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ECOLOGICAL INTERPRETATIONS OF PLIOCENE AND PLEISTOCENE STRATIGRAPHY IN THE GREAT PLAINS REGION

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ECOLOGICAL INTERPRETATIONS OF PLIOCENE AND PLEISTOCENE STRATIGRAPHY IN THE GREAT PLAINS REGION

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ABSTRACT. In the Great Plains the succession of gross ecological conditions through Neogene and Quaternary time may be interpreted from the stratigraphy, geomorphological history, buried soils, and fossil mollusks and plants. A mild humid climate prevailed over a late-mature erosional topography in earliest Neogene. Progressive reduction of topographic relief and lowering of the regional water table, accompanied by an almost uniform drying of the climate, followed. Semiarid, rigorous conditions existed on the constructional plain, temporarily at erosional equilibrium, at the end of the Tertiary. A sharp reversal of climatic trend accompanied by stream incision and minor alluviation marked the beginning of the Pleistocene. The trend toward humidity culminating in the Kansan, was followed by a return to the trend—pulsating and irregular but none the less distinct—of progressive desiccation. The Recent climate is judged to approach in dryness and rigor that which existed on the late Tertiary plain.

INTRODUCTION

Paleoecology of marine sediments has received increasing attention by geologists. The paleoecology of terrestrial "flatlands" deposits, however, has been largely neglected in spite of the fact that the late Cenozoic strata of the continental interior contain a wide variety of interpretable data. From our studies of the stratigraphy and paleontology of the Neogene and Quaternary of the central and southern Great Plains have emerged data including an almost complete succession of fossil molluscan faunas, abundant plant remains through middle and late Neogene time, well preserved and extensive buried soil profiles from latest Neogene and Quaternary time, a distinctive sequence of clastic sediments, and the history of geomorphic development. It is our purpose here to reconstruct the succession of gross environmental conditions that obtained in this region through Pliocene and Pleistocene time.

The portion of this work dealing with Texas was supported by the Bureau of Economic Geology of The University of Texas as part of a continuing program on the Cenozoic geology of the northwestern part of the State.

The region considered extends from central-western Texas northward across western Oklahoma, Kansas, and Nebraska to the southern limit of South Dakota—a north-south strip approximately 200 miles wide and 700 miles long that includes much of the High Plains section of the Great Plains physiographic province. Its present aspect is a relatively undissected plateau, underlain by late Cenozoic deposits and segmented by the valleys of the through-flowing Canadian, Cimarron, Arkansas, and Platte rivers. The broad upland areas have a very coarse-textured drainage pattern and locally lack external drainage.

The climate is semi arid and windy; rates of evaporation greatly exceed precipitation rates. Average annual rainfall is as low as 15 inches in the southern part and nowhere exceeds 25 inches. Temperatures fluctuate widely; extremes of 118° to 120°F and –27° to –47°F have been recorded. The average annual afternoon wind velocity is approximately 15 miles per hour, which contributes significantly to the high evaporation rate.

The Great Plains are virtually treeless, although the hackberry, western Cottonwood, willow, and some woody shrubs are found sparingly along water courses. The uplands support a cover of grasses among which buffalo grass predominates. Cacti and yucca are common, particularly in the south; sagebrush is common along water courses and on dune areas but in the south is replaced by mesquite and other xerophytic shrubs. The native fauna consisted of great herds of American bison and antelope, together with the prairie wolf, coyote, badger, prairie dog, and a great variety of small rodents that still inhabit the region. Molluscan populations are sparse and composed of few species; branchiate snails live in a few isolated localities where cold waters are perennially available from artesian springs, whereas the few widely distributed aquatic pulmonate snails are capable of surviving periods of drought. The grassy plains support few terrestrial snails, although a variety of pulmonate gastropods occur along stream courses where shrubs, mixed grasses, and herbs form the vegetative cover.

STRATIGRAPHY

The succession of environmental conditions is deduced from the deposits and their contained organic remains. The descriptive stratigraphy has been documented, but a statement of stratigraphic framework and a brief summary of depositional history and lithologies is requisite to ecological interpretations. Nomenclature differs somewhat from state to state but correlations within the late Cenozoic are now reasonably well established throughout the region. Figure 1 shows the most widely used terms and their correlation.

