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HYBRIDIZATION IN A UNIONID FAUNAL SUTURE ZONE

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ABSTRACT

Retreat of the Wisconsinan glaciers and expansion of unionid geographic ranges has resulted in re-establishment of contact between Interior Basin and northern Atlantic Slope species isolated by the Appalachian Mountains at the height of glaciation. One suture zone between these faunas occurs in the area around Lake Champlain, and molecular genetic, anatomical, and shell microstructural data indicate hybridization between species of *Anodonta* and *Lampsilis*. Additionally, introgression appears to occur over a wide geographic area. *Elliptio* populations around Lake Champlain exhibit no evidence of hybridization, but form a locally differentiated group when compared to northern Atlantic Slope *E. complanata*. Hybrid *Anodonta* and *Lampsilis* populations contain variant alleles not found among parental species. Probability of hybridization is proposed to be best predicted by similarity of glochidial hosts between unionid species, not necessarily by levels of electrophoretically determined genetic differentiation. Taxonomic implications of the data are discussed.

Key words: hybridization; zoogeography; genetics; Unionidae; Bivalvia.

INTRODUCTION

Hybrid zones have long been of special interest to evolutionary biologists. Introgressive hybridization (Anderson, 1949) can potentially enhance the level of genetic variation and thus the evolutionary flexibility of populations. For instance, Sage & Selander (1979) and Hunt & Selander (1973) observed increased levels of heterozygosity as well as unique alleles in hybrid populations of frogs and mice. Such unique alleles have been proposed to arise through increased mutation rates among hybrid populations (Thompson & Woodruff, 1978), or through intragenic recombination between the different parental alleles (Watt, 1972). Also, Anderson & Stebbins (1954) have proposed that hybridization can trigger episodes of innovative diversification, and certain species of plants are known to have had a hybrid origin (Grant, 1966; Lewis, 1966; Gallez & Gottlieb, 1982).

Hybrid zones are often established by changes in distribution of one or both of the taxa involved. Geographic ranges of all North American unionids have probably fluctuated to some extent during the repeated Quaternary glacial episodes, but such fluctuations are best documented for species of the north-

ern Interior Basin and Atlantic Slope faunas (Simpson, 1896; Ortmann, 1913; Baker, 1920; Johnson, 1970, 1980; Clarke, 1973; Kat, 1982, 1983a, b, c; Smith, 1982; Kat & Davis, 1984). For example, fossil evidence has indicated that populations of at least three Interior Basin species were present on the Atlantic Slope about 200,000 years ago, but were subsequently eliminated by glaciers (Kat, 1983b). Contact between these faunas has recently been re-established by migration out of Wisconsinan refugia. One such suture zone (Remington, 1968) is located in the area around Lake Champlain. This lake has had a varied postglacial history including a saltwater phase and connections to both Interior Basin and Atlantic Slope drainages (Simpson, 1896; Clarke & Berg, 1959; Elson, 1969; Johnson, 1980; Smith, 1982). As a consequence of these historic connections and/or a more recent immigration route (via the Erie Canal system, which links Lake Erie, Lake Champlain, and the Hudson River), Lake Champlain and surrounding drainages contain species of both faunal regions (Smith, 1983). This area thus provides a natural experiment to determine the degree of genetic interaction between various members of these previously isolated faunas.

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Study of hybridization between Interior Basin and Atlantic Slope unionid species is of special interest for two reasons. First, because of patterns of Wisconsinan glaciation and the location of the hybrid zone, there is little uncertainty about its origin. This hybrid zone represents a postglacial secondary contact between taxa that existed in allopatry at the height of glaciation, and therefore can not be explained as differentiation within a continuous series of populations (Ender, 1977; White, 1978). Second, the Lake Champlain fauna allows study of the degree of interaction between species belonging to lineages that are diversifying at different rates, between species that differ in observed levels of heterozygosity and polymorphism, and between species that exhibit various levels of genetic differentiation.

Also included in this study is a genetic and morphological analysis of *Anodonta "cataracta" fragilis*. This taxon was thought by Clarke & Rick (1963) to represent an intergrade between *A. fragilis* from Newfoundland and northern Atlantic Slope *A. cataracta*. Previous studies, however, have indicated that Nova Scotian *A. "c." fragilis* are genetically distinct from *A. cataracta*, and that the taxon is more closely related to European than North American anodontines (Kat, 1983d, e; Kat & Davis, 1984). The taxonomic status of anodontines that resemble *A. fragilis* but occur outside Newfoundland is therefore still uncertain.

METHODS

Populations analysed in this study were collected from Lake Champlain and adjacent areas, as well as the Delmarva Peninsula, Nova Scotia, Michigan, and Wisconsin. The bivalves were maintained in aquaria for at least two weeks. Four individuals from each population were then relaxed (sodium nembutal) and fixed (10% formalin) in preparation for dissection. The remaining 20–25 individuals had wedges of tissue removed from the foot and viscera and these tissue samples were either homogenized and electrophoresed immediately or stored at -20° C for later analysis.

Starch-gel electrophoresis has been used with good success in a series of taxonomic analyses of the Unionidae (Davis *et al.*, 1981; Davis, 1983, 1984; Kat, 1983a, c, d; Kat & Davis, 1984). Methods for electrophoresis and enzyme staining were generally similar to

those of Davis *et al.* (1981), and 15 loci of which at least eight were polymorphic among species were scored using the methods of Ayala *et al.* (1973). Nei's (1972) genetic distances were computer generated using a program written by Green (1979). This genetic distance matrix was then used in the multivariate analysis program NT-SYS (Rohlf *et al.*, 1972). Multidimensional scaling maximized goodness-of-fit of the regression of genetic distance and distance in three-dimensional space, and a minimum spanning tree was derived from these adjusted distances. The minimum spanning tree summarizes taxonomic relationships since distances between closely related taxonomic units are small, whereas those between distantly related taxonomic units are large. Distance between taxonomic units is here defined as a function of the observed Nei distances. Such multivariate analyses are especially useful in elucidation of relationships among taxa such as *Elliptio* that exhibit considerable polymorphism at a number of loci.

Fine detail of unionid stomach anatomy can be used as a taxonomic tool at a variety of taxonomic levels (Kat, 1983a, c, d). Techniques for dissection and illustration are discussed in Kat (1983d). Four individuals from each population were dissected and photographed to determine levels of intrapopulation variability.

Microstructure of conchiolin layers within the shell was examined with a scanning electron microscope. Previous studies (Kat, 1983a, e) reveal that the conchiolin layer is divisible into three distinct regions, of which the central, reticulate region in particular contains species-specific characters. In the past, patterns of resemblance among unionid taxa based on conchiolin layer microstructure have been highly compatible with patterns of resemblance suggested by electrophoretic data, and conchiolin layer microstructure was successfully used to discriminate among two races of *Elliptio complanata* and their hybrids (Kat, 1983a). Techniques for conchiolin layer preparation and microscopy are detailed in Kat (1983e).

RESULTS

A. Molecular genetics

Distributions of alleles among loci that best discriminate species of *Anodonta* and *Lamps-*

TABLE 1. Distribution of alleles among loci of *Anodonta* examined in this study. Loci that do not discriminate among species are not included.

Enzyme	Allele	Species			
		<i>A. cataracta</i>	<i>A. grandis</i> × <i>cataracta</i>	<i>A. grandis</i>	<i>A. fragilis</i>
PGM I	24	1.00	.26	.05	
	22		.74	.95	
	20				1.00
PGM II	32		.29		
	31				1.00
	30	1.00	.71		
	28			1.00	
LAP	34			.35	
	32		.52	.65	
	30	1.00	.48		
	28				1.00
MDH I	18				.50
	15	1.00	1.00	1.00	
	13				.50
MDH II	— 9		.35	.55	
	— 11	1.00	.65	.45	1.00
HEX	34		.20	.20	
	31	1.00	.72	.80	1.00
	28		.08		
MPI	26		1.00	.65	
	23				0 to .15
	20	.33 to .48		.35	.85 to 1.00
	18	.52 to .67			
ODH	15		.61	.72	
	9				1.00
	6	1.00	.39	.28	

ilis are presented in Tables 1 and 2. Similar data are not presented for populations of *Elliptio* because *Elliptio dilatata* from Wisconsin appears to possess only two relatively rare alleles not present among Atlantic Slope *E. complanata* examined to date: MDH I 14 and HEX 34. Also, the number of populations examined and the high levels of polymorphism characteristic of *Elliptio* would require a table of excessive proportions.

