	●		●	●	●	●
Uniomerus tetralasmus	●	●	●		●	●	●	●
Utterbackia imbecillis	●	●	●	●	●	●	●	●
Villosa fabalis	●	●	●	●	●	●	●	●
Villosa iris	●	●	●	H	●	●	●	●

Key to symbols: ● = all specimens examined and all records included in this book; ■ = all specimens examined but only significant records included in this book; H = all specimens from the Hudson River basin examined and included in this book; D = all specimens from the Delaware River basin examined and included in this book.

Museum abbreviations as follows: AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences at Philadelphia; BSM = Buffalo Science Museum; MCZ = Musuem of Comparative Zoology (Harvard University); NYSM = New York State Museum; OSUM = Ohio State University Museum of Biological Diversity; UMMZ= University of Michigan Museum of Zoology; USNM = National Museum of Natural History, Smithsonian Institution.

Erroneous collection localities arise frequently from carelessness in labeling specimens, switches of specimens or labels in museums, etc. Unfortunately, misattributed collection localities are more difficult to detect and evaluate than misidentifications because it is not possible to verify the collection locality. We suspect incorrect attribution of the collection locality if (1) the specimen is correctly identified but far out of its known range or usual habitat; (2) the specimen does not have a lot number or collection locality written on the shell, meaning that a label or specimen switch could have gone undetected; or (3) the specimen belongs to a series of lots with many problematic localities. For example, ANSP contains a series of lots with distinctive, cardboard labels bearing the locality "Mohawk" or "Upper Red Hook". Many of the species in this series are far out of range. Apparently, these lots were labeled with the address of the donor (James Lewis and W.S. Teator, respectively), rather than the site of collection, a fairly common practice in the nineteenth century (cf. Heard 1962). We therefore regard the collection localities of all these distinctively labeled lots as unknown.

Three localities in New York are especially problematic. Three lots in ANSP are attributed to "Dansville, Livingston County" (ANSP 365661: *Lampsilis cariosa*; ANSP 365734: *Pleurobema cordatum*; ANSP 365773: *Lampsilis ovata*, locality written on shell); all these are more or less outside their known ranges. Until field investigations of Canaseraga Creek confirm the existence of at least one of these species in the Dansville area, we are inclined to regard these records as doubtful.

Likewise, Sodus Bay is given as the collection locality and written on the shells for UMMZ 74013 (*Ptychobranchus fasiolaris*) and UMMZ 79338 (*Potamilus alatus*). The former is well out of range, but neither record is entirely implausible, given the eastward extension of many Ohioan species across the Lake Ontario lowlands. Again, we prefer to treat these two records as questionable until they are verified.

The most problematic locality in New York is the Niagara River and nearby western New York. In the late nineteenth century and early twentieth century (Beauchamp 1886; Letson 1905, 1909; Lewis 1874; Marshall 1895a; see also Robertson and Blakeslee 1948), several species that were out of their known ranges were recorded from the Niagara River or western New York. Some of these records arose from misidentifications (e.g., *Epioblasma obliquata*, *Leptodea leptodon*, *Ligumia subrostrata*, *Potamilus ohiensis*, *Venustaconcha ellipsiformis*; see "Species Erroneously Recorded from New York"). Other records are well supported by authentic specimens and truly represent somewhat disjunct or peripheral populations. Examples include *Epioblasma triquetra*, *Quadrula pustulosa*, *Quadrula quadrula*, *Simpsonaias ambigua*, *Truncilla donaciformis, and Truncilla truncata*. Left in limbo are three species (*Lampsilis abrupta*, *Lampsilis teres, and Potamilus capax*), said to have been collected from the Niagara River. These collections are supported by correctly identified specimens. All these species are said to have been collected between 1890 and 1910, when the Buffalo Society of Natural Sciences had an active conchological section led by Elizabeth Letson and Mary Walker (Robertson and Blakeslee 1948). In addition, *L. teres* was said to have been taken from the Buffalo area by Coleman T. Robinson in the mid- to late nineteenth century (Lewis 1874; Marshall 1895a).

All three of these species are well out of range in New York. None has been recorded from elsewhere in the Great Lakes basin; the nearest generally accepted records are from the Wabash basin in Indiana. Nevertheless, specimens of these rare species are attributed to different collectors at different times, and all have "Niagara r." written on the shells, reducing the probability that these records arose from label switches or a misattributed collection. Furthermore, although the Wabash and the Niagara are geographically distant, they once were closely connected. About 14,400 years ago, glacial ice prevented Lake Erie from draining to the north or east. Instead, its outlet was through the Maumee River, which drained southwest across the low divide at Fort Wayne, Indiana, to the Wabash River. Most of the fish and unionoids now living in the Lake Erie basin colonized the basin from the Wabash through the Maumee outlet (Bailey and Smith 1981; van der Schalie 1938). When the Niagara outlet was finally free of ice about 13,300 years ago, the present-day Lake Erie was nearly dry. The Maumee and Detroit Rivers formed the headwaters of a large river which ran northeast to Buffalo. As the elevation of the sill at Niagara relative to the western end of the Lake Erie basin rose due to isostatic rebound, this river was gradually drowned and replaced by present-day Lake Erie. The only large section of this river that remains is the Niagara River.

The Detroit River did not reach its present large size until after much of Lake Erie was filled, and it was therefore isolated from the Niagara River. Thus, any large-river mussels that crossed the Wabash–Erie divide would have found continuous large-river conditions only in the Niagara River, although the Detroit and Maumee Rivers have always been fairly large and do in fact support some large-river species—*Obovaria olivaria*, *Obliquaria reflexa*, *Truncilla* spp. It is at least possible that a relict, disjunct large-river unionoid fauna lives in the Niagara River, and records of *Lampsilis abrupta*, *Lampsilis teres*, and *Potamilus capax* are authentic. This problem will be solved only by careful thorough collecting in the Niagara River.

Collecting and Identifying Pearly Mussels

Collecting and Preserving Pearly Mussels

For routine faunal surveys in shallow, clear water, unionoids are usually collected by handpicking (i.e., collectors find the mussels by visual searches and then pick them up by hand). Some collectors find that a glass-bottomed bucket is advantageous in finding pearly mussels. A mask and snorkel are also very helpful, especially if small species or young mussels are being sought.

Several methods may be used in water too deep to search while wading or snorkeling. SCUBA diving is a very effective way to collect mussels from deep water (Miller et al. 1993). Alternatively, one may use grabs (see below) or dredges in deep water.

Some streams, especially in agricultural areas (e.g., Conewango and Tonawanda Creeks), are rarely clear enough to allow visual searches for mussels. In such cases, one is restricted to finding empty shells along the banks or searching for shells and mussels by feel, taking care to remember that many of our streams are full of broken glass and sharp pieces of metal, especially near bridge crossings.

Quadrats are commonly used for quantitative work. Visual searches of quadrats are quick and non-destructive, but they will not produce reliable estimates of the densities of small or buried animals (Amyot and Downing 1991). Alternatively, quadrats can be excavated and the collected material sieved to collect juveniles as well as adults (Miller and Payne 1993). Excavating and sieving quadrats takes more time than visual searches and may be more disruptive to mussels. Although grabs have sometimes been used in quantitative studies of pearly mussels (Negus 1966; Strayer et al. 1994), they have not been properly tested to see that they actually recover mussels quantitatively. There is some indication that Ekman grabs underestimate mussel numbers (Haukioja and Hakala 1974). If grabs are used, a relatively large grab with a strong bite (e.g., a standard 23 x 23 cm PONAR grab) is preferable. Depending on the minimum size of juveniles to be recovered, a relatively coarse-mesh sieve (e.g., 2 mm) may be used.

It is illegal to collect living pearly mussels in New York without a special scientific collector's permit issued by the Department of Environmental Conservation. Scientific collectors should be careful not to damage mussel populations through excessive collecting or handling of living mussels. Because mussels have long life cycles and populations may be small and local, careless collecting can badly damage pearly mussel populations. It is rarely necessary to collect living specimens during routine surveys; spent shells suitable for vouchers or reference collections are usually readily found. A particularly good spot to find nice, clean spent shells is in muskrat middens, although Watters (1994b) has shown that middens do not contain an unbiased sample of the mussel community. These middens often contain hundreds or thousands of shells, including those of small species.

Alternatively, if spent shells cannot be found, a clear photograph may serve to document the occurrence of a rare species. The few studies that have been made of the effects of handling on pearly mussels suggest that mortality from handling is small but not negligible (Dunn 1993; Imlay 1972). It makes sense to handle living mussels as little as possible and to gently rebed them in their place on the stream or lake bottom.

Because of declines in range and abundance, several species of pearly mussels are now protected under the endangered species laws of New York or the United States (Table 2). Without endangered species permits, which differ from ordinary scientific collectors' permits, from the New York State Department of Environmental Conservation and the United States Fish and Wildlife Service it is illegal to kill, disturb, or possess living or dead specimens of species listed as endangered or threatened. In addition to these listed species, many species of pearly mussels are rare and declining. Because of the current political climate in New York and in the U.S. Congress, it is unlikely that many of these species will soon receive special legal protection. Although not now protected, these species (Table 2) should be treated especially cautiously.

For most purposes, dry shells make adequate specimens. Stansbery and Stein (1983) described a procedure for producing especially fine specimens of dry shells. If the animal itself is to be preserved, 70% ethanol is suitable for long-term storage. The specimen should not be left in formaldehyde over the long term. The best specimens should be relaxed and fixed properly before storing them in alcohol.

Although many procedures have been used to relax and fix mussels (see Coney 1993, for a critical review), D. Smith (1982) described a simple procedure using readily available materials. Animals are placed in water from the collection site to which menthol crystals are added. After the animal is well relaxed (usually 24 to 36 hours), 10% formalin (= 4% formaldehyde) is hypodermically injected into the pericardium.

TABLE 2

Rare or Protected Pearly Mussels of New York.

Species	Status[a]	Legal status
Alasmidonta heterodon	E	NY-E, US-E
Alasmidonta marginata	SC	
Alasmidonta undulata	SC	
Alasmidonta varicosa	T	
Alasmidonta viridis	SC	
Epioblasma triquetra	T	
Lampsilis abrupta	E	US-E
Lampsilis cariosa	T	
Lampsilis fasciola[b]		
Lampsilis ovata	SC	
Lasmigona subviridis	T	
Leptodea ochracea	SC	
Ligumia nasuta	SC	
Ligumia recta	SC	
Margaritifera margaritifera	SC	
Obovaria subrotunda	SC	
Pleurobema clava	E	US-E
Potamilus capax	E	US-E
Simpsonaias ambigua	SC	
Villosa fabalis	SC	

[a] Status taken from Williams et al. (1993), as follows: E = endangered ("in danger of extinction throughout all or a significant portion of its range"); T = threatened ("likely to become endangered throughout all or a significant portion of its range"); SC = special concern ("may become endangered or threatened by relatively minor disturbances to its habitat"). Codes for legal status: NY-E = listed as endangered by the New York State Department of Environmental Conservation; US-E = listed as endangered by the United States Fish and Wildlife Service.

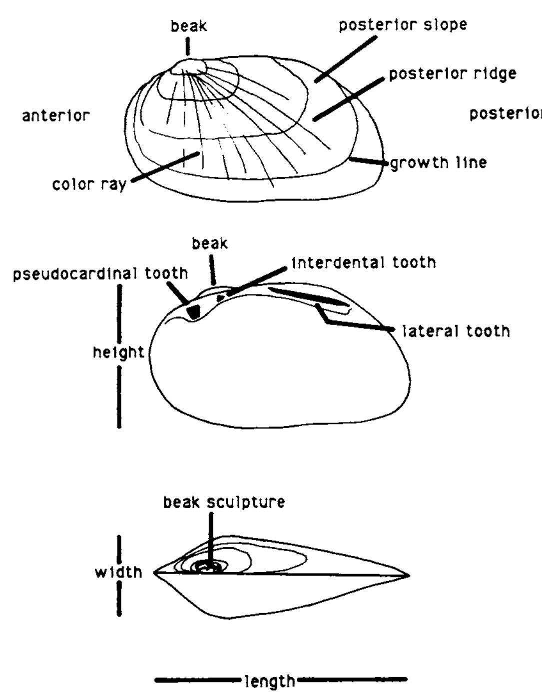
[b] While not listed as threatened or endangered by Williams et al. (1993), *Lampsilis fasciola* is listed by several states (Cummings and Mayer, 1992), and we believe it is rare enough to deserve legal protection in New York.

After 3 to 7 days in formalin, the animals are transferred to 70% ethanol or 70% isopropyl alcohol for long-term storage.

Terms Relevant to the Identification of Pearly Mussels

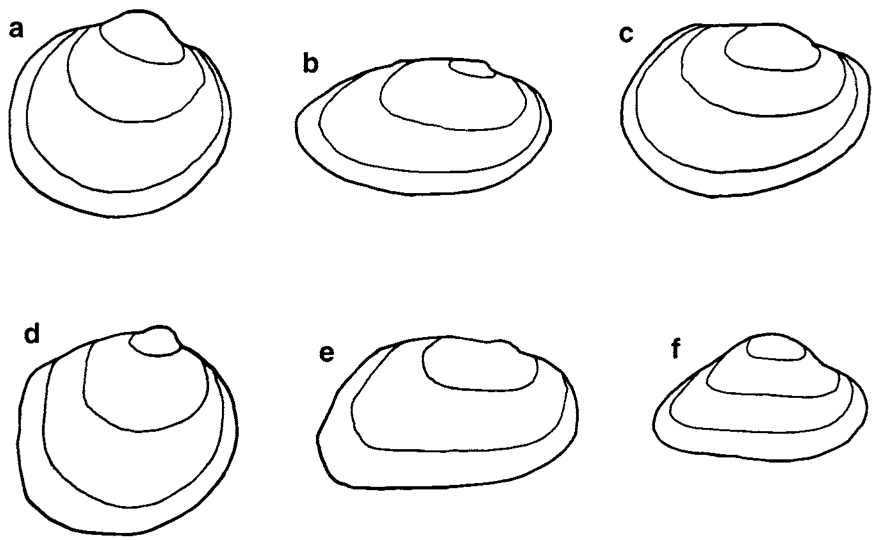
Our keys and species descriptions are based largely on shell characters. This focus on shell characters is not because the shells are so useful in defining species and genera; in fact, the "soft parts," particularly the reproductive organs, provide most of the really important characters that define genera and subfamilies (Davis and Fuller 1981). Nevertheless, we do not advocate killing mussels for routine identification. Species are usually identifiable from shell characters alone. Indeed, living animals can usually be identified from external shell characters alone, and spent shells often are the only material available on which to make an identification. Descriptions of the soft parts of most of New York's unionoids are available in Ortmann (1912).

FIGURE 10



Schematic diagram of a unionoid shell, showing the major features used in identification.

FIGURE 11



Shapes of unionoid shells. a. subcircular; b. subelliptical; c. subovate; d. subquadrate; e. subrhomboidal (=subtrapezoidal); f. subtriangular.

The short end of a unionoid shell is its anterior, and the side along which the two halves of the shell are attached is the dorsal side. The length, width, and height of the shell are measured as shown in Figure 10. The beak (sometimes called the umbo) is the oldest part of the shell and sometimes protrudes well above the dorsal margin of the shell. Unionoid shells are typically marked with dark, concentric growth lines, which may not always be annual (Downing et al. 1992).

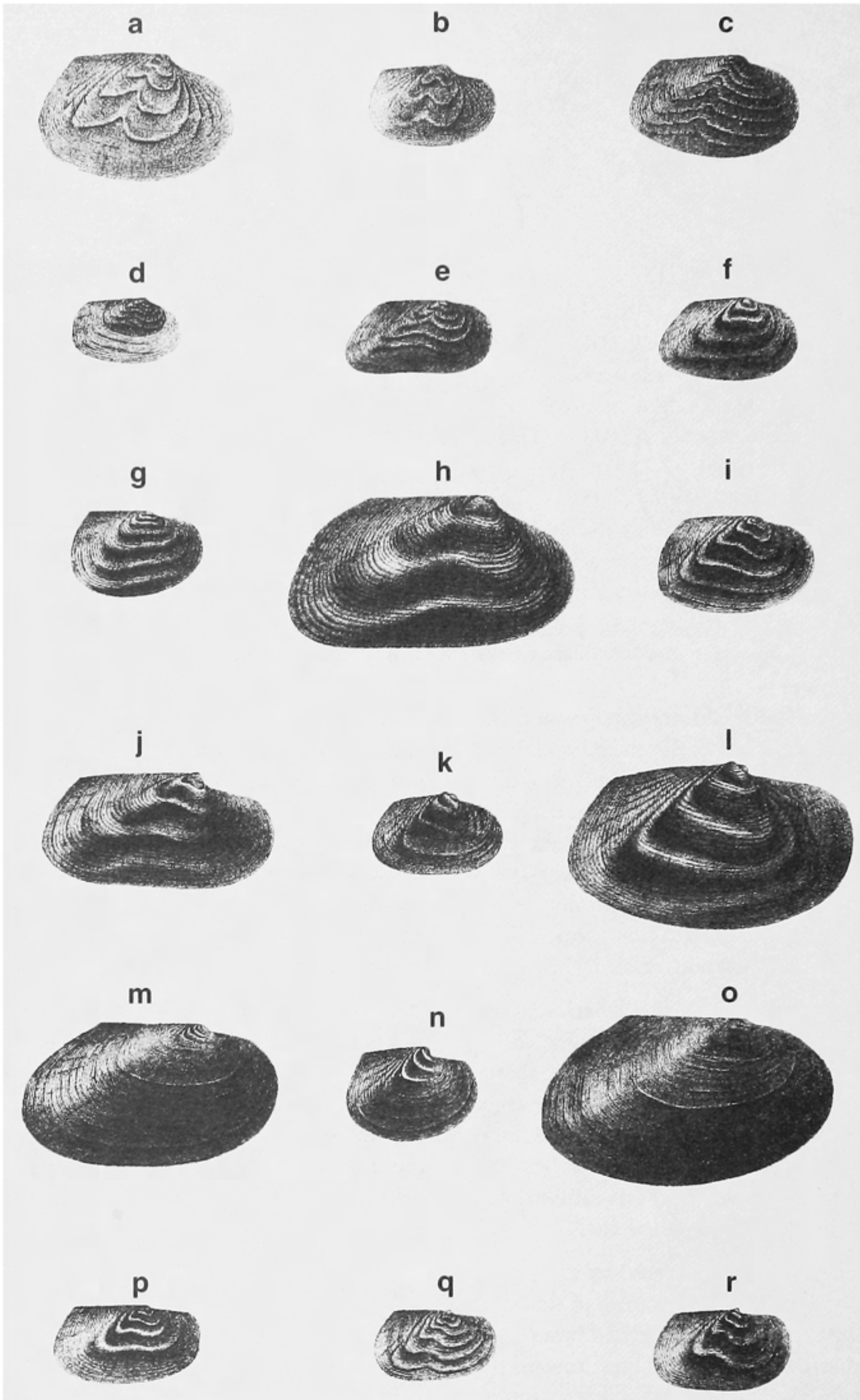
One of the most important external shell characters is the shape of the shell. Shell shapes in lateral view are usually described with reference to the geometric shape they most closely resemble (Figure 11). In dorsal view, a shell can be compressed (narrow) or inflated (wide, especially near the beaks). Often, there is a more or less well-defined ridge (the posterior ridge) separating the posterior slope from the remainder of the shell.

The exterior of a unionoid shell is covered by a colored periostracum. The color and texture of the periostracum and the presence, location, and nature of green "color rays" that radiate from the beak toward the shell margin are useful in distinguishing among mussel species. The shell exterior may be marked with more or less distinct knobs or ridges as well, which also are species-specific. Watters (1994c) analyzed the functional significance of shell sculpture as well as shell shape.

An external character that is rarely used but can be very helpful is the beak sculpture. Beak sculpture refers to the fine, raised lines on the very tip of the beak. The pattern of beak sculpture differs across species (Figure 12) and can often be used to distinguish between otherwise similar species. Unfortunately, in specimens from New York, the beak sculpture is often obliterated, especially in animals that are old or live in soft water.

The interior of the shell is made up of nacre, or mother-of-pearl, which may be white, bluish white, salmon, pink, or purple. The most important characters in the inside of the shell are the presence, type, and shape of the hinge teeth (Figure 10), which are protuberances along the dorsal margin of the shell that help hold the two halves of the shell together. There are two common kinds of hinge teeth: (1) pseudocardinal teeth, usually stumpy or triangular, which are near the beak; and (2) lateral teeth, long, sharp ridges running along the dorsal margin of the shell from the beak region toward the posterior end of the shell. Various species may have one, both, or neither of these two kinds of hinge teeth. In addition, a few species have interdental teeth, which are protuberances lying between the pseudocardinals and the laterals.

FIGURE 12



Beak sculpture of some unionoids, from Marshall (1890). a. *Lasmigona compressa*; b. *Lasmigona subviridis*; c. *Lampsilis siliquoidea*; d. *Lampsilis radiata*; e. *Ligumia nasuta*; f. *Elliptio complanata*; g. *Leptodea ochracea*; h. *Alasmidonta marginata*; i. *Lampsilis cariosa*; j. *Lasmigona costata*; k. *Strophitus undulatus*; l. *Alasmidonta undulata*; m. *Anodontoides ferussacianus* (whole shell of young animal); n. *Anodontoides ferussacianus*; o. *Pyganodon grandis* (whole shell of young animal); p. *Anodonta implicata*; q. *Pyganodon cataracta*; r. *Pyganodon grandis*.

Identification Keys

Notes on the Keys

After much thought, several headaches, and much gnashing of teeth, we have decided that it is probably impossible to write a simple, friendly, reliable key to the species of unionoids found in New York. It is certainly impossible for us. Keys based on shell characters are inevitably filled with vague, subjective terms, are frustrating for beginners to use, and misidentify many shells. Although a key based on soft anatomy (see Ortmann 1919 for a good example) would be less ambiguous and more reliable, the shell is often the only part of the animal available for study. Furthermore, we are very reluctant to encourage the collection of living unionoids, especially merely for routine identification. Our solution to this dilemma has been to write a frustrating, sometimes unreliable key based on shell characters and filled with vague, subjective terms, but to make it the friendliest and most reliable vague, frustrating key that we could. **Users should know that if they rely solely on this key, they will misidentify many shells.** Users should employ the key to make a provisional identification, then carefully compare the specimen with the illustrations and species description, which includes remarks on how to tell the species from other similar species.

Many misidentifications occur when beginners try to use a unionoid key to identify bivalves that are not unionoids. If it is not clear whether a given specimen is a unionoid rather than another bivalve, it may be best to run it through the short key to the families of freshwater bivalves of New York, which precedes the key to unionoid species. Other misidentifications may occur if a specimen has been collected in brackish water where additional bivalves of marine affinities occur (see Gosner 1971 for keys to this fauna), or if it is a discarded shell of an edible marine species (e.g., oysters, hardshell clams) from someone's picnic. The latter are surprisingly common in New York, even at fairly remote sites. These marine shells differ conspicuously from unionoids in shell structure; perhaps most obviously, the hinge teeth do not match those of the unionoid pattern (see above and Figure 10).

Learning to identify pearly mussels is simply a matter of learning to recognize the species by sight. Most of our species can be readily recognized, usually from external characters visible on living specimens. We think the best way to learn our unionoids is to take a favorite guide (e.g., Burch 1975a; Clarke and Berg 1959; Ortmann 1919; ours; D. Smith 1995) to a collection of properly identified shells (e.g., at one of the museums in the state), study the shells, and mark up your guide until you begin to recognize the species. Perhaps two or three days would be required to learn most of New York's species.

The key is in the standard dichotomous format, with alternatives designated as "a" or "b." The number in parentheses which follows the couplet number is the number of the couplet that led to it. This feature allows the user to work backwards through the key in the event of a questionable identification.

Key to the Families of Freshwater Bivalves of New York

1a. Animal attached to the substratum by a tough "beard" of fibers; shell more or less flattened ventrally, so it is triangular in cross-section, and usually marked with light and dark bands; the two halves of the shell attached by a ligament that is inside the shell; hinge teeth absent. . . . . **Dreissenidae**
(zebra mussels and relatives)

1b. Animal usually free-living (juvenile pearly mussels may be attached to substrata by a single, long fiber); shell not flattened ventrally; external color various; the two halves of the shell attached by a ligament that is readily visible from outside the shell; hinge teeth present or absent. 2

2a (1b). Hinge teeth consist of stumpy pseudocardinal teeth near the beaks, flanked on only the posterior side by elongate lateral teeth (either or both of these sets of teeth may be missing or reduced, but there never are lateral teeth anterior to the stumpy teeth near the beaks); inside of shell bright and lustrous white, bluish white, pink, orange, or purple; shell often >50 mm long . . . . **Unionidae** and **Margaritiferidae**
(pearly mussels; see key to species below)

2b. Hinge teeth consist of stumpy cardinal teeth near the beaks, flanked on both sides by elongate lateral teeth; inside of shell dull gray; shell always <50 mm long (usually <25 mm long). . . . 3

3a (2b). Lateral hinge teeth conspicuously serrated; outside of shell with coarse, concentric striae; shell solid, often >20 mm long; found at only a few sites in New York, chiefly on Long Island . . **Corbiculidae**
(*Corbicula fluminea*)

3b. Lateral hinge teeth with smooth surfaces; outside of shell smooth or with fine, concentric striae; shell thin, <25 mm long; widely distributed and common in New York . . . . . . **Sphaeriidae**
(fingernail and pill clams; for identification, see Burch 1975b; Clarke 1981a; Herrington 1962; Mackie et al. 1980; Smith 1995)

Key to the Species of Pearly Mussels of New York

1a. Face of shell with conspicuous, well-defined pustules, knobs, or ridges; hinge teeth massive 2

1b. Shell rough or smooth, but not with well-defined pustules or ridges on the face of the shell (posterior slope may contain ridges); hinge teeth may be strong, weak, or entirely missing. . . 6

2a (1). Outside of shell with ridges (Plate 21, Figures 1 and 3; Plate 22). . . . . . *Amblema plicata*

2b. Outside of shell with knobs or pustules (Plate 12, Figures 2 and 3; Plate 26, Figures 1 through 3; Plate 27, Figure 8) 3

3a (2). Nacre purple . . . . *Cyclonaias tuberculata* (Plate 26, Figures 1 and 2)

3b. Nacre white. 4

4a (3). Outside of shell with a few (<5/valve) large knobs on central part of shell (Plate 26, Figure 3) . . . . *Obliquaria reflexa*

4b. Outside of shell with pustules, which are usually small and numerous (Plate 12, Figures 2 and 3; Plate 27, Figure 8) . . . . *Quadrula* spp. . . 5

5a (4). Shell with a prominent median sulcus; pustules usually extending onto beaks; beak sculpture double-looped . . . . *Q. quadrula* (Plate 27, Figure 8)

5b. Shell more or less evenly rounded, without sulcus; pustules usually absent from beak region; beak sculpture concentric; often with characteristic broad green color ray near beaks . . . . *Q. pustulosa* (Plate 12, Figures 2 and 3)

6a (1). Hinge teeth entirely absent or at most represented by small poorly defined ridges or knobs . . . 7

6b. Conspicuous hinge teeth present 14

7a (6). Beaks not projecting above hinge line (Plate 9, Figures 3 and 4); shell very thin. *Utterbackia imbecillis*

7b. Beaks projecting above hinge line 8

8a (7). Shell small (<50 mm long), about twice as long as high; pseudocardinal teeth small but distinct . . . . *Simpsonaias ambigua* (Plate 19, Figure 7; Figure 13 c)

8b. Shell often >50 mm long, often less than twice as long as high; pseudocardinal teeth entirely absent or represented by an indistinct thickening of the nacre. 9

9a (8). Beak sculpture concentric (Figure 12 k, n). 10

9b. Beak sculpture double-looped (Figure 12 p-r) 11

10a (9). Beak sculpture coarse (Figure 12 k); nacre usually bluish white along the margins and orangish in the beak cavity. . . . . *Strophitus undulatus* (Plate 17, Figures 1 through 3)

10b. Beak sculpture fine (Figure 12 n); nacre usually bluish white throughout. . . . . *Anodontoides ferussacianus* (Plate 17, Figures 4 through 6)

11a (9). Nacre distinctly pink or purple; shell markedly thickened anteriorly. . . . . . *Anodonta implicata* (Plate 15, Figure 1; Plate 26, Figure 4; Figure 12 p)

11b. Nacre usually silvery white or bluish (sometimes discolored and orangish); shell not especially thick anteriorly . . . . *Pyganodon* spp. 12

12a (11). Beak sculpture nodulous (i.e., unequal in height and thickness) (Figure 12 r; Figure 13 a); periostracum often brownish or yellowish . . . . *P. grandis* (Plate 13)

12b. Beak sculpture not nodulous (Figure 12 q; Figure 13 b); periostracum often greenish 13

13a (12). Beak sculpture usually with 7-8 ridges (Figure 13 b); shell very thin . . . . *P. lacustris* (Plate 15, Figures 2 and 3; Plate 16)

13b. Beak sculpture usually with 5 ridges (Figure 12 q; Figure 13 b), shell moderately thin to very thin. . . . . *P. cataracta* (Plate 14)

14a (6). Lateral teeth absent or vestigial. 15

14b. Lateral teeth well developed enough to interlock 22

15a (14). Shell long (H/L = approximately 0.5), often a little arched, and without color rays; lateral teeth usually entirely absent. 16

15b. Shell long to short ($H/L = 0.5-0.7$), not arched, and usually with fine, green color rays; lateral teeth vestigial but usually apparent 17

16a (15). Shell small (<50 mm long) and thin with gray to brown periostracum (western New York) . . . . *Simpsonaias ambigua* (Plate 19, Figure 7; Figure 13 c)

16b. Shell large (adults >75 mm long) and solid with blackish periostracum (eastern New York) . . . . *Margaritifera margaritifera* (Plate 24, Figure 5)

17a (15). Shell very compressed, with a large dorsal wing . . . . *Lasmigona complanata* (Figure 13 d)

17b. Shell compressed to inflated; dorsal wing absent or (on some young specimens) small 18

18a (17). Posterior slope with prominent ridges crossing the growth lines; shell compressed ($W/H < 0.6$) . . . . *Lasmigona costata* (Plate 18, Figures 2 and 3; Figure 12 j)

18b. Posterior slope smooth or with fine ridges crossing the growth lines; shell inflated (W/H usually >0.6) . . . . *Alasmidonta* spp. 19

19a (18). Posterior slope with fine but distinct ridges crossing the growth lines (Plate 20, Figures 1 through 6); pseudocardinal teeth delicate, elongate, and with smooth surfaces (Plate 20, Figure 1b). 20

19b. Posterior slope without distinct ridges crossing the growth lines; pseudocardinal teeth strong, triangular, and with rough surfaces (Plate 18, Figure 1) 21

20a (19). Posterior ridge angular and prominent; posterior slope usually distinctly lighter- colored than the rest of the shell; shell truncate, up to 100 mm long; color rays usually broken up into spots (widespread in New York) . . . . *A. marginata* (Plate 20, Figures 1, 5, and 6; Figure 12 h)

20b. Posterior ridge rounded; posterior slope not lighter-colored than the rest of the shell; shell somewhat rounded, usually less than 70 mm long; color rays usually continuous (southeastern New York). . . . . *A. varicosa* (Plate 20, Figures 2 through 4)

21a (19). Shell subrhomboid, less than 50 mm long (western New York) . . . . *A. viridis* (Plate 18, Figure 1)

21b. Shell subtriangular to subovate, reaching 80 mm long (central and eastern New York) . . . *A. undulata* (Plate 12, Figures 4-6; Figure 12 l)

22a (14). H/L ≤0.48. 23

22b. H/L >0.48 25

23a (22). Periostracum glossy yellow, with or without fine color rays (Plate 10, Figure 4); a very rare species of the Niagara River. . . . . *Lampsilis teres*

23b. Periostracum dark, smooth or a little rough (Plate 8, Figures 1 through 5); common and widespread . . . . *Ligumia* spp. . . 24

24a (23). Posterior ridge prominent, posterior end drawn out into a blunt point; pseudocardinals delicate and elongate; usually <110 mm long . . . . *L. nasuta*
(Plate 8, Figures 2, 3, and 5; Figure 12 e)

24b. Posterior ridge low and rounded; posterior end evenly rounded; pseudocardinals triangular; often >110 mm long . . . . *L. recta*
(Plate 8, Figure 1)

25a (22). Shell compressed, with well-developed dorsal wing (e.g., Plate 9, Figure 1) (This wing may be reduced or lost on older specimens.). 26

25b. Shell without dorsal wing. 29

26a (25). Posterior end of shell and posterior ridge somewhat angular; dorsal wing poorly to moderately well developed (Plate 19, Figures 1 through 6); periostracum usually greenish with many fine rays; nacre white . . . . *Lasmigona* (in part) . . .27

26b. Posterior end of shell smoothly rounded; dorsal wing poorly (Plate 11) to very well developed (Plate 9, Figure 1); periostracum color variable; nacre purple, pinkish, or white. 28

27a (26). Shell often >70 mm long, usually markedly subtrapezoidal; interdental tooth usually prominent, widespread in New York . . . . *L. compressa*
(Plate 19, Figures 1 and 4 through 6; Figure 12 a)

27b. Shell usually <65 mm long, tending toward subovate; interdental tooth usually small; a species of southeastern and central New York. . . . . *L. subviridis*
(Plate 19, Figures 2 and 3; Figure 12 b)

28a (26). Pseudocardinal teeth strong and triangular; nacre purple or dark pink; periostracum usually greenish to blackish . . . . *Potamilus alatus*
(Plate 10, Figures 1 and 2)

28b. Pseudocardinal teeth thin and lamellar; nacre silvery white to light pink; periostracum usually grayish yellow to brownish yellow . . . . *Leptodea fragilis*
(Plate 9, Figures 1 and 2; Plate 11; Figure 13 f)

29a (25). Shell with conspicuous color rays that are made up of V's, W's, or dots (Plate 3, Figure 4; Plate 23, Figure 7; Plate 26, Figure 6), subtriangular or subtriangular-subovate, small (usually <75 mm long); periostracum usually smooth. 30

29b. Shell of various shapes (including subtriangular), but not with color rays as described above. 32

30a (29). Color rays made up of triangular or squarish spots (Plate 3, Figure 4); shell inflated (W/H = 0.7-1.2) and fairly elongate (H/L = 0.55-0.7) . . . . *Epioblasma triquetra*
(Plate 3, Figure 4; Figure 13 g)

30b. Color rays containing dark V's and W's (Plate 23, Figure 7; Plate 26, Figure 6); shell compressed to inflated (W/H = 0.55-0.9) and short (H/L = 0.6-0.85) . . . . *Truncilla* spp. . . . 31

31a (30). Shell strongly subtriangular; posterior ridge sharp, straight, and reaching to the margin of the shell. . . . . *T. truncata*
(Plate 23, Figure 7)

31b. Shell subtriangular to subovate; posterior ridge rounded, bowed downward, and fading out before it reaches the shell margin . . . . *T. donaciformis*
(Plate 26, Figure 6)

32a (29). Nacre purple . . . . *Elliptio* spp. . . . 33

32b. Nacre white or pink. 34

33a (32). Shell subtrapezoidal with angular posterior-ventral margin and posterior ridge; posterior slope broad and well defined; widespread . . . . *E. complanata*
(Plate 23, Figures 1 through 5; Plate 24, Figures 1 through 3; Figure 12 f)

33b. Shell long-subelliptical with rounded posterior-ventral margin and posterior ridge; posterior slope narrow and poorly defined; a species of restricted distribution (chiefly western New York) . . . . *E. dilatata*
(Plate 25, Figures 1 and 3 through 5)

34a (32). Shell subtriangular, subtriangular-subquadrate, or subtriangular-subovate; periostracum usually rough, brownish with few or no color rays; pseudocardinal teeth strong 35

34b. Shell subovate, subelliptical, subrhomboidal, or subcircular; periostracum rough or smooth; color rays may be conspicuous 37

35a (34). Beaks very near the anterior end of the shell; often with a broad band of color rays; a very rare species of the Allegheny basin. . . . . *Pleurobema clava*
(Plate 26, Figure 5)

35b. Distance from beaks to the anterior margin of the shell 5-40% of shell length; color rays absent or fine and reaching across the face of the shell; common species of western and north-central New York 36

36a (35). Shell subtriangular to subquadrate, sides usually flattened or with an indistinct medial sulcus; posterior slope usually sharply defined; distance from beaks to anterior margin of shell usually 20-40% of shell length; nacre white . . . . *Fusconaia flava*
(Plate 21, Figure 2; Plate 23, Figures 6 and 8; Plate 25, Figure 2)

36b. Shell subtriangular to subovate, usually with evenly rounded sides; posterior slope not sharply defined; distance from beaks to anterior margin of shell usually 5-25% of shell length; nacre white or rosy pink. . . . . *Pleurobema cordatum*
(Plate 21, Figures 4 and 5)

37a (34). Shell thick, short (H/L = 0.6- 0.85), subovate with beaks very near the anterior end (Plate 7, Figure 4; Plate 21, Figure 5; Plate 26, Figure 5) 38

37b. Shell of various shapes, but not short-subovate with beaks very near the anterior end 40

38a (37). Shell often with a broad bundle of color rays; a very rare species of the Allegheny basin . . . . *Pleurobema clava*
(Plate 26, Figure 5)

38b. Color rays absent or not in bundles 39

39a (38). Shell evenly rounded with inflated beaks; periostracum smooth, often with distinct color rays; Niagara and St. Lawrence Rivers. *Obovaria olivaria*
(Plate 7, Figure 4)

39b. Shell often somewhat subtriangular; beaks not inflated; periostracum a little rough; color rays absent or fine and indistinct . . . . *Pleurobema cordatum*
(Plate 21, Figures 4 and 5)

40a (37). Right valve with two lateral teeth; shell small (<55 mm long) and subrhomboidal to subtriangular, with a prominent posterior ridge; a rare species of the Atlantic Slope . . . *Alasmidonta heterodon*
(Plate 20, Figures 7 and 8; Figure 13 e)

40b. Right valve with one lateral tooth (rarely, hinge teeth may be reversed); shell shape and size variable; common 41

41a (40). Shell subcircular with nearly central beaks; periostracum distinctly lighter on the posterior slope than elsewhere; a very rare species of western New York . . . . *Obovaria subrotunda* (Plate 27, Figure 1)

41b. Not as above 42

42a (41). Shell very small (<40 mm long), dark green, dark brown, or black, rayless . . . . *Toxolasma parvum* (Plate 6, Figure 4)

42b. Not as above 43

43a (42). Shell with a large, thin, posterio-ventral expansion (female) or with two radial ridges separated by a furrow (male); a very rare species of western New York . . . . *Epioblasma torulosa rangiana* (Plate 27, Figures 3 and 4)

43b. Not as above 44

44a (43). Lateral teeth very stout (wide) or swollen distally; shell subelliptical, compressed, and fairly thick to very thick 45

44b. Lateral teeth delicate to strong, but not remarkably wide; shell subelliptical or subovate, thin to thick 46

45a (44). Shell small (<40 mm long) but very thick; color rays fine or absent . . . . *Villosa fabalis* (Plate 6, Figure 5)

45b. Shell often >40 mm long, moderately thick; color rays in distinct bundles (but absent in some old animals) . . . . *Ptychobranchus fasciolaris* (Plate 12, Figure 1; Plate 24, Figure 4)

46a (44). Shell subrhomboidal; posterior ridge often more or less angular; posterior end of shell angular or squarish. 47

46b. Shell subovate to subelliptical; posterior ridge usually poorly defined or rounded; posterior end of shell usually well rounded. 50

47a (46). Pseudocardinals strong, rough-surfaced, and triangular; interdental tooth absent; beak sculpture trapezoidal. . . . . *Elliptio complanata* (Plate 23, Figures 1 through 5; Plate 24, Figures 1 through 3; Figure 12 f)

47b. Pseudocardinals delicate, lamellar, often with smooth surfaces; interdental tooth present or absent; beak sculpture double-looped or circular 48

48a (47). Periostracum rayless; interdental tooth absent; beak sculpture circular .... *Uniomerus tetralasmus* (Plate 27, Figure 2)

48b. Periostracum often with many fine, green color rays (old specimens may lack rays); interdental tooth usually present; beak sculpture double-looped (Figure 12 a, b) 49

