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ECOLOGY AND ZOOGEOGRAPHY OF THE FRESHWATER MOLLUSKS OF THE HUDSON RIVER BASIN

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ABSTRACT

There has never been a comprehensive treatment of the freshwater mollusk fauna of the Hudson River basin, despite the economic importance of the river, its proximity to major eastern museums and universities, and its significance as a zoogeographic gateway between the Atlantic Slope and Interior Basin regions. To get as complete a picture as possible of the freshwater mollusk fauna of the Hudson River, I examined 2271 museum lots of material collected from the basin, reviewed papers that reported collections from the basin, and surveyed 81 sites on streams in the mid-Hudson valley for mollusks. All of these records are now available on computer databases. The results of this review show the fauna of the basin to include about 96 species of freshwater mollusks: 19 prosobranch snails, about 31 pulmonate snails, 24 unionid clams, and 22 sphaeriid clams. Spot maps and notes on distribution and ecology are given for each species. The fauna is of diverse origin: 20 species are from the Interior Basin, 16 species originated on the Atlantic Slope, 53 species are widespread in North America, and seven species are exotic species introduced into the basin by humans. Although the mollusk fauna has been severely damaged or destroyed at many sites in the Hudson River basin, other areas, including the freshwater tidal Hudson River, still support the same species that they did a century ago.

INTRODUCTION

The drainage basin is, in many ways, the ideal unit for ecological and zoogeographical studies of freshwater organisms. The primary advantage of using a drainage basin instead of a political unit (state, county) as the unit of study is that the boundaries of the study area often correspond to distributional boundaries of species. Such is not the case for political units. Several prominent faunal studies have been based on drainage basins (*e.g.*, van der Schalie, 1938: Clarke, 1973).

This paper is an ecological and zoogeographic study of the freshwater mollusks of one drainage basin: the Hudson River basin of the northeastern United States. The fauna of the Hudson basin is of interest for two reasons. First, the Hudson basin has been used intensively by Europeans for more than 300 years. Some mollusks are of direct or indirect economic value to humans: also, mollusks can serve as indicators of the impacts of human activities on water quality. Second, the Hudson River basin is of special interest to zoogeographers. Because of post-glacial confluences between the Hudson River and Lakes Erie and Champlain, the Hudson basin has served as a gateway for exchange of species between the Atlantic Coastal drainages and the drainages of the Interior Basin (van der Schalie & van der Schalie, 1950: Smith, 1982, 1983).

However, the freshwater mollusks of the Hudson River basin never have been treated comprehensively. A number of publications (*e.g.*, Lewis, 1856, 1860, 1872; Marshall, 1890, 1895b; Townes, 1937; Pate, 1933; Smith, 1982, 1983) describe the mollusk fauna at particular places in the basin, and the mollusks of the Hudson basin have been mentioned peripherally in a number of papers (*e.g.*, DeKay, 1844; Letson, 1905; Clarke & Berg, 1959; Jacobson & Emerson, 1971; Ortmann, 1919; Sepkoski & Rex, 1974), but none of these works gives a detailed picture of the fauna of the entire basin. The purpose of this paper is to provide a critical review of the ecology and distribution of freshwater mollusks in the Hudson River basin, and to use this information to offer a scenario for the postglacial dispersal of freshwater mollusks into the Hudson River basin.

THE STUDY AREA

The Hudson River drains 34, 615 km^2, primarily in eastern New York, but including small parts of Vermont, Massachusetts, New Jersey, and Connecticut (Fig. 1). The basin encompasses several physiographic regions (Fig. 1). The Adirondack Mountains are formed of Precambrian crystalline rocks. As a consequence, most of the surface waters in the Adirondacks are soft and acidic to circumneutral, and pH values below 6.0 are common (Colquhoun *et al.*, 1984). The natural vegetation of the Adirondacks, spruce-fir and northern hardwood forests, reflects the cool climate. The Adirondacks are almost entirely forested today.

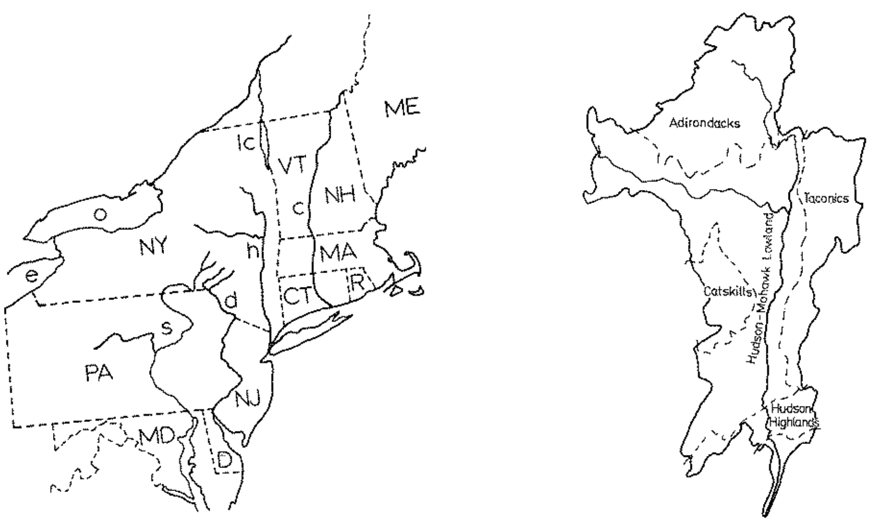

FIG. 1. **Left:** Location of the Hudson River basin in the northeastern United States. Some important bodies of water include: c = Connecticut River, d = Delaware River, e = Lake Erie, h = Hudson River, lc = Lake Champlain, 0 = Lake Ontario, and s = Susquehanna River. **Right:** Physiographic regions of the Hudson River basin, after Thompson (1966).

The Catskill Mountains, along the western edge of the Hudson basin, are made of hard sandstone. Surface waters typically are circumneutral. Most of the Catskill region is covered by northern hardwood forests.

The Taconic highlands form the eastern edge of the Hudson basin. This region contains a variety of bedrock types, including limestone and marble. The original vegetation of the Taconic highlands was northern hardwood forests grading into oak forests, but parts of the region are now used for agriculture.

The Hudson Highlands are a small area of crystalline rocks in the lower part of the Hudson basin. Most of the area is forested, predominantly in oak forests. Surface waters are soft.

The remaining part of the Hudson River basin constitutes the Hudson-Mohawk lowlands. The bedrock of this region is primarily sedimentary in origin, including shale and limestone. Surface waters usually are well buffered, with pH ranging typically from 7.0 to 8.5. Although the Hudson-Mohawk lowlands supported oak and northern hardwood forests prior to European settlement, the area is now a mix of forests, agricultural lands (dairies, orchards, and vegetable farms), and urban and suburban zones. Because of municipal and industrial wastes associated with cities such as New York, Albany-Troy, Utica, and so forth, many of the streams in the Hudson-Mohawk lowlands have been badly polluted at one time or another. This brief account was summarized from Thompson (1966), which contains much more information about the Hudson River basin.

Drainage history of the Hudson River basin

The entire present-day Hudson River basin was covered by glaciers of Wisconsin age, whose southern margin lay just south of New York City. However, because sea level stood about 100 m lower than present during full-glacial times, the full-glacial Hudson River basin would have included an unglaciated portion on the now-submerged continental shelf.

The Wisconsin glaciers began to retreat about 18,000 B.P., and by 14,500 B.P. they had exposed the southern parts of the present day Hudson basin. A terminal moraine in the New York City area dammed the Hudson River, forming a lake (Lake Albany) that extended northward to Albany and beyond as the glaciers retreated. Lake Albany drained about 12,500 B.P., and most of the Hudson basin was ice-free by 12,000 B.P.

To the west of the Hudson basin, the proglacial predecessors to the Laurentian Great Lakes were forming and fluctuating in response to glacial advances and retreats and isostatic rebound and downcutting at key outlets (Hough, 1963). Only one of these stages is critical to the present discussion. About 13,000 B.P., retreating ice uncovered the Mohawk River valley, which provided a lower outlet than others available at that time for the Great Lakes. The Mohawk outlet carried water eastward from Lake Erie for about 1,000 years until a lower outlet at the Niagara River was uncovered. The Mohawk outlet was probably used by some Interior Basin mollusks to enter the Hudson basin from Lake Erie, since Lake Erie presumably received its Interior Basin mollusk fauna through the Wabash River outlet about 14,000 B.P.

The final postglacial confluence of interest occurred between the Hudson and Champlain Valleys about 12,000 B.P. Because the Champlain Valley was newly deglaciated and presumably lacked a mollusk fauna, no mollusk species entered the Hudson basin through this confluence, but several species of mollusks moved from the Hudson basin into the Champlain basin during this time (Smith, 1985a). Further information on the postglacial history of the northeastern United States is available in the works of Hough (1963) and Flint (1971), from which the above account was summarized.

Much more recently, canal-building has connected the Hudson basin to several other surrounding drainage basins (Fig. 2). The Erie Canal, built in 1817-1825, reached from Lake Erie to the Mohawk River, and provided an entryway used by many Interior Basin species to invade central New York and the Hudson basin. Shortly thereafter, the Champlain Canal opened, connecting the upper Hudson with the waters of the Lake Champlain basin. Later canals included the Delaware and Hudson (1829), connecting the Basher Kill of the Delaware basin to the Rondout Creek, the Chenango Canal (1837), which ran from Utica on the Mohawk River to the headwaters of the Chenango River of the Susquehanna drainage, and the Black River Canal (1839-1855), connecting the waters of the upper Mohawk with those of the Black River drainage of the Lake Ontario basin. Further details on these canals were given by Thompson (1966). All of these canals provided potential routes for dispersal across drainage divides.

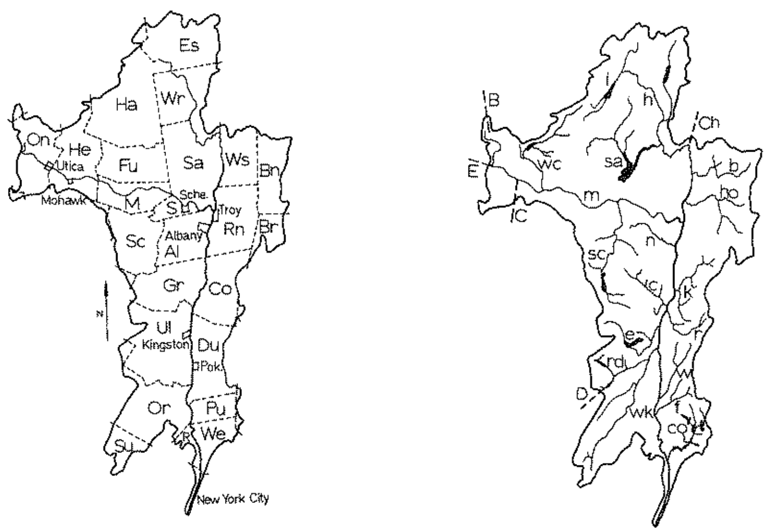

Fig. 2. **Left**: Counties (large letters) and some cities (small letters) of the Hudson River basin. Counties: Al = Albany, Bn = Bennington (Vermont), Br = Berkshire (Massachusetts), Co = Columbia, Du = Dutchess, Es = Essex, Fu = Fulton, Gr = Greene, Ha = Hamilton, He = Herkimer, M = Montgomery, On = Oneida, Or = Orange, Pu = Putnam, R = Rockland, Rn = Renssalaer, S = Schenectady, Sa = Saratoga, Sc = Schoharie, Su = Sussex (New Jersey), Ul - Ulster, We = Westchester, Wr = Warren, Ws = Washington. Cities: Pok = Poughkeepsie, Sche = Schenectady. **Right**: Waterways of the Hudson River basin. Canals (dotted lines): B = Black River Canal, C = Chenango Canal, D = Delaware and Hudson Canal, E = Erie Canal. Major streams of the basin: b = Battenkill, c = Catskill, co = Croton, e = Esopus, f = Fishkill, h = Hudson, ho = Hoosic, i = Indian, k = Kinderhook, m = Mohawk, n = Normanskill, r = Roeliff-Jansen Kill, rd= Rondout, sa = Sacandaga, sc = Schoharie, w = Wappinger, wc = West Canada, wk = Wallkill.

History of malacology in the Hudson basin

The earliest scientific works on the freshwater mollusks of the Hudson River basin were species descriptions by noted naturalists of the early 19th century (*e.g.*, Rafinesque - see Gordon, 1986; Say, 1821; Lea, 1829; DeKay, 1844).

However, the first ecological observations and thorough collections of the fauna were made by James Lewis of Mohawk (Herkimer Co.) in 1853-81. Lewis, a dentist, was a dedicated and talented amateur malacologist (Call, 1881; Clench, 1962). His publications (Lewis, 1856, 1860, 1868a,b, 1872, 1874) gave us the first good idea of the habitats and abundance of freshwater mollusks in our area. Lewis was a thorough collector; probably about half of the museum lots from the Hudson basin are due to Lewis' activities. Unfortunately, although Lewis collected material from throughout the eastern United States, essentially all of his collecting in the Hudson basin was done in the Mohawk River and Erie Canal at Mohawk, so we have a very limited picture of the molluscan fauna of the mid-19th century in the Hudson basin as a whole.

Two contemporaries of Lewis made small but important collections elsewhere in the basin. Truman H. Aldrich, later a mining engineer and congressman from Alabama, surveyed the mollusks of the Troy area in 1867 (Aldrich, 1869). R. Ellsworth Call, known primarily for his work on the mollusks of the Midwest (Johnson, 1975), did some of his first scientific work in the Hudson Valley, collecting both along the Mohawk River (Call, 1878) and at Vassar College, Poughkeepsie, in 1877. Both Aldrich and Call left many of their specimens in museums.

In addition to Aldrich's work, Charles E. Beecher and William B. Marshall of the New York State Museum collected intensively in the Albany-Troy area in the late 19th century (Beecher, 1883; Marshall, 1890, 1892, 1895a,b.). There are many lots of their shells in the New York State Museum and elsewhere. Other important 19th century collections were made by Albert Bailey near Utica (Bailey, 1891) and Edgar A. Mearns, an army surgeon and mammalogist who continued his collections from the Hudson Highlands and Catskills into the early 20th century (Mearns, 1898, 1899, later unpublished collections held in the United States National Museum.).

Next to Lewis, the most productive collector of freshwater mollusks from the Hudson basin was William S. Teator, a fruit grower from Red Hook, in north-western Dutchess Co. (Garlinghouse, 1976). Teator made thorough collections from dozens of sites on lakes and streams around Red Hook around 1887-1892. Although Teator did not publish much (*e.g.*, Teator, 1890), his collections are well represented in all of the major museums in northeastern North America. Teator was unusually careful to document the exact site and date of collection, so his material is especially useful.

The first detailed information on the molluscan fauna of the Hudson River itself came as part of the statewide Biological Survey (Farrell, 1933; Pate, 1933; Townes, 1937). Unfortunately, I could not find any museum specimens resulting from this survey. There have since been several other surveys of the macro-invertebrates of the Hudson River that contain important information on the mollusks (Ristisch *et al.*, 1977; Crandall, 1977; Simpson, 1976; Simpson *et al.*, 1984, 1986).

Other important 20th century collections were made by Morris Jacobson and others from the American Museum of Natural History, chiefly in Westchester and Rockland Co. (Jacobson, 1945), and by M. Pierce, Ruth Turner, and others at Vassar College from Dutchess and Ulster Co. in the 1940's (unpublished collections, mostly in the American Museum of Natural History).

More recently, Willard N. Harman surveyed the mollusks of some lakes in the Adirondacks (Harman, 1981; Buckley & Harman, 1980), and Douglas G. Smith made some important collections in the eastern part of the Hudson basin (Smith, 1982, 1983). Eileen H. Jokinen (pers. comm.) is now undertaking an extensive survey of the freshwater gastropods of New York State, and has already visited dozens of sites in the Hudson basin. The results of her survey should greatly expand our knowledge of gastropod distribution and ecology in our region.

Many others have made collections, some of them important, from the Hudson basin. I was surprised to find how many prominent American malacologists have collected at one time or another in the Hudson basin. Some of the names that I encountered on museum labels include Anthony, Bequaert, Blakeslee, Clapp, Clench, Ferriss, Goodrich, Hubricht, R. I. Johnson, Karlin, Pilsbry, Prime, I. C. Robertson, Sanderson Smith, Solem, Sterki, and van der Schalie.

It is apparent that many people, including some dedicated amateurs, have contributed to the understanding of the mollusks of the Hudson River drainage ever since the early 19th century. Nonetheless, as will be obvious below, knowledge of the ecology and distribution of mollusks in the basin is in many ways incomplete.

MATERIALS AND METHODS

I gathered information from three sources: a review of published literature, an examination of the holdings of major museums, and a field survey of 81 sites in the mid-Hudson Valley in 1985. The raw data (collection records and environmental data) are far too lengthy to include here, but all are available at cost from me either as paper copy or as diskettes containing the data in dBase III files (MS-DOS operating on the DEC Rainbow 100 computer).

I gathered collection records and any other useful information from the following sources: DeKay (1844), Dewey (1856), Lewis (1856, 1860, 1868a,b, 1872, 1874), Aldrich (1869), Call (1878), Gray (1883), Marshall (1890, 1895a,b), Bailey (1891), Mearns (1898, 1899), Walker (1910), Ortmann (1919), Farrell (1933), Pate (1933), Townes (1937), Jacobson (1945), Johnson (1946, 1947,) Freas (1950), Bretet & Carswell (1952), Clench & Turner (1955), Clarke & Berg (1959), Clench (1962), Basch (1963), Clench & Fuller (1965), Jacobson & Emerson (1971), Sepkoski & Rex (1974), Simpson (1976), Ristisch *et al.* (1977), Crandall (1977), Buckley & Harman (1980), Harman (1981), Clarke (1981b, 1985), Smith (1982, 1983), Simpson . (1984, 1986), and Thompson (1984). Many of the collection records from these publications are supported by museum lots. In general, I accepted the identifications reported by the author, unless a mistake was obvious or examination of the museum lot upon which the record was based showed that the species had been misidentified. Because of the high probability of misidentification in the family Sphaeriidae (fingernail and pea clams), I made no effort to gather literature records of this family.

Museum collections were an important source of information about the Hudson basin's freshwater mollusk fauna. I visited the following museums: the University of Michigan Museum of Zoology (UMMZ), Harvard's Museum of Comparative Zoology (MCZ), the United States National Museum (USNM), the American Museum of Natural History (AMNH), the Academy of Natural Sciences at Philadelphia (ANSP), and the New York State Museum (NYSM). Also, through the kindness of Erik Kiviat, I was able to examine the small collection held by Hudsonia, Inc. at Bard College. At each of these museums, I went through the general collection to find material collected from the Hudson basin. With a few exceptions, I examined each of these lots, verified (or corrected) the identifications, and recorded information from the collection label (date and site of collection, collector, and so forth). There is considerable uncatalogued material in some of the museums. I went through such material as well as the general, catalogued collections. In total, I located 2271 lots of freshwater mollusks from the Hudson basin.

Because of time constraints, I was not able to examine holdings of Physidae at the MCZ and the NYSM or Sphaeriidae at the MCZ, AMNH and the NYSM. While it would have been desirable to include these holdings for the sake of completeness, it is likely that most of the locality records represented by these omitted lots are duplicated by holdings from other museums. The amount of lost information is probably therefore small.

I did not feel competent to judge the correctness of identifications for some species. In such cases, I simply accepted the identifications claimed by the museums, and recorded the name of the person responsible for the identification, if known. Thus, I am not responsible for the identifications of museum lots of the Physidae (these are due mostly to George A. Te), the Sphaeriidae, *Gillia altilis* vs. *Birgella subglobosa*, *Fossaria* spp., or *Gyraulus parvus* vs. *G. circumstriatus*.

In 1985, I (and my field assistants) visited 81 sites on running waters in the lower Hudson basin: specifically, the Rondout Creek, Black Creek, Fishkill Creek, and Wappinger Creek basins, along with the Hudson River and its minor tributaries between Tivoli and Beacon in Dutchess and Ulster Co. We searched each site thoroughly for all mollusk species living at the site, and collected representative specimens. These specimens, most of them narcotized with menthol and fixed and stored in alcohol, will be deposited in the New York State Museum in Albany. Those specimens from our collecting shown in the figures of shells and listed as "uncatalogued" will be deposited in the AMNH.

Fig. 3a shows all of the sites from which freshwater mollusks have been recorded, either through museum records, publications, or my survey. At most of these sites collections have been fragmentary, so we know the full mollusk fauna from only a few sites, notably Mohawk, the Albany-Troy region, the tidal Hudson River, and Dutchess, Ulster, and Orange Co. It is apparent that, despite the amount of collecting activity that has gone on in the Hudson basin, the mollusk fauna is unknown or poorly studied in large parts of the basin.

RESULTS AND DISCUSSION

The following section, following Table 1, begins with a species-by-species account of distribution and zoogeography, and concludes with a series of sections devoted to more general matters. Nomenclature follows Burch (1975a,b, 1982). Table 1 lists the freshwater mollusks known from the Hudson River basin.

TABLE 1. List of the freshwater mollusks of the Hudson River basin and their occurrence in museum collections and my 1985 stream survey. The table shows the number of sites from which each species is known and the approximate number of specimens collected from the basin, excluding subfossil shells. Data for the Physidae and Sphaeriidae are not comparable with the rest of the table, because my search of museum specimens of these taxa did not include the MCZ and NYSM collections.

Species	No. Sites	No. Specimens
Prosobranch snails		
Valvata piscinalis	2	3
Valvata sincera	2	7
Valvata tricarinata	23	>1000
Viviparus georgianus	15	ca. 500
Cipangopaludina chinensis	7	19
Campeloma decisum	37	>1000
Lioplax subcarinata	6	ca. 75
Bithynia tentaculata	17	ca. 1000
Probythinella lacustris	3	ca. 700
Gillia altilis	10	ca. 350
Birella subglobosa	6	>1000
Cincinnatia cincinnatiensis	3	ca. 800
Marstonia lustrica	6	ca. 600

TABLE 1 (cont.)

