Fossil Evidence from Fish House Clays for the Origin and Changes in Species Composition through Time of the Northern Atlantic Slope Unionid Fauna (Mollusca: Bivalvia)

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ABSTRACT.—Pre-Wisconsinan unionid fossils within the Fish House clays near Camden, New Jersey, reveal the existence of a fauna composed of ten species. Three of these species are now found only among the Interior Basin unionid fauna, another species is now restricted to a smaller geographic range, and two anodontine species now hybridize where their newly-expanded ranges overlap. The Fish House fossils constitute the only described Pleistocene unionid fauna of the northern Atlantic Slope, and the existence of Interior Basin taxa within this fauna supports hypotheses concerning an Interior Basin origin of certain Atlantic Slope species. The Fish House fossils also indicate that the northern Atlantic Slope fauna did not result from simple processes of dispersal from an ancient center of origin in the south, that one of the northern Atlantic Slope species is relictual in distribution, and that unionids, in contrast to marine bivalves and mammals, did not suffer extinctions during the Wisconsinan glaciation, but only underwent reductions in geographic ranges. [Atlantic Slope, biogeography, evolution, Fish House clays, fossils, Mollusca, Unionidae, Wisconsinan glaciation]

The most fundamental questions about any fauna in any region concern its origins and diversity through time. The unionid fauna of the northern Atlantic Slope (drainages between the York River in Virginia and the St. Lawrence River in Canada) consists of about 16 largely conchologically defined species (Johnson 1970) with diverse origins and a long history of fluctuations in geographic range (Ortmann 1913; Kat 1982a, b, 1983a, b; Kat and Davis in press). This fauna includes species proposed to have close relationships with those of the exceptionally diverse fauna of the Interior Basin. Members of this Interior Basin fauna either immigrated around the northern end of the Appalachian mountains in pre-glacial or inter-glacial times, or crossed drainage divides through stream capture (Simpson 1895; Ortmann 1913), and subsequently differentiated in allopatry. Early circumstantial evidence for a close relationship be-

tween these taxa was provided by Ortmann (1913) and by Clarke and Berg (1959) who described hybrid zones (based on intermediacy of shell characters) in areas of geographic range overlap of such Interior Basin and northern Atlantic Slope taxa as *Lampsilis radiata siliquoidea* (Barnes) and *L. r. radiata* (Gmelin), and *Anodonta grandis* Say and *A. cataracta* Say. Other members of the northern Atlantic Slope fauna are thought to have been derived from southern Atlantic Slope ancestors by northward migration and progressive differentiation (Johnson 1970; Sepkoski and Rex 1974).

More recently gathered taxonomic information based on soft-part anatomy, molecular genetics, and shell microstructure complicates the picture somewhat. For example, the Nova Scotian *Anodonta cataracta fragilis* (sensu Clarke and Rick 1963) exhibits similarities in soft-part characteristics and beak sculpture to the Eurasian taxon *A. cyg-*

nea (Linnaeus) (Clarke and Rick 1963; Kat 1982a), and could thus represent a species with European affinities which survived Wisconsinan (and earlier) glaciers in a refuge either in eastern Canada or on a section of the exposed continental shelf. Whether or not this species, which appears to be extending its geographic range southward from the Canadian maritime provinces, is in fact hybridizing with *A. c. cataracta* as Clarke and Rick (1963) claim remains to be determined; molecular genetic and shell microstructural data (Kat 1982a, 1983c) indicate that *A. c. fragilis* exhibits levels of divergence from *A. c. cataracta* similar to those separating "good" species such as *A. c. cataracta* and *A. gibbosa* Say from Georgia. A similar variety of data reveals that the highly polytypic, widely-distributed, and supposedly southern-derived *Elliptio complanata* (Lightfoot) is in fact divisible into two distinct races on the Delmarva Peninsula: the northern section of the Peninsula is inhabited by a race that recolonized previously glaciated areas such as New England and Nova Scotia, the southern part by a race moving northward from Virginia and North Carolina, and the center of the Peninsula by hybrids between the two races (Kat 1983b). On the basis of such data it was suggested that the *E. complanata* complex should be thought of as a Rassenkreis distributed around the Appalachian mountains, and that hybrid zones between locally differentiated races should be apparent in several areas. Also, the northern Atlantic Slope region contains two strict endemics: *E. fisheriana* (Lea) which is limited to streams on the western side of the Delmarva Peninsula (Davis et al. 1981), and the more widely distributed *Anodonta implicata* Say which seems to have no close relatives either in the Interior Basin or on the southern Atlantic Slope (Kat 1982a).

Despite these various lines of evidence linking species elements of the northern Atlantic Slope fauna to those of Europe, the Interior Basin, and the southern Atlantic Slope, statements on the origins of the northern Atlantic Slope fauna will always lack rigor without fossil evidence. Fossils could be used, for example, to substantiate claims of species immigration from the Interior Basin to the northern Atlantic Slope, and to determine species diversity and composition of faunas through time. However, the unionacean fossil record is at this point difficult to decipher. Mesozoic and many Palaeogene fossils have uncritically been placed in the genus *Unio,* and there seem to have been few attempts to elucidate possible affinities with Recent taxa (White 1883; Henderson 1935). In addition, taxonomic analyses of fossil unionacean bivalves are complicated by high levels of phenotypic variability in shell characters such as overall shape, size, dentition, and ornamentation, and by shell shape convergence and parallelism (see Miller 1978; Kat and Davis 1983). Two Mesozoic (?) fossil taxa which could have bearing on the origins of the Atlantic Slope fauna were described by Woodward (1971) from "Cretaceous–Tertiary" deposits in Greenland. Woodward (1971) pointed out resemblances between these fossils and Recent South American taxa, and the fossils also seem to exhibit some similarities to Recent North American taxa of the genus *Elliptio.* The value of these fossils, however, is diminished by uncertainity as to their age and collection locality.

Pleistocene Unionacea have received by far the most attention, but have been used mainly in paleoclimatic reconstruction (Taylor 1965; Tuthill 1969; Miller 1978). Also, Pleistocene unionacean faunas appear to be rare in the Interior Basin and on the Atlantic Slope; for example, of the 122 Pleistocene molluscan faunas listed by LaRoque (1966) from seven Interior Basin states, only six contain unionid fossils consisting mainly of unidentifiable fragments. Where unionid fossils have been found,

however, they have been useful in documenting stream capture and former drainage patterns (Miller 1970, 1976), changes in species composition and abundance (Smith 1894; Metcalf 1980), and patterns of recolonization of previously glaciated territory (Tuthill et al. 1964; LaRoque 1969; Karrow et al. 1975; Miller et al. 1979).

