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Article abstract

Molluscs are among the most ubiquitous fossils found in Quaternary non-marinesediments. They are found in a wide variety of deposits including: loess, cave, sinkhole and fissure deposits; fluvial, lacustrine, glaciolacustrine and paludal sediments; and spring-fed travertine accumulations.

In spite of problems associated with identification of some species from shell morphology alone and a general inadequacy in our understanding of the factors controlling modern species distribution, Quaternary studies of non-marine molluscs have resulted in some significant contributions. In North America fossil molluscs have been used to: (1) reconstruct former stream confluences; (2) provide a basis for biostratigraphic zonation of sedimentary sequences in the Lake Michigan, Superior and Huronbasins; and (3) reconstruct local habitat and climatic conditions. Isotopic data obtainedf rom the analysis of mollus can shell has provided information about the environment in which the molluscs lived. Amino acid stud-ies of the shell protein have provided infor-mation about the age of fossil assemblagesand a method for estimating post depositional effective temperature histories of fossil sites.

One of the basic problems in Quaternary biogeography concerns the timing, the nature, and the magnitude of biotic changes that accompanied glacial advances and retreats. The ubiquity of non-marine molluscsin Quaternary sediments provides an excellent opportunity to study effects of both short and long scale climatic fluctuations on at least one important part of the non-marinebiota, the molluscs.

Methods in Quaternary Ecology #8. Non-marine Molluscs

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Summary

Molluscs are among the most ubiquitous fossils found in Quaternary non-marine sediments. They are found in a wide variety of deposits including: loess, cave, sinkhole and fissure deposits; fluvial, lacustrine, glaciolacustrine and paludal sediments; and spring-fed travertine accumulations.

In spite of problems associated with identification of some species from shell morphology alone and a general inadequacy in our understanding of the factors controlling modern species distribution, Quaternary studies of non-marine molluscs have resulted in some significant contributions. In North America fossil molluscs have been used to: (1) reconstruct former stream confluences; (2) provide a basis for biostratigraphic zonation of sedimentary sequences in the Lake Michigan, Superior and Huron basins; and (3) reconstruct local habitat and climatic conditions. Isotopic data obtained from the analysis of molluscan shell has provided information about the environment in which the molluscs lived. Amino acid studies of the shell protein have provided information about the age of fossil assemblages and a method for estimating post depositional effective temperature histories of fossil sites.

One of the basic problems in Quaternary biogeography concerns the timing, the nature, and the magnitude of biotic changes that accompanied glacial advances and retreats. The ubiquity of non-marine molluscs in Quaternary sediments provides an excellent opportunity to study effects of both short and long scale climatic fluctuations on at least one important part of the non-marine biota, the molluscs.

Introduction

Molluscs have been reported from a diversity of environments. Sediments known to preserve non-marine molluscs include supraglacial lake deposits (Tuthill *et al.*, 1964); windblown silt (Leonard and Frye, 1960); cave, sinkhole and fissure sediment accumulations (Guilday *et al.*, 1978); alluvial floodplain (Miller and Kay, 1981), back-water channel (Miller, 1983), littoral and lagoonal lacustrine sediments (Karrow *et al.*, 1975; Bajc, 1986), accumulations of spring-fed travertine (Hansel and Johnson, 1986), and peat (Miller and Thompson, 1987). Human activities have accumulated significant shell concentrations in Indian middens (Parmalee and Bogan, 1986).

The widespread occurrence of fossil non-marine molluscs in a variety of environments, has frequently led to their inclusion in reports dealing with Quaternary sites, even though they usually were not the main focus of the study. For example, the panhandle of Oklahoma – southwestern Kansas contains one of the best documented molluscan successions in North America. It includes a sequence of faunas that range in age from the Pliocene to the Holocene, that were collected over a period of three decades by C.W. Hibbard and his associates. The molluscs, which usually formed the most abundant faunal element, were retained during wet-sieving of sediments for the fossil microvertebrate remains: the main focus of the study.

In spite of the large amount of important research that remains to be done in North American Quaternary malacology, few paleontologists have been attracted to this field of study. The reasons for this are probably comparable to those given by Morgan and Morgan (1980) for the paucity of paleoentomologic researchers, *viz.*, it requires ... "a blend of paleontology, stratigraphy"... "taxonomy and zoogeography, so it is rare that any prospective researcher starts in this field fully qualified in all aspects". Add to this the sheer tedium of sorting through large quantities of material for shells, the few well-organized systematic reference collections and taxonomic keys, and the absence of ecological and distributional data for many species, has probably discouraged potential students and driven former workers from the field.

Although these difficulties have hindered, they have not prevented malacology from being an important contributor to North American Quaternary studies. The sections that follow present a short review of Quaternary malacology in North America.

Historical Development

One of the first references to Canadian Quaternary non-marine molluscs was made in 1861 by Robert Bell who reported on collections made between 1838 and 1861 from several mollusc-bearing deposits in the eastern Great Lakes and St. Lawrence valley (Coleman, 1922). Among these are reports of freshwater molluscs enclosed in calcareous nodules from Green Creek near Ottawa; molluscs contained within fluvial gravels of an ancestral Niagara River near Niagara Falls; and mollusc remains recovered from clay pit excavations near Montreal. Subsequent reports of fossil molluscs from the north shore of Lake Superior were published after Bell's visit to the area around 1860 (Coleman, 1922).

Baker's (1920a) classic publication *Life of the Pleistocene or Glacial Period* presents a compilation of the early studies dealing with fossil molluscs in eastern North America, with special reference to the interglacial and post-glacial biota of the Great Lakes region. Reference to interglacial shells at Toronto (Lemon, 1898), and general discussions on fossil land snails in Quaternary paleoecology (Billups, 1902), are among the many significant historical citations found in this publication. As early as 1884, molluscan faunal studies from Canadian archaeological sites were being used to reconstruct cultural and natural environments (Matthew, 1884). Other early work, dealing primarily with taxonomy, distribution, and ecology of modern and fossil molluscs include publications by Sterki (1920) and Baker (1920b). Quaternary molluscan studies of post-glacial and interglacial sites in Saskatchewan were undertaken by Russell (1934) in an attempt to compare distributions of modern populations in the province with their fossil counterparts.

Wittaker (1921) described molluscan faunas from marl deposits in the Ottawa area. The molluscan succession of Holocene basin deposits in Ontario and Quebec were the subject of a series of studies by Shallom (1965), Clowers (1966), Gibson (1967), Warner (1968), and Bickel (1970). These investigations utilized substrata and water depth, chemistry, temperature, and pH data in the interpretation of molluscan paleoecology. Harris and Pip (1973) studied fossil molluscs in southwestern Alberta in an attempt to reconstruct post-glacial climatic change from distribution shifts of extant taxa. A recent study of gastropods from the interglacial Don Formation at Toronto revealed a fossil fauna similar to that found in southern Ontario today (Kerr-Lawson, 1985).

Molluscan studies of Quaternary assemblages from the Ontario (Karrow *et al.*, 1972), Huron (Miller *et al.*, 1985), Agassiz (Ashworth and Cvancara, 1983), and Superior basins (Bajc, 1986) have focussed on the potential for biostratigraphic zonation of these faunas. Data from the Lake Michigan basin suggests faunal changes similar to those observed in the Huron basin during the past 11 Ka B.P. (Miller, unpublished).

A number of modern studies have focussed on the analysis of stable isotopes in molluscan shell for deducing past temperatures, evaporative effects, and productivity levels of fossil environments (Webber and

LaRocque, 1964; Stuiver, 1968; Fritz and Poplawski, 1974; Fritz *et al.*, 1975; Yapp, 1979; Godwin, 1985).