The sub-Ogallala surface.—Throughout the region, except in northern Nebraska, late Cenozoic deposits rest on an erosion surface developed on Mesozoic and Permian rocks, and therefore a record of Paleogene time is lacking. This Miocene erosion surface, offering but slight evidence of surface environment during earliest Neogene, was a late-mature topography of gentle slopes and broad valleys. Maximum relief probably did not exceed 250 feet, although it is judged that locally sharp incision occurred along minor tributaries. In the deeper parts of these Miocene valleys, the deposits that rest upon this erosion surface are commonly coarse clastics, and the soil profile developed on the bedrock has been removed; however, where the profile is partially preserved below the Ogallala it is relatively thin, is importantly influenced by the parent bedrock, and commonly lacks a zone of caliche accumulation.

The early Neogene drainage, generally aligned west to east, initiated sedimentation in the deepest parts of the major valleys and their principal tributaries (Frye, Leonard, and Swineford, 1956). Progressive reduction of topographic relief throughout the Neogene (fig. 2) by gradual engulfment

<table>
<tr><th colspan="3">AGE</th><th colspan="2">W. NEBRASKA</th><th colspan="2">W. KANSAS</th><th colspan="2">W. OKLA.</th><th>N.W. TEXAS</th></tr>
<tr><td rowspan="9">PLEISTOCENE</td><td rowspan="3">WISCONSINAN and RECENT</td><td>Almenan</td><td colspan="2">(Alluvium and dune sand) Bignell</td><td rowspan="5">Sanborn Formation</td><td>(Alluvium, loess, and dune sand) Bignell</td><td rowspan="5">Sanborn Formation</td><td colspan="2">(Alluvium and dune sand)</td></tr>
<tr><td>Bradyan</td><td colspan="2">Brady soil</td><td>Brady soil</td><td rowspan="4"></td><td rowspan="4">(Tahoka)
(Peoria)
(terraces)

"red cover sands"</td></tr>
<tr><td>Scandian</td><td colspan="2">Peorian
Todd Valley</td><td>Peoria
(sand and gr)</td></tr>
<tr><td colspan="2">SANGAMONIAN</td><td colspan="2">Sangamon s</td><td>Sangamon s</td></tr>
<tr><td colspan="2">ILLINOIAN</td><td colspan="2">Loveland
Crete</td><td>Loveland
Crete</td></tr>
<tr><td colspan="2">YARMOUTHIAN</td><td colspan="2">Yarmouth s.</td><td colspan="2">Yarmouth s.</td><td colspan="2"></td><td></td></tr>
<tr><td colspan="2">KANSAN</td><td colspan="2">Sappa
Grand Island</td><td>Meade</td><td>Sappa
Grand Island</td><td colspan="2">Meade Fm.</td><td>Tule Fm</td></tr>
<tr><td colspan="2">AFTONIAN</td><td colspan="2">Afton soil</td><td colspan="2">Afton soil</td><td colspan="2"></td><td></td></tr>
<tr><td colspan="2">NEBRASKAN</td><td colspan="2">Fullerton
Holdrege</td><td>Blanco</td><td>Fullerton
Holdrege</td><td colspan="2">Blanco Fm.</td><td>Blanco Fm.</td></tr>
<tr><td>NEOGENE</td><td colspan="2">(PLIOCENE)

(MIOCENE)</td><td>OGALLALA GROUP</td><td>Kimball
Sidney
Ash Hollow
Valentine</td><td>Ogallala Formation</td><td>Kimball
Ash Hollow
Valentine
(Laverne)</td><td colspan="2">Ogallala Formation

Laverne Formation</td><td>Ogallala Formation</td></tr>
</table>

Fig. 1. Chart showing nomenclature in general use for late Cenozoic stratigraphic units in the central and southern Great Plains region.

of the erosional topography resulted from spread of alluviation onto the valley slopes. Moving laterally from linear initial areas along the streams, sedimentation produced an intricately complex degradational-constructional surface of which the existing record is primarily the depositional portion. Bedrock areas were reduced to isolated circumalluviated hills and small discontinuous linear areas along former major divides. This complex surface, graded to erosional surfaces in central Colorado and in the Flint Hills, maintained effective equilibrium in latest Neogene time. At the beginning of the Pleistocene, topographic evolution was reversed (fig. 2), and relief was accentuated by cyclic entrenchment of streams with resultant dissected alluvial terraces.

