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THE STUDY OF PLEISTOCENE NONMARINE MOLLUSKS IN NORTH AMERICA*

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Most North American Pleistocene shells can be referred to living species. This generally established observation determines the strengths and weaknesses of mollusks for geologic studies. It leads also to the tacitly accepted principle that the basis of interpretation of the fossils includes knowledge of the details of morphology, classification, ecology, and geographic distribution of living mollusks.

Local variations in fauna and sediments make the methods and faunistic literature of one area often unsuited to another area. For the sake of generality I therefore restrict this essay to some broader principles, observations, and conclusions from the study of Pleistocene nonmarine mollusks. The comparisons with the central European record are based on publications by Vojen Ložek and on his extensive comments on a first draft of this paper.

Both in Europe and North America relatively few late Pliocene and early Pleistocene nonmarine molluscan faunas have been described, and generalizations about this interval in both continents are necessarily crude. Rate of differentiation seems to have been more rapid in land snails than in aquatic mollusks, and more rapid in Europe than in central North America. As a corollary the contrast between Pliocene and Pleistocene faunas is more marked in Europe.

The differences between the two regions are probably due mostly to two factors: the different geography of the regions, and their geologic histories. The broad central lowland of North America has practically no sharp ecological boundaries, so the molluscan faunas have consisted almost entirely of widespread species that have survived for a long time. The topographic and ecologic diversity of Europe provides practically no room for such major changes in range as those seen in many faunas of central North America, and it has favored more local differentiation. The Alpine Revolution during the Tertiary may have stimulated the rich and local differentiation of such speciose groups as Helicidae and Clausiliidae. Perhaps one of the consequences of the rapidly changing late Tertiary landscape of Europe was that many molluscan groups in that region were and still are evolving more rapidly than are those in the stable lowland area of central North America.

If rapid ecological changes and local isolation are significant factors in evolution of nonmarine mollusks, then North America has three main areas where late Cenozoic differentiation is likely to have been most rapid: (1) the Great Lakes region, where frequent isolation and reunion of lake and stream habitats has occurred through the Quaternary; (2) the region of Florida and the Bahamas, where sea-level changes can join or isolate many small islands in the archipelagoes situated on shallow platforms; and (3) the Great Basin and central west-coast region of North America, where the Middle Pleistocene orogeny of the Coast Ranges, eustatic changes in sea level, block faulting in the Great Basin, Pleistocene desiccation, and volcanism have changed habitats more rapidly and drastically than in other parts of North America. The Great Plains region is the area where there is the most detailed knowledge of late Cenozoic (particularly Pleistocene) nonmarine mollusks in North America, but the conservative character of its fauna is probably not representative of all of the continent.

I have commented on the interpretation of Quaternary mollusks previously (Taylor, 1960b), but crudely and superficially as it seems in retrospect. Anyone concerned with the principles of paleoecologic interpretation should take the essay by G. H. Scott (1963) as a starting point. The conventional approach to paleoecology (usually tacit) is to interpret former environments upon the assumption that they have changed and that the species have changed less so or not at all. Scott made the telling point that this frame of mind is in ill accord with the evolutionary approach of the biostratigrapher. He concluded (G. H. Scott, 1963, p. 524), "Lyell's particular principle of ecological uniformity is neither a sufficient nor even a necessary condition for paleoecology to be called a science."

Quaternary shells are so like those of living mollusks that interpretation of the past in terms of the present has seemed a commonplace. It is significant both for the general methods of paleoecology and for the Pleistocene history of North America that such a seemingly simple procedure in such a geologically young interval is not straightforward.

Pleistocene assemblages that are referable to living assemblages pose no interpretive problems. Those that are referred to living species, not all of which can be found living in close proximity, require one or another assump-

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tion: either some species have changed their environmental tolerances, or they have not. To take the first stand is to lessen the precision with which these species can be used in the fossil record. To take the second is to say in effect that some environments only a few thousand years old, in which all the species were those still living, cannot be found and studied today. In either case the present is not, in detail, the key to the past.

Pragmatically I am suspicious of strict adherence either to the idea of ecologic nonevolution or to the idea that present environments are standards for the past. As a taxonomic conservative I believe fossils should be referred to living species unless they can be shown to be different; but surely all evolutionary changes in mollusks are not necessarily reflected in their shells. Most fossil assemblages of living species can be rationalized by supposing the species have not changed their ecologic tolerances and that past environments were not precisely like those of today. Even so there are cases (for example the wide Pleistocene distribution of species such as *Omalodiscus pattersoni* (Baker), *Bulimnea megasoma* (Say), *Acroloxus coloradensis* (Henderson), and *Pupilla sinistra* (Franzen) that cannot be disposed of so readily.

Regional Differences in Pleistocene Faunas

The regional differences in the living molluscan fauna of North America are shown also by Pleistocene faunas. In arid areas the fossil assemblage may be more diverse than the modern fauna, but generally the living species are found in adjacent areas. Pleistocene faunas from different faunal provinces may share no species in common, just as with present-day faunas.

Faunal divisions of North America were drawn by Pilsbry (1948) for land snails and by Henderson (1931) for western, land and freshwater mollusks. The faunal differences expressed by such provinces are mainly of pre-Pleistocene origin, as shown by direct fossil evidence, by correlation with geologic structure, and by inferred correlation with probable past events. The major geographic differences in the living fauna probably have their beginnings at least in the Cretaceous, as Henderson (1931) noted. Lesser geographic differences may not be so ancient, but many are of Tertiary origin. The Recent Holarctic element among land snails has been interpreted as the relict Mesozoic to early Tertiary fauna of northern latitudes (Waldén, 1963, p. 163). Local endemism, disjunct distribution, and much observable geographic variation may as readily be of Tertiary as of Pleistocene origin. The fossil record by its nature will never provide all the documentation one could wish and so must be interpreted against a sound biogeographic background.

MODES OF INTERPRETATION OF PLEISTOCENE FAUNAS

The composition of any assemblage of animals and plants is determined by three factors. *Geologic Time* determines the stages present in the myriad lines of descent of various evolving organisms—what genetic combinations are available. *Habitat* includes the range of environments and the physical and biotic factors affecting individuals in an assemblage throughout their lives. *Biogeographic history* includes antecedent factors of regional distribution and dispersal that determine what organisms can occupy newly available habitats in a particular area or can gradually enter and adapt to already present environments.

So far as fossil shells can demonstrate, nearly all species of mollusks have remained virtually unchanged throughout the Pleistocene. The recurrence of similar habitats is the simplest explanation for the known recurrent assemblages. Within the Pleistocene, mollusks show the effects of passing time almost entirely by the gradual extinction of species that were already present in the Pliocene.

Regional differences in geologic history and molluscan fauna, *i.e.* biogeographic differences, are so great that in different parts of North America different problems loom large, calling for different techniques of study and interpretation. The mainly lacustrine faunas of pluvial Lakes Bonneville and Lahontan led Call (1885) to biometric analysis; considerations of the effects of salinity, temperature, and elevation on freshwater mollusks; and study of the living fauna of the now-arid region. Ponds and small lakes that existed in the glaciated region of the eastern United States have been studied by quantitative analysis of stratigraphic sequences by LaRocque and his students (*e.g.* Mowery, 1961), who emphasize limnology. The alluvial deposits of the unglaciated southern Great Plains have favored study of large samples with emphasis on climatic inferences (Hibbard and Taylor, 1960; Taylor, 1960b). Nowhere have studies of buried soils and fossiliferous alluvium and loess reached the refinement and precision of those by Ložek in Czechoslovakia (*e.g.* Kukla *et al.*, 1961, Kukla and Ložek, 1961), although the combined pedological-stratigraphic-paleontological approach promises equally detailed results in parts of North America. Cave-fills and travertine have yielded abundant fossil assemblages in Europe, but so far are virtually unstudied in North America.