Much recent work is currently being directed toward the use of amino acids in shell protein to infer ages of fossil assemblages and estimating post-depositional effective temperature histories of fossil sites (Miller and Hare, 1980).

Field Techniques and Source of Fossils

The quality of preservation of fossil molluscs may vary greatly. Individual shells from some sites may retain the external organic periostracum layer and original shell colour patterns (Figure 1). Preservation of snail eggs in some deposits is not uncommon. Tompa (1976) reported calcified eggs of *Vallonia* from middle Pleistocene sediments associated with a 700 Ka B.P. ash in the Meade County area of southwestern Kansas. Fossil eggs (Figure 2) have also been recovered from magnetically reversed silts at Whites Branch in west-central Indiana (Miller *et al.*, 1987). At the other end of the preservation spectrum is complete destruction of the shell by leaching leaving only a mold of the exterior and/or interior.

Access to natural exposures of fossil assemblages may occur as a consequence of some geologic processes, *e.g.*, wave action along the shores of a lake (Gutschick and Gonsiewski, 1976) or the erosive action of a stream that might expose fossils in its cut bank (Wayne, 1981). Many sites containing molluscs become accessible as a result of such human activities as sand and gravel extraction operations (Leonard, 1953).

In the field, fossil molluscs are often bleached white on the surface of exposures and may stand out in sharp contrast against the colour of the enclosing sediments. All but the smallest (< 2 mm) shells can be seen easily with the unaided eye. To avoid a bias that would favour larger individuals, bulk samples are usually collected at selected stratigraphic intervals of the exposure for systematic analysis.

Extraction of molluscs from the enclosing sediment usually starts by drying the sample to remove most of the interstitial water. The sample is then immersed in a container of cold water. After several hours of soaking the sediments will usually disaggregate, and many shells, insects, seeds, and plant fragments may float to the surface where they are skimmed off with a tea-strainer. The fossils remaining in the water-sediment slurry are then poured through a stacked series of sieves (0.071 mm to 2.0 mm mesh diameter). Washing under a gentle spray of water flushes the fine silt and clay through the sieves and breaks down small clods of sediment that did not completely disaggregate during the soaking.

If this simple procedure was insufficient to free all shells, the sample may be redried, soaked or boiled in a water-soluble deflocculant such as Quaternary-O or sodium hexametaphosphate or placed in an ultrasonic cleaner. This concentrate of shell, organic matter, and the coarse-grained fraction from the sample is then dried, labelled and stored in vials for later examination and sorting under a low-power microscope. The molluscs are sorted on the basis of shell morphology with forceps or a fine sable brush and stored in gelatin capsules or vials.

Identification

Most taxa encountered as fossils in North American Quaternary deposits are referable to extant species. Consequently, reliable identification of fossil molluscs requires access to good collections of identified modern representatives and familiarity with malacological literature. Often taxonomic specialists are needed to confirm identification.

Identification may require the careful scrutiny of minute details in shell microstructure at high magnifications (100 ×). In some genera, (*e.g.*, *Strobilops, Vertigo, Gastrocopta, Carychium*, and *Planorbula*), examination of folds, lamellae, and denticles (Figure 3) that may extend varying distances within the shell may be necessary for species determination. X-radiography (Miller, 1957) or immersion of the opaque shell in oil (refractive index 1.60), which makes the shell translucent to transmitted light (Miller, 1968), provide non-destructive methods for studying internal structures.

Taxa that require the examination of soft parts, (usually the genitalia), for species identification, are of little value in fossil specimens. Although many aquatic species commonly encountered in Quaternary assemblages belong to families in which the shell alone is frequently insufficient to permit specific identification, (for example, many species of the families Succiniidae, Lymnaeidae, Physidae and Hydrobiidae), there are far more taxa that can be confidently identified to the species level on the basis of shell characters alone.

Factors Controlling Fossil Mollusc Assemblages

The suitability of a fossil molluscan assemblage for Quaternary environmental reconstruction is determined by factors related to: natural abundance of taxa in living populations; processes of deposition and preservation; effects of contamination by older or younger shells; adequacy of the sample; and specimen identification (Sparks, 1964). Further consideration of this problem can be found in Pip (1988), Lozek (1982), Birks and Birks (1980), Crisman (1978), Miller (1978), Kerney (1977), LaRocque (1966), and Sparks (1961).

Natural abundance of taxa. The relative abundance of various taxa in their natural habitat is an important consideration for paleoecologic reconstructions. Some freshwater forms, such as *Valvata tricarinata, Lymnaea stagnalis, Sphaerium striatinum,* and *Pisidium casertanum* are ubiquitous, whereas others, such as *Acella haldemani, Pisidium cruciatanum,* and *Pisidium henslowanum* are invariably scarce, even in favourable, present-day environments. The single shell of a rare or uncommon taxon in any paleoecological analysis has quite a different significance than the solitary occurrence of a common species.

Figure 1 Anguispira alternata *from the Chinatown Silt (Illinoian) Bellville, Illinois showing preserved colour pattern in shell.*

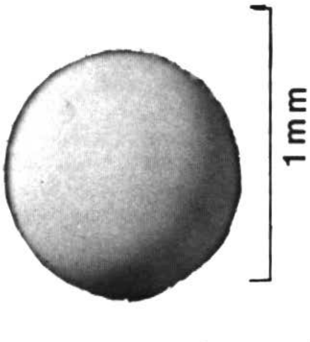


Figure 2 *Fossil calcified egg from magnetically reversed silts (> 730 Ka B.P.) Whites Branch, Indiana (Miller* et al.*, 1987).*

Figure 3 *Angular parietal fold (upper part of aperture) and lower and basal lamellae in* Gastrocopta cf. Gastrocopta armifera *from middle Pleistocene sediments, Little Sioux, Iowa. The number, shape, and distribution of these apertural structures are important features used for the identification of species within certain families of gastropods.*

Allochthonous and autochthonous assemblages. Most Quaternary molluscan assemblages are composed of taxa that have been brought together after death from a variety of habitats. Air trapped in the shells of gastropods frequently permit them to float long distances. Species diversity in an open river deposit, therefore, may be quite high because it could represent an accumulation of shell from a wide spectrum of terrestrial and aquatic habitats indiscriminately brought together during high-water periods. In contrast, a small, spring-fed lake, may yield only a limited number of taxa that were living in the water column near the sampling site.

Interpretation of mixed assemblages, frequently requires invoking the "rule of relative abundance", which assumes that, if all other factors are equal, species native to a given environment (autochthones) should be more abundant than exotic (allochthonous) taxa brought in from outside (LaRocque, 1966). Sparks (1964) has suggested that autochthonous elements in a fossil assemblage can often be recognized by the quality of preservation of the periostracum and the absence of surface abrasion. An allochthonous origin for a mollusc assemblage can be inferred when only a small percentage of the sample shows absence of wear and fragmentation.

Allochthonous assemblages redeposited by fluvial processes are likely to have been subjected to some degree of sorting. The composition of the assemblage may be determined by the size, weight, and surface morphology of the shells in the fossil deposit (Pip, 1988). As stream competence increases, the larger, heavier, and more streamlined shells will tend to settle out, while the smaller, lighter molluscs will remain in suspension and be swept away to a position downstream. Generally, loosely coiled gastropods have the greatest potential for redeposition because of their low mass to volume ratio and high sphericity. In contrast, the streamlined shape of clam valves are more resistant to transport after disarticulation.

