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DOUGLAS G. SMITH

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The zoogeography of the freshwater mussels of the Taconic and southern Green mountain region of northeastern North America (Mollusca: Pelecypoda: Unionacea)

DOUGLAS G. SMITH
Museum of Zoology, University of Massachusetts, Amherst, MA, U.S.A. 01003–0027
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The Taconic and southern Green mountains form a system of ridges drained by four watersheds in eastern New York and western New England: Lake Champlain and the Housatonic, Hudson, and Connecticut rivers. Ten species of mussels distributed among the Margaritiferidae and Unionidae are recorded, based on museum records and recent collections, from the area. The presence of species representing two regional faunas, the Mississippian and Northern Atlantic Slope, indicates that some western streams of the Taconic Mountain region were connected with both the Atlantic coastal and interior Mississippian drainages during the Late Pleistocene. However, a divide has persisted along the north–south trend of the two mountain chains that has prevented late glacial east–west migration between the Hudson River – Lake Champlain systems in eastern New York and the Connecticut River – Housatonic River systems in western New England.

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Le sud des Montagnes Vertes et les monts Taconic constituent un système de crêtes drainé par quatre systèmes hydrographiques dans l'est de l'état de New York et l'ouest de la Nouvelle-Angleterre; le lac Champlain et les rivières Housatonic, Hudson et Connecticut. Dix espèces de moules, Margaritiferidae et Unionidae, retrouvées à la fois dans les collections de musée et les collections récentes, habitent la région. La présence d'espèces de deux faunes régionales différentes, celle du Mississipi et celle du versant de l'Atlantique Nord, indique que certains ruisseaux du versant ouest des monts Taconic ont été reliés à la fois au bassin de la côte Atlantique et au bassin intérieur du Mississipi vers la fin du Pléistocène. Cependant, les gradients nord–sud des deux chaînes de montagnes sont restés séparés et cette division a empêché la migration est–ouest à la fin des glaciations entre les systèmes Rivière Hudson – Lac Champlain dans l'est de l'état de New York et les systèmes Rivière Connecticut – Rivière Housatonic de l'ouest de la Nouvelle-Angleterre.

[Traduit par le journal]

Introduction

The Taconic and southern Green mountains form a continuous divide that separates the Hudson River and Lake Champlain drainages in eastern New York and western New England from the Housatonic and Connecticut River drainages in west-central New England. While conducting a comprehensive study on the late glacial zoogeographical history of the New England physiographic province, it was found that little information was available on the distribution of freshwater mussels in the Taconic – southern Green mountain region. Since the region represents an area of mixing between Atlantic slope and Mississippian mussel faunae (Walker 1913; Johnson 1980) it was decided to survey the region intensively. This report provides distributional and biological data gathered on the mussel species collected and proposes an expanded account of the late glacial zoogeographical history of the mussel fauna.

Methods and materials

Field work was performed during 1977–1980. The study area is within the physiographic borders of the Taconic Mountains and southern Precambrian Green Mountain massif, and encompasses nearly 4500 square miles (11 600 km^2) (Fig. 1).

Collecting was done by hand. Mostly fluvial habitats were sampled although small impoundments were also investigated. Small voucher series of living animals were retained for fluid preservation whereas conchological material was kept only where shells of deceased animals were found. All specimens saved for preservation were held in water from the collection locality and narcotized with ground menthol crystals. Following relaxation, usually after 24 to 36 h, 10% formalin was hypodermically injected into the pericardium of individual specimens. This killing method was especially effective in that the resultant hydrostatic pressure in the vascular system, brought about by the injection, caused the mantle and foot tissues to expand, thus revealing otherwise obscured anatomical details.

All preserved specimens were fixed in 10% formalin and stored in 70% isopropyl alcohol. Preserved material has been deposited at the Museum of Zoology, University of Massachusetts at Amherst (UMA), and conchological material has been deposited at the Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ).

Where sex could not be determined by gill morphology or where hermaphroditism was suspected, gonadal sections were prepared using conventional histological techniques (Smith 1979).