Some of the differences among these various studies are no doubt personal, and others reflect unequal knowledge of different regions. Still for the most part they are reflections of different circumstances. Tectonic events, hydrographic changes, and local endemism are salient problems in the western part of North America (see Taylor, 1960a). Local changes in drainage, vegetation, climate, soil, and geographic distribution of mollusks are stronger themes in the east. Thus west of the Rocky Mountains biogeographic problems are dominant in Pleistocene studies, but to the east the elements of ecology are more conspicuous. The data from the west are fewer and less amenable to generalization. I have emphasized the Great Plains and Midwest region for this reason.

Knowledge of Living North American Mollusks

The ready reference of most Pleistocene shells to living species is an attribute of mixed value. On the one hand it offers a means of interpreting in some detail an ancient environment. But ecologic interpretation of fossils depends on knowledge of the identity and habitat of living species. An illustration will show not only that present knowledge of the living fauna is imprecise, but that at least some recent and widely accepted work is seriously erroneous.

THE *Lymnaea "palustris"* GROUP

"*Lymnaea palustris*" is a name that has been applied widely to pond snails in much of the Northern Hemisphere. Under various generic names it occurs in the following general works on mollusks in northern Eurasia: Kennard and Woodward, 1926, p. 56 (Britain); Germain, 1931, p. 497 (France); Nobre, 1941, p. 188 (Portugal); Adam, 1947, p. 47 (Belgium); van Benthem Jutting, 1933, p. 200 (Netherlands); Mandahl-Barth, 1949, p. 68 (Denmark); Boettger, 1944, p. 255 (Germany); Frömming, 1956, p. 107 (central Europe); Ložek, 1956, p. 239 (Czechoslovakia); Soós, 1943, p. 83 (Hungary); Grossu, 1955, p. 101 (Roumania); Zhadin, 1952, p. 173 (U.S.S.R.). In his monograph on "The Lymnaeidae of North and Middle America", Baker (1911) identified the species as living in most of North America, but later (1928) considered the American snails to represent subspecies different from those of Europe. Hubendick (1951) reviewed the Lymnaeidae as a whole, maintained the species was valid, and extended it to include a number of forms previously considered separate by Baker. These works show that in recent years there has been general agreement on the concept of one species distributed in northern Eurasia and North America, even though some authors have recognized varieties while others have not.

In evidently the first careful study of "*L. palustris*," based on thorough anatomical study of 686 specimens from 75 localities in Poland, Jackiewicz (1959) found that it included three distinct biological entities. These differ in several characters of genitalia and radula and show different but overlapping ecologic and geographic distribution. One can be distinguished often but not always by shell features; two cannot be distinguished by shell features. These three entities were reasonably called separate species by Jackiewicz. Previously applied varietal names were available for *Lymnaea corvus* (Gmelin) and *L. turricula* Held, but no name could be applied surely to the third, named as new *L. occulta* (Jackiewicz). Use of the name *L. palustris* (Müller) does not aid understanding of this complex group or clarity in communication and should be discontinued.

The status of all the North American members of the *Lymnaea "palustris"* group is thus open to question. Perhaps there are no species common to America and Eurasia, or if some are they cannot be recognized in the present state of knowledge. Perhaps the finely dividing classification by Baker (1928) goes too far, perhaps not far enough. Until a detailed morphological study of American representatives of this group is available the number and characteristics of the species will be uncertain. Identification of fossils, and their ecologic interpretation, will likewise be of doubtful value. Clearly, however, the more narrowly drawn species are more likely to prove useful than broad, composite categories such as "*Lymnaea palustris*" or "*L. humilis*".

LIVING SPECIES FIRST DESCRIBED AS FOSSILS

Theoretically the knowledge of living mollusks should precede study of Pleistocene mollusks. In practice the study of the recent North American fauna has advanced so slowly that paleontology has run ahead even at the elementary stage of describing species, and some extant species were first known as fossils. Such discoveries were understandable in the last century, when so much of North America was unknown malacologically. Nevertheless, they are still being made, and other supposedly extinct forms may yet be found alive. The references in Table 1 include original descriptions and authority for occurrence of the species alive.

TABLE 1

Living Species Considered Extinct When First Described

Helicinidae
- *Hendersonia occulta* (Say, 1831). Shimek, 1904.

Hydrobiidae
- *Amnicola pilsbryana* Baily and Baily, 1952. Taylor and Bright, unpublished data.
- *Fluminicola avernalis* Pilsbry, 1935. Gregg, 1941.
- *Pyrgulopsis letsoni* (Walker, 1901). Berry, 1943.
- *Tryonia clathrata* Stimpson, 1865. Stearns, 1893.
- *Tryonia protea* (Gould), 1855. Stearns, 1901.

Physidae
- *Physa skinneri* Taylor, 1954. Taylor, 1960b.

Pupillidae
- *Pupilla sinistra* Franzen, 1946. Hibbard and Taylor, 1960.

Endodontidae
- *Discus macclintocki* (Baker, 1928). Morrison, 1940; Hubricht, 1943, 1955.
- *Discus shimeki* (Pilsbry, 1890). Shimek, 1901.

Polygyridae
- *Stenotrema hubrichti* Pilsbry, 1940. Hubricht, 1943.

LATEST CENOZOIC MOLLUSCAN FAUNAS IN CENTRAL NORTH AMERICA

Most of the known, independently dated late Pliocene and Pleistocene molluscan faunas of central North America are listed in Table 2 in stratigraphic order. The compilation is

TABLE 2

Latest Cenozoic Molluscan Faunas in Central North America (Fig. 1)

A. Late Pliocene (complete)
   1. Saw Rock Canyon local fauna, Rexroad Formation, Seward County, Kansas (Taylor, 1960b).
   2. Red Corral local fauna, Oldham County, Texas (Taylor, 1960b).
   3. Rexroad local fauna, Rexroad Formation, Meade County, Kansas (Miller, 1964; Taylor, 1960b).
   4. Bender local fauna, Rexroad Formation, Meade County, Kansas (Taylor, 1960b).

B. Nebraskan (complete)
   5. Sand Draw local fauna, Brown County, Nebraska (Taylor, 1960b).
   6. David City gravel and Nebraskan till, Doniphan County, Kansas (Frye and Leonard, 1952).

C. Late Nebraskan–early Aftonian (complete)
   7. Dixon local fauna, Kingman County, Kansas (Taylor, 1960b).

D. Aftonian (complete)
   8. Sanders local fauna, Missler Silt Member of Ballard Formation, Meade County, Kansas (Taylor, 1960b).

E. Kansan (incomplete)
   9. Cudahy fauna, associated with the Pearlette ash bed in various locally named formations. Many localities, Iowa to Texas (Leonard, 1950); Phillips County, Kansas (Frye and Leonard, 1954); Randall County, Texas (Johnston and Savage, 1955); Jefferson County, Colorado (Scott, 1962).

Continued

TABLE 2 (*cont.*)

10. Cagle Loess Member of Atherton Formation, Putnam County, Indiana (Wayne, 1958, 1959, 1963).
11. Cloverdale Till Member of Jessup Formation, Parke County, Indiana (Wayne, 1959, 1963).

F. Yarmouth
12. Borchers local fauna, Atwater Silt Member, Crooked Creek Formation, Meade County, Kansas (Hibbard, 1949). This assemblage includes only vertebrates. No mollusks surely referable to the Yarmouth in the light of modern stratigraphy are known.