(Species)	(No. Sites)	(No. Specimens)
Amnicola limosa	48	>1000
Amnicola grana	4	ca. 100
Amnicola pupoidea	3	ca. 100
Elimia livescens	9	>1000
Elimia virginica	17	ca. 600
Pleurocera acuta	3	ca. 800
Pulmonate Snails		
Bulimnea megasoma	2?	3?
Fossaria spp.	80	>1000
Lymnaea stagnalis	2	4
Pseudosuccinea columella	19	ca. 200
Radix auricularia	1	1
Stagnicola elodes	39	>1000
Stagnicola catascopium	29	>1000
Physa vernalis	1	1
Physella ancillaria	14	ca. 250
Physella gyrina	32	ca. 450
Physella heterostropha	58	ca. 800
Physella integra	3	31
Physella vinosa	2	ca. 30
Aplexa elongata	12	ca. 200
Gyraulus deflectus	17	ca. 250
Gyraulus circumstriatus	10	ca. 200
Gyraulus parvus	50	ca. 600
Helisoma anceps	51	ca. 1000
Menetus dilatuats	11	35
Planorbella campanulata	11	ca. 100
Planorbella trivolvis	41	ca. 1000
Planorbula armigera	16	ca. 500
Promenetus exacuous	15	ca. 200
Ferrissia ragilis	8	ca. 60
Ferrissia parallelus	3	ca. 60
Ferrissis rivularis	39	ca. 500
Laevapex fuscus	12	ca. 100
Unionid Clams		
Fusconaia flava	1	2
Elliptio complanata	69	577
Alasmidonta calceolus	0	0
Alasmidonta marginata	3	55
Alasmidonta varicosa	2	3
Alasmidonta undulata	21	163
Lasmigona compressa	8	36
Lasmigona subviridus	7	226
Lasmigona costata	7	84
Anodontoides ferrissacianus	12	109
Anodonta cataracta	47	310
Anodonta grandis	5	107
Anodonta imbecilis	2	2
Anodonta implicata	8	81
Strophitus undulatus	14	91
Proptera alata	1	1
Leptodea fragilis	2	2
Ligumia nasuta	10	49
Lampsilis cariosa	11	107
Lampsilis ochracea	10	129

TABLE 1 (cont.)

(Species)	(No. Sites)	(No. Specimens)
Lamsilis radiata group	22	171
Lamsilis ovata	1?	2?
Villosa iris	0	0
Sphaeriid Clams		
Sphaerium corneum	1?	1?
Sphaerium fabale		na
Sphaerium rhomboideum	5	na
Sphaerium simile	14	na
Sphaerium striatinum	27	na
Sphaerium occidentale	5	na
Musculium lacustre	4	na
Musculium partumeium	11	na
Musculium securis	5	na
Musculium transversum	13	na
Pisidium adamsi	3	23
Pisidium amnicum	0	0
Pisidium casertanum	13	na
Pisidium compressum	7	na
Pisidium dubium	4	na
Pisidium equilaterale	4	na
Pisidium fallax		subfossils only
Pisidium ferrugineum	2	na
Pisidium insigne	1	4
Pisidium nitidum	4	na
Pisidium variabile	7	na
Pisidium ventricosum	1	na
Pisidium walkeri	1	na

Prosobranchs

VALVATIDAE

Valvata piscinalis (Müller) (Fig. 7a)

This European species is known from the Laurentian Great Lakes, Cayuga Lake, and the Hudson River (Harman & Berg, 1971; Clarke, 1981a). The only records from the Hudson basin are a few scattered individuals that I collected from the freshwater tidal Hudson River (Fig. 3b); the species does not appear to be abundant. *Valvata piscinalis* was first recorded in North America in 1913 (Clarke, 1981a); its time of arrival in the Hudson River is not known.

Valvata sincera Say (Fig. 7b)

New York State forms part of the southern range limit for this species of lakes and large streams (Baker, 1928; Harman & Berg, 1971; Clarke, 1981a; Jokinen, 1983). There are only a few records of *Valvata sincera* from the Hudson basin, all from rivers (Fig. 3b), but the presence of this species in postglacial lake deposits suggests that it may once have been more widespread in the Hudson basin.

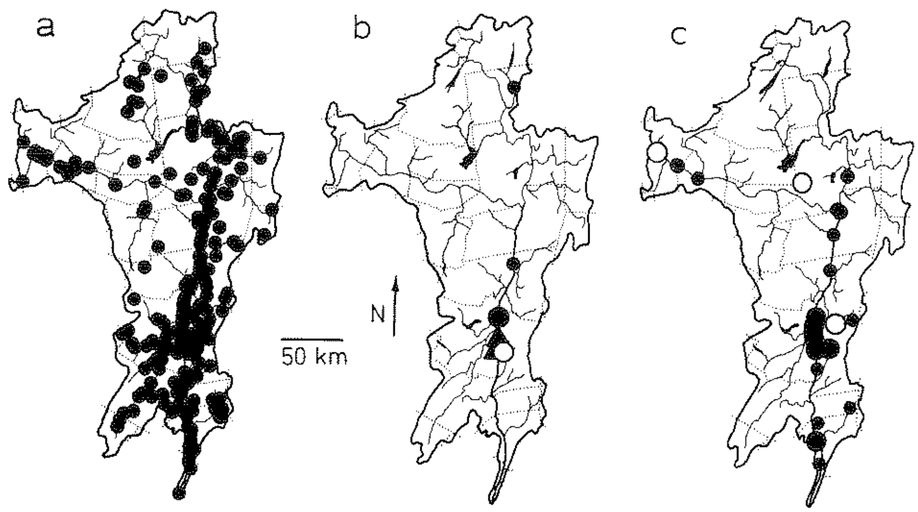

Fig. 3 **a**, Sites in the Hudson basin from which freshwater mollusks have been collected; **b**, distribution of *Valvata sincera* (circles) and *V. piscinalis* (triangles); **c**, distribution of *V. tricarinata* in the Hudson River basin. In this and succeeding figures, large black circles indicate living specimens collected since 1960, large white circles indicate subfossil shells, and small black circles indicate all other distributional records. Records that were not plotted because their exact location could not be determined are noted in the figure legend: there is a record of *V. tricarinata* from the Schroon River.

Valvata tricarinata (Say) (Fig. 7c)

The most common and widespread valvatid in the Hudson basin, *Valvata tricarinata* inhabits quiet water (lakes, permanent ponds, stream backwaters) throughout the basin (Fig. 3c). It was abundant on tidal mud flats (such as Tivoli South Bay) of the Hudson River in 1985.

VIVIPARIDAE

Viviparus georgianus (Lea) (Fig. 5a)

This species is now widespread in lakes, permanent ponds, and rivers in the Hudson basin (Fig. 4a), but it is not native to the basin. This colorful snail is a favorite of aquarists, and so has been introduced widely outside its natural range (the southeastern United States and the Mississippi River basin) (Clench, 1962; Clench & Fuller, 1965). Apparently, it was first introduced into the Hudson basin by James Lewis in 1854 (UMMZ 29145 is a lot of two *Viviparus georgianus*, labeled Erie Canal, Mohawk, NY 1854). This introduction seems not to have been mentioned in Lewis' publications, and apparently was unsuccessful, for Lewis re-introduced the species from Illinois into the Erie Canal at Mohawk in 1867 (Lewis, 1872). This colony was successful, as evidenced by numerous museum lots (*e.g.*, MCZ 166899, MCZ 237897) from Herkimer Co. in the succeeding decade. By 1892, the species had been recorded from Amsterdam (MCZ 166894) and was abun-

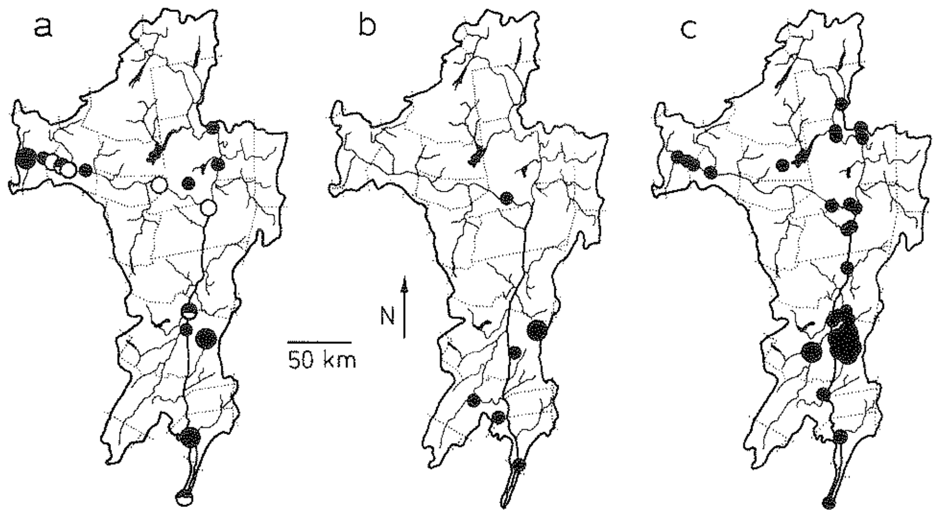

Fig. 4. Distribution of (a) *Viviparus georgianus*, (b) *Cipangopaludina chinensis*, and (c) *Campeloma decisum* in the Hudson River basin. In (a), open circles show records of collections made before 1900, half-filled circles are 1900-1930, small black circles are 1930-1960, and large black circles are 1960-1986. Other symbols as in Fig. 3. The following records are not plotted: *Ci. chinensis*: Hackettstown (Warren Co.) and "upper Hudson and Mohawk drainages" (Buckley & Harman, 1980); *Ca. decisum*: Black Rock Pond (Albany Co.).

dant at Albany (Marshall, 1895b). Teator did not find *V. georgianus* during his intensive work in Dutchess Co. in 1887-1892, but did find the species in the Hudson River, Dutchess Co., in 1926 (AMNH, uncatalogued Teator collection), three years after it was found in the nearby Sawkill at Annandale by Mrs. J.R. Delafield (AMNH 85580). In 1921, the first of many collections of *V. georgianus* from New York City was made (ANSP 129523). It appears that Lewis' colony at Mohawk was the source for populations of *V. georgianus* in the Mohawk and upper Hudson Rivers. The records from New York City may well represent a second introduction of the species.

Cipangopaludina chinensis (Gray) (Fig. 5b)

Cipangopaludina chinensis is an Asian snail that was introduced into North America in the 1890's and now lives throughout North America in quiet waters (Jokinen, 1982). It first appeared in the Hudson basin at Niskayuna, Schenectady Co., in 1920 (ANSP 129315), only six years after it was first recorded in eastern North America (Clench & Fuller, 1965). It is known from scattered sites in the Hudson basin (Fig. 4b).

Campeloma decisum (Say) (Fig. 5c)

This is one of the most abundant snails in the Hudson basin, and lives in lakes and streams throughout the Hudson basin (Fig. 4c).

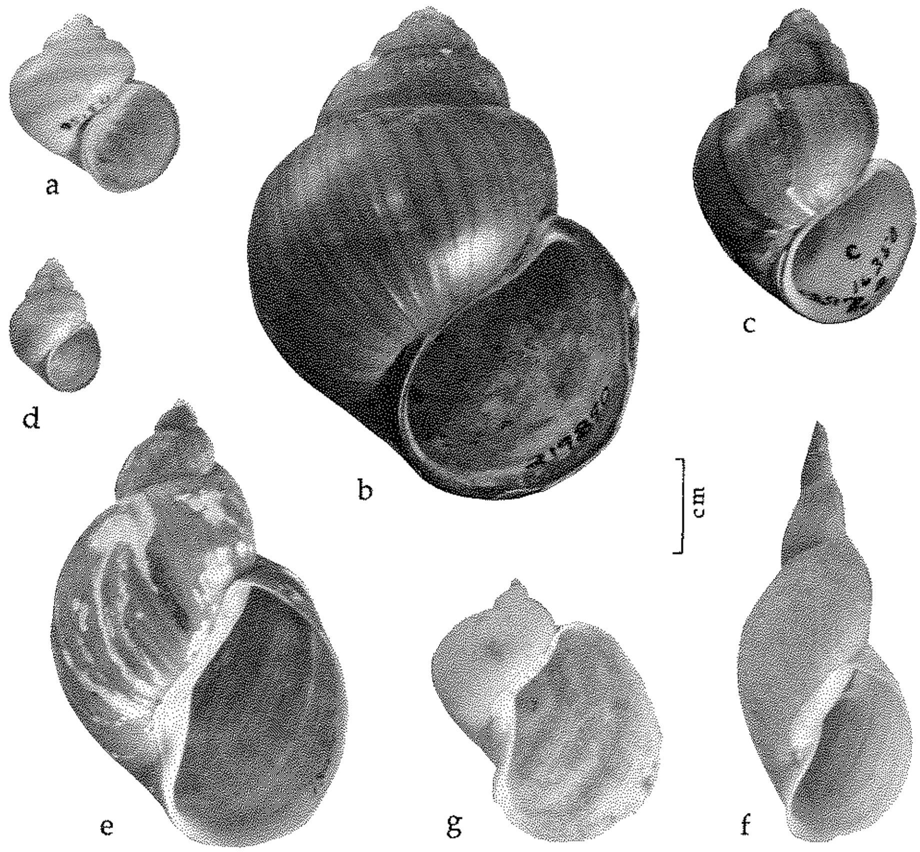

Fig. 5. **a**, *Viviparus georgianus* (AMNH 73156, Erie Canal at Mohawk, N.Y.); **b**, *Cipangopaludina chinensis* (AMNH 219890, Buckingham Lake, Albany Co., N.Y.); **c**, *Campeloma decisum* (AMNH 68512, Mohawk, N.Y.); **d**, *Lioplax subcarinata* (AMNH 68731, Columbia, Pa.); **e**, *Bulimnea megasoma* (AMNH 130175, pond near Albany, N.Y.); **f**, *Lymnaea stagnalis* (AMNH 6784, Plattsburgh, N.Y.); **g**, *Radix auricularia* (AMNH 2618, Davy's Pond, Bloomfield, N.J.). Scale line = 1 cm.

In the 1985 survey, we always found *Campeloma decisum* buried in soft sediments, usually in dense plant beds.

Lioplax subcarinata (Say) (Fig. 5d)

This species lives in the freshwater tidal portion of the Hudson River from Kingston to Albany (Fig. 6a). There are no recent (since 1936) records of this species, although the unidentified viviparid found by Simpson *et al.* (1984) may well be *Lioplax*. The Hudson basin is the northeasternmost extension of the range of *Lioplax*. Clench & Turner's (1955) review of the genus inexplicably omitted records from the Hudson basin, despite the presence of several museum lots and publications (*e.g.*, Marshall, 1895b; Townes, 1937) that document *Lioplax*'s occurrence in the basin. Lewis (in Marshall, 1895b) believed that *Lioplax* invad-

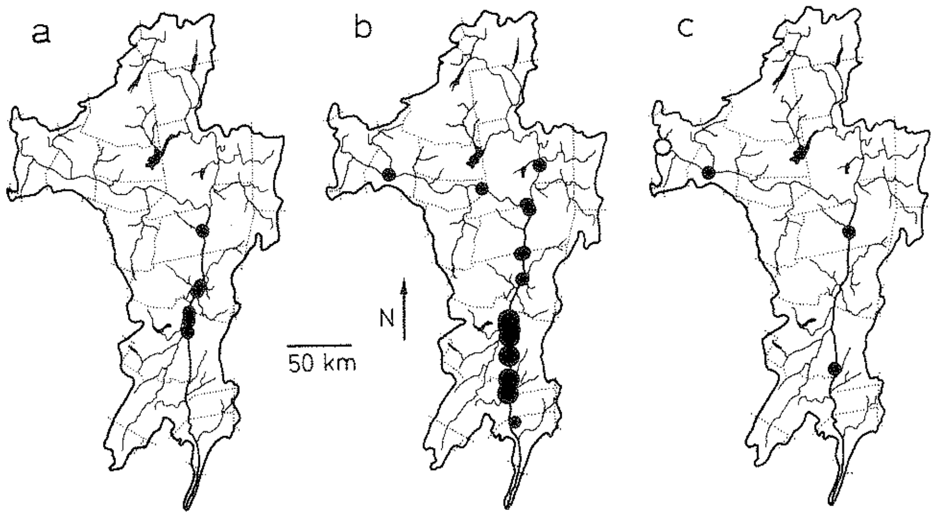

Fig. 6. Distribution of (a) *Lioplax subcarinata*, (b) *Bithynia tentaculata*, and (c) *Probythinella lacustris* in the Hudson River basin. Symbols as in Fig. 3.

ed the Hudson basin from the Delaware River *via* the Delaware and Hudson canal, but I know of no evidence to test this contention.

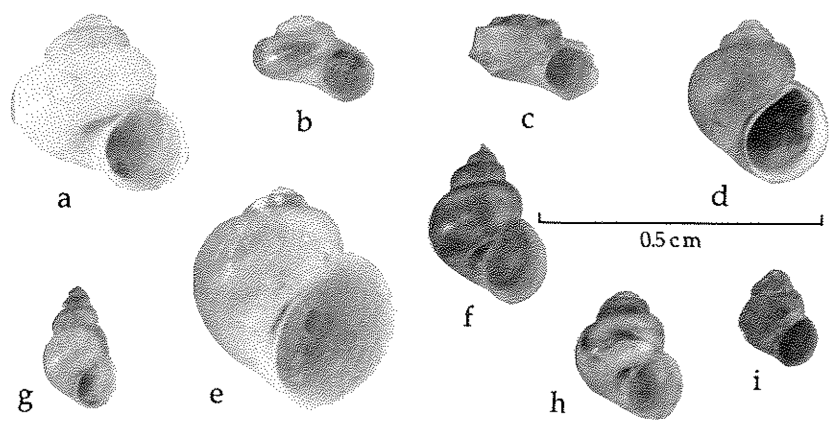

Fig. 7. **a**, *Valvata piscinalis* (AMNH 71202, Scotland); **b**, *V. sincera* (AMNH 60745, New York); **c**, *V. tricarinata* (AMNH 71186, Mohawk River, N.Y.); **d**, *Gillia altilis* (AMNH 65129, Raritan River, N.J.); **e**, *Birgella subglobosa* (AMNH 65119, N.Y., Ill., Wis.); **f**, *Cincinnatia cincinnatiensis* (AMNH 71081 Erie Canal, N.Y.); **g**, *Marstonia lustrica* (AMNH 71078, Erie Canal, N.Y.); **h**, *Amnicola limosa* (AMNH 71088, Mohawk River, N.Y.); **i**, *A. pupoidea* (uncatalogued, Indian Kill at Staatsburg, N.Y.). Scale line = 1 cm.

BITHYNIIDAE

Bithynia tentaculata (Linnaeus) (Fig. 10a)

This European species was introduced into New York State about 1878, appearing almost simultaneously in Lake Ontario at Oswego (Beauchamp, 1886) and the Champlain Canal, West Troy (Marshall, 1895b). James Lewis got specimens of *Bithynia tentaculata* from Oswego to plant in the Mohawk River at Mohawk, where it flourished (Gray, 1883). *Bithynia tentaculata* was apparently scarce in the Hudson River in Dutchess Co. in 1888-1892, since there are only two individuals (MCZ 281946) in museums from W. S. Teator's careful collecting. The species now occurs in the Hudson and Mohawk Rivers, and the extreme lower portions of their tributaries (Fig. 6b). *Bithynia tentaculata* was extraordinarily abundant in 1985 on hard substrata in the intertidal zone of the Hudson River, Dutchess and Ulster Co., to the point of literally covering the undersides of rocks. There is only a handful of records from sites away from the main rivers in the Hudson basin (Jacobson & Emerson, 1971), although the species is known from lakes and streams elsewhere in its range (*e.g.*, Baker, 1928).

Baker (1928) claimed to have found *Bithynia tentaculata* in Pleistocene deposits in Illinois, and argued that North American populations consisted both of native and introduced stocks. Regardless of the validity of Baker's idea, it is clear that *B. tentaculata* was not present in New York prior to its sudden, dramatic appearance in 1878; the species was not listed in any of the early works on our mollusk fauna (DeKay, 1844; Lewis, 1856, 1860, 1872, 1874).

HYDROBIIDAE

Probythinella lacustris (Baker)

This is a species of central Canada and the American Midwest (Baker, 1928; Berry, 1943; Clarke, 1981a), reaching its southeasternmost limit in the Hudson basin. Apparently, it reached the basin prior to the construction of the Erie Canal, shown by a lot (ANSP 134986) of subfossil shells from Oneida Co. Although *Probythinella lacustris* is known from only a few sites in our area, all of them large rivers (Fig. 6c), it may be very abundant. Many of the museum lots from Mohawk (*e.g.*, MCZ 2064) contain dozens to hundreds of specimens. It apparently is a deepwater inhabitant in the Hudson basin, although it occupies other habitats (*e.g.*, small streams) elsewhere in its range (Clarke, 1973; Cvancara, 1983).

Gillia altilis (Lea) (Fig. 7d)

This species lives in large rivers in the Hudson basin (Fig. 8a). According to Thompson (1984), who described the morphology, systematics, and distribution of this species in detail, *Gillia altilis* is a species of Atlantic coastal drainages that reaches its northeastern range limit in the Hudson basin. Although Townes (1937) reported *G. altilis* to be abundant in the shallows of the Hudson River in

Dutchess Co., neither Simpson *et al.* (1984, 1986) nor I found this species in the Hudson in 1983-85.

Birgella subglobosa (Say) (Fig. 7e)

The distribution of *Birgella subglobosa* in the Hudson basin is almost identical to that of *G. altilis*: large rivers (Fig. 8d). *Birgella subglobosa* was first recorded in the Hudson basin at Mohawk in 1860 (Lewis, 1868a, 1872), and presumably invaded from Lake Erie via the Erie Canal. Formerly, the species was abundant in the Hudson (Townes, 1937) and Mohawk Rivers; several museum lots contain hundreds of individuals (*e.g.*, MCZ 282016). The species has not been found in recent surveys (Simpson *et al.*, 1984, 1986; this study).

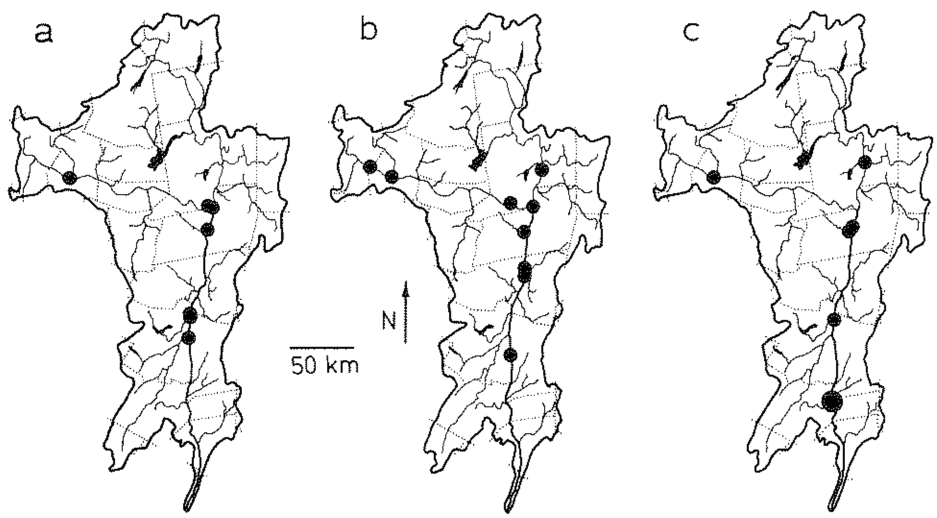

Fig. 8. Distribution of (a) *Gillia altilis*, (b) *Birgella subglobosa*, and (c) *Marstonia lustrica* in the Hudson River basin.. Symbols as in Fig. 3. The following records are not plotted: *G. altilis*: Beck's spring (Dutchess Co.); *M. lustrica*: Williams Bridge (Westchester Co.).