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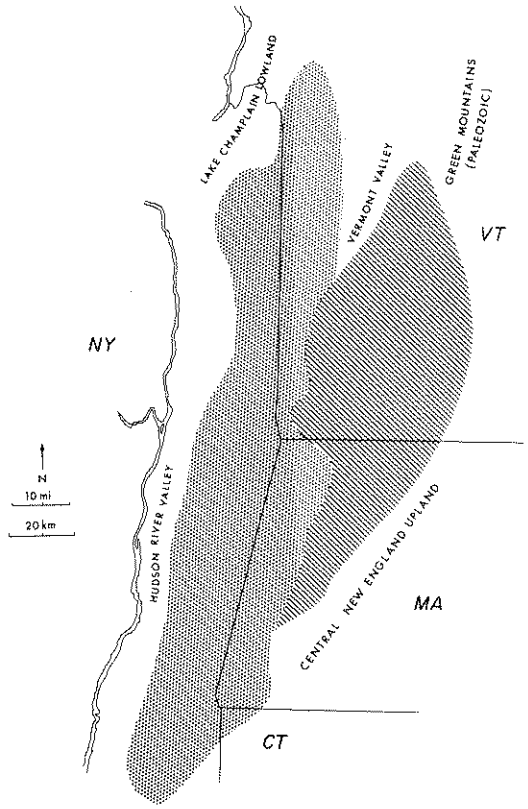

FIG. 1. Map of physiographic characteristics of western New England and eastern New York. Study region indicated by shaded portion. Stipple represents Taconic Mountain system, diagonal lines represent the southern (Precambrian) Green Mountain massif.

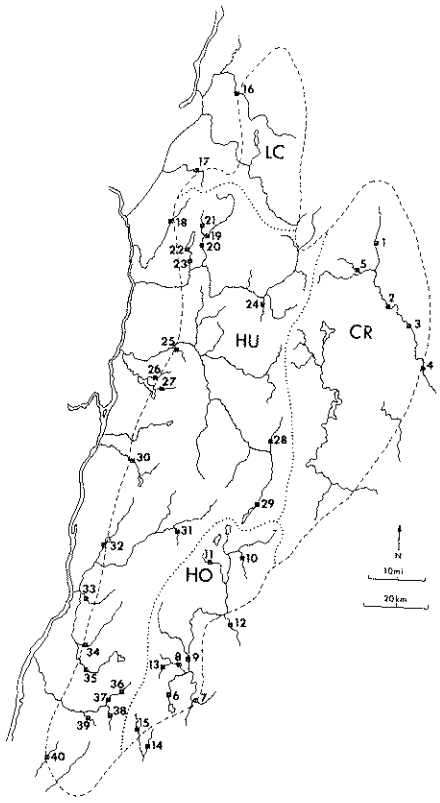

FIG. 2. Map of drainage patterns in the study area (- - -). Large lettered abbreviations indicate major drainage system (...): LC, Lake Champlain; HU, Hudson River; HO, Housatonic River; CR, Connecticut River. Numbers associated with squares indicate collection stations (see above).

During the spring, fish collections were made along with mussel collections. Individual preserved fish were subsequently examined for glochidial attachment.

Mussel collection stations [Fig. 2]

Connecticut River system—(1) West River, 1.2 km N Londonderry, Windham Co., VT; (2) West River, 4.5 km SE Jamaica, Windham Co., VT; (3) West River, 4.0 km S Townshend, Windham Co., VT; (4) West River, 5.5 km NNW Brattleboro, Windham Co., VT; (5) Mill Brook, 7.0 km NW Jamaica, Windham Co., VT.

Housatonic River system—(6) Schenob Brook, 8.0 km SW Sheffield, Berkshire Co., MA; (7) Konkapot River, 6.5 km S Sheffield, Berkshire Co., MA; (8) Hubbard River, 1.5 km N Sheffield, Berkshire Co., MA; (9) Housatonic River, 3.0 km S Great Barrington, Berkshire Co., MA; (10) Konkapot Brook, 0.5 km S Stockbridge, Berkshire Co., MA; (11) Flat Brook, 3.5 km W West Stockbridge, Berkshire Co., MA; (12) Hop Brook, 0.5 km S Tyringham, Berkshire Co., MA; (13) Willard Brook, 2.5 km W Sheffield, Berkshire Co., MA; (14) Mudge Pond Brook, 1.0 km W Sharon, Litchfield Co., CT; (15) Webatuck Creek, 3.0 km S Millerton, Dutchess Co., NY.