The Ogallala formation.—Because the stratigraphy of the Ogallala formation in Kansas recently has been described in detail, we give here only a brief summary as background for ecological interpretations. Stratigraphic classification has varied from place to place and among workers; for this discussion we use units in the sense of the Nebraska type localities (Lugn, 1939) and their equivalents as described in Kansas (Frye, Leonard, and Swineford, 1956).

From the type areas of the Valentine in northern Nebraska southward to central western Texas the initial deposits of the Ogallala consist generally of fine to medium sand and locally coarse gravel representing channel and near-channel floodplain deposits of major streams. Throughout the northern two-thirds of this region, the predominant color of these lowermost Ogallala deposits is greenish gray, and this fact, coupled with the general lack of carbonate cement, preservation of bedding, bentonitic alteration of volcanic ash lentils (Swineford, Frye, and Leonard, 1955), and preserved fauna and flora, indicates a continuously high water table in the floodplain areas. The Valentine member generally is well sorted fine to medium sand. An exception to this occurs in the panhandle area of Oklahoma and adjacent Kansas where

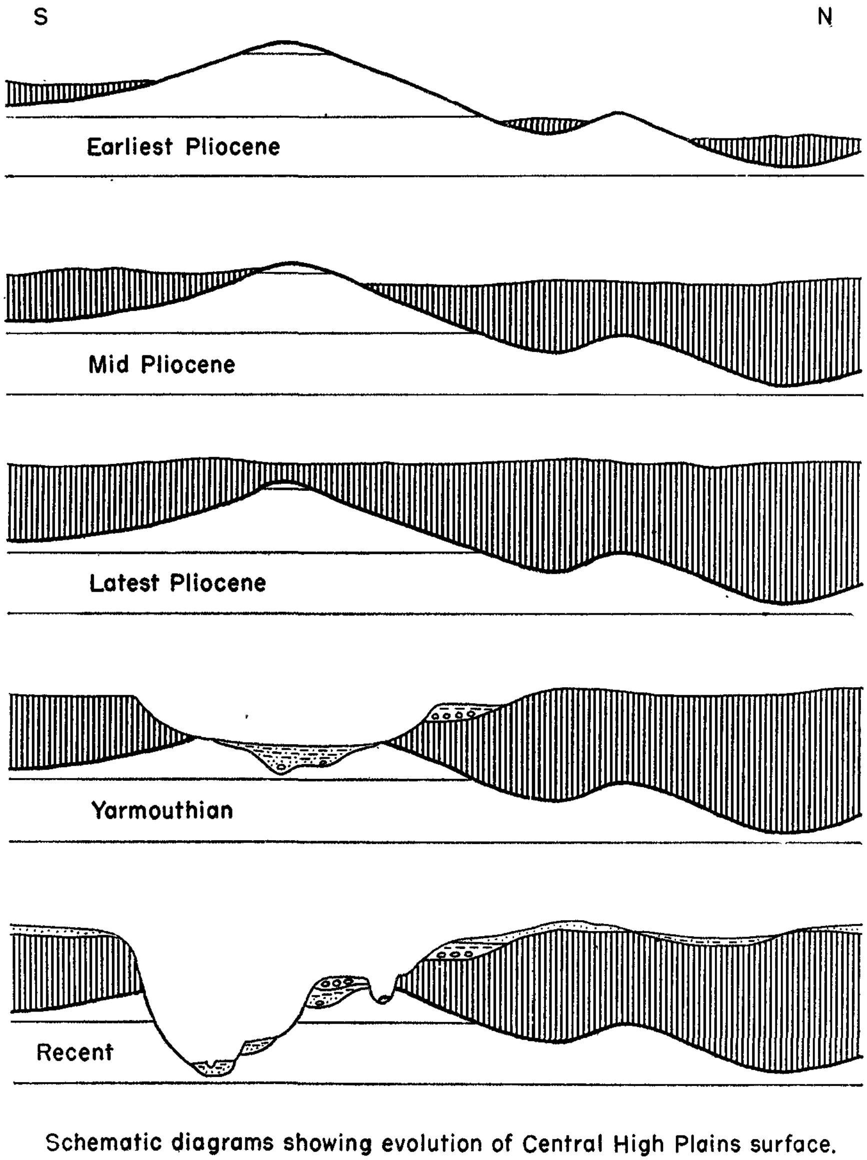

Fig. 2. Generalized diagrammatic cross sections showing evolution of the central and southern High Plains surface in Pliocene and Pleistocene time.

beds of diatomaceous marls and shales (Frye and Hibbard, 1941), locally classed as Laverne, reflect local structurally controlled ponding. This area also has afforded a record of mid-Neogene arboreal flora (Chaney and Elias, 1936) and exceptionally numerous molluscan fauna (Leonard and Franzen, 1944.).

The Ash Hollow member conformably overlying the Valentine is comparable to it in thickness but much more widespread and continuous. By the end of deposition of the Ash Hollow, 80 to 90 percent of the erosional bedrock topography had been buried by these two members, which include most of the thickness of the Ogallala. Although gradational and generally separated arbitrarily by paleontological and paleobotanical evidence (Frye, Leonard, and Swineford, 1956), the two members can in general be distinguished by their gross lithology. The degree of sorting decreases in the transition zone between Valentine and Ash Hollow, and tones of red and red brown and zones of calcium-carbonate cementation appear. Upward into the Ash Hollow, degree of oxidation, irregularly spaced and discontinuous zones of calcium carbonate, strong alternation of channel and floodplain deposits, indications of developed soil profiles, and increased textural contrasts suggest a fluctuating, declining water table during deposition. As the surface was at all times an aggradational alluvial plain, a declining water table could not have been produced by physiographic changes but must have been related to climatic fluctuations.