Cincinnatia cincinnatiensis (Anthony) (Fig. 7f)

This is a midwestern species that probably entered the Hudson basin through the Erie Canal. There are records from only three sites in the basin, all from the 19th century: the Erie Canal and Mohawk River at Mohawk (Herkimer Co.) (Lewis, 1872), the "Mohawk basin" (=Mohawk River?) (Saratoga Co.) (Aldrich, 1869), and "drift of the Hudson River" (specific locality not given - UMMZ 160697). Many of the museum lots contain dozens to hundreds of individuals, so the species was at least locally abundant. I know of no recent collections of this species from the Hudson basin.

Marstonia lustrica (Pilsbry) (Fig. 7g)

This Interior Basin species reaches its eastern limit in the Hudson basin, which it presumably entered through the Erie Canal. Although *Marstonia lustrica* is widespread in many habitats in Wisconsin to central New York (Baker, 1928; Berry, 1943; Harman & Berg, 1971), it is almost restricted to large rivers in the Hudson basin (Fig. 8c).

Amnicola limosa (Say) (Fig. 7h)

One of the most abundant snails in the basin, *Amnicola limosa* is widely distributed in permanent waters, both lakes and streams (Fig. 9a). In 1985, we found it living on various aquatic plants as well as on stones and silty bottoms. It was especially abundant in the Shawangunk Kill and Wallkill River in Ulster Co.

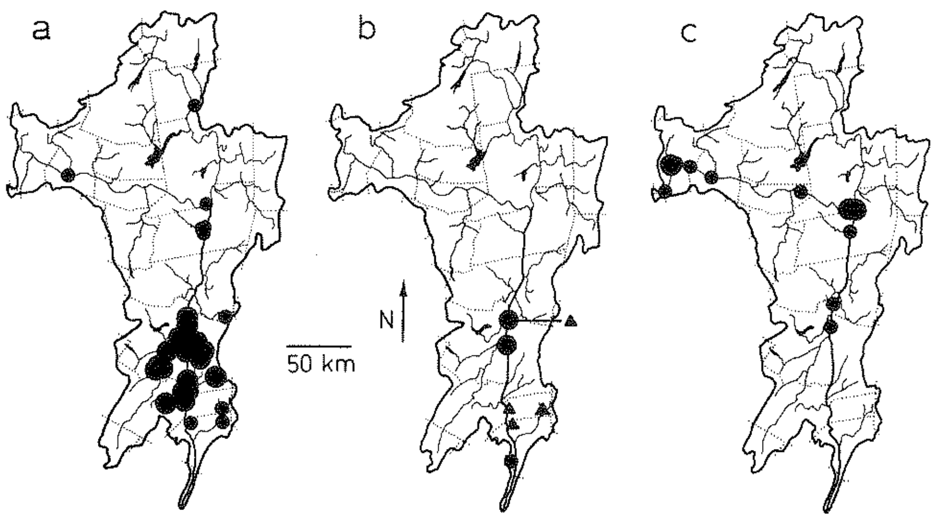

Fig. 9. Distribution of (a) *Amnicola limosa*, (b) *A. pupoidea* (circles) and *A. grana* (triangles), and (c) *Elimia livescens* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *A. limosa*: Williams Bridge (Westchester Co.): *E. livescens*: Stone Creek, 1 mile south of Greenway (Oneida Co.). (This may not be in the Hudson basin.)

Amnicola grana (Say)
Amnicola pupoidea (Gould) (Fig. 7i)

These two tiny hydrobiids have been reported only from a few sites in the southeastern part of the Hudson basin (Fig. 9b). Because of their size, it is possible that they have been overlooked elsewhere, but it is worth noting that both of these species live chiefly on the Atlantic Coastal Plain (Clarke, 1981a; Jokinen, 1983) and do not penetrate very far inland. We found two populations of

Amnicola pupoidea in 1985, both living on rocks and mud just below the high tide mark in northern Dutchess Co.

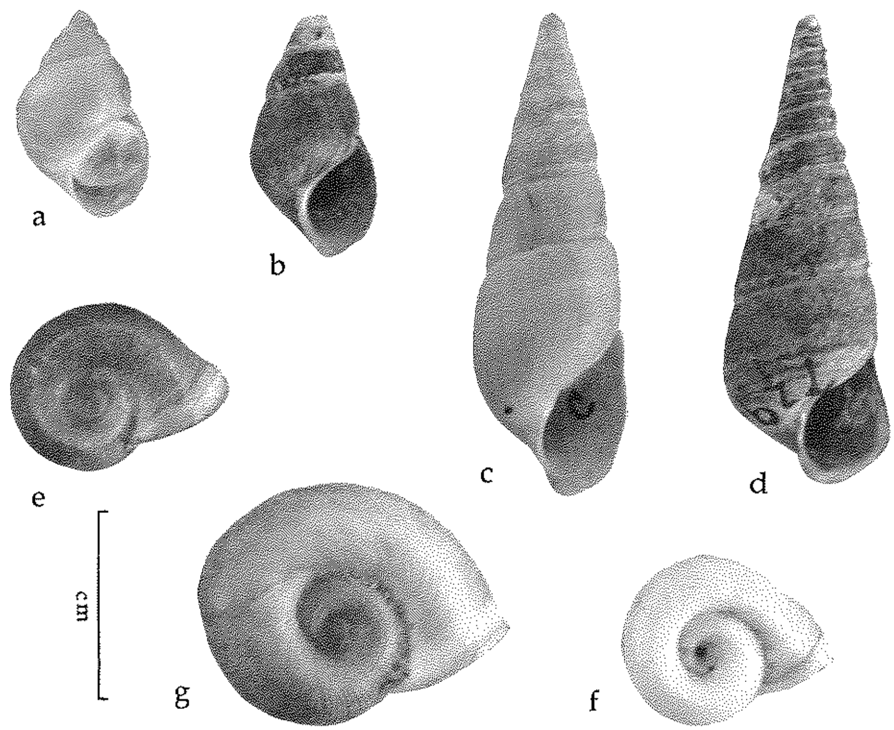

Fig. 10. **a**, *Bithynia tentaculata* (uncatalogued, Hudson River, Dutchess Co., N.Y.); **b**, *Elimia livescens* (AMNH 146046, Mohawk, N.Y.); **c**, *E. virginica* (AMNH 69354, Hudson River, N.Y.); **d**, *Pleurocera acuta* (AMNH 72954, Mohawk River, N.Y.); **e**, *Helisoma anceps* (AMNH 89940, Ossining, Westchester Co., N.Y.); **f**, *Planorbella campanulata* (AMNH 122824, Rockland Lake State Park, Rockland Co., N.Y.); **g**, *P. trivolvis* (AMNH 89934, Sawmill River, Yonkers, N.Y.). Scale line = 1 cm.

PLEUROCERIDAE

Elimia (=Goniobasis) livescens (Menke) (Fig. 10b)

E. livescens is another species of the Interior Basin whose presence in the Hudson basin is usually attributed to the Erie Canal (*e.g.*, Lewis, 1872; Goodrich, 1942; Smith, 1983). Except for Lewis' records for Mohawk, the presence of *Elimia livescens* in the Hudson basin has not been widely recognized by prior authors such as Dazo (1965) (*cf.* Smith, 1983). In the Hudson basin, it is known chiefly from the large rivers (Fig. 9c), where it may be very abundant (Lewis, 1872; Townes, 1937). Records from Oriskany Creek, Oneida Co., are the only indication from Fig. 9c that this species can occupy other habitats; in fact, it is a frequent inhabitant of permanent streams of all sizes as well as springs and lakes in the Midwest (Dazo, 1965).

Elimia (= Goniobasis) virginica (Gmelin) (Fig. 10c)

Elimia virginica lives in the largest rivers of the Atlantic drainages (Goodrich, 1942; Smith, 1980), occasionally moving up into the somewhat smaller upland rivers (Harman & Berg, 1971). In the Hudson basin, it is restricted almost entirely to the Mohawk and Hudson Rivers proper (Fig. 11a). Poland Creek, Albany Co. (a locality that I could not find and which is not plotted in Fig. 11a) is the only site in the Hudson basin that may be in the uplands. Some of the specimens from Poland Creek (a large uncatalogued lot in the MCZ) have an unusual shape, which is more reminiscent of *Leptoxis* than *Elimia*. *Elimia virginiana* was common in the intertidal zone of the Hudson River, Dutchess and Ulster Co., in 1985, where it lived beneath stones and on sandy mud flats.

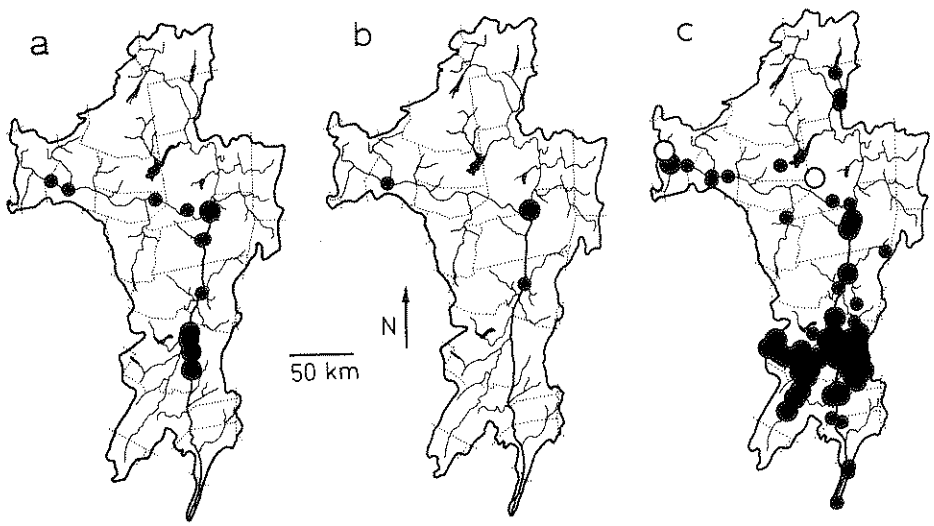

Fig. 11. Distribution of (a) *Elimia virginica*, (b) *Pleurocera acuta*, and (c) *Fossaria* spp. in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *E. virginica*: Poland Creek (Albany Co.); *Fossaria* spp.: Steele's Creek (Herkimer Co.).

Pleurocera acuta Rafinesque (Fig. 10d)

The occurrence of this Interior Basin snail at Mohawk is well known (Lewis, 1872; Goodrich, 1942; Dazo, 1965). It also has been recorded from the vicinity of Troy (Aldrich, 1869, documented by ANSP 27361; Smith, 1983) and the Hudson River at Hudson, Columbia Co. (Townes,1937, from dead shells only). All of these sites are large river habitats (Fig. 11b), although the species lives in lakes and smaller streams elsewhere (Dazo, 1965). It seems likely that *Pleurocera acuta* entered the Hudson basin via the Erie Canal (Goodrich, 1942; Harman & Berg, 1971; Smith, 1983).

Pulmonates

LYMNAEIDAE

Bulimnea megasoma (Say) (Fig. 5e)

Lake Champlain usually is given as the only New York locality for *Bulimnea megasoma*, a snail common to the north and west of New York State (Clarke, 1981a). There are, however, two records from the Hudson River basin. MCZ 104733 is a shell of *B. megasoma* collected by J.G. Anthony and labeled, "Hudson R.". Unfortunately, Anthony was notoriously sloppy about locality labels (Goodrich, 1931), so this record must be regarded as questionable. In 1868, R.P. Whitfield (1882) released specimens of *B. megasoma* derived from a colony near Burlington, Vermont, into ponds and streams near Albany. One of these releases resulted in the successful establishment of a population of *B. megasoma*, as evidenced by a museum lot (AMNH 130175) taken in 1871. The fate of this population is unknown. *B. megasoma* may yet turn up in quiet waters of the upper Hudson basin.

Fossaria spp. (Fig. 12a-e)

The taxonomy of this genus is poorly understood. Most authors recognize several species of *Fossaria* in northeastern North America, based on subtle differences in shell shape (*e.g.*, Baker, 1928; Clarke, 1981a; Burch, 1982; Jokinen, 1983). Prior to the discovery of chromosomal evidence that *Fossaria* contains at least two species (Burch, 1960; Inaba, 1969), some authors lumped all northeastern *Fossaria* into a single species, *F. humilis* (Say) (*e.g.*, Hubendick, 1951; Harman & Berg, 1971; Jacobson & Emerson, 1971). I have not tried to treat *Fossaria* at the species level for two reasons. First, on purely practical grounds, I cannot confidently assign all of the material collected from the Hudson basin to species of *Fossaria* using the criteria given by Baker (1928), Clarke (1981a), Burch (1982), and Jokinen (1983). Second, I am not convinced that the species-level taxonomy of *Fossaria* s.s. used by these authors has been adequately supported by detailed work on genetic and ecophenotypic variation in these snails.

The following "species" of *Fossaria* are known from the Hudson River basin (listed in order of their frequency in museum collections): *Fossaria obrussa* (Say), *F. humilis* (Say), *F. modicella* (Say), *F. parva* (Lea), *F. rustica* (Lea), and *F. galbana* (Say) (known only from subfossil shells) (Fig. 11c). Taxa belonging to *Fossaria* are very widespread and abundant in the Hudson basin: I found them at 67% of the stations that supported mollusks in my 1985 survey. Invariably, I found *Fossaria* (all of which keyed to *F. obrussa* group in Burch, 1982) living just above the water line, especially on gently sloping muddy banks.

Lymnaea stagnalis (Linnaeus) (Fig. 5f)

Although this conspicuous species is known both from Lake Champlain (DeKay, 1844; Letson, 1905) and central New York (Harman & Berg, 1971), it is very rare in the Hudson basin, and appears to have entered the basin only recent-

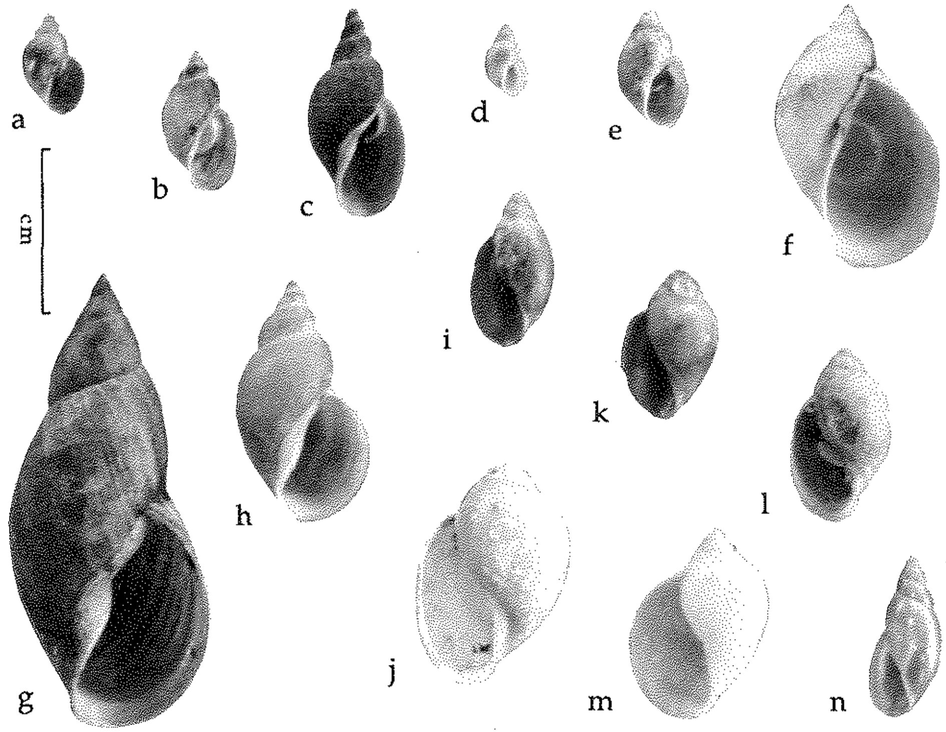

Fig. 12. **a**, *Fossaria humilis* (AMNH 89931, Beechwood Lake, Westchester Co., N.Y.); **b**, *F. modicella* (AMNH 70843, Yetman, N.J.); **c**, *F. obrussa* (AMNH 85653, Old Bilop Farm, Staten Island, N.Y.); **d**, *F. parva* (AMNH 70842, Rahway, N.J.); **e**, *F. rustica* (AMNH 115662, Van Cortlandt Park, Bronx Co., N.Y.); **f**, *Pseudosuccinea columella* (AMNH 70389, Mohawk, N.Y.); **g**, *Stagnicola elodes* (AMNH 70390, Mohawk, N.Y.); **h**, *S. catascopium* (AMNH 70340, Mohawk, N.Y.); **i**, *Physa vernalis* (uncatalogued, pond near Millbrook, Dutchess Co., N.Y.); **j**, *Physella ancillaria* (AMNH 44667, Cold Spring, N.Y.); **k**, *P. gyrina* (uncatalogued, unnamed brook near Millbrook, Dutchess Co., N.Y.); **l**, *P. heterostropha* (uncatalogued, Black Creek, Esopus, Ulster Co., N.Y.); **m**, *P. vinosa* (AMNH 69775, Mackinaw Is., Mich.); **n**, *Aplexa elongata* (AMNH 69995, New York). Scale line = 1 cm.

ly. Lewis (1871) found a single dead specimen from the Erie Canal, Herkimer Co., in 1871, and UMMZ 154088 contains two shells taken from the Erie Canal at Canajoharie (Montgomery Co.) in 1940. ANSP 58408 is two *Lymnaea stagnalis* attributed to Aldrich from Troy, although Aldrich (1869) did not mention finding this species. *Lymnaea stagnalis* is usually found in quiet weedy waters (Baker, 1928; Clarke, 1981a), although it occasionally occurs in other habitats (Harman & Berg, 1971). It may well spread into such habitats in the Hudson basin in the coming decades.

Pseudosuccinea columella (Say) (Fig. 12f)

Pseudosuccinea columella has been reported from quiet water throughout the Hudson basin (Fig. 13a). I found it only occasionally in my 1985 survey of the streams of the mid-Hudson region, usually in marshy places. I assume that *P. columella* would be shown to be abundant and widespread in the Hudson basin if suitable habitats - marshes and weedy lakes and ponds (Baker, 1928; Jokinen, 1983) - were examined.

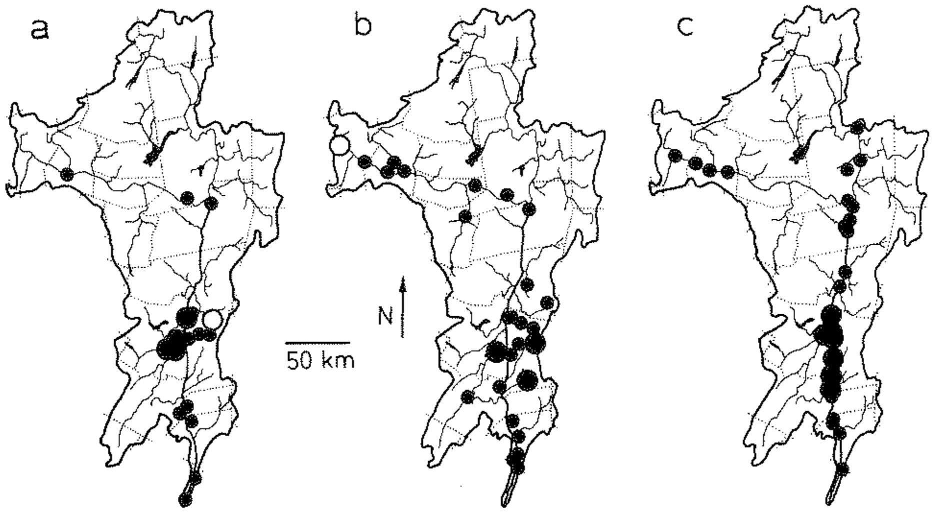

Fig. 13. Distribution of (a) *Pseudosuccinea columella*, (b) *Stagnicola elodes*, and (c) *S. catascopium* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *P. columella*: Riverdale (Westchester Co.); *S. elodes*: Greendale (Columbia Co.), Gardnertown (Orange Co.), Riverdale (Westchester Co.), Greene Co., Croton River.

Radix auricularia (Linnaeus) (Fig. 5g)

This European species has been introduced into scattered sites across North America (Harman & Berg, 1971; Jacobson & Emerson, 1971; Clarke, 1981a; Burch, 1982). It is known from the Hudson basin from only a few shells taken at two sites. Aldrich (1869) reported a few specimens of *Radix auricularia* near Troy, and UMMZ 73544 is a single, battered shell taken from Robinson Pond, Columbia Co. by E.C. Brown.

Stagnicola elodes (Say) (Fig. 12g)

Stagnicola elodes is a widespread species of quiet waters, including temporary ponds (Baker, 1928; Harman & Berg, 1971; Clarke, 1981a; Jokinen, 1983). It is common in such habitats in the Hudson basin (Fig.13b). The few records along the Mohawk and Hudson Rivers are from canals and marshes; it does not live in the main channel of these rivers. I found it only rarely in streams in 1985, and only in marshy backwaters.

Stagnicola catascopium (Say) (Fig. 12h)

This species also is widespread in the Hudson basin (Fig. 13c), but its distribution is almost perfectly complementary to that of its relative, *Stagnicola* *elodes*. *S. catascopium* is abundant in the main channels of the Hudson and Mohawk Rivers, and rarely extends upland more than a kilometer or two from these rivers. I found it to be abundant on hard substrata in the intertidal zone of the Hudson River, Dutchess and Ulster Co., and in swift water in the lower stretches of Fishkill and Rondout Creeks. Although *S. catascopium* lives in lakes (Baker, 1928; Harman & Berg, 1971; Clarke, 1981a), it has been reported from only one lake (Saratoga Lake) in the Hudson basin.

Following Clarke (1973, 1981a), I have included the morph *emarginata* (Say) under *Stagnicola catascopium*. Specimens of *S. catascopium* from many sites on the Hudson River, especially in brackish water, are stunted and are < 10 mm high. Such specimens may be incorrectly identified as *Fossaria*, if some widely available keys are used (eg., Harman & Berg, 1971). It seems likely that at least some of Simpson's (1976) records of *Fossaria humilis* from the Hudson River actually refer to these dwarfed *S. catascopium*.

PHYSIDAE

Taxonomical difficulties have also plagued studies of the Physidae. Differences in shell morphology among species often are subtle. As a consequence, published identifications of physids must be accepted with caution. Recently, George Te revised the taxonomy of the Physidae based on shell morphology and internal anatomy; my treatment of physid species follows his work (Te, 1975, 1978, 1980).

Physa vernalis Taylor & Jokinen (Fig. 12i)

This species was described only recently (Taylor & Jokinen, 1984), so there are not yet many definite records of its occurrence in the Hudson basin. Taylor & Jokinen (1984) reported it from West Albany (NYSM 31464), and I found a single specimen from a flowing, weedy swamp near Millbrook in Dutchess Co. *Physa vernalis* will presumably show up throughout our area in its preferred habitats - small ponds and ditches.