49a (48). Shell small (<65 mm long) and thin, shape tending toward subovate; interdental tooth usually small; a species of southeastern and central New York.. .... *Lasmigona subviridis* (Plate 19, Figures 2 and 3; Figure 12 b)

49b. Shell often >70 mm long, fairly solid, usually markedly subtrapezoidal; interdental tooth usually prominent; widespread in New York. .... *Lasmigona compressa* (Plate 19, Figures 1 and 4 through 6; Figure 12 a)

50a (46). Shell subelliptical (i.e., height of shell not much less in front of the beaks than behind the beaks) and elongate (H/L <0.6); beaks usually low 51

50b. Shell subovate (i.e., height of shell markedly less in front of the beaks than behind the beaks) or subelliptical; often short (H/L >0.6); beaks often prominent 52

51a (50). Periostracum usually brown and a little rough; rays absent or thin and indistinct; hinge teeth strong.. .... *Elliptio dilatata* (Plate 25, Figures 1 and 3 through 5)

51b. Periostracum usually smooth to glossy (except in old specimens); usually with conspicuous, broad rays that often are interrupted at the growth lines; hinge teeth delicate .... *Villosa iris* (Plate 5, Figures 3 and 4)

52a (50). Shell subovate to subtriangular, solid; periostracum a little rough, brown; rays absent or fine and indistinct .... *Pleurobema cordatum* (Plate 21, Figures 4 and 5)

52b. Shell subovate or subelliptical, thin to thick, periostracum usually yellow to green; often smooth; rays usually conspicuous. 53

53a (52). Shell short, very inflated (especially near the beaks); periostracum shiny but rayless; hinge-line conspicuously S-shaped; a very rare species of western New York .. .... *Potamilus capax* (Plate 27, Figures 5 and 6)

53b. Not with the above combination of characters 54

54a (53). Periostracum clear yellow, often glossy; color rays absent or restricted to the posterior slope .... *Lampsilis cariosa* (Plate 3, Figures 1, 2, 5, and 6; Figure 12 i)

54b. Periostracum yellow to greenish, glossy or a little rough; color rays usually present across the face of the shell (except in old specimens). 55

55a (54). Shell extremely thick, short (H/L >0.67); nacre often pinkish; periostracum usually brownish; rays absent or indistinct; an extremely rare species recorded only from the Niagara River . . . . *Lampsilis abrupta*
(Plate 27, Figure 7)

55b. Not with the above combination of characters 56

56a (55). Shell short (H/L = 0.65-0.75); beaks prominent; shell often inflated near the beaks 57

56b. Shell elongate (H/L = 0.5-0.7); beaks not especially prominent; shell not particularly inflated near the beaks 59

57a (56). Periostracum a little rough; rays numerous but poorly defined; hinge teeth delicate; shell thin; Hudson (and possibly St. Lawrence) River . . . . *Leptodea ochracea*
(Plate 3, Figure 3; Figure 12 g)

57b. Periostracum smooth; rays few to many, but sharply defined; hinge teeth strong; shell moderately thick to thick. 58

58a (57). Rays numerous, wavy; shell small (<75 mm long); western New York . . . . *Lampsilis fasciola*
(Plate 7, Figures 1 and 2)

58b. Rays few, straight; shell often >75 mm long; widespread . . . . *Lampsilis ovata*
(Plate 1; Plate 2; Figure 13 h)

59a (56). Pseudocardinals stout, triangular; shell thick, often subelliptical. . . . . . . *Actinonaias ligamentina*
(Plate 7, Figure 3; Plate 26, Figure 7)

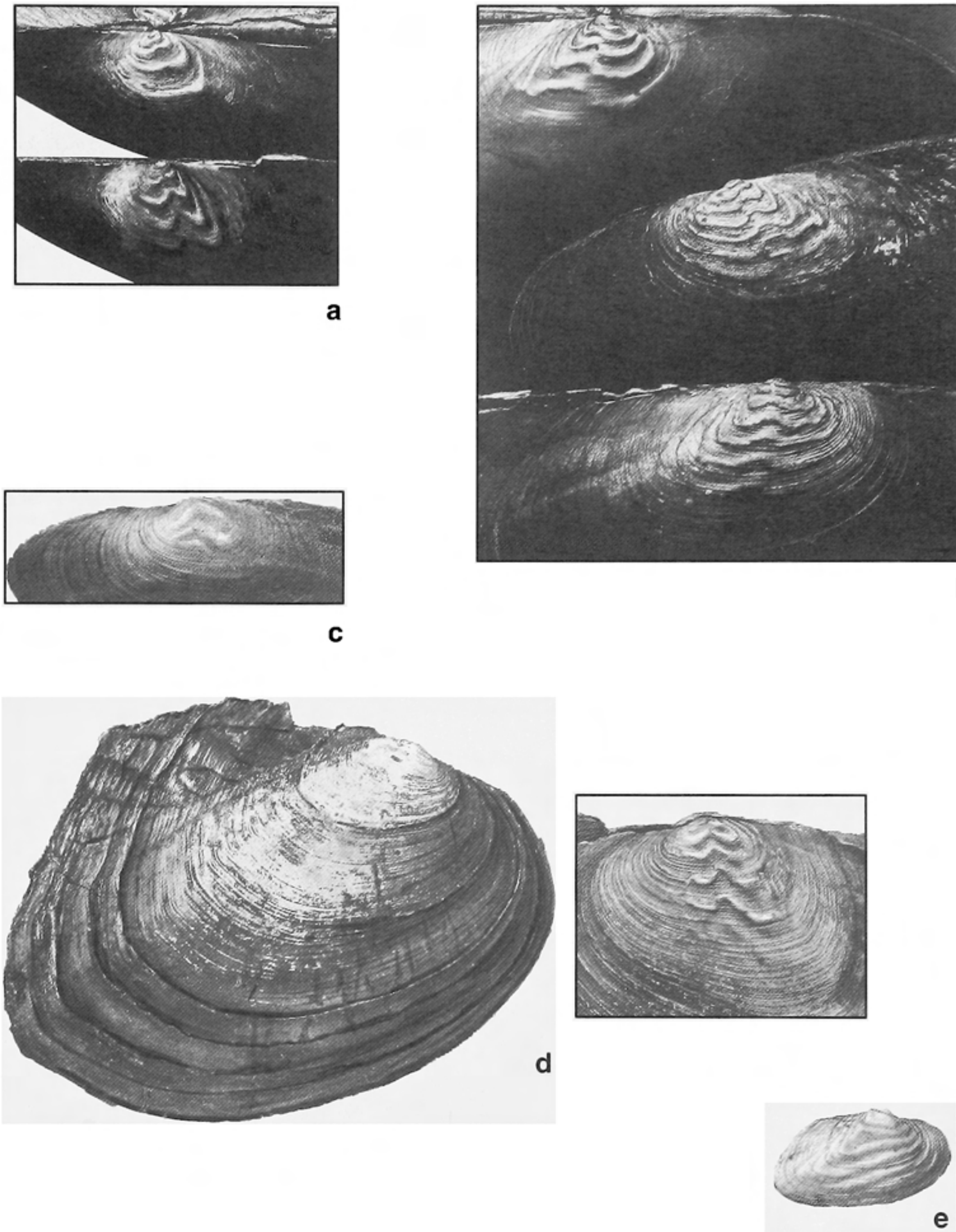
59b. Pseudocardinals delicate to moderately strong, often flexed upward; shell moderately thin to moderately thick, usually distinctly subovate 60

60a (59). Periostracum greenish, slightly roughened by fine wrinkles that are parallel to the growth lines; rays usually numerous; nacre often pink; shells usually not strongly sexually dimorphic . *Lampsilis radiata*
(Plate 4; Plate 5, Figures 1, 2, and 5; Figure 12 d)

60b. Periostracum often yellowish to brownish, glossy; rays often few; nacre rarely pink; shells strongly sexually dimorphic . . . . *Lampsilis siliquoidea*
(Plate 5, Figures 6 and 7; Plate 6, Figures 1 through 3; Figure 12 c)

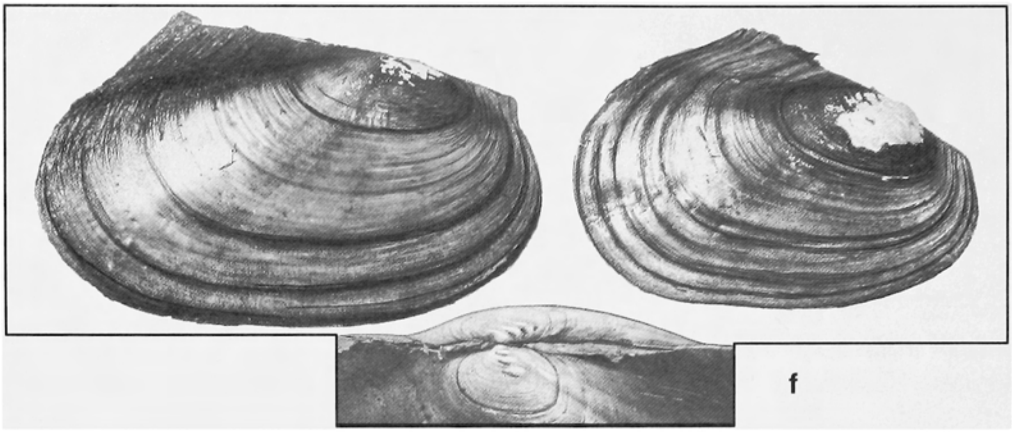
FIGURE 13

Details of Selected Unionoid Shells



a. Beak sculpture of *Pyganodon grandis* (upper: Erie Canal; lower: Mohawk River; both Mohawk, Herkimer County, New York), three times life size; b. beak sculpture of *Pyganodon cataracta* (upper; Dover Plains, Dutchess County, New York) and *Pyganodon lacustris* (?) (middle and lower; Beaver Creek, and Mohawk, respectively; both Herkimer County, New York), three times life size; c. beak sculpture of *Simpsonaias ambigua* (ANSP 41067), enlarged; d. *Lasmigona complanata* (Erie Canal, Pittsford, Monroe County, NY), life size, with enlargement of beak sculpture; e. juvenile of *Alasmidonta heterodon* (Schuylkill River, Pennsylvania, ANSP 27344) at four times life size, showing beak sculpture.

FIGURE 13, *continued*



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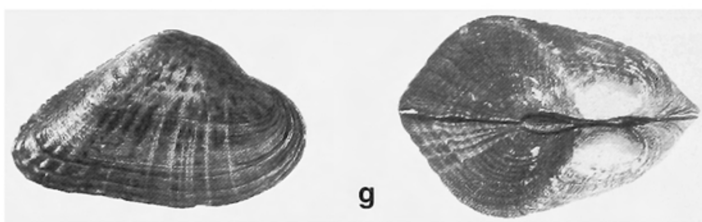

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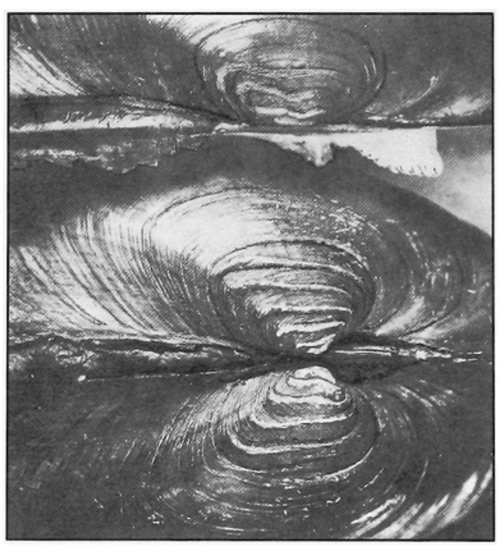


h

f. *Leptodea fragilis* (Lake Erie, Presque Isle, Pennsylvania) at 75% of life size, with enlargement of beak sculpture; g. lateral and dorsal views of a female of *Epioblasma triquetra* (Ohio), life size; h. beak sculpture of *Lampsilis ovata* (upper: Erie Canal, Pittsford, Monroe County, New York; lower: Seneca River, New York), 150% of life size. All from Pilsbry (1925).

Species Accounts

Actinonaias ligamentina (Lamarck)

Mucket

PLATE 7, FIGURE 3; PLATE 26, FIGURE 7

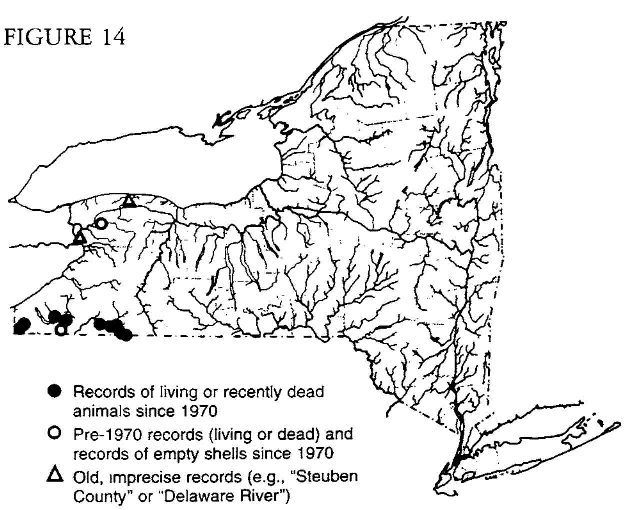
Shell subelliptical to subovate, H/L=usually 0.55–0.7, W/H=usually about 0.65, thick, often greater than 100 mm long. Beak sculpture indistinct. Periostracum yellowish or greenish in young animals, brownish in old animals. Broad or indistinct color rays often present, especially in young animals. Hinge teeth strong: pseudocardinals heavy, triangular, and with rough surfaces; laterals long and heavy. Nacre white.

This species is distinguished by its large, heavy, subelliptical shell, but it can easily be confused with some species of *Lampsilis*. *Lampsilis* spp. typically have more delicate pseudocardinal teeth, more ovate and thinner shells, and narrower, sharper color rays than *A. ligamentina*. In young specimens of *Lampsilis* spp., typically double-looped beak sculpture will be visible (e.g., Figures12 c-d, 13 h), while *A. ligamentina* rarely has visible beak sculpture. *A. ligamentina* can be especially difficult to separate from large males of *Lampsilis* spp. (*siliquoidea*, *ovata*, and *radiata*), which may lack the narrow color rays and bright periostracum characteristic of young *Lampsilis*. Female *Lampsilis* spp. are much higher and more inflated posteriorly than *A. ligamentina*. *A. ligamentina* can be distinguished from males of *L. ovata* by its low, rounded posterior ridge and beaks that project only a little above the hinge line. Male *L. ovata* usually have steep, well-defined posterior ridges and beaks that project well above the hinge line.

A. ligamentina is widespread in many parts of the Mississippi and Great Lakes basins. In New York, it is widespread in the Allegheny basin (Figure 14), where it is still abundant (Strayer 1995; Strayer et al. 1991). The distribution of *A. ligamentina* elsewhere in New York has been misunderstood because of confusion with *Lampsilis* spp. The following records are based on correctly identified specimens and seem to be reliable: Niagara River (Letson 1909; Robertson and Blakeslee 1948; NYSM 31651; a specimen in NYSM with no lot number but with "Niagara r." written on the shell; this latter specimen is shown in Plate 7, Figures 3, 3a, and 3b); Oak Orchard Creek (OSUM 25248); and possibly Tonawanda Creek (MCZ 228496). These records are old, and the museum lots are small, so *A. ligamentina* seems to have been rare and may no longer be extant in the Great Lakes basin in New York, contrasting with its abundance in the nearby Allegheny basin. The following reports of *A. ligamentina* from central New York are doubtful and are probably based on misidentifications of *Lampsilis* spp.: Cross Lake (Beauchamp 1886; Clarke and Berg 1959; Marshall 1895a), Oneida Lake (Baker 1916; Clarke and Berg 1959), and the Susquehanna River (Harman 1982).

In the Allegheny basin of western New York, *A. ligamentina* is a common inhabitant of rivers and large creeks, where it occurs in habitats ranging from stony riffles to soft-bottomed pools. It is known to use many species of warmwater fish as hosts, including banded killifish, white bass, many centrarchids, sauger, and yellow perch (Hoggarth 1992; Watters 1994a).

FIGURE 14



Alasmidonta heterodon (Lea)

Dwarf wedgemussel

PLATE 20, FIGURES 7 AND 8; FIGURE 13E

Shell small (<55 mm long), thin, subrhomboidal to subtriangular, with a prominent posterior ridge. Beak sculpture consists of two concentric ridges surrounded by two or three more or less trapezoidal ridges drawn out along the posterior slope. Periostracum greenish to brownish, often with numerous fine green color rays. Both pseudocardinal and lateral teeth present but delicate. Two lateral teeth in the right valve and one in the left. Nacre white.

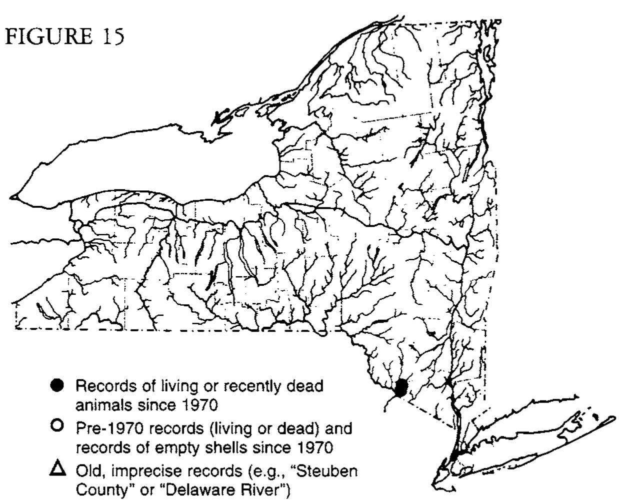
This small mussel can be recognized immediately by its reversed lateral teeth. Two occur in the right valve and one in the left, the opposite of what is normally found in other unionoid species. Note, however, that specimens with reversed hinge teeth are occasionally found in other unionoid species. *A. heterodon* also can be identified by its small size, distinctive shell shape, and prominent posterior ridge.

A. heterodon lives in streams along the Atlantic Slope from North Carolina to New Brunswick (USFWS 1993). Never common, *A. heterodon* has declined to about two dozen small populations worldwide and is listed as endangered by both the United States Fish and Wildlife Service and the New York State Department of Environmental Conservation. In New York, it is known only from a short reach of the lower Neversink River (Figure 15; Strayer and Ralley 1991), where at approximately 20,000 animals (Strayer et al. 1996), one of the world's largest populations of this rare species remains. It has been reported from nearby New Jersey (Passaic River basin) and Connecticut (Housatonic River basin) (both Clarke 1981b), so it may yet turn up elsewhere in the Atlantic drainage of southeastern New York.

A. heterodon lives in running waters of all sizes, from small brooks less than 5 m wide to large rivers more than 100 m wide (USFWS 1993). It does not show any strong preference for particular habitats or microhabitats (USFWS 1993; Strayer 1993; Strayer and Ralley 1993; see also Michaelson and Neves 1995).

Its habitat in New York is a small (40 m wide), coolwater river, where it lives bedded in the fine sediments that accumulate between cobbles. The known hosts of *A. heterodon* include the tessellated darter, the johnny darter, and the mottled sculpin (Michaelson and Neves 1995), all of which are widespread in New York (C.L. Smith 1985).

FIGURE 15



Alasmidonta marginata Say

Elktoe

PLATE 20, FIGURES 1, 5, AND 6; FIGURE 12H

Shell trapezoidal with a prominent posterior ridge, inflated, thin, up to 100 mm long. Posterior slope with fine but well-defined ridges running perpendicular to the growth lines. Beak sculpture two or three coarse, weakly double-looped wrinkles. Periostracum yellowish or greenish, usually with bright, blue-green rays that often are speckled with dots. The posterior slope is typically lighter-colored and less rayed than the rest of the shell. Pseudocardinals distinct and interlocking, but thin, lamellar, and with smooth surfaces. Laterals absent or reduced to low, rounded thickenings along the hinge line. Nacre bluish white.

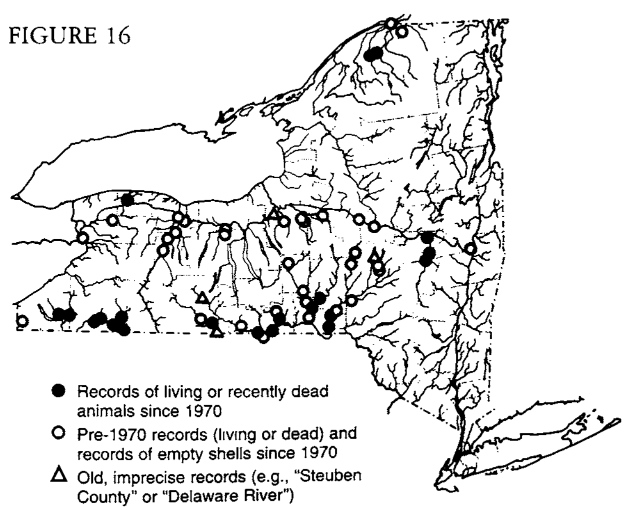
This species is easily recognized by its trapezoidal shape, its colorful bluish spotted color rays, and, in living animals, its bright orange foot. It is most easily confused with *Alasmidonta varicosa*. The two species are similar in shape and color, but *A. varicosa* is smaller (<70 mm long) and less truncate, and has a more rounded posterior ridge. In *A. marginata*, the posterior slope is usually distinctly lighter in color than the rest of the shell, while in *A. varicosa*, the posterior slope is usually the same color or darker than the rest of the shell. Furthermore, the two species have different distributions in New York; they overlap only in the Susquehanna basin. *A. marginata* might possibly be confused with *Epioblasma triquetra* as well, but the latter species has much stronger hinge teeth, a different color pattern on the periostracum, and a very restricted range in New York.

A. marginata is an Interior Basin species that lives throughout much of the Mississippi and Great Lakes basins (Clarke 1981b). In New York, it is widespread in the Allegheny basin and is found at scattered sites along the course of the Erie Canal from the Niagara River to Albany (Figure 16). It also lives in the St. Lawrence River and its tributaries in northern New York. It is one of only two or three Interior Basin species to have reached the Susquehanna basin, where it is widely distributed. The route by which this species reached the Susquehanna is not clear. It may have gone from the Allegheny to the upper Genesee to the Susquehanna via postglacial confluences (see "Dispersal Routes"), but the lack of any records of *A. marginata* from the upper Genesee basin is problematic. Alternatively, early postglacial confluences between the Finger Lakes and the Susquehanna (von Engeln 1961) might have been used, *A. marginata* might have moved along the Chenango Canal (cf. Figure 5), or it may have been introduced by humans into the Susquehanna. Harman's (1975) report of this species from the West Branch of the Delaware River probably refers instead to *A. varicosa*. Ortmann (1919) recognized populations in the Susquehanna basin as a distinct subspecies (*A. marginata susquehannae*), but later authors (e.g., Clarke and Berg 1959) have not regarded this subspecies as valid.

A. marginata was considered to merit special concern status by Williams et al. (1993). It usually forms only a small part of the unionoid community in New York, but is still seen regularly and has not obviously declined in historic sites that have been resurveyed (Jirka 1991; Strayer 1995; Strayer et al. 1995).

A. marginata usually lives in running waters of various sizes, from small creeks to medium-sized rivers. It is said to be characteristic of riffles (e.g., Ortmann 1919). It may use shorthead redhorse, northern hog sucker, white sucker, rock bass, and warmouth as hosts, although the evidence is not definitive (Hoggarth 1992).

FIGURE 16



Alasmidonta undulata (Say)

Triangle floater

PLATE 12, FIGURES 4 THROUGH 6; FIGURE 12L

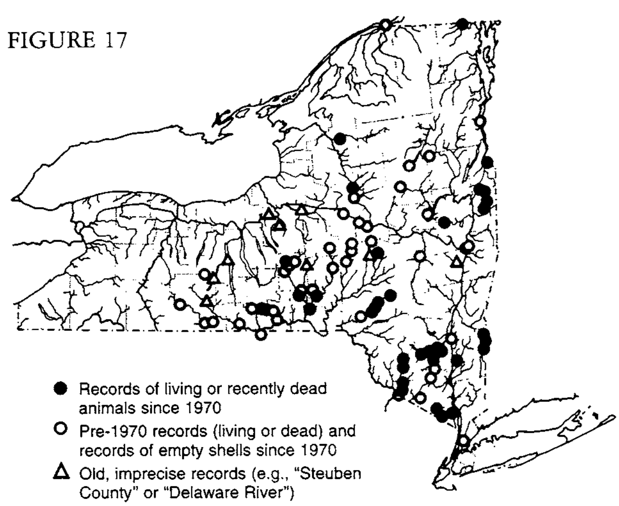
Shell subovate to subtriangular, thick anteriorly and thin posteriorly, not more than 80 mm long (usually <60 mm). Beaks usually prominent. Beak sculpture coarse, uneven in height, more or less concentric. The periostracum of young animals is shiny and yellowish to greenish, often with many green color rays, but is often dark brown or blackish and rayless in old animals. Pseudocardinals strong and triangular, but laterals vestigial, represented by thin, low ridges parallel to the hinge line. Nacre usually white, sometimes pink.

Externally, this species can be recognized by its triangular-ovate shape. It is more triangular than *Lampsilis* spp. and *Strophitus undulatus* and more ovate than *Alasmidonta varicosa*. Also distinctive are its coarse, uneven beak sculpture, and its shiny periostracum and bright color rays. Internally, the combination of strong pseudocardinal teeth and vestigial laterals and the dramatic decrease in shell thickness from anterior to posterior are characteristic. Very young animals of *A. undulata* may have fine but distinct ridges on the posterior slope and may therefore key out as *Alasmidonta varicosa*. These two species are easily distinguished by differences in shell shape and hinge teeth. *A. undulata* is not easily confused with any other species in New York.

This Atlantic Slope species is widespread in southeastern and south-central New York (Figure 17). It has been reported from scattered sites in the Lake Champlain (D. Smith 1985a), St. Lawrence (Clarke and Berg 1959; Erickson and Fetterman 1996), and Black River (Buckley 1977) basins as well. The degree to which *A. undulata* moved westward along the Erie Canal is not clear. Records from western New York (AMNH 139031: "Lake Erie;" BSM 364L-4/9: "Lancaster;" Clarke 1981b: "Monroe County") are almost certainly incorrect, but reports from Oneida Lake and Onondaga County (Beauchamp 1886; Baker 1916; Clarke and Berg 1959; Clarke 1981b) may represent a modest invasion westward along the Erie Canal. Although *A. undulata* apparently has been declining in parts of its range and is a subject of concern in some states (D. Smith, pers. comm.; Williams et al. 1993), it is still widespread and abundant in New York.

A. undulata lives in creeks, rivers, and lakes (Clarke and Berg 1959; Ortmann 1919; Strayer 1993). It sometimes is abundant, especially in large creeks and small rivers. Dr. Barry Wicklow (pers. comm.) and his colleagues at St. Anselm College have found that common shiners, blacknose dace, and longnose dace serve as hosts for this species.

FIGURE 17



Alasmidonta varicosa (Lamarck)

Brook floater

PLATE 20, FIGURES 2 THROUGH 4

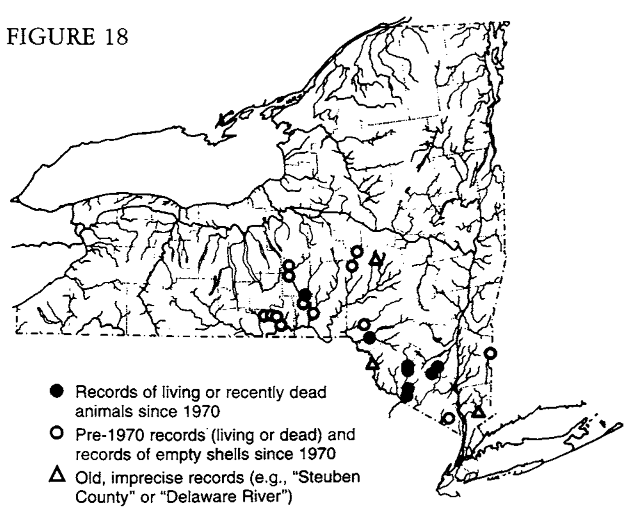
Shell subtrapezoidal to almost subovate, thin, <70 mm long, with a prominent but rounded posterior ridge. Posterior slope with fine but well-defined ridges running across the growth lines. Beak sculpture coarse, variable in shape. Periostracum greenish with dark green color rays that are usually continuous, in contrast to the dotted rays of *A. marginata*. Pseudocardinals thin, lamellar, with smooth surfaces. Laterals absent or represented as low, rounded ridges along the hinge line. Nacre bluish white, but sometimes discolored.

This species can be recognized by its shape, its prominent posterior ridge, and the fine corrugations on the posterior slope. Characters for distinguishing *A. varicosa* from the similar *Alasmidonta marginata* are given in the account of the latter species. Very young animals of *Alasmidonta undulata* may have ridges on the posterior slope and therefore be misidentified as *A. varicosa*.

Formerly widespread in southeastern New York (Figure 18) and elsewhere on the Atlantic Slope from South Carolina to New Brunswick (Clarke 1981b), this species has disappeared from many sites and is now rare. In New York, populations in the Housatonic and Passaic basins have apparently disappeared (Strayer 1992, 1994), and surveys of eleven historic populations in the Susquehanna basin in 1991 and 1995 turned up only one living animal (Jirka 1991; Schneider, pers. comm.). Populations in the Shawangunk Kill (Hudson basin) and upper Delaware basin (Harman 1975, as *A. marginata*; Fichtel, pers. comm.) are sparse and limited in extent. In New York, only the Neversink River population (Strayer and Ralley 1991) is large at approximately 10^5 animals (Strayer, unpublished). The report of this species from the Canandaigua Lake outlet (UMMZ 101159) is highly doubtful and may refer instead to the Canadarago Lake outlet (Oaks Creek), from which *A. varicosa* is known. *A. varicosa* was listed as threatened by Williams et al. (1993).

A. varicosa is strictly a running-water species and is said to favor gravelly riffles in creeks and small rivers (Clarke and Berg 1959; Ortmann 1919; but see Strayer and Ralley 1993). It is found most frequently in nutrient-poor streams of fairly low calcium content (Strayer 1993). Where it occurs, it is usually uncommon. Dr. Barry Wicklow (pers. comm.) and his colleagues at St. Anselm College have found that longnose dace, golden shiners, pumpkinseeds, and slimy sculpins serve as hosts for this species.

FIGURE 18



Alasmidonta viridis (Rafinesque)

Slipper shell

PLATE 18, FIGURE 1

Shell subquadrate to subovate, thin, usually <40 mm long (occasionally reaching 60 mm), with a truncated posterior end. Beak sculpture fairly coarse, concentric to weakly double-looped. Periostracum yellow-green to gray-green with many fine green color rays. Pseudocardinals strong, triangular, with rough surfaces. Laterals low, weak, and rounded or entirely absent. Nacre bluish white.

Small size, a squarish posterior end, and a gray-green periostracum characterize this species. No other New York species closely resembles *A. viridis*. Young *A. marginata* have corrugated posterior slopes and a different color pattern, and *Epioblasma triquetra* has much stronger lateral teeth and a distinctively colored periostracum.

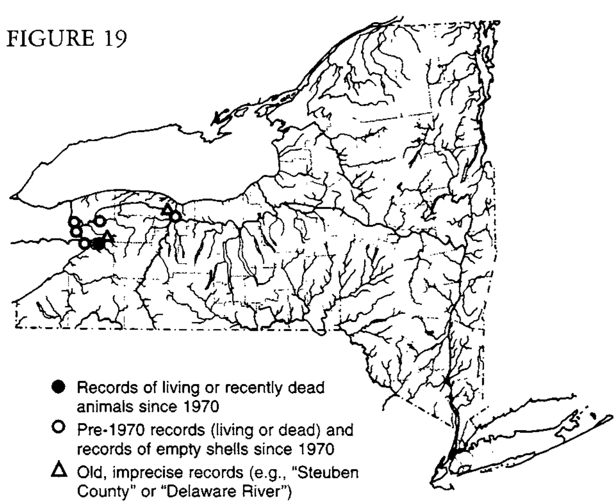
In New York, *A. viridis* has been seen at only a few places in the western part of the state (Figure 19) as follows: the Buffalo River basin (Letson 1905; Robertson and Blakeslee 1948; Strayer et al. 1991; plus records in BSM, UMMZ); the Niagara River (Letson 1905; Robertson and Blakeslee 1948; plus records in BSM and MCZ); Tonawanda Creek (Strayer 1995: Tonawanda Creek at Transit Road); and the lower Genesee basin (Baker 1898; Walton 1891; UMMZ 101281: "Mud Creek," presumably in Monroe County.). It is not to be expected from the Allegheny basin in New York because it does not occur in the upper Ohio basin (Ortmann 1919).

Reports of *A. viridis* from further east in New York are doubtful and require confirmation; we have not seen specimens to support any of the following records. Clarke's (1981b) maps showed *A. viridis* from Beaver Creek (Susquehanna basin) and the Black River. The former record is based on a misidentified *A. undulata* (MCZ 254784). No records were reported by Clarke (1981b) or Buckley (1977), nor did any museum we visited contain any records of *A. viridis* from the Black River basin. Clarke and Berg (1959) reported that Athearn found *A. viridis* from Oriskany Creek at Oriskany Falls (Oneida County).

The current status of this species in New York is not well known because of insufficient recent survey work in the area between Buffalo and Rochester. It may be more widespread in this area than Figure 19 indicates. Williams et al. (1993) listed it as a species of special concern.

Although *A. viridis* is typically a species of small streams (Strayer 1983; van der Schalie 1938), it occupies a wide range of habitats in New York, from small streams to large rivers. In fact, the largest collections of this species made in New York have come from the Niagara River. It occurs also infrequently in lakes. The banded sculpin, johnny darter, and mottled sculpin may serve as fish hosts (Clarke and Berg 1959; Zale and Neves 1982, for the possibly synonymous *A. minor*).

FIGURE 19



Amblema plicata (Say)

Three-ridge

PLATE 21, FIGURES 1 AND 3; PLATE 22

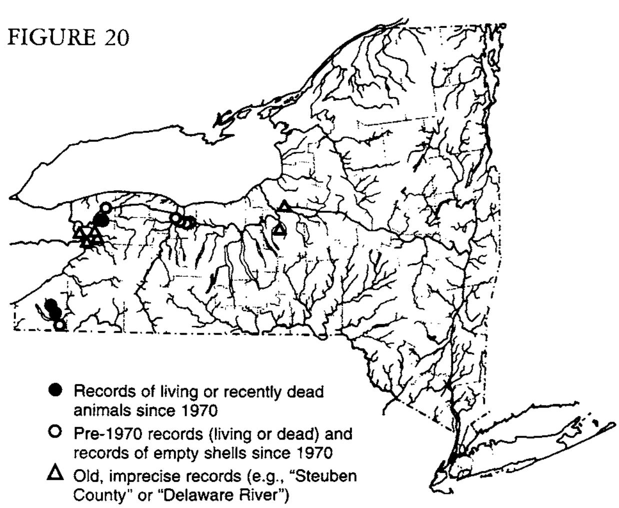
Shell subovate to subtrapezoidal, thick and heavy, often >100 mm long, with prominent transverse ridges running across the face of the shell. Beak sculpture concentric, nodulous. Periostracum olive-brown (in young specimens) to blackish brown (in old specimens), without color rays. Hinge teeth very strong, with rough surfaces on the pseudocardinals. Nacre white.

With its prominent undulations, squarish outline, and heavy teeth, this species is unmistakable. Occasionally, specimens that are nearly smooth are seen, but these are readily recognized by their shape, color, and hinge teeth.

A. plicata has been recorded from low-gradient streams of the Allegheny basin (Strayer 1995), the Erie–Niagara basin (Robertson and Blakeslee 1948; Strayer et al. 1991), and several sites along the Erie Canal near Rochester (Baker 1901; Clarke and Berg 1959; Marshall 1895a) (Figure 20). In addition, a few old but poorly documented records of this distinctive species from central New York (Oneida River: Marshall 1895a; Skaneatales Lake: Harman, unpublished; old Erie Canal, Onondaga County: Beauchamp 1886) suggest that it followed the Erie Canal well into central New York. More recent surveys of central New York (Clarke and Berg 1959; Harman 1970a) did not locate this species, so *A. plicata* may have been eliminated from this area. It apparently has been eliminated from the Buffalo River basin as well (Strayer et al. 1991), but it remains abundant in Tonawanda and Cassadaga Creeks (Strayer et al. 1991; Strayer 1995). It should be sought in low-gradient streams between Niagara and Monroe Counties as well.

A. plicata lives in lakes, creeks, and rivers, where it is often one of the dominants of the unionoid community. In New York, as in other parts of its range (Strayer 1983), it is especially common in muddy, low-gradient creeks and rivers. Many fish are suitable hosts, including shortnose gar, white and black crappie, rock bass, large-mouth bass, bluegill, green sunfish, pumpkinseed, and yellow perch (Hoggarth 1992).

FIGURE 20



Anodonta implicata Say

Alewife floater

PLATE 15, FIGURE 1; PLATE 26, FIGURE 4; FIGURE 12 P

Shell subelliptical, elongate, thin posteriorly but much thicker anteriorly, often >100 mm long. Beak sculpture double-looped, not nodulous. Periostracum greenish, brownish, or blackish, sometimes with fine rays. Hinge teeth absent. Nacre pinkish to purplish. The color is best seen on the anterior part of the shell.

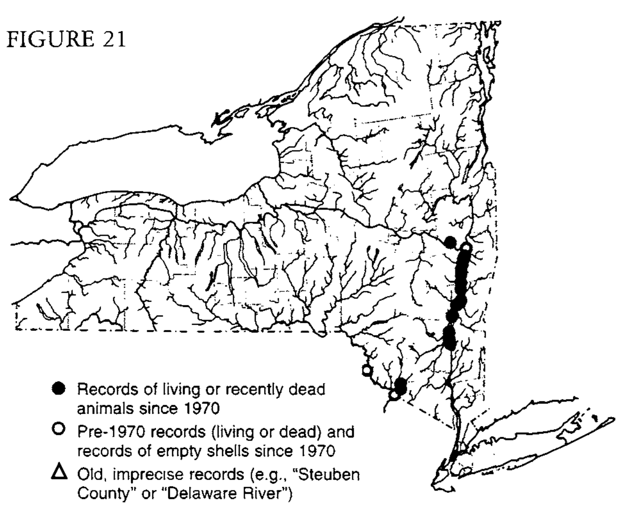
This species is distinguished by its toothless hinge, its pink to purple nacre, its shell thickness, which increases markedly from posterior to anterior, and its double-looped beak sculpture. *Pyganodon* species have bluish-white (occasionally coppery-orange) nacre and thin shells, while *Anodontoides ferussacianus* and *Strophitus undulatus* have concentric beak sculpture and bluish-white nacre. Note in addition that *A. implicata* has a limited distribution in New York (Figure 21).

A. implicata occurs on the Atlantic Slope from South Carolina to Nova Scotia (Williams et al. 1993). In New York, there are authentic records from only two areas (Figure 21): the freshwater tidal Hudson River to the lower Mohawk River (Strayer 1987; Strayer et al. 1994; INHS 12256: Mohawk River at Schenectady [We have examined this specimen, and it is authentic]), and the lower Delaware River basin, including the Neversink River (Strayer and Ralley 1991) and the Delaware River (Narrowsburg: UMMZ 103652). The older literature and most museum collections contain records of "*A. implicata*" from sites throughout New York, including the central and western parts of the state. We reject all records other than those shown in Figure 21. The museum specimens mistakenly attributed to *A. implicata* that we have examined are typically large (sometimes huge) specimens of *Pyganodon* spp., often with a pathologically coppery-orange nacre (see Ortmann's [1919] discussion of *Anodonta grandis* form *salmonia* Lea) that were attributed to *A. implicata* before malacologists had developed a clear conception of this species.

In New York, this species maintained a large population at 400 million individuals in 1991–1992 (Strayer et al. 1994) only in the Hudson River estuary. It now appears that this population is declining sharply in response to the zebra mussel invasion (Strayer and Smith 1996), so *A. implicata* may be on the verge of disappearing from New York.