Lake Champlain drainage—(16) Poultney River, 8.0 km N Hampton, Washington Co., NY; (17) Big Creek, 3.2 km W Hartford, Washington Co., NY.

Hudson River system—(18) Moses Kill, Argyle Center, Washington Co., NY; (19) Black Creek, West Hebron Village, Washington Co., NY; (20) Black Creek 4.8 km NW Salem, Washington Co., NY; (21) West Branch Black Creek, 3.2 km N West Hebron Village, Washington Co., NY; (22) S end Cossayuna Lake (impoundment), Washington Co., NY; (23) Whittaker Brook, 4.5 km E North Greenwich Village, Washington Co., NY; (24) Warm Brook, 2.2 km S Arlington, Bennington Co., VT; (25) Nipmoose Creek, 9.5 km NNE Pittstown, Rensselaer Co., NY; (26) Otter Creek, 6.0 km NE Pittstown, Rensselaer Co., NY; (27) Sunkauissia Creek, 0.8 km N Pittstown, Rensselaer Co., NY; (28) Mauserts Pond (impoundment), Clarksburg, Berkshire Co., MA; (29) Hoosic River (Cheshire Reservoir outlet), Cheshire, Berkshire Co., MA; (30) Wyants Kill, 4.7 km W Sand Lake, Rensselaer Co., NY; (31) South Branch Wyomanock Creek, 0.5 km S New Lebanon, Columbia Co., NY; (32) Valatie Kill, Nassau Center, Rensselaer Co., NY; (33) Fitting Creek, 15.0 km E Stockport, Columbia Co., NY; (34) Claverack Creek, 1.2 km S Claverack, Columbia Co., NY; (35) Taghkanic Creek, 2.0 km SE Taghkanic, Columbia Co., NY; (36) Roeliff Jansen

TABLE 1. Distribution of species collected by faunal affinity, elevation, and locality

Species	Faunal affinity	Elevation range (m)[a]	Collection stations
Margaritifera margaritifera	A[b]	164–350	1, 2, 5
Elliptio complanata	A	61–277	3, 6, 7, 8, 9, 10, 11, 12, 14, 15, 16, 18, 27, 30, 32, 33, 35, 36, 37, 38, 40
Lasmigona costata	M	61–91	16, 17
Lasmigona compressa	M	61–151	16, 17, 18, 19, 20, 21, 25, 33
Alasmidonta undulata	A	61–227	7, 10, 12, 13, 15, 16, 17, 19, 20, 23
Alasmidonta varicosa	A	79–164	2, 3, 4
Anodonta c. cataracta	A	61–197[c]	6, 9, 19, 22, 26, 28, 29, 31, 32, 33, 36
Anodontoides ferussacianus	M	61–161	16, 17, 18, 19, 20, 33, 39
Strophitus undulatus	C	61–277	2, 4, 5, 10, 11, 12, 13, 17, 24
Lampsilis ovata	M	61	17

[a]Above sea level.
[b]A, Atlantic; M, Mississippian; C, Cosmopolitan (A and M).
[c]Populations were found in impoundments up to 328 m, but these may represent introductions.

Kill, 1.5 km NW Copake, Columbia Co., NY; (37) Roeliff Jansen Kill, 4.8 km N Ancramdale Village, Columbia Co., NY; (38) Punch Brook, 3.0 km E Ancram, Columbia Co., NY; (39) Shekomeko Creek, Pachin Mills Village, Dutchess Co., NY; (40) Little Wapinger Creek, Clinton, Dutchess Co., NY.

Results

The present study revealed 10 species occurring in the Taconic and southern Green mountain region. Most of the species encountered are typically referred to as "creek" species (Ortmann 1919; Baker 1928) and are characteristic of upland streams. Two species, *E. complanata* and *A. c. cataracta*, are ubiquitous throughout the northern Atlantic and parts of the Great Lakes drainages and are ordinarily found at various altitudes in both lotic and lentic environments.

Among the four watersheds surveyed, the Lake Champlain drainage contained the most diverse fauna comprising seven species. The Hudson River contained six species, whereas the Housatonic River and Connecticut River systems contained four each.