One of the most diverse Pleistocene unionid faunas thus far described, and one which has direct bearing on the origin of the northern Atlantic Slope fauna, occurs in the so-called Fish House clays near Camden, New Jersey. The unionid fossils were first described by Lea (1868) and Whitfield (1885) who assumed them to be from Cretaceous sediments. Later, Woolman (1896) placed the Fish House clays within the Pennsauken Formation, and revised the age of the fossils to mid-Pleistocene, an age subsequently adopted by Ortmann (1913) and Baker (1920). Henderson (1935) again revised the age of the fossils to late Pleistocene, and stated that the fossils belonged to extant taxa. More recent evaluation reveals that the clays cut into the Pennsauken (itself revised to late Miocene–early Pliocene) and are probably correlative with the Accomack beds on the Delmarva Peninsula dated by a variety of methods to about 200,000 B.P. (J. P. Owens, USGS, pers. comm.; see also Cronin et al. 1981; McCartan et al. 1982; Wehmiller and Belknap 1982). The climate at that time, as inferred from pollen analyses, was warm-temperate and suggestive of interglacial conditions (Cronin et al. 1981).

Twelve unionid species were originally described from this fauna, seven of which were believed to have strong Interior Basin affinities (Lea 1868; Whitfield 1885). Both Ortmann (1913) and Baker (1920) were unconvinced of such western affinities, but neither saw the actual fossil material. Also, Ortmann (1913) stated that there were more likely to be three or four species rather than 12. Despite this controversy, the Fish House fauna appears not to have been examined since the turn of the century. Further collection is made difficult by the presence of a sewage disposal facility on the original Fish House site, but a number of Lea's type specimens as well as over 70 specimens from subsequent collections are housed at the Academy of Natural Sciences of Philadelphia (ANSP). The purposes of this study were to re-examine the members of this fauna in the ANSP collections, to re-evaluate the supposed affinities of members of this fauna to Interior Basin taxa, and to re-evaluate the species composition of the Fish House clays.

THE FISH HOUSE FOSSILS

In his original description of the Fish House fossil unionid fauna, Lea (1868) named ten species, to which Whitfield (1885) added two additional species based on material from subsequent collections. Lea was aware of the morphological similarities between modern and Fish House taxa, but because the Fish House clays were at that time still considered to have been deposited during the Cretaceous, did not consider the possibility that the Fish House fossils could be related to Recent taxa. Nevertheless, his system of nomenclature reflects putative similarities in shell shape to Recent taxa; for example, the Fish House fossil taxa *Unio nasutoides* Lea and *U. radiatoides* Lea were named for their supposed resemblances to *Ligumia nasuta* (Say) and *Lampsilis radiata*. As Whitfield (1885) already observed, the state of preservation of the fossils is a drawback to a rigorous comparison with Recent taxa. With few exceptions, the fossils consist of interior casts in a poor state of preservation, and for that reason, only type specimens and those which are best preserved were used in this study. The identification of the fossils was made by comparisons of such specimens to a number of extant species with regard to overall shell shape, dentition, muscle scars, and where possible, shell sculpture. In addition, those

TABLE 1. Summary of curvatures at various points on the shell edge of fossil and Recent taxa. Location of each measurement of curvature is determined by rotation of a line passing through the umbo through the specified number of degrees. Measurements begin at the posterior section of the shell and continue to the anterior section. Abbreviations: LCR 1 = *Lampsilis ochracea*, LCR 2 = *Unio subrotundoides*, LEF 1 = *Leptodea fragilis*, LEF 2 = *U. alatoides*; LIN 1 = *Ligumia nasuta*, LIN 2 = *U. praeanodontoides*; LIR 1F = *Ligumia recta* female, LIR 2F = *U. praeanodontoides*; LIR 1M = *Ligumia recta* male, LIR 2M = *U. rectoides*; ANC 1 = *Anodonta cataracta*, ANC 2 = *A. grandioides*, AGR 1 = *Anodonta grandis*, AGR 2 = *A. corpulentoides*; ELA 1 = *Elliptio fisheriana*, ELA 2 = *E. producta*, ELA 3 = *U. nasutoides*.