The alewife is thought to be a host for this species (Johnson 1946). Other species of *Alosa* may be hosts as well. The shad-restoration program on the Connecticut River increased the range of *A. implicata* in the Connecticut River (D. Smith 1985b). Although *Anodonta* species are usually said to prefer quiet waters, in New York *A. implicata* lives in the strong currents of the tidal Hudson River and among cobbles in the Neversink River (Strayer and Ralley 1993; Strayer et al. 1994).

FIGURE 21



Anodontoides ferussacianus (Lea)

Cylindrical papershell

PLATE 17, FIGURES 4 THROUGH 6; FIGURE 12 M–N

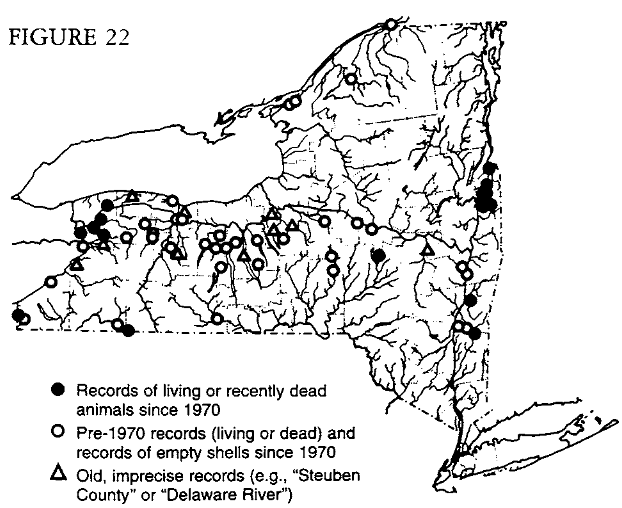
Shell subelliptical, elongate, thin, small (usually <75 mm long). Beak sculpture fine and concentric. Periostracum usually gray-green, often with indistinct rays, and sometimes with a few broad, dark rays on the posterior slope. Hinge teeth absent. Nacre bluish white.

Among species with no hinge teeth, *A. ferussacianus* can be recognized by its fine, concentric beak sculpture (Figure 12 m–n), which is conspicuously finer than that of *Strophitus undulatus*. *Anodonta*, *Pyganodon*, and *Utterbackia* all have double-looped beak sculpture. Also, the nacre of *A. ferussacianus* is bluish white, while that of *S. undulatus* is bluish white along the margins, but salmon-orange to pure white in the beak cavity.

A. ferussacianus occurs widely in the Mississippi River and Great Lakes basins from Oklahoma to Quebec, as well as in parts of the Hudson Bay drainage. In New York, it is widely distributed from the Erie–Niagara basin east to Syracuse in the Ontario drainage (Figure 22). It crossed the Oswego–Mohawk divide, probably by natural means well before the opening of the Erie Canal (cf. Strayer 1987), and is scattered throughout the Mohawk, mid-Hudson, and southern Champlain basins. It is present, but infrequent, in the St. Lawrence (Clarke and Berg 1959; Erickson and Fetterman 1996; Ortmann 1919) and Allegheny basins (Strayer et al. 1991; Allegheny River at Olean: ANSP 8493; West Branch of French Creek: INHS 3354). Records from the Susquehanna and Delaware basins (e.g., Marshall 1895a) are difficult to interpret. Because of potential confusion with *Strophitus undulatus* and *Pyganodon cataracta*, some authors (e.g., Strayer and Ralley 1991) rejected these early records. Nevertheless, there certainly are authentic specimens of *A. ferussacianus* from the Susquehanna drainage (Chemung River at Corning, ANSP 366071; Chemung River, Chemung County, UMMZ 105563; Chenango River at Earlville and one mile east of North Norwich: OSUM 21545 and 21617, respectively; also Otsego Lake, Harman 1970b; Weir 1977). It is probably more widespread in the Susquehanna and perhaps the Delaware basin than Figure 22 suggests. The distribution and origin of *A. ferussacianus* in the Susquehanna and Delaware basins needs further study. It may have crossed either the Allegheny–Genesee–Susquehanna divide or the Oswego–Susquehanna divide by postglacial confluences or canals, or it may have reached the Susquehanna through human introduction. This species still seems to be common in New York and elsewhere throughout its range (cf. Williams et al. 1993).

A. ferussacianus is usually said to be a species of small streams and occasionally lakes (e.g., Ortmann 1919; van der Schalie 1938), but in New York it occurs in large rivers (e.g., the Niagara) as well as creeks. It has been found in several lakes (Erie, Seneca, Cayuga, Otsego) in the state. *A. ferussacianus* uses the spotfin shiner, largemouth bass, bluegill, and black crappie as hosts (Hove et al. 1995a; Watters 1995); it may use the sea lamprey and the mottled sculpin as well (Hoggarth 1992).

FIGURE 22



Elliptio complanata (Lightfoot)

Eastern elliptio

PLATE 23, FIGURES 1 THROUGH 5; PLATE 24, FIGURES 1 THROUGH 3; FIGURE 12 F

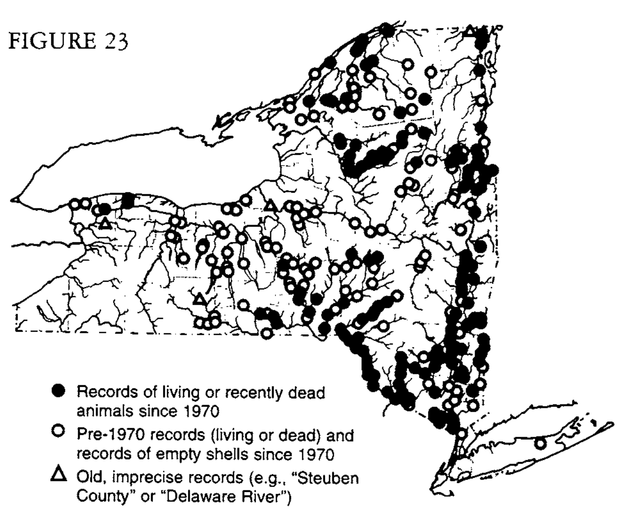
Shell subtrapezoidal, compressed or inflated, moderately thick, usually 50–80 mm long (but reaching >100 mm in length), usually with a pronounced posterior ridge. Beak sculpture trapezoidal. Periostracum usually rough, yellowish with many fine, green rays in young animals and dark brown in old animals. Hinge teeth well developed; pseudocardinals triangular with rough surfaces, laterals long and sharp. Nacre purple, white, or salmon, sometimes discolored.

This is a variable species that usually can be recognized by its trapezoidal shape, angular posterior ridge, and prominent posterior slope. *Elliptio dilatata* has a much narrower posterior slope than *E. complanata* and scarcely overlaps *E. complanata* in its New York distribution (Figure 24).

E. complanata occurs on the Atlantic Slope from Florida to Nova Scotia, as well as in the northern parts of the Great Lakes basin from Lake Ontario to the Lake Superior drainage. It is the most abundant and widespread unionoid in New York, absent only from the upper Genesee, Allegheny, and Erie basins, and from most of the Niagara basin above the falls (Figure 23). There is a single specimen of *E. complanata* (UMMZ 94198, "Tonawanda Creek") from the upper Niagara basin. If this record is authentic, it suggests that this species moved west along the Erie Canal, but only to a very limited degree.

Within its range in New York, *E. complanata* is found in nearly every site that supports unionoids, from brooks to the largest rivers, and in many lakes (Clarke and Berg 1959; Strayer 1993). It is usually the most abundant unionoid in the community. *E. complanata* is still abundant at many sites in New York; in fact, it often persists after other unionoids have declined or disappeared. Yellow perch is the only demonstrated host, but other species certainly must serve as hosts; banded killifish and several sunfish have been implicated as possible hosts as well (Hoggarth 1992; Young 1911; Watters 1994a).

FIGURE 23



Elliptio dilatata (Rafinesque)

Spike

PLATE 25, FIGURES 1 AND 3 THROUGH 5

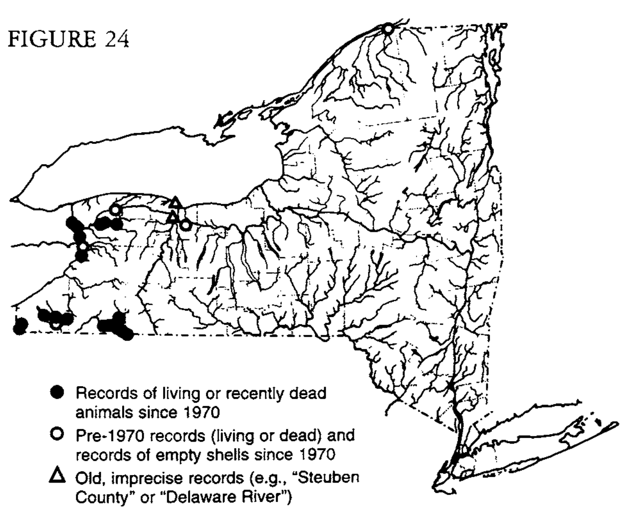
Shell elongate (H/L = usually 0.46–0.54), subelliptical to subovate, thick, sometimes (especially in old specimens) a little humped. Posterior ridge indistinct, and posterior slope small and poorly defined. Beak sculpture trapezoidal. Periostracum usually rough, brownish, and rayless, but in young animals it may be yellowish and fairly glossy, with many fine, green rays. Pseudocardinals strong, with rough surfaces, laterals long and strong. Nacre usually purple, but sometimes white or salmon.

Three species in New York are most likely to be confused with this species: *Elliptio complanata*, *Ligumia recta*, and *Ptychobranchus fasciolaris*. *E. complanata* has a more trapezoidal outline and a much broader posterior slope than *E. dilatata*. *L. recta* is more elongate and straighter ventrally than *E. dilatata*, which usually has a humped appearance. The periostracum of *L. recta* is typically green to black to *E. dilatata*'s brown. The lateral teeth of *P. fasciolaris* are shorter and thicker than those of *E. dilatata*. Also, *P. fasciolaris* is usually more trapezoidal than *E. dilatata* and often has bundles of fine, green color rays (Plate 24, Figure 4).

E. dilatata is a common species of the Mississippi and Great Lakes basins. It reaches the edge of its range in New York. It is abundant and widely distributed in the Allegheny and Erie–Niagara basins (Figure 24), but records further east are rare. There are positive records from the Rochester area (Baker 1898; Robertson and Blakeslee 1948; Walton 1891), possibly as a result of movement along the Erie Canal, and from the St. Lawrence River (Clarke and Berg 1959). Records from Keuka Lake (Marshall 1895a) and the Mohawk River (Call 1878) are very doubtful (see Clarke and Berg 1959; Strayer 1987); they are probably based on misidentifications of *E. complanata*. Although restricted in its range in New York, *E. dilatata* is still abundant in western New York (Strayer 1995; Strayer et al. 1991).

In New York, as elsewhere in its range, *E. dilatata* occupies a wide range of habitats: creeks, rivers, and large lakes (cf. Ortmann 1919; van der Schalie 1938). It is often one of the most abundant unionoids in the community. Definitive studies of host fish have not been made, but various authors have suggested that gizzard shad, flathead catfish, white and black crappie, and sauger probably serve as hosts (Hoggarth 1992).

FIGURE 24



Epioblasma triquetra (Rafinesque)

Snuffbox

PLATE 3, FIGURE 4; FIGURE 13 G

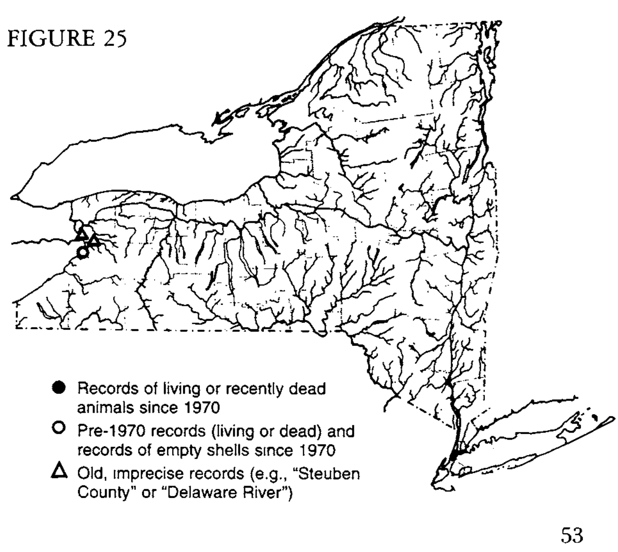
Shell subtriangular, inflated (W/H = 0.7–0.85 in males and 0.8–1.2 in females), fairly thick, small (males <70 mm long, females <50 mm long), with a well-defined posterior ridge. Beak sculpture indistinct. Periostracum yellow to light green, with dark green color rays that are broken up into triangular spots. Pseudocardinals strong, with rough surfaces, laterals short, strong, and sharp. Nacre white. Shell strongly sexually dimorphic, the female shell much smaller than the male, and with a ribbed posterio-ventral extension.

The female of this species is unmistakable. The male superficially resembles *Alasmidonta marginata* and the two species of *Truncilla*, but the hinge teeth of *E. triquetra* are much stronger than those of *A. marginata* and the color markings on the periostracum of *E. triquetra* are distinctly different from those of *A. marginata* or *Truncilla* spp.

E. triquetra belongs to a large and formerly widespread genus of evolutionarily advanced unionoids that has been nearly eliminated by human activities (Johnson 1978; Neves 1993; Stansbery 1970; Williams et al. 1993). Of the 20 species of *Epioblasma*, 11 are extinct and 6 others are listed as endangered on the federal endangered species list (Neves 1993). *E. triquetra* is by far the most common and widespread member of this genus, but even it is regarded as threatened (Williams et al. 1993). Its range occupies the Mississippi and Great Lakes drainages from Oklahoma and Alabama to Wisconsin and New York. In New York (Figure 25), it has been collected from Lake Erie at Bay View (Robertson and Blakeslee 1948; RMSC 49.421.98, one specimen), Buffalo Creek (BSM 365A-1/8, one specimen), and the Niagara River (Marshall 1895a; BSM 365A-1/3: "Niagara River, Buffalo," three specimens; BSM 365A-1/5: "Buffalo," 18 specimens). All these collections were made before 1950, so it is uncertain whether *E. triquetra* still lives in New York. It should be sought in the Niagara River and perhaps the larger tributaries of Lake Erie and the Niagara River. It may also turn up in the Allegheny basin in New York, as it has been seen in Pennsylvania only a few kilometers from the state line (Ortmann 1919).

E. triquetra lives in large creeks and rivers, chiefly in riffles, and in a few lakes (Ortmann 1919; van der Schalie 1938). In southeastern Michigan, it was most commonly seen in clear, hydrologically stable, low-gradient streams in glacial lake districts (Strayer 1983). It typically buries itself deeply in the substratum (Ortmann 1919; van der Schalie 1932). The logperch and banded sculpin are known to be hosts (Hoggarth 1992; Sherman 1993).

FIGURE 25



Fusconaia flava (Rafinesque)

Wabash pigtoe

PLATE 21, FIGURE 2; PLATE 23, FIGURES 6 AND 8; PLATE 25, FIGURE 2

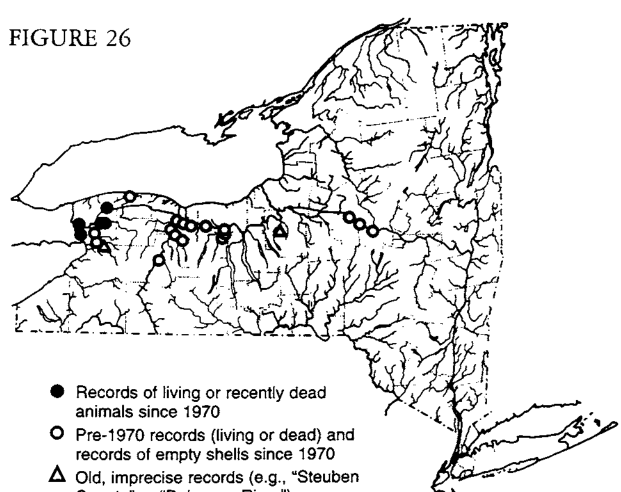
Shell subtriangular to short subtrapezoidal, thick, medium size (up to 100 mm long, but usually <80 mm long). Beak sculpture faint or obscure. Periostracum a little rough, brownish, occasionally with fine, green rays in young specimens. Hinge teeth heavy. Nacre white.

This species is difficult to tell from *Pleurobema cordatum*. *F. flava* tends to be more angular and less rounded than *P. cordatum*, has a more distinct posterior ridge, and has beaks placed 20–40% of the way from the anterior end of the shell (versus 5–25% for *P. cordatum*). In addition, in gravid females of *F. flava*, all four gills are filled with developing glochidia and are red, whereas in *P. cordatum* only the two outer gills contain glochidia, and they are white. The names *F. undata*, *F. trigona* (Plate 25, Figure 2), and *F. parvula* have occasionally been used for *Fusconaia* collected from New York; these are ecophenotypes of *F. flava* (Ortmann 1919).

F. flava is found throughout the Mississippi, Great Lakes, and Red River of the North drainages. In New York, which forms the northeastern edge of its range, *F. flava* occurs from the Erie–Niagara basin eastward into the Mohawk River (Figure 26). The easternmost records (Mohawk River from Utica to Mohawk: compiled from various sources by Strayer 1987; Old Erie Canal, Onondaga County: Beauchamp 1886, and NYSM 31998) almost certainly represent a range extension through the Erie Canal. It is unclear whether populations in the lower Genesee basin (e.g., Clarke and Berg 1959) and Canandaigua Outlet (Harman 1970a) arose via natural, pre-Columbian dispersal or via the Erie Canal. Curiously, *F. flava* has never been seen in the Allegheny basin in northern Pennsylvania or New York (Ortmann 1919), although it is common further south and west in the Ohio basin. *F. flava* is still encountered regularly in western New York (Strayer et al. 1991), but its current status in the Genesee and Oswego basins is not known.

F. flava lives in running waters of all sizes, from small creeks to the Niagara River. It occurs occasionally in lakes, especially Lake Erie (see Ortmann's [1919] discussion of *F. flava parvula*). It seems to do well in muddy, hydrologically unstable, low-gradient streams (Strayer 1983). The bluegill and perhaps the black and white crappie are suitable hosts (Hoggarth 1992).

FIGURE 26



Lampsilis abrupta (Say)

Pink mucket

PLATE 27, FIGURE 7

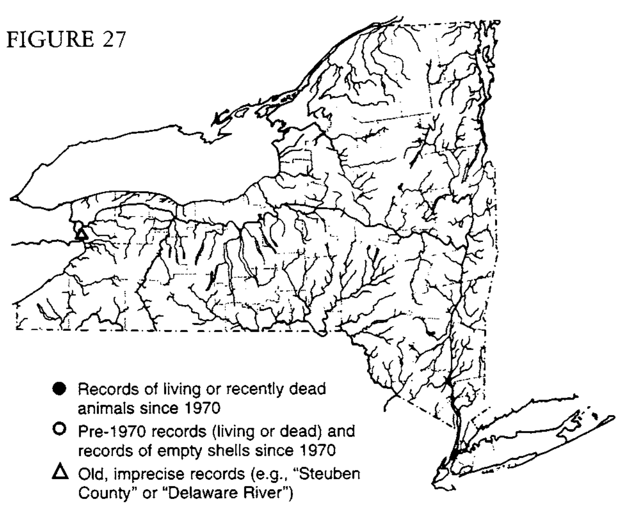
Shell subovate to subelliptical, very thick, reaching up to about 100 mm long. Beak sculpture indistinct or double-looped. Periostracum brown, sometimes with fine, indistinct rays in young animals. Hinge teeth strong. Nacre white to pink.

The most conspicuous characteristic of *L. abrupta* is its extremely thick shell, which is unequalled by that of any other species in New York. The male of *L. abrupta* is, however, very similar to *Actinonaias ligamentina*; often, *L. abrupta* has less distinct and finer color rays than *A. ligamentina* (Ortmann 1919). The female of *L. abrupta* (Plate 27, Figure 7) is much less elongate than *A. ligamentina*.

Only one specimen of this rare species has been found in New York (Figure 27). This specimen (BSM 365B-22/2), which we illustrate here (Plate 27, Figure 7), was mentioned by both Robertson and Blakeslee (1948) and Johnson (1980), but it is not generally recognized as legitimate in discussions of the range of *L. abrupta* (e.g., Burch 1975a; USFWS 1985; Williams et al. 1993), probably because the nearest populations of *L. abrupta* are in the lower Allegheny River of Pennsylvania and the Wabash basin in Indiana (Cummings and Mayer 1992; Johnson 1980; Ortmann 1919; USFWS 1985). The right valve of the New York specimen is labelled "Niagara r., Miss Walker!" in pencil; the left is labelled "*L. fasciola*." "Miss Walker" is Mary E. Walker (1844–1925), who was a cousin of the renowned amateur malacologist Bryant Walker and who had the largest shell collection in Buffalo at the time (Robertson and Blakeslee 1948). The handwriting on the right valve matches that on many of the shells taken from the Niagara River around the turn of the century, and may be that of Elizabeth Letson. Because of the marking on the shell and the reasons discussed under "Erroneous and Questionable Records," we believe there is a good chance that this record of *L. abrupta* is legitimate. Note, however, that the name "*Lampsilis fasciola*" did not come into wide use until the teens, suggesting that at least the left valve was labeled well after the purported collection in 1906. Robertson and Blakeslee wrote that the specimen was labeled "*Lampsilis multiradiatus*," an old name for *L. fasciola*. We tentatively accept *L. abrupta* as a part of New York's fauna. If it still lives in New York, it may be found in the Niagara River above the falls.

L. abrupta has been found in the large rivers of the Ohio River basin, in the Illinois River and Mississippi River in Illinois, and in some rivers in the Ozarks (Johnson 1980; USFWS 1985; note, however, that the systematic status of the western populations is unclear). Apparently never abundant (Johnson 1980; Ortmann 1919; USFWS 1985), *L. abrupta* has disappeared from many sites and is now listed as endangered by the United States Fish and Wildlife Service (USFWS 1985). Its fish hosts are not known, but the closely related *L. higginsii* uses northern pike, largemouth and smallmouth bass, green sunfish, bluegill, walleye, yellow perch, and perhaps sauger and freshwater drum as hosts (Hoggarth 1992).

FIGURE 27



Lampsilis cariosa (Say)

Yellow lampmussel

PLATE 3, FIGURES 1, 2, 5, AND 6; FIGURE 12 I

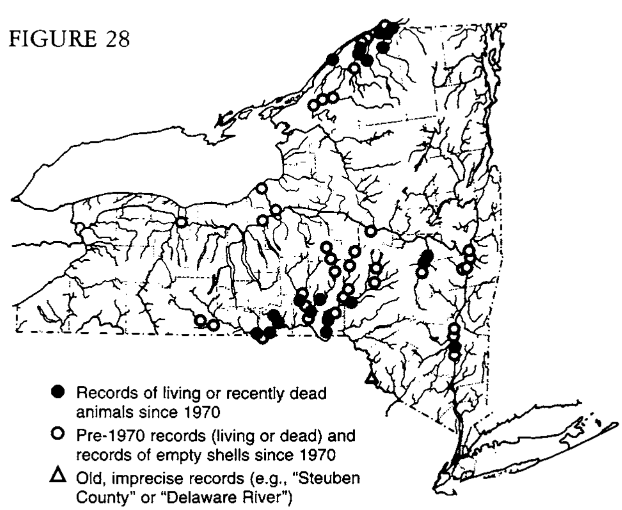
Shell subovate, margin evenly rounded, of variable size and thickness (thick and reaching >100 mm long in some sites, but fairly thin and rarely >75 mm long in others). Beak sculpture weakly double-looped, but often obliterated. Periostracum usually glossy, a distinctive clear yellow, and often without rays. If rays are present, they are well defined and restricted to the posterior slope and ridge. Pseudocardinal and lateral hinge teeth both well developed, but variable in shape and strength. Pseudocardinals often strong and triangular, but sometimes delicate and lamellar, especially in young animals or in specimens from northern New York. Nacre white. Shells sexually dimorphic, with males more elongate than females.

L. cariosa can be recognized by its clear yellow periostracum on which color rays are absent or are confined to the posterior part of the shell. Both *Lampsilis ovata* and *Leptodea ochracea* are similar to *L. cariosa*, but they usually have color rays widely distributed on the shell.

L. cariosa lives on the Atlantic Slope from Georgia to Nova Scotia (Johnson 1947; Williams et al. 1993). In New York, there are many records from the Susquehanna and Hudson basins (Figure 28). Curiously, although the species is not known from the Champlain basin (see also D. Smith 1985a), it is widespread in the St. Lawrence basin in northern New York (see "Dispersal Routes"). Records from elsewhere in the state are scattered. Marshall (1895a) reported it from the "Delaware River system," and it is known from the Delaware basin in Pennsylvania (Ortmann 1919), but we have not seen any specimens or definite records from the Delaware basin in New York. It may have occurred in the Passaic system in New York because it has been found just over the state line in the Ramapo River, New Jersey (Rick Dutko, pers. comm.) ANSP 365657 is labelled "Passaic River at Passaic Bridge, NY," but the Passaic River proper does not reach New York and we have been unable to locate Passaic Bridge, New York. Although records of *L. cariosa* from central New York are questionable because of potential confusion with *L. ovata*, the following records (all old) seem to be authentic: "Oswego" (UMMZ 83842); Oswego River, Onondaga County (Beauchamp 1886); Seneca River (Marshall 1895a); Cross Lake (MCZ 252120); and [Erie?] Canal, Rochester (UMMZ 83839). It is unclear whether *L. cariosa* reached the Oswego basin via the Erie Canal or was present in the basin in pre-Columbian times. The following records from western New York all are questionable and probably refer to *Lampsilis ovata:* Buffalo River (Dewey 1856); Honeoye Lake, Ontario County (Marshall 1895a); Cayuga Lake (Maury 1916). Specimens marked "Dansville, Livingston County" (ANSP 365660, 365661) are *L. cariosa*, but the locality is suspect (see "Erroneous and Questionable Records").

Continued

FIGURE 28



L. cariosa has declined over parts of its range and was listed as threatened by Williams et al. (1993). Nevertheless, it is still relatively common and widespread in New York. Although it seems to be rare in the Hudson River (Strayer 1987), it is still common and reproducing in the Susquehanna basin (Jirka 1991) and lower Schoharie Creek (Strayer 1995). It also still occurs in several tributaries of the St. Lawrence in northern New York (Douglas Carlson, pers. comm.; Erickson and Fetterman 1996; Jirka 1991).

In New York, *L. cariosa* lives in small to large rivers, especially in riffles (Ortmann 1919; Strayer 1993). It is often fairly abundant where it occurs. *L. cariosa* also lives in lakes in Maine (Johnson 1947), but no records are known from New York lakes. The hosts of *L. cariosa* are not known.

Lampsilis fasciola Rafinesque

Wavy-rayed lampmussel

PLATE 7, FIGURES 1 AND 2

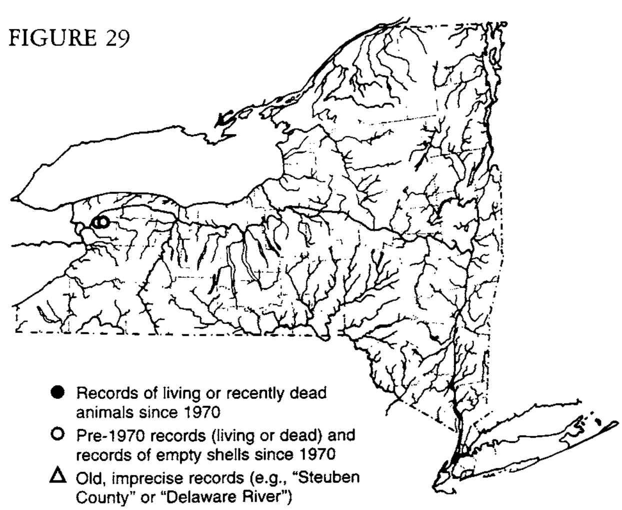
Shell short-subovate (H/L = usually 0.65–0.75) with prominent beaks and an evenly rounded margin, somewhat inflated (W/H = usually 0.5–0.7), moderately thick to thick, usually less than 75 mm long. Beak sculpture a few faintly double-looped bars, not conspicuous. Periostracum yellow to olive with many conspicuous, fine, wavy, green color rays. Hinge teeth strong. Nacre white. Shell sexually dimorphic, the female expanded posterio-ventrally and relatively shorter than the male.

This beautiful species is easily recognized by its rounded, short, ovate shell with many fine, wavy color rays. The only similar species in New York are *Lampsilis ovata*, which has many fewer color rays, and *Leptodea ochracea*, whose range does not overlap with that of *L. fasciola*.

L. fasciola is known from throughout the Ohio River basin, and in the tributaries of Lake St. Clair, Lake Erie, southern Lake Huron, and southwestern Lake Ontario. Records from New York are few (Figure 29). It has been collected in the Great Lakes basin from the Niagara River (Letson 1909; Robertson and Blakeslee 1948; BSM 365D-1/2, one specimen; BSM 365D-1/4, two specimens), Medina (presumably Oak Orchard Creek, ANSP 323383, two specimens), and the Genesee River (Marshall 1895a; NYSM 31385, one specimen). The small number of specimens known from this area suggests that *L. fasciola* was never common or widespread in the Great Lakes basin in New York. It has not been collected from this area since 1906, although it may survive in the Niagara River or in creeks in Niagara, Orleans, or Genesee County. *L. fasciola* also has been seen in French Creek and the eastern Allegheny basin, where it occurs in small numbers (Strayer 1995; Strayer et al. 1991). The record of *L. fasciola* from Butternut Creek, Otsego County (Marshall 1895a) is based on a deformed specimen of *Lampsilis radiata* (ANSP 323391). *L. fasciola* is a rare species in New York; fewer than twenty specimens have ever been seen in the state. Williams et al. (1993) listed *L. fasciola* as "currently stable," but it has declined, at least in the upper Midwest, and it is legally protected in several states (Cummings and Mayer 1992).

L. fasciola typically lives in and around riffles in large creeks and rivers, especially in clear, hydrologically stable streams (Ortmann 1919; Strayer 1983; van der Schalie 1938). It is rarely abundant. The smallmouth bass is a known host (Hoggarth 1992).

FIGURE 29



Lampsilis ovata (Say)
Pocketbook

PLATES 1 AND 2; FIGURE 13 H

Shell solid, short-subovate (H/L = usually 0.65–0.75) with prominent beaks, W/H = usually 0.55–0.65; sometimes very large (>150 mm). Beak sculpture weakly double-looped. Periostracum yellow-green to brown, usually with several, well-defined, broad, green rays distributed across the shell, except in old specimens, which may be rayless. Hinge teeth strong. Nacre white.

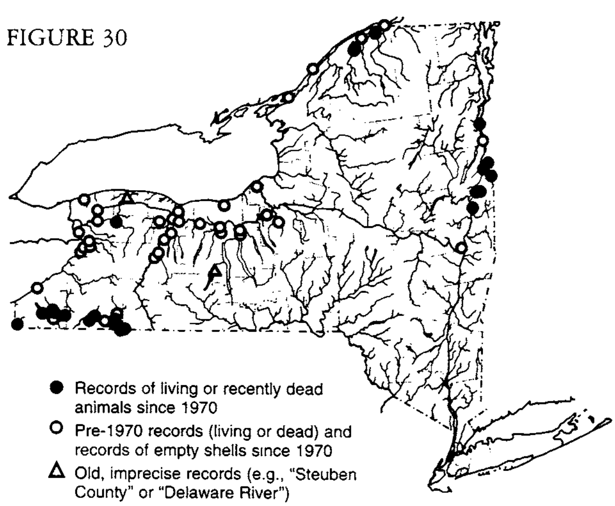
L. ovata can be confused with *Actinonaias ligamentina* and with other species of *Lampsilis*. Shells of *L. ovata* are usually a little shorter than those of *A. ligamentina*, and they have more prominent beaks and more delicate pseudocardinal teeth. Small specimens of *L. ovata* might be misidentified as *Lampsilis fasciola*, but they lack the numerous, fine, wavy color rays that are so characteristic of that species. Males of *L. ovata* are typically higher than those of *Lampsilis siliquoidea* or *Lampsilis radiata*. Typically, *L. ovata* is greenish or brownish, with color rays across the face of the shell, while *Lampsilis cariosa* is yellow, with color rays absent or restricted to the posterior slope.

Many recent authors (e.g., Cummings and Mayer 1992; Stansbery 1983; Turgeon et al. 1988; Watters 1993; Williams et al. 1993) have distinguished *L. ovata* s.s., which has an angular posterior ridge and lives in large rivers, from *L. cardium* (= *L. ventricosa* of earlier authors), which has a rounded posterior ridge and is ecologically widespread. Because the evidence for this separation has not been published and because traditional morphological analyses (Cvancara 1963; Ortmann 1919) suggest that *L. ovata* and *L. cardium* are continuously intergrading ecophenotypes of a single species, we are conservatively including both under *L. ovata*. Almost all New York material is "*L. cardium*," but a few specimens from the Allegheny River proper would be classified as "*L. ovata*" in the strict sense.

L. ovata is widespread in the Mississippi and St. Lawrence basins, as well as the Potomac River (where it was introduced) and the Red River of the North. In New York, it has been found at many sites in the Allegheny, Erie–Niagara, Genesee, Oswego, and Champlain basins (Figure 30). It is also known from a few places in the St. Lawrence River basin in northern New York (Clarke and Berg 1959; Erickson and Fetterman 1996; INHS 9173: St. Lawrence River 2 miles southwest of Morristown; NYSM 8401: Raquette River at village of Raquette River; OSUM 21924: Grass River at Madrid) and from two sites in the Hudson basin near the entrance of the Champlain Canal (D. Smith 1982; OSUM 9098: "Albany"). According to recent surveys (D. Smith 1985a; Strayer 1995; Strayer et al. 1991), *L. ovata* is still common in parts of New York, but Williams et al. (1993) gave it special concern status.

L. ovata is widespread in large creeks and rivers; it occurs in some lakes as well (e.g., Ortmann 1919; van der Schalie 1938). It is often one of the most abundant unionoids in the community. Known hosts include white crappie, largemouth and smallmouth bass, bluegill, walleye, and yellow perch (Hoggarth 1992, as *L. ventricosa*; Watters 1994a).

FIGURE 30



Lampsilis radiata (Gmelin)

Eastern lampmussel

PLATE 4; PLATE 5, FIGURES 1, 2, AND 5; FIGURE 12 D

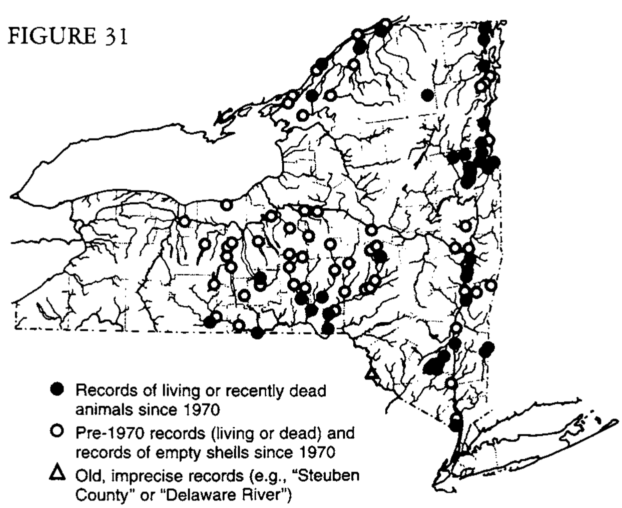
Shell subovate, margin evenly rounded, of medium thickness and size (up to about 100 mm long), H/L = usually 0.5–0.6, W/H = usually 0.6–0.66 (Clarke and Berg 1959). Beak sculpture double-looped. Periostracum a little rough, yellow-green to green, usually with many dark green rays over the whole shell. Hinge teeth well developed but not heavy. Nacre white or pink. Shell slightly sexually dimorphic, with the female shell a little expanded posterio-ventrally.

This species closely resembles *Lampsilis siliquoidea*, with which it apparently hybridizes (Clarke and Berg 1959; Kat 1983c, 1986). In fact, many authors consider *L. radiata* and *L. siliquoidea* to be subspecies; we tentatively recognize them as full species until critical studies are made. Typical *L. radiata* has a slightly rough, wrinkled, greenish-yellow periostracum and numerous dark green color rays, while typical *L. siliquoidea* has a smooth, glossy, brownish-yellow periostracum with a few, widely spaced color rays. Sexual dimorphism is much more pronounced in *L. siliquoidea* than in *L. radiata*. Typical specimens of the two species are not difficult to separate. Nevertheless, because intergrades may be found in parts of New York (Clarke and Berg 1959), it may be impossible to assign some specimens to *L. radiata* or *L. siliquoidea*. *L. radiata* is more elongate than *Lampsilis cariosa*, *Lampsilis ovata*, and *Leptodea ochracea*. Also, color rays (if present) are restricted to the posterior part of the shell of *L. cariosa*, while *L. radiata* usually has color rays across the face of the shell. *L. radiata* may closely resemble *Actinonaias ligamentina* externally, but it usually has a thinner shell and much more delicate hinge teeth. In addition, the two species have non-overlapping ranges in New York.

L. radiata lives along the Atlantic Slope from South Carolina to Nova Scotia and reaches inland from Lake Ontario through the Lake Huron and Lake Superior basins. Its exact distribution in New York is unclear because of confusion and perhaps hybridization with *L. siliquoidea*. Figure 31 shows the distribution of *L. radiata* based on specimens we examined or literature records that we think are reliable. *L. radiata* is widespread in the Susquehanna, Hudson, and Champlain basins, and in the St. Lawrence basin in northern New York. There also are scattered records from other basins: the Delaware (Marshall 1895a: "Delaware River system"), the Passaic (Strayer 1994), the Housatonic (Strayer 1992), and Lake Ontario basins (Clarke and Berg 1959). The westernmost record that we found was from the Erie Canal at Pittsford (NYSM 31845). *L. radiata* overlaps widely with *L. siliquoidea* in the Oswego and Mohawk basins. *L. radiata* is still common and widespread in New York.

L. radiata is an ecologically tolerant species that lives in creeks, rivers, and lakes. Often, it is one of the most abundant unionoids in the community. No definitive studies have been made of the fish hosts of this species, but the closely related *L. siliquoidea* uses many warm-water fish species (see following account).

FIGURE 31



Lampsilis siliquoidea (Barnes)

Fat mucket

PLATE 5, FIGURES 6 AND 7; PLATE 6, FIGURES 1 THROUGH 3; FIGURE 12 C

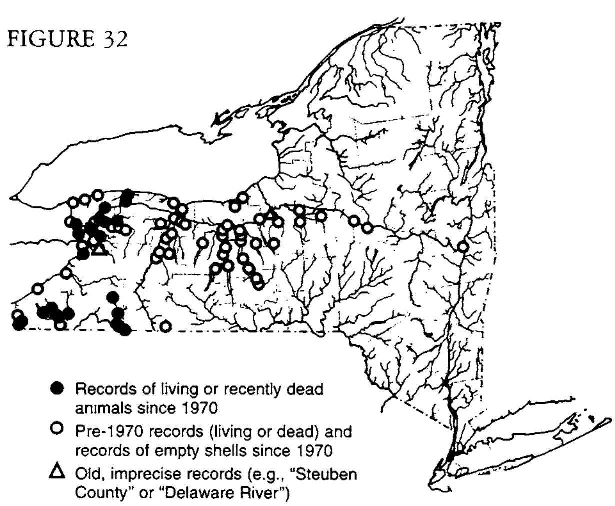
Shell subovate, moderately long (H/L = usually 0.5–0.65, W/H = usually 0.5–0.8) and thick, sometimes exceeding 100 mm in length. Beak sculpture double-looped (or sometimes with more than two loops). Periostracum glossy, usually yellow to brown (sometimes yellow-green) with a few prominent rays. Hinge teeth well developed but not heavy. Nacre usually white, but sometimes pink. Shells strongly sexually dimorphic, the female shell expanded posterio-ventrally.

This species is most likely to be confused with *Lampsilis radiata* (see previous account). *L. siliquoidea* also resembles *Actinonaias ligamentina* and *Villosa iris*. *A. ligamentina* is more elliptical than *L. siliquoidea*, and has a thicker shell, stouter pseudocardinal teeth, and broader, less distinct color rays. *V. iris* is small (<75 mm), more elongate and elliptical than *L. siliquoidea*, and has broad, often interrupted, color rays.