Family Margaritiferidae

Margaritifera (*Margaritifera*) *margaritifera* (Linné)

Marshall (1895) listed Lake Champlain drainage records for this species. Two specimens of this species presently exist (NYSM[1] 31875) that were collected from Lake Champlain. However, no other information is available. Elsewhere, in the Lake Champlain drainage, the species has been collected from the Winooski River, Montpelier, "High Bridge" (presumably Washington Co.), Vermont, by C. Goodrich (MCZ 146611 and 152024). However, W. Clench and R. Turner (MCZ records) did not collect this species in the same vicinity during the 1940s. Marshall (1895) gave the Winooski River as a locality, listing B. Walker as the authority. Adams (1841) recorded *M. margaritifera* from the Onion River, Burlington (presumably Chittenden Co.), Vermont, which is near Lake Champlain. However, no specimens, supposedly part of the Adams collection and now at the MCZ, presently exist. All these records are in need of confirmation.

All four individuals collected were histologically determined to be gonochoristic, which is consistent with other *M. margaritifera* populations from New England (Smith 1979).

Family Unionidae

Elliptio complanata (Lightfoot)

In the study area the species has been previously collected in lakes Bomoseen (MCZ 187042) and St. Catherine (MCZ 187041 and 197382), both in Poultney Tp., Rutland Co., Vermont, and in the Lake Champlain drainage. During the present investigation, a subsequent collection was made in Lake St. Catherine, Rutland Co., Vermont, 21 September 1978 (UMA MO. 1068). Other previous collectors have found the species in Pontoosac Lake (MCZ 147862), and Crane Pond (MCZ 14864), both in Berkshire Co., Massachusetts and both draining to the Housatonic River. The species occurs in all four drainages investigated.

Lasmigona (*Lasmigona*) *costata* (Rafinesque)

A species of the Mississippian region, *L. costata* previously has been reported from the Mohawk River (Lewis 1861; Ortmann 1919) and the "canals" around Troy, New York (Aldrich 1869). Extant specimens collected during the nineteenth century from the Hudson River system are distributed among the following localities: Norman's Kill, Albany (MCZ 252180, NYSM 31434), the Mohawk River, Cohoes (NYSM 31650), and the Hudson River, Albany (NYSM 31832).

[1]New York State Museum.

In the Lake Champlain system in Vermont, *L. costata* was collected by Adams (1841). During the present study, *L. costata* was found only in the Lake Champlain drainage.

Lasmigona (*Platynaias*) *compressa* (Lea)

A common inhabitant of the upper Mississippi and Great Lakes drainages, *L. compressa* has been known from the Hudson River system since its description, and still others discussed by Marshall (1890) (extant in NYSM), came from Norman's Kill, near Albany. The presence of this species in the Mohawk River system has been noted by Lewis (1861), Call (1878), and Gray (1883). Elsewhere, Aldrich (1869) mentioned the rare occurrence of *L. compressa* in the "Northern canal" around Troy. He also indicated that the species was known "to be plentiful in Hoosic River, farther north." This last statement would represent the only evidence for the occurrence of *L. compressa* in an eastern Hudson River tributary. In the Lake Champlain drainage in Vermont, *L. compressa* was collected by Adams (1841) and, 100 years later, by H. Athearn, W. Clench, and R. Turner (unpublished MCZ records). Collections made during the present investigation firmly establish the presence of *L. compressa* in the middle and upper eastern Hudson River system as well as the upper Lake Champlain drainage.

The species has been alleged to be hermaphroditic based on assessment of gross morphological characters (Ortmann 1911, 1919) and histological analysis (van der Schalie 1970). Histological investigation of 22 specimens collected in the present study substantiates earlier reports. Specimens of *L. compressa* in the study region are predominantly female–hermaphroditic (preponderance of female tissue). Occasionally specimens displayed neoplasia of unknown origin in gonadal tissue.

Alasmidonta (*Alasmidonta*) *undulata* (Say)

This species was collected in three out of four drainages investigated. It was absent from the Connecticut River drainage. *Alasmidonta undulata* in the past has been reported from all four drainage systems (Adams 1841; Marshall 1895; Letson 1905; Johnson 1915).

The host fish for *A. undulata* has never been determined. In Warm Brook, which is unispecific for *A. undulata*, large populations of two cyprinid fish species occur; the common shiner, *Notropis cornutus*, and the creek chub, *Semotilus atromaculatus*. At the time of collection, 22 May 1980, several fish, particularly creek chubs, contained encysted glochidia of *A. undulata* attached to the gills, the soft lining of the gill chamber, and, rarely, the trailing edges of ventral fins. Development of glochidia was not ascertained, although it is suspected that the above fish species serve as hosts for *A. undulata*.