Typically, collections of fossils are assumed to be the same age unless evidence warrants rejection of this hypothesis. Taylor (1965), for example, utilized the worn and etched condition of most of the shells from the Rezabeck local fauna, Lincoln Co., Kansas, in contrast with the normal fresh condition of shells from other nearby Quaternary age sites in the area, as evidence for probable reworking of this assemblage. A wide range of values obtained from amino acid racemization analyses of shells from the same taxa and stratigraphic level, would suggest that the fossils include reworked shells from different age deposits. Failure to recognize the possibility of contamination from older deposits may result in misleading ecological, biogeographic, and age interpretation.

The reworking of post-glacial mollusc-bearing sediments within the Great Lakes basins is a serious potential problem given the history of water level changes, particularly transgressive phases that have reworked sediments from older and lower lake levels. Within the Huron basin, alluvial deposits transitional in age between Algonquin and Nipissing phases, may well contain reworked fossils from the oldest Algonquin sediments (Miller *et al.*, 1985). Along the north shore of Lake Superior, the potential for reworking of older shells also exists as continuously falling post-glacial water levels resulted in the insetting of progressively younger terraces into older lacustrine and alluvial deposits (Bajc, 1986).

Preservation of fossil molluscs. The preservation of fossil molluscs can be related to both the biological and chemical attributes of the depositional environment as well as the strength of the individual shell structures. In non-calcareous environments, molluscs are quickly leached after deposition. Generally, fossil molluscs are absent from large areas of the Canadian Shield containing acidic overburden and bedrock. The scarcity of fossil mollusc sites along the northern parts of the Huron basin has been attributed to this phenomenon (Miller *et al.*, 1985). Calcareous drift on Precambrian bedrock is responsible for the preservation of fossil molluscs along the north shore of Lake Superior (Bajc, 1986), east of Lake Nipigon (Kristjansson, pers. comm.), and in the Fort Frances-Rainy River area (Bajc and Gray, 1987).

Solution features are commonly found in molluscs recovered from sand and gravel deposits because high groundwater flow rates through permeable sediments greatly enhance the leaching process. Calcareous, low permeability (fine-grained) sediments, tend to favour preservation of gastropods and pisidiid clams whereas, better drained sediments favour preservation of the larger unionid clams.

Differential destruction of species occurs during transportation and deposition, sediment compaction from burial, and the laboratory extraction of fossils from the enclosing matrix. Factors that contribute to differential destruction of molluscan shell include relative weakness of: larger *versus* smaller shells, thin *versus* thick shells, and loosely-coiled and elongate *versus* tightly coiled, compact shells (Sparks, 1964). Over-representation of small species, juveniles and the broken early whorls of larger forms, often results from the operation of these factors. Molluscan paleoecologists must be aware of such problems to avoid overestimating the abundance of a particular taxon or group of taxa.

Uses of Fossil Non-marine Molluscs

Stratigraphy. As Quaternary North American non-marine molluscs have apparently undergone little change in shell morphology, they have proven useful indicators of environmental change that locally have stratigraphic significance. Miller *et al.* (1985) have shown that the Algonquin, Stanley, and Nipissing lake phases of the Huron basin are characterized by distinctive assemblages of molluscs that relate to climatic changes, retreat of ice margins, and isostatic rebound which altered the drainage. The widespread occurrence of well-preserved non-marine molluscs in a variety of environments has led to their use in stratigraphic studies utilizing amino acid racemization ratios obtained from shell protein (Miller and Hare, 1980). Miller *et al.* (1987) have shown that changes in the ratio of alloisoleucine to isoleucine (alle/Ile) in fossil gastropods from west-central Indiana could be used to differentiate four distinct groupings (Figure 4). The lowest alle/Ile values were from shells collected from sites within the Trafalgar Formation (*ca.* 20 Ka B.P.), while the highest values were associated with the magnetically reversed (>730 Ka B.P.) Jessup and Atherton Formations.

Habitat reconstruction. Most interpretations of Quaternary non-marine molluscs start with the tacit assumption that fossils with shell morphology similar to those of living forms represent the same species, and therefore, probably responded in the same manner to environmental factors as their living counterparts (Taylor, 1960, 1965, 1988). Some support for the belief that many non-marine molluscs have been evolutionary conservatives during the Quaternary comes from examination of a large number of fossil faunas in which the same ecologic association of species reappear. These assumptions have frequently provided the basis for reconstruction of local paleohabitat and paleoclimatic conditions.

Analysis of molluscs for environmental reconstructions usually involves sorting of extant species into habitat associations in which they most frequently occur. These data may be plotted as relative abundance histograms. Miller and Thompson (1987) used this approach to graphically illustrate habitat changes in a core from the Cowles Bog area of northern Indiana that they interpreted as responses to water-level oscillations (Figure 5).

Although most species may be found in a range of habitats today, many of them seem to occur more frequently in only a few. This point is illustrated by Pip (1986) in an ecological study of 38 aquatic gastropods species in central Canada. She found that most of the species were not restricted to a single habitat, but many were far more common in lakes and ponds that in river and creek habitats. While many species are generalists and can tolerate a broad range of environmental conditions (*e.g.*, *Pisidium casertanum*, Figure 6) other species, for example, *Discus macclintocki*, are limited to a few sites in northeastern Iowa which are kept cool during the summer months by cold-air drainage (Frest and Fay, 1980a). *Sphaerium occidentale*, (Figure 7) is a species that is found only in aquatic habitats that dry up for parts of each year. It is more amphibious than any other North American bivalve and often occurs among damp leaves (Clarke, 1981).

Some species develop special shell modifications that reflect habitat conditions. The development of a septum that partially closes the aperture in some species of *Ferrissia* living in habitats subjected to periodic drought has been reported by Basch (1963) and Richardot (1978). Fossil septate individuals of *F. fragilis* in the Kanopolis local fauna near Ellsworth, Kansas, therefore, were considered *prima facie* evidence for the presence of temporary water bodies near the depositional site (Miller and Kay, 1981). Six habitats were inferred from the gastropods of the Kanapolis local fauna (Figures 8 and 9). The general compatibility between interpretations based on molluscs, and those derived from the study of other fossil organisms in the assemblage (*e.g.*, Hall, 1980), suggests that this approach is valid.

Migration patterns and dispersal routes. In his review of the distribution of fossil freshwater molluscs, Yen (1947) suggested several mechanisms by which dispersal can occur. River and lake currents can transport molluscs effectively. Often, molluscs attach themselves to floating objects and have been observed on aquatic insects, amphibians, birds, and fish (Kew, 1893; Cooke, 1895). Molluscs have also been found floating within ice on rivers and lakes; some species have been known to survive after being frozen for several months. Malone (1965) suggested that snails could also be dispersed by being regurgitated from the crop of water birds. The dispersal of many species of unionid clam is highly dependent upon fish migrations (Taylor, 1988). During their glochidial stage, the clams are parasitic upon a host fish and therefore, are easily spread.