L. siliquoidea is widespread throughout most of the Mississippi, Great Lakes, and Red River of the North basins. For reasons discussed under *L. radiata*, the distribution of *L. siliquoidea* in New York is a little unclear. Figure 32 shows our best assessment of its range, based on specimens we examined and on literature reports that we consider reliable. *L. siliquoidea* lives in many places throughout the Allegheny, Erie–Niagara, Genesee, and Oswego River basins, as well as in small tributaries of Lake Ontario east to the Oswego River. Significantly, the only record of the *L. radiata* complex from the upper Genesee basin is *L. siliquoidea* (ANSP 365677: creek at Richberg, Allegany County). *L. siliquoidea* is also known from a few places in the Mohawk River as far east as Cohoes (Strayer 1987; ANSP 365698), which it undoubtedly reached through the Erie Canal. Reports of this species from Lake Champlain (Marshall 1895a) and the Susquehanna basin (Harman 1970a) are probably based on *L. radiata*. *L. siliquoidea* is still one of the most abundant unionoid species in western New York (Strayer 1995; Strayer et al. 1991).

Like *L. radiata*, *L. siliquoidea* lives in a wide range of habitats: small and large lakes, creeks, and rivers. It is often one of the most abundant species in the mussel community. In streams, *L. siliquoidea* often lives along the margins of pools, while other mussel species live in the riffles. *L. siliquoidea* uses many hosts, including white bass, many centrarchids, sauger, walleye, and yellow perch (Hoggarth 1992; Watters 1994a).

FIGURE 32



Lampsilis teres (Rafinesque)

Yellow sandshell

PLATE 10, FIGURE 4

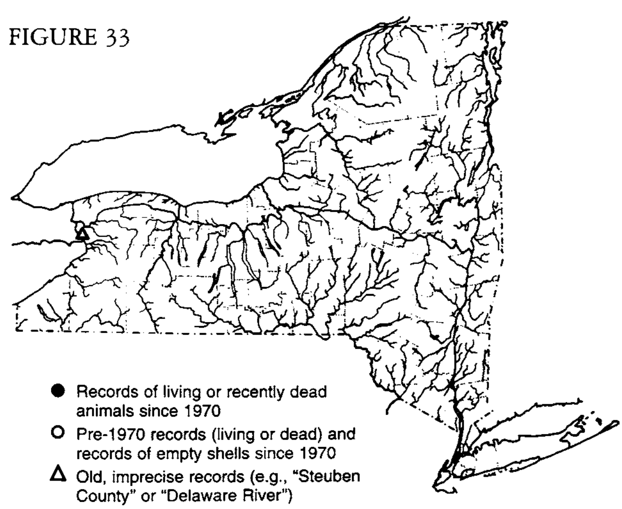
Shell elongate-subelliptical, moderately thick, up to 150 mm long (but New York specimens are much shorter). Beak sculpture double-looped. Periostracum glossy, bright yellow, rayless or with many fine, green rays. Pseudocardinal teeth elongate; lateral teeth long and nearly straight. Nacre white.

The long shell and shiny yellow or green periostracum of *L. teres* distinguish it from other species. *Lampsilis siliquoidea* has a shorter, higher shell; *Ligumia recta* has a much darker periostracum; and *Ligumia nasuta* has a rough periostracum.

L. teres is found throughout the Mississippi River and Gulf basins. New York is not generally recognized as part of its range (e.g., Burch 1975a; Williams et al. 1993), and there are no records from elsewhere in the Great Lakes basin. Nevertheless, there are a few records of *L. teres* from the Niagara River. Several early authors recorded this distinctive species from "western New York" (Beauchamp 1886; Call 1895; Lewis 1874), "near Buffalo" (Marshall 1895a), or "Niagara River" (Letson 1909), without giving specific localities. In addition, we have seen two authentic specimens of *L. teres* attributed to New York: NYSM 31864 (shown in Plate 10; definitely collected before 1925 and probably collected ca. 1900) and ANSP 42080 (Letson! 1891). Both specimens have "Niagara r." penciled on the shell, possibly in Letson's hand. We believe that these old records are probably genuine (see "Erroneous and Questionable Records"), but they badly need to be confirmed through careful surveys of the Niagara River.

L. teres lives in medium-sized to large rivers, often on sandy bottoms (Cummings and Mayer 1992). The Niagara River probably provides the only suitable habitat in New York. Known hosts include alligator, longnose, and shortnose gar, and perhaps several centrarchids (Hoggarth 1992).

FIGURE 33



Lasmigona complanata (Barnes)

White heelsplitter

FIGURE 13 D

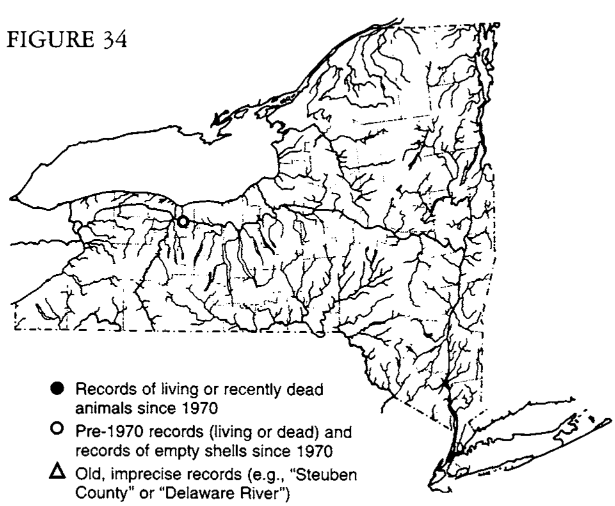
Shell short, subovate to subrhomboidal, strongly compressed, with a prominent dorsal wing, of moderate thickness, reaching over 150 mm in length. The dorsal wing may be marked by irregular, low ridges. Beak sculpture conspicuous, double-looped. Periostracum brownish, sometimes with faint, thin, green color rays. Pseudocardinals strong, but laterals represented only by low ridges; interdental tooth present in left valve. Nacre white.

This distinctive species can be confused only with the other two heel-splitters in New York. *Potamilus alatus* has purple nacre and strong lateral teeth, and *Leptodea fragilis* has a smooth yellowish periostracum, and distinct, but delicate, lateral teeth. *L. complanata* has white nacre, only traces of lateral teeth, and a brownish periostracum.

L. complanata is very widely distributed in North America. It is known from nearly the entire Mississippi basin, large parts of the Great Lakes basin, and parts of the Hudson Bay and Gulf of Mexico drainages (Clarke 1985). Several specimens of *L. complanata* were taken from Erie Canal at Pittsford, Monroe County by Shelley G. Crump in the 1920s (Pilsbry 1925). Figure 13 d illustrates one of these specimens. We were not able to locate these specimens in ANSP or NYSM. This is the only definite record of the species from New York (Figure 34), although there are a few old, indefinite records from western New York (Beauchamp 1886) or Buffalo (Lewis 1874; Marshall 1895a). *L. complanata* should be sought in low-gradient streams and canals from Buffalo to Rochester. Although apparently now rare or absent from New York, *L. complanata* is common elsewhere in its range.

L. complanata is a common species of creeks, rivers, and reservoirs, often in muddy, low-gradient habitats (Strayer 1983; van der Schalie 1938). It occasionally lives in lakes as well. It is one of few unionoids that seem to do well in disturbed habitats. Known hosts include the carp, banded killifish, white crappie, large-mouth bass, orangespotted sunfish, and green sunfish (Hoggarth 1992; Watters 1994a).

FIGURE 34



Lasmigona compressa (Lea)

Creek heelsplitter

PLATE 19, FIGURES 1 AND 4 THROUGH 6; FIGURE 12 A

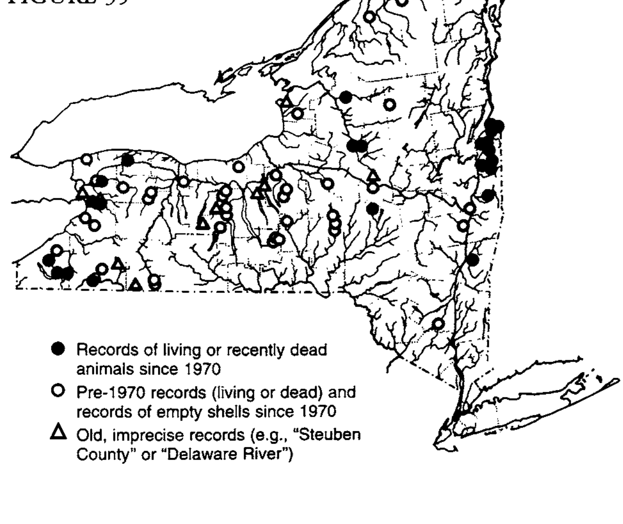
Shell subtrapezoidal, compressed, moderately thick, sometimes with a small dorsal wing in young specimens, usually <100 mm long. Beak sculpture obvious, double-looped. Periostracum greenish with many fine, green rays in young animals, greenish black in old animals. Pseudocardinals lamellar, usually smooth; laterals delicate, but functional and interlocking. In addition, there is a more or less prominent interdental tooth in the left valve between the pseudocardinals and the laterals. Nacre white, sometimes a little orangish in the beak cavity.

L. compressa is characterized by its compressed, trapezoidal shape, its small dorsal wing, its many fine green color rays, and its large interdental tooth. The only species likely to be confused with *L. compressa* is *Lasmigona subviridis*, which is smaller, thinner-shelled, more ovate, and has a much smaller interdental tooth. Typically, the beak sculpture of *L. compressa* consists of 4–5 large, deeply double-looped bars of even height, while that of *L. subviridis* is 3–4 smaller, less deeply curved and distinctly nodulous bars (Figures 12 a, b). In addition, the ranges of these two species scarcely overlap (Figures 35 and 37).

L. compressa lives in the Mississippi River basin from Kentucky north, as well as in the Hudson Bay basin, the Great Lakes basin, the lower St. Lawrence basin, and the Hudson River basin (Clarke 1985). It is one of the most widespread of the Interior Basin species in New York (Figure 35). It is found throughout the Allegheny (Strayer 1995; Strayer et al. 1991), Erie–Niagara, Lake Ontario (including the upper Genesee: Marshall 1895a; NYSM 31838; ANSP 366135, ANSP 365707), and Champlain basins. It crossed into the Hudson basin, probably by natural means well before the opening of the Erie Canal (Strayer 1987). There are a few positive records (Erickson and Fetterman 1996; Raquette River one mile south of Potsdam: Clarke 1985; Cook's Corners, St. Lawrence County: ANSP 365861) from the St. Lawrence basin in northern New York. Remarkably, *L. compressa* has been found in the northeastern headwaters of the Susquehanna system (Chenango River at Earlville: OSUM 21547; Chenango River one mile east of North Norwich: OSUM 21622; Chenango River east of Shelburne: OSUM 14897; West Branch of Tioughnioga River above mouth of Factory Brook, Homer: OSUM 21930; all C. Stein! 1965; Herkimer Creek, Otsego County: Harman 1973), perhaps arriving by the same, still undefined, route (or maybe by the Chenango Canal?) as *Anodontoides ferussacianus*. *L. compressa* is still abundant in New York and elsewhere.

L. compressa is typically a creek species, sometimes living in streams too small to support other unionoids (Ortmann 1919; Strayer 1983; van der Schalie 1938). It occasionally lives in rivers and (rarely) lakes as well (e.g., pond at Griswold Station, Erie County: BSM 364K-1/57; Brown's Tract Pond, Hamilton County: ANSP 97784). *L. compressa* is one of the few unionoids that are hermaphroditic (van der Schalie 1970). Hove et al. (1995b) found that slimy sculpin, spotfin shiner, black crappie, and yellow perch were suitable hosts.

FIGURE 35



Lasmigona costata (Rafinesque)
Fluted shell

PLATE 18, FIGURES 2 AND 3; FIGURE 12 J

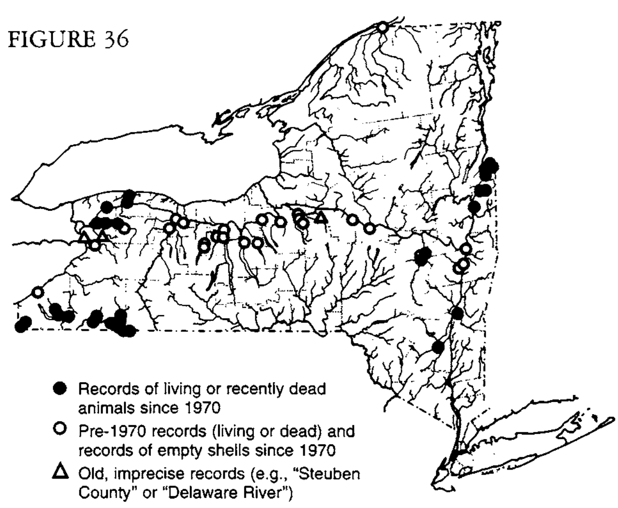
Shell subtrapezoidal, compressed, moderately thick, up to about 150 mm long. Posterior slope with prominent ridges crossing the growth lines. Beak sculpture coarse, weakly double-looped. Periostracum greenish or brownish with fine, green rays in young specimens, brown or dark green in old specimens. Pseudocardinals moderately strong, but laterals represented by faint ridges along the hinge line; prominent interdental tooth in left valve. Nacre white or cream.

The coarse ridges on the posterior slope make this species easy to identify. Even if these ridges are obscure or overlooked, *L. costata* is easily identified by its flattened, subtrapezoidal shell and distinctive hinge teeth.

L. costata lives throughout the Mississippi and Great Lakes basins, as well as in the Hudson Bay system and the lower St. Lawrence basin. In New York, its range (Figure 36) is similar to that of *Lasmigona compressa* (Figure 35), except that *L. costata* does not inhabit the smallest creeks, so it has not gone as far into the headwaters. Also, *L. costata* has never been seen in the Susquehanna basin. According to recent surveys (D. Smith 1985a; Strayer 1995; Strayer et al. 1991), *L. costata* is still abundant at many sites in New York.

L. costata is abundant in large creeks and small rivers. It has been found in a few lakes (Erie, Canandaigua, Cayuga, Cross, Onondaga) in New York as well. Known hosts include the carp, bowfin, northern pike, bluegill, largemouth bass, yellow perch, and walleye (Hoggarth 1992; Hove et al. 1994a).

FIGURE 36



Lasmigona subviridis (Conrad)

Green floater

PLATE 19, FIGURES 2 AND 3; FIGURE 12 B

Shell subovate to subtrapezoidal, fairly thin, less than 65 mm long (often less than 50 mm). Young specimens may have a small dorsal wing. Beak sculpture conspicuous, double-looped. Periostracum yellowish to greenish, with many fine color rays. Hinge teeth well developed but delicate. As in *Lasmigona compressa*, there is an interdental tooth in the left valve between the pseudocardinals and the laterals. This interdental tooth is small in *L. subviridis*, and it may be continuous with the pseudocardinals. Nacre white.

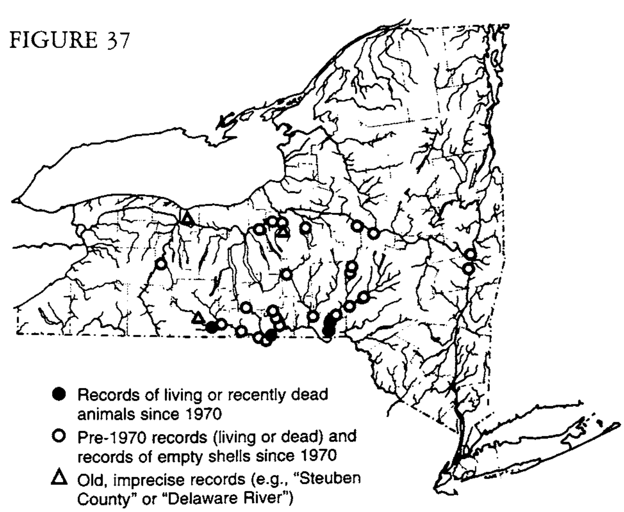
This species most closely resembles *Lasmigona compressa*. See the account of that species for tips on distinguishing the two species.

L. subviridis is a species of the Atlantic Slope from North Carolina to New York, as well as the Kanawha River basin of the Ohio River drainage system in North Carolina, Virginia, and West Virginia (Clarke 1985). Most of the records from New York are from the Susquehanna River drainage, where the species was formerly widespread (Figure 37). It also has reliably been recorded from a few sites in the Mohawk and Hudson Rivers (Strayer 1987), the Oswego River basin near Syracuse (Beauchamp 1886; Clarke 1985; Clarke and Berg 1959; Erie Canal near Baldwinsville: ANSP 41019), and the lower Genesee drainage (UMMZ 247519, UMMZ 104147). Erickson and Fetterman (1996) tentatively reported two specimens of *L. subviridis* from the Grass River drainage in northern New York, but this record is well out of the known range of the species and must be verified. Other reports of *L. subviridis* from central and western New York (e.g., Baker 1898, 1901; Marshall 1895a; Walton 1891) are uncertain, and may be based on misidentifications of *L. compressa*, which was not always properly distinguished from *L. subviridis* by early authors.

L. subviridis has declined throughout much of its range and was listed as threatened by Williams et al. (1993). Apparently, relatively few populations remain in New York. *L. subviridis* has not been seen this century in the Hudson River, despite intensive sampling (Bode et al. 1986; Simpson et al. 1986; Strayer et al. 1994; Townes 1937). It is very doubtful that the species remains in the Mohawk River, which has been badly polluted since 1891, the last time *L. subviridis* was seen there (Bailey 1891). The most recent surveys of the Oswego and Genesee basins (Clarke and Berg 1959; Harman 1970a) turned up this species only in Chittenango Creek, a tributary of Oneida Lake, in 1956. Surveys of eleven historical sites in the Susquehanna basin in New York, formerly a stronghold of this species, turned up *L. subviridis* at only four (Jirka 1991; Schneider, pers. comm.).

L. subviridis is found most frequently in the quiet parts of large creeks and small rivers (Clarke and Berg 1959; Ortmann 1919). It seems to occur more often in hydrologically stable streams than in those subject to severe floods and droughts (Strayer 1993). *L. subviridis* is one of few hermaphroditic unionoids (van der Schalie 1970). Its fish hosts are not known.

FIGURE 37



Leptodea fragilis (Rafinesque)

Fragile papershell

PLATE 9, FIGURES 1 AND 2; PLATE 11; FIGURE 13 F

Shell thin, subovate, compressed, with a dorsal wing, sometimes >100 mm long. Dorsal wing typically well developed in young specimens and in animals living in lakes, but low or even absent in old, river-dwelling animals. Beak sculpture indistinct, double-looped. Periostracum shiny, light grayish yellow to brownish yellow, sometimes with faint, green rays. Hinge teeth present but delicate. Pseudocardinals lamellar, weak. Nacre silvery white to light pink. Shells sexually dimorphic, the female shell more extended posterio-ventrally.

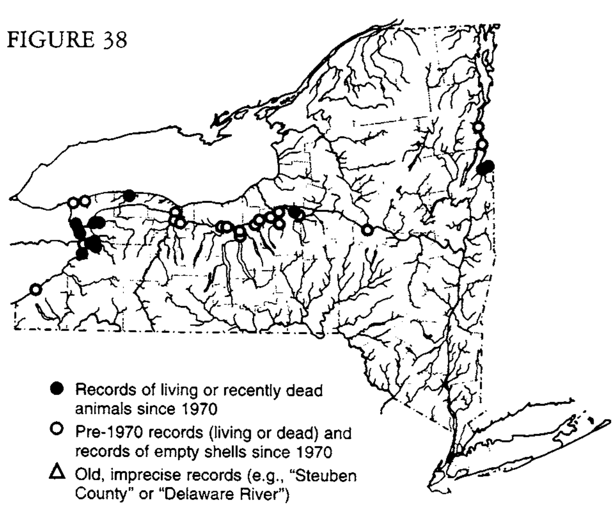
This species could be confused with *Potamilus alatus* or *Lasmigona complanata*. *P. alatus* has a dark green or black periostracum, strong triangular pseudocardinal teeth, and a distinctly purple nacre, and *L. complanata* has a brownish periostracum, a white nacre, and vestigial lateral teeth.

In New York, as elsewhere in its range (e.g., Ortmann 1919), *L. fragilis* varies considerably in nacre color and wing size. Nacre color varies from silvery white, which is said to be typical for the species, to a pale but distinct shell pink. Many specimens from creeks in western New York are almost wingless, while other specimens, especially from Lake Champlain, have a large, sharp dorsal wing. We believe this variation is the source of erroneous reports of *Leptodea leptodon* and *Potamilis ohiensis* from New York (see "Erroneous and Questionable Records").

L. fragilis lives throughout the Mississippi and Great Lakes basins, as well as in parts of the Gulf of Mexico and lower St. Lawrence River basins. It entered New York from two directions (Figure 38). From Lake Erie, it moved east to Oneida Lake, and based on a single specimen, the mid-Mohawk River (MCZ 252205: Hydraulic Canal at Herkimer, Lewis!). At least part of this range was probably invaded via the Erie Canal, but pre-Columbian natural confluences may have been used as well. *L. fragilis* also moved south from the St. Lawrence River into Lake Champlain and its tributaries (cf. D. Smith 1985a). Although it has not been seen in the St. Lawrence or its tributaries in northern New York, it may very well occur in this region. This species recently has been encountered regularly in the Erie–Niagara (Strayer et al. 1991) and Champlain (D. Smith 1985a; Fichtel and Smith 1995) basins, sometimes in good numbers.

L. fragilis is especially characteristic of the quiet waters of canals and lakes, but it also occurs in riffles in creeks and rivers (e.g., Tonawanda Creek, Erie and Niagara Counties). According to Ortmann (1919), it is one of the speediest and most active of the unionoids. The freshwater drum may be a host (Hoggarth 1992).

FIGURE 38



Leptodea ochracea (Say)

Tidewater mucket

PLATE 3, FIGURE 3; FIGURE 12 G

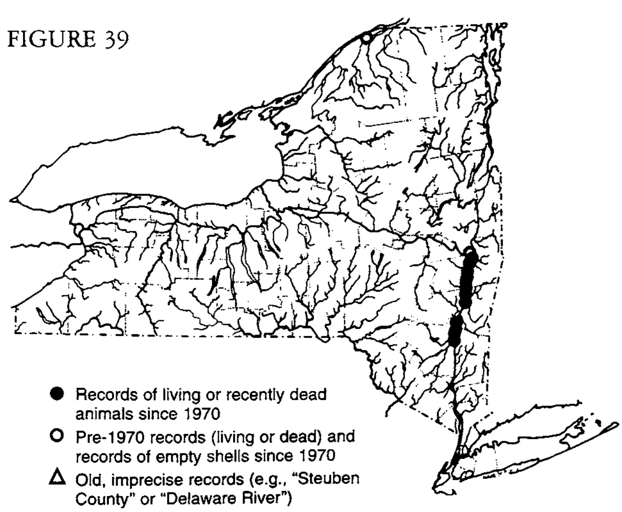
Shell short, subovate, thin, reaching about 75 mm long. Beak sculpture weakly double-looped. Periostracum a little rough, drab brownish yellow to greenish yellow, usually with many fine rays covering the shell. Hinge teeth well developed but delicate; pseudocardinals compressed. Nacre white to reddish pink.

The shell of this species is similar to those of several species of *Lampsilis*. Until recently, most authors placed *Leptodea ochracea* in the genus *Lampsilis*. Typically, *L. ochracea* has fine color rays across the face of the shell, while *Lampsilis cariosa* has no color rays or rays only on the posterior slope. Often, the periostracum of *L. cariosa* is glossy, while that of *L. ochracea* is satiny, and the shell and hinge teeth of *L. cariosa* are heavier than those of *L. ochracea*, although specimens of *L. cariosa* from tributaries of the St. Lawrence in New York are very delicate. Furthermore, *L. ochracea* often has pink nacre, whereas *L. cariosa* always has white nacre. *Lampsilis radiata* has a more elongate shell and is much greener than *L. ochracea*. While *Lampsilis fasciola* superficially resembles *L. ochracea*, it has wavy color rays and, except in old specimens, a bright periostracum; furthermore, their ranges do not overlap (Figures 29 and 39).

L. ochracea lives in coastal ponds and quiet tidal waters from Georgia to Nova Scotia. In New York, it was common only in the freshwater tidal Hudson River (Figure 39), where in 1991–1992, it constituted about 5% of the unionoid community of over one billion animals (Strayer et al. 1994). Since the arrival of the zebra mussel, the population of *L. ochracea* in the Hudson River appears to have declined considerably (Strayer and Smith 1996), so this species may soon disappear from New York. Williams et al. (1993) gave it a status of special concern.

Remarkably, a single, old, spent shell of *L. ochracea* was collected in 1965 from the Grass River at Louisberg by Carol B. Stein (OSUM 14909). Erickson and Fetterman (1996) likewise reported a questionable occurrence of this species in the Grass River. Far from previously known populations of the species, the origins and status of this population are obscure. It may represent a remnant population that survived glaciation in an offshore refugium (cf. *Lampsilis cariosa*), or the specimens found by Stein and Erickson may have been strays, brought up the St. Lawrence by anadromous fish. For example, C.L. Smith (1985) pointed out that stray specimens of *Alosa sapidissima* occasionally make it all the way up the St. Lawrence to Lake Ontario. The host of *L. ochracea* is not known, although it is presumably an anadromous fish such as *Alosa* (Johnson 1947, 1970).

FIGURE 39



Ligumia nasuta (Say)

Eastern pondmussel

PLATE 8, FIGURES 2, 3, AND 5; FIGURE 12 E

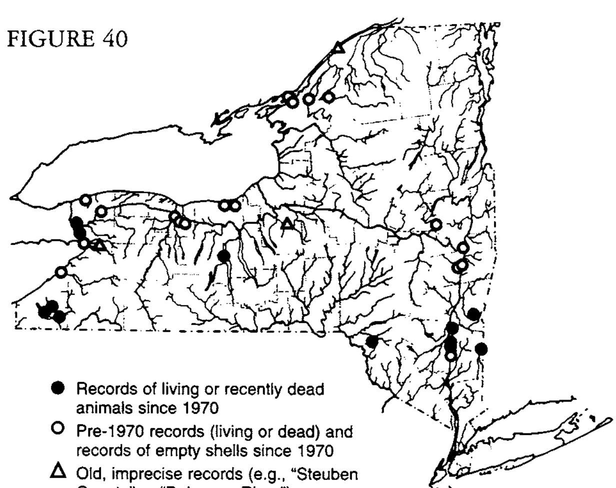
Shell elongate (W/L usually 0.4–0.5), subelliptical, with a distinct posterior ridge, medium thick, rarely >100 mm long and often <75 mm long. The posterior end of the shell is drawn out into a more or less well-defined blunt point near the midline of the shell. Beak sculpture double-looped. Periostracum dark, green to brown, sometimes with fine rays over the posterior part of the shell. Hinge teeth well developed, sharp, and delicate. Nacre bluish white to creamy white.

The long shell, with its distinctive posterior end, makes this species easy to recognize. Other diagnostic characters include the rough periostracum, often with fine color rays posteriorly, the delicate pseudocardinal teeth, and the thin, sharp lateral teeth. *Elliptio* spp. usually have shorter shells and much heavier hinge teeth than *L. nasuta*, and *Ligumia recta* has a smoother periostracum, heavier hinge teeth, and a more rounded posterior end.

Although *L. nasuta* originated on the Atlantic Slope, it has dispersed into much of New York (see "Dispersal Routes") and is most common in the western part of the state (Figure 40). On the Atlantic Slope in New York, it is found only sporadically in the Hudson (Strayer 1987), Delaware (Tennanah Lake, Sullivan County: Harman, unpublished) and Housatonic (Webatuck Creek near mouth: Strayer 1992) basins. It seems to be missing altogether from the Susquehanna basin (cf. Ortmann 1919). It is scattered in the Erie–Niagara drainage (Robertson and Blakeslee 1948; Strayer et al. 1991), central New York (Clarke and Berg 1959; Harman 1970a) and the St. Lawrence and its tributaries (Clarke and Berg 1959; Erickson and Fetterman 1996; Harman 1970a; Oswegatchie River at Gouverneur: OSUM 19352, Stein! 1965; St. Lawrence River: BSM 365d-2/1, Letson! 1906). Remarkably, since 1980, *L. nasuta* has been found at three sites in the Allegheny basin (Chautauqua Lake: NYSM 8502, Jokinen! 1985; OSUM 55808, Forrer and Krull! 1983; Cassadaga Creek at Red Bird: Strayer 1995; Chadokoin River at mouth: Strayer 1995). Because *L. nasuta* is not widespread in the Ohio River basin (e.g., Ortmann 1919) and was not reported by any of the several collectors who visited the Chautauqua Lake area during the early 1900s (Baker 1928b; Maury 1916; plus many lots held in various museums), *L. nasuta* was probably recently introduced into the Chautauqua area, perhaps with stocked fish. Although not very widespread in New York, *L. nasuta* is still encountered regularly, and sometimes it is abundant. It was listed as a species of special concern by Williams et al. (1993).

L. nasuta is found most often in quiet waters in estuaries, lakes, canals, or slow streams, but it has also been found regularly in the Niagara River. Its fish hosts are not known, but its close relative *Ligumia subrostrata* uses several centrarchid species (Hoggarth 1992).

FIGURE 40



Ligumia recta (Lamarck)

Black sandshell

PLATE 8, FIGURE 1

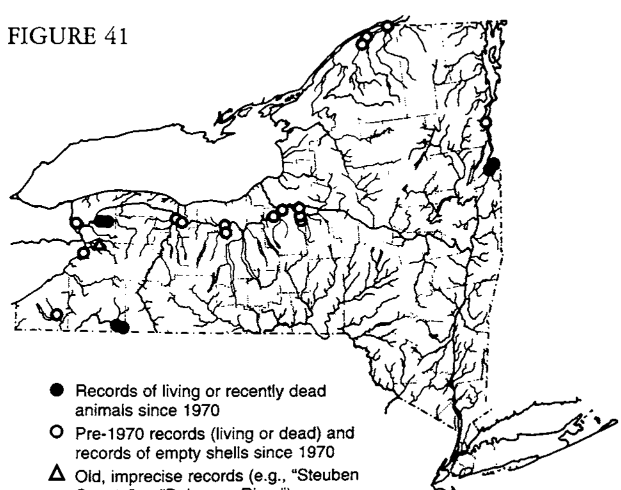
Shell elongate (H/L = usually 0.37–0.49), subelliptical, thick, reaching about 200 mm long. Beak sculpture obscure. Periostracum shiny and dark green with rays in young animals, dark brown to black in old animals. Hinge teeth heavy; pseudocardinals triangular or a little compressed. Nacre usually white, but often pinkish or purple, especially in the beak cavity. Shells sexually dimorphic, broader and more rounded posteriorly in females than in males.

Adult shells of this species are distinctive: large, heavy, and elongate with a black periostracum and strong hinge teeth. Young *L. recta* may be confused with *Elliptio dilatata*, but *L. recta* has a shiny green or black periostracum, while the periostracum of *E. dilatata* is a little rough and usually brown. Also, *E. dilatata* is not usually as elongate as *L. recta*.

L. recta has three ranges in New York: the Allegheny basin, the Erie–Ontario basin, and the St. Lawrence–Champlain basin (Figure 41), reflecting its three routes of entry into the state. In the Allegheny basin, it has been found only in the Allegheny River proper and in one of its largest tributaries, Cassadaga Creek (Strayer 1994; Strayer et al. 1991). It has been recorded from Lakes Erie (BSM 365D-3/1) and Oneida (Clarke and Berg 1959; Harman and Forney 1970), and in rivers and large creeks in between these lakes (Clarke and Berg 1959; Harman 1970a; Robertson and Blakeslee 1948; Strayer et al. 1991; Walton 1891). Finally, there are scattered records from the St. Lawrence River and one of its tributaries, the Grass (Clarke and Berg 1959; Erickson and Fetterman 1996), Lake Champlain (USNM 308864 and 452102), and the Poultney River (Fichtel and Smith 1995), which flows into Lake Champlain. Although widespread in New York, *L. recta* is usually seen in small numbers. Because much of its range in New York has not been surveyed recently, its current status is not well known. Probably, it is still extant but uncommon through much of its range in New York. Williams et al. (1993) listed it as being of special concern.

L. recta lives in large creeks, rivers, and some large, shallow lakes (Ortmann 1919; Strayer 1983; van der Schalie 1938). Its thick, lustrous shell was valued by the pearl-button industry (e.g., Clark and Wilson 1912). Known hosts include the banded killifish, white crappie, largemouth bass, bluegill, green sunfish, orangespotted sunfish, and walleye (Hoggarth 1992; Hove et al. 1994 a, 1994b).

FIGURE 41



Margaritifera margaritifera (Linneaus)

Eastern pearlshell

PLATE 24, FIGURE 5

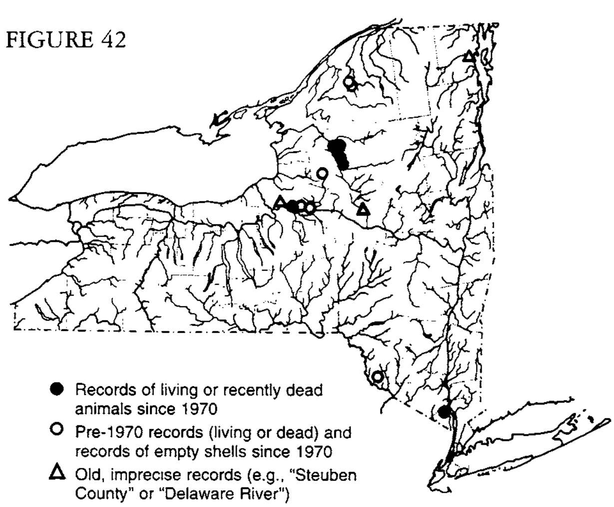
Shell elongate (H/L = usually 0.45–0.5), subelliptical to arched, thick (but often cracking when dried), reaching up to 150 mm long. Beak sculpture coarse, concentric (but usually obliterated). Periostracum dark brown to black, without rays. Pseudocardinals strong, laterals nearly or entirely absent. Nacre pearly white, sometimes with pink or purple tones.

In New York, this species is likely to be confused only with *Elliptio complanata*. The shell of *M. margaritifera* has a blackish, rayless periostracum, no lateral teeth, and conspicuous pores on the interior of the shell. Old specimens of *M. margaritifera* often have distinctly arched shells. The shell of *E. complanata* is not arched, usually has a brownish periostracum, sometimes has fine color rays, has well-developed lateral teeth, and lacks shell pores.

M. margaritifera is the only Holarctic species in our unionoid fauna, occurring in Europe and Asia as well as North America. The center of its North American distribution is in New England and the Maritimes. New York and Pennsylvania (Ortmann 1919) form the southern and western edges of its range. Its exact distribution and current status in New York are poorly known. *M. margaritifera* lives in cold, softwater, mountain streams that often are overlooked in surveys for other mussel species. It is probably widespread along the margins of the Adirondacks, where it has been seen in the Oneida Lake (Clarke and Berg 1959; Fish Creek, town of High Market: UMMZ 107587; Harman 1970a; Walker 1910;), Black River (Buckley 1977); Grass River (Erickson and Fetterman 1996; Grass River at and one mile below Russell: OSUM 14773 and 15752, both Stein!), and Lake Champlain (Saranac River near Lake Champlain: USNM 477123; Boquet River: Mark Gretch, personal communication; Fichtel and Smith 1995) basins. It may also occur in the Hudson basin in the southern Adirondacks (Clarke and Berg 1959; Marshall 1895a). Only two colonies are known from outside this region in New York. A single shell taken from Silver Lake, Sullivan County, in 1949 (AMNH 164659, H.S. Feinberg!) establishes its presence in the Delaware basin in New York. It is known from a few places in the Delaware basin in Pennsylvania as well (Ortmann 1919). It also has been known to live in the upper Hackensack River basin in Rockland County since DeKay's time (DeKay 1844; Jacobson and Emerson 1971). Although this colony was thriving in the early 1950s, it had almost disappeared by 1994 (Strayer 1994), probably a casualty of intensive residential development of the watershed. Records from Lake Erie (Letson 1905), the St. Lawrence River (UMMZ 4338), and Lake Champlain (Lewis 1874) are suspect. Undiscovered populations of *M. margaritifera* may occur throughout eastern New York in nutrient-poor, softwater trout streams.

Continued

FIGURE 42



M. margaritifera is the only member of the family Margaritiferidae in New York, and its biology and distribution are unique among the state's unionoids. *M. margaritifera* uses various trout and salmon species as hosts (Hoggarth 1992), so it is restricted to coldwater habitats. Although its shell is heavy and rich in calcium, it usually lives in calcium-poor (<20 mg/L [D. Smith 1976]) waters, where it is often the only unionoid species (Clarke and Berg 1959; Ortmann 1919; Strayer 1993). Furthermore, Bauer (1988) has shown that enrichment of streams by nutrients, especially nitrate, has caused declines in *M. margaritifera* populations in Europe. *M. margaritifera* was considered by Williams et al. (1993) to merit special concern.

"*Margaritifera*" means pearl-bearer, and *M. margaritifera* has been fished for pearls at least since Roman times; Julius Caesar is said to have invaded Britain in part for its *Margaritifera* pearls (Ziuganov et al. 1994). In fact, overfishing for pearls and mother-of-pearl has been a major reason for the decline of this species in Europe (Bauer 1988; Young and Williams 1983b; Ziuganov et al. 1994). Closer to home, the city of Pearl River, New York, was probably named for pearls taken from *M. margaritifera* in Muddy Brook (Knight 1973).

Obovaria olivaria (Rafinesque)

Hickory nut

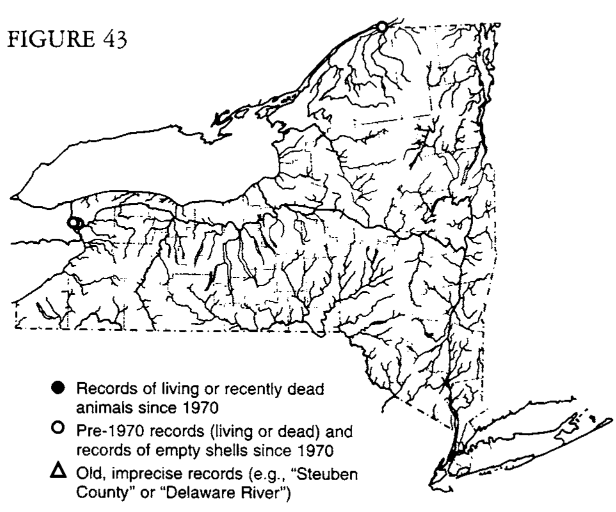
PLATE 7, FIGURE 4

Shell thick, subovate, H/L = usually 0.65–0.8, evenly rounded, <100 mm long (usually <75 mm long). Beaks near the anterior of the shell; distance from the anterior end to the beaks about 10% of the shell length in mature specimens, more in juveniles. Beak sculpture faint, weakly double-looped, usually obliterated. Periostracum smooth, yellow-green, often with rays. Hinge teeth heavy. Nacre white.

The rounded, heavy shell of this species, with the beaks located so far forward, is distinctive, although it might be mistaken for the lake form (*"pauperculum"*) of *Pleurobema cordatum*. Usually, *O. olivaria* has color rays and is inflated near the beaks, while *P. cordatum* is rayless (except in some young animals) and is flattened in the region of the beaks.

O. olivaria is widely distributed in large rivers in the Mississippi, Great Lakes, and St. Lawrence basins. In New York, it has been seen only in our two largest rivers, the Niagara (Robertson and Blakeslee 1948; plus numerous museum lots) and the St. Lawrence (Clarke and Berg 1959) (Figure 43). It seems to have been fairly abundant in the Niagara because museum lots often contain multiple specimens. Old records from Cayuga Lake (Marshall 1895a) and Onondaga Lake (Clarke and Berg 1959, after Beauchamp 1886) are not supported by specimens in any major museum and are probably spurious. The current status of this species in New York is not known. Its only known host is the shovelnose sturgeon (Hoggarth 1992), which does not live in New York.