It is clear from Table 1 that the *Anodonta* population in Lake Champlain shares alleles characteristic of both Atlantic Slope *A. cataracta* and Interior Basin *A. grandis*. However, the Lake Champlain population also possesses alleles not present in either parental species (HEX 28 and PGM II 32), and is fixed

for MPI 26. Over 15 loci examined, *A. cataracta* possesses 17 alleles, *A. grandis* 22, and *A. cataracta* × *grandis* 24: *A. grandis* shares 13 alleles with *A. cataracta* and 18 alleles with *A. cataracta* × *grandis*, while *A. cataracta* shares 14 alleles with *A. cataracta* × *grandis*. *A. "cataracta" fragilis*, however, is quite different from both *A. cataracta* and *A. grandis*. *A. "c." fragilis* has 18 alleles at the loci examined of which it shares 10 with *A. cataracta* and *A. grandis*. There is no evidence from electrophoresis to suggest any genetic exchange between *A. cataracta* and *A. fragilis*.

Table 2 presents allele frequencies for nine loci at which Atlantic Slope *Lampsilis radiata* differ from Interior Basin *L. siliquoidea*. Again, there is good evidence to support a hybrid

TABLE 2. Distribution of alleles among loci of *Lampsilis* examined in this study. Loci that do not discriminate among the parental species are not included.

Enzyme	Allele	Species		
		<i>L. radiata</i>	<i>L. radiata</i> × <i>siliquoidea</i>	<i>L. siliquoidea</i>
GPI	16	1.00	.90	.45
	10		.10	.55
PGM I	18	0 to .34		.20
	16	.62 to 1.00	.92	.80
	14		.08	
	12	.04 to .20		
PGM II	30		.05	.45
	28	.85 to 1.00	.95	.55
	26	.05 to .15		
LAP	34	.03 to .47	.35	.35
	32	.53 to 1.00	.50	.45
	30	.04 to .30		
	28		.15	.20
MPI	24	1.00	1.00	.70
	22			.30
6PGD	6	0 to .10		
	4	.70 to 1.00	.40	.45
	2	.04 to .30	.60	.55
G3PDH	11	0 to .13		
	9	0 to .60	.40	
	7	.40 to 1.00	.60	1.00
GPDH	32	1.00	.95	.70
	30		.05	.30
SOD II	- 7	1.00	.70	.08
	- 9		.30	.92

origin of the *Lampsilis* population in Lake Champlain, and this population also possesses an allele not present in either parental species (PGM I 14). *L. radiata* possesses a total of 26 alleles over the 15 loci examined, *L. siliquoidea* 25, and *L. radiata* × *siliquoidea* 26. *L. radiata* shares 19 alleles with *L. siliquoidea*, and 20 alleles with *L. radiata* × *siliquoidea*, while *L. siliquoidea* shares 24 alleles with the hybrid population.

In contrast to these examples of hybridization between species of *Anodonta* and *Lampsilis*, the population of *Elliptio* in Lake Champlain presents no evidence that it is of hybrid origin between Atlantic Slope *E. complanata* and Interior Basin *E. dilatata*. Rather, this

population exhibits affinities to regional populations of *E. complanata* in Vermont and Maine.

Nei's (1972) genetic distances and similarities between all pairs of *Anodonta*, *Lampsilis*, and *Elliptio* populations examined are presented in Tables 3, 4, and 5, respectively. Table 3 indicates that *A. "cataracta" fragilis* is genetically almost invariant from Nova Scotia through Maine and Vermont, and is distantly related to *A. cataracta* and *A. grandis*. *A. cataracta* and *A. grandis* are genetically similar at a level of $0.649 \pm .012$, which is comparable to levels of similarity among other species in the *cataracta* clade such as *A. gibbosa* from Georgia (Kat, 1983d). *A. cataracta* × *grandis* exhibits intermediate levels of

TABLE 3. Genetic distances (above the diagonal) and similarities (below the diagonal) between all pairs of *Anodonta* populations examined in this study. See Appendix for locations of the collection sites.

	Population										Species
	ME1	VT3	NS4	NS6	NS2	NJ2	DE2	NJ1	VT1	MI	
ME1	—	.001	.001	.001	.003	.544	.561	.568	.622	.585	<i>A. fragilis</i>
VT3	.999	—	.001	.001	.002	.542	.559	.566	.620	.583	<i>A. fragilis</i>
NS4	.999	.999	—	.001	.003	.541	.558	.564	.616	.538	<i>A. fragilis</i>
NS6	.999	.999	.999	—	.003	.541	.558	.564	.616	.538	<i>A. fragilis</i>
NS2	.998	.998	.999	.999	—	.542	.557	.563	.609	.581	<i>A. fragilis</i>
NJ2	.581	.582	.582	.582	.582	—	.003	.003	.222	.453	<i>A. cataracta</i>
DE2	.571	.572	.572	.572	.573	.999	—	.001	.224	.420	<i>A. cataracta</i>
NJ1	.567	.568	.569	.569	.570	.998	.999	—	.225	.423	<i>A. cataracta</i>
VT1	.537	.538	.540	.540	.544	.801	.800	.799	—	.124	hybrid
MI	.557	.558	.584	.584	.560	.636	.657	.655	.883	—	<i>A. grandis</i>

TABLE 4. Genetic distances (above the diagonal) and similarities (below the diagonal) between all pairs of *Lampsilis* populations examined. See Appendix for locations of collection sites.

	Population												Species
	NS7	NS4	NS1	NB	NS3	VT3	DE3	MD1	ME4	DE1	VT1	MI	
NS7	—	.014	.004	.009	.021	.022	.020	.023	.029	.051	.056	.209	<i>L. radiata</i>
NS4	.986	—	.011	.012	.033	.025	.024	.019	.031	.047	.052	.199	<i>L. radiata</i>
NS1	.999	.984	—	.011	.025	.026	.022	.027	.033	.059	.064	.212	<i>L. radiata</i>
NB	.991	.988	.989	—	.014	.018	.011	.011	.017	.029	.047	.218	<i>L. radiata</i>
NS3	.979	.968	.976	.986	—	.017	.003	.016	.014	.031	.052	.231	<i>L. radiata</i>
VT3	.978	.975	.974	.982	.983	—	.019	.016	.016	.027	.027	.204	<i>L. radiata</i>
DE3	.980	.977	.978	.989	.996	.981	—	.011	.010	.026	.043	.218	<i>L. radiata</i>
MD1	.977	.981	.974	.989	.984	.984	.989	—	.003	.012	.038	.208	<i>L. radiata</i>
MD4	.971	.970	.968	.983	.986	.984	.990	.995	—	.013	.037	.203	<i>L. radiata</i>
DE1	.950	.954	.943	.971	.970	.973	.974	.988	.987	—	.029	.220	<i>L. radiata</i>
VT1	.946	.950	.938	.954	.950	.973	.958	.963	.964	.971	—	.124	hybrid
MI	.811	.820	.809	.804	.794	.804	.812	.816	.802	.815	.881	—	<i>L. siliquoidea</i>

TABLE 5. Genetic distances (above the diagonal) and similarities (below the diagonal) between all pairs of *Elliptio* populations sampled in this study. See Appendix for locations of the collection sites.

	Population																Species
	VT1	VT3	ME1	VT2	MD4	MD2	MD3	PA	ME2	DE3	MD1	NJ2	NS8	NS7	NS5	WI	
VT1	—	.026	.046	.066	.041	.076	.059	.072	.052	.068	.041	.045	.052	.035	.033	.087	<i>E. complanata</i>
VT3	.976	—	.015	.072	.016	.059	.041	.089	.016	.057	.017	.012	.016	.015	.033	.044	<i>E. complanata</i>
ME1	.955	.985	—	.069	.016	.060	.048	.099	.025	.059	.023	.012	.024	.016	.040	.044	<i>E. complanata</i>
VT2	.936	.931	.932	—	.063	.088	.093	.078	.098	.101	.076	.076	.087	.063	.097	.124	<i>E. complanata</i>
MD4	.960	.984	.984	.939	—	.027	.023	.107	.035	.045	.022	.018	.028	.023	.053	.054	<i>E. complanata</i>
MD2	.927	.943	.942	.916	.973	—	.013	.144	.085	.035	.055	.057	.064	.064	.099	.072	<i>E. complanata</i>
MD3	.943	.960	.954	.911	.977	.987	—	.129	.064	.027	.040	.042	.044	.049	.073	.070	<i>E. complanata</i>
PA	.931	.915	.905	.925	.898	.866	.879	—	.089	.134	.089	.120	.126	.089	.094	.157	<i>E. complanata</i>
ME2	.949	.984	.975	.907	.965	.919	.938	.915	—	.067	.018	.019	.017	.020	.035	.053	<i>E. complanata</i>
DE3	.934	.944	.943	.904	.956	.966	.974	.874	.935	—	.043	.052	.052	.061	.086	.070	<i>E. complanata</i>
MD1	.960	.983	.977	.927	.978	.946	.960	.915	.982	.958	—	.017	.019	.014	.035	.059	<i>E. complanata</i>
NJ2	.956	.989	.988	.927	.982	.944	.959	.887	.981	.949	.983	—	.007	.015	.037	.051	<i>E. complanata</i>
NS8	.949	.984	.976	.917	.972	.938	.957	.882	.983	.949	.982	.993	—	.022	.037	.051	<i>E. complanata</i>
NS7	.966	.985	.984	.939	.977	.938	.953	.915	.980	.941	.987	.985	.979	—	.014	.046	<i>E. complanata</i>
NS5	.968	.967	.961	.907	.948	.906	.930	.910	.966	.917	.966	.964	.963	.986	—	.048	<i>E. complanata</i>
WI	.917	.957	.957	.883	.948	.930	.932	.855	.948	.932	.943	.951	.950	.955	.953	—	<i>E. dilatata</i>