G. Illinoian (incomplete)
13. Berends local fauna, Sanborn Group, Beaver County, Oklahoma (Miller, in press).
14. Doby Springs local fauna, Harper County, Oklahoma (Miller, in press).
15. Butler Spring local fauna, Sanborn Group, Meade County, Kansas (Miller, in press).
16. Mt. Scott local fauna, Kingsdown Formation, Meade County, Kansas (Miller, 1961, in press).
Kansas (Frye and Leonard, 1954; Leonard, 1952).
Oklahoma (Kitts, 1959).
Illinois (Rubey, 1952).
Indiana (Gooding, 1963; Wayne, 1958, 1959).

H. Sangamon (complete)
17. Slocum alluvium, Douglas and Jefferson counties, Colorado (Scott, G. R., 1962, 1963).
18. Cragin Quarry local fauna, Kingsdown Formation, Meade County, Kansas (Hibbard and Taylor, 1960).
19. Slaton local fauna, Lubbock County, Texas (Taylor, unpublished data).
20. Jinglebob local fauna, Kingsdown Formation, Meade County, Kansas (Hibbard and Taylor, 1960).
21. Don beds, Toronto, Ontario, Canada (Baker, 1931a; Watt, 1954).

I. Wisconsin (incomplete)
29. Jones local fauna, Vanhem Formation, Meade County, Kansas (Hibbard and Taylor, 1960).
Colorado (Scott, 1962, 1963).
Illinois (Leonard and Frye, 1960; Rubey, 1952).
Indiana (Wayne, 1959, 1963; Gooding, 1963).
Kansas (Goodrich, 1940; Hibbard and Taylor, 1960; Leonard, 1952).
Minnesota (Tuthill, 1963).
Nebraska (Miller and Scott, 1955, 1961).
North Dakota (Tuthill, 1961; Tuthill *et al.*, 1964).
Ohio (Clark, 1961; Cornejo, 1961; LaRocque, 1952; LaRocque and Conley, 1956; LaRocque and Forsyth, 1957; Leonard, 1953; Mowery, 1961).
Oklahoma (Kitts, 1959).
Texas (Cheatum and Allen, 1963; Dalquest, 1962; Frye and Leonard, 1964; Slaughter *et al.*, 1962; Wendorf, 1961).

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intended primarily to show how few late Pliocene, Nebraskan, and interglacial assemblages there are on which to base inferences about effects of the first glaciation, long-term climatic trends, glacial-interglacial shifts in range, or progressive faunal changes. Illinoian faunas are relatively abundant compared to interglacial assemblages, and I have listed only a sample, principally the more reliably dated ones. Some fossil shells of Wisconsin or post-Wisconsin age can be found nearly anywhere. Their study can become most meaningful as local sequences with detailed stratigraphy and radiocarbon dates are described. A few of these are available and listed, but most localities of Wisconsin mollusks have been omitted. For access to older literature, with stratigraphy of variable reliability, see Baker (1920).

REVISED OR QUESTIONED AGES

Some assemblages have been omitted from Table 2 or appear there under a revised age assignment, for reasons discussed below. The list is arranged from younger to older:

22. Mollusks attributed to the Yarmouth in Howard County, Nebraska (Miller and Scott, 1955) have been shown by radiocarbon dates to be of late Wisconsin age (Miller and Scott, 1961). The fossils attributed to the late Wisconsin originally are also younger than supposed, but still of late Wisconsin age.

23. The Sulphur River Formation (of Slaughter and Hoover, 1963) in Delta County, Texas, ranges in age from about 12,000 to 9,000 years B.P. Mollusks from this unit were identified as both late Kansan and early Wisconsin by Frye and Leonard (1963, locality 12 and section 6), according to Slaughter and Hoover.

24. Mollusks from the Hardeman terrace, Hardeman County, Texas, were assigned a late Kansan age by Frye and Leonard (1963, p. 34, locality 8; p. 38, section 7). Shells collected by W. W. Dalquest from the locality cited by Frye and Leonard yielded a radiocarbon date of 16,775 ± 565 years B.P. (Socony Mobil laboratory, mean of five dates, including comparison of interior and exterior of shells; Dalquest, personal communication, 1964).

25. Mollusks from near Byers, Clay County, Texas, were described by Allen and Cheatum (1961) as of Illinoian age. Frye and Leonard (1963) considered the assemblage as Kansan on the basis of the fauna as well as geomorphic evidence (tracing of the Hardeman terrace). Shells of *Physa gyrina* Say from this locality were dated as 16,920 ± 665 years old (SM-694, SMU-P 17).

26. The Clear Creek local fauna, Denton County, Texas (Slaughter and Ritchie, 1963; Cheatum and Allen, 1963), has been dated as 28,840 ± 4740 years B.P. (SM-534; Slaughter and Ritchie, 1963, p. 129). Of the interglacial *vs.* interstadial alternatives considered by Slaughter and Ritchie, this date tends to favor an interstadial early Wisconsin age.

27. The Hill-Shuler local faunas, Dallas and Denton counties, Texas, were ascribed to "the last interglacial or a major interstadial of the last glacial" (Slaughter *et al.*, 1962, p. 10). They occur in the T-2 terrace fill, representing the same episode of alluviation as that which yielded the Clear Creek local fauna (Slaughter and Ritchie, 1963, p. 129), and like that fauna are referred here to an early Wisconsin interstadial. Occurrence of such now-northern mollusks as *Gyraulus circumstriatus*, *Lymnaea caperata*, and *Aplexa hypnorum* is also more consistent with a Wisconsin than Sangamon age. A radiocarbon date of greater than 37,000 years B.P. (Slaughter *et al.*, 1962, p. 52) is in keeping with an interstadial age.

28. The Good Creek Formation of Dalquest (1962), in Foard County, Texas, is referred here to the early Wisconsin instead of the Sangamon interglacial. Occurrence of several mollusks in the Easley Ranch local fauna now found only considerably to the north (especially striking is *Pupilla muscorum*), is more consistent with a Wisconsin than Sangamon age. The mammalian fauna most similar to that from the Good Creek Formation is the Jinglebob local fauna, Meade County, Kansas, ascribed to the late Sangamon (Hibbard and Taylor, 1960). At this level of precision I think the mammals may not be age-diagnostic—not sufficiently different to permit one to distinguish early Wisconsin from late Sangamon, and I prefer to rely on ecological interpretation of the mollusks.

29. The Jones local fauna, Meade County, Kansas (Hibbard and Taylor, 1960), has been dated as more than 30,000 years old (M-1103; Crane and Griffin, 1961). In terms of the local sequence the fauna is Wisconsin, and from the radiocarbon date evidently early Wisconsin. If molluscan assemblages like that of the Jones occurred as far south as central Texas, they are older than those referred to an early Wisconsin interstadial.