The dispersal of terrestrial gastropods tends to be a much slower process. Common dispersal mechanisms include: natural locomotive processes; organic agents, such as mammals and birds; and physical agents, such as wind and water. Factors such as natural abundance; resistance to desiccation, drowning and cold; and the fertility of

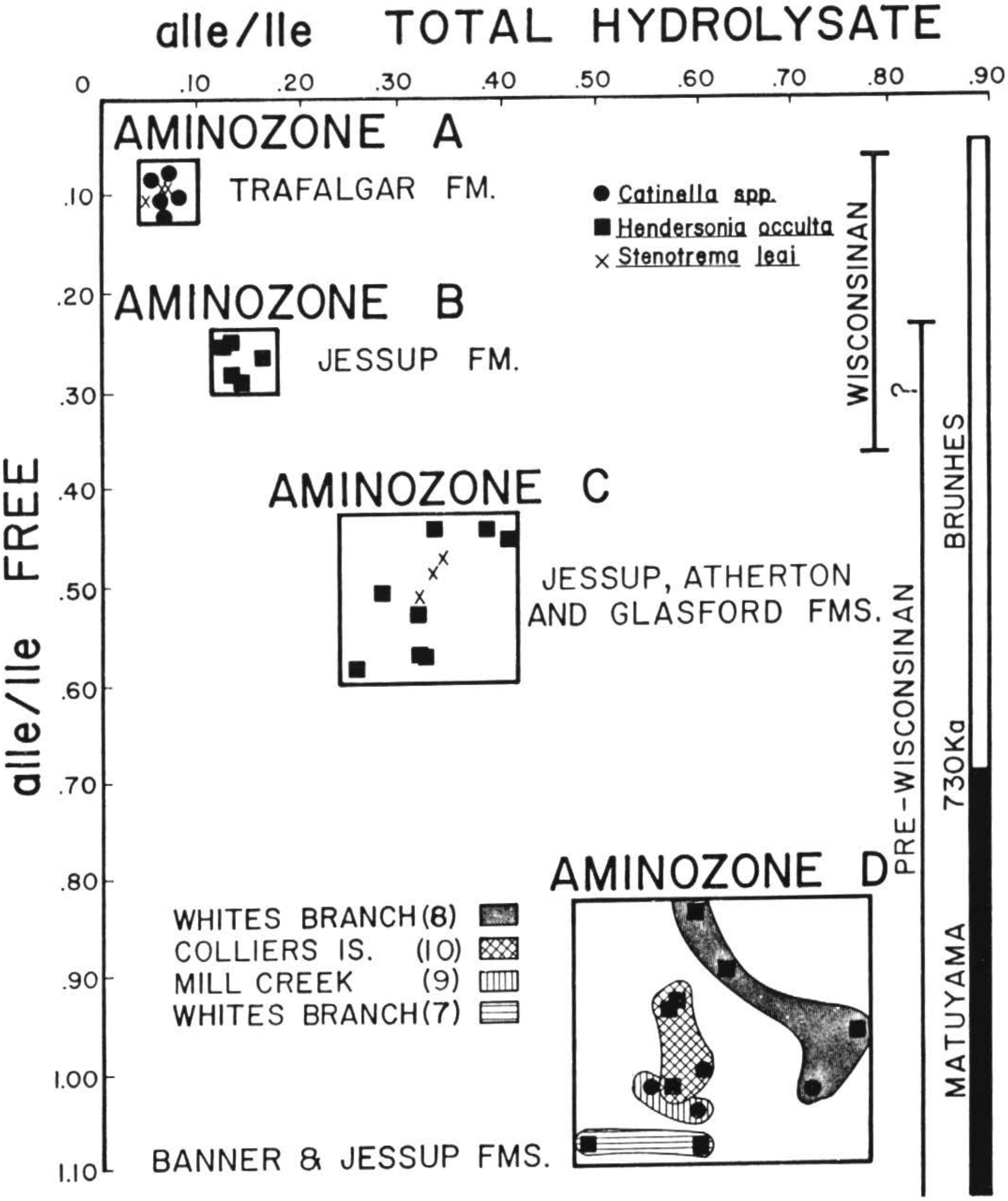


Figure 4 *Plot of free versus total alloisoleucine/isoleucine from fossil mollusc shell protein. The ratio of free to total hydrolysate increases asymptotically with age. The sites with the highest ratios are magnetically reversed and should be older than the Brunhes-Matuyama boundary or > 730 Ka B.P. (Miller et al., 1987).*

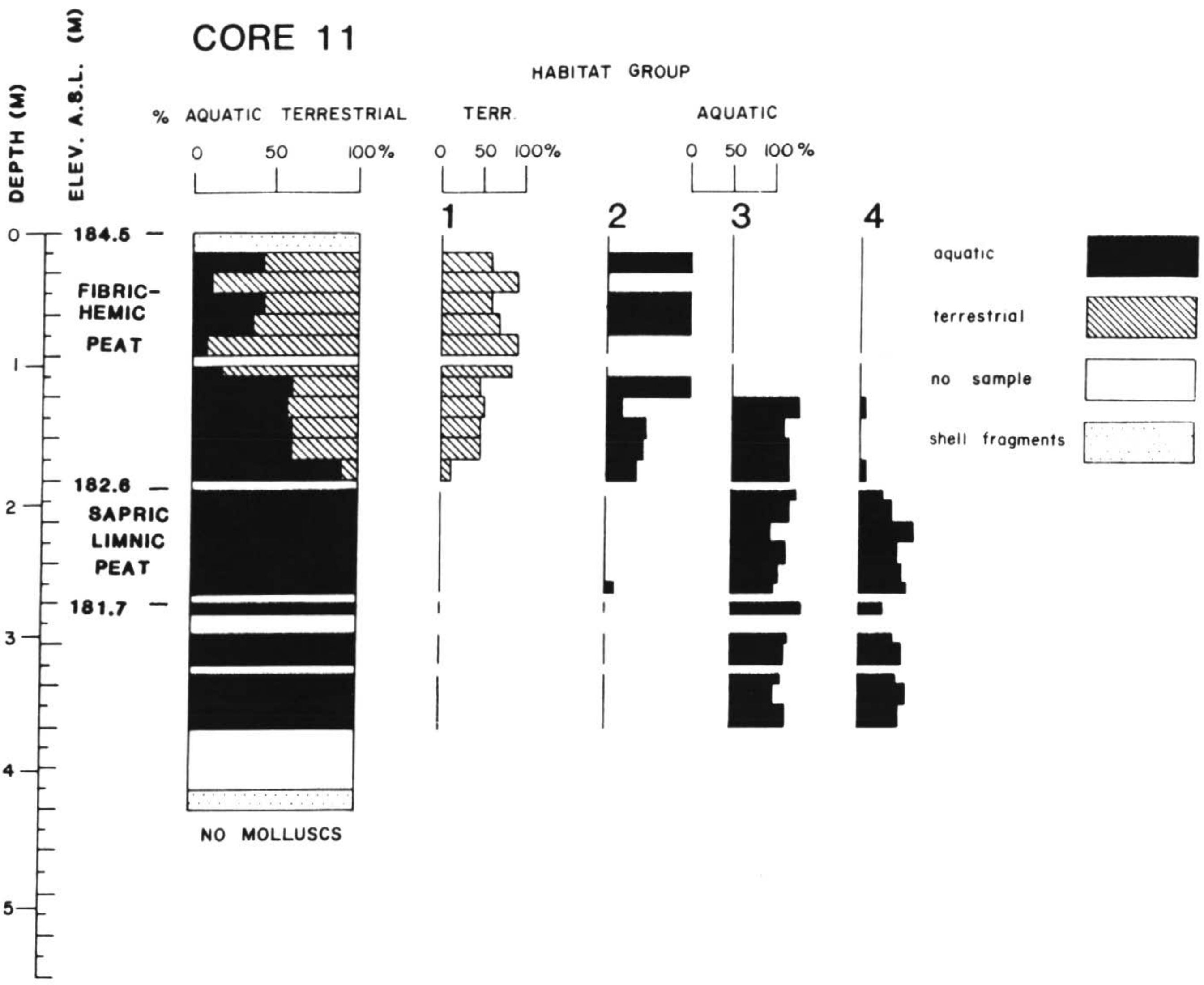


Figure 5 *Plot showing the change in abundance of molluscan habitat groupings in core 11 from Cowles Bog, Indiana (Miller and Thompson, 1987).*
Habitat group 1 *includes terrestrial species living in wooded, damp lowland areas, close to water, with moist areas available throughout the year.*
Habitat group 2 *contains species associated with bodies of water subject to significant seasonal drying and with areas of submerged vegetation.*
Habitat group 3 *includes species associated with eutrophic, perennial bodies of water that are not subject to significant seasonal drying.*
Habitat group 4 *includes species that live in perennial unpolluted water bodies containing aquatic vegetation.*