similarity to both *A. grandis* (0.883) and *A. cataracta* (0.800).

Populations of *Lampsilis radiata* from the Delmarva Peninsula to Nova Scotia exhibit an average level of interpopulation similarity of $0.979 \pm .012$, and *L. radiata* and *L. siliquoidea* resemble each other at a level of $0.808 \pm .007$ (Table 4). This degree of resemblance is comparable to that observed among other species of the *radiata* clade such as southern Atlantic Slope *L. splendida* (Kat, 1983c). *L. radiata* \times *siliquoidea* from Lake Champlain resembles *L. radiata* at a level of $0.954 \pm .010$ and *L. siliquoidea* at a level of 0.881: the higher degree of resemblance to *L. radiata* reflects greater similarity in the frequencies of shared alleles. Interestingly, Clarke & Berg (1959) also classified the Lake Champlain *Lampsilis* population as more *radiata*-like than *siliquoidea*-like based on conchological characters.

Populations of *Elliptio complanata* from the Delmarva Peninsula to Nova Scotia, Maine, and Vermont exhibit characteristically high levels of variability in genetic resemblance among populations, ranging from 0.993 to 0.866, with an average degree of resemblance of $0.950 \pm .030$ (Table 5). *E. complanata* resembles *E. dilatata* from Wisconsin at a level of $0.934 \pm .028$. This high level of resemblance among species within diversifying *Elliptio* clades is common (see Davis *et al.*, 1981; Davis, 1984). Table 5 indicates, however, that the Lake Champlain *Elliptio* population is most closely related to populations of *E. complanata* from Vermont, Maine, and Nova Scotia, and in fact exhibits less affinity with *E. dilatata* than other northeastern populations of *E. complanata*.

Minimum spanning trees based on genetic distances and connecting all populations of *Elliptio*, *Lampsilis*, and *Anodonta* are illustrated in Fig. 1. The distance measure between populations is a function (variable over each analysis) of the Nei genetic distances, and thus corresponds to taxonomic relatedness. Such distances are small, for example, among populations of *A. cataracta* and *A. "cataracta" fragilis*, but considerable between these species. *A. cataracta* \pm *grandis* is shown to be almost equidistant between *A. cataracta* and *A. grandis*, while *L. radiata* \times *siliquoidea* clusters considerably closer to *L. radiata* than *L. siliquoidea*. The minimum spanning tree between *Elliptio* populations generally connects geographically neighbor-

ing populations. Divergent populations within this group are those from Joes Pond, Vermont, and the Susquehanna River, Pennsylvania, both due to high frequencies of otherwise rare alleles at loci such as LAP and MPI.

Table 6 contains levels of observed heterozygosity and polymorphism for all populations of *Elliptio*, *Lampsilis*, and *Anodonta* examined. Populations of *Elliptio* exhibit characteristically high levels of H and P (average H = $0.139 \pm .014$; average P = $0.517 \pm .054$) except among peripheral populations in Nova Scotia (see Kat & Davis, 1984). Heterozygosity and polymorphism among populations of *Lampsilis* are characteristically lower than those observed among *Elliptio*, except in the case of *L. siliquoidea* from Michigan, which possesses the highest level of H and P thus far observed for any lampsiline population (see Kat, 1983c). *L. radiata* \times *siliquoidea* from Lake Champlain is not more heterozygous than either parent (average H for central range populations of *L. radiata* = $0.058 \pm .004$), but exhibits a level of polymorphism equal to that of *L. siliquoidea*. Levels of heterozygosity for anodontine populations presented here are higher than those published earlier (Kat, 1983d) due to inclusion of loci with fixed heterozygosities (GPI for all species and MDH I for *A. "c." fragilis*). *A. cataracta* \times *grandis* from Lake Champlain is considerably more heterozygous than either parent species.

B. Stomach anatomy

Fine detail of stomach anatomy can be used to discriminate between hybrids and parental species of the lampsilines and anodontines examined in this study. The *Elliptio* population in Lake Champlain (Fig. 2) is very similar in stomach anatomy to *E. complanata* from eastern Canada (see Kat, 1983a), as well as *E. dilatata* from Wisconsin (not figured). Stomach anatomy of *L. radiata* \times *siliquoidea* from Lake Champlain (Fig. 3) is quite similar to that of *L. radiata* from eastern Canada (see Kat, 1983c) and the Delmarva Peninsula (Fig. 4), and also that of *L. siliquoidea* from Michigan (Fig. 3A). Differences are apparent, however, in the curvature of the minor typhlosole fold. *A. cataracta* \times *grandis* in Lake Champlain (Fig. 5) also differs from *A. cataracta* from Virginia and *A. grandis* from Tennessee and Michigan in details of the minor typhlosole fold. This fold is gently rounded