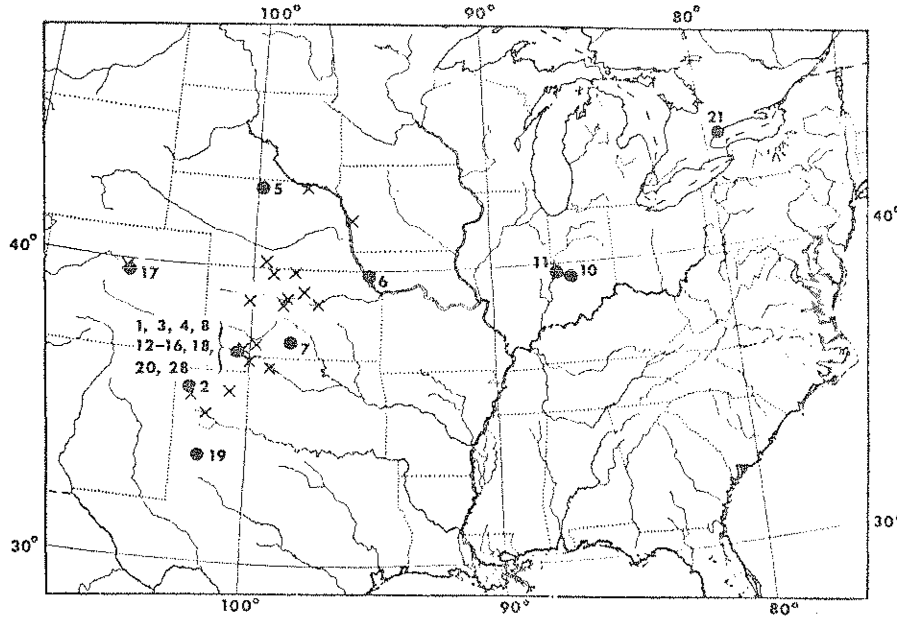

Figure 1. Location of fossil molluscan faunas in central North America. Numbers correspond to those in Table 2. X's mark localities of the Cudahy fauna (9, Table 2) associated with Pearlette ash.

30. The Rezabek local fauna, Lincoln County, Kansas (Hibbard, 1943) is considered of Illinoian age (Hibbard, 1963, and personal communication). A sample of the shells in the University of Michigan Museum of Paleontology collected by Hibbard seems to me to be reworked from older Pleistocene deposits, probably Kansan. Most of the shells are worn or etched in contrast to those of other Pleistocene assemblages from the Great Plains that I have studied. Possibly both Illinoian and Kansan shells are represented, but for the present they had better be ignored.

31. Mollusks from the Swingle locality, Kingman County, Kansas (Lane, 1960), were interpreted previously as Nebraskan or Aftonian. There is still no basis for a more precise age assignment.

GENERAL OBSERVATIONS ON THE FOSSIL RECORD

Analysis of the late Pliocene and Pleistocene molluscan assemblages in central North America (Table 2) leads to the following generalizations.

1. Nearly all species in the Pleistocene faunas are still living, either locally or in adjacent areas (Table 4).

2. Percentage of extinct species in general decreases gradually with time. Irregularities in detail can be ascribed to variably complete samples of the fauna.

3. Evolutionary novelties are rare. The only species for which evidence is adequate to support a Pleistocene origin is the freshwater snail *Promenetus exacuous exacuous*. It may have developed in the late Pleistocene from the Pliocene to Middle Pleistocene *P. exacuous kansasensis* (Hibbard and Taylor, 1960; Miller, in press).

4. The faunas may represent a terrestrial environment only, as in most loess, but ordinarily consist of aquatic mollusks of a pond or small stream together with a sample from some adjacent terrestrial habitats. Large-stream faunas are unknown; those of large lakes are known only from the latest Pleistocene Great Lakes.

5. Extant species mostly occur in associations that can be duplicated today. Exceptions can nearly all be grouped in two classes. (i) Late Pleistocene assemblages, especially from loess, in the central Great Plains and Ohio River valley include several elements now restricted far to the north or at high elevations in the Rocky Mountains. Species such as *Pupilla muscorum*, *Columella columella alticola*, and *Discus shimeki* are found as fossils in the lowlands in association with species with which they do not now coexist. (ii) Many Pleistocene assemblages in the southern Great Plains include species now found only far to the north of their fossil occurrences, such as *Lymnaea stagnalis*, *Gyraulus deflectus*, and *Physa skinneri*. In interglacial or interstadial faunas these may be found associated with species of generally southern distribution, whose range they do not now overlap.

6. Differences between successive faunas are more conspicuous toward the south and west. As Wayne (1963, p. 58) noted in Indiana, "nearly identical ecologic conditions near the ice margin prior to, during, and following each glaciation have resulted in the recurrence of relatively similar faunas at successively higher stratigraphic positions. Distinctions between faunal assemblages in the Pleistocene formations in Indiana are more subtle than those recorded for Kansas." The more conspicuous faunal contrasts to the south and west can be explained simply as due to fluctuations from semiarid to humid and from continental to maritime climates that had little or no expression in more humid eastern regions. A corollary is that the stratigraphic value of Pleistocene mollusks will be greatest where climatic variations were most extreme, hence generally in the semiarid southern Great Plains.

PARALLELISM WITH EUROPE

There are some clear, even striking, parallels between the Pleistocene molluscan faunas of Czechoslovkia and those of central North America. These parallels are instructive in showing how generally different molluscan faunas have reacted to events of the Pleistocene in similar ways. Interpretations of the better-known European assemblages are also pertinent to interpretation of analogous aspects of the

American record. Abundant literature on the Czech mollusks is available through Ložek (1955, 1961, 1963), Ložek and Kukla (1959), and Kukla *et al.* (1961).

1. The major features of change in molluscan faunas are similar: progressively smaller numbers of extinct or regionally extinct species, and changes in composition associated with major shifts in temperature and precipitation.

2. Postglacial aridity is marked in both central Europe and the southern High Plains. In southwestern Kansas the living molluscan fauna is poorer in species than any of the adequately sampled Pleistocene faunas. "The present-day relatively continental climate of Meade County is similar to no known ancient climate that is to be inferred from fossils in the area" (Hibbard and Taylor, 1960, p. 24-25).

3. The Last Glacial in Czechoslovakia is characterized by the widespread and abundant *Columella*-fauna, named after the dominant species *Columella columella columella*. This assemblage is a subarctic steppe fauna made up of several wide-ranging, ecologically tolerant species together with arctic and arctic-alpine species. *C. columella columella* lives in Scandinavia north of 67° and eastward in Siberia to the Yenisei between 61° and 69° 15′; it is known in central Europe in lower Pleistocene deposits but is most common in those of the Last Glacial (Forcart, 1959).

A later Wisconsin cold-steppe fauna is likewise known in the northern Great Plains. It includes two species, now living in the higher Rocky Mountains, that are unknown from the earlier parts of the Pleistocene. These alpine elements are *Columella columella alticola* and *Discus shimeki*. Characteristic associates in the assemblage are other northern and montane species known also from earlier glacial deposits, such as *Pupilla muscorum*, *P. blandi*, and *Vertigo modesta*. *Oreohelix strigosa cooperi*, living in the Black Hills of South Dakota and Cypress Hills of Alberta, occurred also in this cold-steppe fauna far to the east into Iowa. As in the European *Columella* fauna the association is not one found living today; it is a combination of arctic-alpine elements together with widely tolerant species and lacks southern and hygrophilous species (for discussion and different interpretation see Shimek, 1930, 1931). Available stratigraphic data suggest that these arctic-alpine species spread eastward only, or most commonly, in the "classical" or post-Farmdale Wisconsin interval.

4. The last interglacial assemblages in Czechoslovakia include *Banatica* faunas, named after *Helicigona banatica*. This species and some of its associates are extinct in the region or are found only in local populations. The interglacial faunas have a high percentage of warmth- and moisture-loving species. Kukla *et al.* (1961, p. 24) interpreted these assemblages as indicating a climate like that of the present, or 2° − 3° C warmer, but with annual precipitation at least 50% greater than at present. The climate approximated that of the northern Balkan Peninsula.

In southwestern Kansas the late Sangamon Jinglebob local fauna provides a parallel to the Riss-Würm *Banatica* faunas. The climate was more humid than that of today and had no marked seasonal extremes. Thermophiles occur among the vertebrates though not the mollusks.