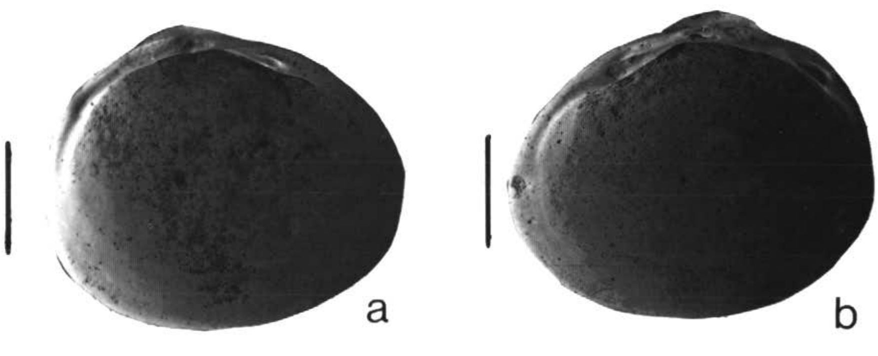


Figure 6 *Right and left valve of* Pisidium casertanum, *a species which can tolerate a broad range of environmental conditions. Scale bars equal 1 mm.*

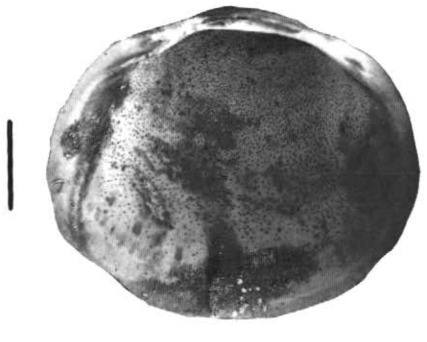


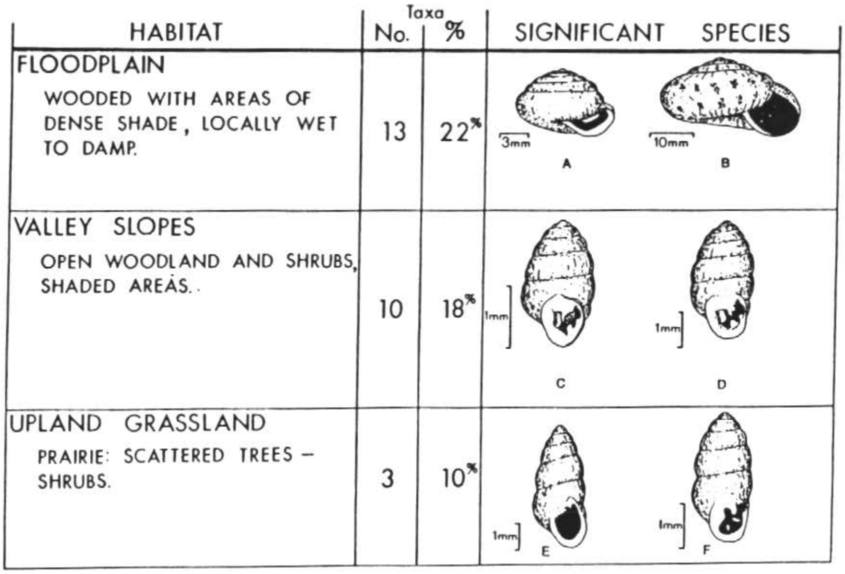
Figure 7 *Right valve of* Sphaerium occidentale, *one of the most amphibious species of North American bivalves (Clarke, 1981). Scale bar equals 1 mm.*

taxa play important roles in dispersal (Oughton, 1948).

Ice-marginal positions and intra-basin confluence appear to have imposed constraints on mollusc migration patterns within the Great Lakes basins. Between 12 and 10 Ka B.P., the Huron, Michigan, and southeast corner of the Superior basins were confluent and formed Lake Algonquin (Figure 10a). Freshwater molluscs followed the retreating ice margin in the Superior basin and reached the north shore by 9.5 Ka B.P. (Figure 10b). Aquatic mollusc assemblages (9-8 Ka B.P.), recovered from the north shore of the Superior basin are remarkably similar to those found in Algonquin age sediments of the Huron basin (12-10 Ka B.P.) (Bajc, 1986). Basin confluence appears to be the primary controlling factor responsible for this similarity. Between 10 and 6 Ka B.P., the Michigan and Huron basins stood at the Chippewa and Stanley low-water levels, respectively, and the transitional levels while the Superior basin remained perched above the lower lakes at the Minong through Houghton water levels. It was during this time that important migrations of terrestrial molluscs from the upper peninsula of Michigan to the north shore of Lake Superior occurred (Figures 10b and 10c). By 6 Ka B.P., confluence of the upper Great Lake was again restored due to isostatic processes, the water body standing at the Nipissing shoreline (Figure 10d). Basin confluence resulted in rapid dispersal of aquatic taxa and hence, a great increase in diversity in Nipissing faunas of the Huron basin and the introduction of 16 new taxa of aquatic molluscs to the north shore of the Superior basin (Bajc, 1986).

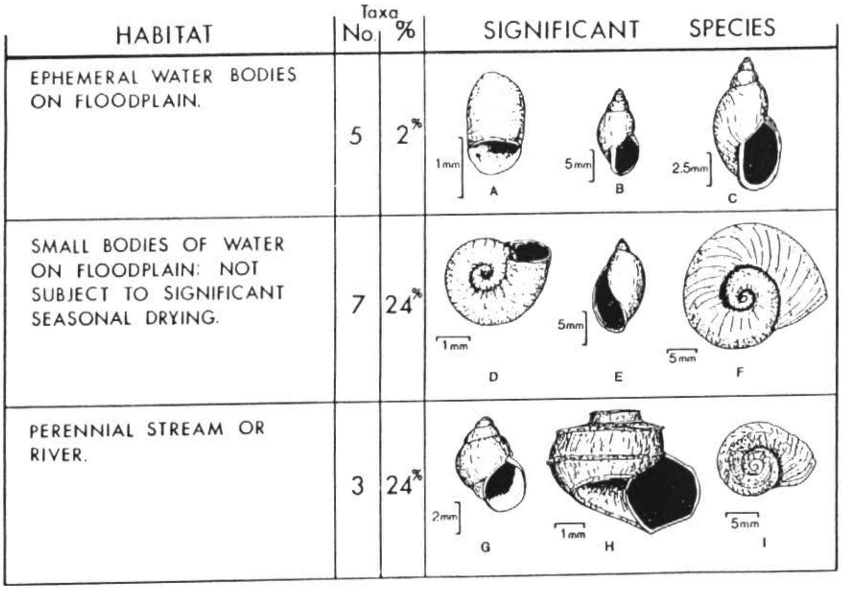
It is also possible to suggest directions of intra-basin migrations by plotting the temporal occurrences of various taxa in adjoining basins. For example, if one plots the temporal occurrences within the Agassiz, Superior, and Huron basins of aquatic taxa that first occur in the Superior basin between 7 to 4 Ka. B.P., a better sense of migration is achieved (Figure 11). The majority of migrations appear to be in the westerly direction, however, some exceptions exist (*e.g.*, *Ferrissia rivularis* and *Pisidium idahoense*). Terrestrial taxa appear to demonstrate similar trends to those documented by the aquatic molluscs (Figure 12).