The Kimball (including in its base the Sidney gravels of Nebraska classification) marks the top of the Ogallala formation and the culmination of the Neogene alluvial plain. Much thinner than either of the other members, it is more widespread, overlapping the Ash Hollow and at places resting directly on bedrock. The base is conformable and gradational except locally where it can be drawn sharply at the base of gravel lentils (Sidney). Depositional trends that were evident in the Ash Hollow are accentuated in the Kimball. Although the member is predominantly fine textured floodplain sediments, contained gravel lentils are exceptionally coarse; the colors, where not masked by caliche, are dark reds and red browns; bedding is almost nowhere preserved; indications of developed soil profiles are common; and the upper part of the member is everywhere characterized by conspicuous accumulations of calcium carbonate. These characteristics, accounted for only by a water-table position significantly below the surface, point to continued climate change in the late Neogene.

Pliocene-Pleistocene unconformity.—The relationships associated with the Pliocene-Pleistocene unconformity have obvious ecological implications. Neogene deposition culminated in a plain of low relief (fig. 2) marked only by natural levees, channel scars, and small low swells in local areas where the bedrock surface was not buried. This practically featureless surface maintained stability for a significant but unknown period of time, and indications of declining water table reached a maximum. A thick and widespread mantle of dense calcium carbonate, locally encrusted at the top, developed over most of the region. Although a variety of origins have been advanced, this mantle recently has been attributed directly or indirectly to soil-forming processes- (Bretz and Horberg, 1949; Swineford, Frye, and Leonard, 1956). This hypothesis depends on a continued low water table with a balance between precipitation and evaporation tending to reduce downward percolation of dissolved carbonates, followed by the removal (by wind, water, or both) of the friable A horizon. The solution effects and secondary encrustations now observable on this irregular and uneven limestone layer must have been produced by a subsequent episode of increased precipitation.