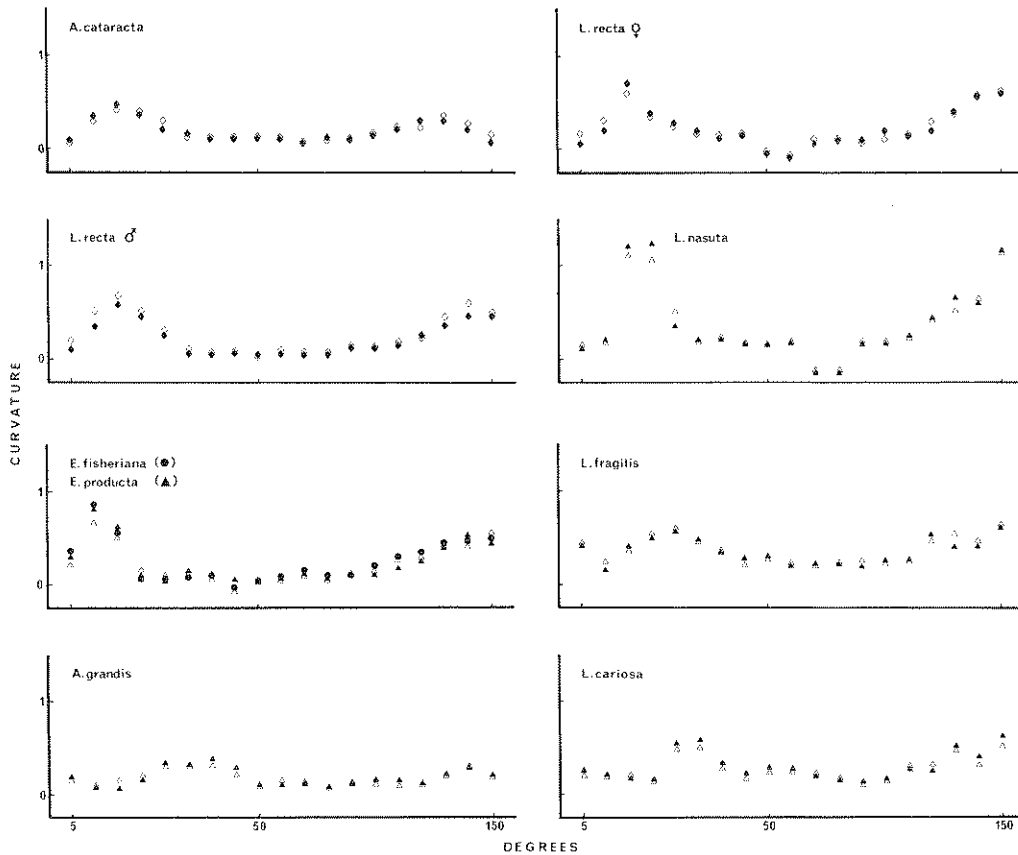| | Degrees | | | | | | | | | | | | | | | | | | |
	5	10	15	20	25	30	35	40	50	60	70	80	90	100	110	120	130	140	150
LCR 1	.24	.21	.17	.15	.51	.57	.33	.22	.29	.26	.21	.14	.15	.18	.28	.25	.51	.41	.63
LCR 2	.16	.18	.19	.16	.46	.49	.27	.19	.22	.23	.20	.14	.11	.16	.30	.32	.46	.30	.50
LEF 1	.41	.14	.41	.51	.58	.47	.34	.29	.31	.20	.23	.21	.20	.25	.27	.52	.40	.41	.62
LEF 2	.45	.23	.38	.56	.61	.48	.34	.23	.34	.19	.20	.22	.25	.21	.24	.45	.55	.47	.67
LIN 1	.12	.22	1.20	1.23	.36	.18	.18	.16	.15	.18	-.17	-.16	.18	.18	.24	.44	.64	.60	.93
LIN 2	.19	.26	1.09	1.05	.52	.18	.16	.13	.16	.14	-.15	-.14	.17	.16	.21	.46	.50	.65	.88
LIR 1F	.08	.21	.70	.42	.28	.21	.11	.14	-.06	-.10	.05	.09	.12	.19	.22	.24	.41	.54	.59
LIR 2F	.16	.32	.58	.36	.24	.16	.16	.15	-.05	-.08	.09	.09	.06	.11	.19	.31	.42	.52	.59
LIR 1M	.10	.34	.57	.45	.23	.07	.05	.05	.05	.06	.03	.07	.12	.12	.14	.24	.35	.46	.44
LIR 2M	.20	.50	.67	.50	.28	.12	.05	.06	.02	.11	.07	.05	.13	.15	.17	.23	.43	.59	.50
ANC 1	.08	.36	.45	.36	.21	.14	.08	.07	.08	.08	.06	.12	.08	.13	.21	.27	.28	.20	.07
ANC 2	.05	.29	.39	.40	.29	.10	.09	.08	.07	.05	.08	.08	.10	.18	.20	.19	.31	.26	.15
AGR 1	.19	.08	.09	.15	.32	.33	.37	.28	.09	.08	.09	.07	.10	.14	.15	.12	.22	.26	.24
AGR 2	.14	.06	.19	.21	.29	.31	.30	.20	.08	.13	.07	.05	.09	.11	.08	.12	.21	.28	.20
ELA 1	.34	.84	.55	.07	.05	.08	.09	-.06	.03	.11	.15	.10	.09	.20	.30	.36	.44	.46	.47
ELA 2	.29	.81	.62	.11	.11	.14	.09	.05	.04	.04	.11	.11	.09	.10	.17	.29	.40	.48	.44
ELA 3	.20	.66	.49	.18	.03	.03	.03	-.05	.04	.09	.12	.06	.08	.15	.26	.25	.39	.39	.53

FIG. 1.   Analysis of curvature along the shell margins of fossil taxa and their recent analogs. In each case, the Recent taxa are denoted by black symbols and the fossil taxa by open symbols. The axis labelled "DEGREES" represents the curvature at a point on the shell edge intersected by a line rotated through the indicated number of degrees from the umbo. Curvatures shown begin at the posterior section of the shell (5 degrees) and end at the anterior section (150 degrees).

fossil species with complete shell outlines were compared to Recent taxa by analyses of curvature along the shell edge. Shell outlines were digitized on a Numonics digitizing tablet, and coordinates of 250–400 points along the shell edge fed to an Apple II computer. Circles were fit to sets of points along the outline of the valve using a best-fit criterion outlined by Bookstein (1978: 39) involving a multiple linear regression of $x^2 + y^2$ as the dependent variable against x and y as independent variables (Kaufman and Kat in prep.). Centroids of point clusters along the outline were determined by the point of intersection of lines rotated through pre-determined numbers of degrees from the umbo and the shell outline. Curvature is defined as the inverse of the radius of the fitted circle. Curvature analyses in this study were limited to comparisons between fossil specimens and specimens of a Recent taxon which was visually determined to resemble the fossil closely in overall shape. Curvature along the shell edge is presented in Table 1 and in Fig. 1.

Recent taxonomic investigations based

TABLE 2. List of the Fish House unionid taxa identified by Lea (1868) and Whitfield (1885), and their re-evaluation in the present study.

Unio nasutoides	Elliptio fisheriana
Unio radiatoides	Lampsilis radiata
Unio subrotundoides	Lampsilis cariosa
Unio carriosoides	Lampsilis ochracea
Unio humerosoides	type = L. radiata, others = Elliptio complanata
Unio roanokoides	Elliptio complanata
Unio ligamentinoides	type = L. fragilis, others = L. cariosa
Unio alatoides	Leptodea fragilis*
Unio praeanodontoides	type = Ligumia nasuta, others = L. recta*
Unio rectoides	Ligumia recta*
Anodonta grandioides	Anodonta cataracta
Anodonta corpulentoides	Anodonta grandis*

* Species with present distributions largely restricted to the Interior Basin.

on characters with high heritability reveal that members of the family Unionidae often show considerable variability in shell characters such as overall shape, size, sculpture, and patterns of dentition (see Kat and Davis 1983). This high variability is presumably ecophenotypic in nature, although levels of intrapopulation variability at any one site can also be high. Consequently, since a number of the specimens originally designated as species by Lea (1868) fall within the boundaries of variability exhibited by modern representatives, I reduced the number of species in the Fish House fauna from 12 recognized by Lea (1868) and Whitfield (1885) to ten. The probable relationships among Recent and Fish House species are listed in Table 2.

A brief summary of the salient features of each of Lea's and Whitfield's fossil taxa and their proposed modern analogs which best seem to fall within the exhibited character complexes is provided below: more complete descriptions are provided by Lea (1868) and Whitfield (1885).