Physella ancillaria (Say) (Fig. 12j)

This is a species of rivers and lakes in northeastern North America (Te, 1978; Burch, 1982; Jokinen, 1983). In the Hudson basin, it occurs in the tidal Hudson River and a few upland sites (Fig. 14a). *Physella ancillaria* was the commonest physid along the margins of the Hudson River in 1985.

Physella gyrina (Say) (Fig. 12k)

Physella gyrina is one of the most common and widespread members of its genus, living in a wide variety of habitats (Te, 1975; Clarke, 1981a; Jokinen, 1983). In the Hudson basin, it lives in upland lakes and streams and, much less frequently, in the Hudson River (Fig. 14b). Museum lots from the Hudson basin are listed under several names, including *P. gyrina gyrina* (Say), *P. gyrina sayi*

(Tappan), *P. gyrina alba* (Crandall), *P. gyrina cylindrica* (Newcomb), and the morphs *elliptica* (Lea) and *hildrethiana* (Lea).

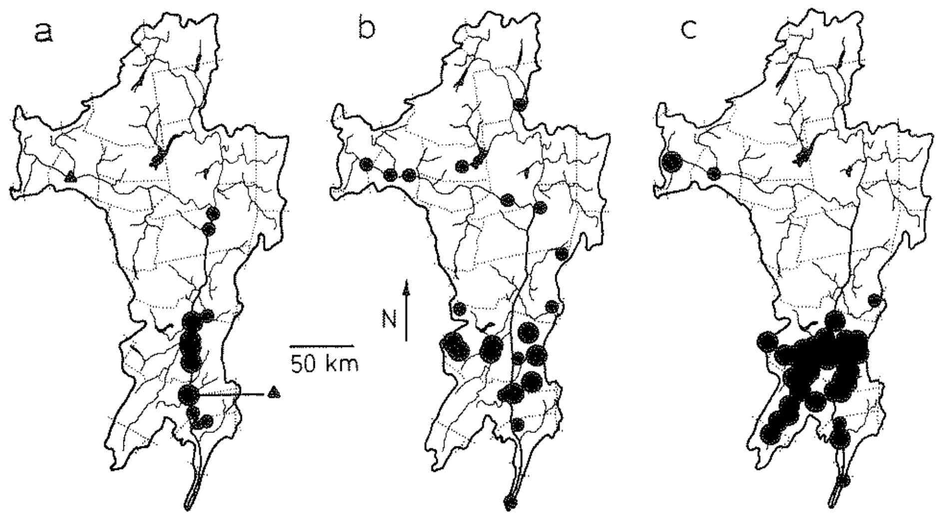

Fig. 14. Distribution of (a) *Physella ancillaria* (circles) and *P. integra* (triangles), (b) *P. gyrina* , and (c) *P. heterostropha* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *P. gyrina*: Orangeburg (Rockland Co.), Nevis (Columbia Co.); *P. heterostropha*: Riverdale, New York City.

Physella heterostropha (Say)(Fig. 12l)

This was the most abundant physid in my 1985 survey of streams, and is also found in ponds through the Hudson basin (Fig. 14c). *Physella heterostropha* is a eurytopic species of northeastern North America (Te, 1978; Clarke, 1981a; Burch, 1982; Jokinen, 1983).

Physella integra (Haldeman)

Physella integra is a midwestern species that is ecologically tolerant, but especially frequent in rivers and lakes (Te, 1975; Clarke, 1981a; Burch, 1982). The Hudson basin is apparently the eastern edge of its range, because *P. integra* was not found in Connecticut by Jokinen (1983). Within the Hudson basin, *P. integra* seems to be uncommon, judging by the number and size of museum lots, and is found chiefly in rivers (Fig. 14a; Townes, 1937). I did not find this species in 1985.

Physella vinosa (Gould) (Fig. 12m)

Physella vinosa lives chiefly in large lakes in the Great Lakes region (Te, 1975; Burch, 1982). It is known from our area by two museum lots from Mohawk, Herkimer Co. (UMMZ 43096 and 119165), possibly the easternmost records for the species.

Aplexa elongata (Say) (Fig. 12n)

There are records of this species from sites scattered throughout the Hudson basin (Fig. 15a). It probably lives throughout the basin in appropriate habitats: temporary ponds and ditches (Harman & Berg, 1971; Clarke, 1981a).

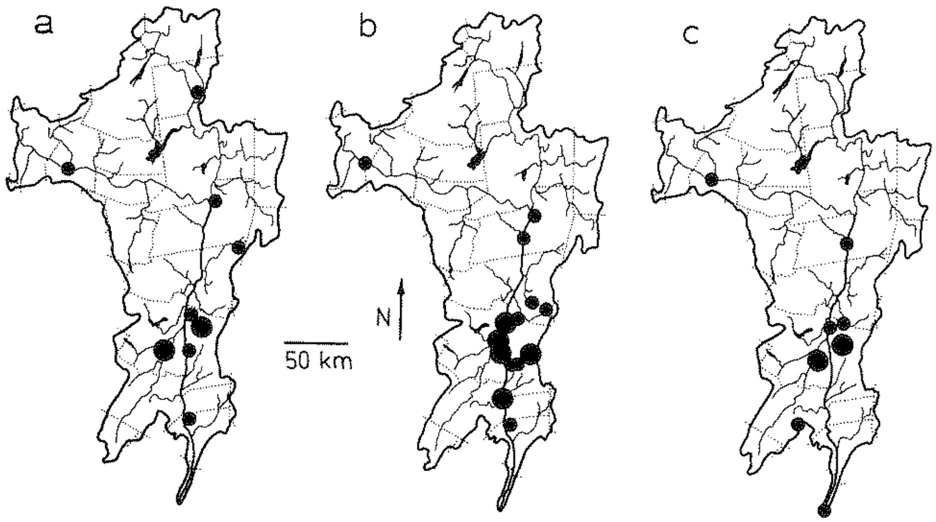

Fig. 15. Distribution of (a) *Aplexa elongata*, (b) *Gyraulus deflectus*, and (c) *G. circumstriatus* in the Hudson River basin. Symbols as in Fig. 3. The following record is not plotted: *G. deflectus*: Schroon River.

PLANORBIDAE

Gyraulus deflectus (Say) (Fig. 18a)

This species lives in lakes in the Hudson basin, as well as the tidal Hudson River and the backwaters of streams (Fig. 15b). It is widely distributed in our area, and large museum lots show that it may be abundant, but it is not especially frequent. *Gyraulus deflectus* usually lives in lakes, ponds, and quiet backwaters of streams (*e.g.*, Baker, 1928; Harman & Berg, 1971; Clarke, 1981a; Jokinen, 1983).

Gyraulus circumstriatus (Tryon) (Fig. 18b)

Gyraulus circumstriatus is an inhabitant of quiet, weedy waters, and is especially frequent in temporary pools (Clarke, 1981a; Jokinen, 1983). It closely resembles *G. parvus*, so I am not certain that Fig. 15c accurately shows the distribution of *G. circumstriatus* in the Hudson basin. Most of the records from our area are from ditches, small creeks, and ponds, although there are specimens from the Erie Canal and Mohawk River at Mohawk (Herkimer Co.).

Gyraulus parvus (Say) (Fig. 18c)

This small snail is abundant nearly everywhere in the Hudson basin, from the tidal Hudson River to lakes and small streams (Fig. 16a). In 1985, I found it living chiefly on rocks and aquatic plants in streams. *G. parvus* is one of the most eurytopic and widespread freshwater snails in North America (Baker, 1928; Harman & Berg, 1971; Clarke, 1981a; Jokinen, 1983).

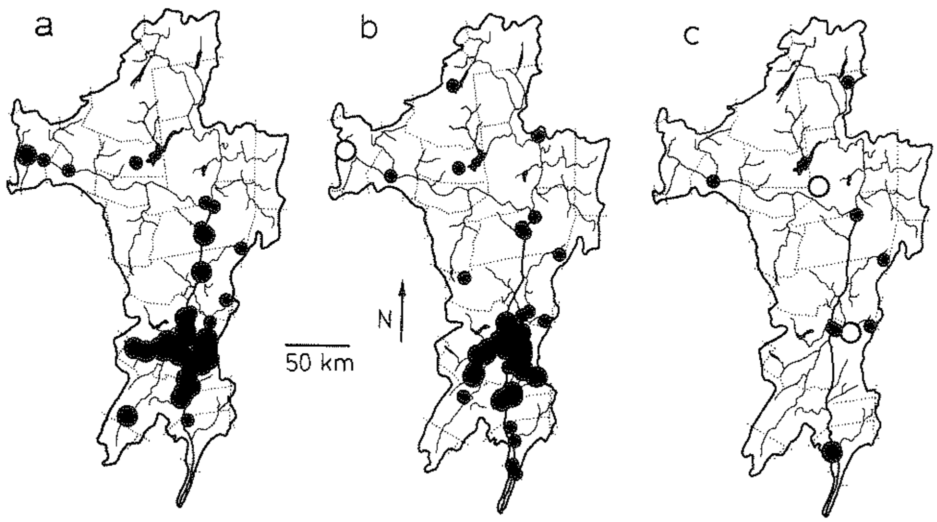

Fig. 16. Distribution of (a) *Gyraulus parvus*, (b) *Helisoma anceps*, and (c) *Planorbella campanulata* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *G. parvus*: Schroon River; *H. anceps*: Schroon River (Warren Co.); *P. campanulata*: marl bed (Greene Co.).

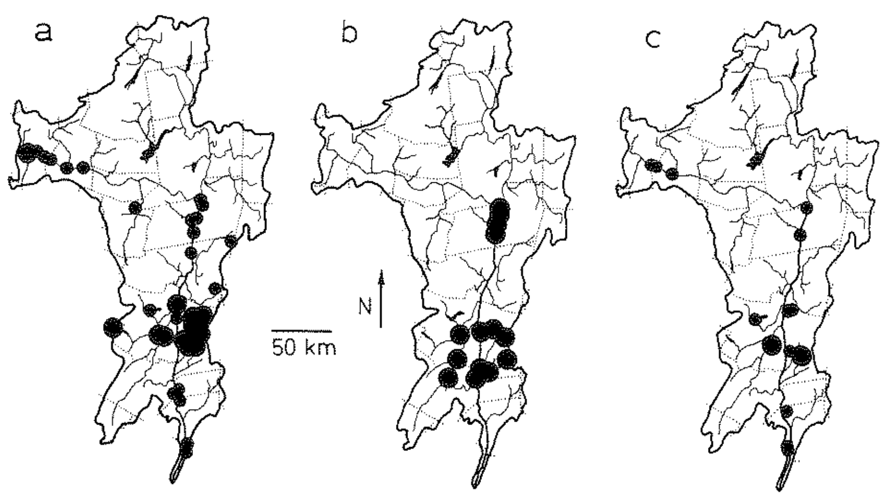

Fig. 17. Distribution of (a) *Planorbella trivolvis*, (b) *Menetus dilatatus*, and (c) *Planorbula armigera* in the Hudson River basin. Symbols as in Fig. 3. The following record is not plotted: *Planorbula armigera*: Riverdale (Westchester Co.).

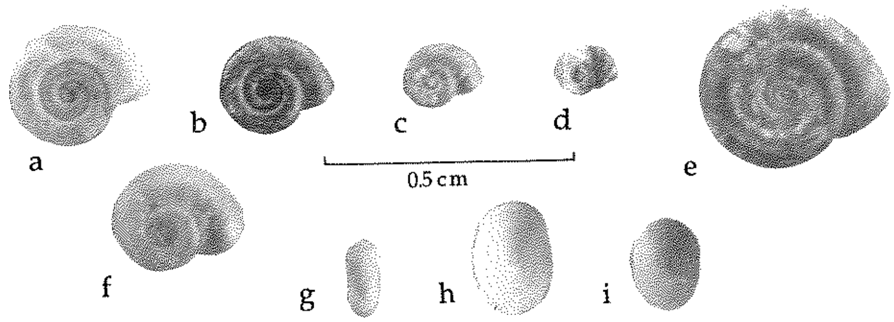

Fig. 18. **a**, *Gyraulus deflectus* (AMNH 62795, Staten Island, N.Y.); **b**, *G. circumstriatus* (AMNH 63021, Staten Island, N.Y.); **c**, *G. parvus* (uncatalogued, Black Creek, Esopus, Ulster Co., N.Y.); **d**, *Menetus dilatatus* (uncatalogued, Dutchess Co., N.Y.); **e**, *Planorbula armigera* (AMNH 63033, Mohawk, N.Y.); **f**, *Promenetus exacuous* (AMNH 62747, New York); **g**, *Ferrissia fragilis* (AMNH 71148, Greenport, Long Island, N.Y.); **h**, *F. rivularis* (AMNH 1819, Ashokan, N.Y.); **i**, *Laevapex fuscus* (AMNH 146653, Lake Mohegan, Westchester Co., N.Y.). Scale line = 1 cm.

Helisoma anceps (Menke) (Fig. 10e)

Helisoma anceps has been found at sites scattered throughout the Hudson basin (Fig. 16b). Unlike many planorbids, *H. anceps* lives in upland streams as well as lakes, a tendency noticed by earlier authors (*e.g.*, Baker, 1928; Buckley, 1977). I found it most frequently on silt or sand in quiet areas along the margins of streams.

Menetus dilatatus (Gould) (Fig. 18d)

I found this tiny snail regularly in upland streams and the Hudson River in Dutchess, Orange, and Ulster Co., especially living on aquatic plants. Prior to this, the only records of *Menetus dilatatus* from the Hudson basin were those of Simpson (1976) from the Hudson River near Albany (Fig. 17b). This species was almost certainly overlooked by earlier collectors in the Hudson basin, so Fig. 13 probably does not show its true distribution in our area.

Planorbella campanulata (Say) (Fig. 10f)

This distinctive species is known from a few sites from lakes and rivers in the Hudson basin (Fig. 16c). Although it is not frequently encountered, large museum lots show that it may be locally abundant in our area. The occurrence of *Planorbella campanulata* in postglacial marl beds in the Hudson basin suggests that the species may have been more widespread in our region in earlier times. *Planorbella campanulata* is a widespread species of quiet waters, but is somewhat uncommon in the northeastern states (Harman & Berg, 1971; Jokinen, 1983).

Planorbella trivolvis (Say) (Fig. 10g)

This is a very common species in the Hudson basin, occupying quiet waters in lakes, some upland streams, and rivers (Fig. 17a). There are no records from the Adirondacks in the Hudson basin, but this lack may reflect the paucity of collections from the area rather than the absence of this species. I found it on silt, sand, and stones in the quiet marginal areas of streams. *Planorbella trivolvis* is a widespread, eurytopic species (e.g., Baker, 1928; Harman & Berg, 1971; Jokinen, 1983).

Planorbula armigera (Say) (Fig. 18e)

Planorbula armigera is a species of marshes, ponds, and temporary waters (Baker, 1928; Harman & Berg, 1971; Jokinen, 1983). The scattered records from the Hudson basin are from such habitats (Fig. 17c). Museum lots of *P. armigera* from the Hudson basin frequently are large, as this species may be very abundant in suitable habitats.

Promenetus exacuous (Say) (Fig. 18f)

This widely distributed species frequents quiet waters (Baker, 1928; Harman & Berg, 1971; Jokinen, 1983). In our area , it is known from marshes, ponds, and the freshwater tidal Hudson River (Fig. 19a).

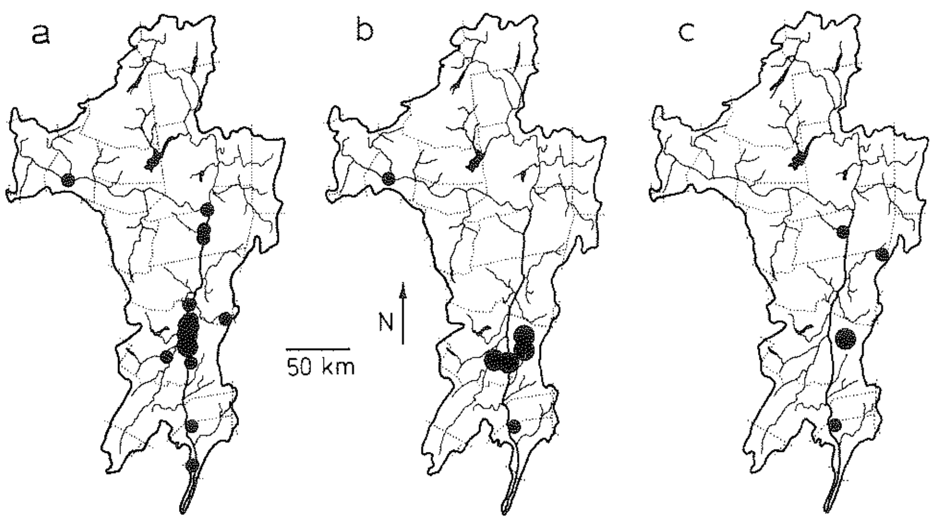

Fig. 19. Distribution of (a) *Promenetus exacuous*, (b) *Ferrissia fragilis*, and (c) *F. parallelus* in the Hudson River basin. Symbols as in Fig. 3.

ANCYLIDAE

Ancylids, or freshwater limpets, seem to have been largely overlooked by early collectors in the Hudson basin. Most of the records of ancylids from the Hudson basin are from my 1985 survey, so we have a poor idea of the basin-wide distribution of ancylids.

Ferrissia fragilis (Tryon) (Fig. 18g)

This tiny, inconspicuous limpet lives on aquatic vegetation in quiet waters (Basch, 1963; Clarke, 1981a; Jokinen, 1983), which is where collections were made in the Hudson basin (Fig. 19b).

Ferrissia parallelus (Haldeman)

Ferrissia parallelus is another species of quiet waters (Basch, 1963; Harman & Berg, 1971; Clarke, 1981a; Jokinen, 1983). Although it is known from only a few such places in the Hudson basin (Fig. 19c), it probably is widespread in our area, since it is well known from nearby regions (Harman & Berg, 1971; Buckley, 1977; Jokinen, 1983).

Ferrissia rivularis (Say) (Fig. 18h)

In contrast to the previous two species, *F. rivularis* is almost entirely restricted to flowing waters (Basch, 1963; Harman & Berg, 1971; Jokinen, 1983). It was very abundant and widespread in upland streams in my 1985 survey, and also lives in the mainstem Hudson River (Fig. 20a).

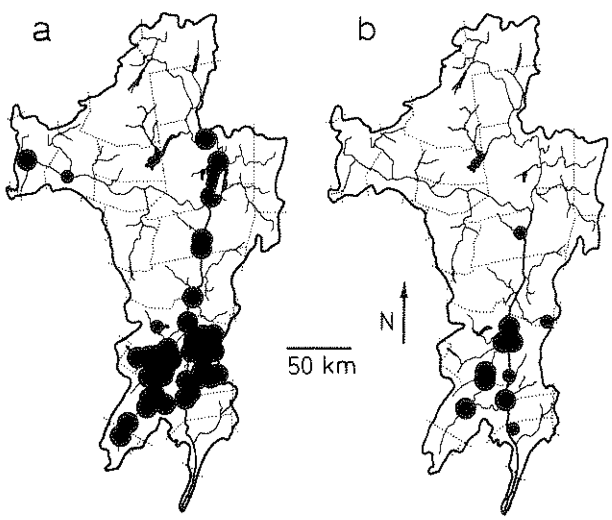

Fig. 20. Distribution of (a) *Ferrissia rivularis* and (b) *Laevapex fuscus* in the Hudson River basin. Symbols as in Fig. 3. The following record is not plotted: *L. fuscus*: Senachivine Lake (Putnam Co.).

Laevapex fuscus (Adams) (Fig. 18i)

Laevapex fuscus lives chiefly in the quiet waters of impoundments, lakes, and streams (Basch, 1963; Clarke, 1981a; Jokinen, 1983). I found it at several river sites, including the Hudson River, in my 1985 survey; it was abundant at two sites in the Rondout-Wallkill system. The few records from elsewhere in the basin are from lakes and rivers (Fig. 20b).

Bivalves

UNIONIDAE

Fusconaia flava (Rafinesque) (Fig. 22a)

There are a few records of this Interior Basin species from the upper Mohawk drainage: the Erie Canal at Mohawk (Call,1878; UMMZ 93043), the Erie Canal between Ilion and Utica (Bailey, 1891), and Utica (Marshall, 1895a). These collections all were made between 1877 and 1895; the present status of *F. flava* in the Hudson basin is not known. *Fusconaia flava* is a widespread species of creeks and rivers of the Midwest (Ortmann, 1919; van der Schalie, 1938) and almost certainly entered the Hudson basin through the Erie Canal.

Elliptio complanata (Lightfoot) (Fig. 22b)

This species lives in streams and lakes throughout the Hudson basin (Fig. 21a). It was the most abundant and widespread unionid in our 1985 survey. The species is the most eurytopic and abundant of the northeastern unionids (Ortmann, 1919; Clarke & Berg, 1959).

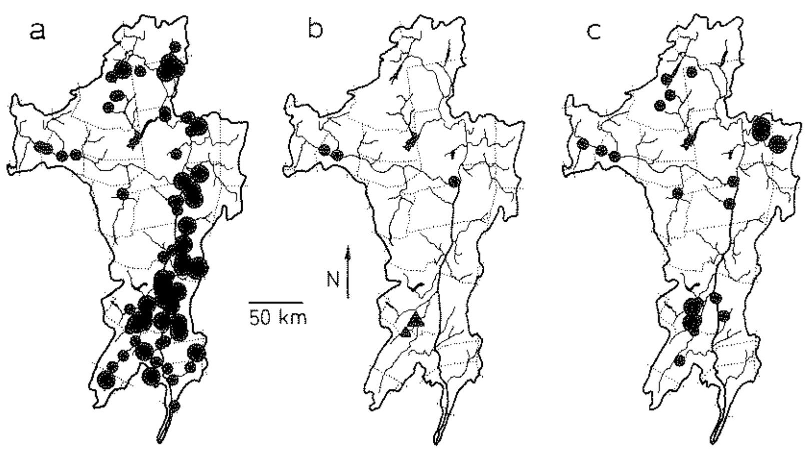

Fig. 21. Distribution of (a) *Elliptio complanata*, (b) *Alasmidonta marginata* (circles) and *Alasmidonta varicosa* (triangles), and (c) *Alasmidontaundulata* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *E. complanata*: Long Lake (Herkimer Co.), Chilson Lake (Essex Co.), Long Pond (Orange Co.).