The equilibrium of this surface was interrupted with relative suddenness throughout the plains by what is judged to be the sharpest climatic change of the late Cenozoic. That stream incision was, at least locally, governed by climatic rather than tectonic factors is suggested by the fact that it took place along streams that rose on the plains surface as well as along those that flowed through the plains from the mountainous regions to the west. This initial episode of dissection, coming between the culmination of Ogallala deposition and the initiation of Blancan-Nebraskan deposition, is considered to mark the break between the Pliocene and Pleistocene.

The Pleistocene formations.—The depositional history of the Pleistocene contrasts strongly with that of the Neogene. In contrast to the progressive and gradually changing depositional trends of the Neogene, the Pleistocene is marked by comparatively shorter and more violent episodes of stream incision and alluviation (fig. 2) alternating with intervals of equilibrium recorded by widespread buried soils. Major stratigraphic units and their correlations (fig. 1) have been described in some detail (Condra and Reed, 1950; Evans and Meade, 1945; Frye and Leonard, 1951; 1952; Frye, Swineford and Leonard, 1948; Lugn, 1935; Schultz, Lueninghoener and Frankforter, 1951; Schultz and Stout, 1945; 1948).

The depth of initial Pleistocene incision varied widely, but, with the exception of some areas in Texas, the first episode of deposition (Blanco, Holdrege-Fullerton) was characterized by coarse gravels—generally coarser than the Ogallala deposits of the same region—grading upward into finer-textured elastics marked at the top by a lime-accumulating soil profile (Afton buried soil). In drainage ways originating in the plains, these sediments are largely reworked Ogallala and the coarser texture is due to removal of fines; but in through-flowing streams, Rocky Mountain-derived gravels locally are coarser than the coarsest elements of the adjacent Ogallala.

The episodes of stream incision following the Nebraskan were profound and general throughout the region. Kansan alluviation (Tule, Meade, Grand Island-Sappa) displays a coarse texture and is indicative of a degree of stream competence somewhat greater than that in the Nebraskan. A widespread fall of volcanic ash (Pearlette bed) occurred in the late phase of Kansan deposition and, although of slight ecological significance in itself, it trapped abundant molluscan faunas and furnishes a precise time datum throughout the plains (Frye, Swineford, and Leonard, 1948). Kansan sediments are widely preserved as terrace remnants. The Yarmouth soil that caps the sequence is deep and has strongly developed structure and caliche zone.

The Illinoian deposits (Crete-Loveland) at many places indicate a departure from the general cyclic pattern of the Pleistocene in the plains. Although there was local incision of the Kansan sediments, Illinoian deposits commonly overlie the Kansan with only minor incision, which suggests lack of stream competence. This relationship also is true along drainage ways that originate within the plains, suggesting a decrease in the quantity of water available to the streams of the area. Moreover, the Illinoian is the first Pleistocene depositional cycle to have significant quantities of eolian deposits in upland areas. In the central and northern parts of the region the upland eolian deposits are largely "Loveland loess" and some local dune sand, whereas in the southern part extensive, well oxidized "cover sands" mantle many upland areas. The strongly developed Sangamon soil, readily traceable throughout the region, distinguishes the top of the Illinoian.

Renewed regional valley deepening preceded Wisconsinan deposition. This suggests increased stream competence, but as the Wisconsinan knickpoints have fallen far short of those reached by Kansan streams in the plains, the climatic implication is not clear. Furthermore, early Wisconsinan (Scandian) time witnessed the most extensive development of upland eolian deposition of the Pleistocene. Loess correlated as Peoria from northern Texas to northern Nebraska attained thicknesses of well over 100 feet, and extensive dune tracts formed in Texas, Kansas and Nebraska.

This major episode of Wisconsinan deposition was terminated by a brief interval of stability distinguished by the Brady buried soil. Post-Bradyan (Almenan) history is not consistent throughout the Plains. In the northern half, thin Bignell loess overlies the Brady soil at many places on the uplands, and sand dune tracts were developed; in valley areas post-Bradyan alluviation consists generally of a minor increment above the surface of the Brady soil followed by minor episodes of channel incision that have resulted in low narrow terraces and the present active floodplain. In the southern half of the region the Bradyan interval was marked by slight but general stream incision followed by minor alluviation that left the pre-Bradyan deposits standing as a low terrace. Here in upland areas, eolian activity was limited to local shifting of fine-textured materials, mostly from nearby blowout areas.