Climatic interpretations. Although evidence directly implicating climate as a prime factor in controlling the distribution of molluscs is difficult to obtain, there are observations concerning distribution of some terrestrial gastropods which strongly suggest that temperature may be a major control. Miller (1975) reviewed field observation and laboratory experiment data that suggested temperature extremes and available moisture as two of the major factors controlling non-marine gastropod distributions. In a more recent study, Frest and Fay (1980a) have shown that three species of terrestrial



HABITAT	Taxa No.	Taxa %	SIGNIFICANT SPECIES
FLOODPLAIN WOODED WITH AREAS OF DENSE SHADE, LOCALLY WET TO DAMP.	13	22%	A (3mm) B (10mm)
VALLEY SLOPES OPEN WOODLAND AND SHRUBS, SHADED AREAS.	10	18%	C (1mm) D (1mm)
UPLAND GRASSLAND PRAIRIE: SCATTERED TREES – SHRUBS.	3	10%	E (1mm) F (1mm)

Figure 8 *Kanopolis local fauna terrestrial habitats inferred from molluscs (Miller and Kay, 1981). The total number of species and their abundance expressed as a percentage of the total number of individuals counted is also included. The significant species illustrated are: **(A)*** Stenotrema leai, ***(B)*** Anguispira alternata, ***(C)*** Gastrocopta contracta, ***(D)*** Gastrocopta armifera, ***(E)*** Pupoides albilabris, *and **(F)*** Gastrocopta cristata.



HABITAT	Taxa No.	Taxa %	SIGNIFICANT SPECIES
EPHEMERAL WATER BODIES ON FLOODPLAIN.	5	2%	A (1mm) B (5mm) C (2.5mm)
SMALL BODIES OF WATER ON FLOODPLAIN: NOT SUBJECT TO SIGNIFICANT SEASONAL DRYING.	7	24%	D (1mm) E (5mm) F (5mm)
PERENNIAL STREAM OR RIVER.	3	24%	G (2mm) H (1mm) I (5mm)

Figure 9 *Kanopolis local fauna aquatic habitats inferred from molluscs (Miller and Kay, 1981). The total number of species and their abundance expressed as a percentage of the total number of individuals counted is also included. The significant species listed are: **(A)*** Ferrissia fragilis, ***(B)*** Stagnicola caperata, ***(C)*** Fossaria obrussa, ***(D)*** Gyraulus parvus, ***(E)*** Physa gyrina, ***(F)*** Promenetus exacuous kansasensis, ***(G)*** Amnicola integra, ***(H)*** Valvata tricarinata, *and **(I)*** Helisoma anceps.

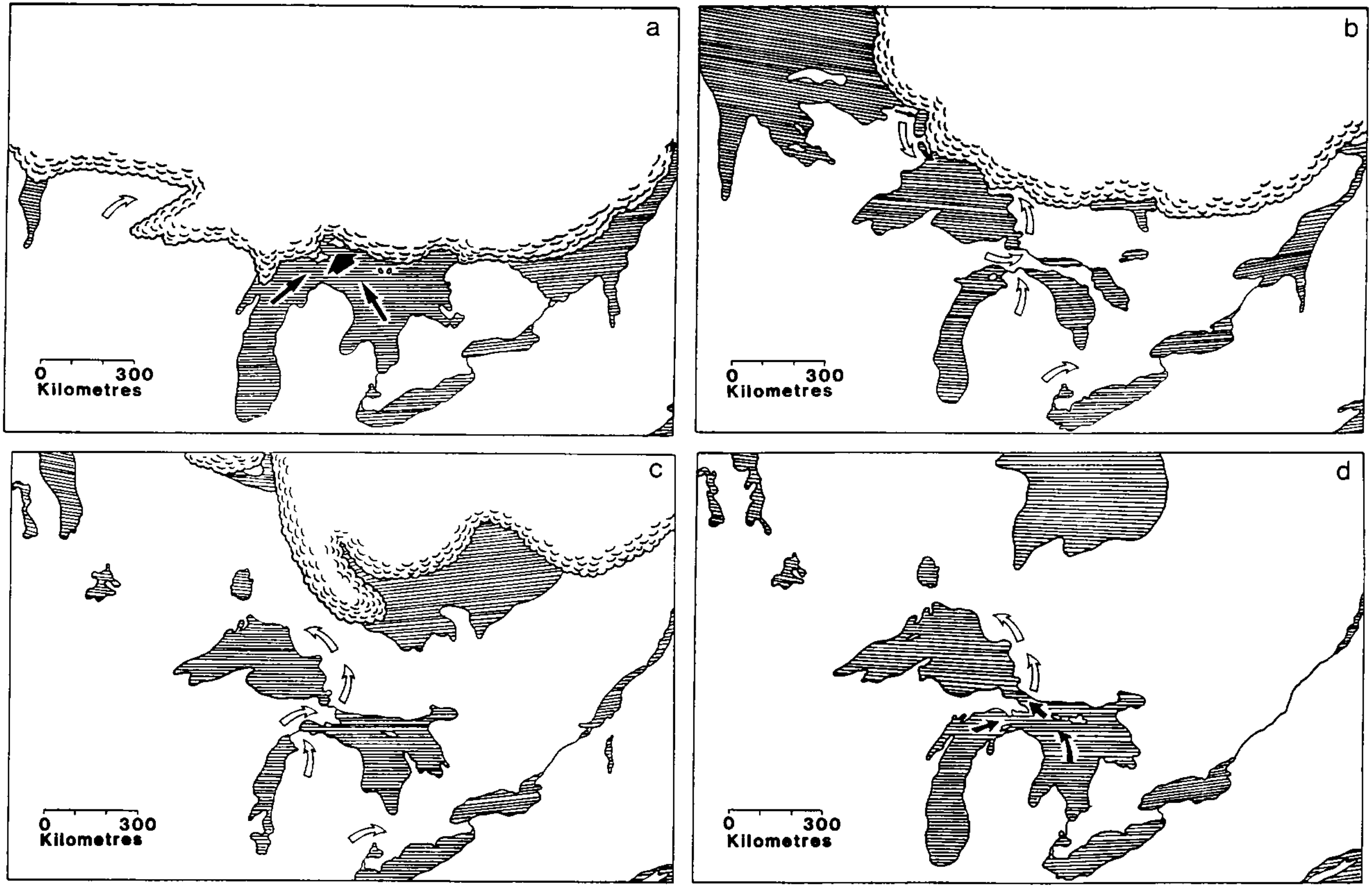


Figure 10 *Major mollusc migration pathways in the Great Lakes drainage basins. Solid arrows indicate migration pathways of aquatic molluscs and open arrows indicate migration pathways of terrestrial molluscs.*

(a) *Migration of Algonquin aquatic fauna into the southeastern corner of the Superior basin between 12 and 10 Ka B.P.*

(b,c) *migration of terrestrial molluscs from southern Michigan into southwestern Ontario and from the upper peninsula of Michigan to the north shore of Lake Superior between 10 and 8 Ka B.P.*

(d) *Migration of Michigan and Huron basin aquatic faunas into the Superior basin between 7 and 4 Ka B.P. during the Nipissing phase of the upper Great Lakes.*