The amplitude of climatic change is more marked in some areas than in others. Central Europe shows the greatest differences in that continent between the warm and cold intervals. The warm ones are often of submediterranean character, while the cold intervals have a subarctic fauna. To the north and south, climatic shifts are not so evident. In Czechoslovakia the interglacials are very moist-maritime, the glacials more or less dry-continental. Only the late postglacial is dry, so that the lowlands are a cultivated chernozem steppe, whereas in the interglacials they were woodland with gray-brown podzolic soils.

In North America relatively few sequences of Pleistocene faunas are known, but the record is consistent with the belief that climatic shifts were strongest in the southern High Plains.

The significance of the ecological similarities and differences in Pleistocene molluscan faunas of Europe and North America can be evaluated soundly only when their chronological correspondence has been established. At present no intercontinental glacial or interglacial correlations older than the limit of C_{14} dating are reliable.

Climatic Interpretation of Latest Cenozoic Faunas in High Plains Region

Knowledge of nonmarine fossil mollusks in North America is insufficient for more than a few generalizations. That of widest interest to students of Pleistocene phenomena is the inferred sequence of climatic changes in the High Plains region, for it can be checked by many lines of evidence and is pertinent to general hypotheses of Pleistocene climatic change.

The span of Pleistocene time has been brief compared to the duration of molluscan species as identified by shells. Hence if one can eliminate the effects of biogeographic history, then the composition of a Pleistocene fauna is largely determined by the range of habitats available. The High Plains region is a large, relatively featureless area with no sharp biogeographic discontinuities; it is all in one "faunal province." Within this area regional climate and local habitats are the main variables, and if local habitat is understood then regional climate can be evaluated.

Inferences about the climatic significance of mollusks come from geographic distribution, habitat, and associated species. There are virtually no experimental data. The plausibility of such inferences can be tested by comparison with similarly derived inferences from other kinds of animals associated with the mollusks, by whether or not diverse faunal elements can be reconciled, and by comparison with ecologic interpretation of associated plant remains. The mollusks and several groups of associated vertebrates of various faunas in southwestern Kansas and northwestern Oklahoma can be interpreted simply and plausibly under an hypothesis of major climatic shifts (Hibbard and Taylor, 1960; Taylor, 1960b). Associated pollen, so far as known, is consistent with these inferences and confirms the principle of interpretation (Kapp, in press). As more information about recent mollusks becomes available and as more fossils are studied, the rather broad climatic inferences summarized in Table 3 can be refined. Writing of the Pleistocene mollusks of Czechoslovakia, Ložek (1961, p. 119) stated: "Although in the older literature their significance is underestimated with reference to assessing the climate it still is possible to state, on the basis of all observations carried out with due care, that they are equally sensitive from this point of view as plants."

SEQUENCE OF INFERRED CLIMATES

The climates inferred from the series of late Pliocene and Pleistocene faunas of southwestern Kansas and northwestern Oklahoma are summarized in Table 3. Most of the elements of the former hypothetical climates are given in terms of contrast with the present local climate.

Meade County, in southwestern Kansas, now has a continental, temperate, generally moisture-deficient climate. Precipitation and temperatures are variable, both from year to year and within a given year. Mean annual rainfall is 19.66 in. (49 mm) for 45 years. The lowest recorded annual precipitation is 9.35 in. (337 mm), for 1910; the highest, 31.62 in. (803 mm), for 1915. The climate is dry, with no seasonal water surplus; Meade County is on the boundary between semiarid and dry subhumid climatic types. Summer is the wettest season, and nearly three-quarters of the annual precipitation comes during the warmer half year. Mean annual temperature is about 56° F (13° C). January, the coldest month, has a mean temperature of about 32° F (0° C); July, the hottest month, has a mean temperature of about 80° F (26° C). Recorded temperature extremes are −20° F (−29° C) and 110° F (43° C). Normal annual evaporation from pans is slightly over 90 in. (about 2,290 mm); from May to October 65 in. (about 1,650 mm) (Hibbard and Taylor, 1960).

A conservative approach has been employed in interpreting earlier climates. The inferred climates differ from the present one only by the minimum differences considered necessary to account for observed faunal differences. Names of the animals interpreted as especially significant climatic indicators are listed under the heading "Significant fossils" in Table 3; not all are mollusks. In general, a given species has been regarded as significant for only one climatic element or pair of elements, such as minimum winter temperature, effective warm-season precipitation, temperatures of summer hot spells, and the like.

GENERAL OBSERVATIONS ON PLEISTOCENE CLIMATES

The inferred Pleistocene climates of central North America (Table 3; Hibbard, 1960; Hibbard and Taylor, 1960; Taylor, 1960b) have significance not only for hypotheses of Pleistocene climatic change but also for stratigraphy. The general observations that follow illustrate the close interaction between theoretical research (geologic history and Pleistocene climatology) and applied research (stratigraphy of Pleistocene deposits).

1. Through all of Pleistocene time prior to the Wisconsin, glacial-interglacial changes were broadly similar. The record is consistent with the hypothesis of cyclic changes (Taylor, 1960b) but inadequate to document such an interpretation beyond reasonable doubt. Significantly, however, Karlstrom (1961) considered the Pleistocene record most simply interpreted as a system of harmonic or near-harmonic cycles of climatic change.

2. All of the pre-Wisconsin climates were more maritime than the modern climate at the sites where the fossils were collected. None of the pre-Wisconsin faunas known could live in the present combination of hot summers and bitterly cold spells during the winter. Recurrence of similar climates —all different from that of the present—produced similar molluscan faunas at various times.

3. "If the circulation of air masses in the Sangamon was generally like that today, in that there were winter incursions of air from Canada and the Arctic southward over the Plains, the Jinglebob and Cragin Quarry assemblages imply that there were no continental glaciers and no ice on the Arctic Ocean. Aside from the matter of much milder winters, the considerably greater precipitation suggested by the pine pollen and vertebrate fauna from the Jinglebob site can be explained most simply by the postulation that the moisture was derived from an ice-free Arctic Ocean" (Hibbard and Taylor, 1960, p. 24).

4. The land snail *Columella columella alticola*, living at high elevations in the Rocky Mountains (Leonard, 1952, p. 33; Pilsbry, 1948), appears in the Pleistocene of the Great Plains only in the Wisconsin. This snail and its associates make up a cool-steppe fauna that seems to reflect a time when summers were cooler and mean annual temperature lower than at any other time in the Pleistocene. The correlative *Columella-fauna* in Czechoslovakia is a similar association due to the same cause. The synchroneity of these cool-steppe faunas suggests more extreme glacial climates during the Wisconsin-Würm than previously in the Pleistocene.

5. The present is a poor guide to the past so far as geographic distribution and faunal associations of mollusks go. In southwestern Kansas all of the adequately sampled Pleistocene faunas, glacial as well as interglacial, are more diverse than the living molluscan fauna (Hibbard and Taylor, 1960, p. 18-19). The record there is more detailed than elsewhere, but in general everywhere in the arid and semiarid regions of North America the Pleistocene faunas are richer than the local living assemblages. Aridity and strong seasonal contrast are a late Wisconsin or post-Wisconsin development, not only in the Great Plains but generally in the American Southwest (Malde, 1964). Sure these unprecedented climatic changes, following hard on the most intense of the glacial climates, played a role in extinction of the large vertebrates.