Early and late Wisconsinan water-laid deposits present a textural gradation, as do the older cycles, but on the average they are finer. Subsequent to the Bradyan, several minor soils formed and were locally buried, indicating a complex of minor depositional cycles.

ECOLOGICAL TRENDS

The succession of gross ecologies of the Great Plains through late Cenozoic time becomes reasonably clear when we add to the history of sedimentation the data from the almost continuous sequence of populous molluscan faunas, the distinctive floras of the Neogene, and climatic and floral implications of the buried soils. These data are summarized and environmental interpretations are shown diagrammatically in figure 3.

The rigors of the present climate have largely exterminated the rich and varied faunas of gastropods that thrived on the Great Plains during one part or another of late Cenozoic time, but most of the species, or their near relatives, still live somewhere in North America. This fact makes possible accurate interpretations of past ecologies in terms of present environmental requirements of these animals. In general the same may be said for Tertiary fossil

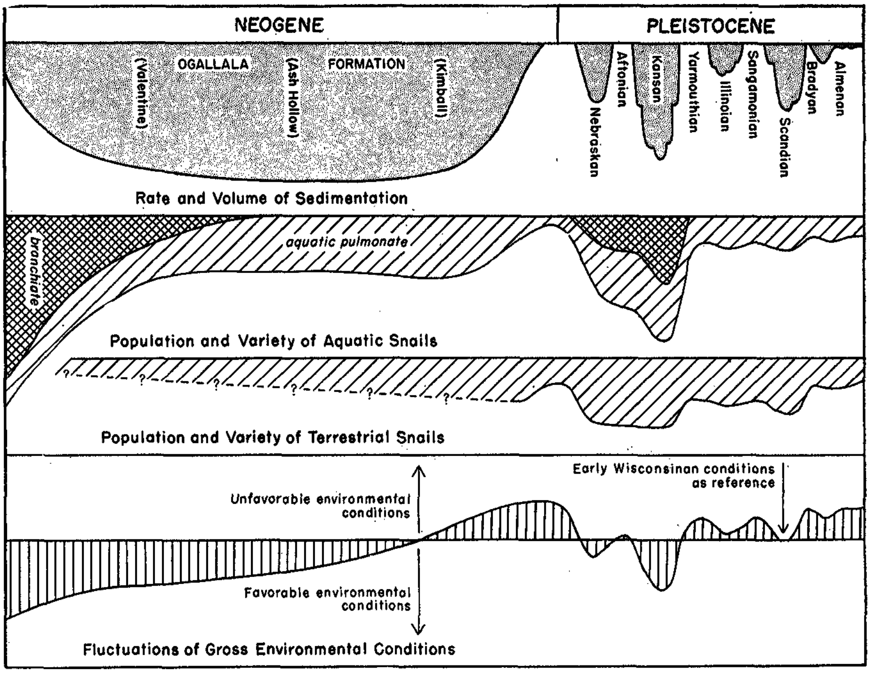

Fig. 3. Schematic diagrams showing ecological trends in the central Great Plains during late Cenozoic time. The curves depicting sedimentation, and population and variety of moluscan faunas, are generalities for the region (Texas to Nebraska) and are not intended as an accurate picture for any specific locality.

plants (Elias, 1942; Frye, Leonard, and Swineford, 1956), but plant remains in Pleistocene deposits in this region are too rare to have any practical utility.

At the initiation of Ogallala deposition, in approximately mid-Neogene time, organic remains confirm the existence of somewhat moist conditions. Western Oklahoma has furnished particularly abundant materials from the Laverne beds (lower Valentine member). Plentiful and stable water conditions are required by such branchiate gastropods as *Amnicola, Calipyrgula,* and *Viviparus,* which lived in association with species of the aquatic pulmonates *Lymnaea, Helisoma, Gyraulus,* and others. The terrestial gastropods that occur in this assemblage (*Pupoides albilabria, Vertigo ovata, Hawaiia minuscula,* and others) are largely wide-ranging species that have persisted on the plains to the present in spite of climatic fluctuations. The presence in these earliest Ogallala deposits of leaves of the persimmon (*Diospyros pretexana*) (Chancy and Elias, 1936) seems to point to a somewhat higher average annual temperature, but this may be only the effect of a more stable climate.