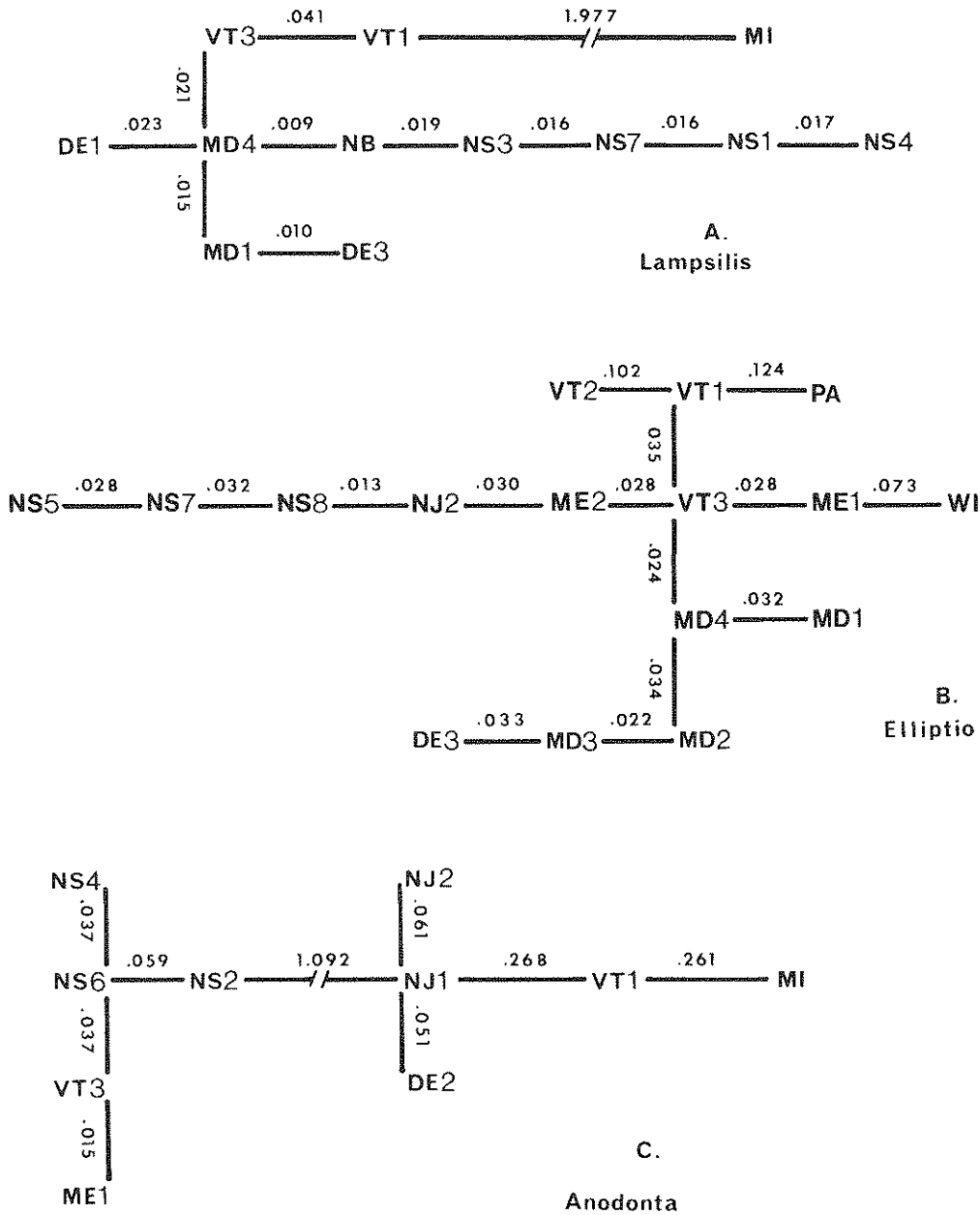


FIG. 1. Minimum spanning trees for all populations of *Lampsilis*, *Elliptio*, and *Anodonta*. Among the lampsilines, all populations except MI (*L. siliquoidea*) and VT1 (hybrid) are *L. radiata*. Among *Elliptio*, all populations except WI (*E. dilatata*) are *E. complanata*, although populations from Joes Pond, Vermont (VT2) and the Susquehanna River, Pennsylvania (PA) are relatively distant from other *E. complanata* populations. Among the anodontines, NS4, NS6, NS2, VT3, and ME1 are populations of *A. fragilis*, NJ2, NJ1, and DE2 are populations of *A. cataracta*, VT1 is a hybrid, and MI represents *A. grandis*. The distance measure between populations is a function of the Nei genetic distance

TABLE 6. Levels of heterozygosity (H) and polymorphism (P) for all species included in this study.

	H	P
<i>Elliptio complanata</i>	0.122 ± .037	0.499 ± .066
<i>Elliptio dilatata</i>	0.104	0.428
<i>Lampsilis radiata</i>	0.038 ± .023	0.305 ± .132
<i>Lampsilis siliquoidea</i>	0.113	0.600
<i>L. radiata</i> × <i>siliquoidea</i>	0.053	0.600
<i>Anodonta cataracta</i>	0.098 ± .003	0.142
<i>Anodonta grandis</i>	0.192	0.500
<i>A. grandis</i> × <i>cataracta</i>	0.256	0.570
<i>Anodonta fragilis</i>	0.148 ± .006	0.185 ± .039

in *A. cataracta* (see Kat, 1983d) but becomes more angular in *A. cataracta* × *grandis* (Fig. 5, 5A), and is V- or U-shaped in *A. grandis* (Fig. 5B, 5C). Overall stomach anatomy among anodontines of the *cataracta* group (*A. cataracta*, *A. grandis*, *A. gibbosa*) is quite similar (Kat, 1983d). *A. "cataracta" fragilis*, however, differs strongly from *A. cataracta* in stomach anatomy (Fig. 6, 6A) and there is no evidence from this character to suggest that *A. cataracta* and *A. fragilis* hybridize either in Nova Scotia or in New England.

C. Conchiolin layer microstructure

Conchiolin layers among unionids are composed of three parts: an upper, homogeneous region; a central, reticulate region that consists of a number of thin, usually vertically arranged lamellae that form chambers of various shapes and dimensions; and a lower, very thin homogeneous region (Kat, 1983e). Microstructure of conchiolin layers can discriminate among parental species and Lake Champlain hybrids of *Anodonta* and *Lamps-*

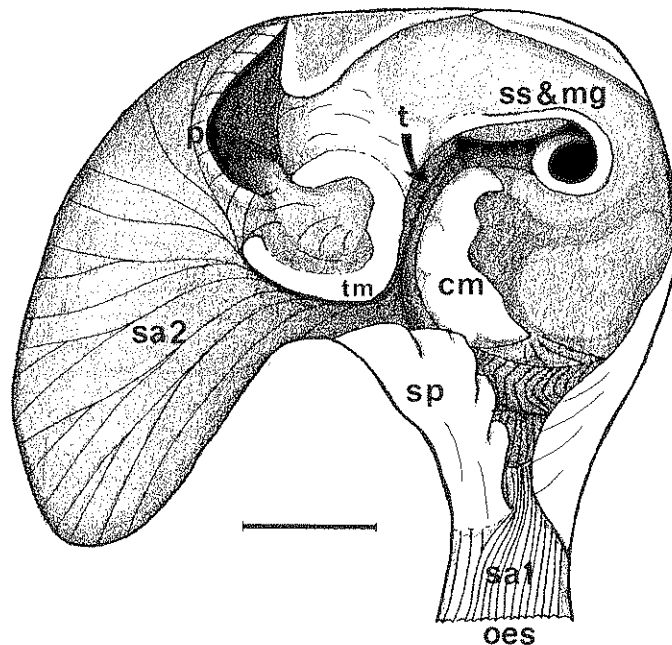


FIG. 2. Stomach floor of *Elliptio complanata* from Lake Champlain. Abbreviations: cm - conical mound, oes - oesophagus, p - sorting pouch, sa1 - sorting area 1, sa2 - sorting area 2, sp - sorting platform, ss & mg - style sac and midgut, t - major typhlosole, tm - minor typhlosole fold. Scale bar = 2 mm.

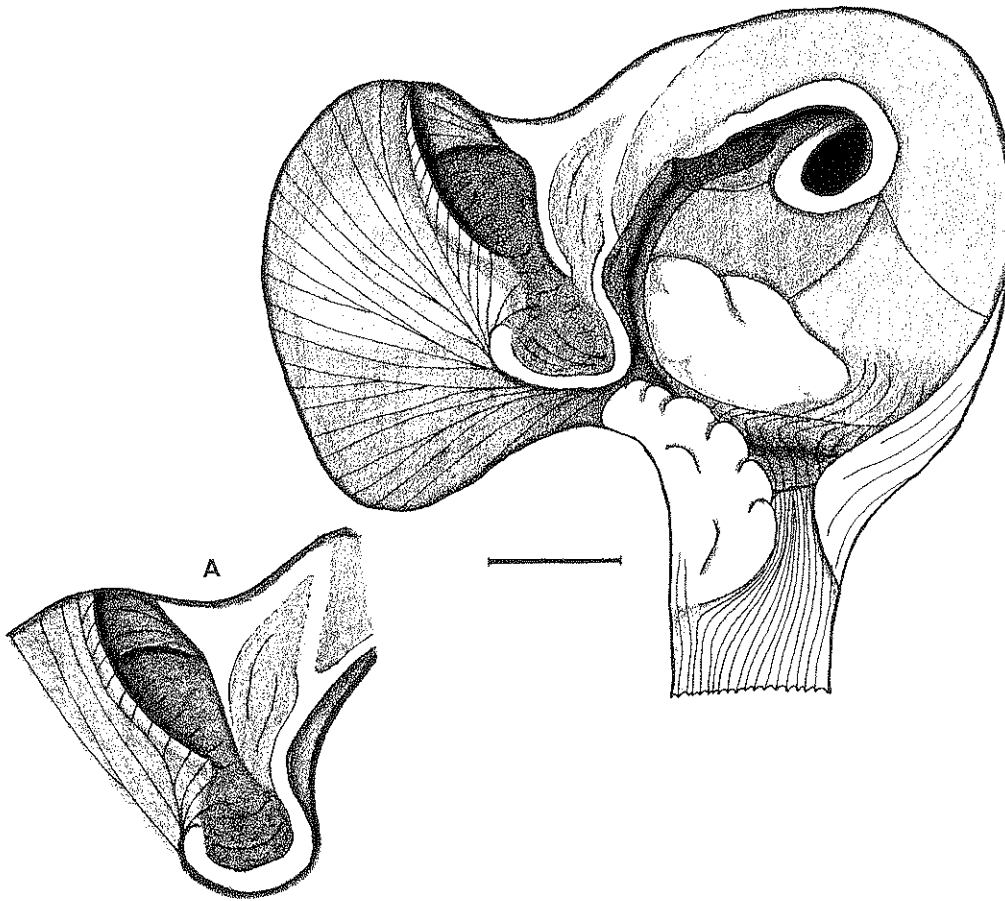


FIG. 3. Stomach floor of *Lampsilis radiata* × *siliquoidea* from Lake Champlain; inset A depicts the minor typhlosole of *L. siliquoidea* from Michigan. Scale bar = 2 mm; structures as in Fig. 2.