6. In summary the fossil record can be interpreted most simply and consistently by hypothesizing major climatic fluctuations. Pre-Wisconsin climates, both glacial and interglacial, were less continental than those of today and differed among themselves mainly in amount and effectiveness of mean annual precipitation, and summer temperatures. Perhaps glacial climates became gradually more severe through the Pleistocene; at any rate the Wisconsin seems to have been most severe. The dry, seasonal climates of today are a late Wisconsin or post-Wisconsin development. The events that brought about these changes evidently affected global circulation to a considerable extent, though not necessarily by altering its pattern. The most plausible speculation I can make is that during the Wisconsin the Arctic Ocean became frozen and has remained so longer than at any time previously, if indeed it was ever frozen

TABLE 3

Late Cenozoic Climates Inferred from Fossil Assemblages in Southwestern Kansas and Northwestern Oklahoma and Compared with Modern Climate
(Numbers refer to Table 2 and Fig. 1)

Age	Local fauna	Climate	Significant fossils
Recent		Semiarid to dry subhumid, generally moisture deficient, continental, temperate. January mean 32° F, July mean 80° F. Mean ann. precip. 19.35 in.; mean ann. pan evaporation 90+ in.	
Early Wisconsin	29. Jones	Semiarid to dry subhumid. Mean ann. precip. no greater, perhaps less. Summers much cooler. Continentality reduced	Mammals: *Sorex cinereus, Microtus pennsylvanicus;* mollusks: *Pisidium ferrugineum, P. lilljeborgi, Valvata tricarinata, Lymnaea stagnalis, Pupilla blandi*
Late Sangamon	20. Jinglebob	Humid, no seasonal moisture deficiency. Mean ann. precip. 40-45 in. Winters much milder. Summers much wetter, slightly cooler. Continentality much reduced	Tortoise: *Terrapene llanensis;* mammals: *Oryzomys, Microtus pennsylvanicus;* mollusks: *Lacrapex kirklandi, Strobilops labyrinthica, Punctum minutissimum*
Early Sangamon	18. Cragin Quarry	Semiarid. Mean ann. precip. little different. Freezing temperatures rare or absent. Summers slightly cooler. Continentality much reduced	Tortoises: *Terrapene llanensis,* medium-sized *Geochelone;* lizards: *Phrynosoma cornutum, P. modestum;* shrew: *Notiosorex crawfordi;* snail: *Gastrocopta pellucida hordeacella*
Late Illinoian	16. Mt. Scott	Moist subhumid. Mean ann. precip. slightly greater (20-25 in.). Summers much cooler, winters slightly warmer. Continentality reduced	Fishes: *Esox masquinongy, Perca flavescens;* tortoise: *Terrapene llanensis;* mammals: *Sorex cinereus, S. arcticus, Blarina brevicauda carolinensis, Oryzomys fossilis;* mollusks: *Pisidium subtruncatum, P. variabile, Valvata tricarinata, Physa skinneri, Gastrocopta cristata, G. pellucida hordeacella*
Illinoian	15. Butler Spring	Dry subhumid. Mean ann. precip. little different. Summers much cooler, winters perhaps like those today. Continentality reduced	Fishes: *Ictalurus* cf. *I. punctatus, Perca flavescens;* mollusks: *Valvata tricarinata, Probythinella lacustris, Lymnaea stagnalis, Physa skinneri, Pupilla muscorum, Vertigo elatior, Vallonia cyclophorella*
Illinoian	14. Doby Springs	Dry subhumid. Mean ann. precip. little different. Summers much cooler, winters perhaps like those today. Continentality reduced	Fishes: *Catostomus commersoni, Perca flavescens;* mammals: *Sorex arcticus, S. cinereus, Blarina brevicauda brevicauda;* mollusks: *Sphaerium sulcatum, Valvata tricarinata, Probythinella lacustris, Lymnaea stagnalis, Gyraulus deflectus, Pupilla muscorum, Vertigo elatior*
Illinoian	13. Berends	Dry subhumid. Mean ann. precip. little different. Summers much cooler. Continentality reduced	Fishes: *Perca flavescens, Esox masquinongy;* mammals: *Sorex* cf. *S. cinereus, Blarina* cf. *B. brevicauda, Microtus pennsylvanicus;* mollusks: *Valvata tricarinata, Physa skinneri*
Early Yarmouth	12. Borchers	Dry subhumid. Freezing temperatures rare or absent. Mean ann. precip. slightly greater or summers slightly cooler. Continentality much reduced	Tortoise: *Geochelone* (large); mammals: *Sigmodon hilli, Spilogale ambarvalis*
Kansan	9. Cudahy	Dry subhumid. Mean ann. precip. little different. Summers much cooler. Continentality reduced	Mammals: *Sorex cinereus, S. lacustris, Microsorex pratensis, Microtus paroperarius, Synaptomys meltoni;* mollusks: *Valvata tricarinata, Gyraulus deflectus, Planorbula campestris, Physa skinneri, Pupilla muscorum, Vallonia pulchella, V. cyclophorella*
Late Aftonian	8. Sanders	Subhumid. Mean ann. precip. greater, but perhaps only slightly. Summers cooler. Winters no cooler. Continentality reduced	Mammals: *Sigmodon* cf. *S. intermedius, Bensonomys meadensis;* mollusks: *Lymnaea bulimoides techella, L. caperata, Promenetus umbilicatellus, Physa skinneri, Aplexa hypnorum, Helicodiscus singleyanus*
Late Pliocene	4. Bender	Semiarid-dry subhumid. Mean ann. precip. little different. Summers slightly cooler. Winters little if at all cooler. Continentality reduced	Mollusks: *Lymnaea bulimoides techella, L. caperata, L.* cf. *L. exilis, Promenetus umbilicatellus, Gastrocopta cristata, Helicodiscus singleyanus, Polygyra rexroadensis*
Late Pliocene	3. Rexroad	Dry subhumid. Mean ann. precip. slightly greater. Freezing temperatures rare or absent. Summers slightly cooler. Continentality much reduced	Tortoise: *Geochelone rexroadensis;* lizard: *Phrynosoma cornutum;* mammals: *Notiosorex jacksoni, Baiomys* spp., *Sigmodon intermedius;* mollusks: *Lymnaea exilis, Helisoma anceps, Nesovitrea electrina*

TABLE 3 (*cont.*)

Age	Local fauna	Climate	Significant fossils
Early late Pliocene	1. Saw Rock Canyon	Dry subhumid. Mean ann. precip. slightly greater. Winters slightly warmer. Summers slightly cooler. Continentality reduced	Turtle: *Kinosternon flavescens;* mammals: *Baiomys sawrockensis, Onychomys larrabeei;* mollusks: *Marstonia* spp., *Helisoma anceps, Strobilops labyrinthica, Gastrocopta holzingeri*

TABLE 4

Progressive Change in Late Cenozoic Mammals and Mollusks of Southern Kansas and Northwestern Oklahoma
Data from Hibbard (1963), Hibbard and Taylor (1960), Miller (in press), and Taylor (1960b)

	Extinct genera				Extinct species			
	Mammalia		Mollusca		Mammalia		Mollusca	
Local fauna	Percent	Number	Percent	Number	Percent	Number	Percent	Number
Jones (Wisconsin)	13	2	0	0	23	3	0	0
Jinglebob (Sangamon)	14	3	0	0	50	9	2	1
Cragin Quarry (Sangamon)	25	7	0	0	50	14	6	2
Mt. Scott (Illinoian)	0	0	0	0	28	5	1	1
Butler Spring (Illinoian)	0	0	0	0	0	0	4	2
Adams (Illinoian)	50	4	0	0	85	6	5	1
Doby Springs (Illinoian)	12	3	0	0	39	8	3	2
Berends (Illinoian)	29	3	0	0	54	5	2	1
Sanders (Aftonian)	62	8	0	0	100	13	20	4
Dixon (Nebraskan)	27	3	0	0	100	7	16	7
Rexroad (late Pliocene)	54	30	0	0	98	64	25	9
Saw Rock Canyon (late Pliocene)	67	8	0	0	100	11	28	7

before. The Arctic air masses that dominate the central part of North America throughout the colder half-year are thus drier and colder than previously, and seasonal contrasts are intense.