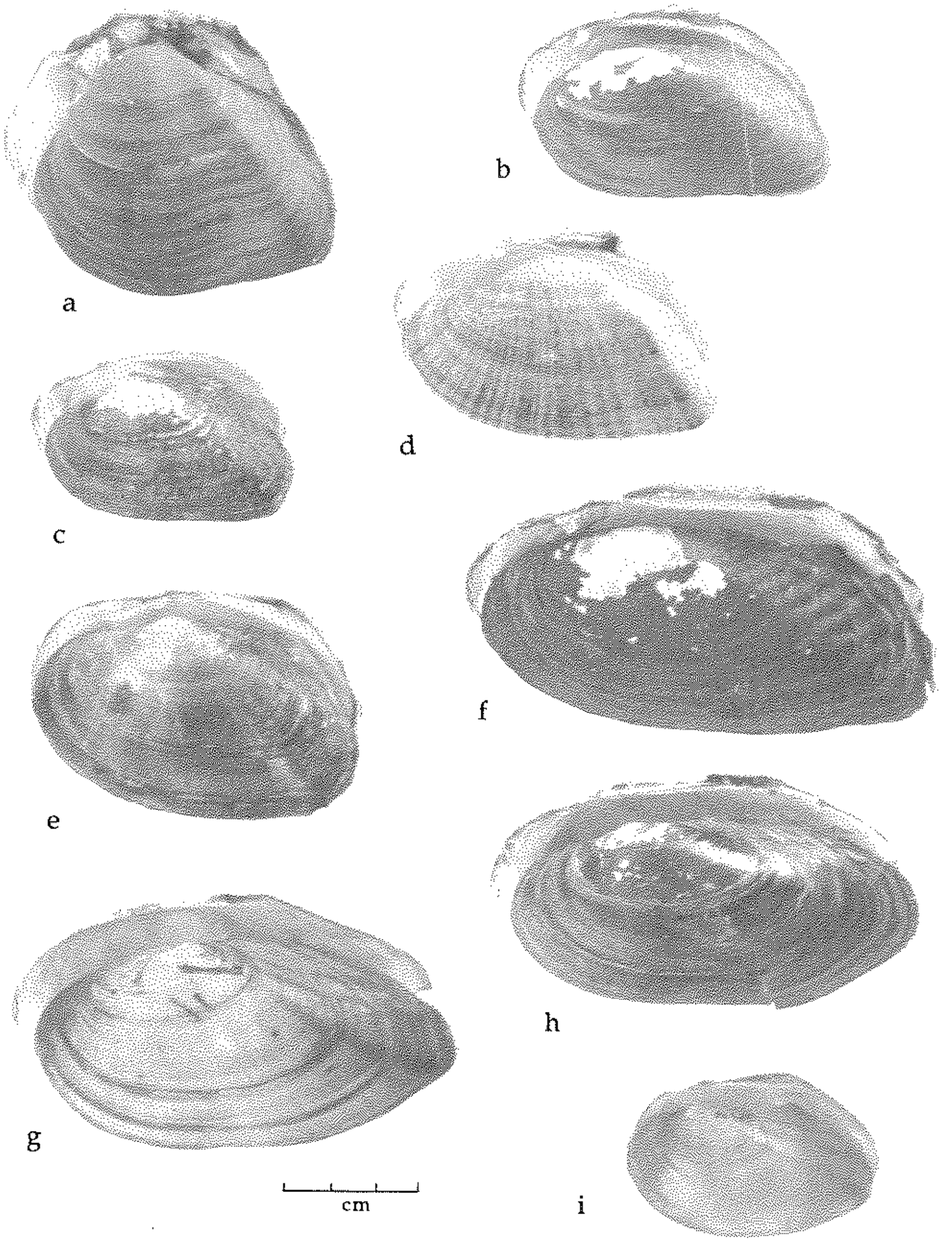

Fig. 22. **a**, *Fusconaia flava* (AMNH 35462, Erie Canal, Rochester, N.Y.); **b**, *Elliptio complanata* (uncatalogued, Hudson River, Ulster Co., N.Y.); **c**, *Alasmidonta varicosa* (uncatalogued, Shawangunk Kill, Ulster Co., N.Y.); **d**, *Al. marginata* (AMNH 30424, New York); **e**, *Lasmigona compressa* (AMNH 149071, Thomas Creek, Monroe Co., N.Y.); **f**, *L. costata* (uncatalogued, Rondout Creek near Rosendale, Ulster Co. N.Y.); **g**, *Anodonta cataracta* (AMNH 30323, Hudson River, N.Y.); **h**, *An. implicata* (uncatalogued, Hudson River, Ulster Co., N.Y.); **i**, *An. grandis* (AMNH 30345, Mohawk R. N.Y.). Scale line = 1 cm.

Alasmidonta calceolus (Lea) (Fig. 24a)

There is a single record of this species from the Hudson basin: Oriskany Creek, Oriskany Falls, Oneida Co. (Clarke & Berg, 1959). I have not found any museum specimens to support this record, and it is possible that the record is based on a misidentified *Alasmidonta undulata*, since the two species are occasionally confounded. However, I am inclined to accept the record, since it was made by a reliable collector (H. D. Athearn), and because *A. calceolus* is known from scattered sites elsewhere in New York State (Clarke & Berg, 1959; Clarke, 1981b). Nonetheless, it would be desirable to verify this record with further collections.

Clarke's (1981b) distribution map for this species is incorrect for New York State. The record for Beaver Creek, Herkimer Co. (in the Susquehanna drainage, not the Lake Ontario drainage as stated by Clarke) is based on a misidentified lot of *Alasmidonta undulata* (MCZ 254784). Furthermore, Clarke showed two records of *A. calceolus* from the Black River drainage which are not supported by any records in Clarke's text. Buckley (1977) did not find the species in his survey of the mollusk fauna of the Black River basin.

Alasmidonta marginata (Say) (Fig. 22d)

The existence of this Interior Basin species in the Hudson basin has been regarded as questionable. Although recorded by early authors (*e.g.*, Aldrich, 1869; Marshall, 1895a), later workers (*e.g.* Smith, 1982) have been reluctant to accept these records, in part because of the potential confusion between *A. marginata* and *Alasmidonta varicosa*. However, nine museum lots (*e.g.*, MCZ 146953) establish *A. marginata* as an authentic, if rare, member of the 19th century fauna of the Mohawk River (Fig. 21b). It has not been collected since 1891, so its continued presence in our area is uncertain. It apparently invaded the Hudson basin *via* the Erie Canal.

Alasmidonta varicosa (Lamarck) (Fig. 22c)

Alasmidonta varicosa is a common unionid in streams of the Atlantic coastal drainages (*e.g.*, Ortmann, 1919; Clarke & Berg, 1959; Clarke, 1981b; Smith, 1982) and has been quoted as belonging to the Hudson's fauna (*e.g.*, Sepkoski & Rex, 1974). I was therefore surprised to find that there were no museum lots or original literature records of this species from the Hudson basin. USNM 150514 contains two shells of this species, marked "Conidoguinit Pond, Prof. Burns, Westchester Co., NY." I was unable to find such a pond in Westchester Co., but Ortmann (1919) collected *A. varicosa* from Conedoguinet Creek, Pennsylvania. I suspect that the USNM lot is from Pennsylvania and acquired an erroneous label somewhere along the way. However, during 1985-86, I found several fresh shells of this species at two sites in the Shawangunk Kill, a gravel-bottomed large creek in Ulster Co. (Fig. 21b). I have no explanation of why this species should be so rare in the Hudson basin, while it is widespread in streams in surrounding areas.

Alasmidonta undulata (Say) (Fig. 24b)

This is the only common *Alasmidonta* in the Hudson basin, and is found in streams and lakes throughout the basin (Fig. 21c). As in Pennsylvania (Ortmann, 1919), *A. undulata* avoids the largest rivers in the Hudson basin.

Lasmigona compressa (Lea) (Fig. 22e)

This species is known from a few scattered streams in the Hudson basin (Fig. 23a). It seems to prefer small streams, in agreement with observations elsewhere (*e.g.*, van der Schalie, 1938; Strayer, 1983). Although *Lasmigona compressa* is an Interior Basin species, it probably did not enter the Hudson basin through the Erie Canal, but rather through postglacial confluences with the Laurentian Great Lakes. It was recorded from the Normanskill in Albany (Lea's type locality) in 1829, only four years after the opening of the Erie Canal. Furthermore, it inhabits scattered sites above the fall line in the Hudson basin (Call, 1878; Smith, 1982), a distributional pattern unlikely to have been established since 1825.

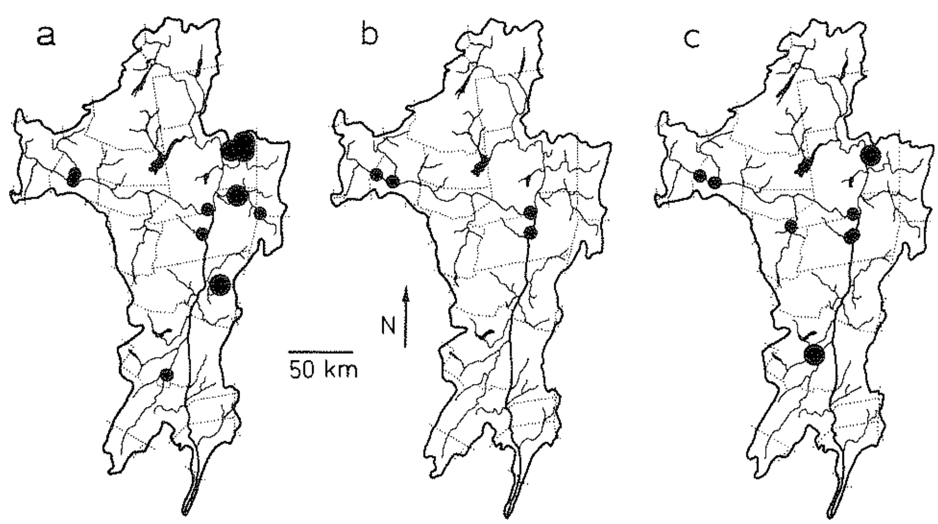

Fig. 23. Distribution of (a) *Lasmigona compressa*, (b) *L. subviridus*, and (c) *L. costata* in the Hudson River basin. Symbols as in Fig. 3.

Lasmigona subviridus (Conrad) (Fig. 24c)

Although *Lasmigonasubviridus* is usually thought of as a species of small- to medium-sized streams (Ortmann, 1919; Clarke & Berg, 1959), it is known only from rivers and canals in the Hudson basin (Fig. 23b). It was abundant at these sites, at least in the 19th century, when the species was last collected in our area. For instance, Bailey (1891) collected 350 *Lasmigona subviridus* in a collection of 598 unionids from the Erie Canal between Ilion and Utica. Aldrich (1869) and Lewis (1872) also remarked that the species was very local. It is puzzling to me

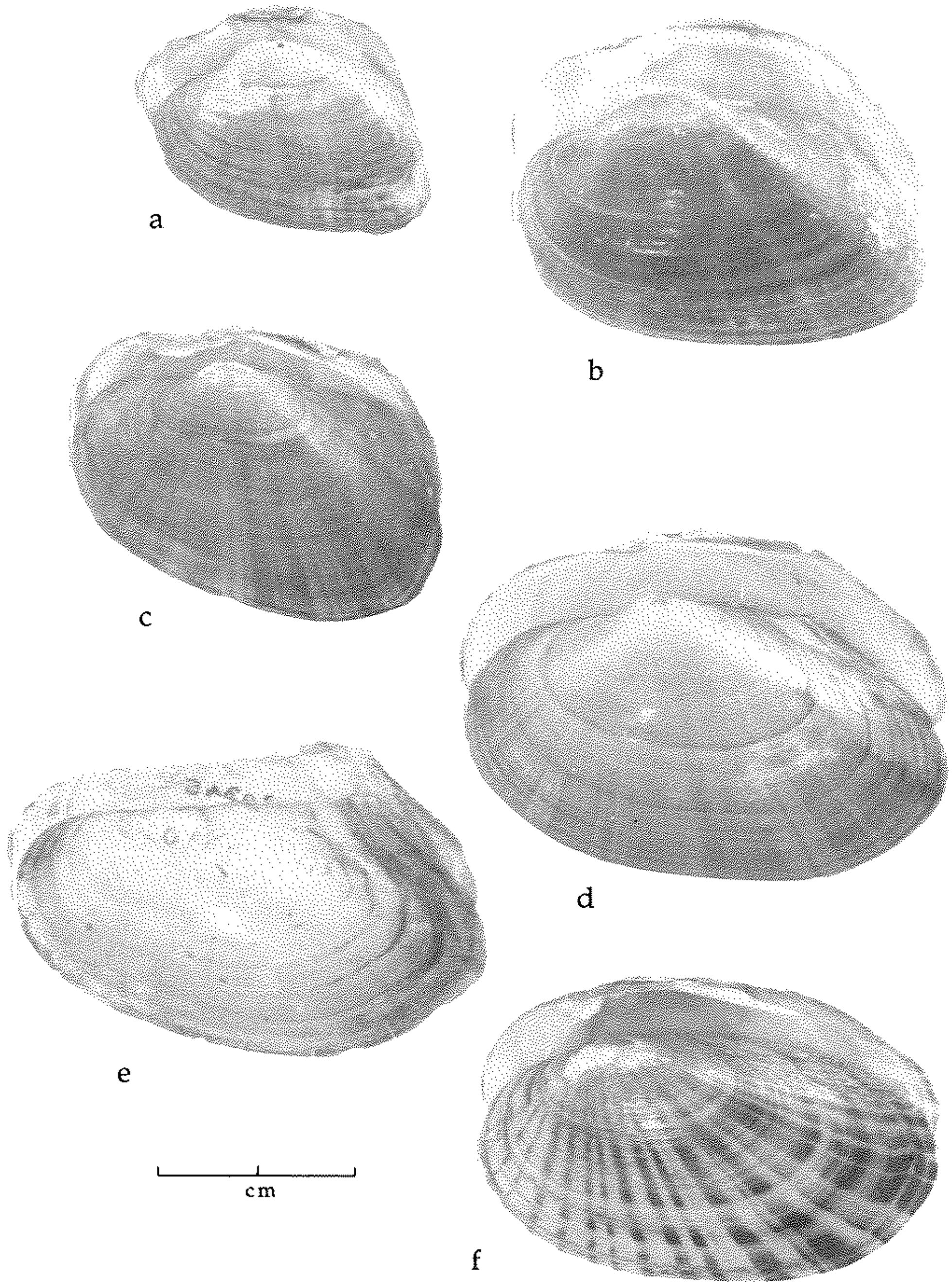

Fig. 24. **a**, *Alasmidonta calceolus* (AMNH 31154, Ohio); **b**, *Al. undulata* (AMNH 73387, Erie Canal, Mohawk, N.Y.); **c**, *Lasmigona subviridus* (AMNH 35494, Mohawk River, N.Y.); **d**, *Anodontoides ferussacianus* (AMNH 31119); **e**, *Anodonta imbecilis* (AMNH 223432, Mohawk River, N.Y.); **f**, *Villosa iris* (AMNH 29005, New York). Scale line = 1 cm.

why *L. subviridus* is found at only a few sites, not even in its prime habitat, in the Hudson basin.

Lasmigona costata (Rafinesque) (Fig. 22f)

This Interior Basin species is known from scattered sites on medium-sized to large streams in the Hudson basin (Fig. 23c). It may well have entered our area prior to the opening of the Erie Canal, since it is fairly widespread in the basin and is found in the Lake Champlain drainage (Smith, 1985a). The locality from Ulster Co. (Rondout Creek) is isolated from the Hudson River by several waterfalls: it appeared to contain a thriving colony of *Lasmigona costata* in 1985.

Anodontoides ferussacianus (Lea) (Fig. 24d)

There are records of this Interior Basin species from sites scattered throughout the Hudson basin (Fig. 25a). It seems likely that this species entered the basin prior to the opening of the Erie Canal. In the Hudson basin, as elsewhere (*e.g.*, Ortmann, 1919; van der Schalie, 1938), *Anodontoides ferussacianus* is primarily a species of small streams. There are records of the species from the Mohawk River, but it was not abundant there (Lewis, 1856, 1860, 1872; Bailey, 1891).

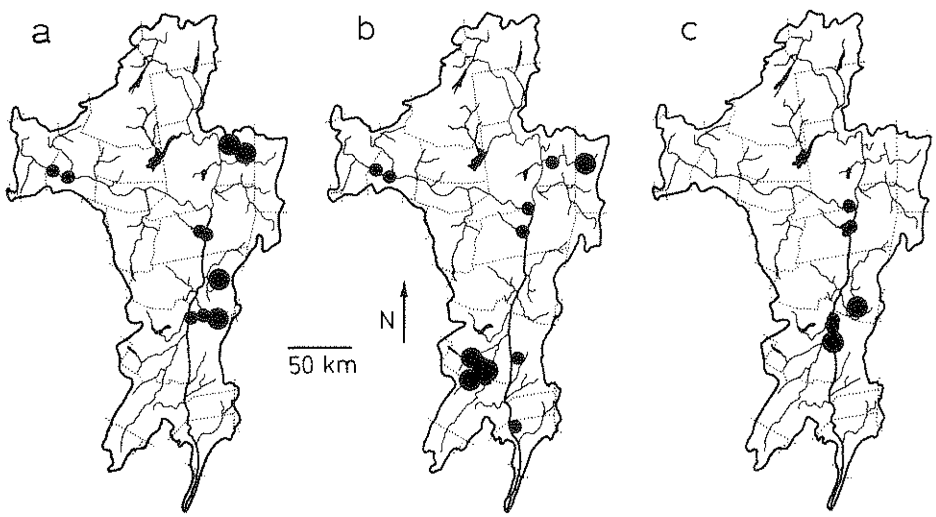

Fig. 25. Distribution of (a) *Anodontoides ferussacianus*, (b) *Strophitus undulatus*, and (c) *Ligumia nasuta* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *A. ferussacianus*: Schoharie Valley (Schoharie Co.); *S. undulatus*: Kinderhook Creek.

Anodonta cataracta Say (Fig. 22g)

This is the most ecologically widespread unionid in the Hudson basin, and has been recorded from lakes, streams, and rivers throughout the basin (Fig. 26a). It is most frequently found in quiet waters (Ortmann, 1919; Clarke & Berg, 1959; Clarke, 1981a).

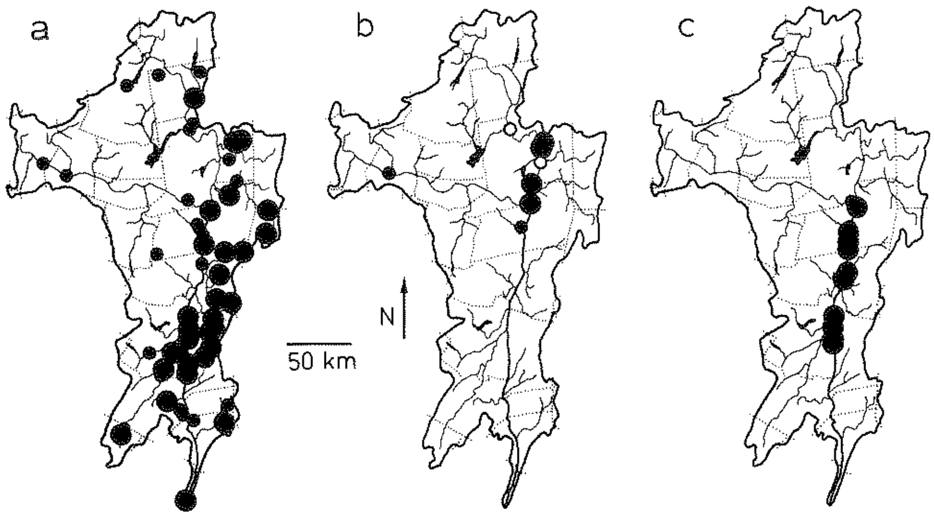

Fig. 26. Distribution of (a) *Anodonta cataracta*, (b) *A. grandis*, and (c) *A. implicata* in the Hudson River basin. In (b), the small white circles show literature records not backed by museum specimens; other symbols as in Fig. 3. The following records are not plotted: *A. cataracta*: Lake Chilson (Essex Co.), Highland Lake (Orange Co.); *A. grandis*: Schoharie (Marshall, 1895b).

Anodonta grandis Say (Fig. 22i)

Anodonta grandis, the Interior Basin counterpart of *A. cataracta*, is known from several sites along the mainstem Mohawk and Hudson Rivers and the mouths of a few of their tributaries (Fig. 26b). Smith (1985a) argued that *A. grandis* was one of the Interior Basin species that entered the Hudson basin before the opening of the Erie Canal. However, *A. grandis* is much more restricted in distribution in our area than are these other species (*Lasmigona compressa* and *L. costata* - Fig. 23a,c; *Anodontoides ferussacianus* - Fig. 25a), even though it is more ecologically tolerant than these species (Ortmann, 1919; van der Schalie, 1938; Clarke & Berg, 1959; Strayer, 1983). I suggest that the restricted distribution of *A. grandis* in the Hudson basin reflects its recent arrival. It may have invaded *via* the Erie Canal, the Champlain Canal, or both. Kat (1986) presented evidence that *Anodonta* living in Lake Champlain are hybrids between *A. cataracta* and *A. grandis*. It seems likely that some populations of *Anodonta* in the Hudson basin, especially in the Mohawk and upper Hudson Rivers, are hybrids.

Anodonta imbecilis Say (Fig. 24e)

This Interior Basin species is known from two specimens taken from Mohawk, Herkimer Co., in the 19th century (Lewis, 1856, 1860, 1872; UMMZ 103877;

AMNH 30345). It presumably entered the Hudson basin *via* the Erie Canal and its present status in our area is not known.

Anodonta implicata Say (Fig. 22h)

This interesting species is abundant in the freshwater tidal estuary of the Hudson River, but it is found almost nowhere else in the basin (Fig. 26c). In 1985, we found shells of this species to be abundant in the Kingston area, and Simpson *et al.* (1984, 1986) reported densities of 200-400m^2 in Albany Co. *Anodonta implicata* is characteristically found in fresh coastal waters (Ortmann, 1919; Johnson, 1946), being one of two species (*Lampsilis ochracea* is the other) in our area that frequent such habitats. Species of *Alosa* (the American shad *A. sapidissima*, the alewife *A. pseudoharengus*, and perhaps the blueback herring, *A. aestivalis*) serve as hosts for *A. implicata* (Johnson, 1946; Davenport & Warmuth, 1965; Smith, 1985b). It is curious that there are no records of *A. implicata* from above the Capital District, even though *Alosa* spp. formerly ascended the Hudson River to Hudson Falls.

Strophitus undulatus (Say) (Fig. 27a)

This species is known from scattered sites, chiefly creeks and small rivers, throughout the Hudson basin (Fig. 25b). Although Lewis (1856, 1860) found *Strophitus undulatus* in the Erie Canal and Mohawk River at Mohawk, he commented that it was scarce, as it usually is in large rivers (*e.g.*, Ortmann, 1919; van der Schalie, 1938; Clarke & Berg, 1959).

Proptera alata (Say) (Fig. 27b)

This distinctive Interior Basin species has been known from the Troy area since DeKay's (1844) time (also Aldrich, 1869; Marshall, 1895a). It apparently has always been rare in the Hudson basin; I found only a single specimen in museum collections (ANSP 129314, Mohawk River, Niskayuna, 1921) (ANSP 42414, "Mohawk," is probably mislabeled - see the section on species questionably or erroneously recorded from the basin). *Proptera alata*, a species of rivers and large lakes (Ortmann, 1919; Clarke & Berg, 1959), is known both from Lake Champlain (Smith, 1985a) and central New York (Clarke & Berg, 1959; Harman, 1970; Harman & Forney, 1970), and probably entered the Hudson basin through canals.