ilis, and suggests that Lake Champlain and surrounding areas are inhabited by a distinct subgroup of *Elliptio complanata*. *E. complanata* from Virginia and the southern Delmarva Peninsula are characterized by reticulate regions with short, widely-spaced lamellae that enclose triangular or rectangular chambers of various sizes (Kat, 1983a; Pl. 1:1). *E. complanata* on the northern Atlantic Slope possesses longer, straighter lamellae that enclose rather elongate, narrow chambers (Kat, 1983a; Pl. 1:2). *E. dilatata* from western North Carolina (Pl. 1:3), Wisconsin (Pl. 2:2), and western Ontario (Pl. 2:1) are characterized by a thin upper homogeneous region and long, vertical lamellae. *E. complanata* from Ver-

mont (Pl. 1:4 and 1:5) and Lake Champlain (Pl. 1:6) all possess highly characteristic curved and striated lamellae that enclose variably shaped chambers. This particular conchiolin layer microstructure has not been observed in any other region of the geographic range of *E. complanata*, although similarly striated lamellae occur in a hybrid zone between races of *E. complanata* on the Delmarva Peninsula (Kat, 1983a).

Conchiolin layer microstructure of *Anodonta cataracta* (Pl. 2:4) consists of a thin upper homogeneous layer underlain by a poorly defined reticulate region composed of small, irregular chambers. *A. grandis* possesses a better defined reticulate region

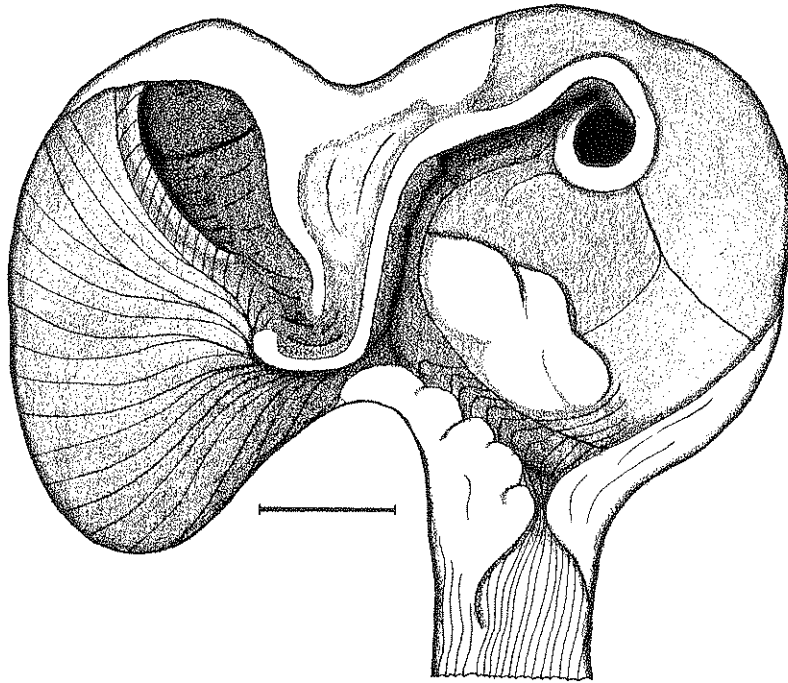


FIG. 4. Stomach floor of *Lampsilis radiata* from the Delmarva Peninsula (Andover Branch). Scale bar = 2 mm.

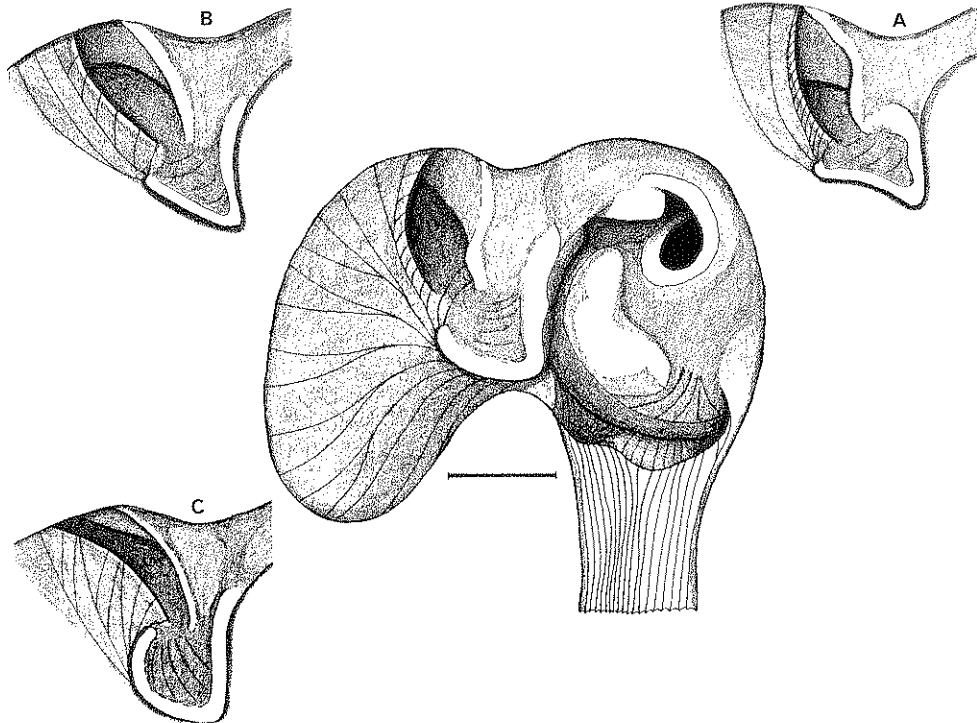


FIG. 5. Stomach floor of *Anodonta cataracta* x *grandis* from lake Champlain; inset A represents an extreme variant in the same population; inset B depicts the minor typhlosole fold of *A. grandis* from Tennessee; inset C shows the minor typhlosole fold of *A. grandis* from Michigan. Scale bar = 2 mm.

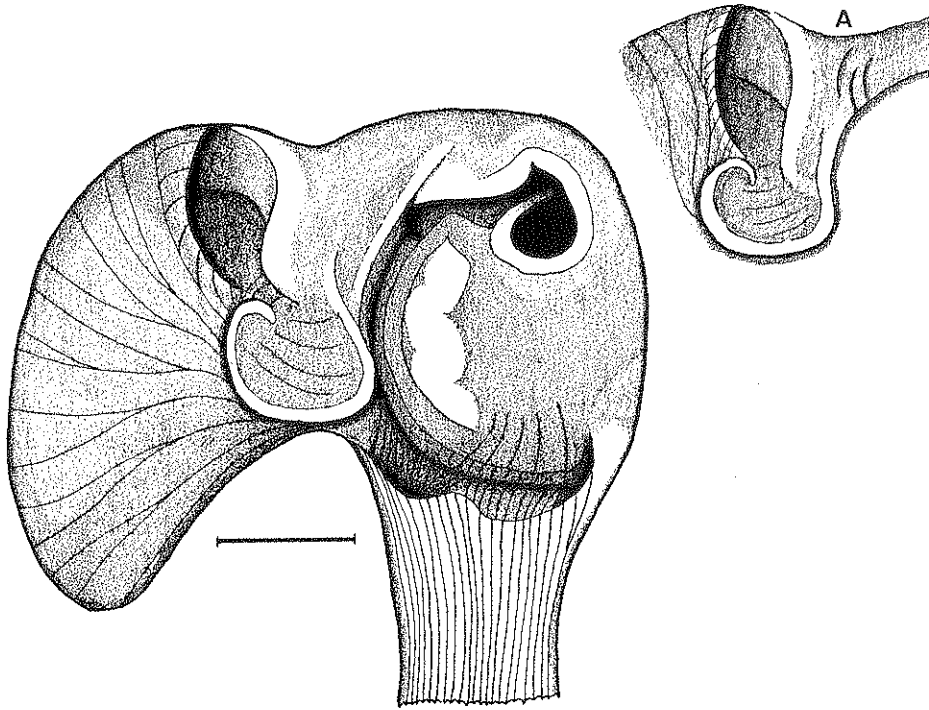


FIG. 6. Stomach floor of *Anodonta fragilis* from Maine (Lake St. George). Inset shows the minor typhlosole fold of *A. fragilis* from Nova Scotia (Placide Lake). Scale bar = 2 mm.