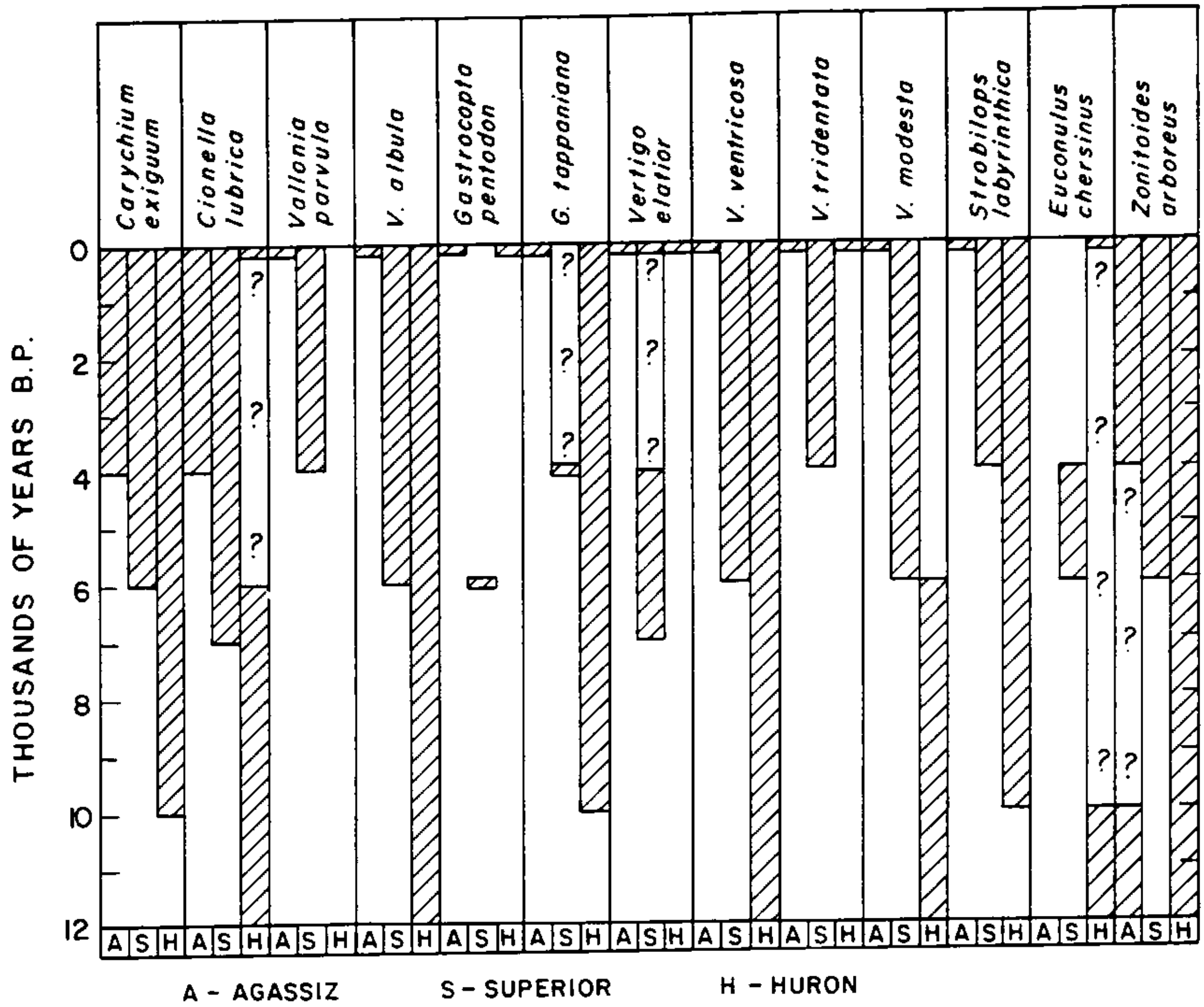


Figure 11 *Temporal occurrences of aquatic molluscs in the Agassiz, Superior, and Huron basins for those taxa that occur first on the north shore of Lake Superior between 7 and 4 Ka B.P. Note the overwhelming westerly migration of aquatic molluscs (Bajc, 1986).*

gastropods first described from Pleistocene loess deposits of the American midwest, *Vertigo hubrichti*, *V. briarensis*, and *Discus macclintocki*, can now be found living as isolated relict colonies in the Driftless Area of northeastern Iowa. The molluscs at these sites are associated with "cold air slopes" which buffer the maximum summer temperature to about 10°C and provide a climatically acceptable refugia for species that were widely distributed in the region during the Pleistocene.

Unfortunately, no standard methods of analyses are now in use to infer climatic data from molluscan assemblages. Some workers have tried to make qualitative statements about climate by dividing molluscs, on the basis of their modern distribution patterns, into what are considered climatically significant groupings (Harris and Pip, 1973). Changes in relative abundance of these species-groupings are interpreted as responses to climatic change (Zakrewski and Kolb, 1982). In other studies, an area of sympatry for the majority of the extant faunal elements is established, and the climate of the overlap area is considered to be an approximation of climatic conditions locally at the time the fossil assemblage lived (Taylor, 1960, 1965; Miller, 1966).

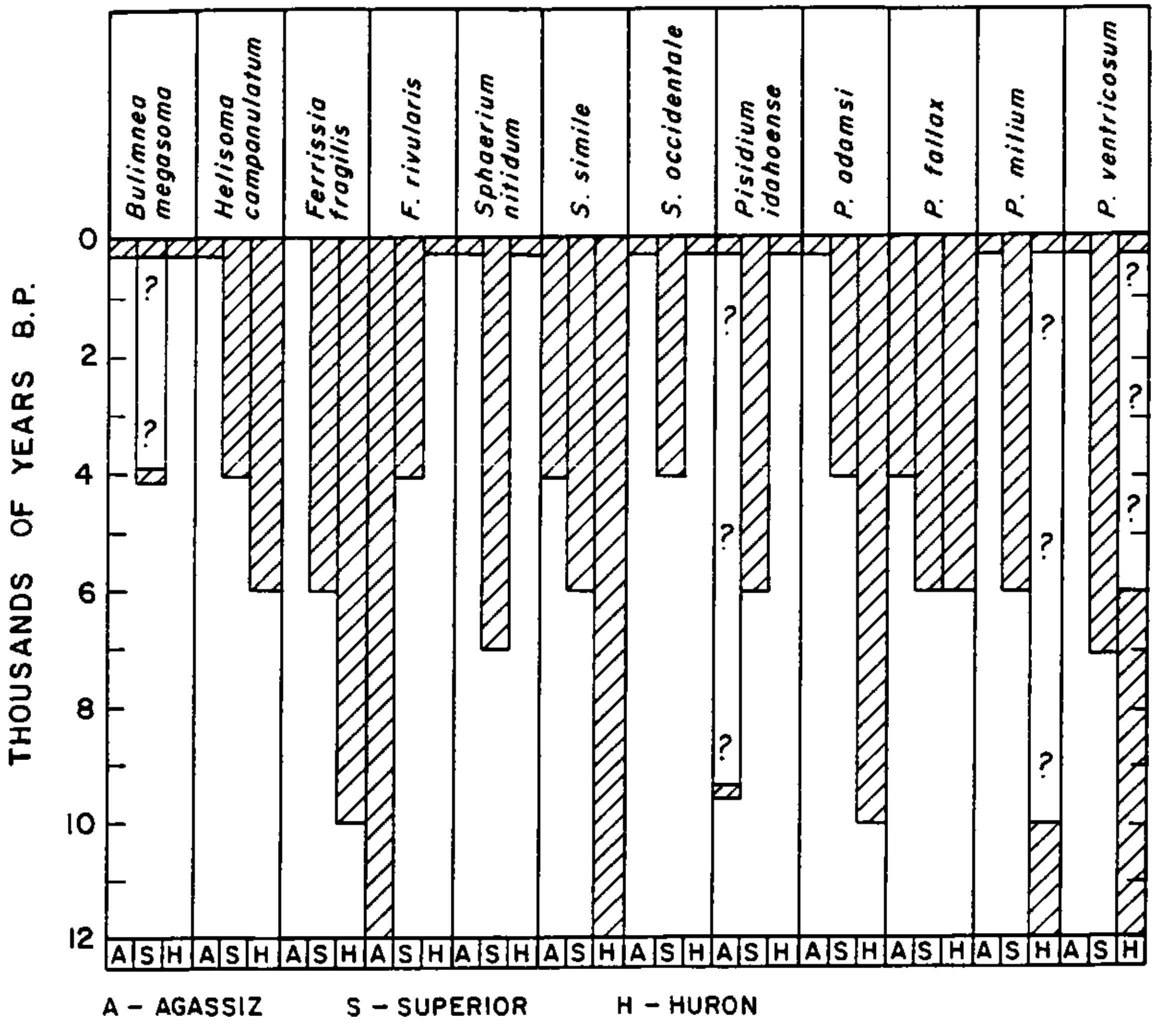
Some recent workers have tried to relate variation in shell morphology to climatic parameters. Baerreis (1980) produced a climatic reconstruction for the interval between 6.35 and 10.5 Ka B.P., at the Cherokee Site in northwestern Iowa, in which climatic interpretations were derived from equations that regressed variation in shell size of extant land snails against a series of climate variables.