A. Unio nasutoides Lea (Plate 3C, see also Whitfield (1885) plate XXIV, figs. 4 and 5).

The length of these specimens is more than 2.5 times their height, and all are rounded anteriorly and quite pointed posteriorly. The umbos are located in the anterior third of the shells. The shell surface is smooth, and the anterior shell edge forms a distinct angle where it joins the dorsal edge. The ventral edge is almost straight. The lateral teeth are long, straight, and well developed, while the cardinal teeth are relatively small, thin, and striated. Lea (1868) remarked that this species exhibited resemblances to both *Ligumia nasuta* and *Elliptio fisheriana*. Curvature analysis (Fig. 1; Table 1) reveals a good fit between *U. nasutoides* and *E. fisheriana* (level of similarity = 89%) and *E. producta* (Lea) (83%) (Plate 3C). The lanceolate fossil is slightly less curved anteriorly and posteriorly than both Recent lanceolate taxa, and although the overall shell shape of the fossil is closer to that of *E. fisheriana*, curvature analysis does not clearly identify the fossil as either *E. fisheriana* or *E. producta*. This could imply that the fossil taxon is ancestral to both Recent taxa, or that it is ancestral to one of the Recent taxa which differentiated over time. Curvature analysis does indicate, however, that the fossil is clearly not a specimen of
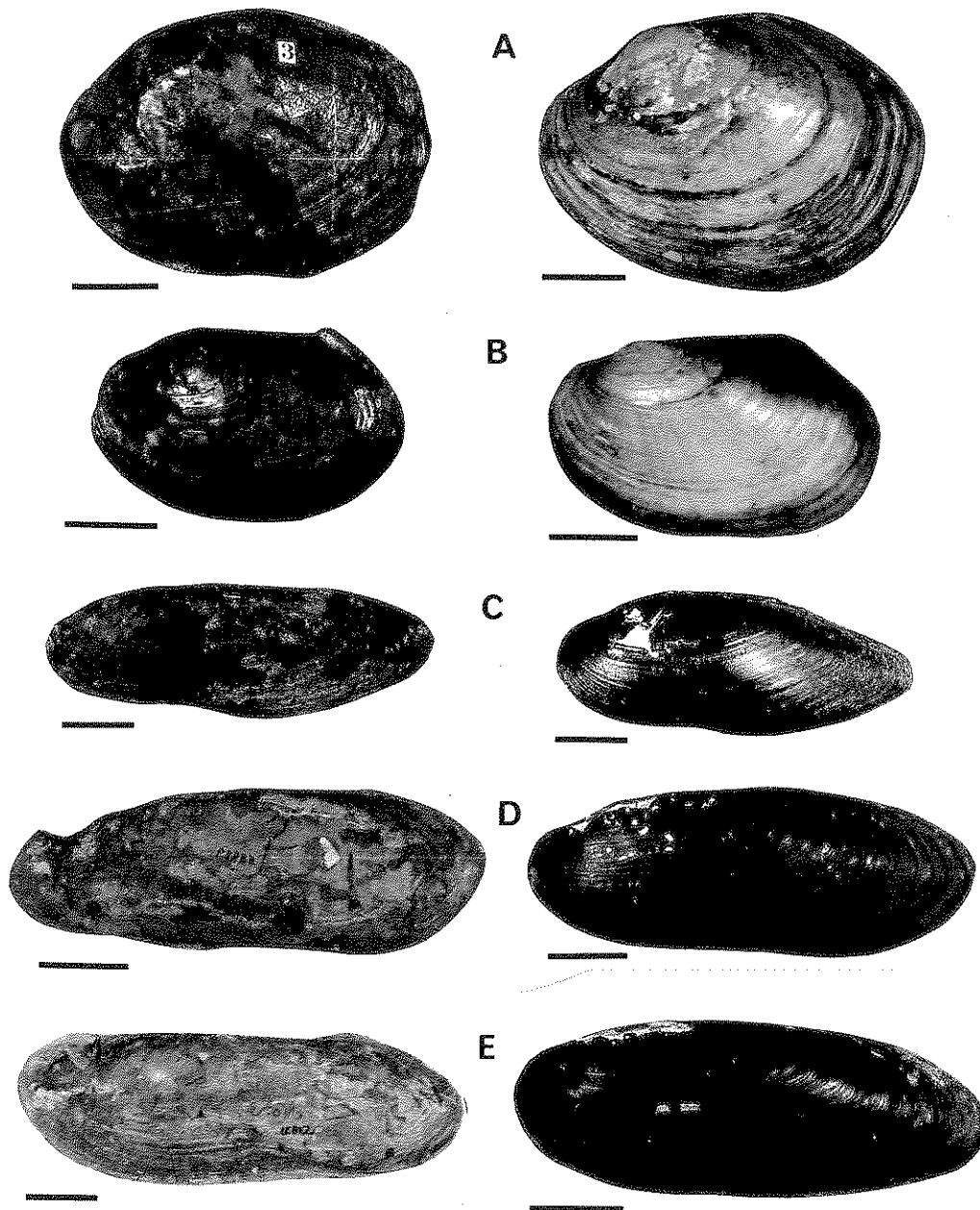
PLATE 1.   **A.** Left: type specimen, *Unio subrotundoides* Lea (ANSP 31524); right: *Lampsilis cariosa* (Say. **B.** Left: *Unio alatoides* Lea (ANSP 36081); right: *Leptodea fragilis* (Rafinesque). **C.** Left: Holotype, *Unio praeanodontoides* Whitfield (ANSP 31523); right: *Ligumia nasuta* (Say). **D.** Left: *Unio praeanodontoides* Whitfield (ANSP 53829); right: female *Ligumia recta* (Lamarck). **E.** Left: *Unio rectoides* Whitfield (ANSP 53831); right: male *Ligumia recta* (Lamarck). Scale bars = 20 mm.

L. nasuta, which has a much more curved anterior and posterior shell edge, and a concave ventral shell edge (Fig. 1).

B. Unio radiatoides Lea (Plate 2C, see also Whitfield (1885) plate XXXIV, figs. 1–3).

These shells are rather large, generally oval in shape, with moderately inflated umbos located in the anterior half of the shell. The height of the posterior section is larger than that of the anterior region. The shell surface is smooth and marked only with concentric growth lines. The posterodorsal shell edge is relatively straight while the ventral shell edge is gently rounded. The lateral teeth are long and moderately curved while the cardinal teeth are comparatively weakly developed. Features of these specimens agree in all details with those of Recent *Lampsilis radiata* collected from the same geographic area, and there can be little doubt that these fossils are indeed representatives of *L. radiata.*

C. Unio subrotundoides Lea (Plate 1A, see also Whitfield (1885) plate XXXII, fig. 5).

Whitfield (1885) describes this species as "very broad ovate in outline . . . the greatest height considerably behind the [umbos] . . . valves . . . convex with strong concentric striae; hinge line strongly arcuate, lateral teeth long, thin, and strongly arched." I agree with Whitfield that this specimen exhibits almost no resemblance to *Fusconaia subrotunda* (Lea) (range: Ohio, Cumberland, and Tennessee River systems) after which Lea (1868) named the species. In fact, the overall shape of the shell, hinge line, and appearance of the lateral teeth (especially their pronounced arcuate shape) of the type specimen closely resemble the widely distributed and locally common northern Atlantic Slope species *Lampsilis cariosa* (Say) (see below). Curvature analysis of the shell outline (Fig. 1) confirms a close fit (88%)

between *L. cariosa* and *U. subrotundoides;* the Recent specimen is slightly more curved anteriorly and posteriorly.