(Pl. 2:5), and *A. cataracta* × *grandis* possesses a reticulate region characterized by thick, roughly vertical lamellae that enclose variably sized and shaped chambers (Pl. 2:6). *A. "cataracta" fragilis* (Pl. 2:3) has a conchiolin layer microstructure very different from that of *A. cataracta*.

The conchiolin layer of *Lampsilis radiata* (Pl. 3:1, 3:2, 3:3, and 3:4) is characterized by a thick upper homogeneous region and a reticulate region composed of poorly defined, digitiform to blocky lamellae. *L. siliquoidea* (Pl. 3:6) also possesses a thick homogeneous region but has a reticulate region composed of densely packed, jagged lamellae. *L. radiata* × *siliquoidea* (Pl. 3:5) has a rather disorganized reticulate region composed of irregular, blocky lamellae.

DISCUSSION

Studies dealing with genetics of hybrid zones and dynamics of hybridization are nu-

merous. Some of these studies indicate considerable genetic exchange within the hybrid zone and some, possibly asymmetrical, introgression elsewhere (e.g. Hunt & Selander, 1973; Avise & Smith, 1974; Patton *et al.*, 1979; Moran *et al.*, 1980; Hafner, 1982). Other studies report hybridization without any or much introgression beyond the often narrow hybrid zone (e.g. Nevo & Bar-El, 1976; McDonnell *et al.*, 1978; Sage & Selander, 1979; Barton *et al.*, 1983). While hybridization between *Anodonta grandis* and *A. cataracta* and *Lampsilis radiata* and *L. siliquoidea* is documented here, too few Interior Basin localities in particular were examined to be able to determine the extent of introgression. There is some evidence, however, that introgression takes place over a wide geographic area: Atlantic Slope *L. radiata* and *A. cataracta* exhibit a much higher frequency of fixed alleles among the 15 loci examined than do *A. grandis* and *L. siliquoidea* from Michigan, which both possess many "Atlantic Slope" alleles in low frequencies. Also, two of the loci

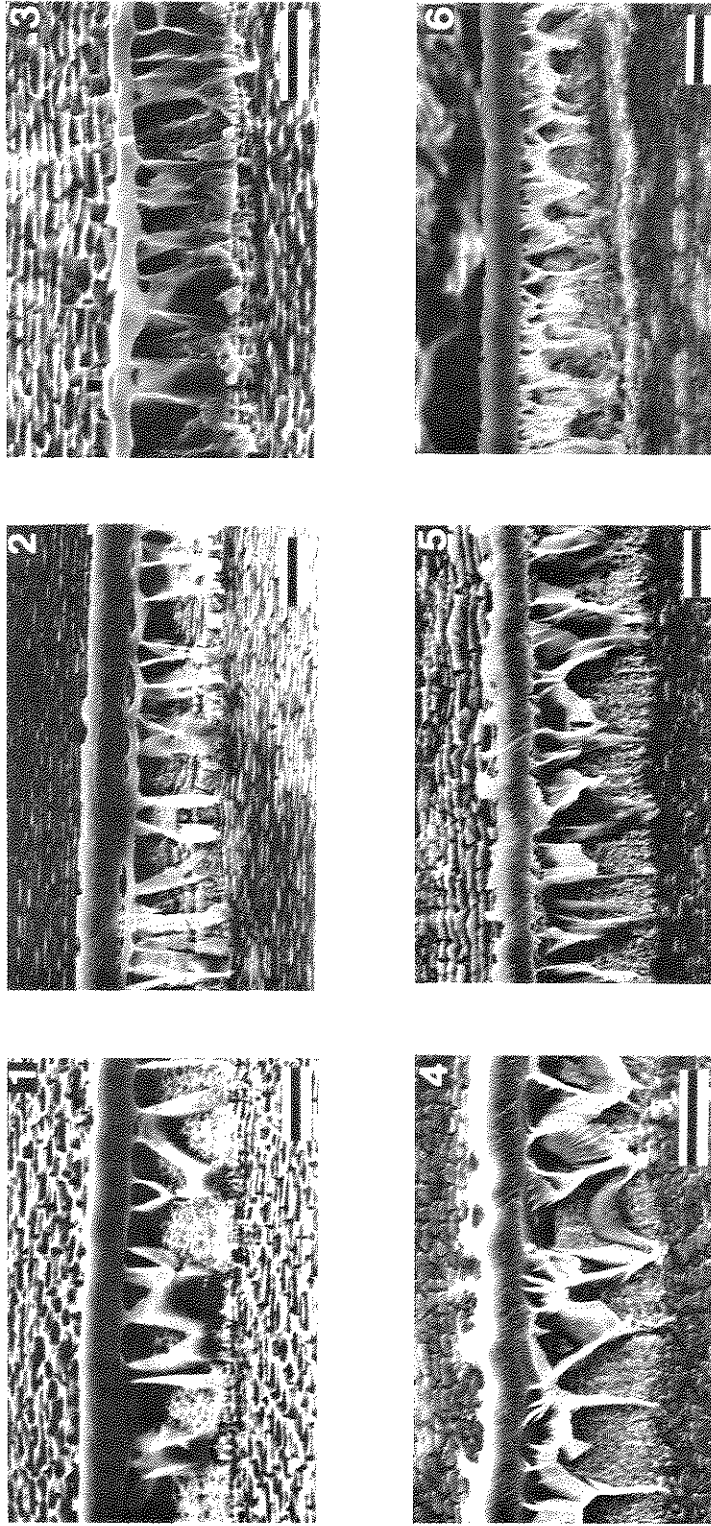


PLATE 1. Conchiolin layer microstructure of *Elipito*. 1. Southern Atlantic Slope *E. complanata*; 2. Northern Atlantic Slope *E. complanata*; 3. *E. dilatata*; 4, 5. *E. complanata* from Vermont; 6. *E. complanata* from Lake Champlain. Scale bars = 10 μ m.