Leptodea fragilis (Rafinesque) (Fig. 27c)

Of similar appearance and habits to the preceding species, *Leptodea fragilis* is another Interior Basin species that probably entered the Hudson basin via the Erie Canal. There are two records from the Hudson basin. MCZ 252205 is a single valve of *L. fragilis* collected by James Lewis from the Hydraulic Canal at Herkimer (Herkimer Co.) in 1853. I have no explanation for the origin of the population of *L. fragilis* represented by AMNH 35331 ("near Goshen, NY"

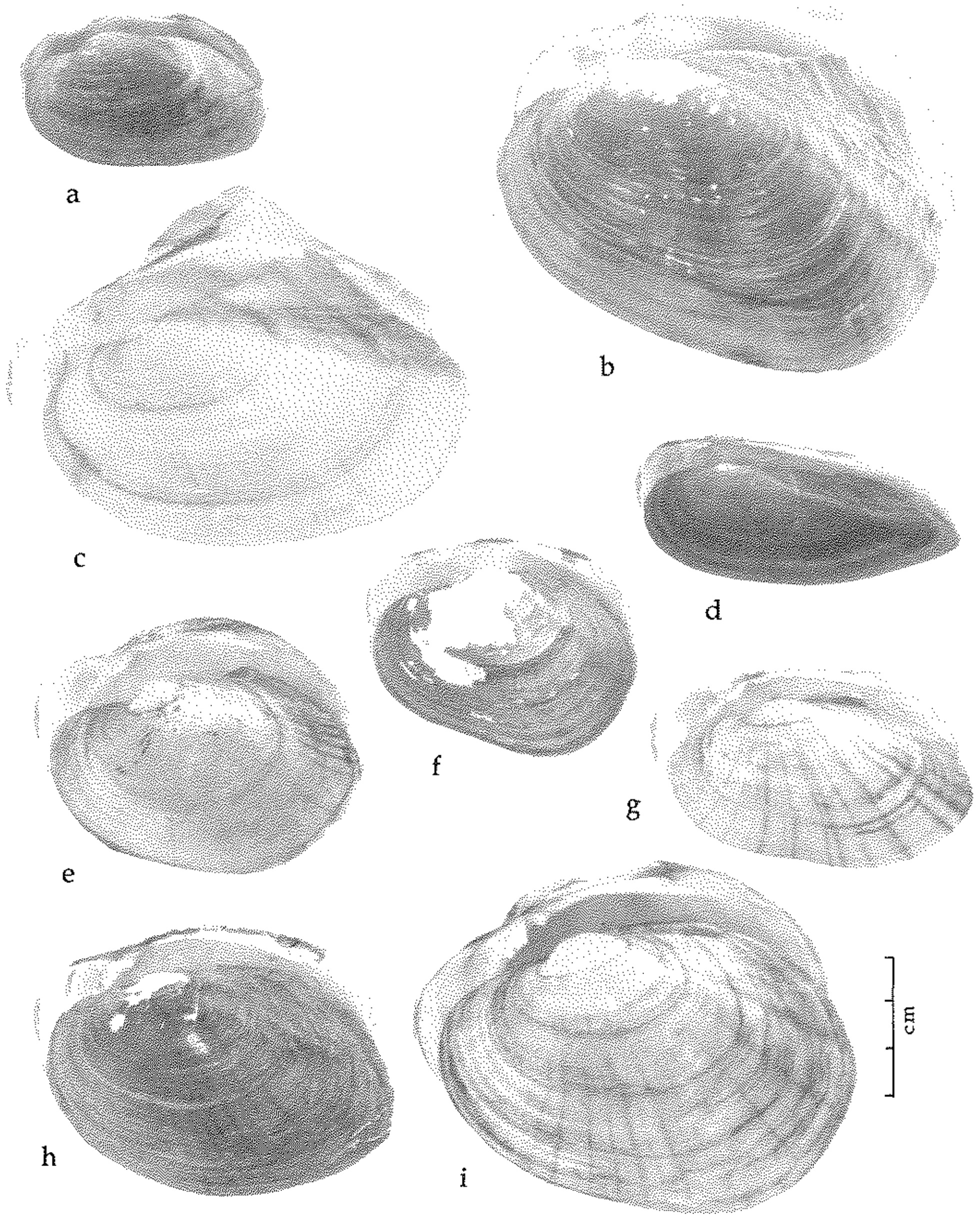

Fig. 27. **a**, *Strophitus undulatus* (AMNH 149068, Lake Mohegan, Westchester Co., N.Y.); **b**, *Proptera alata* (AMNH 29059, Lake Champlain, N.Y.); **c**, *Leptodea fragilis* (AMNH 28998, Lake Champlain); **d**, *Ligumia nasuta* (AMNH 35310, Erie Canal, Pittsford, Monroe Co., N.Y.); **e**, *Lampsilis cariosa* (AMNH 29003, Hudson River, N.Y.); **f**, *La. ochracea* (uncatalogued, Hudson River, Ulster Co., N.Y.); **g**, *La. siliquoidea* (AMNH 29049, Mohawk River, N.Y.); **h**, *La. radiata* (uncatalogued, Hudson River, Ulster Co., N.Y.); **i**, *La. ovata* (AMNH 127891, Honeyoye Creek, Monroe Co., N.Y.). Scale line = 1 cm.

(Orange Co.) written on the shell, collected some time before 1893), nor do I know if the species persists in the Hudson basin.

Ligumia nasuta (Say) (Fig. 27d)

Ligumia nasuta is a species of quiet waters in rivers and lakes, and is especially common in tidewater along the Atlantic Coast (Ortmann, 1919; Clarke & Berg, 1959). In the Hudson basin, it is known from the freshwater tidal estuary of the Hudson, the canal in West Troy, and Lake Taghkanic (Columbia Co.) (Fig. 25c). Judging by the size of museum lots, *L. nasuta* has never been abundant in the Hudson basin. We found a few specimens of *L. nasuta* in the Hudson River, Dutchess and Ulster Co., in 1985-86. It is surprising that *L. nasuta* has not been recorded from more lakes in the Hudson basin, since it is found in inland lakes elsewhere in its range (*e.g.*, Goodrich, 1932; Harman, 1970).

Lampsilis cariosa (Say) (Fig. 27e)

Lampsilis cariosa is a species of Atlantic Coastal drainage rivers (Ortmann, 1919, Clarke & Berg, 1959; Harman, 1970). In the Hudson basin, *L. cariosa* has been collected from the Mohawk and Hudson Rivers, and from Schoharie Creek, a large creek (Fig. 28a). According to Lewis (1856, 1860, 1872), it was not common in the Mohawk area, and the largest museum lots are from the Albany-Troy area (Aldrich, 1869). We found a single recently dead shell of this species in the 1985 survey, from the tidal mouth of the Indiankill.

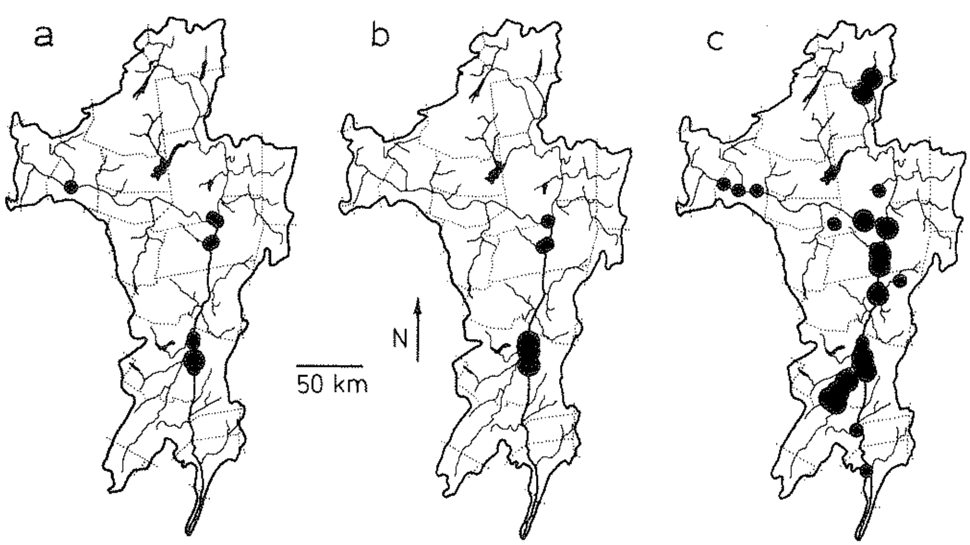

Fig. 28. Distribution of (a) *Lampsilis cariosa*, (b) *L. ochracea*, and (c) *L. radiata s. l.* in the Hudson River basin. Symbols as in Fig. 3. The following record is not plotted: *L. cariosa*: Schoharie Creek (Schoharie Co.).

Lampsilis ochracea (Say) (Fig. 27f)

This species is ecologically similar to *Anodonta implicata*, being characteristic of coastal ponds and rivers (Ortmann, 1919; Johnson, 1947). It is reliably known from the freshwater tidal Hudson River and the extreme lower Mohawk River (Fig. 28b). I found many freshly dead shells of this species in Ulster Co. in 1985, so it apparently is still abundant in this stretch of the Hudson River, where it apparently lives in fairly deep water. Lewis (1856, 1860) recorded *L. ochracea* from Mohawk, but in view of the widespread misunderstanding of this species in the 19th century (Ortmann, 1919; Johnson, 1947), the absence of the species from Lewis' last (1872) list of Herkimer Co. shells, and the absence of any museum lots of *L. ochracea* from the upper Mohawk River, I am inclined to regard Lewis' early reports as erroneous.

Lampsilis radiata (Gmelin) group (Fig. 27g,h)

Two taxa belonging to this group are found in the Hudson basin: *Lampsilis radiata*, of the Atlantic Slope, and *L. siliquoidea* (Barnes) from the Interior Basin. These taxa have been regarded as subspecies (Clarke & Berg, 1959) or full species (Kat, 1986) that hybridize freely in zones of contact. Because the conchological differences between these taxa are slight, it is possible that specimens may not always have been assigned to the correct taxon. Furthermore, following Kat (1986), we would expect many populations in the Mohawk and Hudson Rivers to be hybrids between *L. radiata* and *L. siliquoidea*, with pure *L. radiata* existing only in upland sites. For what they are worth, historical records (Fig. 28c) show *L. radiata* to be widespread in the basin, although scarce in the upper Mohawk basin (*e.g.*, USNM 452007, 51254, MCZ 5920, 5921, 89764). *L. siliquoidea* has been recorded only from Herkimer Co. (DeKay, 1844; Lewis, 1856, 1860, 1872; Bailey, 1891) and a single shell from Cohoes (Marshall, 1895a; USNM 85437). Both species are eurytopic, living in lakes, rivers, and creeks.

Lampsilis ovata (Say) (Fig. 27i)

This species is definitely established in the Lake Champlain basin (Smith, 1985a) and central New York (Clarke & Berg, 1959; Harman, 1970), but there is only one definite record from the Hudson basin: from the Moses Kill at Fort Edward, Washington Co. (Smith, 1983). As Smith suggested, *Lampsilis ovata* probably entered the Hudson basin via the Champlain Canal.

There are two other records of this species from the Hudson basin. Table 1 of Harman (1981) listed *Lampsilis ovata* from Pack Forest Lake, Warren Co., although Harman stated in the text of his paper that he found the species only in Lake Champlain. It appears that the record of *L ovata* from Pack Forest Lake is a typographical error for *Anodonta cataracta*, which Harman did collect from this lake (MCZ 252075). UMMZ 89473 (Troy, Renssalaer Co., collected by Aldrich in 1868) is labelled as *L. ovata*. I examined this lot at the beginning of this study, before I had a clear conception of the range of variation of *L. cariosa*, a species that can be very similar in appearance to *L. ovata*. I was not able to positively identify this lot as either *ovata* or *cariosa*, but it could very well be *cariosa*, a common species in the Troy area (Fig. 28a; Aldrich, 1860).

Villosa iris (Lea) (Fig. 24f)

I have included this Interior Basin species in the fauna of the Hudson basin on the strength of a single lot in the Carnegie Museum from the Mohawk River (Ortmann, 1919, p. 269). I have found no other evidence of its occurrence in the Hudson basin, although it is abundant in tributaries of Oneida Lake a few miles to the west of the Mohawk-Oswego drainage divide (Clarke & Berg, 1959).

SPHAERIIDAE

Twenty-three species of sphaeriid clams are known from the Hudson basin. Many previous workers in the Hudson basin overlooked sphaeriids, so the distributions shown in Figs. 29 and 31 probably greatly understate the distribution of sphaeriids in our area.

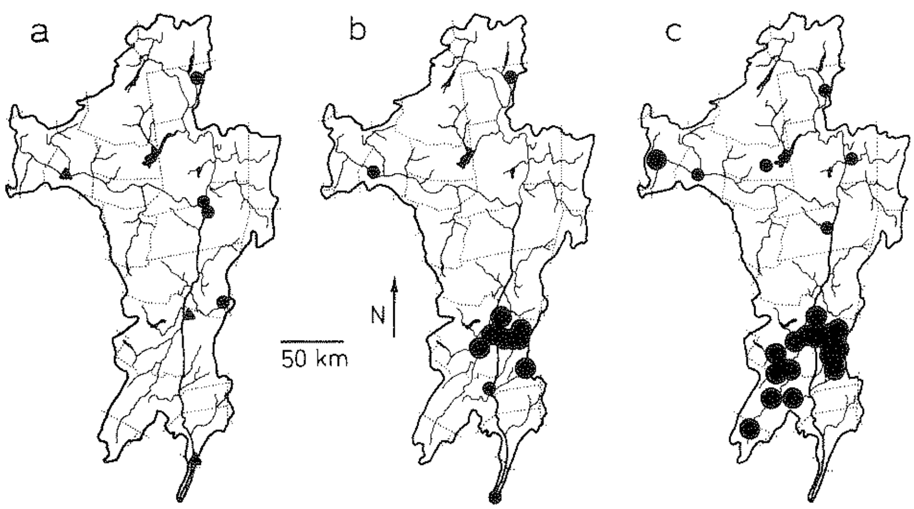

Fig. 29. Distribution of (a) *Sphaerium rhomboideum* (circles) and *S. occidentale* (triangles), (b) *S. simile*, and (c) *S. striatinum* in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *S. occidentale*: Williams Bridge and Riverdale (both Westchester Co.); *S. simile*: Westchester Co.; *S. striatinum*: Westchester Co.

Sphaerium corneum (Linnaeus) (Fig. 30a)

This is a European species that is known from several large rivers and lakes in the Great Lakes region (Herrington, 1962; Burch 1975b). Simpson (1976) reported finding *Sphaerium corneum* from the Hudson River near Albany, and I picked up a single empty shell that resembles this species from the Hudson River at Ulster Landing County Park near Kingston in 1985. Its presence in the Hudson basin needs confirmation.

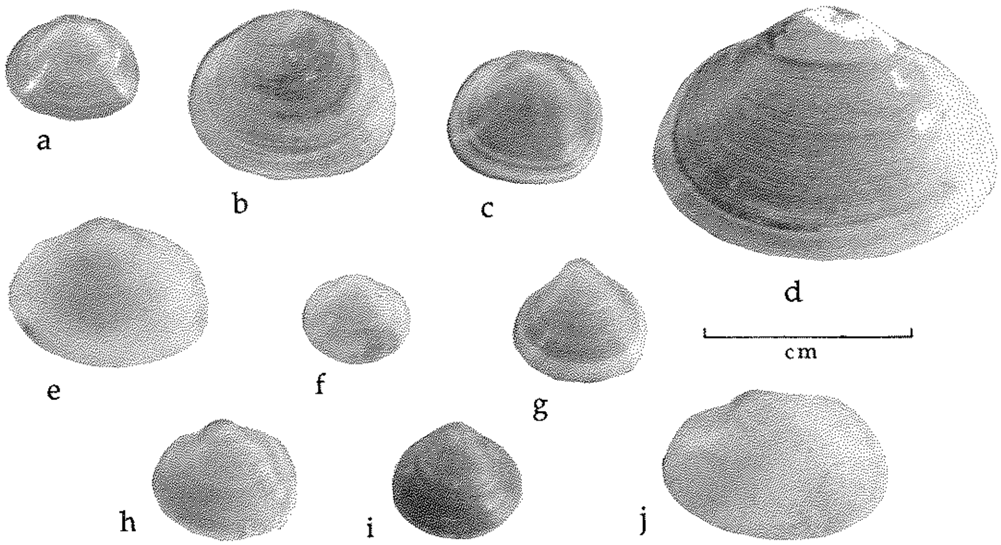

Fig. 30. **a**, *Sphaerium corneum* (AMNH 110639, Lake Ontario, Canada); **b**, *S. fabale* (AMNH 70872, Pennsylvania); **c**, *S. rhomboideum* (AMNH 64682, Vermont); **d**, *S. simile* (AMNH 64601, New York); **e**, *S. striatinum* (AMNH 64857, Mohawk River, N.Y.); **f**, *S. occidentale* (AMNH 64835, Mohawk, New York); **g**, *Musculium lacustre* (AMNH 64656, Massachusetts); **h**, *M. partumeium* (AMNH 70870, Mohawk, N.Y.); **i**, *Musculium securis* (AMNH 70880, Riverdale, N.Y.); **j**, *M. transversum* (Canal, Mohawk, N.Y). Scale line = 1 cm.

Sphaerium fabale (Prime) (Fig. 30b)

Sphaerium fabale is a species of creeks and rivers, and is widespread in the Great Lakes region (Heard, 1962; Herrington, 1962; Burch, 1975b). Although I would expect *S. fabale* to live in the Hudson basin, the only record of its occurrence is UMMZ 102775 ("Westchester Co., NY").

Sphaerium rhomboideum (Say) (Fig. 30c)

According to Heard (1962), Herrington (1962), and Clarke (1981a), *Sphaerium rhomboideum* lives in lakes, ponds, and quiet areas of creeks and rivers. Although I did not find it in my 1985 survey, this species is known from a few widely scattered sites in the Hudson basin (Fig. 29a).

Sphaerium simile (Say) (Fig. 30d)

Sphaerium simile is a very widespread sphaeriid said to live in sand and mud in a variety of perennial-water habitats (Heard, 1962; Herrington, 1962; Clarke, 1981a). There are records from lakes and streams throughout the Hudson basin (Fig. 29b), as well as the tidal Hudson River (Townes, 1937). I did not find *S. simile* to be abundant during my 1985 survey, but it occupied a distinct habitat. Nearly all of the my records are from marginal mud banks in small trout streams.

Sphaerium striatinum (Lamarck) (Fig. 30e)

One of the most common sphaeriids in North America, *Sphaerium striatinum* is especially frequent in permanent streams, but also occurs in lakes (Heard, 1962; Herrington, 1962; Clarke, 1981a). It is widely distributed in the Hudson basin (Fig. 29c). In the 1985 survey, I found *S. striatinum* in many creeks in the mid-Hudson region. It was especially numerous in coarse gravel (often under cobbles) in riffles.

Sphaerium occidentale (Prime) (Fig. 30f)

This widely distributed species is characteristic of, and often very abundant in, ditches, swamps, and woodland temporary ponds (Herrington, 1962; Clarke, 1981a). Not surprisingly, I did not find it in my 1985 stream survey. There are scattered records of *Sphaerium occidentale* from throughout the Hudson basin (Fig. 29a); undoubtedly it is widespread in temporary waters in our area.

Musculium lacustre (Müller) (Fig. 30g)

Musculium lacustre typically lives on muddy bottoms in the quiet water of ponds, lakes, and streams (Herrington, 1962; Clarke, 1981a). Scattered records suggest that it is widespread in the Hudson basin (Fig. 31a). I found it only once in 1985, in the soft bottom of a brown-water flowing swamp.

Mŭsculium partumeium (Say) (Fig. 30h)

This is a common species of temporary and permanent ponds, lakes, and slow-moving streams, usually living on muddy bottoms (Heard, 1962; Herrington, 1962; Clarke, 1981a). It is probably common and widespread in the Hudson basin (Fig. 31b). I found it at four places in my 1985 survey, two of them flowing swamps and two of them medium-sized creeks.

Musculium securis (Prime) (Fig. 30i)

This is another geographically and ecologically widespread species, frequenting soft sediments in ponds, lakes, and streams of all sizes (Heard, 1962; Herrington, 1962; Clarke, 1981a). Again, there are records from throughout the Hudson basin (Fig. 31c), suggesting that the species is widespread in our area. I did not find *Musculium securis* in my 1985 survey.

Musculium transversum (Say) (Fig. 30j)

This species usually is found in the soft sediments of rivers, although it also occurs in large lakes (Heard, 1962; Herrington, 1962; Clarke, 1973, 1981a). All of the records from the Hudson basin are from running water, chiefly rivers (Fig. 31c). I found *Musculium transversum* to be abundant in the muddy rivers of the Rondout-Wallkill basin, typically in gravel under cobbles or among plants.

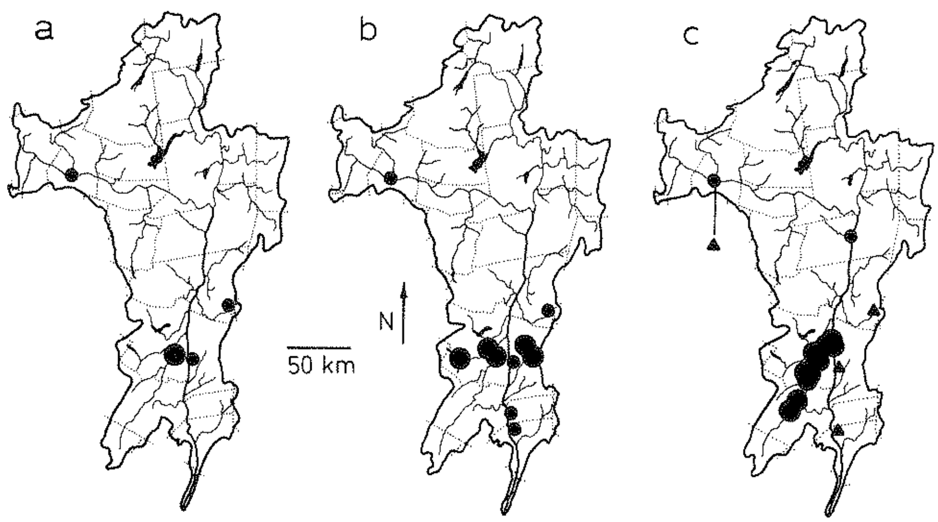

Fig. 31. Distribution of (a) *Musculium lacustre*, (b) *M. partumeium*, and (c) *M. transversum* (circles) and *M. securis* (triangles) in the Hudson River basin. Symbols as in Fig. 3. The following records are not plotted: *M. partumeium*: Riverdale (Westchester Co.?); *M. securis*: Williams Bridge (Westchester Co.).