D. Unio carriosoides Lea (Plate 2B, see also Whitfield (1885) plate XXII, fig. 3).

Lea's type specimen is the only example of this species in the collection at ANSP, and it appears to have been slightly distorted and compressed during fossilization. The shell is rather large, oval in shape, with moderately inflated umbos located in the anterior ⅓ of the shell. The specimen is mostly an internal cast, but retains a small section of the original shell. The anterior edge is gently rounded, the posterior edge pointed, and the ventral edge curved. The lateral teeth are long and gently curved, and there is a suggestion of a well-developed cardinal tooth. I find no resemblance to *Lampsilis cariosa* for which Lea named the specimen; rather, this fossil is probably a specimen of *L. ochracea* (Say). Whitfield (1885) also mentioned a resemblance to *L. radiata.* There are clearly specimens of *L. cariosa* within the Fish House fauna, which are classified as either *U. subrotundoides, U. ligamentinoides,* and even *U. radiatoides.*

E. Unio humerosoides Lea (not figured here) and *U. roanokoides* Lea (Plate 2A, see also Whitfield (1885) plate XXXI, fig. 4; plate XXXIII, figs. 1 and 2; plate XXXIV, fig. 7).

The type specimen of *Unio humerosoides* is actually a specimen of *Lampsilis radiata;* other specimens in the collection with this label are all specimens of *Elliptio complanata. U. roanokoides* and *U. humerosoides* were so named by Lea for their close resemblances to *U. humerosus* Lea and *U. roanokensis* Lea, both of which were synonymized under *Elliptio complanata* by Johnson (1970). The range of variability of these fossil specimens, in which the shape
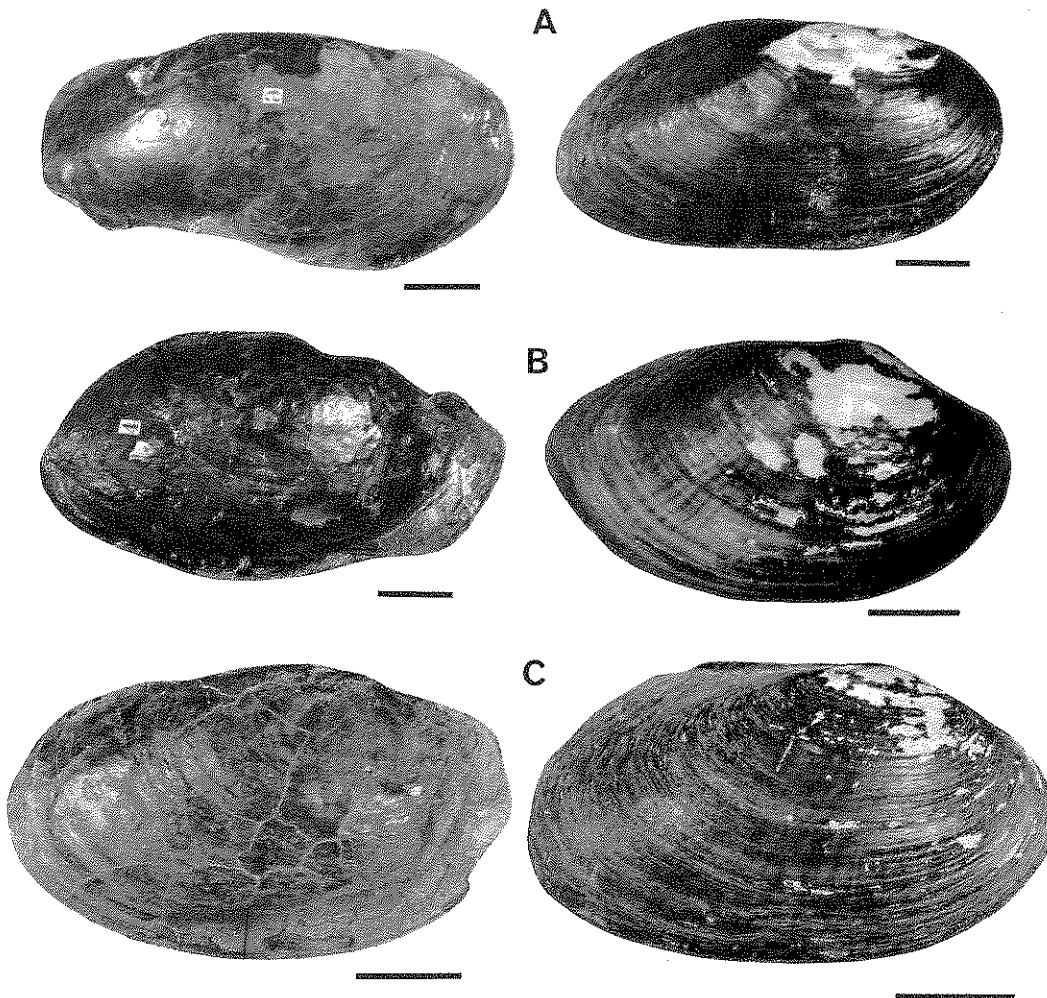
PLATE 2. **A.** Left: Type specimen, *Unio roanokoides* Lea (ANSP 31520); right: *Elliptio complanata* (Lightfoot). **B.** Left: Type specimen, *Unio carriosoides* Lea (ANSP 31517); right: male *Lampsilis ochracea* (Say). **C.** Left: *Unio radiatoides* Lea (ANSP 367073); right: *Lampsilis radiata* (Gmelin). Scale bars = 20 mm.

ranges from trapezoidal to elliptical, is typical of Recent *E. complanata*. Also, the specimens are quite compressed, with the umbos located in the anterior third of the shell, and the dentition consists of well-developed cardinal teeth and long lateral teeth, all of which are suggestive of *E. complanata*. These specimens are among the most common in the collection from the Fish House locality.