UNIONID HYBRIDIZATION

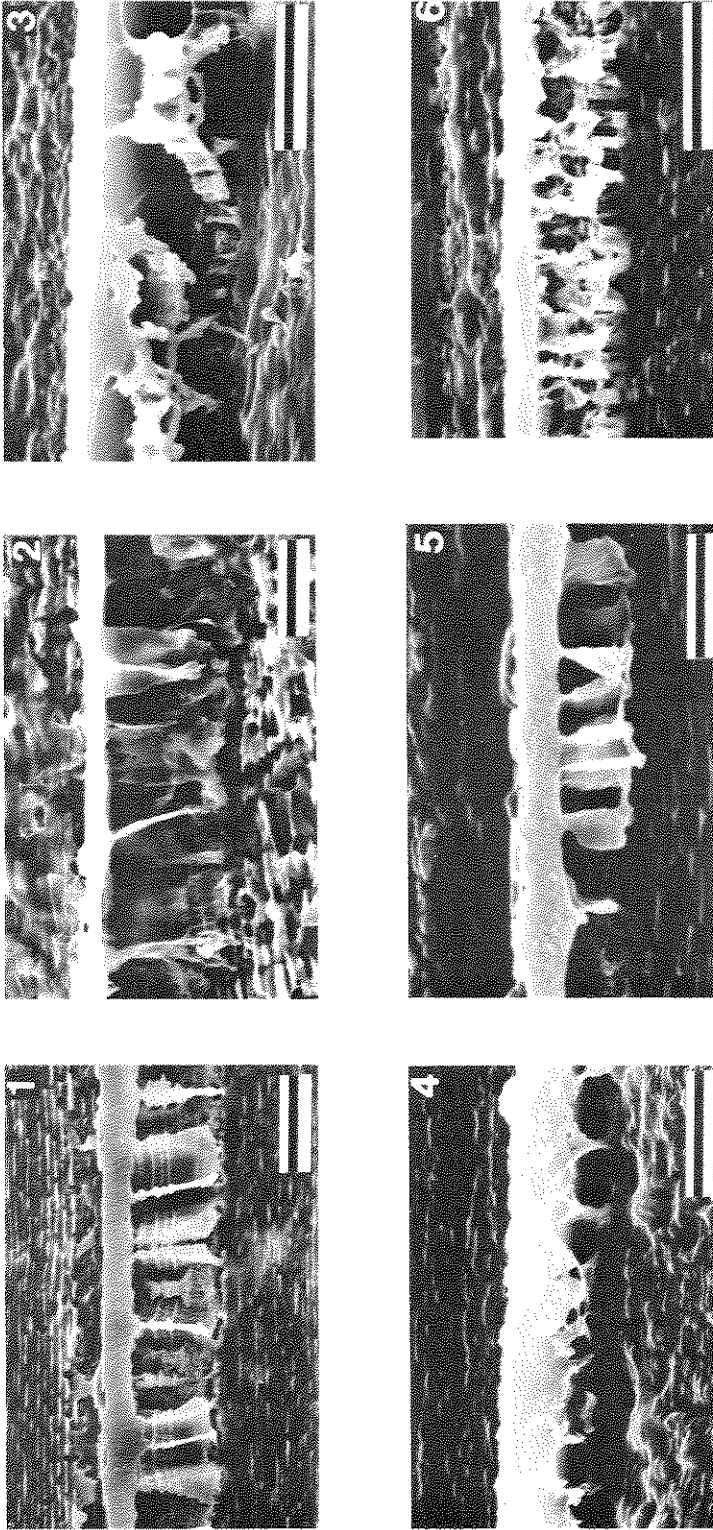


PLATE 2. Conchiolin layer microstructure of *Elipifio* and *Anodonta*. 1. *E. dilatata* from Ontario; 2. *E. dilatata* from Wisconsin; 3. *A. fragilis* from Nova Scotia; 4. *A. grandis* from Pennsylvania; 5. *A. grandis* from Michigan; 6. *A. cataracta* from Lake Champlain. Scale bars = 10 μ m.

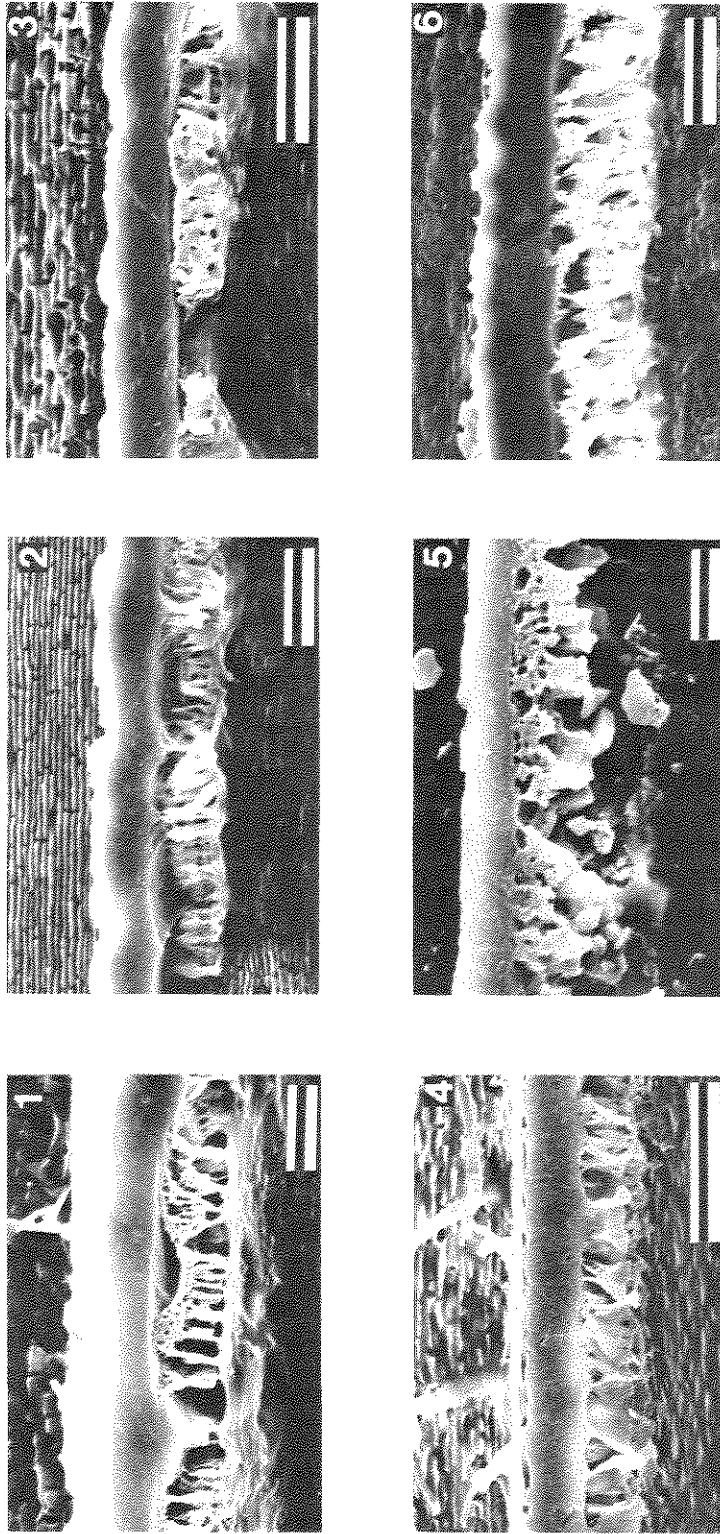


PLATE 3. Conchiolin layer microstructure of *Lampsilis*. 1. *L. radiata* from Nova Scotia; 2. *L. radiata* from Nova Scotia; 3. *L. radiata* from Nova Scotia; 4. *L. radiata* from Vermont; 5. *L. radiata* × *siliquioidea* from Lake Champlain; 6. *L. siliquioidea* from Michigan. Scale bars = 10µm.

A

B

C

D

E

F

G

H

I

J

K

L

M

N

O

P

Q

R

S

T

U

V

W

X

Y

Z

surveyed possess soluble as well as mitochondrial forms: MDH and SOD (Davidson & Cortner, 1967; Beckman, 1973; Harris & Hopkinson, 1978). Since mitochondrial genes are exclusively inherited through maternal lines, alleles at these loci can be used to estimate relative parental contributions to hybrids and thus levels of introgression. Lake Champlain populations of *Anodonta* and *Lampsilis* contain 65% *cataracta* and 70% *radiata* alleles at these loci, for example, while Michigan populations contain 45% *cataracta* and 8% *radiata* alleles. If incidence of introgression is confirmed by genetic examination of "pure" populations of *A. grandis* and *Lampsilis siliquoidea* south of the maximal glacial advance, it would suggest that hybrids between these species are not inferior to their parents in terms of maladaptation to external environments and/or disruption of balanced gene complexes (Sage & Selander, 1979; Moore, 1977; see below). The population of *Elliptio* in Lake Champlain exhibits no evidence of a hybrid origin, and is genetically and morphologically related to populations of Atlantic Slope *E. complanata*. Conchiolin layer microstructure of populations of *E. complanata* from Lake Champlain and Vermont is different from that of other northern Atlantic Slope populations, but such divisions of *E. complanata* into locally differentiated populations have been observed before and are apparently characteristic of this species (Kat, 1983a; Kat & Davis, 1984). If *E. complanata* and *E. dilatata* hybridize, it probably occurs farther west than Lake Champlain, and the location of the hybrid zone could well reflect differences in routes of recolonization taken by *Elliptio* when compared with *Lampsilis* and *Anodonta*. For example, Interior Basin *Anodonta* and *Lampsilis* apparently followed retreating glaciers closely: subfossil *A. grandis* and *L. siliquoidea* occur in Lake Algonquin (12,000 to 10,000 B.P.) and Transitional (10,000 to 6,000 B.P.) sediments, respectively, in southwestern Ontario (Miller *et al.*, 1979), and subfossil *Lampsilis* (species undetermined) occur in 7,000 year old sediments around Lake Champlain (Elson, 1969). *E. complanata*, according to Clarke & Berg (1959), occurs westward to the upper great lakes (Ontario, Huron, Superior), and probably colonized this area via Lake Newbery, which inundated the present Finger Lakes basin in New York and drained into the Susquehanna River of the Atlantic Slope.

Clarke & Berg (1959) also state that *E. dilatata* co-occurs with *E. complanata* in the St. Lawrence River drainage, but geographic ranges of these phenotypically variable species need to be confirmed with more reliable taxonomic methods than the conchological characters of previous authors.