FIGURE 43



Obovaria subrotunda (Rafinesque)

Round hickorynut

PLATE 27, FIGURE 1

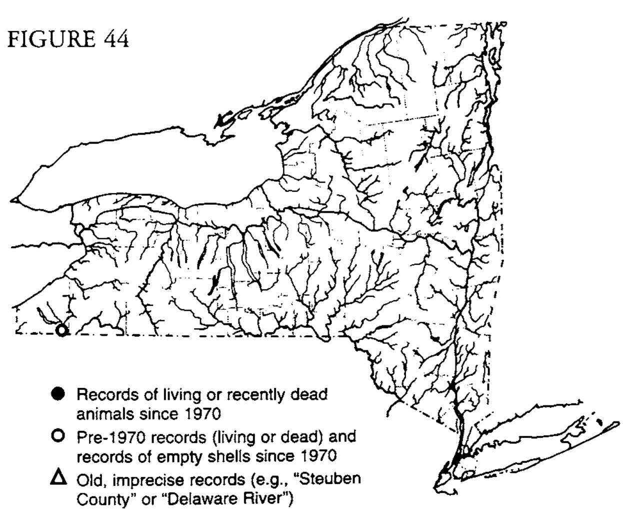
Shell subcircular, H/L = usually 0.75–0.95, thick, usually <50 mm long. Beak sculpture a few faint, weakly double-looped bars. Periostracum gray-green to brown, rarely with rays; posterior slope distinctly lighter and yellower than remainder of shell. Hinge teeth strong. Nacre white.

This species is easily recognized by the circular outline of its shell and the distinctly lighter periostracum on the posterior slope. In New York only smooth specimens of *Quadrula pustulosa* even remotely resemble the species.

O. subrotunda lives in the Ohio River and Lake Erie–Lake St. Clair basins. Only a single, broken, weathered shell of this species has been collected from New York (Strayer et al. 1991) (Figure 44). An old record of *O. leibii* = *O. subrotunda* from Onondaga Lake (Beauchamp 1886) is almost certainly spurious. It has probably been eliminated from the state, although it may turn up in the Allegheny or Erie–Niagara basins. It has declined through much of its range and was listed as a species of special concern by Williams et al. (1993). It is protected by several midwestern states.

O. subrotunda lives in rivers, especially on sandy riffles (Ortmann 1919; van der Schalie 1938) as well as in Lakes Erie and St. Clair. In Michigan, it occurred chiefly in low-gradient, turbid, hydrologically unstable rivers (Strayer 1983). The fish host is not known, although Clark (1977) suggested that the eastern sand darter might be a host of *O. subrotunda* because the two species often co-occur.

FIGURE 44



Pleurobema clava (Lamarck)

Club shell

PLATE 26, FIGURE 5

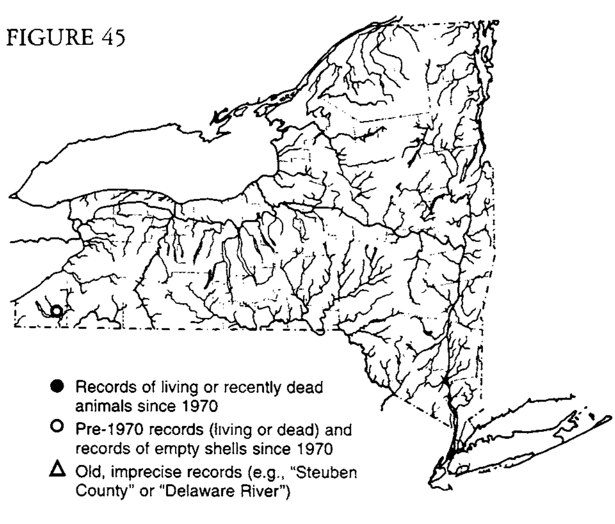
Shell subovate (young animals) to subtriangular (old animals), a little inflated near the beaks, but compressed posteriorly, thick, usually <60 mm long (although reaching 80 mm). Beaks near the anterior end of the shell. Beak sculpture a few poorly defined lumps. Periostracum yellow-brown, typically with broad bundles of fine, green rays. Hinge teeth strong. Nacre white.

Typical shells of *P. clava*, which have a triangular outline, beaks near the anterior end, and broad bundles of color rays, are easy to recognize. Young specimens, in which the beaks are not so far forward, might perhaps be mistaken for *Ptychobranchus fasciolaris*, but even these specimens are more triangular and have more anterior beaks than *P. fasciolaris*.

P. clava lived throughout the Ohio River basin and in a few streams in the Maumee River basin, which is a tributary to western Lake Erie (USFWS 1994). In New York, it has been seen at only one site on Cassadaga Creek (Figure 45), where six subfossil shells were collected in 1995 (Strayer 1995; shells in NYSM). This species may have been scattered through the upper Allegheny basin in New York (cf. Ortmann 1919), but it has probably now been eliminated from the state. It is nevertheless possible that populations still live in the Cassadaga and Conewango Creek systems, which have not been well surveyed. Although formerly widespread from eastern Illinois through Pennsylvania, only a few populations of *P. clava* remain (USFWS 1994), and it is listed as endangered by the United States Fish and Wildlife Service.

P. clava typically lives in gravelly riffles of creeks and small rivers. Because it buries itself deeply into the stream bottom (Clark 1977; USFWS 1994), living animals may be hard to find. Its hosts are unknown, but the related *Pleurobema oviforme* uses the whitetail shiner, common shiner, river chub, central stoneroller, and fantail darter (Weaver et al. 1991).

FIGURE 45



Pleurobema cordatum (Conrad)

Round pigtoe

PLATE 21, FIGURES 4 AND 5

Two forms of this variable species exist in New York. In both forms, the periostracum is yellow-brown to chestnut-brown without rays except in some young specimens, which have fine, green rays. The beak sculpture is faint and poorly defined. The hinge teeth are strong. The form that lives in the Allegheny basin (form *coccineum*) is short (H/L = approximately 0.62–0.84), compressed (W/L = approximately 0.33–0.5), subtriangular to subovate, thick, and fairly large (up to about 100 mm long). The nacre is white or a beautiful rosy pink. In Lake Erie and the Niagara River, form *pauperculum* is found. It is a smaller shell than *coccineum* (rarely >75 mm long), and more inflated (W/L = approximately 0.45–0.55) and subovate than *coccineum*.

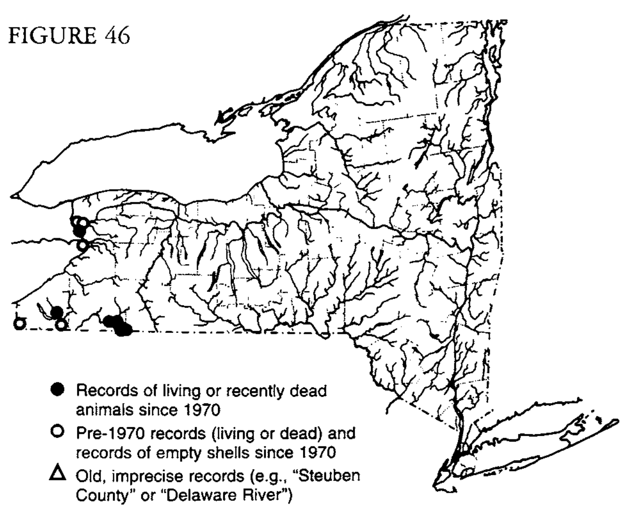
This species is difficult to tell from *Fusconaia flava* (see for distinguishing characteristics). The lake form of *P. cordatum* (form *pauperculum*) is somewhat similar to *Obovaria olivaria*, but it has flatter sides, a duller periostracum, and is less likely to have color rays.

P. cordatum is part of a complex of closely related species or ecophenotypes (*P. cordatum*, *P. coccineum* = *P. sintoxia*, *P. plenum*, *P. rubrum* = *P. pyramidatum*) that are found throughout the Ohio River drainage and in parts of the Mississippi and Great Lakes basins. Earlier this century, these were widely regarded as intergrading ecophenotypes (e.g., Ortmann 1919), but more recently they have been recognized as distinct species (e.g., Stansbery 1983; Williams et al. 1993). Clearly, a critical study of these taxa is needed to resolve their status.

Whatever the taxonomic status of these forms, only the *coccineum* form (and its large lake ecophenotype, form *pauperculum*) has been seen in New York. It is known from only a few sites: Lake Erie, the Niagara River, and the larger streams in the Allegheny basin (Figure 46). It has been recorded from Tonawanda Creek (Robertson and Blakeslee 1948), but the only specimens labeled as *P. cordatum* that we saw from Tonawanda Creek (UMMZ 81551) are *Fusconaia flava*, which is common in the creek. Nevertheless, *P. cordatum* may very well live in creeks tributary to Lake Erie and the Niagara River. A record from Dansville (ANSP 365734) may be spurious (see "Erroneous and Questionable Records").

P. cordatum lives in creeks and rivers of all sizes, but it is especially frequent in large creeks and small-to medium-sized rivers (e.g., Ortmann 1919; Strayer 1983). It is a common species in parts of its range, but it is uncommon at its New York localities, constituting only a few percent of the unionoid community. Various minnows and possibly the bluegill serve as hosts for *P. cordatum* (Hoggarth 1992; Hove 1995b).

FIGURE 46



Potamilus alatus (Say)

Pink heelsplitter

PLATE 10, FIGURES 1 AND 2

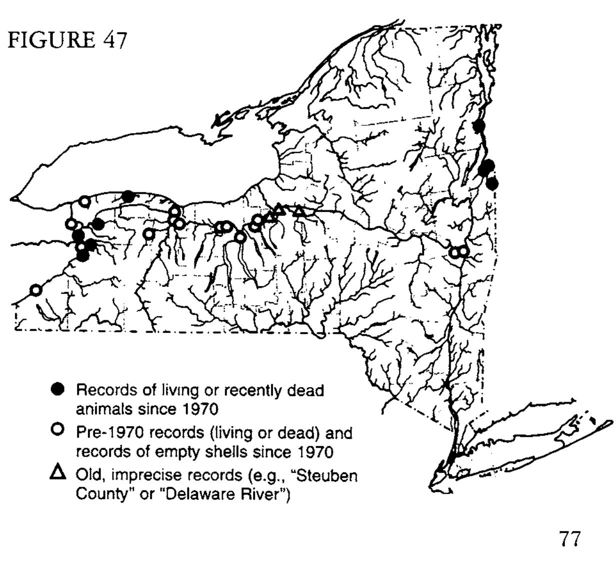
Shell subovate, compressed, fairly thick, large (sometimes >150 mm long), with a more or less prominent dorsal wing. Dorsal wing best developed in young animals and in animals living in quiet waters. Beak sculpture indistinct. Periostracum dark green, dark brown, or black, sometimes with fine rays in young specimens. Pseudocardinals strong, triangular, with rough surfaces; laterals strong. Nacre purple.

P. alatus superficially resembles other heelsplitters in New York (*Lasmigona complanata* and *Leptodea fragilis*), but it can be readily identified by its strong, well-developed pseudocardinal and lateral hinge teeth. Also, its nacre is purple and its periostracum is usually greener than those of our other heelsplitters.

P. alatus is widely distributed in the Mississippi and Great Lakes drainages and is also found in the Hudson Bay and lower St. Lawrence basins. In New York, it has been seen at many sites in a band from Buffalo to Oneida Lake as well as in Lake Champlain and its larger tributaries (Figure 47). In addition to the records shown in Figure 47, this species was collected from Canandaigua Lake at Vine Valley (RMSC 49.421.547). The few old records from the Albany area (summarized by Strayer 1987) probably represent recent range extensions through the Erie or Champlain canals. Although *P. alatus* has not been reported from the St. Lawrence or its tributaries in northern New York, it may turn up in these waters. The following records seem out of range and require confirmation: Sodus Bay (UMMZ 79338, locale on shell) and south end of Tully Lake, Cortland County (Susquehanna basin) (ANSP 135034).

P. alatus is especially common in quiet waters and is often found in lakes and canals. Nevertheless, it also lives on riffles in creeks and rivers (cf. Ortmann 1919). The freshwater drum may be a host (Hoggarth 1992).

FIGURE 47



Potamilus capax (Green)

Fat pocketbook

PLATE 27, FIGURES 5 AND 6

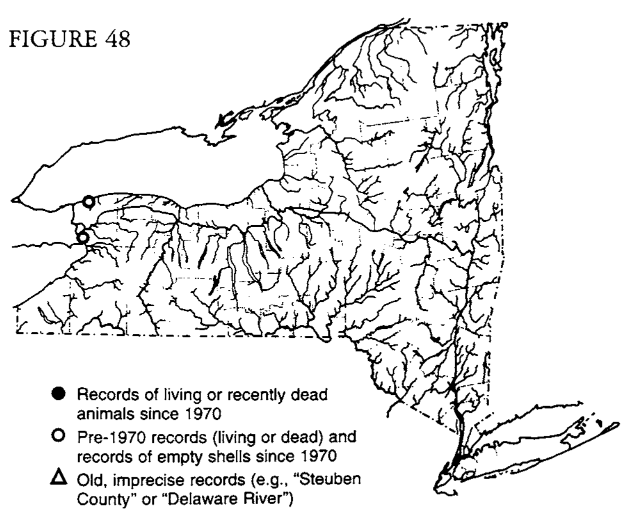
Shell short-subovate, very inflated (especially in the beak region), moderately thin, usually <100 mm long. Hinge line strongly S-shaped. Beak sculpture indistinct. Periostracum shiny, yellow-brown to gray-brown, rays absent or very faint. Pseudocardinals compressed, flexed upward; laterals well developed, but short and curved. Nacre white.

This species most closely resembles *Lampsilis ovata*, which is usually less inflated, has a less S-shaped hinge line than does *P. capax*, and has well-defined color rays.

This rare species lives in large rivers in parts of the Mississippi basin; the nearest records to New York are from central Indiana (Johnson 1980; USFWS 1989). Nevertheless, authentic specimens of *P. capax* have been reported from two sites in New York (Figure 48). BSM 3651-6/2 (Plate 27, Figure 6) contains a pair of broken, slightly weathered valves labeled "Niagara river, Buffalo, Letson! 1906." The right valve is marked in pencil "capax, Niagara r., only one I ever found," in addition to the lot number. BSM 3651-6/1 is labeled "Wilson's Ck., Niagara County, N.Y." and consists of a pair of broken, slightly weathered valves.

The left valve contains some faint, illegible markings in pencil in addition to the lot number. "Wilson's Creek" is Twelvemile Creek, a tributary of Lake Ontario. These collections were made almost a century ago, so we do not know whether *P. capax* still lives in New York. It should be sought in the Niagara River. *P. capax* is listed by the United States Fish and Wildlife Service as endangered (USFWS 1989). The freshwater drum has been reported to be a host (Watters 1994a).

FIGURE 48



Ptychobranchus fasciolaris (Rafinesque)

Kidneyshell

PLATE 12, FIGURE 1; PLATE 24, FIGURE 4

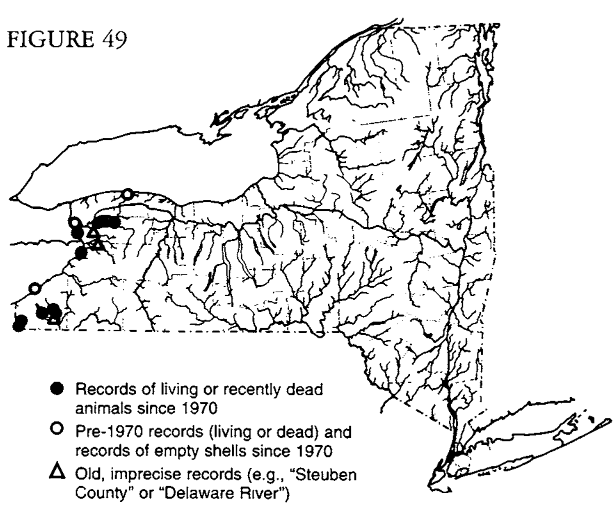
Shell subelliptical, more or less compressed (W/L usually approximately 0.18–0.36), sometimes humped in old specimens, thick, usually <100 mm long, but sometimes reaching more than 150 mm. Beak sculpture poorly developed. Periostracum yellow to medium brown, typically with broad bundles of fine, green color rays. Hinge teeth solid; laterals (especially in the right valve) swollen distally. Nacre white. Females have a conspicuous groove on the inside of the shell that runs from the beak cavity towards the posterio-ventral part of the shell.

The peculiar, bundled color rays, the compressed subelliptical shell, and the heavy lateral hinge teeth distinguish this species from others in New York. Old, rayless specimens might be mistaken for *Elliptio dilatata*, which, however, is more elongate, has less stout lateral teeth, and usually has purple nacre. The external coloring of *Pleurobema clava* is reminiscent of *P. fasciolaris*, but the former species has a triangular outline with very anterior beaks.

P. fasciolaris is a species of the Ohio River and lower Great Lakes drainage that reached New York via both the Allegheny River and Lake Erie (Figure 49). It is common and widespread in the western parts of the Allegheny basin in New York, but it seems to be missing from the eastern parts of the basin. It also occurs in Lake Erie, the Niagara River, and their tributaries. Robertson and Blakeslee (1948) reported it from Johnson Creek, Orleans County, in the Lake Ontario drainage. The record "Sodus Bay" (Wayne County) (UMMZ 74013) seems doubtful; the shell is *P. fasciolaris* and the locality is written on the shell. It needs to be verified. There is no other indication that this species reached east of Orleans County, despite the existence of much suitable habitat in Monroe and Wayne Counties. Although *P. fasciolaris* does not have a wide range in New York, it is often abundant where it occurs.

P. fasciolaris is especially common in large creeks and small rivers, although it lives in large rivers and some lakes (Erie, Chautauqua) as well (Ortmann 1919; van der Schalie 1938). Although it is said to favor gravelly riffles (Ortmann 1919), there is some evidence that it occurs most frequently in low gradient streams (Strayer 1983). Other species of *Ptychobranchus* release their glochidia in packages (conglutinates) that mimic food items of fish, thereby presumably increasing the probability of infecting a host (Barnhardt and Roberts 1996; Hartfield and Hartfield 1996). The conglutinates of *P. fasciolaris* should be examined. Various darters (*Etheostoma* spp.) serve as hosts for this species (White et al., 1996).

FIGURE 49



Pyganodon cataracta (Say)

Eastern floater

PLATE 14; PLATE 15, FIGURE 3 (?); FIGURES 12 Q AND 13 B

Shell thin, subelliptical to subovate, elongate, often >100 mm long. Beak sculpture of five to seven double-looped bars of uniform height. Periostracum usually greenish, often shiny, and usually with fine, green color rays. Hinge teeth absent. Nacre bluish white or silvery, sometimes discolored.

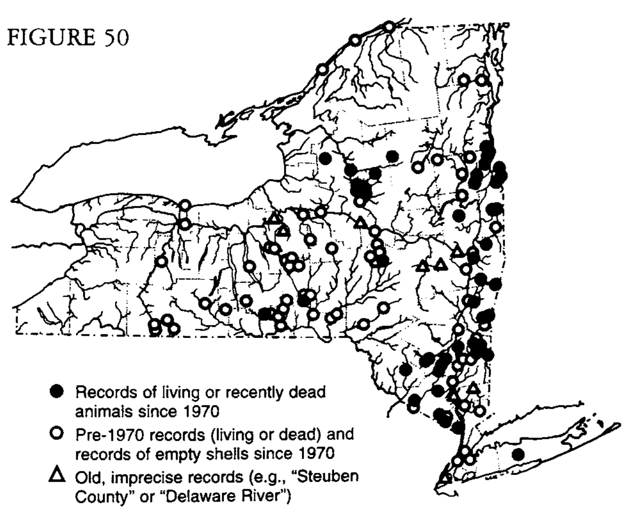
Pyganodon contains several closely related and similar species whose limits and relationships have not yet been resolved (Hoeh 1990; Hoeh and Burch 1989; Kat 1983b, 1986). Apparently, three species (*P. cataracta*, *P. grandis*, and *P. lacustris*) occur in New York. At least two of these (*P. cataracta* and *P. grandis*) are thought to hybridize (Kat 1985, 1986), and all three are difficult to distinguish from one another. The best character for separating *P. cataracta* from *P. grandis* is beak sculpture. In *P. cataracta*, the beak sculpture is low and evenly raised above the surface of the shell, while the beak sculpture of *P. grandis* is nodulous (i.e., different parts of the sculpture are raised different heights above the shell surface) (Figures 12 q, r, and 13 a, b). In specimens with intact beaks, this character usually allows for ready identification of the specimens. In addition, *P. cataracta* usually has a greenish periostracum, while *P. grandis* is more often brownish. In ponds, *P. cataracta* usually has a long, drawn-out posterior end and a posterior slope that is distinctly bowed, while that of *P. grandis* is usually relatively short. *P. lacustris* was re-recognized only recently on the basis of electrophoretic evidence (Hoeh and Burch 1989), so its morphological characters have not been well established. Specimens labelled "*P. lacustris*" (or "*P. marginata* = *P. lacustris*") that we have seen in museums look like thin, stunted *P. cataracta*, with silvery nacre and from six to nine non-nodulous, double-looped bars on the beaks.

Externally, *P. cataracta* resembles *Anodonta implicata*, but the latter species has pink to purple nacre, while the nacre of *P. cataracta* is bluish white (sometimes coppery-orange in deformed specimens). Also, at least in older specimens, the shell of *A. implicata* is markedly thickened anteriorly, while *P. cataracta* is only modestly thicker anteriorly. The other toothless unionoids in our area (*Anodontoides ferussacianus* and *Strophitus undulatus*) both have concentric beak sculpture, in contrast to the double-looped sculpture of the *Pyganodon* species. Finally, with some practice it is possible to recognize *Pyganodon* by its shell shape, particularly the pointed posterior end.

P. cataracta lives along the Atlantic Slope from the St. Lawrence River to Georgia (Johnson 1970). Its distribution in New York is not completely clear because of confusion with other *Pyganodon* species. Figure 50 is based on specimens we examined or on relatively recent literature records that we consider to be reliable. *P. cataracta* is widespread in the Susquehanna, Delaware, and Hudson basins. It also occurs in the eastern part of the Oswego River basin

Continued

FIGURE 50



(Clarke and Berg 1959; Harman 1970a), and in the Passaic (Strayer 1994), Housatonic (Strayer 1992), Lake Champlain (D. Smith 1985a), and St. Lawrence River basins (Clarke and Berg 1959). Remarkably, there are several authentic records of *P. cataracta* from the upper Genesee River basin (e.g., Genesee River, Stannard's Corners: ANSP 365592; Genesee River, Wellsville: ANSP 366023; marsh at West Union, Steuben County: ANSP 366030) suggesting that *P. cataracta* crossed over from the upper Susquehanna basin (cf. *Alasmidonta marginata*). Some of the records from the lower Genesee basin may be authentic (e.g., canal at Mount Morris: ANSP 366062, *sub Anodonta implicata*; Erie Canal, Pittsford: Walton 1891, *sub Anodonta excurvata*; Lake Ontario, Braddock Bay, Monroe County: Ortmann 1919), but they need confirmation. Reports of *P. cataracta* from the Erie, Niagara, and Allegheny basins (e.g., Letson 1909; Marshall 1895a) are probably all based on misidentifications of *P. grandis*. *P. cataracta* is one of the most common, widespread unionoids in central and eastern New York.

P. cataracta occupies a wide range of habitats, from marshes, lakes, and ponds to creeks and rivers (Clarke and Berg 1959; Ortmann 1919; Strayer 1993). It is especially common in quiet, protected waters. Only the carp is known to be a host, but the closely related *P. grandis* uses many warmwater fish species as hosts (see following account), so it is likely that many other fish species are suitable hosts for *P. cataracta*.

Pyganodon grandis (Say)

Floater

PLATE 13; FIGURES 12 O, R; 13 A

Shell thin, subelliptical to subovate, often >100 mm long. Beaks prominent, bearing several nodulous, double-looped ridges. Periostracum yellowish, brownish, or greenish, shiny, sometimes with fine green rays. Hinge teeth absent. Nacre usually silvery white, but often discolored (especially coppery orange).

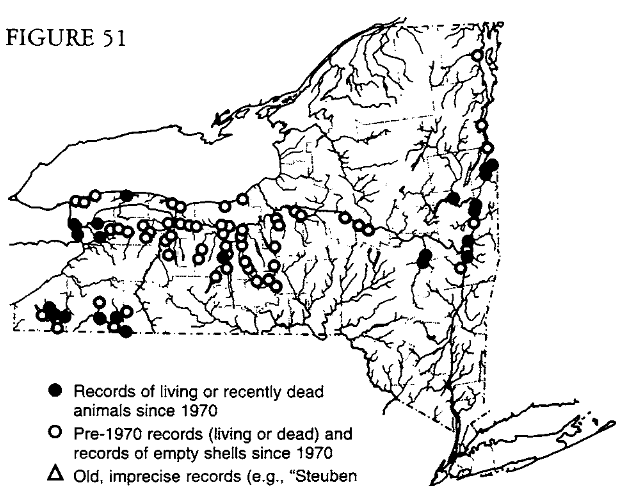
See remarks under *Pyganodon cataracta* for tips on separating *P. grandis* from other *Pyganodon* species. *P. grandis* is the only local unionoid species without hinge teeth and with nodulous, double-looped beak sculpture.

P. grandis is widely distributed in the Mississippi, Great Lakes, and Hudson Bay basins. Its exact distribution in New York is unclear for the reasons given under *P. cataracta*. Our best interpretation of available records (Figure 51) shows that *P. grandis* is widespread in the Allegheny, Erie, Niagara, lower Genesee, and Oswego basins. It also occurs in the lowland parts of the Mohawk (Strayer 1987, 1995) and Champlain (D. Smith 1985a) basins. The restricted distribution of *P. grandis* in the latter basins suggest that it is a recent immigrant to eastern New York, perhaps arriving by way of the Erie and Champlain Canals (cf. Strayer 1987). We tentatively reject records of *P. grandis* from the upper Genesee (Andover: ANSP 366058, 366059) and Susquehanna basins (Harman 1970a; Marshall 1895a; Maury 1916) pending further investigation because some or all of these probably refer to *P. cataracta*. *P. grandis* is still a common species in New York.

Kat (1985, 1986) showed that *P. grandis* may hybridize with *P. cataracta*. The two species come into contact at several places in New York: the middle Genesee, the eastern Oswego, the Mohawk, and the Lake Champlain basins. It would be interesting to know the extent of hybridization in each of these areas.

Like *P. cataracta*, *P. grandis* is an ecologically widespread mussel, living in standing and running waters of all sizes (e.g., Strayer 1983; van der Schalie 1938). It is often said to prefer quiet waters, but it is known from rough waters (e.g., the Niagara River) and riffles as well. It uses many fish hosts, including longnose gar, golden shiner, blacknose dace, pearl dace, creek chub, redfin shiner, common shiner, blacknose shiner, blackchin shiner, central stoneroller, bluntnose minnow, banded killifish, brook silverside, brook stickleback, black crappie, rock bass, largemouth bass, green sunfish, bluegill, longear sunfish, pumpkinseed, orangespotted sunfish, yellow perch, johnny darter, Iowa darter, and rainbow darter (Hoggarth 1992).

FIGURE 51



Pyganodon lacustris (Lea)

Lake floater

PLATE 15, FIGURES 2 AND 3; PLATE 16; FIGURE 13 B

Shell very thin, subelliptical to subovate, elongate. Beak sculpture of six to nine, non-nodulous, double-looped bars. Periostracum grayish green, sometimes with fine, green rays. Hinge teeth absent. Nacre silvery white. Because of uncertainty as to the characteristics and limits of this species, we are not sure whether the illustrations that we tentatively attribute to this species actually show *P. lacustris* rather than other *Pyganodon* species.

See remarks under *P. cataracta* for remarks on how to distinguish *P. lacustris* from other *Pyganodon* species.

Although this species was recognized as valid by malacologists in the late nineteenth and early twentieth centuries, it was assumed to be an ecophenotype of *P. grandis* by later authors (e.g., van der Schalie 1938). Recent electrophoretic studies (Hoeh 1990; Hoeh and Burch 1989) suggest that *P. lacustris* is specifically distinct from *P. grandis* and *P. cataracta*. Because this species was re-recognized only recently and is easily confused with the other species of *Pyganodon*, we do not know where it occurs in New York. The type locality of *P. lacustris* is in New York ("Little Lakes" = Weaver and Young Lakes in the Susquehanna basin in Herkimer County). Many records of this species from the old literature (e.g., Letson 1905; Lewis 1874; Marshall 1895a) are probably unreliable, but museum collections contain specimens from a number of lakes throughout New York that match Lea's description of *P. lacustris*. Until this species is better defined, it is not possible to map its precise distribution in New York.

The ecology of this species likewise is poorly known. As its name suggests, *P. lacustris* seems to be primarily a species of lakes, where it may be fairly common. Its hosts are not known.

Quadrula pustulosa (Lea)

Pimpleback

PLATE 12, FIGURES 2 AND 3

Shell subcircular to subquadrate, thick, reaching about 75 mm in length. Beak sculpture concentric but indistinct. Surface of shell typically marked by few to many irregular pustules, which may, however, be absent. Pustules absent from the beak region. Periostracum yellow-brown to brown, often with a broad bundle of fine, green color rays near the beak. Hinge teeth heavy. Nacre white.

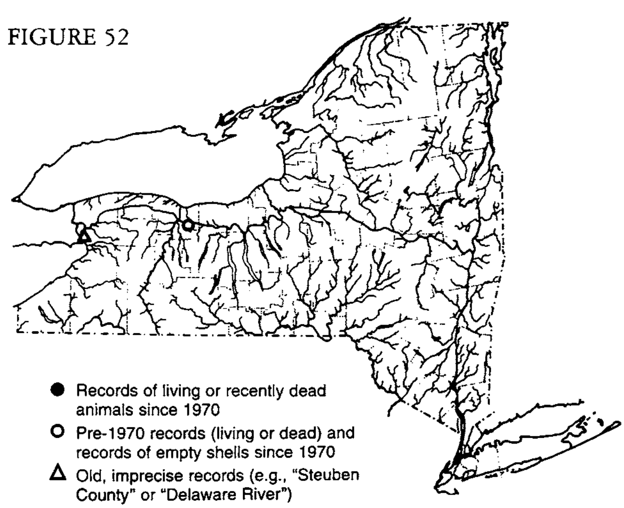
Typical specimens of this species, with white nacre, a broad green ray near the beak, and pustules on the face of the shell, are not easily mistaken for any other species in New York. The pustules and color rays of some specimens from New York are faint or altogether absent. Such a specimen may be confused with *Obovaria subrotunda*, from which it can be distinguished by its squarish profile and lack of a distinctly lighter posterior slope.

Although *Q. pustulosa* is common and widespread in the Mississippi and Great Lakes basins, its range scarcely reaches New York (Figure 52), and it is not a common species in the state. Several records (Letson 1909; LaRocque and Oughton 1937; Robertson and Blakeslee 1948; BSM 362E-12/4, one specimen; INHS 4643, two specimens; INHS 4910, three specimens; UMMZ 77316, one specimen) document its occurrence in the Niagara River, but it does not seem to have been abundant. In addition, four specimens of *Q. pustulosa* were collected from the Erie Canal at Pittsford by Shelly Crump about 1920 (ANSP 129660), which suggests that the species moved east some distance along the Erie Canal. One perfectly smooth specimen of *Q. pustulosa* in the BSM (362E-12/3) bears the locality "Saint Lawrence River," and was taken by Elizabeth Letson in 1906. There is no special reason to doubt this record, but it is well out of range for *Q. pustulosa* and should be confirmed.

Q. pustulosa has not been taken in New York for over 50 years, so its status in the state is unclear. It should be sought in Lake Erie (cf. Masteller et al. 1993) and large streams from Rochester west, especially the Niagara River.

Q. pustulosa usually lives in medium-sized to large rivers (Cummings and Mayer 1992). It occurs in the Great Lakes as well (Clarke and Stansbery 1988). Known hosts include channel catfish, flathead catfish, and black and brown bullheads (Hoggarth 1992).

FIGURE 52



Quadrula quadrula Rafinesque

Mapleleaf

PLATE 27, FIGURE 8

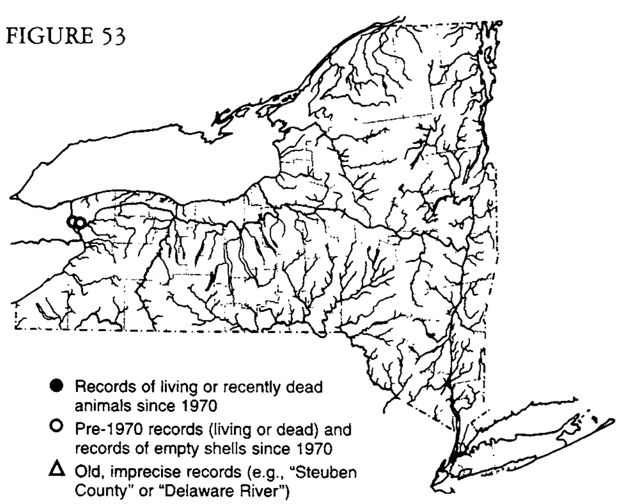
Shell short-subtrapezoidal to subquadrate (H/L = approximately 0.8–0.85), fairly thick, reaching about 100 mm in length, but often smaller, with a more or less prominent sulcus in front of the posterior ridge. Shell covered with a variable number of pustules, which are especially dense near the beaks. Beak sculpture double-looped. Periostracum yellowish to brown, sometimes with indistinct, green rays. Hinge teeth strong. Nacre white.

No other species in New York has a median sulcus and distinct pustules on the face of the shell.

Like the preceding species, *Q. quadrula* is widespread and abundant west of New York, but it is barely present in our state (Figure 53). Three specimens were taken from the Niagara River between 1917 and 1934 (LaRocque and Oughton 1937; Robertson and Blakeslee 1948; UMMZ 198119). It may still occur in Lake Erie, the Niagara River, or their larger tributaries.

Q. quadrula is a common species of rivers and reservoirs (e.g., Bates 1962; Cummings and Mayer 1992); it also lives in Lake Erie (Ortmann 1919; Masteller et al. 1993). The flathead catfish, which does not occur in New York (C.L. Smith 1985), may serve as a host (Hoggarth 1992).

FIGURE 53



Simpsonaias ambigua (Say)

Salamander mussel

PLATE 19, FIGURE 7; FIGURE 13 C

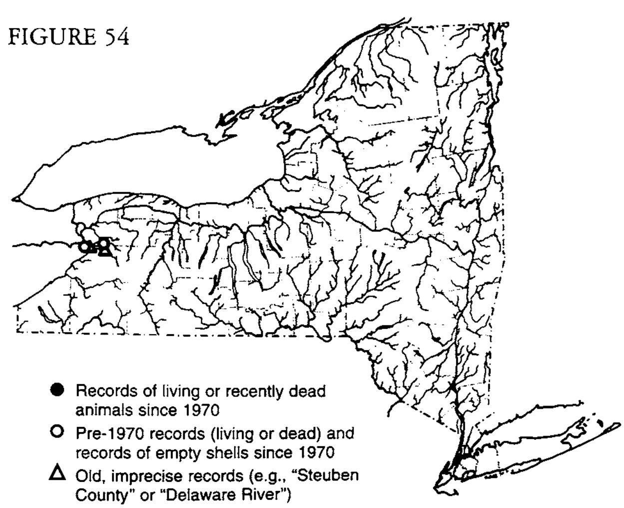
Shell elongate (H/L = usually approximately 0.45–0.55), subelliptical, often inflated (W/H = often 0.6–0.8) and somewhat cylindrical, thin, rarely >50 mm long. Beak sculpture consists of several V's, their apices pointed toward the beak (Figure 13 c), but often obscure. Periostracum gray-brown to yellow-brown, rayless. Pseudocardinal teeth weak and rounded; laterals altogether missing. Nacre white, iridescent, sometimes discolored in the beak cavity.

This small, drab mussel is easy to overlook but simple to identify once collected. *S. ambigua* is most likely to be confused with *Anodontoides ferussaccianus*, which often exceeds 50 mm in length, often has some color rays, has no pseudocardinal teeth, and has fine, concentric beak sculpture.

S. ambigua is sporadically but widely distributed in the Mississippi and Great Lakes basins from Arkansas and Tennessee to Iowa and New York (Clarke 1985). It was collected from several sites near Buffalo in the nineteenth century (Figure 54): Lake Erie at Buffalo (Clarke 1985; ANSP 126779), Buffalo Creek (or Buffalo River) at Buffalo (Clarke 1985; UMMZ 107843; AMNH 31311), and Cayuga Creek at Lancaster (BSM 364M-1/4). Recent surveys (Strayer et al. 1991) turned up no trace of *S. ambigua* and showed that the Buffalo River drainage, which includes Buffalo and Cayuga Creeks, has been badly damaged by urban development. Nonetheless, the size and cryptic habits of *S. ambigua* make it especially hard to find, and its host is still widespread around Buffalo (M. Wilkinson, New York State Department of Environmental Conservation, pers. comm.), so it is possible that it may still occur in Lake Erie, the Niagara River or their tributaries.

S. ambigua uses the mudpuppy, *Necturus maculosus*, as a host. It is the only unionoid known to use an amphibian as a host. *S. ambigua* is rarely collected live or in large numbers, but when it is found in abundance, it is typically living beneath large, flat rocks, which are probably used as shelters by its host. It has been collected from creeks and rivers of all sizes as well as from Lake Erie (Clarke 1985). *S. ambigua* was considered to merit special concern status by Williams et al. (1993).

FIGURE 54



Strophitus undulatus (Say)

Squawfoot

PLATE 17, FIGURES 1 THROUGH 3; FIGURE 12 K

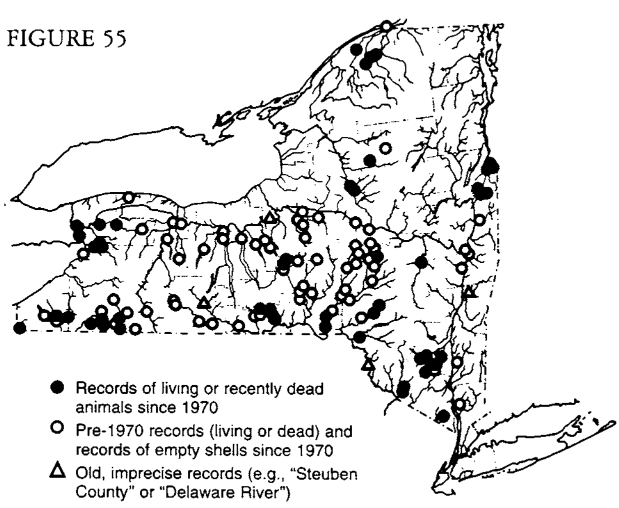
Shell subovate to subelliptical, often with a somewhat blunt posterior end, moderately thin, reaching a little more than 100 mm in length, although often much smaller, particularly in eastern New York. Beak sculpture fairly coarse and sharply defined, concentric. Periostracum variable in color, sometimes with fine, green rays, especially on the posterior slope. Hinge teeth usually absent, although the pseudocardinals may be present as indistinct thickenings of the nacre. Nacre bluish white near the edge of the shell, often cream to pale salmon in the beak cavity.

This variable species probably causes more problems with identification than any other unionoid in New York. An ideal specimen of *S. undulatus* can be recognized by the absence of hinge teeth and by the concentric beak sculpture, which is distinctly coarser than that of *Anodontoides ferussacianus*, but finer than that of *Alasmidonta undulata*. Further, the typically bicolored nacre contrasts with the uniform bluish-white nacre of *A. ferussacianus* or *Pyganodon* spp. Less-than-ideal specimens, especially those without clear beak sculpture, can be difficult to tell from these species. Living specimens, which can be confused with many other species, are best recognized by their beak sculpture. Other useful external characters include the somewhat inflated shell; the blunt posterior end; the fine green color rays, which often are most obvious on the posterior slope; the S-shaped hinge line; and usually the slight gape at the posterior end of the shell. Many anodontines have this gape.

S. undulatus is the only unionoid that is widely distributed on both sides of the Alleghenian Divide. Populations on either side of this divide were formerly considered to belong to separate species, and although current opinion is that a single species is involved, it is at least possible that *S. undulatus* contains two closely related species (Strayer 1987). In New York, *S. undulatus* has been found in all major drainage systems (Figure 55). It is sometimes abundant.

S. undulatus is especially common in creeks and small rivers, but it is found in other habitats, including brooks, large rivers, and some lakes. Some old research (Lefevre and Curtis 1911) suggests that its glochidia can develop without a fish host, but it can also develop using spotfin shiner, fathead minnow, creek chub, yellow bullhead, black bullhead, plains killifish, largemouth bass, bluegill, green sunfish, and walleye as hosts (Hoggarth 1992; Hove 1995a).