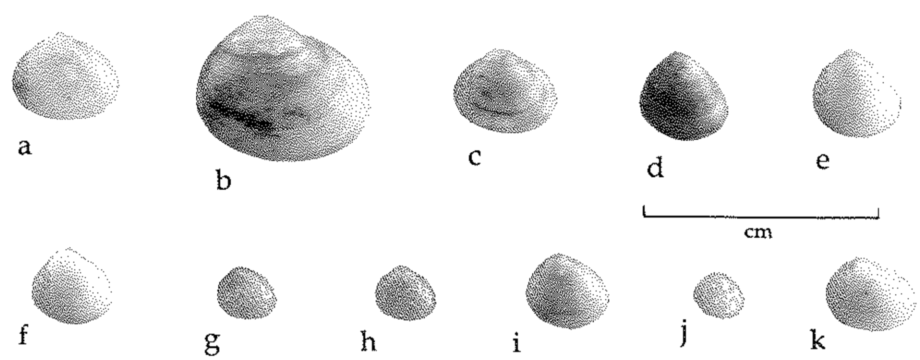

Fig. 32. **a**, *Pisidium adamsi* (AMNH 70856, New Hampshire); **b**, *P. amnicum* (AMNH 64808, France and Britain); **c**, *P. casertanum* (AMNH 64885, Mohawk River, N.Y.); **d**, *P. compressum* (AMNH 64886, Mohawk River, N.Y.); **e**, *P. dubium* (AMNH 64772, Canal at Mohawk, N.Y.); **f**, *P. equilaterale* (AMNH 64724, Canal at Mohawk, N.Y.); **g**, *P. ferrugineum* (AMNH 70849, Mohawk, N.Y.); **h**, *P. nitidum* (AMNH 64834, Mohawk, N.Y.); **i**, *P. variabile* (AMNH 64723, Canal at Mohawk, N.Y.); **j**, *P. ventricosum* (AMNH 64887, Mohawk, N.Y.); **k**, *P. walkeri* (AMNH 64827, Erie Canal). Scale line = 1 cm.

Pisidium spp. (Fig. 32a-k)

I will not attempt a species-by-species account of these small, taxonomically difficult clams. Although *Pisidium* can be abundant in many habitats, records of most species in the Hudson basin are scarce, offering very little idea as to the geographic or ecological distribution of individual species in our area. Furthermore, I have not identified the material collected in my 1985 survey (even this consists of only 18 lots).

The following species of *Pisidium* are represented by museum lots from the Hudson basin: *P. adamsi* Stimpson, *P. casertanum* (Poli), *P. compressum* Prime, *P. dubium* (Say), *P. equilaterale* Prime, *P. fallax* Sterki (known only as subfossil shells from postglacial deposits in Oneida Co. and through the unverified record of Townes (1937) from the Hudson River at Barrytown, Dutchess Co.), *P. ferrugineum* Prime, *P. insigne* Gabb (ANSP 186672), *P. nitidum* Jenyns, *P. variabile* Prime, *P. ventricosum* Prime, and *P. walkeri* Sterki (UMMZ 113024). Simpson *et al.* (1984, 1986) reported *P. amnicum* (Müller) from the Hudson River, Albany Co.

Species erroneously or questionably recorded from the Hudson basin

In the text, I recognized approximately 96 species of freshwater mollusks as reliable recorded from the Hudson River basin. I have found records of an additional 15 species, but without adequate documentation to unequivocally establish their presence in the basin. In some of these cases, the records are so implausible as to be clearly erroneous; but in others I can neither accept nor reject the records with certainty.

Many of the clearly erroneous records are due to a series of lots at the ANSP which bear distinctive labels and are attributed to "Mohawk" or "Upper Red Hook." These lots were apparently received from James Lewis and W. S. Teator and erroneously labeled with the address of the donor rather than the locality of collection, a fairly common practice (cf. Heard, 1962). Species whose presence in the Hudson River basin is based solely on these lots are designated with an asterisk in the following list. These species certainly do not belong to the Hudson basin's fauna.

**Valvata perdepressa* Walker - ANSP 12002, "Mohawk."

Valvata bicarinata Lea - The collection catalogue at UMMZ lists a lot (#143545) of *V. bicarinata* from Mohawk. I could not find this lot in the UMMZ collection. Lewis did not record the species from the Hudson basin in any of his writings, nor are there any other records of the species from the basin.

Amnicola walkeri Pilsbry - There are two lots in the MCZ that are catalogued as this species. I could not find one of the lots (no catalogue number, "Erie Canal at Mohawk"), and the other (34043, "Normanskill at Albany") is *Marstonia lustrica*.

**Acella haldemani* ('Deshayes' W. G. Binney) - ANSP 58538. Although there are no authentic records from the Hudson River basin, this species is known from nearby Schuyler's Lake in Herkimer Co. and from Lake Champlain.

Stagnicola caperata (Say) - DeKay (1844) figured this species from the Mohawk River, although there are no authentic museum lots or subsequent literature records of this species from the Hudson basin. Museum lots catalogued under *S. caperata* (UMMZ 73668, USNM 121511a, ANSP 43752, AMNH 1760) from the Hudson basin all have proved to be *Fossaria* or *Stagnicola catascopium*. However, despite Clarke's (1973, 1981a) assertions to the contrary, there are at least a few genuine records of this distinctive species from New York State (*e.g.*, MCZ 20466, "Niagara").

Margaritifera margaritifera (Linnaeus) - Although this species is found in the Oneida Lake, Lake Champlain, Hackensack River, and Connecticut River drainages adjoining the Hudson basin (Clarke & Berg, 1959; Jacobson & Emerson, 1971; Smith, 1982, 1985a), I have not found any definite records of *M. margaritifera* from the Hudson basin. Marshall (1895a) reported that Call found the species in "tributaries of the Mohawk," Walker (1910), cited it from the Hudson River, and Sepkoski & Rex (1974) listed it in the fauna of the Hudson River basin. None of these indefinite records is supported by museum specimens, so the presence of *M. margaritifera* in the Hudson basin is questionable. The species should be looked for in the mountain streams of the Catskills and Adirondacks.

Amblema plicata (Say) - Lewis introduced this species into the Erie Canal at Mohawk prior to 1860 (Lewis, 1860) but, as far as I can tell, the species never established itself in the Hudson basin. The ANSP has a lot of *A. plicata* from "Mohawk" (129711) which is almost certainly erroneous, and MCZ 240243 is a specimen of *A. plicata* labeled "Nyack". The latter locality is probably a transcription error for "NYork," as the species is known from western New York State (*e.g.*, Robertson & Blakeslee, 1948).

**Quadrula cylindrica* (Say) - ANSP 41711, "Mohawk."

Cyclonaias tuberculata (Rafinesque) - ANSP 43146, a lot of *C. tuberculata*, is attributed to "Mohawk R." This locality is almost certainly incorrect; the species is not reliably known east of the Niagara and Allegheny River drainages. Lewis never mentioned *Cyclonaias tuberculata* in his writings on the fauna of the Mohawk River.

Elliptio dilatata Rafinesque - Call (1878) claimed that Lewis found a single specimen of this species in the Erie Canal at Mohawk, and Ortmann (1919) repeated this record. Lewis did not mention finding *E. dilatata* himself, and there are no specimens of this species from the Hudson basin in the collections that I examined. Call's record may be based on an aberrant specimen of the variable *E. complanata*.

**Pleurobema cordatum* (Rafinesque) - ANSP 43118, "Mohawk."

Uniomerus tetralasmus (Say) - Lewis introduced this species into the Erie Canal, Mohawk, prior to 1860 (Lewis, 1860, as *Unio camptodon*). Although there are no subsequent records from the Hudson basin, a lot of *U. tetralasmus* (ANSP

140870) from the Erie Canal at Rochester (the only New York State record of this species) suggests that Lewis' introduction may have been successful.

**Actinonaias carinata* (Barnes) - ANSP 56434, "Mohawk."

Carunculina parva (Barnes) - Another species introduced by Lewis into the Erie Canal, Mohawk, prior to 1860 (Lewis, 1860). There is no evidence that *C. parva* established itself in the Hudson basin. NYSM 31840, from the Mohawk River at Cohoes, is *C. parva*, but is labeled as *Alasmidonta marginata*. This is most likely a case of label-switching with the correct record being that of *A. marginata* in the Mohawk River, Cohoes, a part of its known range (Fig. 21b).

**Obovaria subrotunda* (Rafinesque) - ANSP 56599, "Mohawk."

Ecological distribution of mollusks in the Hudson River basin

Following the approach of van der Schalie (1938), we can define several major habitat types and describe the molluscan faunas typically present in each. I will recognize eight broad habitat types: brooks (streams with a mean annual discharge [MAD] of less than $0.3 m^3/sec$), small streams (MAD = 0.3-$3 m^3/sec$), creeks and small rivers (MAD = 3-$30 m^3/sec$). large rivers (MAD > $30\ m^3/sec$), the freshwater tidal Hudson River, lakes (standing water with a surface area of > 10 ha), ponds (area < 10 ha) and marshes, and temporary pools and ditches. I have listed the mollusks typically found in each of these habitats in Table 2.

TABLE 2. Summary of ecological distribution of freshwater mollusks in the Hudson River basin. Habitats are: 1 = brooks, 2 = small streams, 3 = medium-sized streams, 4 = rivers, 5 = freshwater tidal Hudson River, 6 = lakes, 7 = ponds, 8 = temporary pools and ditches. Key to table: 3 = nearly always found in the habitat, often abundant; 2 = often found in the habitat, sometimes abundant; 1 = occasionally found in the habitat, rarely abundant; - = rarely or never found in the habitat*.

Species	Habitats*							
Prosobranch Snails	1	2	3	4	5	6	7	8
Amnicola grana	1	-	-	-	1	-	-	-
Marstonia lustrica	1	-	-	2	2	-	-	-
Elimia livescens	-	-	1	2	1	-	-	-
Amnicola pupoidea	1	-	-	-	1	1	-	-
Cincinnatia cincinnatiensis	-	-	-	2	-	-	-	-
Amnicola limosa	1	2	2	3	3	3	2	-
Campeloma decisum	1	2	2	2	2	2	1	-

*Because of insufficient information for *Physella* and the Sphaeriidae, I have simply marked (+) the habitats in which each species is known to occur in the Hudson basin. Rare species omitted.

TABLE 2 (cont.)

(Species)	(Habitats)*							
Pleurocera acuta	-	-	-	2	1	-	-	-
Probythinella lacustris	-	-	-	2	2	-	-	-
Gillia altilis	-	-	-	2	2	-	-	-
Birgella subglobosa	-	-	-	2	2	-	-	-
Valvata tricarinata	-	1	1	2	2	2	1	-
Elimia virginica	-	-	-	1	2	-	-	-
Bithynia tentaculata	-	-	-	1	3	1	-	-
Cipangopaludina chinensis	-	1	-	-	-	1	1	-
Valvata sincera	-	-	-	-	1	-	-	-
Lioplax subcarinata	-	-	-	-	1	-	-	-
Viviparus georgianus	-	-	-	1	1	2	1	-
Pulmonate Snails								
Ferrissia rivularis	1	3	3	3	1	-	-	-
Fossaria spp.	2	3	3	2	2	3	2	2
Helisoma anceps	1	2	2	2	1	2	2	-
Gyraulus circumstriatus	1	-	-	-	-	-	1	1
Physella gyrina	+	-	+	+	+	+	+	-
Laevapex fuscus	-	-	1	2	1	1	-	-
Planorbella trivolvis	1	1	1	2	1	-	3	-
Gyraulus parvus	1	2	2	2	2	3	3	-
Gyraulus deflectus	1	1	1	1	1	2	2	-
Menetus dilatatus	-	1	1	-	1	-	2	-
Stagnicola catascopium	-	-	-	2	3	1	-	-
Stagnicola elodes	1	-	-	1	1	-	3	3
Physella integra	-	-	-	+	+	-	+	-
Physella ancillaria	-	-	-	-	+	+	-	-
Pseudosuccinea columella	1	-	-	-	1	2	3	-
Physella heterostropha	-	-	-	+	-	+	+	-
Planorbula armigera	-	-	-	-	1	1	2	2
Promenetus exacuous	-	-	-	-	1	1	2	-
Ferrissia fragilis	-	-	-	-	1	1	2	-
Planorbella campanulata	-	-	-	-	-	1	1	-
Aplexa elongata	-	-	-	-	-	1	2	3
Unionid Clams								
Lasmigona compressa	1	1	1	-	-	-	-	-
Anodontoides ferussacianus	1	2	1	1	-	-	-	-
Strophitus undulatus	1	1	1	1	1	-	-	-
Alasmidonta undulata	1	2	2	2	-	1	-	-
Elliptio complanata	1	2	3	3	3	3	-	-
Anodonta cataracta	1	2	2	2	2	2	1	-
Lasmigona costata	-	-	1	2	1	-	-	-
Alasmidonta marginata	-	-	-	1	-	-	-	-
Anodonta grandis	-	-	-	2	1	-	-	-
Lasmigona subviridus	-	-	-	2	1	-	-	-
Lampsilis radiata group	-	1	1	2	2	2	-	-
Lampsilis cariosa	-	-	-	1	1	-	-	-
Ligumia nasuta	-	-	-	1	2	1	-	-
Anodonta implicata	-	-	-	-	3	-	-	-
Lampsilis ochracea	-	-	-	-	2	-	-	-
Sphaeriid Clams								
Sphaerium striatinum	+	+	+	+	+	-	-	-
Musculium transversum	-	+	+	+	+	-	-	-

TABLE 2 (cont.)

(Species)	(Habitats)*							
Sphaerium simile	+	+	-	+	-	+	+	-
Musculium partumeium	-	+	+	-	-	+	+	+
Pisidium dubium	-	-	-	+	+	+	-	-
Pisidium compressum	-	-	-	+	-	+	-	-
Sphaerium corneum	-	-	-	-	+	-	-	-
Pisidium casertanum	-	-	-	+	-	+	+	-
Musculium lacustre	-	-	-	-	-	+	+	-
Musculium securis	-	-	-	-	-	+	+	-

Habitat type 1: brooks

It is difficult to generalize about the mollusk fauna of brooks, because ecological conditions (and mollusk faunas) in these streams vary so widely. At one end of the spectrum are shaded, cool, high gradient brooks where mollusks often are rare or entirely absent. At the other extreme, slow, warm, weedy ditches often support a dense and varied community of mollusks, especially pulmonate snails. If any general statement can be made, it is that *Fossaria* is the only mollusk frequently found here, but that about two dozen other species appear occasionally in such habitats (Table 2).

Habitat type 2: small streams

The mollusk community is much better developed here than in habitat 1; mollusks rarely are absent from small streams, unless the water is very acid. The fauna of small streams typically contains 3-8 species, chiefly drawn from the following list.

Campeloma decisum
Amnicola limosa

Fossaria sp.
Physella gyrina
Gyraulus parvus
Helisoma anceps
Ferrissia rivularis

Elliptio complanata
Alasmidonta undulata
Anodonta cataracta
Anodontoides ferussacianus

Sphaerium striatinum
Sphaerium simile
(*Pisidium* spp.?)

Habitat type 3: creeks and small rivers

This habitat often contains several well developed microhabitats: stony riffles, sand and gravel bars, quiet pools, and, importantly, weedy backwaters and oxbows. Mollusks are conspicuous in this habitat, and the fauna typically contains 6-10 species, mostly those in the following list.

Campeloma decisum
Amnicola limosa

Fossaria sp.
Physella gyrina
Gyraulus parvus
Helisoma anceps
Ferrissia rivularis

Elliptio complanata
Alasmidonta undulata
Anodonta cataracta

Sphaerium striatinum
Musculium transversum
(*Pisidium* spp.?)

The faunal list is almost identical to the previous list, but the molluscan fauna is richer here than in habitat 2, as shown by the higher species richness.

Habitat type 4: large rivers

Included in this category are the Mohawk and upper Hudson Rivers, as well as the lower parts of their larger tributaries, such as the Rondout Creek. I visited only a few sites that fall into this category, but it appears that many species of mollusks can be found in the large rivers of the Hudson River basin. Species richness is on the order of 10-25 species.

Valvata tricarinata
Campeloma decisum
Probythinella lacustris
Gillia altilis
Birgella subglobosa
Cincinnatia cincinnatiensis
Marstonia lustrica
Amnicola limosa
Elimia livescens
Pleurocera acuta

Fossaria sp.
Stagnicola catascopium
Physella gyrina
Physella heterostropha
Physella integra
Gyraulus parvus
Helisoma anceps
Planorbella trivolvis
Ferrissia rivularis
Laevapex fuscus

Elliptio complanata
Alasmidonta undulata
Anodonta cataracta
Anodonta grandis
Lasmigona costata
Lasmigona subviridus
Lampsilis radiata

Sphaerium striatinum
Musculium transversum
(*Pisidium* spp.?)

There obviously has been a sharp increase in faunal richness over that in small rivers, particularly among the hydrobiid snails and unionid clams. This increase is partly zoogeographic, rather than ecological, in nature, since the Hudson and especially the Mohawk Rivers have had access to a rich Interior Basin fauna that is largely absent from the smaller upland streams.

Habitat type 5: the freshwater tidal Hudson River

I have listed the freshwater tidal Hudson River separately from other large rivers both because it is very distinctive ecologically and because its mollusk fauna contains several species not found elsewhere in the basin. The freshwater tidal Hudson includes intertidal mudflats, stony shores, and marshes subject to a tide of > 1m, as well as a main channel that contains extensive beds of macrophytes along with substrata ranging from sand to cobbles. The mollusk fauna is diverse and distinctive; the following species are frequently found.

Valvata tricarinata
Campeloma decisum
Bithynia tentaculata
Probythinella lacustris
Gillia altilis
Birgella subglobosa
Cincinnatia cincinnatiensis
Marstonia lustrica
Amnicola limosa
Elimia virginica

Fossaria sp.
Stagnicola catascopium
Physella ancillaria
Physella gyrina
Physella integra
Gyraulus parvus

Elliptio complanata
Anodonta cataracta
Anodonta implicata
Lampsilis ochracea
Lampsilis radiata
Ligumia nasuta

Sphaeriidae spp.

The sphaeriid fauna is not known well enough for me to list it here. The distinctive elements of this fauna include *Bithynia tentaculata, Elimia virginica, Anodonta implicata, Lampsilis ochracea, Ligumia nasuta,* and the rarer *Lioplax subcarinata,* all of which are rare or absent elsewhere in the basin.

Habitat type 6: lakes

I am including here standing waters of more than 10 ha in surface area, and usually deep enough to stratify. Mollusks often are abundant here, especially if the lake is productive and calcium-rich.

Valvata tricarinata
Viviparus georgianus
Campeloma decisum
Amnicola limosa

Fossaria sp.
Pseudosuccinea columella
Physella ancillaria
Physella gyrina

Physella heterostropha
Gyraulus deflectus
Gyraulus parvus
Helisoma anceps

Elliptio complanata
Anodonta cataracta
Lampsilis radiata
Sphaeriidae spp.

Again, the sphaeriids of lakes in the Hudson basin are too poorly known to list.

Habitat type 7: ponds

Included here are marshes and the weedy edges of lakes and streams. Mollusks, especially pulmonate snails, are often abundant in this habitat, although total species richness is not especially high.

Amnicola limosa

Fossaria sp.
Pseudosuccinea columella
Stagnicola elodes
Physella gyrina
Physella heterostropha
Physella integra
Aplexa elongata
Gyraulus deflectus
Gyraulus parvus
Planorbella trivolvis
Planorbula armigera
Promenetus exacuous
Ferrissia fragilis

Sphaerium simile
Musculium partumeium
(*Pisidium* spp.?)

Habitat type 8: temporary pools

As noted by Wiggins *et al.* (1980), the fauna of temporary pools is distinctive. This fauna typically includes the following species of mollusks, which may be very abundant.

Fossaria sp.
Stagnicola elodes
Aplexa elongata
Planorbula armigera

Sphaerium occidentale
Musculium partumeium
?*Musculium securis*
?*Musculium lacustre*

Historical changes in the fauna

Although collections of mollusks have been made for more than 150 years in the Hudson basin, very few sites have been revisited to assess temporal changes in the fauna. As a result, it is not possible to present a detailed picture of the changes in the fauna since 1800. Collections from the two sites that have been revisited and recollected thoroughly are compared in Tables 3 and 4.

TABLE 3. The mollusk fauna of the Hudson River, Dutchess and Ulster Co., in 1887-1900, 1936, and 1973-1985. Records from Townes (1937), Simpson (1976), Simpson et al. (1984), this study, and unpublished collections by Teator, van Ingen, and others. Sphaeriids not included.

	1887-1900	1936	1973-1985
Prosobranch snails			
Valvata piscinalis			x
Valvata sincera			x
Valvata tricarinata		x	x
Viviparus georgianus		x	x
Campeloma decisum	x	x	
Lioplax subcarinata	x	x	
Bithynia tentaculata	x	x	x
Probythinella lacustris		x	
Gillia altilis	x	x	
Birgella subglobosa		x	
Amnicola limosa	x		x
Amnicola pupoidea			x
Elimia livescens		x	
Elimia virginica	x	x	x
Pulmonate snails			
Fossaria sp.	x		x
Pseudosuccinea columella			x
Stagnicola elodes	x		
Stagnicola catascopium	x	x	x
Physella sp.	x	x	x
Gyraulus deflectus	x		x
Gyraulus parvus	x	x	x
Helisoma anceps	x	x	x
Menetus dilatatus			x
Planorbella trivolvis	x	x	x
Promenetus exacuous		x	x
Ferrissia fragilis	x		x
Ferrissia parallelus			x
Laevapex fuscus		x	
Unionid clams			
Elliptio complanata	x	x	x
Anodonta cataracta			x
Anodonta implicata			x
Lampsilis cariosa	x	x	x
Lampsilis ochracea	x		x
Lampsilis radiata	x	x	x
Ligumia nasuta	x		x

The only conclusion that can be made from these tables is that the molluscan fauna of the freshwater tidal Hudson River seems not to have changed its composition markedly over the last 100 years or so. However incomplete our knowledge is, it is at least clear that the situation in the Hudson River estuary is very different from that in many rivers, where much of the molluscan fauna was

TABLE 4. The mollusk fauna of the Hudson River in Albany Co. in 1867-1890 and 1972-1984. Data from Aldrich (1869), Marshall (1895b), Simpson (1976), Smith (1983 and pers. comm.), Simpson *et al.* (1984), and unpublished collections by Aldrich, Beecher, Marshall, Simpson, and others. Sphaeriid clams not included.

Species	1867-1890	1972-1984
Prosobranch snails		
Valvata sincera		x
Valvata tricarinata	x	x
Campeloma decisum	x	
Bithynia tentaculata	x	x
Probythinella lacustris	x	x
Gillia altilis	x	
Marstonia lustrica	x	
Amnicola limosa	x	x
Elimia livescens	x	x
Elimia virginica	x	x
Pleurocera acuta		x
Pulmonate snails		
Fossaria sp.	x	x
Stagnicola catascopium	x	?
Physella sp.	x	x
Gyraulus parvus		x
Helisoma anceps		x
Planorbella trivolvis	x	x
Menetus dilatatus		x
Promenetus exacuous		x
Ferrissia parallelus		x
Ferrissia rivularis		x
Unionid clams		
Elliptio complanata	x	x
Anodonta cataracta		x
Anodonta grandis		x
Anodonta implicata		x
Lasmigona costata	x	
Lasmigona subviridus	x	
Lampsilis cariosa	x	
Lampsilis ochracea	x	x
Lampsilis radiata	x	x
Ligumia nasuta	x	

destroyed in the 20th century (*e.g.*, Isom, 1969; Starrett, 1971; Strayer, 1979, 1980; Suloway, 1981). Because most of the collections making up Tables 3 and 4 were not quantitative, nothing can be said about changing abundances of any of the species.