F. Unio ligamentinoides Lea (not figured here, see Whitfield (1885) plate XXXII, fig. 4; plate XXXIV, fig. 8).

The shell of the type specimen (which is the only specimen in the collection) is ovate in outline, with the umbo located in the anterior third of the shell. The valves are quite compressed. The lateral teeth are slender and curved, and the cardinal teeth com-

paratively large. Lea compared this specimen with *Actinonaias carinata* (Barnes) (range: Ohio–Mississippi Rivers, St. Lawrence drainage?) with which it exhibits only a very superficial resemblance. It is in fact much closer in all details to specimens of *Leptodea fragilis* (Rafinesque) (Plate 1B), discussed further below.

G. Unio alatoides Lea (Plate 1B, see also Whitfield (1885) plate XXXIII, figs. 3 and 4; plate XXXIV, fig. 6).

The shell is compressed and broadly ovate, with a distinct posterior alation. The umbos are very compressed and hardly elevated, and are located in the anterior half of the shell. The surface of the shell appears to have been wrinkled on the posterior surface. Lea named this species after the highly inflated *Proptera alata* (Say) (range: Mississippi River drainage) with which it has almost no resemblance; in fact the specimens closely resemble *Leptodea fragilis* in many details, including the sculpturing on the posterior surface of the shell. Curvature analysis of the shell outline reveals a very close fit (96%) between the shapes of *L. fragilis* and *U. alatoides* (Fig. 1). This phenotype is no longer represented among the present northern Atlantic Slope unionid fauna. Some specimens labelled as *U. alatoides* in the Fish House collection are quite inflated, and therefore likely to be specimens of *Lampsilis ochracea* and *L. cariosa*.

H. Unio praeanodontoides Whitfield (Plate 1C, 1D) and *U. rectoides* Whitfield (Plate 1E, see also Whitfield (1885) plate XXXI, fig. 2; plate XXXII, figs. 1 and 2).

Specimens of these species are elongate, with straight hinge lines, slightly raised umbos, and compressed valves. The lateral teeth are generally long and slender, and the cardinal teeth well developed. The ventral margin of *U. rectoides* is straight or slightly

curved, while that of *U. praeanodontoides* is concave. These species were named by Whitfield for resemblances to *Lampsilis anodontoides* (Lea) (=*L. teres* (Lea); range: entire Mississippi drainage) and *Ligumia recta* (Lamarck) (range: Mississippi drainage north to St. Lawrence River). I agree with the latter identification, but am of the opinion that the type specimen of *U. praeanodontoides* is a specimen of *Ligumia nasuta,* while other specimens in the collection labelled as *U. praeanodontoides* are females of the sexually dimorphic *L. recta.* Curvature analysis reveals that the shell outline of *L. nasuta* exhibits a complex series of curvatures (Fig. 1), ranging from a highly curved posterior section to a concave (negatively curved) ventral section. Nevertheless, the *U. praeanodontoides* fossil fits this pattern of curvature almost exactly (level of similarity = 96%), although it is slightly less curved than *L. nasuta* in the posterior region. Curvature analysis also reveals a very close (97%) fit between female *L. recta* and the other "*U. praeanodontoides*" specimens in the collection; note the profound differences, however, in outline curvature between *L. recta* and *L. nasuta* (Fig. 1). Curvature analysis between male *L. recta* and *U. rectoides* reveals a moderate (83%) fit (Fig. 1). The fossil specimen is more highly curved anteriorly and posteriorly than *L. recta.* The *Ligumia recta* phenotype is no longer represented among the present northern Atlantic Slope unionid fauna.

I. Anodonta grandioides Lea (Plate 3A, see also Whitfield (1885) plate XXXV, figs. 2 and 3).

Shells of these specimens are large and smooth, and subelliptical in shape. The umbos are small and located in the anterior third of the shell. The anterior edge is gently rounded, while the posterior shell edge is much more pointed, with a pronounced
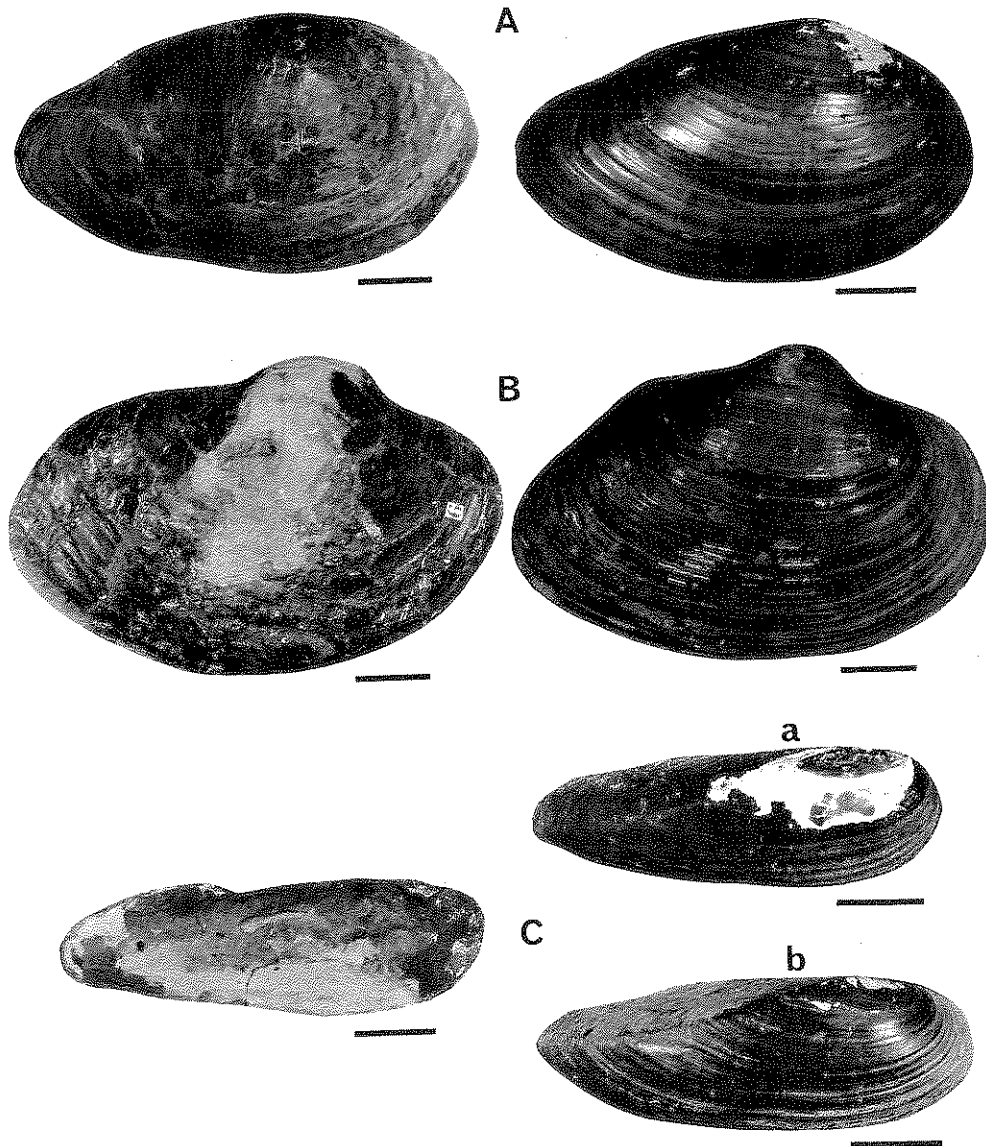
PLATE 3. **A.** Left: Type specimen, *Anodonta grandioides* Lea (ANSP 36075); right: *Anodonta cataracta* Say.
B. Left: Type specimen, *Anodonta corpulentoides* Lea (ANSP 31516); right: *Anodonta grandis* Say. **C.** Left: *Unio nasutoides* Lea (ANSP 36076); right, a: *Elliptio producta* (Conrad); right, b: *Elliptio fisheriana* (Lea). Scale bars = 20 mm.