FIGURE 55



Toxolasma parvum (Barnes)

Lilliput

PLATE 6, FIGURE 4

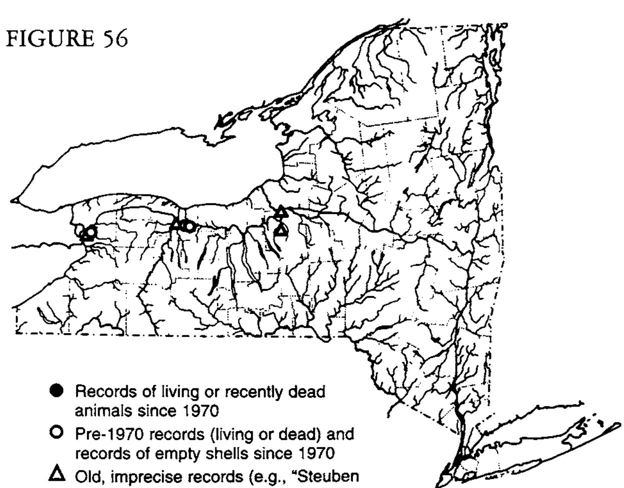
Shell subelliptical, inflated (W/H = approximately 0.65–0.8), of moderate thickness, small (<40 mm long). Beak sculpture sharply defined, concentric, sometimes a little angular posteriorly. Periostracum green, black, or brown, not glossy, and rayless. Hinge teeth well developed but delicate; pseudocardinals lamellar. Nacre white.

This small shell is difficult to mistake for any other in New York. The equally small *Villosa fabalis* has a very thick shell and stout lateral teeth.

T. parvum is common throughout the Mississippi and Great Lakes basins. There are only a few, widely scattered records from New York (Figure 56) as follows: Erie Canal, Buffalo (INHS 1632); Ives Ice Pond, Tonawanda, Erie County (AMNH 164903, UMMZ 168612); Genesee Canal, Monroe County (NYSM 31402); Erie Canal, 2 km west of Macedon and at Pittsford (Clarke and Berg 1959); Seneca River (Marshall 1895a; UMMZ 99551); Syracuse (NYSM 31546); and Old Erie Canal, Onondaga County (Beauchamp 1886; UMMZ 99548). Apparently this species followed the Erie Canal eastward into central New York. None of these collections of *T. parvum* from New York is recent, and most are small. Nevertheless, *T. parvum* probably still lives at scattered sites in quiet streams, canals, and reservoirs between Buffalo and Syracuse.

T. parvum typically lives in quiet waters of low-gradient creeks, rivers, and reservoirs (Bates 1962; Ortmann 1919; Strayer 1983; van der Schalie 1938), often on muddy bottoms. Some, but not all, populations of this species consist of hermaphrodites (Ortmann 1919; Tepe 1943; van der Schalie 1970); the sexuality of New York specimens has not been investigated. Various centrarchids serve as hosts (Hoggarth 1992; Hove 1995c).

FIGURE 56



Truncilla donaciformis (Lea)

Fawnsfoot

PLATE 26, FIGURE 6

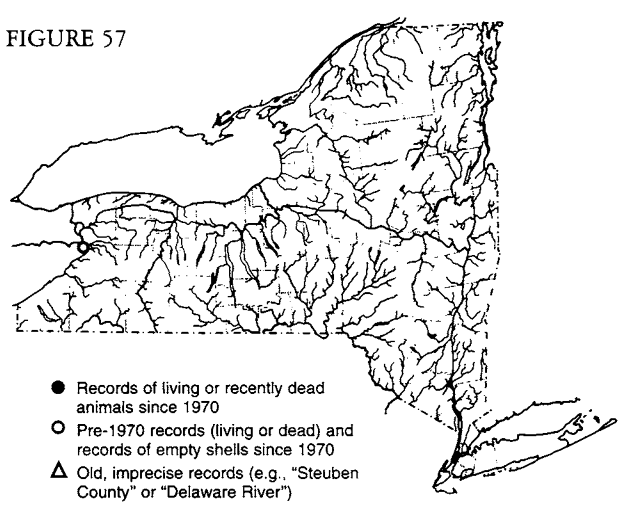
Shell subtriangular to subovate, H/L = 0.6–0.75, of moderate thickness, reaching to about 100 mm long, but almost always <50 mm long in the Great Lakes basin. Posterior slope more or less prominent, a little bowed. Beak sculpture faint, double-looped. Periostracum greenish to brownish yellow, marked with rays that contain dark V's. Hinge teeth high and sharp; pseudocardinals compressed. Nacre white.

Usually the characteristic zig-zag markings on the epidermis will serve to identify this species. It might be confused with *Truncilla truncata*, which, however, has a sharp, straight posterior ridge. The posterior ridge of *T. donaciformis* is usually bowed and a little rounded. Also, *T. donaciformis* usually has more delicate, compressed pseudocardinal teeth and is smaller and a little more elongate than *T. truncata*.

T. donaciformis is widespread in the Mississippi and lower Great Lakes basins, and it occurs also in parts of the Gulf basin. It is common in western Lake Erie, but it is much less common in the eastern parts of the lake. A few specimens have been taken at Presque Isle Bay, Pennsylvania (Masteller et al. 1993) and Buffalo (BSM 365N-2/9). The latter is the only record from New York (Figure 57); the species should be sought in Lake Erie and the Niagara River.

T. donaciformis is a common species of large rivers and Lake Erie. The freshwater drum and perhaps the sauger are hosts (Hoggarth 1992).

FIGURE 57



Truncilla truncata Rafinesque

Deer toe

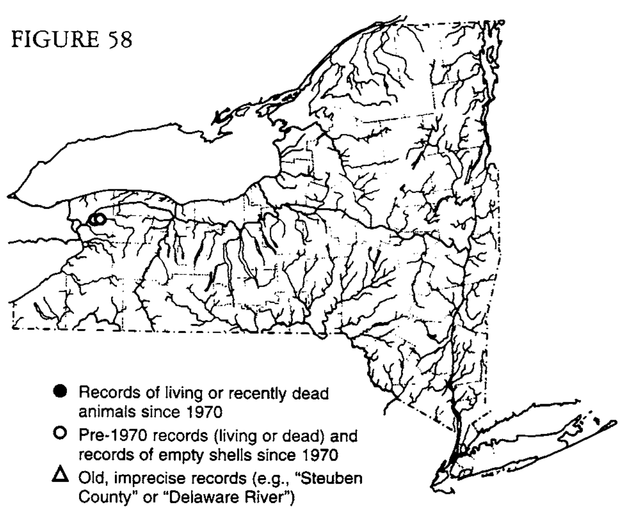
PLATE 23, FIGURE 7

Shell subtriangular, of moderate thickness, H/L = 0.63–0.83, compressed (W/H = 0.55–0.7), usually <75 mm long. Posterior ridge straight, obvious, sharply separating the flat posterior slope from the remainder of the shell. Beak sculpture obscure. Periostracum greenish to brownish green (sometimes dark brown and rayless), usually with rays that contain conspicuous dark V's or W's. Pseudocardinals strong, triangular, with rough surfaces, laterals sharp and high. Nacre white.

T. truncata is distinctive, but might be mistaken for *Truncilla donaciformis* (see for distinguishing remarks) or *Epioblasma triquetra*. The markings on the epidermis of *T. truncata* are different from those of *E. triquetra*, and the latter species is usually more elongate and inflated than *T. truncata*.

Like the preceding species, *T. truncata* is widespread in the large rivers of the Interior Basin, and in some shallow areas of the Great Lakes. Early authors (Beauchamp 1886; Lewis 1874; Marshall 1895a) recorded the species from indefinite localities in western New York, but there are only two definite records from the state (Figure 58). Blakeslee found three specimens in lower Tonawanda Creek (Robertson and Blakeslee, 1948; RMSC 49.421.456), from which we picked up a single spent valve in 1994 (specimen now in NYSM). It has been found in nearby Presque Isle Bay in Pennsylvania (Masteller et al. 1993), so a few individuals probably live in Lake Erie, the Niagara River, and lower Tonawanda Creek in New York. The sauger and freshwater drum may serve as hosts (Hoggarth 1992).

FIGURE 58



Utterbackia imbecillis (Say)

Paper pondshell

PLATE 9, FIGURES 3 AND 4

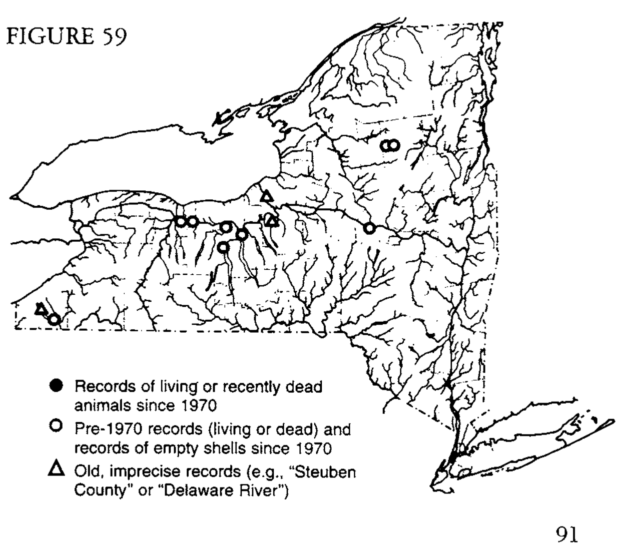
Shell very thin, subelliptical, elongate, not large (usually <70 mm long). Beaks not projecting above the hinge line. Beak sculpture fine, the outer ridges usually weakly double-looped. Periostracum greenish, shiny, usually with fine, green color rays and with two or three dark green rays on the posterior slope. Hinge teeth absent. Nacre bluish or silvery white.

This species is easily recognized by its beaks, which are not raised at all above the hinge line, and by its delicate shell, which is thin enough to see through.

U. imbecillis is widespread in central and southeastern North America. In New York, records are few and scattered (Figure 59), as follows: Chautauqua Lake (Marshall 1895a) and its outlet (ANSP 366061); Erie Canal from Pittsford to Macedon (Clarke and Berg 1959); Irondequoit Creek (Walton 1891); Seneca Lake near Geneva (OSUM 13946); Clyde River near Marengo and Seneca River at the north end of Cayuga Lake (both Harman 1970a); Onondaga County (Beauchamp 1886); Oswego River (Marshall 1895a); Mohawk River, Herkimer County (Lewis 1856, 1860, 1872; UMMZ 103877; AMNH 30345); Brown's Tract Pond, Hamilton County (ANSP 97771); and Raquette Lake, Hamilton County (UMMZ 57686). This distribution is remarkable for its wide extent and erratic character, which unlike distributions of other unionoids, does not closely follow drainage patterns other than the central part of the Erie Canal. *U. imbecillis* is one of few hermaphroditic unionoids (Hoeh et al. 1995; van der Schalie 1970), and it is said to be able to develop directly from glochidium to juvenile mussel without the use of a fish host (Howard 1914). These characteristics may make *U. imbecillis* an unusually good colonizer among unionoids and may free it to some extent from the constraint of dispersing within drainage basins. *U. imbecillis* is an uncommon species in New York that has not been reported in recent years. Nevertheless, it is common and widespread elsewhere in its range, and it probably still lives in New York.

This species is most typically found in soft substrata in quiet waters of lakes, creeks, and rivers (Clarke and Berg 1959; Harman 1970a; van der Schalie 1938). Although it may be able to develop without a fish host, it also can complete its life cycle in the usual way, using spotfin shiner, creek chub, banded killifish, black crappie, rock bass, largemouth bass, green sunfish, longear sunfish, bluegill, pumpkinseed, and yellow perch as hosts (Hoggarth 1992; Hove et al. 1995b; Watters 1994a).

FIGURE 59



Villosa fabalis (Lea)

Rayed bean

PLATE 6, FIGURE 5

Shell subelliptical, compressed, very thick, usually <40 mm long. Beak sculpture faint, double-looped. Periostracum yellow-green and nearly covered by fine, blue-green rays in young animals, chestnut brown to nearly black in old animals. Hinge teeth heavy: pseudocardinals strong and triangular, laterals short and stout. Nacre white, sometimes a little pinkish. Shells sexually dimorphic, the female shell a little broader posteriorly than the male.

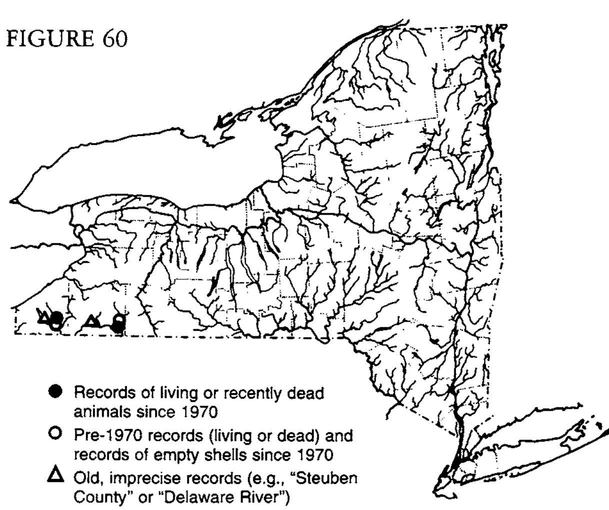
The small but very thick shell of this species, with its stout lateral teeth, is distinctive. Small shells of other species are usually much thinner. The periostracum color is also characteristic.

V. fabalis ranges throughout the Ohio River, Lake Erie, and Lake St. Clair basins. In New York, it has been seen at several sites in the Allegheny basin (Figure 60). Small populations still persist at two of these sites (Strayer 1995; Strayer et al. 1991). In addition to the records shown in Figure 60, UMMZ 92818 is an old record of *V. fabalis* from the Chemung River. Later collectors did not report this species from the Susquehanna basin, so the record is probably erroneous. Nevertheless, some fish and mussels from the Interior Basin did enter the Susquehanna basin (see "Dispersal Routes"), so it is possible that *V. fabalis* does live in the western tributaries of the Susquehanna. Although *V. fabalis* is known from western Lake Erie and its tributaries (e.g., van der Schalie 1938), it has not yet been collected from the eastern part of the basin in Ontario, Pennsylvania, or New York (Clarke 1981a; Masteller et al. 1993; Ortmann 1919; Robertson and Blakeslee 1948).

Typically an uncommon species, *V. fabalis* has declined or disappeared over most of its range and was listed as a species of special concern by Williams et al. (1993). It is legally protected in several midwestern states (Cummings and Mayer 1992).

V. fabalis is most often found in shallow riffles in creeks or small rivers, often among aquatic plants (Ortmann 1919; van der Schalie 1938). The remaining colonies in New York are in exactly such habitats. It also occurs in some lakes (Erie, Chautauqua). Spent shells are persistent and are found much more often than living animals, which are small and live in habitats (riffles) that are hard to search without mask and snorkel. Its hosts have not been investigated systematically, but they include the Tippecanoe darter (White et al., 1996).

FIGURE 60



Villosa iris (Lea)

Rainbow

PLATE 5, FIGURES 3 AND 4

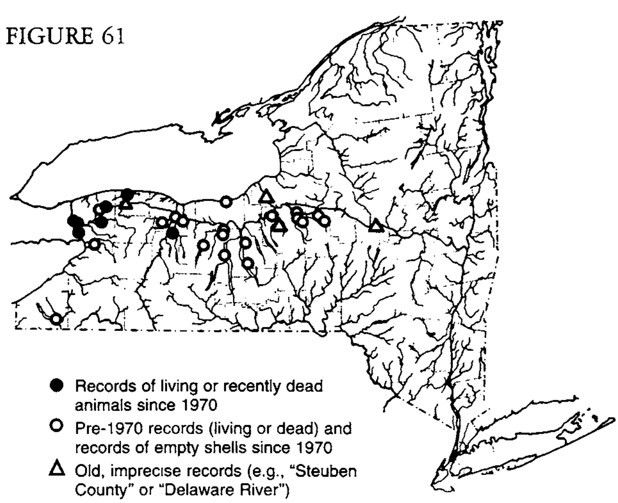
Shell subelliptical, with the margin evenly rounded, elongate (H/L = approximately 0.5–0.6), compressed, of moderate thickness, usually <75 mm long. Beak sculpture faint, double-looped. Periostracum yellow to yellow-green, usually with broad, green color rays that may be interrupted. Hinge teeth well developed but delicate. Nacre white, iridescent.

Typical specimens of *V. iris* are easy to identify by their small size, broad, interrupted color rays, and iridescent nacre. Young specimens of *Lampsilis* spp. might be misidentified as *V. iris*, but *Lampsilis* spp. tend to be ovate rather than elliptical and have continuous color rays. Old specimens of *V. iris*, which may be drab brown, could be taken for white-nacred *Elliptio dilatata*. The beak sculpture of *V. iris* is double-looped, while *E. dilatata* has concentric to trapezoidal beak sculpture.

V. iris is common and widespread in the Mississippi and Great Lakes basins. In New York, it is widespread in the Erie–Niagara, lower Genesee, and Oswego basins, as well as in several small tributaries of Lake Ontario (Figure 61). Curiously, it has been found at only one place in the Allegheny basin ("outlet of Chautauqua Lake;" ANSP 366230, ANSP 366231; BSM 365C-5/7), and it is infrequent in the upper Allegheny basin in Pennsylvania (Ortmann 1919). A single, indefinite record ("Mohawk River;" Ortmann 1919) shows that *V. iris* may have used the Erie Canal to cross the Alleghenian Divide. Erickson and Fetterman (1996) reported this species from the Grass River basin in northern New York, the first report of the species from this region. *V. iris* is still relatively common in the parts of its range in New York that have been surveyed recently (Strayer et al. 1991).

V. iris is typically thought of as a species of creeks and small rivers (Ortmann 1919; van der Schalie 1938), but it occurs in lakes (e.g., Canandaigua, Seneca, Cayuga, Oneida) and large rivers (e.g., Niagara, Seneca, Oswego) as well. It is often fairly abundant. Its hosts are not known.

FIGURE 61



Hypothetical Species

There is a good chance that four additional species of pearly mussels occurred in New York, even though there are no definitive records from the state. We tentatively include them here as part of New York's fauna.

Cyclonaias tuberculata (Rafinesque)

Purple wartyback

PLATE 26, FIGURES 1 AND 2

Shell subcircular to subquadrate, compressed, thick, reaching about 100 mm in length. Surface of the shell (except the anterior part) covered with pustules. Beak sculpture double-looped to zigzag. Periostracum brown and rayless. Hinge teeth very strong. Nacre purple.

No other species in our area has external pustules and a purple nacre. Also, *C. tuberculata* is typically more compressed and has more numerous and smaller pustules than our other pustulate species.

C. tuberculata was found scattered throughout the Allegheny basin in Pennsylvania by Ortmann (1919), and it was taken by Beecher from the Allegheny River in Pennsylvania, "near the NY border" (NYSM 32018; Plate 26, Figure 2), presumably near Warren, Pennsylvania. It probably used to live in the lower part of the Allegheny River in New York as well. This part of the Allegheny is now impounded by Kinzua Dam and is not suitable habitat for *C. tuberculata*. This species has not been found in the Allegheny above the influence of Kinzua Dam (Clark n.d.; Strayer 1995; Strayer et al. 1991). *C. tuberculata* probably no longer occurs in New York, although it may yet live in the Allegheny or in Conewango Creek. There is an outside chance that it may turn up in the Niagara River. Although it has not been seen in eastern Lake Erie or its tributaries (Masteller et al. 1993; Ortmann 1919; Robertson and Blakeslee 1948), it is widespread in the western parts of the Lake Erie basin (e.g., Clark 1977, 1987; van der Schalie 1938).

C. tuberculata lives in large creeks and rivers, often in riffles. Williams et al. (1993) gave it a status of special concern. The only known hosts are yellow bullheads and channel catfish (Hove et al. 1994c). Haggerty et al. (1995) described the reproductive cycle of this species in Tennessee.

Epioblasma torulosa rangiana (Lea)

Northern riffleshell

PLATE 27, FIGURES 3 AND 4

Shell fairly thick, <75 mm long. Beak sculpture obscure. Periostracum yellow to olive, usually with many fine rays. Hinge teeth strong. Nacre white. Shells strongly sexually dimorphic. The female shell (Plate 27, Figure 4) has a large, thin, expansion of the posterio-ventral part of the shell. The male shell (Plate 27, Figure 3) has a well-marked posterior ridge and another ridge on the face of the shell, with a prominent furrow between the two ridges. Occasionally, there are low, indistinct knobs on the ridges.

The thin posterio-ventral expansion of the shell of the adult female of this species is utterly distinctive. The furrowed male shell also does not closely resemble any other species in New York.

Like the preceding species, *E. torulosa rangiana* was widespread in the Allegheny basin of Pennsylvania, reaching nearly to New York (Ortmann 1919). Specifically, *E. torulosa rangiana* was collected from the Allegheny River "near the New York boundary" (presumably near Warren) by Beecher (NYSM 31533; Plate 27, Figures 3 and 4) and Ortmann (1919), and from Conewango Creek at Russell (Ortmann 1919). Because these localities are only a few kilometers from New York, *E. torulosa rangiana* almost certainly lived in the New York portions of these streams at one time, although it has never been reported from New York. Because the mussel fauna of lower Conewango Creek in New York seems to have been destroyed (Strayer 1995; Strayer et al. 1991) and because Kinzua Dam impounded much of the lower Allegheny in New York, it is doubtful whether this species still survives in New York. The most likely places to hold this species are Cassadaga and Conewango Creeks. *E. torulosa rangiana* is known from western Lake Erie and some of its tributaries (Johnson 1978; USFWS 1994), so there is a remote chance that it might be found in the Niagara–Erie basin in New York. *E. torulosa rangiana* was always relatively uncommon, and like most other members of its genus, it has declined sharply in recent times (USFWS 1994). It is listed as endangered by the United States Fish and Wildlife Service.

E. torulosa rangiana is chiefly a species of riffles in small to medium-sized rivers (Ortmann 1919; USFWS 1994). Occasionally, as in parts of the Allegheny basin in Pennsylvania, it is abundant, but it is usually a minor part of the unionoid community. Hosts are not known, but other species of *Epioblasma* typically use darters and sculpins (Hoggarth 1992).

Obliquaria reflexa Rafinesque

Threehorn wartyback

PLATE 26, FIGURE 3

Shell subtrapezoidal, short (H/L = approximately 0.8–0.9), thick, usually <60 mm long. A row of up to four or five large knobs extends down the face of the shell; in end view, these knobs alternate in position on the opposite valves. Beak sculpture concentric, with a nodule at the posterior ridge. Periostracum yellow to brown, sometimes with fine rays. Hinge teeth heavy. Nacre white.

The large, distinct knobs on the shell give this species its common name and distinguish it from any other local species.

There are no records of this species from New York other than Call's (1895) highly questionable report from "western New York." Possibly, the old record of *Unio pustulatus* = *Quadrula nodulata* from western New York (Lewis 1874) refers to this species. Nevertheless, it has been collected from the Grand River in Ontario, a tributary of Lake Erie only about 75 km from New York. It is also found in western Lake Erie and the Maumee River (Brown et al. 1938; Clark 1987), although it has not been seen in Presque Isle Bay in Pennsylvania (Masteller et al. 1993; Ortmann 1919). *O. reflexa* is a common species of large rivers, so there is a good chance that it will be found in the Niagara River or Lake Erie in New York. The hosts of *O. reflexa* are unknown.

Uniomerus tetralasmus (Say)

Pondhorn

PLATE 27, FIGURE 2

Shell subelliptical to subrhomboidal, posterior ridge prominent, posterior end a little squarish, shell moderately thin, up to about 125 mm long. Beak sculpture concentric. Periostracum yellow-green to dark brown, rayless. Hinge teeth well developed but delicate; pseudocardinals lamellar. Nacre white.

With its prominent posterior ridge and rayless brown periostracum, the shell of this species resembles *Elliptio complanata*. The beak sculpture of *U. tetralasmus* is circular, while that of *E. complanata* is more or less trapezoidal. Furthermore, the pseudocardinal teeth of *U. tetralasmus* are delicate and compressed, in contrast to the strong, ragged pseudocardinal teeth of *E. complanata*. Also, there are differences between the soft parts of *U. tetralasmus* and *E. complanata* (Fuller 1977; Shelley 1987).

The range of *U. tetralasmus* covers most of the Midwest as well as the Atlantic Slope north to North Carolina. Two pieces of evidence suggest that it might be part of New York's fauna. James Lewis deliberately released specimens of *U. tetralasmus* (as "*Unio camptodon*") from Illinois into the Erie Canal at Mohawk before 1860 (Lewis 1860). More significantly, ANSP 140870 is a single specimen of *U. tetralasmus* labeled "Erie Canal, Rochester" (Phillip Nell, collector). This specimen is shown in Plate 27. None of the other collectors who collected in the Erie Canal near Rochester (e.g., Baker, Blakeslee, Clarke, Harman, Walton) reported this species, although they might have overlooked occasional specimens of *U. tetralasmus* as *E. complanata*. We are unsure whether this single record is authentic and whether it arose from Lewis's introduction or from an independent introduction of the species.

U. tetralasmus usually lives in quiet waters, in creeks, ponds, and reservoirs (Cummings and Mayer 1992). It is one of few North American unionoids that can tolerate dessication. It seems to be more "weedy" than other unionoids, and it appears to be extending its range through human introductions (e.g., Clark 1944, 1987; Taylor 1984). The golden shiner may be a host (Hoggarth 1992).

Species Erroneously Recorded from New York

Several species have been incorrectly attributed to New York, through either misidentifications or mistakes in assigning the collection locality. Two sources are responsible for many of these errors. Call's (1895) paper contains many erroneous records, including several from "western New York." A series of lots at ANSP bearing distinctive cardboard labels and attributed to either "Mohawk" or "Upper Red Hook" were apparently labeled with the address of the donors (James Lewis and W.S. Teator, respectively) rather than the locality of collection. We believe that reports of the following species from New York are incorrect.

Elliptio crassidens (Lamarck)

Elephant ear

Marshall (1895a) suggested that this species might be found in New York on the basis of Beecher's collection of the species from the Allegheny River in Warren County, Pennsylvania, near the New York border. A specimen collected by Beecher from the Warren County (NYSM 31547) labeled as *E. crassidens* is *Pleurobema clava*. As Ortmann (1919) pointed out, *E. crassidens* does not occur in the upper Allegheny basin near the New York line.

Epioblasma obliquata (Rafinesque)

Catspaw

Johnson (1978) listed a specimen of this species (UMMZ 91414) from the Niagara River. Hoggarth (USFWS 1990) examined this specimen and determined that it is *Obovaria olivaria*, a species that often has been seen in the Niagara, and which superficially resembles the male of *E. obliquata*. Although we were not able to examine this specimen, Dr. David Stansbery kindly examined this specimen at our request and confirmed Hoggarth's determination.

Fusconaia ebena (Lea)

Ebonyshell

Call (1895) reported this large-river species from "western New York," but it is not known east of south-central Ohio (Cummings and Mayer 1992; Ortmann 1919). *F. ebena* is almost certainly not part of New York's fauna.

Leptodea leptodon (Rafinesque)

Scaleshell

PLATE 9, FIGURE 5

This rare species was reported from Buffalo by Simpson (1900) and Letson (1905). The basis for these reports may have been USNM 86051 ("*Leptodea leptodon*, Buffalo, New York," Robinson coll., ex. Lea collection, 2 specimens). We believe these specimens are nearly wingless examples of *Leptodea fragilis*, as are often seen in western New York (see species account of *L. fragilis*). We are not aware of any authentic records of *L. leptodon* from the Great Lakes basin.

Ligumia subrostrata (Say)

Pondmussel

PLATE 8, FIGURE 4

This species, which is found through much of the Midwest and lower Mississippi Valley (Cummings and Mayer 1992), is similar to *Ligumia nasuta*. Reports of *L. subrostrata* from New York (Letson 1905, 1909) are presumably based on misidentified specimens of *L. nasuta*.

Potamilus ohiensis (Rafinesque)

Pink papershell

This species presents special problems. It has been recorded from the Buffalo area (Letson 1905, 1909; Robertson and Blakeslee 1948; BSM 3651-4/2; see Plate 11, which is supposed to be this species), central New York (Harman 1970a), and Lake Champlain (BSM 3651-4/3-4), but we doubt that it really occurs in New York. The shell of this species is very similar to that of *Leptodea fragilis*, which is widespread in New York (Figure 38). The shell characters typically used to distinguish *P. ohiensis* from *L. fragilis* (i.e., beaks not protruding above wings, pink or purple nacre) also apply to some specimens of *L. fragilis* from New York. A positive separation of the two species requires examination of the glochidia, which are large (0.12 by 0.18 mm) and shaped like an ax-head in *P. ohiensis* and small (0.07 by 0.09 mm) and rounded in *L. fragilis* (Ortmann 1919). Until a positive identification using glochidial characters is made of *P. ohiensis*, we tentatively reject all records of *P. ohiensis* from New York.

Quadrula cylindrica (Say)

Rabbitsfoot

This beautiful, distinctive shell was reported from "Mohawk" (ANSP 41711) and "western New York" (Call 1895). The Mohawk record is surely based on erroneous label, and Call's record is unsupported and very likely incorrect. Nevertheless, *Q. cylindrica* is known from the Allegheny basin in Pennsylvania, although not close to the New York state line (Ortmann 1919), so it is just possible that it might occur in one of the larger streams of the Allegheny drainage in New York.

Tritogonia verrucosa (Rafinesque)

Pistolgrip

This is another highly distinctive species reported from "western New York" by Call (1895) but not otherwise known from our state. It is known from the Allegheny basin in western Pennsylvania (Ortmann 1919), but not from any sites near New York. Call's report is almost certainly incorrect.

Unio pictorum Linneaus

This European species was reported by Jay from Lake Champlain (Letson 1905). As it has never been reliably reported from North America, Jay's record must be incorrect, based on a misidentification of *Elliptio complanata* or a mislabeled European specimen.

Venustaconcha ellipsiformis (Conrad)

Ellipse

PLATE 10, FIGURE 3

Beauchamp (1886), Letson (1905), Lewis (1874), and Marshall (1895a) all reported this species from New York, either without locality or from "western New York" or "near Buffalo." We have not seen any authentic specimens from New York of this species, which is easily confused with *Villosa iris* and *Ptychobranchus fasciolaris*. Because of these considerations and because most or all reports of this species from the Lake Erie and Ohio River basins are suspect, we reject all reports of *V. ellipsiformis* from New York.

Synonymy

This informal synonymy, compiled chiefly from Burch (1975a) and Letson (1905), is intended to help readers interpret the older literature on the fauna and contains only names that we have seen in the literature on New York unionoids. A more complete synonymy was given by Burch (1975a).

anodontoides Lea (*Unio*)=*Lampsilis teres*

arcuata Barnes (*Alasmodonta*) = *Margaritifera margaritifera*

atra Rafinesque (*Anodonta*) = *Anodonta implicata*

attenuata Rafinesque (*Obliquaria*) = *Ligumia nasuta*

aurata Rafinesque (*Unio*) = *Elliptio complanata*

benedictensis Lea (*Symphynota*) = *Pyganodon grandis*

borealis Gray (*Unio*) = *Lampsilis radiata*

boydianus Lea (*Unio*) = *Lampsilis radiata*

buchanensis Lea (*Anodonta*) = *Anodontoides ferussacianus*

calceolus Lea (*Unio*) = *Alasmidonta viridis*

canadensis Lea (*Unio*) = *Lampsilis ovata*

cardium Rafinesque (*Lampsilis*) = *Lampsilis ovata*

carinatus Barnes (*Unio*) = *Actinonaias ligamentina*

Carunculina Baker = *Toxolasma*

coccineus Conrad (*Unio*) = *Pleurobema cordatum*

cornutus Barnes (*Unio*) = *Obliquaria reflexa*

corrugata DeKay (*Alasmodon*) = *Alasmidonta varicosa*

costata Rafinesque (*Amblema*) = *Amblema plicata*

Crenodonta Schuter = *Amblema*

cuneata Rafinesque (*Anodonta*) = *Pyganodon cataracta*

cylindrica Lea (*Anodonta*) = possibly *Anodontoides ferussacianus*; we found no species described by Lea under this name, but perhaps Dewey (1856) meant to refer to *subcylindracea* Lea.

decora Lea (*Anodonta*) = *Pyganodon grandis*

deltoidea Lea (*Margaritana*) = *Alasmidonta viridis*

distans Anthony (*Unio*) = *Lampsilis siliquoidea*

Dysnomia Agassiz = *Epioblasma*

edentula Say (*Alasmodonta*) = *Strophitus undulatus*

elegans Lea (*Unio*) = *Truncilla truncata*

ellipsis Lea (*Unio*) = *Obovaria olivaria*

eriganensis Grier (*Lasmigona*) = *Lasmigona costata*

excurvata DeKay (*Anodon*) = *Pyganodon cataracta*

ferruginea Lea (*Anodonta*) = *Anodontoides ferussacianus*

fluviatilis Dillwyn (*Mytilus*) = *Pyganodon cataracta*

fluviatilis Green (*Unio*) = *Elliptio complanata*

footiana Lea (*Anodonta*) = *Pyganodon grandis*

georgina Lamarck (*Unio*) = *Elliptio complanata*

gibbosus Barnes (*Unio*) = *Elliptio dilatata*

gigantea Lea (*Anodonta*) = *Pyganodon grandis*

gracilis Barnes (*Unio*) = *Leptodea fragilis*

Hemilastena Agassiz = as used in the literature on New York, this name refers to *Simpsonaias*

hildrethiana Lea (*Margaritana*) = *Simpsonaias ambigua*

hippopaeus Lea (*Unio*) = *Amblema plicata*

inflatus Barnes (*Unio*) = *Lampsilis siliquoidea*

katherinae Lea (*Unio*) = *Lasmigona complanata*

kennicottii Lea (*Anodonta*) = *Pyganodon grandis*

lachrymosus Lea (*Unio*) = *Quadrula quadrula*

lacustris Baker (*Lampsilis*) = *Leptodea fragilis*

lacustris Baker (*Ptychobranchus*) = *Ptychobranchus fasciolaris*

laevissimus Lea (*Symphynota*) = *Potamilus ohiensis*

latissima Rafinesque (*Unio*) = *Ligumia recta*

leibii Lea (*Unio*) = *Obovaria subrotunda*

lewisii Lea (*Anodonta*) = *Pyganodon grandis*

lurida Simpson (*Lampsilis*) = *Lampsilis ovata*

luteolus Lamarck (*Unio*) = *Lampsilis radiata* (but this name was used most commonly for *L. siliquoidea*)

Margaritana Schumacher = in the nineteenth century, this name was used for species now assigned to *Margaritifera*, *Simpsonaias*, *Lasmigona*, and *Alasmidonta*; in the twentieth century, it was used in a more restricted sense for *Margaritifera.*

marginata Say (*Anodonta*) = *Pyganodon* species, probably *P. lacustris*

megaptera Rafinesque (*Megaptera*) = *Potamilus alatus*

Micromya Agassiz = *Villosa*

modesta Lea (*Anodonta*) = *Anodontoides ferussacianus*

multiradiatus Lea (*Unio*) = *Lampsilis fasciola*

novi-eboraci Lea (*Unio*) = *Villosa iris*

occidens Lea (*Unio*) = *Lampsilis ovata*

oneidensis Baker (*Lampsilis*) = *Lampsilis radiata*

orbiculata Hildreth (*Unio*) (in the sense used by New York authors) = *Lampsilis abrupta*

ovata Lea (*Anodonta*) = *Pyganodon grandis*

pallida Rafinesque (*Lampsilis*) = *Lampsilis cariosa*

parvula Grier (*Fusconaia*) = *Fusconaia flava*

patulus Lea (*Unio*) = *Pleurobema clava*

paupercula Simpson (*Quadrula*) = *Pleurobema cordatum*

pavonia Lea (*Anodonta*) = *Strophitus undulatus*

pepinianus Lea (*Anodonta*) = *Pyganodon grandis*

perplexus Lea (*Unio*) = *Epioblasma torulosa*

phaseolus Hildreth (*Unio*) = *Ptychobranchus fasciolaris*

Plagiola Rafinesque= this name has been used for species now in *Truncilla*, species now in *Ellipsaria*, and most recently for species now in *Epioblasma*

plana Lea (*Anodonta*) = *Pyganodon grandis*

plebius Adams (*Unio*) = *Lasmigona compressa*

pressus Lea (*Unio*) = *Lasmigona compressa*

Proptera Rafinesque = *Potamilus*

purpurascens Lamarck (*Unio*) = *Elliptio complanata*

pustulatus Lea (*Unio*) = *Quadrula nodulata*

rarisulcata Lamarck (*Unio*) = *Elliptio complanata*

rhombula Lamarck (*Unio*) = *Elliptio complanata*

rosaceus DeKay (*Unio*) = *Lampsilis radiata* or *L. siliquoidea*

rosea Rafinesque (*Lampsilis*) = *Leptodea ochracea*

rubiginosa Lea (*Unio*) = *Fusconaia flava*

rugosa Barnes (*Alasmodonta*) = *Lasmigona costata*

salmonia Lea (*Anodonta*) = *Pyganodon grandis*

simpsoniana Lea (*Anodonta*) = *Pyganodon grandis*

Simpsoniconcha Frierson = *Simpsonaias*

solidus Lea (*Unio*) = *Pleurobema cordatum*

spatulatus Lea (*Unio*) = *Venustaconcha ellipsiformis*

sterkii Grier (*Elliptio*) = *Elliptio dilatata*

subcylindracea Lea (*Anodonta*) = *Anodontoides ferussacianus*

superiorensis Marsh (*Unio*) = *Lampsilis siliquoidea*

Symphynota Lea = used by some earlier authors to include species chiefly now in *Lasmigona* and *Leptodea*

tappanianus Lea (*Unio*) = *Lasmigona subviridis*

tenuissima Lea (*Symphynota*) = *Leptodea leptodon*

triangularis Barnes (*Unio*) = *Epioblasma triquetra*

trigonus Lea (*Unio*) = *Fusconaia flava*

truncata Wright (*Alasmidonta*) = *Alasmidonta marginata*

Truncilla = before its present usage, this name was used for species now in *Epioblasma*

tryonii Lea (*Anodonta*) = *Pyganodon cataracta*

tuberculatus Barnes (*Unio*) = *Tritogonia verrucosa*

unadilla DeKay (*Anodon*) = *Strophitus undulatus*

undulata Barnes (*Unio*)= *Megalonaias nervosa*, but used in New York for *Amblema plicata* as well

Unio Retzius = this name was formerly applied to any species with complete hinge teeth (e.g., *Quadrula*, *Elliptio*, *Lampsilis* and many others)

ventricosus Barnes (*Unio*) = *Lampsilis ovata*

verrucosus Barnes (*Unio*) = *Cyclonaias tuberculata*

viridis Conrad (*Unio*) = *Lasmigona subviridis*

williamsii Lea (*Anodonta*) = *Pyganodon cataracta*

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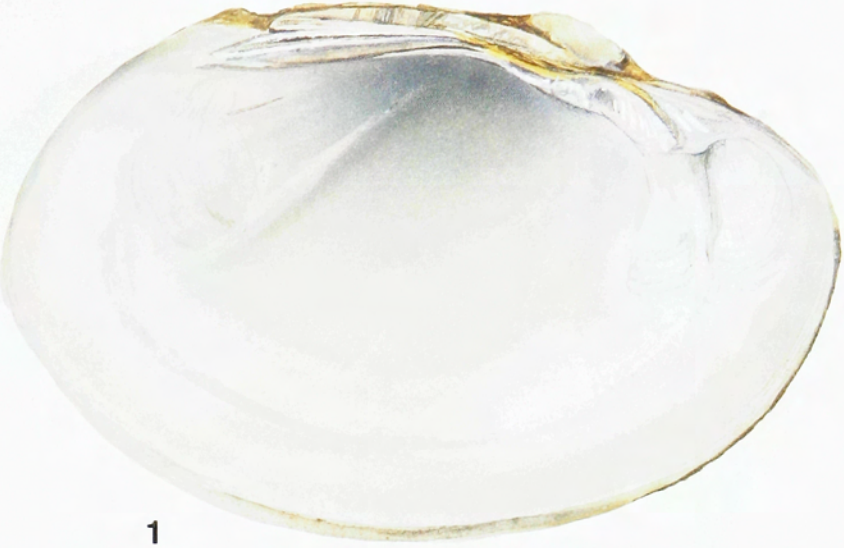
Plates

PLATE 1

Lampsilis ovata

Cayuga Creek, Buffalo, New York.