However, even without good historical records from other parts of the basin, it is clear that human activities have had a devastating effect on the mollusk fauna of some streams. The Wallkill River has been channelized in the intensively farmed mucklands of Orange Co.; it supports a sparse fauna of three species (*Ferrissia rivularis*, *Physella heterostropha*, and *Gyraulus parvus*) rather than the eight to ten species to be expected in a small river. Likewise, the tidal mouth of the Fishkill Creek in Dutchess Co. is eerily devoid of macroinvertebrates and contains only three species of mollusks (*Bithynia tentaculata*, *Gyraulus parvus*, and *Fossaria* sp.). Presumably, industrial pollution from Beacon is responsible for this situation, since other tidal creek mouths in the mid-Hudson region support 10-20 species of mollusks. Thus, it is possible to conclude only that human activities have destroyed much of the original mollusk fauna in some parts of the Hudson basin, but not in others. Little more can be said without a better historical record.

Origin of the freshwater mollusk fauna of the Hudson River basin

Because many species of mollusks are so slow at crossing drainage divides (van der Schalie, 1945), it often is possible to trace the zoogeographic origins of mollusk species. The Hudson River basin has had a complicated history of confluences with surrounding drainage basins. Nonetheless, it is possible to divide most of its mollusk fauna into four zoogeographic groups: introduced species, widely distributed species, Interior Basin species, and Atlantic Slope species.

Exotic species

Seven species of freshwater mollusks have become established in the Hudson basin through introduction by humans (Table 5). Most of these species are European in origin, presumably a result of commercial traffic between Europe and

Table 5. Species that have become established in the Hudson River basin through introductions by humans. The list excludes unsuccessful introductions and species that entered the basin through canals. The dates listed in the table are those when the species entered the Hudson River basin.

Species	Origin	Year
Prosobranch snails		
Valvata piscinalis	Europe	before 1976
Viviparus georgianus	Illinois	1868
Cipangopaludina chinensis	Japan	1890-1920
Bithynia tentaculata	Europe	ca. 1878
Pulmonate snails		
Radix auricularia	Europe	before 1867
Sphaeriid clams		
*Sphaerium corneum**	Europe	before 1976
*Pisidium amnicum**	Europe	before 1983

* Identification not positive (see text).

northeastern North America. *Viviparus georgianus* was deliberately introduced from Illinois by James Lewis (see above). *Cipangopaludina chinensis* was brought to California in the 1890's (Jokinen, 1982) and may have been released in the Hudson basin by amateur aquarists. Except in the case of *V. georgianus* (Fig. 4), we do not have enough information to sketch even the outlines of the spread of these seven species within the Hudson basin.

Some of these introduced species have become common (*Viviparus georgianus, Cipangopaludina chinensis*) or even dominant (*Bithynia tentaculata*) members of the local mollusk fauna. Exotic species are likewise prominent in other parts of the biota of the Hudson basin. For example, 21 of the 124 fish species known from the Hudson basin are introduced (Schmidt, 1986), and especially in the tidal Hudson River, exotic species are conspicuous and abundant (the black basses *Micropterus* spp., the water chestnut *Trapa natans*, the Eurasian water milfoil *Myriophyllum spicatum*, etc.). The prominence of exotic species in the Hudson basin is likely due both to the intensive human activity in the basin and to the relatively impoverished native biota of the basin, which may not have offered much competitive resistance to invaders. We know little about the role such exotic species play in the community and the ecosystem, and little about how communities and ecosystems functioned prior to the arrival of these dominant exotics.

It is interesting that Table 5 is dominated by prosobranch snails, and includes no unionid clams. I would have expected the list of exotics to be dominated by pulmonate snails. Pulmonates are air-breathers, hermaphrodites, and ecologically tolerant, all of which should make them good candidates for introduction. I have no explanation for the lack of European pulmonates in Table 5, except to repeat Te's (1978) suggestion that some European pulmonates might not be recognized as exotics without careful study. Many European pulmonates closely resemble American relatives (*e.g., Stagnicola palustris* and *Stagnicola elodes, Physella acuta* and *Physella heterostropha, Aplexa hypnorum* and *Aplexa elongata*) and would be misidentified as common American species unless they were examined carefully. As for the unionids, these large clams seem much less likely to be transported accidentally by humans. However, Lewis did bring some unionids from the Interior Basin into the Mohawk basin in Herkimer Co. (Lewis, 1867), but none of these introductions seems to have taken hold.

Species of wide distribution

Many mollusks apparently spread cross-country over drainage divides readily, forming broad geographic ranges that are not clearly related to drainage patterns or historical events. About half of the species in the Hudson basin, including almost all of the pulmonate snails and sphaeriid clams, belong to this category (Table 6). Both the pulmonates and the sphaeriids are hermaphroditic, and many species are small, ecologically widespread, or both. The few prosobranchs that fall into this category are either small and easily transported (all of the species except *Campeloma decisum*), or have a means of reproduction that is unusual among the prosobranchs and which probably facilitates colonization (the *Valvata* spp. are hermaphrodites, *C. decisum* is a parthenogen, while most other prosobranchs are gonochores.). There also is a unionid included in Table 6; I will discuss this species in more detail in the section on the Atlantic region species.

Table 6. Species of wide distribution belonging to the fauna of the Hudson River basin.

Prosobranch snails	Pulmonate snails
Valvata sincerac *Valvata tricarinata* *Campeloma decisum* *Marstonia lustrica* *Amnicola limosa*	ca. 27 species
Unionid clams	**Sphaeriid clams**
Strophitus undulatus	20 species

Table 7. Species from the Interior Basin known from the Hudson River basin.

A. Species that probably entered the Hudson basin *via* postglacial confluences with the Great Lakes

Prosobranch snails	Unionid clams
Probythinella lacustris? *Lasmigona compressa* *Lasmigona costata*	*Anodontoides ferussacianus* *Lasmigona compressa* *Lasmigona costata*

B. Species that probably entered the Hudson basin *via* the Erie Canal

Prosobranch snails	Unionid clams
*Birgella subglobosa** ? *Cincinnatia cincinnatiensis** ? *Elimia livescens* *Pleurocera acuta*	*Fusconaia flava* *Alasmidonta calceolus* *Alasmiconta marginata* *Anodonta grandis* *Anodonta imbecilis*
Pulmonate snails	*Lampsilis ovata* *Lampsilis siliquoidea*
Physella integra? *Physella vinosa?*	*Leptodea fragilis** *Proptera alata** *Villosa iris*

* Species of large rivers (see text for explanation.)

Interior Basin species

The Hudson basin is unusual among the Atlantic coastal drainages in containing many freshwater mollusks from the Interior Basin (Table 7). FollowingSmith (1985a), we can divide these species into two groups based on their distribution within the Hudson basin. Three species of unionids are widely distributed in the Hudson basin, occurring in several subbasins both above and below the fall line (Figs. 23a,c and 25 a). These same three species are the only Interior basin unionids that occur regularly in the Lake Champlain basin above the fall line (Smith, 1985a). It thus seems likely that these species entered the Hudson basin during early postglacial times and then dispersed into the Cham-plain basin during the Fort Ann stage of Lake Vermont, a scenario already discus-ed by Smith, 1982, 1983, 1985a).

Although *Probythinella lacustris* is not widespread in the Hudson basin, its presence in post-glacial marl deposits in Oneida Co. suggests that it too may have entered the basin from the west long before the opening of the Erie Canal.

Smith (1983) suggested that *Anodonta grandis* also entered the Hudson basin in early postglacial times. However, I believe that the species probably is a recent immigrant to the basin *via* the Erie and Champlain Canals. *Anodonta grandis* is one of the most eurytopic of the unionids, and occupies habitats similar to those used by *A. cataracta*. *A. grandis* has been found only near the upper Hudson and Mohawk Rivers (Fig. 26b), and was found only once above the fall line in the Lake Champlain basin (Smith, 1985a). In contrast, *A. cataracta* is very widespread in the Hudson and Champlain basin (Fig. 26a; Smith 1985a). If *A. grandis* had been an early immigrant to the Hudson basin, I would expect that its present-day distribution to resemble that of *A. cataracta*.

The other Interior Basin species listed in Table 7 are all more or less restricted to the Mohawk and Hudson Rivers, the Erie Canal, and immediately adjoining waters in the Hudson basin. These species probably entered the Hudson basin through the Erie Canal, and have not had the time or opportunity to disperse to suitable habitats in other parts of the Hudson basin. Several species, noted in Table 7, live chiefly in rivers and large lakes everywhere in their range. These species would not necessarily be expected to disperse into water away from the Mohawk and Hudson Rivers, regardless of their time of entry into the basin, so it is more difficult to determine when they entered the Hudson basin. I suspect that most, if not all, of these species entered the Hudson basin through the Erie Canal.

Atlantic Slope species

Finally, the Hudson basin contains 16 species, chiefly prosobranchs and unionids, that belong to the Atlantic Slope fauna (Table 8). I have included the unionid *Ligumia nasuta* in Table 8, although previous authors (Ortmann, 1919; Johnson, 1970) thought that this species belonged to the Interior Basin fauna, and moved east along the Erie Canal. *L. nasuta* is widespread in Atlantic Coastal drainages from Virginia to the St. Lawrence River, Canada (Johnson, 1970). In the Interior Basin, *L. nasuta* is found only in the drainages of Lakes Ontario, Erie, St. Clair, and Huron (Ortmann, 1919; van der Schalie, 1936, 1938; LaRocque & Oughton, 1937; Clarke & Berg, 1959). It is not known from any part of the Mississippi River basin, and is found south of the glacial border only on the Atlantic Slope. It seems likely that *L. nasuta* is an Atlantic Coast species that moved west up the Trent or Ottawa River outlets to the upper Great Lakes, following the route described for *Elliptio complanata* (= *E. violaceus*) by Ortmann (1919).

Table 8. Species of the Atlantic region found in the Hudson River basin.

Atlantic Slope species	
Prosobranch snails	**Unionid clams**
Lioplax subcarinata	*Elliptio complanata*
Gillia altilis	*Alasmidonta undulata*
Amnicola grana	*Alasmidonta varicosa*
Amnicola pupoidea	*Anodonta cataracta*
Elimia virginica	*Anodonta implicata*
	Lasmigona subviridus
Pulmonate snails	*Lampsilis cariosa*
	Lampsilis ochracea
Physella ancillaria?	*Lampsilis radiata*
	Ligumia nasuta

There are at least five ways that Atlantic Slope species could have entered the Hudson basin. During the height of the Wisconsin glaciation, sea level stood about 100 m lower than the present-day level, exposing parts of the continental shelf (Flint, 1971). Thus, although all of the current drainage of the Hudson River was glaciated, destroying its mollusk fauna, part of the now-submerged lower Hudson basin of full glacial mollusk fauna could have survived the glaciation in this refugium, and then spread north into the upper Hudson basin following deglaciation.

Similarly, parts of Georges Bank, the Sable Island Banks, and the Grand Banks may have been exposed during full glacial times, and might have provided a refuge for freshwater mollusks, which could have then dispersed west into the Hudson basin. Schmidt (1986) presented evidence to suggest that about 20 species of freshwater fish may have used this refuge.

I know of no evidence that could be used to tell which, if any, of the species of Table 8 rode out glaciation anywhere on the continental shelf.

A third route into the Hudson basin was provided by the opening of the Delaware and Hudson Canal in 1829, which linked the Neversink River of the Delaware basin with the Rondout Creek of the Hudson basin. Lewis (in Marshall, 1895b) believed that *Lioplax subcarinata* entered the Hudson basin *via* this route. I have no way of knowing if Lewis was right, or if any other of the species from Table 8 used the Delaware and Hudson Canal to enter the Hudson basin.

The Chenango Canal, which linked the waters of the upper Susquehanna drainage with those of the upper Mohawk, could also have allowed for the dispersal of Atlantic Slope species into the Hudson basin. I know of no examples of species that used this route.

Finally, species could have moved north along the coast, along brackish coastal waters or ephemeral postglacial drainage confluences, or across drainage divides.

Origin and relations of the Atlantic Slope fauna

Ortmann (1913) discussed the origin of the Atlantic Slope fauna and its relationships to the fauna of the Interior Basin. Ortmann's conclusions were reviewed and extended by Johnson (1970), who was especially interested in the history and zoogeography of the fauna of the southern Atlantic Slope: *i.e.*, south of the Potomac River. Ortmann's primary conclusions were:

i) the Appalachian Mountains have formed an effective zoogeographic barrier for unionids and some other freshwater invertebrates, resulting in distinct Atlantic slope and interior Basin faunas.

ii) the Atlantic Slope fauna is a depauperate and essentially derivative fauna. With a few exceptions (*e.g.*, *Lexingtonia*), species of the Atlantic Slope fauna are derived from Interior Basin species, and there has not been much evolutionary radiation on the Atlantic Slope. Most of the species and genera of the Interior Basin have not been successful in crossing the Appalachians. Ortmann suggested that unionids had dispersed around both the southern and northern ends of the Appalachians, as well as crossing the central Appalachians *via* stream captures in a few cases (*e.g.*, *Lasmigona subviridus*).

iii) the unionid fauna is almost uniform among drainage basins of the Atlantic Slope, suggesting to Ortmann that confluences have been common on the coastal plain.

iv) species richness of unionids declines slowly from mouth to headwaters in streams of the Atlantic basin, in contrast to the situation in Interior Basin streams, where there is a marked loss of species from mouth to headwaters. Ortmann attributed this difference to the relatively smooth longitudinal profiles of streams of the Atlantic Slope, which allowed unionid species to penetrate into the headwaters more easily.

Ortmann's main conclusions were well supported by zoogeographic and geological data, and I do not wish to dispute them. Nonetheless, it may be useful to add a few notes to Ortmann's ideas on the origin of the Atlantic Slope unionacean fauna.

First, I can offer an alternative explanation for (iv), the relatively small decline in species richness from mouth to headwaters in Atlantic Slope streams. The species most likely to be successful at crossing or going around the Appalachians, by stream capture, passive dispersal, or whatever, are eurytopic or small-stream species. Thus, we would not expect to find that specialized or large-river genera such as *Plethobasus*, *Quadrula*, *Dysnomia*, *Megalonaias*, and so on, had been successful at crossing the Appalachians. Indeed, the Atlantic Slope fauna is dominated by genera characteristic of small streams (*Lasmigona*, *Alasmidonta*) or genera with eurytopic species (*Elliptio*, *Anodonta*, *Lampsilis*). This scenario results in a mollusk fauna impoverished in large-river species. Ortmann's observation can be reworded as the lack of an increase in species richness in large rivers, rather than the enhanced penetration of headwaters by unionids, and seen as a consequence of the inability of large-river species to cross the Appalachians.

Such an interpretation immediately draws attention to the several Atlantic Slope unionids that are found chiefly in large rivers. There are three such species in the Hudson basin: *Anodonta implicata*, *Lampsilis ochracea*, and *Ligumia nasuta*. *L. nasuta* apparently is related to *L. subrostrata* of the Interior Basin, which lives in lakes, ponds, sloughs, and the backwaters of rivers, habitats similar to those used by *L. nasuta*. *A. implicata* and *L. ochracea* have traditionally been considered as close relatives of *A. grandis* and *L. ovata* of the Interior Basin (Ortmann, 1913; Johnson, 1970), but Kat's (1983a,b) recent work has shown both *A. implicata* and *L. ochracea* to be only distantly related to other members of their genera. Both of these species live in peculiarly coastal environments (tidal rivers, coastal ponds), and presumably use anadromous fish as hosts (Johnson, 1946, 1947; Davenport & Warmuth, 1965; Smith, 1985b), although little is known of the life history of *L. ochracea*. All of this evidence suggests that the ancestors of these two species crossed the Appalachians a long time ago, and that *A. implicata* and *L. ochracea* have had considerable time to adapt to an environment and host fish that were foreign to their Interior Basin progenitors.

There are two more species, both commented upon by Ortmann (1913), that deserve special attention: *Strophitus undulatus* and *Margaritifera margaritifera*. *S. undulatus* is the only species of unionid that is widespread on both sides of the Appalachians. Ortmann (1913) believed that *S. undulatus* crossed the Appalachians from the Interior Basin through stream capture, probably in the headwaters of the West Branch of the Susquehanna River, and then spread throughout the Atlantic Slope. It would be remarkable for enough time to have elapsed for *S. undulatus* to spread throughout Atlantic Slope drainages, even above fall lines, without there being evolutionary differentiation from the Interior Basin population, at least at the subspecific level. Malacologists formerly recognized two species of *Strophitus*; the Atlantic Slope *S. undulatus* and the Interior Basin *S. rugosus* (= *edentulus*), but Ortmann (1919) and Clarke & Berg (1959) synonymyzed the two species. Shells of *Strophitus* are variable and relatively featureless, so that investigations of shell characters alone, as most previous taxonomists have done, might not reveal subtle genetic differentiation. I would suggest that two species (or subspecies) of *Strophitus* may now be included under *S. undulatus*, and that the situation should be investigated using modern taxonomic methods.

Finally, *Margaritifera margaritifera* has a distribution unlike that of any other unionacean (Walker, 1910; Ortmann, 1913). *Margaritifera margaritifera* is a circumboreal species found on the Atlantic Slope from Pennsylvania to Labrador, and in Iceland, northern and western Europe, northern Asia and Japan (Walker, 1910). The closely related or conspecific *M. falcata* inhabits coastal streams from New Mexico and California to southern Alaska, plus streams of the upper Missouri River basin in Montana (Clarke, 1981a). Both species are known chiefly from cold, softwater streams, and both use salmonids as hosts (Fuller, 1974). *Margaritifera margaritifera* is the only unionacean known both from Europe and North America, and it is difficult to explain how a single species could have such a broad distribution. Previous explanations (Walker, 1910; Johnson, 1970) have suggested that *M. margaritifera* migrated between continents on land bridges or attribute its distribution to continental drift (Smith, 1976). Although the distribution of *M. margaritifera* may well have originated through continental drift, it is difficult to believe that obvious genetic and morphological differences between European and North American populations would not have arisen in the millions of years since the continents were separated.

As an entirely speculative alternative, I suggest that *Margaritifera margaritifera* is carried between drainages and between continents by the migrations of anadromous salmonids such as the Atlantic salmon, *Salmo salar*. Once *M. margaritifera* has reached appropriate habitats in a basin visited by anadromous salmonids, it could use local salmonids (*e.g.*, the brook charr *Salvelinus fontinalis* in northeastern North America and the brown trout *Salmo trutta* in Europe) as hosts. Young salmon migrating into the ocean do carry glochidia for at least a few days after their entry into the estuary (Hare & Burt, 1976). However, I have found no records of glochidia on ocean-going salmonids (*e.g.*, Heitz, 1920), nor do I have any evidence that a glochidium of *M. margaritifera* can remain quiescent but alive for the 1-5 years that salmonids remain at sea. Nonetheless, the distribution of *M margaritifera* is highly suggestive of such an alternative. *Margaritifera margaritifera* is absent from the entire North American interior Basin (excepting the extreme upper Missouri River, which it apparently reached by stream capture), despite the widespread occurrence of salmonids there, perhaps reflecting the inaccessibility of this region to migraory salmonids. *Salmo salar* is (or was, prior to European settlement) widespread in rivers from the Connecticut River northeast to Newfoundland and Labrador. *Margaritifera margaritifera* also is widespread throughout this range, but is known from a few sites southwest of the Connecticut River: Tributaries of Oneida Lake, New York (Clarke & Berg, 1959), the headwaters of the Hackensack River, New York (Jacobson & Emerson, 1971), and the headwaters of the Little Schuykill River, Pennsylvania (Ortmann, 1919). Atlantic salmon formerly spawned in the tributaries of Oneida Lake (Forney, 1980). As for the other two sites, I suggest that these streams may have been used by salmon during glacial times. All of the streams presently used by Atlantic salmon were covered by Wisconsin glaciers (Flint, 1971), so the salmon must have spawned elsewhere, perhaps south of the glacial border. It is striking that *M. margaritifera* is not known from streams in the Appalachians south of Pennsylvania, although brook charr are native along headwater streams in the Appalachians south to Georgia. The distributions of *M. margaritifera* and *M. falcata* likewise closely follow those of anadromous salmonids throughout the world. However attractive the coincidence between salmonid and margaritiferid distribution, my scenario cannot be accepted unless glochidia of *Margaritifera* are found on ocean-going salmonids.

To summarize, the Hudson River basin has had a complicated history of natural and man-made drainage confluences with other drainage basins, and consequently its mollusk fauna contain species of several different zoogeographic origins. Of the 96 species of freshwater mollusks known from the basin, seven were introduced by humans (Table 5), 53 species are broadly distributed in North America (Table 6), 20 species entered the basin from the Interior Basin, 4 species in pre-Columbian times and the remaining 16 probably through the Erie and

Champlain Canals (Table 7), and 16 species belong to the fauna of the Atlantic Slope (Table 8).

Some interactions between zoogeography and ecology

I have emphasized at several points that ecological characteristics of a species, such as its size, life history, and habitat specificity, may influence its dispersal ability. Thus, as we move further from glacial refugia, I would expect the mollusk fauna to become relatively rich in small species, hermaphroditic or parthenogenetic species, ecologically tolerant species, and short-lived species. Thus, we would expect the mollusk fauna to become rich in pulmonates and sphaeriids and poor in prosobranchs and unionids as we move to zoogeographically more remote regions. Available data support this trend (Table 9).

TABLE 9. Species composition of the freshwater mollusk fauna in areas of different distances from the presumed refugium and evolutionary center in the Tennessee River drainage. Basins are listed in order from near to far. Un = unionaceans, Pr = prosobranchs, Pu = pulmonates, Sp = sphaeriids.

Basin	Un	Pr	Pu	Sp	% (Un + Pr)	Source*
Tennessee R.	~85	~70	~25	~15	79	2, 3, 4
Wabash R.	66	35	34	~19	66	6, 3
L. Erie (MI)	38	~18	~32	25	50	1, 4, 8, 11
L. Erie (NY)	28	19	30	~27	45	3, 10
Central NY	27	16	25	~27	45	3, 5, 7
Hudson R.	24	19	~31	22	45	this study
State of Connecticut	12	11	26	~20	33	3, 9

* Sources: 1 = Berry (1943); 2 = Burch (1975a); 3 = Burch (1975b); 4 = Burch (1982); 5 = Clarke & Berg (1959); 6= Goodrich & van der Schalie (1938); 7 = Harman & Berg (1971); 8 = Heard (1962); 9 = Jokinen (1982); 10 = Robertson & Blakeslee, modified (1948); 11 = van der Schalie (1938).

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