posterior ridge. Lea named these specimens for their resemblance to *Anodonta grandis* (range: entire Interior Basin) but this is clearly wrong; these specimens much more closely resemble the northern Atlantic Slope anodontine *A. cataracta*. Curvature analysis confirms this resemblance: the fit between the outlines of the two taxa is ex-

tremely close (99%). Note that there are profound differences, however, in both the amount of curvature as well as the location of maximal curvatures when *A. cataracta* is compared with *A. grandis* (Fig. 1, Table 1).

J. Anodonta corpulentoides Lea (Plate 3B, see also Whitfield (1885) plate XXXV, fig. 1).

Shells of these specimens are smooth, large, and very inflated. The umbos are very well developed and located almost in the center of the shell. The anterior edge is gently rounded, while the posterior shell edge is much more pointed. Lea named these specimens for their resemblance to *Anodonta grandis corpulentis* Cooper with which I concur; curvature analysis indicates a close fit (93%) between *A. corpulentoides* and *A. grandis* (Fig. 1). This phenotype is no longer represented among the present northern Atlantic Slope unionid fauna.

ORIGINS OF THE ATLANTIC SLOPE FAUNA

Five species in the Fish House fauna are of special interest to the origin and evolution of the present northern Atlantic Slope unionid fauna. The first of these species, *Unio nasutoides,* which Lea (1868) apparently named for its resemblance to *Ligumia nasuta* but which is morphologically much more similar to lanceolate members of the genus *Elliptio* such as *E. fisheriana* and *E. producta,* is interesting for a number of reasons. Several species belonging to different phylogenetic groups within *Elliptio* apparently have converged on a lanceolate shape, and were all previously synonymized under *E. lanceolata* (see Davis et al. 1981). The northernmost representative of this lanceolate group, *E. fisheriana,* is at present endemic to the Delmarva Peninsula in rivers draining into the Chesapeake Bay. The Fish House taxon, which closely resembles *E. fisheriana* in shell characters, is encountered

further north than modern representatives, and therefore could represent a population which subsequently became extinct. If these are indeed specimens of early *E. fisheriana,* then it would indicate that the geographic range of this species was greater in the past, and that the present populations on the Delmarva Peninsula are relictual rather than necessarily locally evolved.

The second and third species, *Unio praeanodontoides* and *U. rectoides,* which Whitfield (1885) named for resemblances to *Lampsilis teres* and *Ligumia recta,* are probably *Ligumia nasuta* and female and male specimens of *L. recta. Ligumia recta,* however, is presently restricted to the Interior Basin and only occurs far north on the Atlantic Slope in the St. Lawrence River system; this morphotype is otherwise absent from the entire Atlantic Slope. *L. nasuta* is now the only species of *Ligumia* which occurs on the northern Atlantic Slope. *L. nasuta* and *L. recta* seem closely related: both Ortmann (1913) and Johnson (1970) propose that *L. nasuta* differentiated from *L. recta* very recently in the northeastern part of the Interior Basin and colonized the northern Atlantic Slope through the Hudson River, and then spread north and south to cover its present range (James River of Virginia (?) to St. Lawrence system). The presence of Fish House unionids with close morphological resemblance to *L. recta,* however, indicate that both ligumias were already present on the northern Atlantic Slope prior to the Wisconsinan glacial period. Ortmann's (1913) scenario could still apply but clearly has to be moved back in time. Anatomical and molecular genetic studies to elucidate the degree of resemblance between *L. nasuta* and *L. recta* are called for.

There are quite clearly two morphologically distinct species of *Anodonta* in the Fish House fauna (*A. grandoides* and *A. corpulentoides*), which exhibit close resemblances to *A. cataracta* and *A. grandis* respectively

(Fig. 1; Plate 3A, 3B). The present geographic range of *A. cataracta* (which might well be a complex of morphologically similar races or species) extends from the Altamaha River in Georgia to the St. Lawrence River in Canada and westward to Michigan; the range of *A. grandis* covers the entire American and Canadian Interior Basins. The *A. grandis* phenotype is now entirely absent from the Atlantic Slope (although some resemblance is found among *A. gibbosa* endemic to the Altamaha drainage in Georgia), and the presence of Fish House fossils with this phenotype could indicate a much more extensive geographic range of this species in the past. However, sympatry of these distinct taxa (without intergrades) in the past conflicts to some extent with reports (see Ortmann 1914; Clarke and Berg 1959) of hybrid zones in areas of sympatry (e.g. Lake Champlain, the Erie Canal) of these taxa in the Recent. Once genetic and behavioral barriers to hybridization have been established among related taxa, there are no examples that I am aware of which document a subsequent breakdown of those barriers. It is true, however, that selection against hybridization only operates in areas of sympatry among related taxa, and that allopatric populations might therefore not evolve the genetic or behavioral components of these barriers (see Grant 1963, 1971; Levin 1979; Thompson 1982). Evidence for enhancement of reproductive barriers involving behavior and morphology in zones of sympatry has been gathered for a variety of organisms such as plants (Lewis and Lewis 1966; Levin and Kerster 1967; Whalen 1977), *Drosophila* (Ehrman 1969; Ehrman and Probber 1978; Wasserman and Koepfer 1977; Zouros and d'Entremont 1980; Markow 1981), amphibians (Blair 1955; Mecham 1961; Littlejohn 1965), and mice (McCarley 1964). Character displacement among related species in sympatry is a related phenomenon (Brown and Wilson 1956; Grant 1966; Williams 1969; Fenchel

1975; Dunham et al. 1979; but see Grant 1975). If populations in which these barriers against reproduction have been established are eliminated by such processes as glaciation, and if the genetic and/or behavioral components of such barriers are thereby lost, newly sympatric populations of later generations will likely again initially hybridize (see discussion of newly-established "suture zones" in Remington 1968). This is the first presentation of historical fluctuation in levels of hybridization.