Drawn by W.P. Davison.



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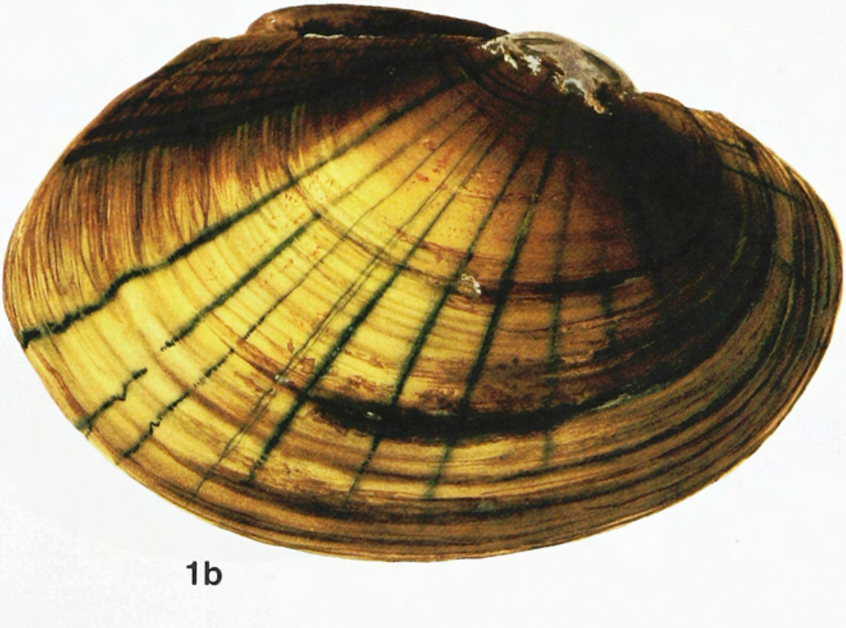
1a



1b

PLATE 2

Lampsilis ovata

1, 1a. Female, Seneca River, Onondaga County, New York;
2. Half-grown specimen, Seneca River, Onondaga County, New York;
3, 3a. Erie Canal, Pittsford, Monroe County, New York;
4. Lake Champlain, Crown Point, Essex County, New York;
5. Lake Champlain, Ticonderoga, Essex County, New York.

Drawn by Helen Winchester.

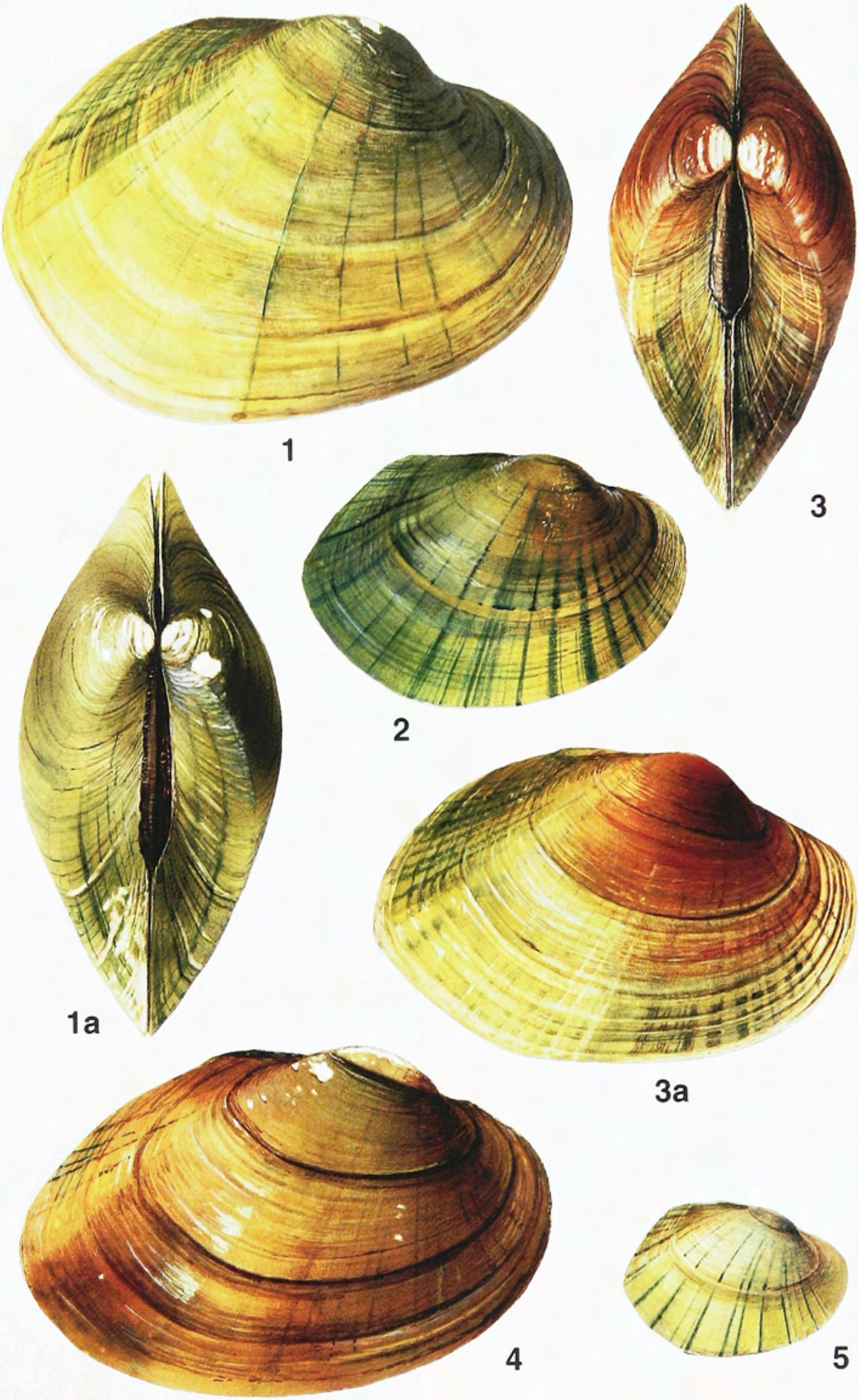

1
3
1a
2
3a
4
5

PLATE 3

Lampsilis cariosa

1. Female, Normanskill, Albany County, New York;
2. Female, Champlain Canal, West Troy, Saratoga County, New York;
5, 6. Champlain Canal, West Troy, Saratoga County, New York.

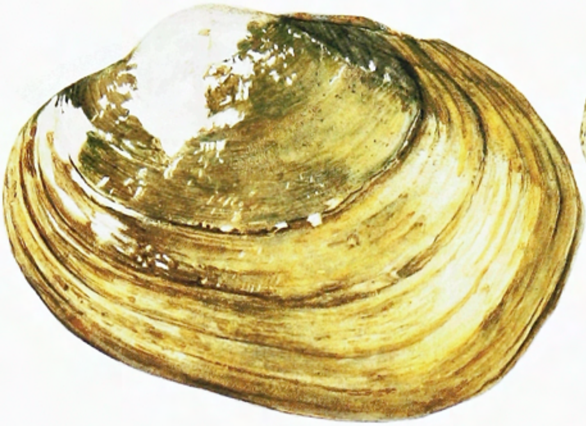
Leptodea ochracea

3, 3a. Champlain Canal, West Troy, Saratoga County, New York.

Epioblasma triquetra

4, 4a, 4b. Male, locality unknown.

Figures 4, 4a, and 4b drawn by W.P. Davison; all others drawn by Helen Winchester.



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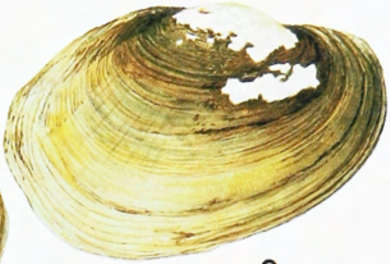
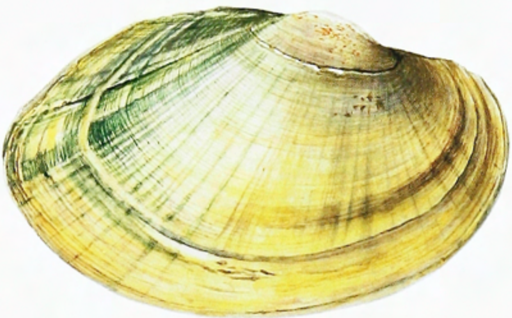


2

4



3

4a

3a

4b

5

6

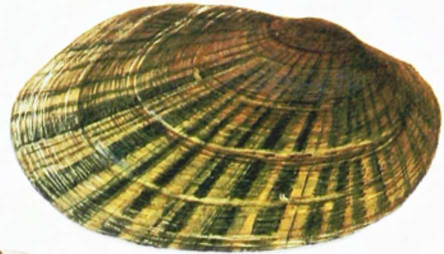
PLATE 4

Lampsilis radiata

1, 1a. Female, Lake Champlain, Crown Point, Essex County, New York, ANSP 129226;
2, 2a, 2b. Male, Albany, Albany County, New York;
3, 4. Oneida Lake, Lower South Bay, Oswego County, New York, ANSP 114854
("cotypes" of *Lampsilis radiata oneidensis* Baker);
5. Lake Champlain, McNeil's Bay, New York, ANSP 129225.

Figures 2, 2a, and 2b drawn by W.P. Davison; all others drawn by Helen Winchester.

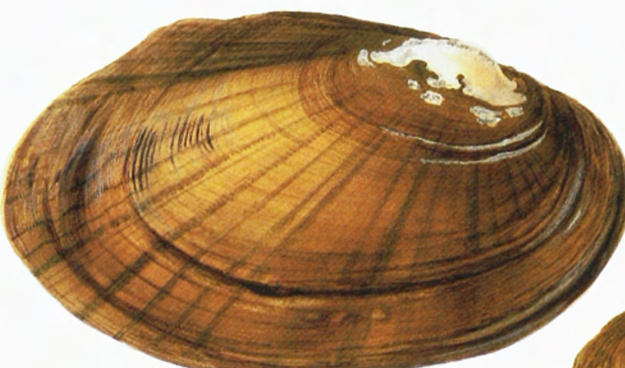
1



1a

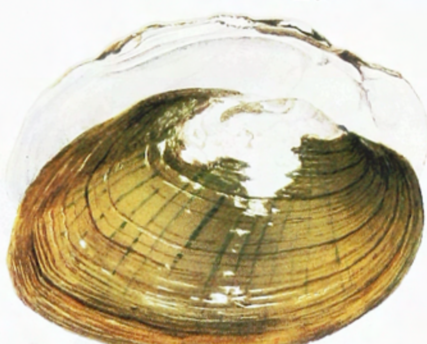
2

2b

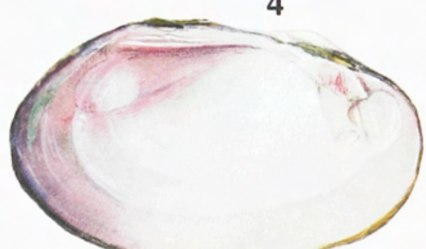


2a

4



3



5

PLATE 5

Lampsilis radiata

1, 2. Lake Champlain at head of Willsboro Bay, Essex County, New York, ANSP 129409; 5. Reproduction of Conrad's figure of *Unio melinus*, Salina Lake.

Villosa iris

3. Erie Canal near Baldwinsville, Onondaga County, New York, ANSP 56469; 4, 4a, 4b. Locality unknown.

Lampsilis siliquoidea

6, 7. Females, Chautauqua Lake, Chautauqua County, New York, ANSP 48009.

Drawn by Helen Winchester, except for Figure 5.

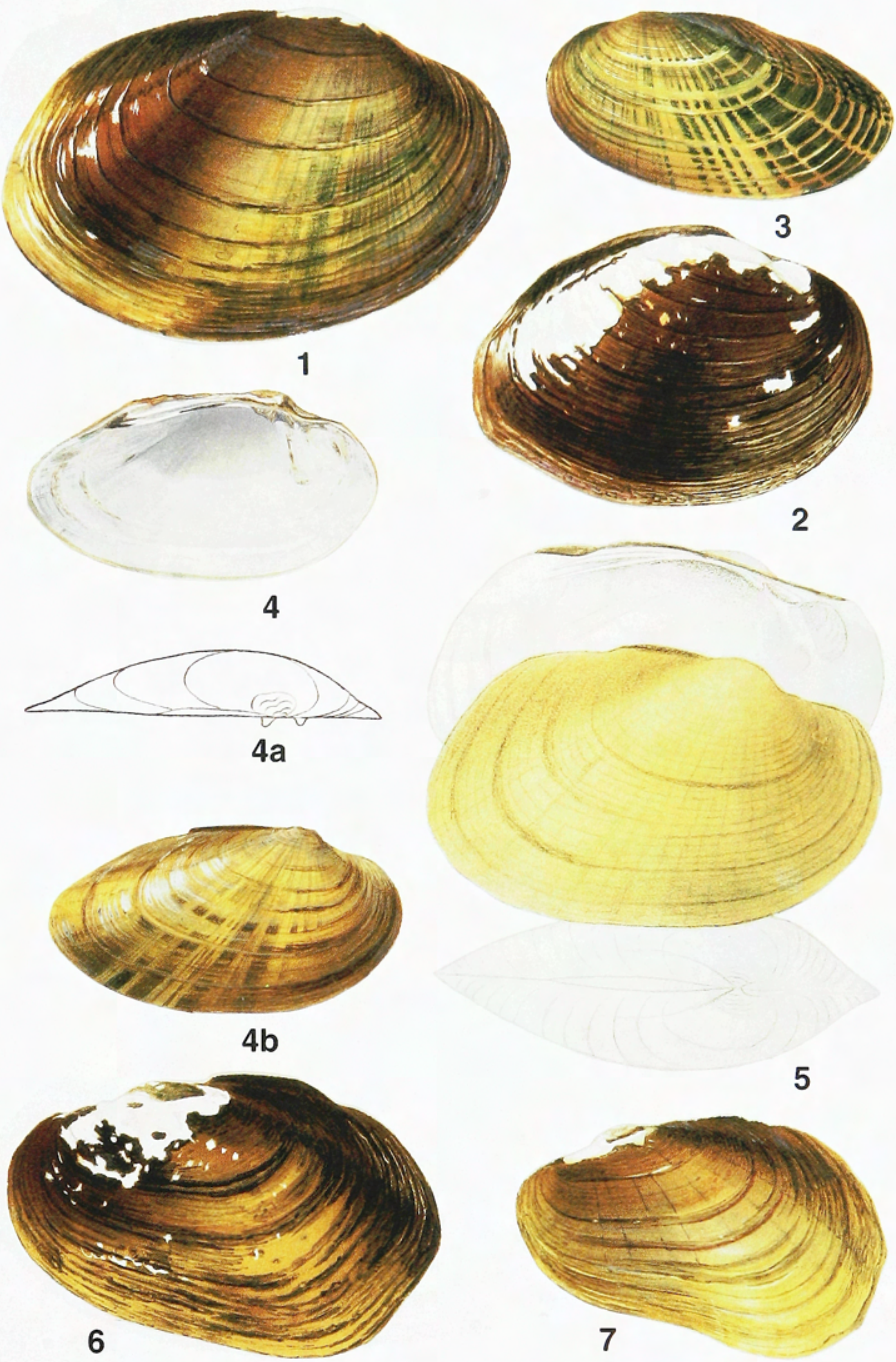

1
2
3
4
4a
4b
5
6
7

PLATE 6

Lampsilis siliquoidea

1. Female, Buffalo, Erie County, New York, ANSP 126079;
2, 2a, 2b. Female (this form was formerly called subspecies *rosacea* DeKay);
3, 3a, 3b. Male, Cayuga Creek, Buffalo, Erie County, New York.

Toxolasma parvum

4, 4a. Erie Canal, New York.

Villosa fabalis

5, 5a, 5b. Allegheny River.

Figure 1 drawn by Helen Winchester; Figures 4 and 4a drawn by George Barkentin; all others drawn by Wilfred Davison.

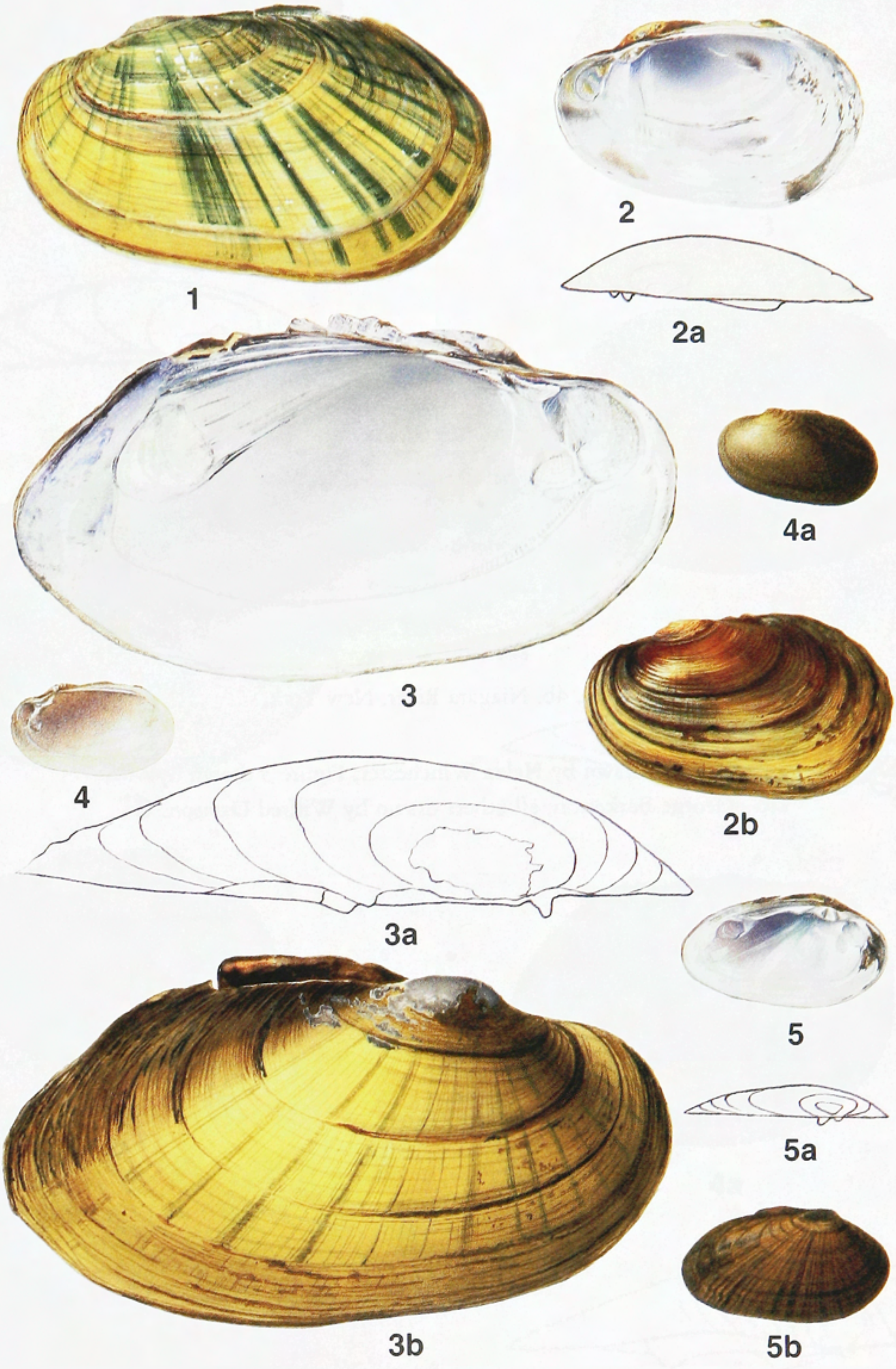

1
2
2a
3
4a
4
2b
3a
5
5a
3b
5b

PLATE 7

Lampsilis fasciola

1, 1a, 1b, 2. Medina, Orleans County, New York.

Actinonaias ligamentina

3, 3a, 3b. Niagara River, New York.

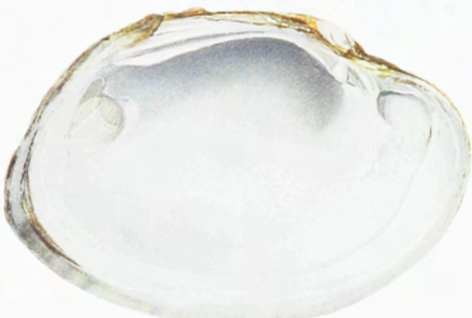
Obovaria olivaria

4, 4a, 4b. Niagara River, New York.

Figure 2 drawn by Helen Winchester; Figure 3 drawn by George Barkentin; all others drawn by Wilfred Davison.

1

1a



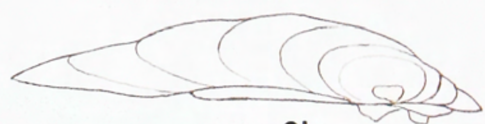
1b

2

4

3

3a



3b

4a

4b

PLATE 8

Ligumia recta

1, 1a. Erie Canal, Erie County, New York.

Ligumia nasuta

2, 5. Lake Erie, Buffalo, Erie County, New York, ANSP 126174;
3. Champlain Canal, Albany County, New York.

Ligumia subrostrata

4, 4a. Locality unknown.

Figures 2 and 5 drawn by Helen Winchester; Figure 3 drawn by George Barkentin; Figures 1 and 4 drawn by Wilfred Davison.

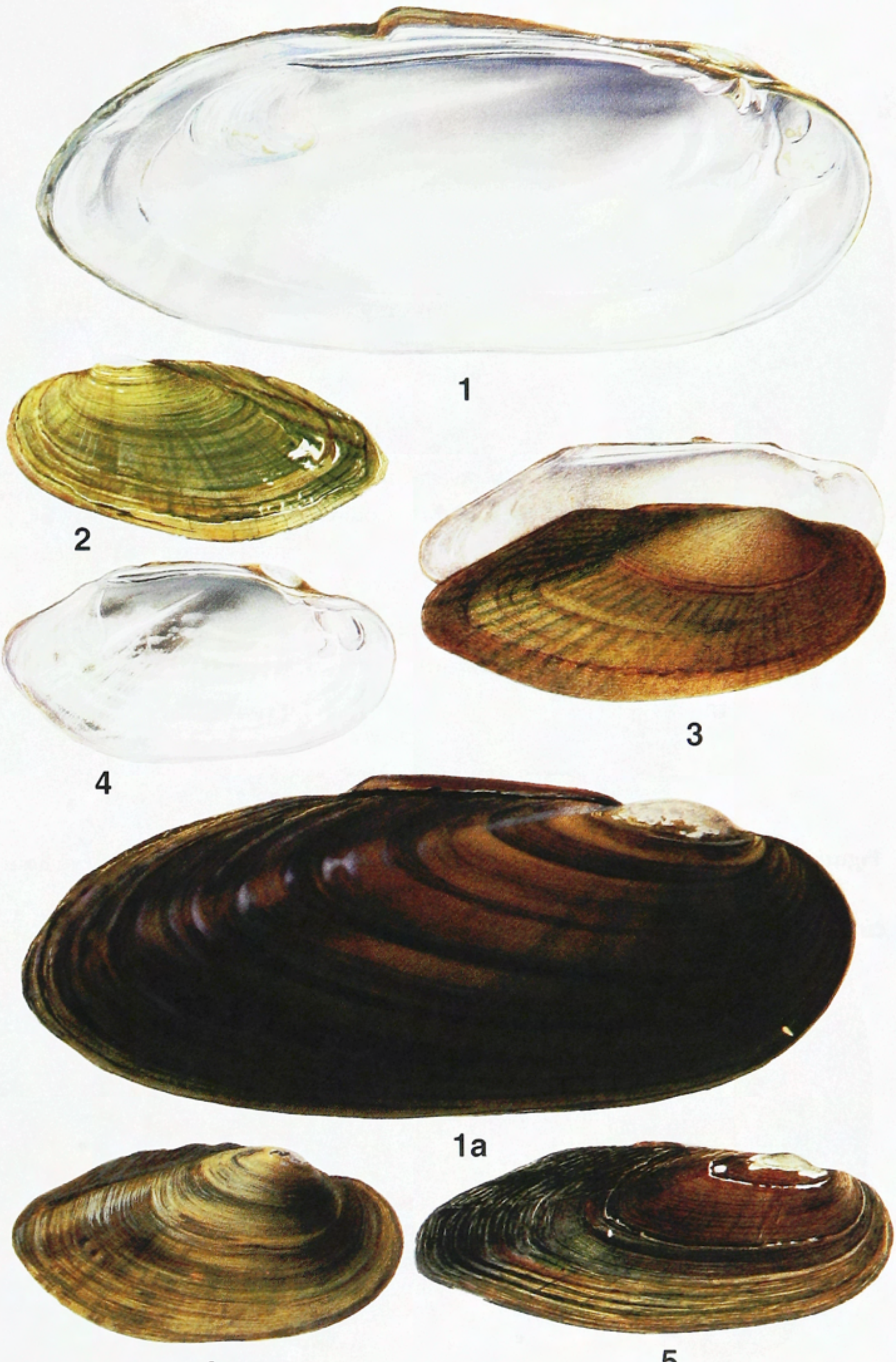

1
2
3
4
1a
4a
5

PLATE 9

Leptodea fragilis

1. Locality unknown, ANSP 126356;
2. Lake Erie, Buffalo, Erie County, New York.

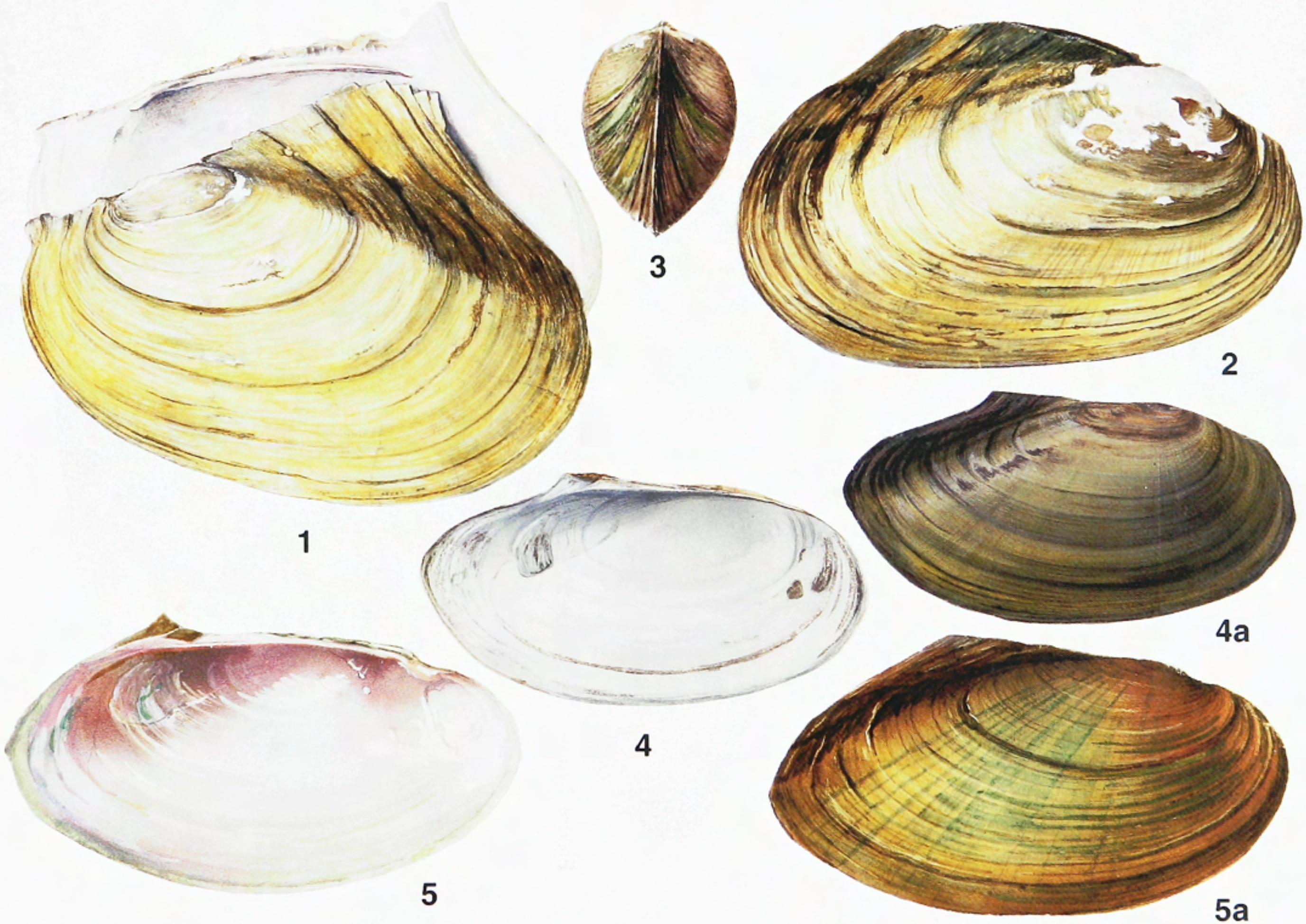
Utterbackia imbecillis

3. Brown's Tract Pond, Hamilton County, New York;
4, 4a. Locality unknown.

Leptodea leptodon

5, 5a. Ohio, ANSP 126630.

Figures 4 and 4a drawn by Wilfred Davison; all others drawn by Helen Winchester.



1
2
3
4
4a
5
5a

PLATE 10

Potamilus alatus

1, 2. Buffalo Creek, Erie County, New York.

Venustaconcha ellipsiformis

3. Grand Rapids, Michigan, ANSP 126275.

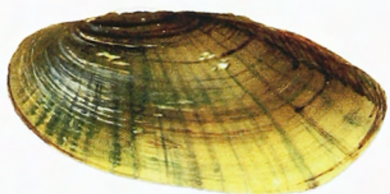
Lampsilis teres

4. Niagara River, New York, ANSP 42080.

Figure 2 drawn by George Barkentin; all others drawn by Helen Winchester.

1

3



4

2

PLATE 11

Leptodea fragilis ("*Potamilus ohiensis*")

Buffalo Creek, Erie County, New York.

Drawn by Wilfred Davison.

PLATE 12

Ptychobranchus fasciolaris

1, 1a. Allegheny River, Pennsylvania, near the New York boundary.

Quadrula pustulosa

2, 2a, 2b. Locality unknown;
3. Erie Canal, Pittsford, Monroe County, New York, ANSP 129660.

Alasmidonta undulata

4, 4a, 5. Normanskill, Albany County, New York, ANSP 56750, 56753;
6. Unadilla River, New York.

Figures 2, 2a, and 2b drawn by Wilfred Davison; all others drawn by Helen Winchester.

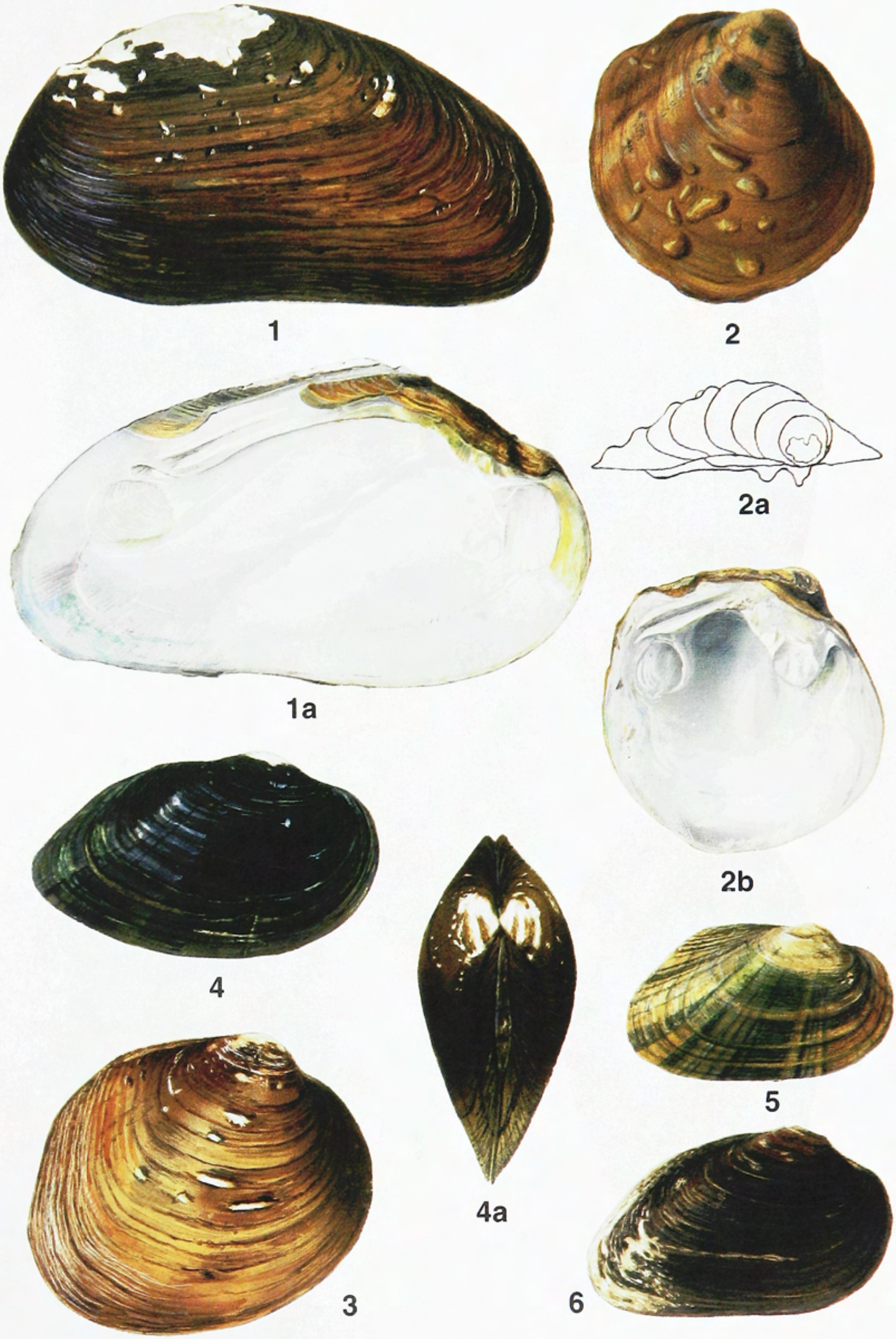

1
2
2a
1a
2b
4
4a
5
3
6

PLATE 13

Pyganodon grandis

1, 2. Lake Champlain, Crown Point, Essex County, New York;
3. Presque Isle Bay, Erie County, Pennsylvania, ANSP 10302;
4. Lake Ontario, ANSP 97853;
5. Irondequoit Bay, Monroe County, New York, ANSP 126598.

Drawn by Helen Winchester.

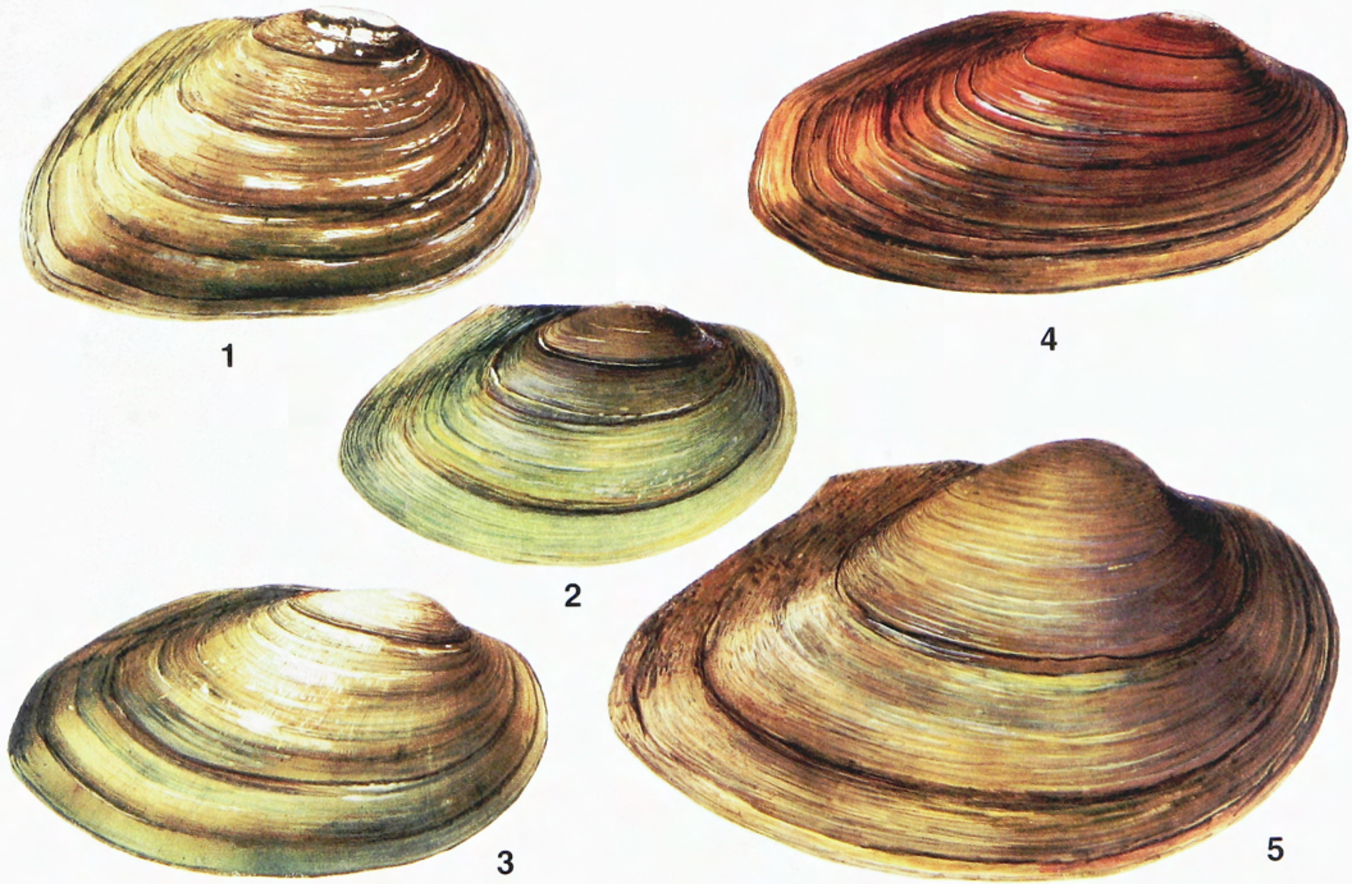
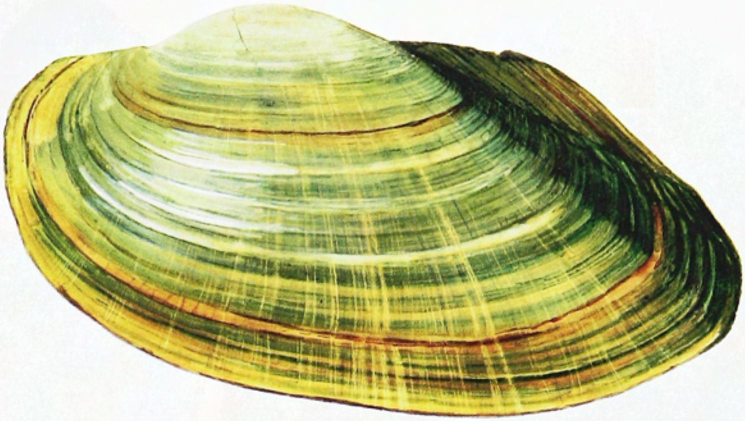

1
2
3
4
5

PLATE 14

Pyganodon cataracta

1, 1a. Pond near Dover Plains, Dutchess County, New York, ANSP 60165;
2. Black Rock Pond, Albany, Albany County, New York.

Figures 1 and 1a drawn by Helen Winchester; Figure 2 drawn by George S. Barkentin.



1

1a

2

PLATE 15

Anodonta implicata

1, 1a, 1b. Locality unknown.

Pyganodon lacustris?

2, 2a. Lake Charlotte (=Lake Taghkanic), Columbia County, New York, ANSP 64579.