EFFECTS OF PLEISTOCENE EVENTS ON MOLLUSKS IN CENTRAL NORTH AMERICA

Within the limitations imposed by the scarcity of faunas of pre-Wisconsin age and the state of taxonomic knowledge, some generalizations can be made about the effects of the Pleistocene on mollusks.

1. The net effect has been a reduction in variety of the fauna. Many more species became extinct than developed during the Pleistocene. These extinctions were most marked in western North America; in central North America they are not nearly so conspicuous as in the west and much less marked than among mammals (Table 4, 5). The number of supposedly extinct invalid and dubious species is greater by far than that of the extinct valid species.

2. Environmental changes of the Pleistocene may have stimulated evolution of *Promenetus exacuous exacuous* from *P. exacuous kansasensis* (Hibbard and Taylor, 1960). This interpretation is entirely speculative; if valid, it would be the only exception to the statement that the effects of the Pleistocene have been entirely destructive, not creative, at the specific level.

3. Over large areas of the arid Great Plains, mollusks were more diversified and abundant in the Pleistocene than now (Table 6). There is no such contrast with Pliocene mollusks, however. It is more accurate to say that the Recent has brought adverse conditions than to claim that the Pleistocene brought favorable ones. Many mollusks with present northern distributions are known in the southern High Plains and probably do represent southward faunal dispersal. Yet the magnitude of such changes in range dur-

TABLE 5

Extinct Valid Species of Pleistocene Mollusks in Central North America
(Many other described forms are synonyms or dubiously valid)

A. Species terminating with no descendents
- Planorbidae
  - *Omalodiscus pattersoni* (Baker). Pliocene to Wisconsin. Leonard, 1953; Taylor, 1958, 1960b.
- Strobilopsidae
  - *Strobilops sparsicostata* Baker. Pliocene to Nebraskan. Taylor, 1960b.
  - *Strobilops lonsdalei* Ho and Leonard, 1961. Kansan to Wisconsin.
  - *Strobilops lonsdalei cansasiana* Ho and Leonard, 1961. Kansan.
- Pupillidae
  - *Gastrocopta chauliodonta* Taylor. Nebraskan to Aftonian. Taylor, 1960b.
  - *Gastrocopta paracristata* Franzen and Leonard. Pliocene to Aftonian. Taylor, 1960b.
  - *Gastrocopta scaevoscala* Taylor. Pliocene to Nebraskan or Aftonian. Taylor, 1960b.
  - *Vertigo gouldi hannai* Pilsbry. Pleistocene. Pilsbry, 1948.
- Limacidae
  - *Deroceras aenigma* Leonard. Pliocene to Wisconsin. Hibbard and Taylor, 1960; LaRocque and Conley, 1956.

B. Species becoming extinct through evolution
- Planorbidae
  - *Promenetus kansasensis* (Baker). Pliocene to Sangamon. Hibbard and Taylor, 1960.

TABLE 6

Number of Species of Mollusks in Late Cenozoic Faunas of Southwestern Kansas and Northwestern Oklahoma Data from Hibbard and Taylor (1960), Miller (in press), Taylor (1960b).

Fauna	Pelecypoda	Prosobranchia	Basommatophora	Stylommatophora	Total Mollusca
Recent, Meade County	4	0	8	17	29
Jones (Wisconsin)	5	1	15	10	31
Jinglebob (Sangamon)	10	1	17	24	52
Cragin Quarry (Sangamon)	2	0	12	21	35
Mt. Scott (Illinoian)	15	1	20	28	64
Butler Spring (Illinoian)	9	2	19	24	54
Adams (Illinoian)	2	1	5	14	22
Doby Springs (Illinoian)	11	2	21	26	60
Berends (Illinoian)	8	1	17	17	43
Sanders (Aftonian)	0	0	10	13	23
Bender (late Pliocene)	3	0	15	19	37
Rexroad (late Pliocene)	3	1	12	23	39

ing, say, the Sangamon and Wisconsin may have been much less than one would judge using present distribution patterns as a standard.

4. The southward and eastward spread in the Great Plains and Ohio Valley of a cold-steppe fauna during part of Wisconsin glacial times is an event that is unknown previously in the Pleistocene. The alpine Rocky Mountain land snail *Columella columella alticola* "has not been found in deposits older than Wisconsin in Kansas, Illinois, Indiana, or Ohio" (LaRocque and Forsyth, 1957, p. 87).

5. Virtually all the Pliocene nonmarine mollusks of northern North America must have been extinguished or displaced by the ice sheets. Perhaps most of the endemic species were destroyed. The most likely remnants or descendents of the preglacial northern fauna are the locally endemic forms occurring within the limits of glaciation or close to it, and species in northern areas (Alaska, Newfoundland, etc.) that might have survived in their present areas of distribution. The slow rate of differentiation in most mollusks (Table 4) would seem to imply that local endemics in a glaciated area are more likely preglacial relicts than postglacial novelties. In the Great Plains region the locally endemic snails *Pupilla sinistra* and *Oreohelix strigosa cooperi* are known to have been much more widespread in the late Pleistocene than now. Perhaps they were also more widespread in the Pliocene than in the Pleistocene.

GLACIAL-INTERGLACIAL CHANGES

Pleistocene molluscan assemblages within the same area of the Great Plains or Central Lowland that show different proportions of locally extinct northern and southern elements have been interpreted in terms of glacial-interglacial changes. Strict superposition in one exposure of a single depositional sequence is rare. The mollusks from three horizons in one such exposure in southwestern Kansas are listed in Table 7, together with the local Recent fauna. The stratigraphically lowest locality is UM-K2-59, ascribed to the Mt. Scott local fauna of late Illinoian age. It has yielded more than twice as many species as are now living in the county. The higher localities are referred to the Cragin Quarry local fauna of early Sangamon age. They have about as many species as are living in the vicinity, and virtually all occur in the older Mt. Scott assemblage. In this stratigraphic section the changes from Illinoian glacial to Sangamon interglacial fauna were principally the local extinction of many species now living only to the north and/or east of the fossil locality. The Sangamon fauna has practically no immigrants; it is the Illinoian fauna reduced by more than half, with different relative abundance of species. (The fossil localities are in the SE¼ sec. 18, T.32S., R.28W., Meade County, Kansas. See Miller, in press; Hibbard, 1963; and Hibbard and Taylor, 1960, for geology, measured section, relative abundance of species, present distribution of species, and associated fauna.)

THE COURSE OF FUTURE WORK

The most profitable lines of future research on Pleistocene nonmarine mollusks in North America can now be seen, even though only in broad outlines. I have selected those problems and methods which may benefit other areas of research and those which may resolve current difficulties in stratigraphic study of mollusks.

1. In many ways the most significant of all problems involving Pleistocene mollusks would entail a detailed study of the biota associated with the Pearlette ash, with special attention to climatic zonation. The wide area over which the fauna is known (crosses, Fig. 1) and the stratigraphic contemporaneity established by the ash provide a unique opportunity to study zonation of climate during a glacial interval.

2. Refinement of stratigraphic application of mollusks will accompany increasingly detailed knowledge of the geographic shifts of various species. Establishing when, how often, and how far south and east such species as *Pupilla muscorum*, *P. blandi*, *Vertigo alpestris oughtoni*, *Vallonia cyclophorella*, and *Discus shimeki* have moved would not only increase their value for stratigraphy but provide rich data for understanding Pleistocene climatic changes.