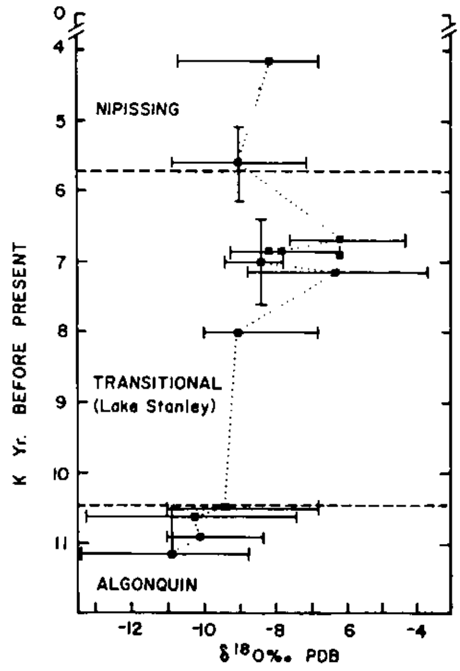
Godwin (1985) used changes in the ^{18}O isotopic composition in freshwater shell carbonate to calculate water temperature changes in the Huron basin between 11 and 4 Ka B.P. Her calculations suggest a 2.5°C increase in water temperature between the pro-glacial, main Algonquin lake phase and the transitional, low-water, Lake Stanley and a drop of 1°C between Lake Stanley and the Nipissing levels (Figure 13).

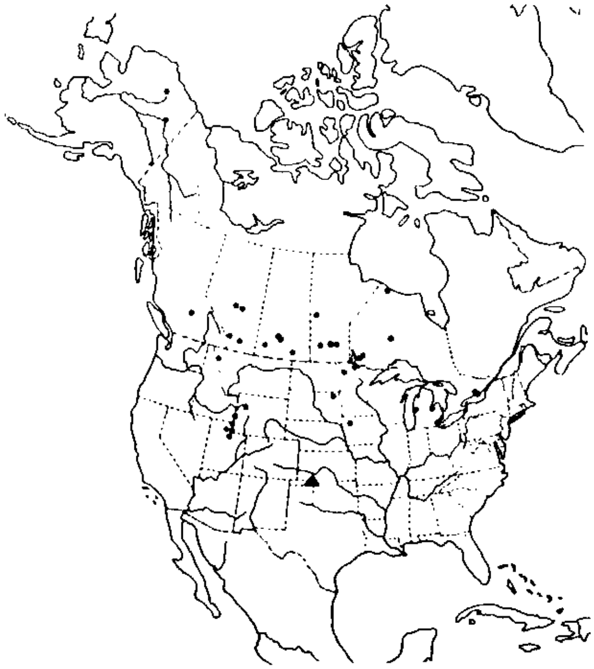
Figure 12 ***(opposite page - top)*** *Temporal occurrences of terrestrial molluscs in the Agassiz, Superior, and Huron basins for those taxa that occur first on the north shore of Lake Superior between 7 and 4 Ka B.P. Note the overwhelming westerly migration of terrestrial molluscs (Bajc, 1986)*

Figure 13 ***(opposite page - lower left)*** *Oxygen-18 isotope data from fossil shell collected at 13 sites along Lake Huron. The molluscs range from about 4000 to 11,000 years B.P. The change in the oxygen isotope values from Lake Algonquin to Nipissing age sites is equivalent to about a 1.5°C increase in temperature (Godwin, 1985).*

Figure 14 ***(opposite page - lower right)*** *Distribution map showing modern geographic range (dots) of* Physa skinneri. *The triangle indicates the fossil occurrence of this species from Illinoian sites in southwestern Kansas (Miller, 1966)*


Bulimnea megasoma
Helisoma campanulatum
Ferrissia fragilis
F. rivularis
Sphaerium nitidum
S. simile
S. occidentale
Pisidium idahoense
P. adamsi
P. fallax
P. milium
P. ventricosum
THOUSANDS OF YEARS B.P.
0
2
4
6
8
10
12
?
A S H
A - AGASSIZ
S - SUPERIOR
H - HURON


K Yr. BEFORE PRESENT
0
4
5
6
7
8
9
10
11
NIPISSING
TRANSITIONAL
(Lake Stanley)
ALGONQUIN
-12
-10
-8
-6
-4
δ18O‰ PDB



Amino acid epimerization rates of isoleucine from shell protein of non-marine gastropods have been used to estimate the average post-depositional integrated thermal history in a region. Unpublished data for molluscs from Late Wisconsinan sites in Ohio and Indiana, suggest an average temperature during the past 20 Ka that was about 1.5°C lower than the present mean annual temperature at these sites.

Pleistocene assemblages frequently include a greater diversity of species than now exist in the area of the fossil sites (Miller, 1976). These faunas usually include associations of species with modern geographic ranges that may approach, but do not reach the area of the fossil localities (Figure 14). The Peoria loess, in parts of northern Missouri, south central Illinois and southern Indiana, present well-documented examples of molluscan species associations that have no modern analogues (Frest and Fay, 1980b). The most parsimonious explanation that can account for the former co-existence of species that now have such disjunct geographic distributions is to assume that these assemblages lived at a time that combined cooler, moister summers (allowing boreal and montane species to extend their range southward and to lower elevations), with shorter, less severe winters (permitting southern forms to range further north during a longer growing season).

Disjunctive molluscan assemblages persisted in the southern Great Plains until about 10 Ka B.P. (Miller, 1975). In the Huron basin disjunct molluscan faunas continued on until 6 to 8 Ka B.P., when climatic warming probably led to a local extirpation of the northern species (Miller *et al.*, 1985).

The relative ease with which large numbers of fossil molluscs can be collected from sites, together with their increasing use as a source of stratigraphic information from amino acid studies of shell protein, virtually guarantees that they will continue to be an important component of Quaternary stratigraphic and paleoecologic studies.

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