Pyganodon cataracta? (or *P. lacustris?*)

3, 3a. Little Lakes (= Weaver and Young Lakes), Herkimer County, New York [i.e., the type locality of *P. lacustris*], ANSP 126529.

Figures 1, 1a, and 1b drawn by Wilfred Davison; all others drawn by Helen Winchester.

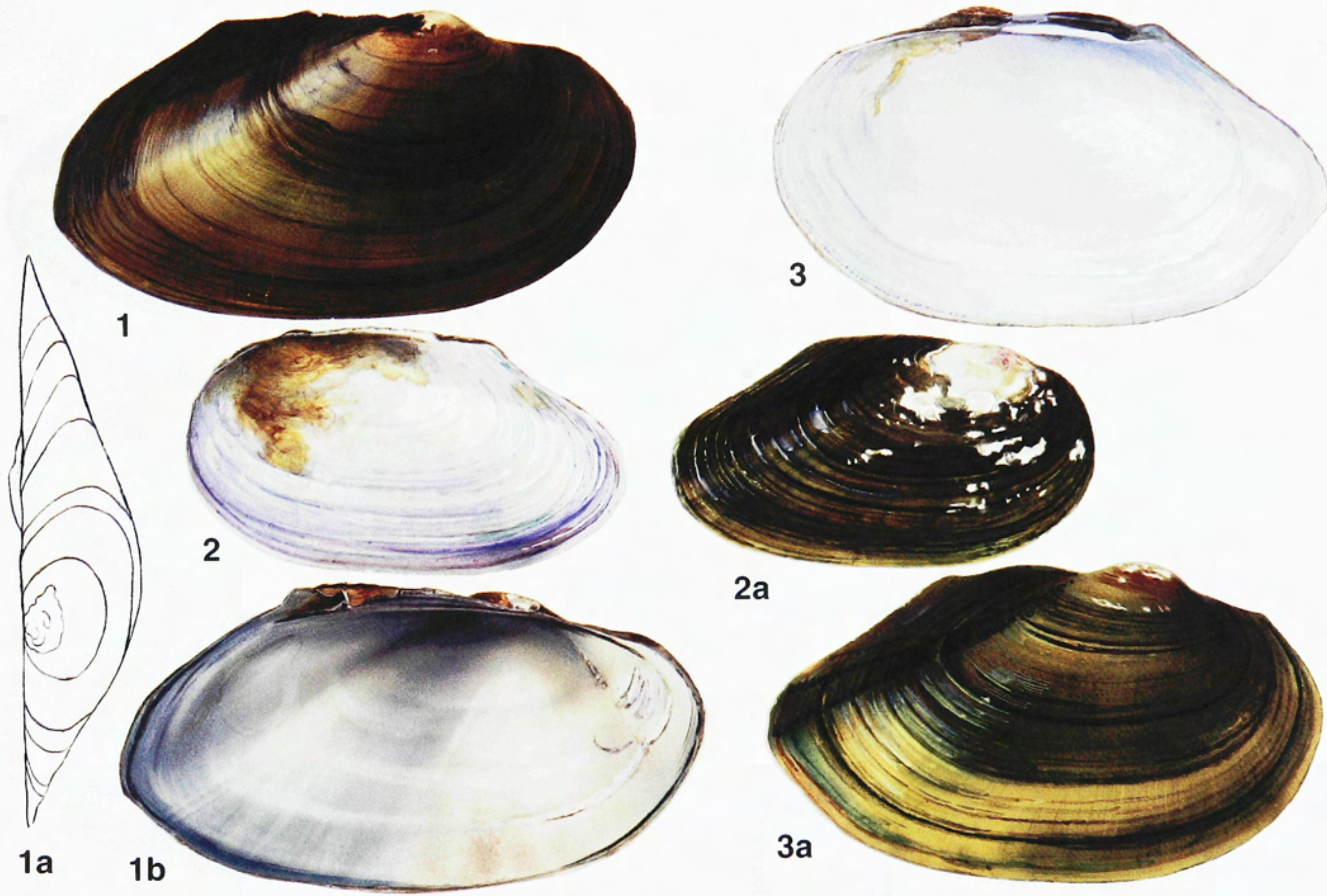

1
1a
1b
2
2a
3
3a

PLATE 16

Pyganodon lacustris?

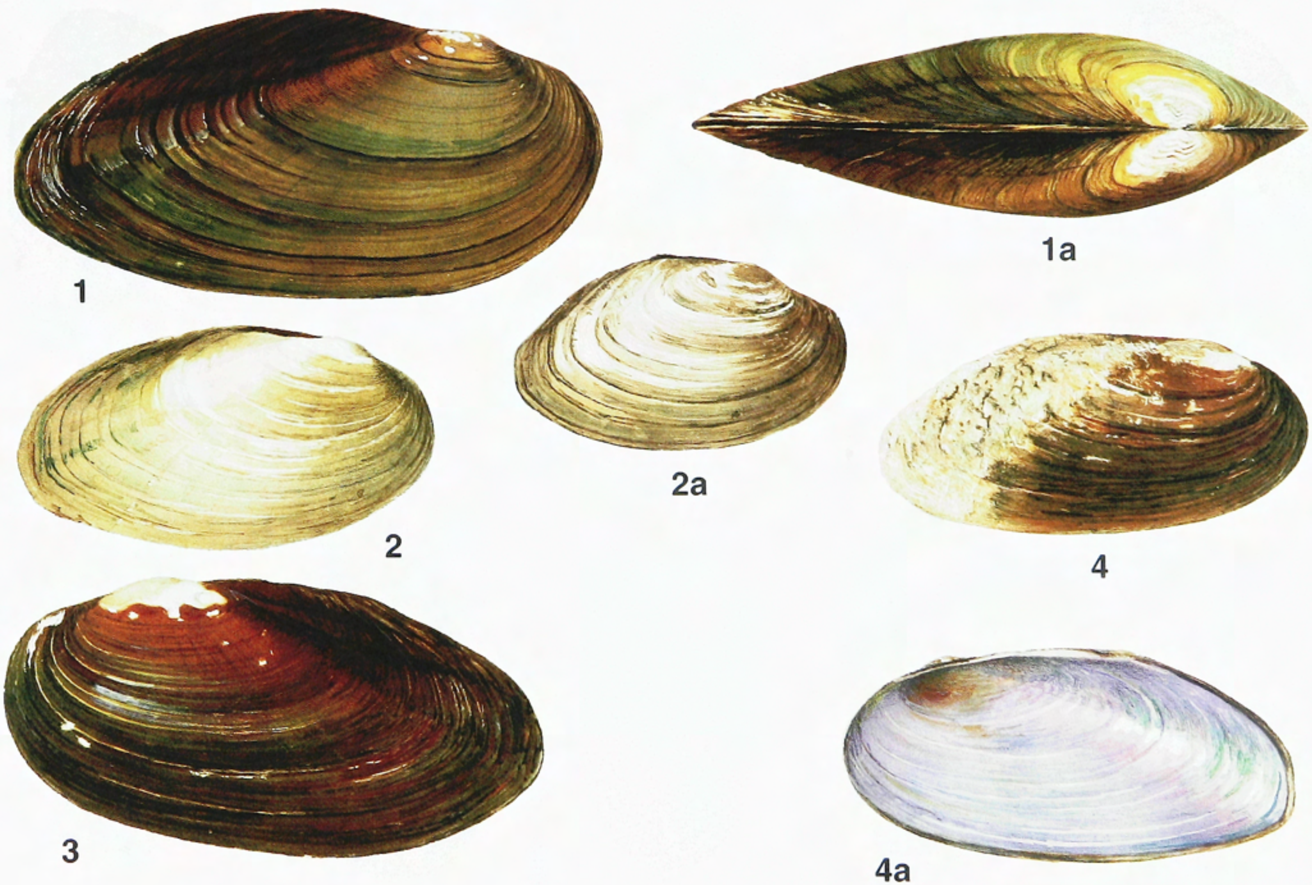
1, 1a. Mohawk, Herkimer County, New York, ANSP 41174;

2, 2a. Skaneatales Lake, Onondaga County, New York;

3. White's Mill Pond, Upper Red Hook, Dutchess County, New York;

4, 4a. Beaver Creek, 8 miles south of Mohawk, Herkimer County, New York, ANSP 126549.

All drawn by Helen Winchester.



1
1a
2
2a
3
4
4a

PLATE 17

Strophitus undulatus

1, 1a, 1b. Locality unknown;
2, 2a. Locality unknown;
3. (Variety *pavonia*) Maine, ANSP 56734.

Anodontoides ferussacianus

4, 4a. Roanoke, Genesee County, New York, ANSP 28626;
5. Beach pools of Lake Erie, Presque Isle, Erie County, Pennsylvania, ANSP 97890;
6. Erie Canal, Rochester, Monroe County, New York, ANSP 29659.

Figures 1 through 2a drawn by Wilfred Davison; all others drawn by Helen Winchester.

1

1a

1b

2

2a

3

4

4a

5

6

PLATE 18

Alasmidonta viridis

1, 1a, 1b. Niagara River, New York.

Lasmigona costata

2, 2a, 2b. Cayuga Creek, Erie County, New York;
3. (Immature) Erie Canal, Mohawk, Herkimer County, New York, ANSP 129771.

Figure 3 drawn by Helen Winchester; all others drawn by Wilfred Davison.

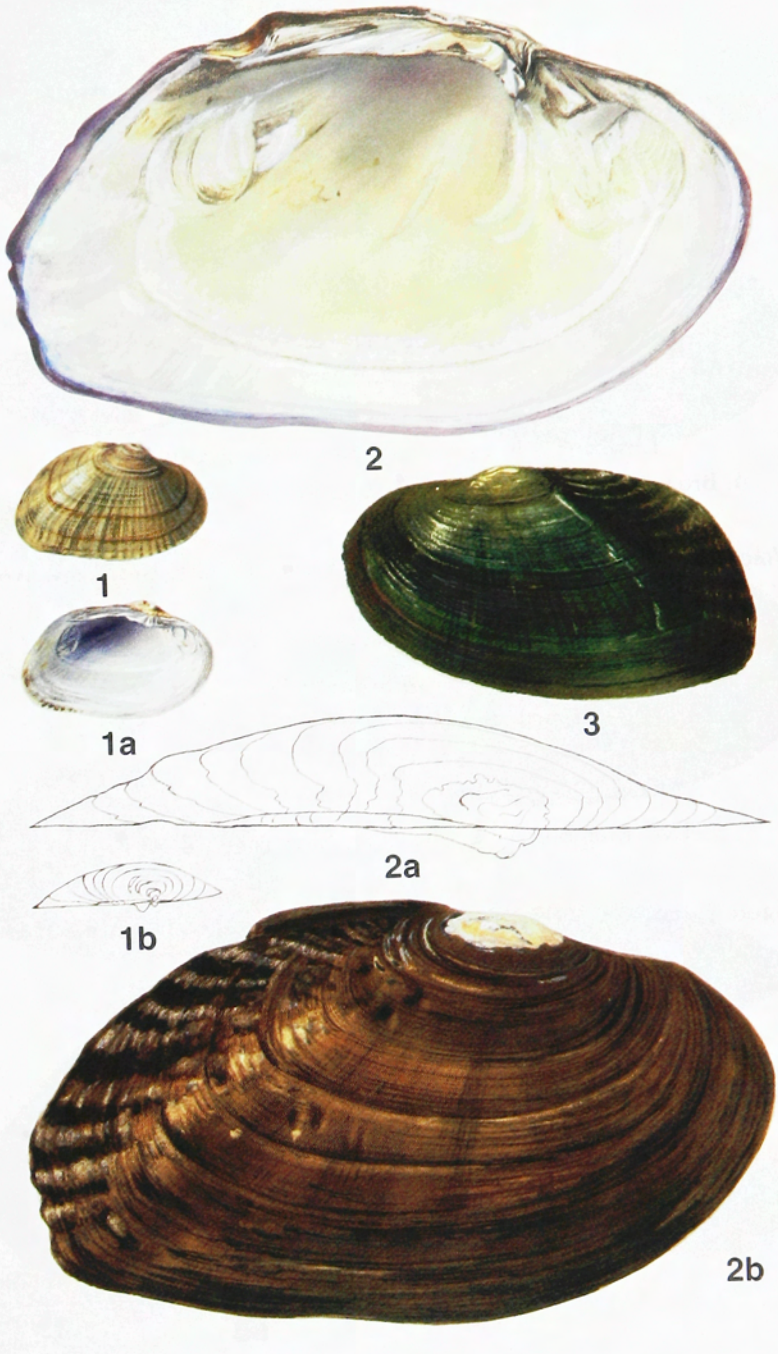

2
1
3
1a
2a
1b
2b

PLATE 19

Lasmigona compressa

1. Albany, Albany County, New York, ANSP 41017;
4. Brown's Tract Pond, Hamilton County, New York, ANSP 97784;
5. Mannsville, Jefferson County, New York, ANSP 48260;
6, 6a. Wolcott Creek, 2 miles north of Wolcott, Wayne County, New York, ANSP 44149.

Lasmigona subviridis

2. Erie Canal, West Troy, Saratoga County, New York;
3, 3a, 3b. Erie Canal, Herkimer County, New York, ANSP 41022.

Simpsonaias ambigua

7. Lake Erie, Buffalo, Erie County, New York, ANSP 126779.

Figure 2 drawn by Wilfred Davison; all others drawn by Helen Winchester.

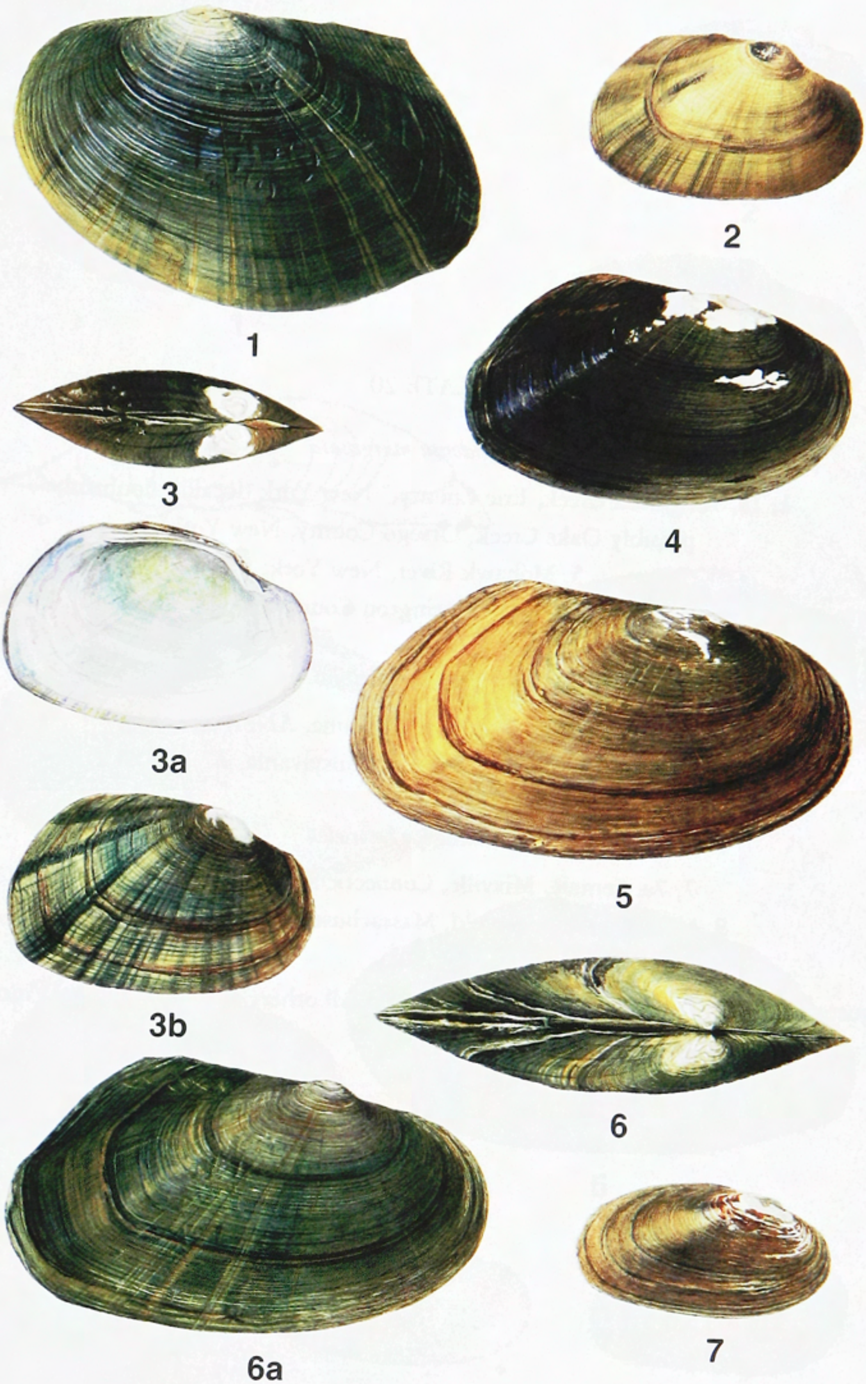

1
2
3
4
3a
5
3b
6
6a
7

PLATE 20

Alasmidonta marginata

1, 1a, 1b. "Oaks Creek, Erie County," New York (locality doubtful; possibly Oaks Creek, Otsego County, New York);
5. Mohawk River, New York;
6. (Variety *susquehannae*) Mt. Union, Huntington County, Pennsylvania, ANSP 69833.

Alasmidonta varicosa

2, 3. Perkiomen Creek, Pennsylvania, ANSP 126752;
4. Sancony Creek near Coatstown, Pennsylvania, ANSP 101555

Alasmidonta heterodon

7, 7a. Female, Mixville, Connecticut, ANSP 41003;
8. Male, Canal, Westfield, Massachusetts, ANSP 126740.

Figures 1, 1a, and 1b drawn by Wilfred Davison; all others drawn by Helen Winchester.

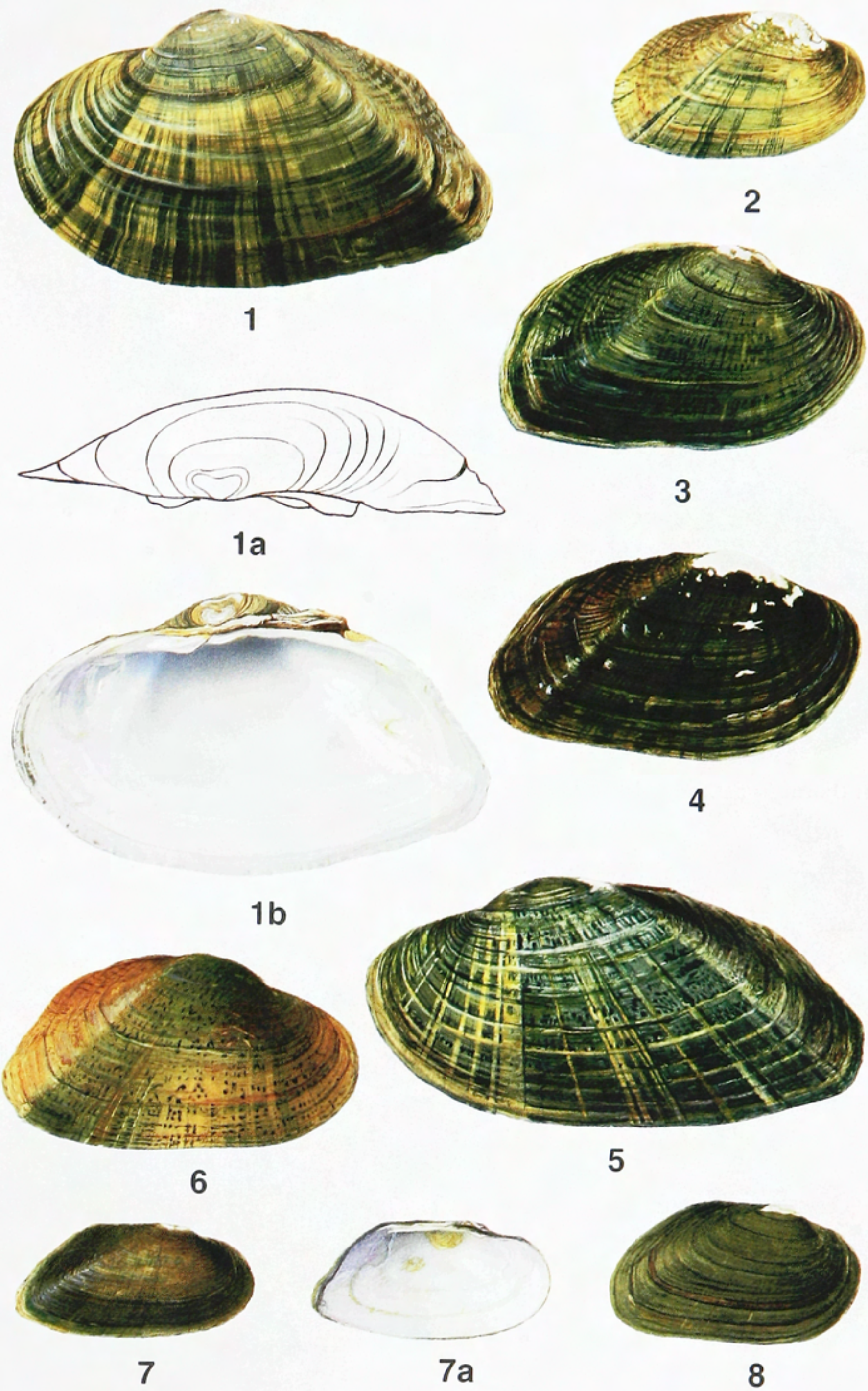

1
2
3
1a
4
1b
5
6
7
7a
8

PLATE 21

Amblema plicata

1. Erie Canal, Rochester, Monroe County, New York, ANSP 129700;
3, 3a. Lake Erie, Presque Isle Bay, Pennsylvania, ANSP 103016.

Fusconaia flava

2, 2a. Locality unknown.

Pleurobema cordatum

4, 4a. (Form *coccineum*) Locality unknown;
5. (Form *pauperculum*) Big Bend of Presque Isle Bay, Pennsylvania, ANSP 103017.

All drawn by Helen Winchester.

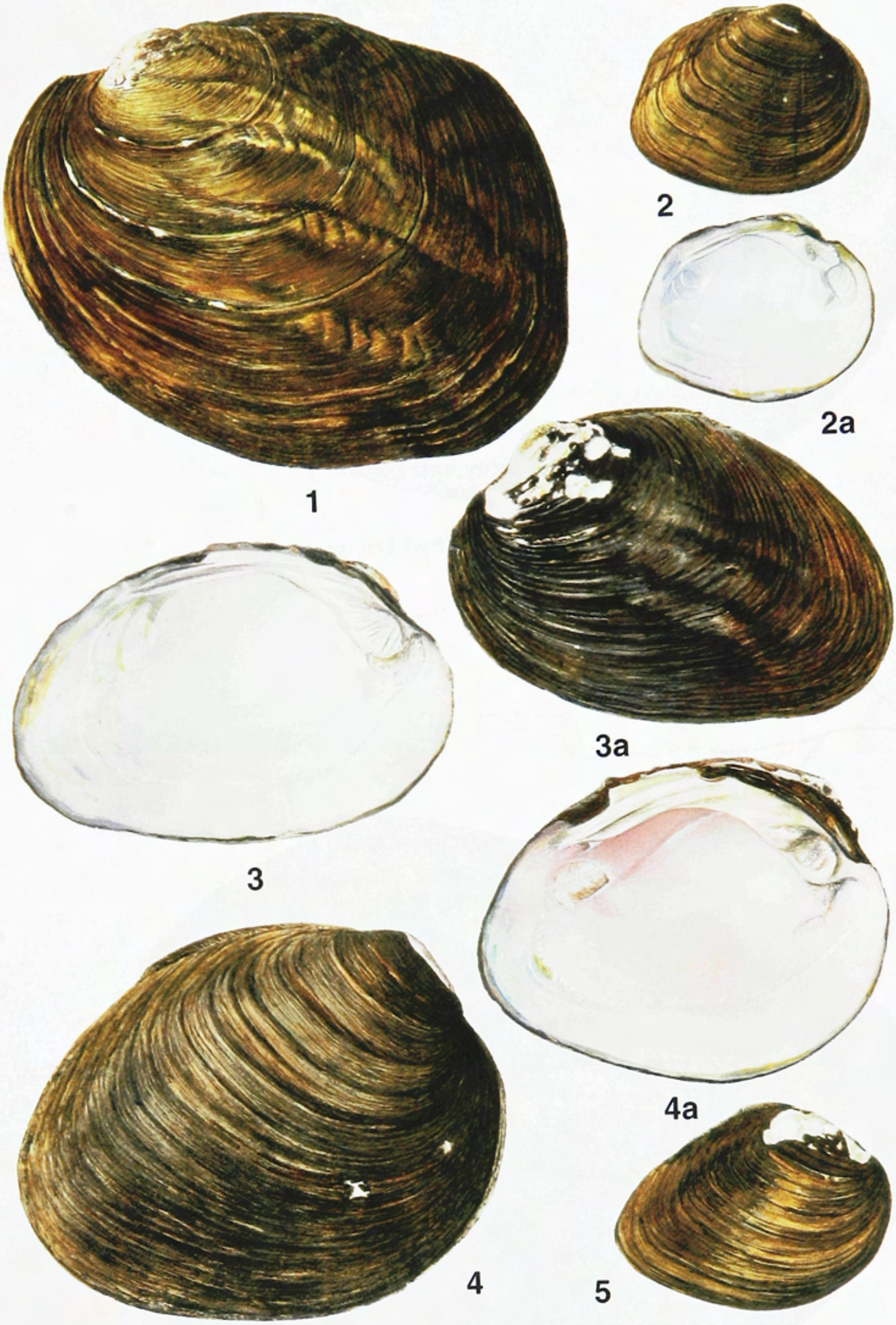
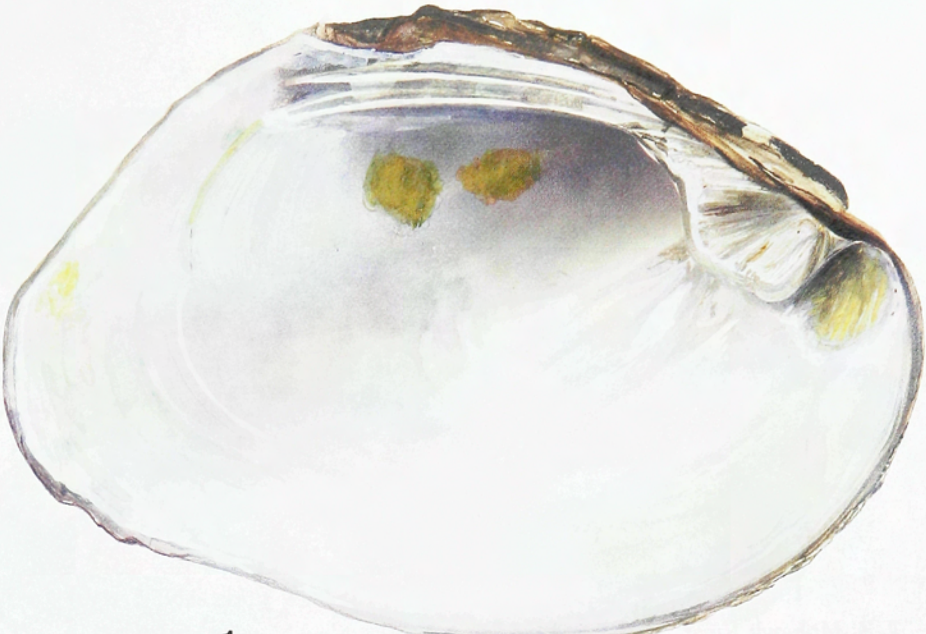

1
2
2a
3
3a
4
4a
5

PLATE 22

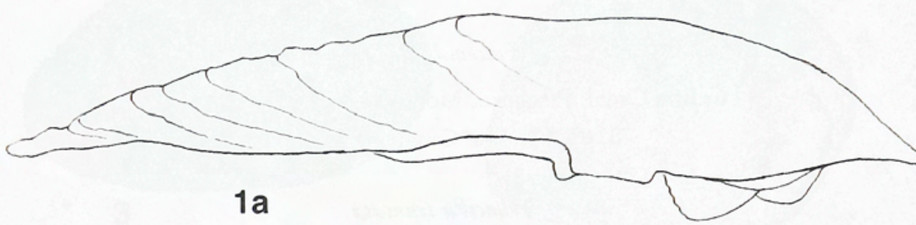
Amblema plicata

Locality unknown.

Drawn by Wilfred Davison.



1



1a

1b

PLATE 23

Elliptio complanata

1. Erie Canal, Mohawk, Herkimer County, New York, ANSP 41368;
2, 3. Mohawk River, Mohawk, Herkimer County, New York, ANSP 129715, 126906;
4. Brown's Tract Pond, Hamilton County, New York, ANSP 97772;
5. Lake Champlain, Crown Point, Essex County, New York, ANSP 129240.

Fusconaia flava

6. Erie Canal, Pittsford, Monroe County, New York;
8, 8a, 8b. Erie Canal, New York.

Truncilla truncata

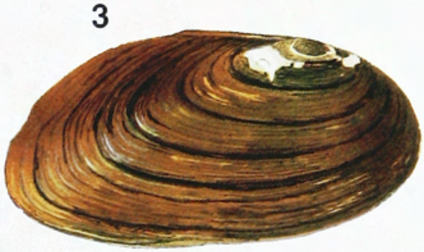
7. Locality unknown.

Figure 7 drawn by George S. Barkentin; all others drawn by Helen Winchester.

1

2

3



4

5

6

7

8

8a

8b

PLATE 24

Elliptio complanata

1. Rochester, Monroe County, New York, ANSP 129713;
2. Schuyler's Lake (=Canadarago Lake), Otsego County, New York, ANSP 129712;
3. Wolcott Creek, north of Wolcott, Wayne County, New York.

Ptychobranchus fasciolaris

4, 4a. Chautauqua Lake, Chautauqua County, New York.

Margaritifera margaritifera

5, 5a. Still Creek, Schuylkill County, Pennsylvania.

All drawn by Helen Winchester.

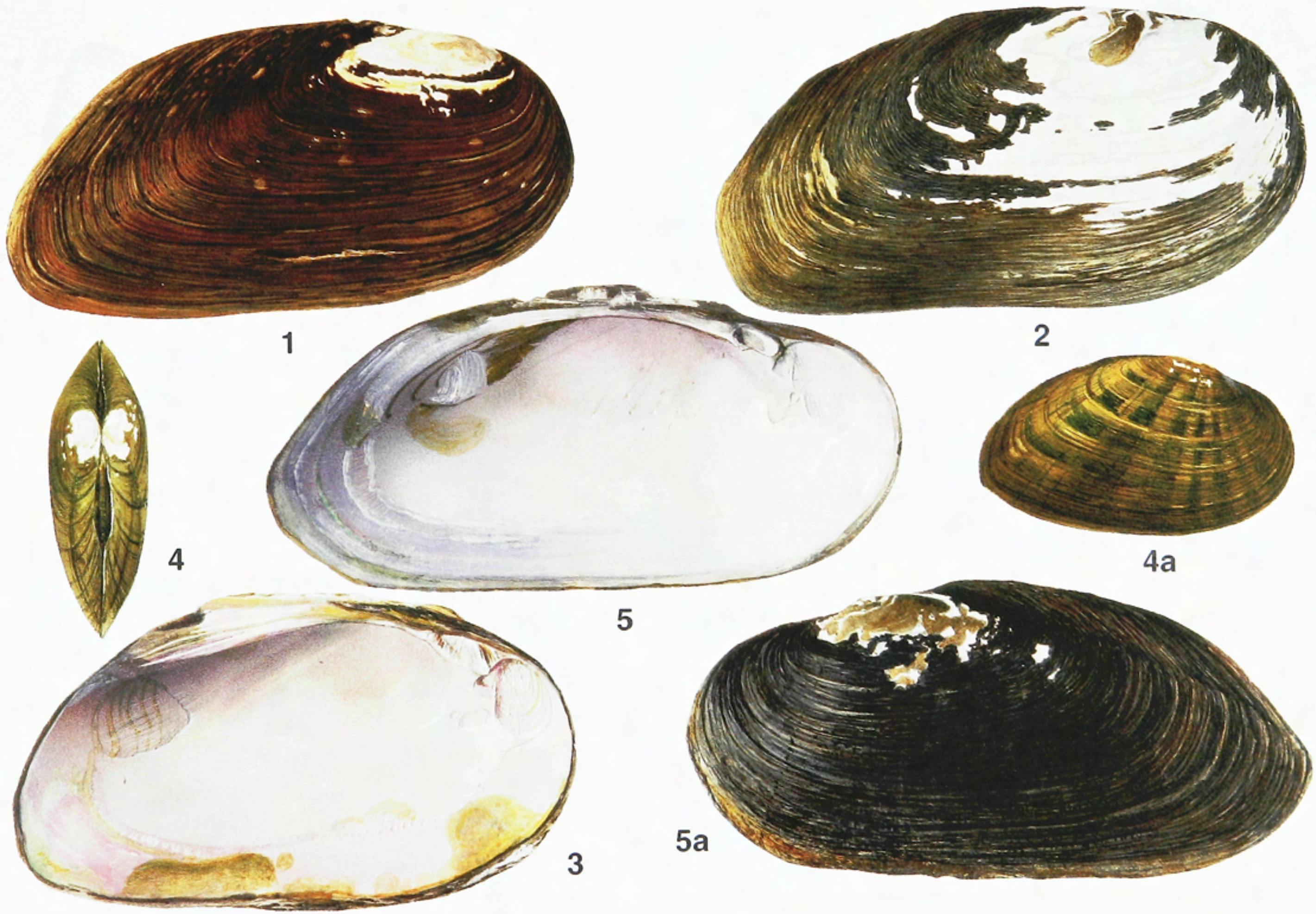

1
2
4
4a
5
3
5a

PLATE 25

Elliptio dilatata

1, 1a. Allegheny River, Kelly, Pennsylvania, ANSP 97888.

Elliptio dilatata (form *sterkii*)

3, 3a. Lake Erie, Presque Isle Bay, Pennsylvania, ANSP 103026;
4, 4a. Niagara River, Buffalo, Erie County, New York;
5. Monroe County, New York.

Fusconaia flava

2, 2a, 2b. (form *undata trigona*). Locality unknown.

Figures 2, 2a, 4, and 4a drawn by Wilfred Davison; all others drawn by Helen Winchester.

1

2

2a

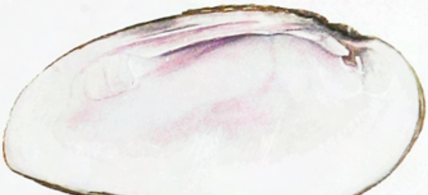
1a

2b

4

3

4a



3a

5

PLATE 26

Cyclonaias tuberculata

1. Butler, Kentucky, NYSM 30672 (73 mm long);
2. Allegheny River, Pennsylvania, near New York border, NYSM 32018 (111 mm long).

Obliquaria reflexa

3. Licking River, Kentucky, NYSM 30654 (41 mm long).

Anodonta implicata

4. Champlain Canal, Watervliet, Albany County, New York, NYSM 31396 (108 mm long).

Pleurobema clava

5. Allegheny River, Pennsylvania, near New York boundary, NYSM 31568 (37 mm long).

Truncilla donaciformis

6. Lake Erie, Catawba Island, Ottawa County, Ohio, UMMZ 54742 (27 mm long).

Actinonaias ligamentina

7. Allegheny River, Olean, Cattaraugus County, New York, NYSM 9062 (91 mm long).


1


2


3


4


5


6


7

PLATE 27

Obovaria subrotunda

1. Coshocton, Coshocton County, Ohio, UMMZ 106270 (40 mm long).

Uniomerus tetralasmus

2. Erie Canal, Rochester, Monroe County, New York, ANSP 140870 (79 mm long).

Epioblasma torulosa rangiana

3. Male, Allegheny River, Pennsylvania, near New York boundary, NYSM 31533 (59 mm long);
4. Very large female, Allegheny River, Pennsylvania, near New York boundary, NYSM 31533 (79 mm long).

Potamilus capax

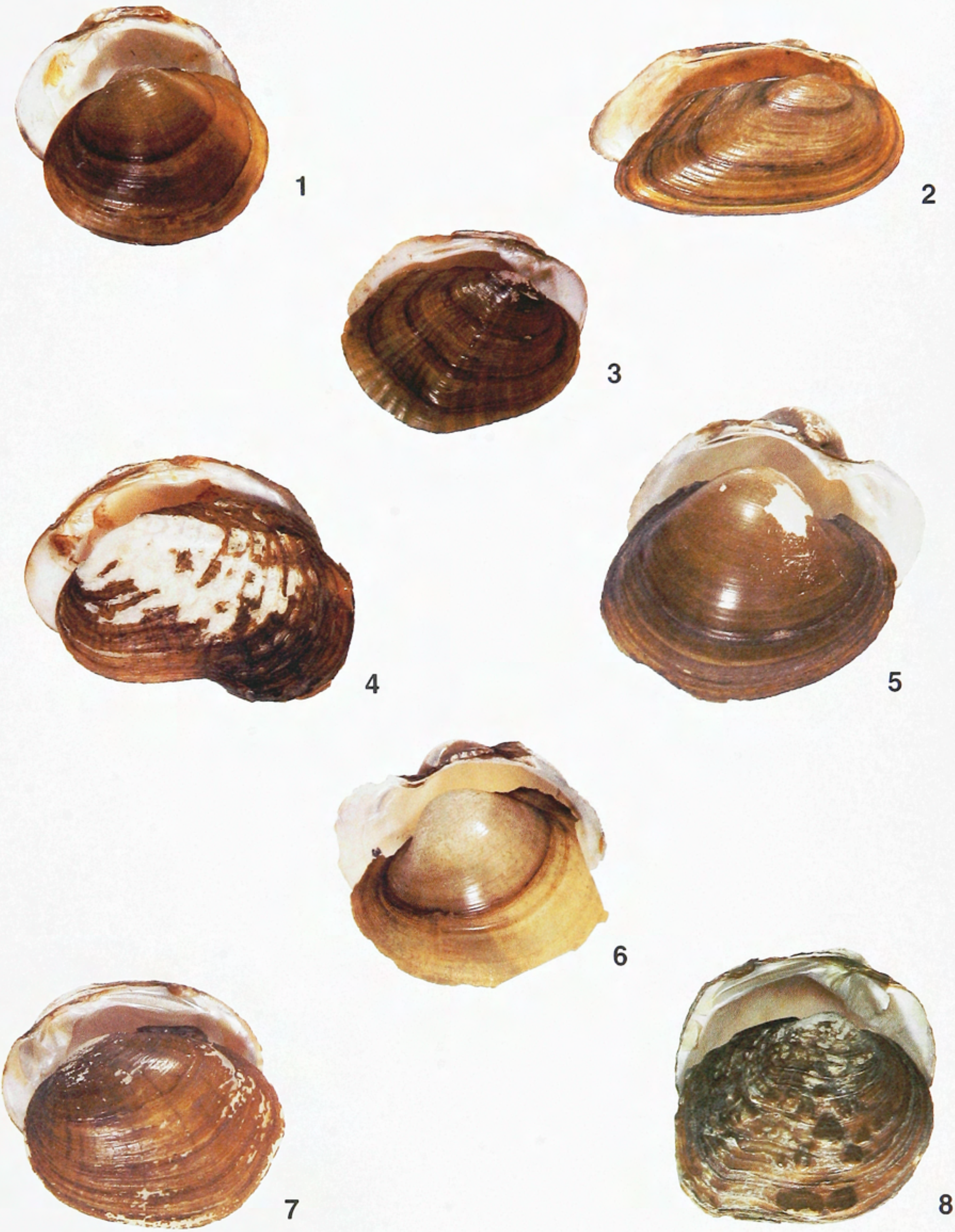
5. Mercer County, Illinois, BSM 365I-6/6 (76 mm long);
6. Niagara River, New York, BSM 365I-6/2 (fragment is 67 mm long).

Lampsilis abrupta

7. Female, Niagara River, New York, BSM 365B-22/2 (64 mm long).

Quadrula quadrula

8. Niagara River, 1 mile above Niagara Falls, Ontario, UMMZ 198119 (67 mm long).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