Alasmidonta (*Decurambis*) *varicosa* (Lamarck)

This species is apparently confined to the Connecticut River system within the study area and the present records constitute the first for the Connecticut River system in Vermont.

Specimens listed as "*Margaritana marginata*?" by Aldrich (1869) and reported as occurring rarely in the "Northern canal" may be referrable to *A. varicosa*. However, uncertainty of the exact identity of "*Margaritana marginata*" in subsequent reports (e.g., Marshall 1895) precludes a solution as to whether *A. varicosa*, or its Mississippian counterpart, *A. marginata*, was encountered (see Ortmann 1919). No specimens from the eastern Hudson River – Lake Champlain region exist in the New York State Museum collections or at the Museum of Comparative Zoology, and early accounts regarding "marginata"-morph mussels in the Taconic Mountain region are in need of verification.

Anodonta (*Pyganodon*) *cataracta cataracta* (Say)

During the present study the species was found in the Hudson River and Housatonic River systems. In the study area, the establishment of *A. c. cataracta* populations in impoundments well within headwater regions of streams or in areas formerly polluted can best be explained as the result of successful introductions of glochidia-infected fish.

Anodontoides ferussacianus (Lea)

The presence of *A. ferussacianus* in northern Atlantic drainages has been in question since Marshall (1895) listed the species as occurring in the Delaware, Susequehanna, and Hudson river systems. Clarke and Berg (1959) did not consider Marshall's (1895) citations trustworthy and did not include the above drainages within the range of *A. ferussacianus*. Baker (1928) and La Rocque (1967) included both the upper St. Lawrence River system and the upper Mohawk River system in New York in its range (La Rocque 1967, p. 197, Fig. 87). Clarke and Berg (1959) did cite a collection of *A. ferussacianus* made by H. Athearn in Lake Champlain. Harman (1970) documented *A. ferussacianus* from the upper Susequehanna River system and, although allowing for the possibility of a recent transfer to the Susequehanna River system, stated that Marshall's (1895) data should be reconsidered.

Lewis (1861) listed the species from "canals and rivers" around Mohawk, presumably in the Mohawk River system, and several lots of *A. ferussacianus* from the Mohawk River system exist in the MCZ. Aldrich (1869) did not record the species from the Troy area, although Marshall (1890) listed material (extant in NYSM) from Norman's Kill, Albany Co. (description for Fig. 14 of Plate), a stream well within the Hudson River system near Albany. Two additional lots of *A.*

ferussacianus (MCZ 254649 and 260946, formerly of the NYSM collection) were collected from Norman's Kill, near Albany. Other previously overlooked series of collections of *A. ferussacianus* that were secured during the late nineteenth century from the lower and middle Hudson River system presently exist (MCZ 226246, 226260, and 226267, and NYSM 31381). The above listed records plus those added by the present study unquestionably establish this species' presence in the Hudson River and Lake Champlain drainages.

Strophitus undulatus (Say)

Prior to this study, two collections of *S. undulatus* are known to have been made in the Taconic Mountain region. Two shells of this species, collected in the nineteenth century, and formerly in the C. B. Adams collection (MCZ 154182), are labeled "Greenwich, New York." Greenwich is in Washington Co. and is situated near the Hudson River. The specimens were probably collected from the Batten Kill system, which drains to the Hudson River. Several valves of this species were also collected during the nineteenth century in the Hudson River system by J. G. Anthony (MCZ 161974), in "Kinderhook, New York" (Columbia Co.) and presumably from Kinderhook Creek. In the present study, *S. undulatus* was found in all four drainage systems.

The largest size record for *S. undulatus* is provided by Ortmann (1919), who listed 106 mm as maximum shell length for specimens from Pennsylvania. Clarke and Berg (1959) state that the species ranges between 60 and 90 mm shell length in New York. During the current investigation, specimens occurring in Willard Brook (UMA MO. 1119), just below a small impoundment, were commonly near or over 100 mm shell length. Shell measurements of the three largest specimens collected are given below (in millimetres).