Evolutionary biologists disagree on the stability of hybrid zones through time. Remington (1968) has argued, for example, that suture zones are ephemeral, leading either to fusion of parental gene pools or separation with perfection of reproductive isolating mechanisms. In contrast, others have indicated that zones of hybridization can be temporally stable and of ancient age (Short, 1972; Hunt & Selander, 1973; Sage & Selander, 1979). There can be little doubt that the hybrid zone between Interior Basin and Atlantic Slope *Anodonta* and *Lampsilis* is of postglacial origin, and the position of the hybrid zone in a repeatedly glaciated area implies that it will last only as long as the present interglacial stage. Evidence that a previous suture zone between these faunas was disrupted by glaciers is provided by the Fish House fossil assemblage near Camden, New Jersey (Kat, 1983b). Interestingly, this fauna contains no morphologic intermediates between sympatric *A. cataracta* and *A. grandis* to suggest that those species were then hybridizing. This lack of genetic interaction was proposed to have resulted from perfection of isolating mechanisms in the zone of sympatry. These adaptations were subsequently lost as sympatric populations were eliminated by glaciers and the geographic range of *A. grandis* restricted to refuges west of the Appalachian mountains. Re-establishment of contact between these species would thus again, at least initially, involve hybridization (Kat, 1983b).

Observations that alleles that are either rare or absent in parental populations occur in appreciable frequencies in hybrid zones are not uncommon. This phenomenon was first described from a land snail hybrid zone (Clarke, 1968) and since then, Hunt & Selander (1973) have found variant esterase alleles in a hybrid zone between semispecies of house mice, and Sage & Selander (1979) described unusual alleles at five of ten loci among hybrid frog populations. Other examples of rare alleles occurring within hybrid zones have been documented by Woodruff (1981) and Barton *et al.* (1983). In this study, the hybrid *Anodonta* population possesses

three variant alleles, while that of *Lampsilis* contains one. Hunt & Selander (1973) proposed that introgression modifies parental gene pools to relax incorporation against new alleles, and Stebbins (1971) suggested that minor alleles could be favored in low frequencies in the new genetic environment created by hybridization. More recently, Thompson & Woodruff (1978) and Woodruff *et al.* (1982) suggested that these new alleles might result from increased mutation rates among hybrids (as a consequence of heterozygosities involving dissimilar alleles), and Watt (1972) proposed that such new alleles could result from intragenic recombination between parental alleles. Such intragenic recombination has been proposed to explain patterns of allelic variability by various authors (Ohno *et al.*, 1969; Koehn & Eanes, 1976; Morgan & Strobeck, 1979; Tsuno, 1981), and Golding & Strobeck (1983) showed mathematically that sympatry of two previously isolated populations can increase the effective number of alleles maintained in the hybrid as well as parental populations. Whether these novel alleles do actually spread from hybrid zones to contribute to allelic diversity of parental populations has not been documented. In this study, increased levels of heterozygosity could be proposed to account for the appearance of variant alleles in the Lake Champlain population of *Anodonta* but not for that of *Lampsilis*, since levels of heterozygosity of the hybrid lampsiine population are comparable to, or lower than, those of its parent species.

Anodonta cataracta and *A. grandis*, and to a lesser extent *Lampsilis radiata* and *Lampsilis siliquoidea*, are genetically divergent species that apparently hybridize readily where their geographic ranges come into contact. The large and fertile (demibranchs of both hybrids were filled with glochidia at the time of collection) populations in Lake Champlain and elsewhere in the hybrid zone would appear to indicate that there is little selection against hybridization, although relative levels of fitness of hybrids and parents are not known. Unionids seem susceptible to accidental hybridization because of their external mode of fertilization, but could theoretically experience penalties for hybridization because of their complicated life cycle that includes an obligate parasitic stage. Parasitism involves genes controlling host recognition as well as genes involved with glochidial survival

while on the host, and such gene complexes would appear to be highly species-specific (Bush, 1975a, b; Kat, 1984). Hybridization will likely disrupt adapted gene complexes, except possibly among unionid species possessing very generalized survival and host recognition genes. Such species are perhaps epitomized by *A. grandis*, which parasitizes over 30 fish hosts (Trdan & Hoeh, 1982), and to a lesser extent by *L. siliquoidea*, which parasitizes about 12 hosts (Trdan, 1981). Species like *E. complanata* and *A. implicata*, however, are only known to parasitize two and one hosts, respectively. Hybridization should be most strongly selected against among these more specialized unionids, unless both parental species parasitize the same host, an occurrence likely in the case of two *E. complanata* races that hybridize on the Delmarva Peninsula (Kat, 1983a). Similarity of hosts should therefore be a more reliable predictor of hybridization between related unionid species than levels of electrophoretically detected differentiation.

The data gathered in this study also have bearing on two taxonomic questions. First, Clarke & Berg (1959) suggested that in view of the width of the hybrid zone, *Lampsilis siliquoidea* should be reduced to the subspecies *L. radiata siliquoidea*. I disagree with this interpretation: *L. siliquoidea* from Michigan (which might constitute a periphery of the zone of introgression) already exhibits the same level of genetic divergence from *L. radiata* as do other recognized lampsiine species such as *L. splendida* from Georgia and *Lampsilis* sp. from Lake Waccamaw, North Carolina (Kat, 1983c). Also, stomach anatomy and conchiolin layer microstructure of these taxa are quite different. I suggest, therefore, that the taxon *L. radiata siliquoidea* be reserved to describe hybrid populations such as that in Lake Champlain, and that *L. siliquoidea* be used to describe Interior Basin populations outside the hybrid zone. Second, Clarke & Rick (1963) named *Anodonta cataracta fragilis* to describe phenotypic (umbonal sculpture) intergrades between *A. fragilis* from Newfoundland and *A. cataracta*. In this study and others (Kat, 1983d, e; Kat & Davis, 1984) genetic, anatomical, and conchiolin layer microstructural data suggest that all populations of *A. "cataracta" fragilis* are very distinct from *A. cataracta*, and that there is no evidence to suggest any hybridization between these taxa. I propose that, unless an

analysis of *A. fragilis* (based on a diversity of data) from Newfoundland (the type locality) reveals substantial differences from *A. "cataracta" fragilis* from Nova Scotia and northern New England, these taxa be considered synonymous and distinct from *A. cataracta*.

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APPENDIX

Classification of species mentioned in the text, and location of the collection sites.

Unionidae	
Anodontinae	
	<i>Anodonta cataracta</i> Say
	<i>Anodonta fragilis</i> Lamarck
	<i>Anodonta gibbosa</i> Say
	<i>Anodonta grandis</i> Say
Ambleminae	
Lampsilini	
	<i>Lampsilis radiata</i> (Gmelin)
	<i>Lampsilis siliquoidea</i> (Barnes)
	<i>Lampsilis splendida</i> (Lea)
Pleurobemini	
	<i>Elliptio complanata</i> (Lightfoot)
	<i>Elliptio dilatata</i> (Rafinesque)
DE1	Andover Branch, Millington, Kent Co., Delaware
DE2	Concord Pond, Sussex Co., Delaware
DE3	Deep Creek, Nanticoke Acres, Sussex Co., Delaware
MD1	Chester River, Millington, Kent Co., Maryland
MD2	Mason Branch, Queen Anne, Queen Annes Co., Maryland
MD3	Norwich Creek, Queen Anne, Talbot Co., Maryland
MD4	Sassafras River, Sassafras, Cecil Co., Maryland
ME1	Lake St. George, Waldo Co., Maine
ME2	Kennebec River, Somerset Co., Maine
MI	Wiggins Lake, Gladwin Co., Michigan
NB	French Lake, Oromocto, Sunbury Co., New Brunswick
NJ1	Delaware River, Burlington Co., New Jersey
NJ2	Swartswood Lake, Sussex Co., New Jersey
NS1	Lake Egmont, Cooks Brook, Halifax Co., Nova Scotia
NS2	First Lake O' Law, Baddeck, Victoria Co., Nova Scotia
NS3	Mattatall Lake, Wentworth Centre, Cumberland Co., Nova Scotia
NS4	Newville Lake, Halfway River East, Cumberland Co., Nova Scotia
NS5	Placide Lake, Havelock, Digby Co., Nova Scotia
NS6	Shaw Lake, Arichat, Isle Madame, Richmond Co., Nova Scotia
NS7	Grand Lake Shubenacadie, Grand Lake, Halifax Co., Nova Scotia
NS8	Sydney River, Sydney, Cape Breton Co., Nova Scotia
PA	Susquehanna River, Cumberland Co., Pennsylvania
VT1	Lake Champlain, South Hero, Grand Isle Co., Vermont
VT2	Joes Pond, Danville, Caledonia Co., Vermont
VT3	Lake Memphremagog, Newport, Orleans Co., Vermont
WI	St. Croix River, Hudson, St. Croix Co., Wisconsin

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