3. The recurrence of similar assemblages of mollusks at various times necessitates the use of independent sources of evidence to establish the stratigraphic horizon of such assemblages. Detailed and relatively complete stratigraphic sections are rarely available. In the present state of knowledge fossil mammals provide the most useful data. The far more rapid progressive change of Pleistocene mammals compared to mollusks is shown in Table 4.

4. Collecting Pleistocene mollusks without stratigraphic data, or studying fossil mollusks while ignoring the associated biota, is analogous to collecting stream-drift for a survey of living mollusks. In regions poorly known scientifically such collections may have some value. In the present state of knowledge none of these practices is worthwhile, for the information gained lacks the detail necessary for incorporation into the body of scientific data. Study of Pleistocene history will be most advanced by combined re-

TABLE 7

Faunal Change in Meade County, Kansas.
The Three Fossil Localities Are in a Single Exposure

	Mt. Scott loc. UM-K2-59	Cragin Quarry loc. 2	Cragin Quarry loc. 3	Recent, Meade County
Unionidae				
Anodonta grandis Say				×
Uniomerus tetralasmus (Say)				×
Sphaeriidae				
Sphaerium occidentale Prime	×			
partumeium (Say)	×			
striatinum (Lamarck)	×			
sulcatum (Lamarck)	×			
transversum (Say)	cf.			×
Pisidium casertanum (Poli)	×		×	×
compressum Prime	×			
nitidum Jenyns	×			
obtusale (Lamarck)	×			
variabile Prime	×			
Valvatidae				
Valvata tricarinata (Say)	×			
Ellobiidae				
Carychium exiguum (Say)	×	×	×	
Lymnaeidae				
Fossaria dalli (Baker)	×	×		×
obrussa (Say)	×			×
Lymnaea caperata Say	×	×	×	
exilis Lea	×			
reflexa Say	×			
Lymnaea bulimoides techella (Haldeman)				×
cockerelli (Pilsbry & Ferriss)				×
Ancylidae				
Ferrissia meekiana (Stimpson)	×			
Laevapex fuscus (Adams)	×			
kirklandi (Walker)	×			
Planorbidae				
Gyraulus circumstriatus (Tryon)	×	×	×	
parvus (Say)	×			×
Armiger crista (Linnaeus)	×		×	
Planorbella trivolvis (Say)	×			×
Promenetus exacuous exacuous (Say)	×			×
exacuous kansasensis (Baker)			×	
Promenetus umbilicatellus (Cockerell)	×			
Physidae				
Physa anatina Lea	×	×	×	×
gyrina Say	×			
skinneri Taylor	×			
Aplexa hypnorum (Linnaeus)	×			
Strobilopsidae				
Strobilops labyrinthica (Say)	×			
Pupillidae				
Gastrocopta armifera (Say)	×	×	×	×
contracta (Say)	×	×	×	
cristata (Pilsbry & Vanatta)	×	×	×	×
holzingeri (Sterki)	×	×	×	
pellucida hordeacella (Pilsbry)	×	×	×	×
procera (Gould)	×			×
tappaniana (Adams)	×	×	×	×
Pupoides albilabris (Adams)	×	×	×	×
Pupilla blandi Morse	×		×	
Vertigo milium (Gould)	×	×	×	
ovata (Say)	×	×	×	×

TABLE 7 (*cont*)

	Mt. Scott loc. UM-K2-59	Cragin Quarry loc. 2	Cragin Quarry loc. 3	Recent, Meade County
Valloniidae				
Vallonia gracilicosta Reinhardt	×		×	
parvula Sterki	×	×	×	×
Succineidae				
cf. *Succinea*	×			×
Oxyloma cf. *O. retusa* (Lea)	×			×
Endodontidae				
Discus cronkhitei (Newcomb)	×			
Helicodiscus parallelus (Say)	×	×	×	×
singleyanus (Pilsbry)			×	×
Zonitidae				
Hawaiia minuscula (Binney)	×?	×	×	×
Nesovitrea electrina (Gould)	×	×	×	
Zonitoides arboreus (Say)	×	×	×	
nitidus (Müller)	×			
Limacidae				
Deroceras aenigma Leonard	×	×	×	
laeve (Müller)				×
Euconulidae				
Euconulus fulvus (Müller)	×	×	×	
Polygyridae				
Stenotrema leai (Binney)	×	×	×	
Number of species	55	22	27	26

Mt. Scott. loc. UM-K2-59	%
Cragin Quarry loc. 2	%
Cragin Quarry loc. 3	%
Recent, Meade County	%

searches on stratigraphy, soils, fauna, and flora; through such investigations research on fossil mollusks will not only yield more but receive more from neighboring sciences.

5. Anyone attempting to interpret in detail the environment represented by Pleistocene mollusks finds abruptly how little is known of the living American fauna. In studying a late Wisconsin assemblage in Ohio, LaRocque (1952) provided a model study that wrung as much as possible from available ecological data. It is a measure of the primitive state of malacology that there was only one study of freshwater mollusks on which he could draw for measurements of pH and simple water quality, that by Morrison (1932).

6. Theoretically it might seem a straightforward matter to begin gathering ecological data on mollusks. To a considerable extent this is true; many geologists and paleontologists who began the study of Pleistocene shells have also collected Recent shells for ecological or distributional data. Qualitative analysis should precede quantitative analysis, however; it would be fruitless to gather detailed ecologic data on a composite species. Refined morphologi-

cal and taxonomic studies are a necessary prelude to meaningful ecologic studies, and these in turn to detailed paleoecologic interpretations.

7. The lack of detailed systematic analysis of living mollusks has already begun to hinder study of Pleistocene fossils, as illustrated by the discussion, earlier in this chapter, of the *Lymnaea "palustris"* group. This is not an isolated example. Virtually none of the species supposed to be common to North America and Eurasia, or pairs of related species with this distribution, has been studied critically with material from representative localities. Such studies are prerequisites for evaluating the extent and timing of possible faunal exchanges between the continents, and for understanding similarities and differences in ecology of supposedly identical species. Especially rewarding subjects for detailed study would seem to lie in the genera *Pupilla* and *Columella*. One can scarcely doubt that analysis of these groups as careful as that which has been carried out in Europe (Forcart, 1959; Ložek, 1954, 1955) would result in useful refinement of current American classification.

Mere describing of new species is not an illuminating response to the lack of systematic study of mollusks. Shimek's (1930, p. 682) words have even greater force, alas, today: "It is true that recent efforts have been made to segregate as species certain fossil forms of several variable species, but the variation in the fossils is duplicated in the modern forms and there is no warrant for the separation." Such spurious species are a disservice to taxonomy by distorting the relative rank of morphologic units, to stratigraphy by establishing supposedly extinct forms, and to paleoecology by depriving it of the evidence of variation within a living species.

8. If paleontological study of Pleistocene mollusks suffers now from lack of basic biological research, it will do so to a much greater degree in the immediate future. This gloomy prediction is based on the belief that Pleistocene research is still in an early stage; on the complete absence from this field of individuals qualified to deal with gross morphology of living mollusks, ecology, biogeography, and stratigraphy all together; and on the observation that there is no prospect for such students soon. Conventional conchological-stratigraphic research has proved to have some use, but in the long run strictly zoological study will advance Pleistocene paleontology more.

Finally it should be noted that Ložek (1961, p. 123) considered that, in Czechoslovakia, "the research methods and the application of Quaternary molluscs are in a test stage at present and they will require considerable improvement." By this standard, in America only a few wistful glances have been cast at the subject.

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