Length	Height	Width
107.3	57.4	38.4
111.5	55.5	43.4
113.1	56.8	41.9

Lampsilis ovata (Say)

A single record of this species was secured in the Lake Champlain drainage. This species has not been previously reported from the Lake Champlain drainage in New York although its presence in Lake Champlain has long been known (Adams 1841).

Discussion

The present distribution of freshwater mussels in the Taconic and Green mountain regions (Table 1) is the result of late-glacial and post-glacial migration from refugia south of the terminus of the Wisconsin glaciation. Simpson (1896) provided an anecdotal history of late-glacial migration of mussel species into the study region. The present account expands Simpson's (1896) ideas and, using recent geological data, suggests a specific chronology of dispersal events.

Founder populations of mussels were derived from southern Atlantic coastal and central Mississippian refugia. Several species, including *L. compressa* and *A. ferussacianus*, entered glacial Lake Iroquois from the south or west following its filling about 12 600 BP (Karrow et al. 1961) and sometime before its draining to modern Lake Ontario levels and the closing of the Rome outlet in the Mohawk Valley (Hough 1963). At this point ice was permanently gone from the Lake Iroquois shore and modern lacustrine conditions were developing. Prior to the final retreat of Port Huron ice from the lakeshore, tremendous influx of sediments into the lake from preglacial outwash would have probably made habitation by infaunal mollusks nearly impossible (Muller 1977).

Lasmigona compressa and *A. ferussacianus*, as well as *L. costata*, eventually became established in the Glacio–Iromohawk River via the Rome outlet and, following its course downstream, reached the Hudson River valley during the Lake Fort Ann stage about 12 000 BP when shallow "river-like" rather than "lake-like" conditions prevailed (Dineen and Rogers 1979). Near the mouth of the Glacio–Iromohawk River the channel divided and water flowed through any of three outlets to Lake Fort Ann before permanently using the current, most southerly course at Albany as the drainage route (La Fleur 1979). Collectively, these water passages opened along a broad north–south stretch of Lake Fort Ann and probably permitted dispersal further north towards the Lake Champlain lowland. The presence of *L. compressa* and *A. ferussacianus* in the southern Lake Champlain drainages (Poultney River and Big Creek) suggests that the establishment of a Mississippian group of mussel species in Lake Champlain could have, in part, resulted from a northern dispersal via Lake Fort Ann. The "river-like" water occupied the Lake Champlain lowland as well and drained southward through the Hudson River valley (Coates 1976; Dineen and Rogers 1979). Alternatively, it is possible that the Champlain canal, connecting the Hudson River and Lake Champlain, allowed species exchanges to occur between the two drainage systems during historical times.

The absence of *L. costata* from any of the investigated upper Hudson River tributaries is unclear. Although only rarely documented from the middle Hudson River region, exclusive of the Erie canal, the species definitely belongs to the postglacial Hudson River fauna. Since

surveys in the eastern Hudson River system were undertaken in small upland streams, it might be that certain biological (e.g., absence of suitable host fish) or physical barriers precluded the species presence there. It is also possible that populations formerly established in eastern Hudson River tributary streams have since become extinct.

The presence of *Lampsilis ovata* in the southern Lake Champlain watershed (Big Creek) probably is best explained by a secondary invasion of modern Lake Champlain from the St. Lawrence River following the draining of the St. Lawrence Sea about 10 200 BP (Gadd 1976).

Atlantic slope mussel species dispersed northward into the Taconic and Green mountain regions from Atlantic coastal refugia. Occupation of upland streams probably did not occur until postglacial times following the final melting of residual ice blocks isolated in the higher altitude hills.

In the Hudson River valley, Atlantic slope species were probably contemporaneous with the Mississippian species found there, and possibly followed the same northerly route into the southern Lake Champlain lowland during the Lake Fort Ann stage. Further dispersal eastward into eastern Hudson River tributaries draining the Taconic and Green mountain ridge system continued into postglacial times. However, migration was halted somewhere west of the ridge as both *L. compressa* and *A. ferussacianus* are not now, nor have been, known to occur in the upper Connecticut and Housatonic river systems. Therefore, for mussel species dispersing into the Hudson River valley area from Mississippian refugia, the Taconic Mountain – Green Mountain divide was an absolute barrier to further dispersal eastward.

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