Finally, *Unio alatoides,* which Lea (1868) named after *Proptera alata,* actually exhibits a much closer resemblance to *Leptodea fragilis.* This morphotype is absent from the present northern Atlantic Slope fauna, but *L. fragilis* is presently distributed throughout the Interior Basin and also occurs in the St. Lawrence River and the Hudson River. This eastern distribution implies a recolonization of the Atlantic Slope subsequent to glacial retreat, but if the Fish House specimens indeed represent an early population of *L. fragilis,* then this present eastward dispersal represents a recolonization of sections of a previously more extensive geographic range.

Informative as the Fish House fossils are in terms of origins and species diversity of the northern Atlantic Slope through time, a number of species present today in this region are not represented as fossils. For example, none of the four species of *Alasmidonta* are represented as fossils, and neither are *Strophitus undulatus* (Say), *Lasmigona subviridis* (Conrad), *Anodonta implicata,* and *Margaritifera margaritifera* (Linnaeus). Some of these species are rather small and could have been overlooked by the early collectors, but the environment of Fish House, which was proposed to have been a slough by Baker (1920) and which was certainly an area of reduced flow in a large river as evidenced by dominance of poorly sorted and clay-size sediments (Woolman 1896), offers a partial explanation for the absence

TABLE 3. Comparison between faunas: probable species assemblage at Fish House and that of the nearby and environmentally similar Nanticoke River in Delaware.

Fish House	Nanticoke River
Elliptio fisheriana	*Elliptio fisheriana*
Elliptio complanata	*Elliptio complanata*
Lampsilis radiata	*Lampsilis radiata*
Lampsilis ochracea	*Lampsilis ochracea*
Lampsilis cariosa	*Lampsilis cariosa*
Anodonta cataracta	*Anodonta cataracta*
Ligumia nasuta	*Ligumia nasuta*
Anodonta grandis*	
Leptodea fragilis*	
Ligumia recta*	
	Anodonta implicata**

* Species presently largely restricted to the Interior Basin.
** Species presently widely distributed on the northern Atlantic Slope, the morphotype of which is absent from Fish House.

of these species: the alasmidontines, *S. undulatus*, and *L. subviridis* are presently restricted to small streams with gravel and sandy sediments, and *M. margaritifera* is found only in cold, fast flowing water of low alkalinity (Johnson 1970). The Fish House environment, however, is similar to that in which *A. implicata* occurs today, and this species is commonly found together with species such as *Elliptio complanata, Lampsilis radiata,* and *A. cataracta* (see Table 3), which are proposed to have been present at Fish House. *A. implicata* presently ranges from the Potomac to the St. Lawrence Rivers, and appears not to be closely related to other Atlantic Slope or Interior Basin anodontines (Kat 1982a).

IMPORTANCE OF THE FISH HOUSE FOSSILS

There are several reasons why the fossil unionid assemblage at Fish House is important. The first is associated with its apparent uniqueness: while the present northern Atlantic Slope assemblage ranks among the most intensively studied of the American unionid faunas, these Fish House fossils represent a valuable source of historic information critical to adequate assessment of the various theories concerning the origins and diversification of the northern Atlantic Slope unionid fauna. The presence of fossil unionids at Fish House with phenotypes now absent from the Atlantic Slope but present among the diverse Interior Basin fauna certainly supports hypotheses that these presently rather distinct faunas exhibited a greater amount of overlap during previous interglacial stages (Simpson 1895). This evidence of immigration of Interior Basin elements into the northern Atlantic Slope region also supports hypotheses that species within these two faunas could at one time have been more closely related, but then progressively diverged during repeated periods of allopatry resulting from the repeated glaciations of this region during the Pleistocene. Levels of molecular genetic and anatomical resemblance between proposed sister species from the northern Atlantic Slope and the Interior Basin should be compared to further evaluate such hypotheses.

Second, the Fish House fossils indicate that the species composition of faunas is subject to considerable change over time by repeated immigration and extinction events. Hence analyses which claim that Recent faunas of a particular geographic region result from simple processes of dispersal from an ancient center of origin, as has been proposed for the northern Atlantic Slope unionids (Sepkoski and Rex 1974), are likely to be both overly simplistic and misleading unless available historic and past climatic evidence has been adequately considered. Even largely sedentary organisms restricted to discontinuous habitats can be surprisingly mobile over spans of time encompassing tens or hundreds of generations, and any fauna in any region is likely to have undergone considerable fluctuation and change in species composition with historical fluctuations in such parameters as temperature, sea level, rainfall, and the po-

sitions of land masses (Williams 1969; Webb 1978, 1979; Davis 1979; Pragill and Olsen 1981; Stanley and Campbell 1981; Stanley 1982).

Third, elements of the Fish House fauna such as the proposed ancestral forms of *Elliptio fisheriana* indicate that, while the present geographic ranges of northern Atlantic Slope unionids are likely the result of net migration into previously glaciated territory from refugia, some species within this fauna remain restricted to smaller ranges than they once occupied, and should be considered relictual in distribution. The previously more extensive range of *E. fisheriana* should also serve as an example of the potentially misleading connections which can be drawn between narrow endemism in the Recent and the necessity that the species in question differentiated within that area of endemism.

Finally, the Fish House fossils provide at least an initial data point on the effects of Pleistocene climatic fluctuations on the Atlantic Slope unionid fauna. It is well-documented that the North American mammal fauna (e.g. Webb 1978; Kurten and Anderson 1980) and tropical Western Atlantic mollusk faunas (Stanley and Campbell 1981) underwent extinctions during that time, and that Recent faunas of these groups are depauperate assemblages of survivors. In contrast, the Fish House fauna indicates that those Atlantic Slope and Interior Basin unionids represented did not suffer a comparable extinction event: the phenotypes of all the Fish House taxa continue to be represented in either the Interior Basin or northern Atlantic Slope faunas. The only effect of the Wisconsinan glaciers seems to have involved a reduction of geographic ranges. Baker (1920) reached a similar conclusion based on comparisons between fossil and Recent Interior Basin unionids, and freshwater and land gastropods.

In sum, and in contrast to earlier views expressed by Ortmann (1913) and Baker

(1920), I am of the opinion that the Fish House fauna provides invaluable insight into the history, origins, and differentiation of the northern Atlantic Slope unionid fauna, and strongly encourage the use of similar historical data in other biogeographical and faunistic analyses.

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