Ascending the stratigraphic column to the transition zone at the top of the Valentine member and into the Ash Hollow member, the evidence of declining water-table and progressively irregular stream flow is augmented by indications of declining and less stable surface moisture conditions. Branchiate gastropods, prevalent in the Valentine, disappear in the Ash Hollow. In the upper Valentine member the flora is dominated by species of prairie grasses (*Stipidium commune, S. coloradense, S. breve, S. elongatum, S, kansasense, Berrichloa amphoralis, B. conica, B. tuberculata,* and others) and forbs (*Krynitzkia coroniformis, K. auriculata, Biorbia fossilia*), which replace the arboreal vegetation that was at least locally common in the early Neogene. These floral elements change through the remainder of the Neogene, but *Biorbia fossilia* and the single tree *Celtis willistoni* persist well into the Kimball, where they are associated only with *Prolithospermum johnstoni* and a single species of *Stipidium*. In the upper Ogallala deposits the gastropod fauna is likewise sparse and is composed almost entirely of species of *Physa, Helisoma,* and *Gyraulus,* which are capable of surviving long periods of desiccation.

The organic remains in Neogene strata corroborate the interpretations reached from the clastic sediments. Progressive desiccation of surface moisture conditions and deterioration of the mild and tolerant climate of the early Neogene is clearly denoted by disappearance of the local arboreal flora, followed by deterioration of the succeeding prevalent lush prairie flora, and accompanied by gradual disappearance of the large and diversified assemblage of branchiate gastropods and eventual elimination of many of the aquatic pulmonate forms.

Organic remains are not available to furnish climatic evidence for the period of virtual equilibrium that forms the erosional-depositional hiatus between the Pliocene and Pleistocene. However, because the climatic trends of the Neogene seem orthogenic and the lithologic and geomorphic evidence points to this interval as the culmination of the trend toward aridity, it is judged that conditions on this stable surface were at least as dry and unfavorable to organic life as are those of the present. In fact, it seems likely that the generally featureless surface, low regional water table and resultant scarcity or lack of permanent streams, and the almost universal surficial blanket of caliche coming at the end of a long period of increasing dryness denote the most adverse conditions to plant and animal life of any time during the Cenozoic.

A distinct climatic reversal characterizes the beginning of the Pleistocene. This is indicated not only by the geomorphological and stratigraphic evidence but also by the reappearance of branchiate snails and a marked increase in the abundance and kinds of the total gastropod fauna in the plains.

The reversed climatic trend toward moist and tolerant conditions reached its climax during Kansan time. The deep stream entrenchment and coarse-textured deposits throughout the plains was accompanied by a resurgence of a varied branchiate gastropod assemblage (Leonard, 1950). *Amnicola,* which first reappeared in Nebraskan deposits, was joined by *Valvata* as a dominant form, along with a wide variety of aquatic pulmonates including *Physa, Helisoma, Gyraulus, Menetus, Ferrissia,* and *Lymnaea.* Terrestrial gastropods point to a dominant prairie vegetation, associated with belts of trees and shrubs along valleys. The fauna included *Hendersonia occulta,* several species of *Gastrocopta, Vertigo,* and *Pupilla, Retinella indentata* and *R. electrina, Stenotrema leai, Strobiliops sparsicosta, Euconulus fulvus,* several species of *Succinea,* and other terrestrial gastropods of less importance. These terrestrial gastropods are species characteristic of the prairies or forest borders, and it is noteworthy that the large "helicine" gastropods, such as *Polygyra, Anguispira, Triodopsis, Mesodon,* and *Allogona,* which flourish in the forests a few hundred miles east of the Great Plains, do not occur. The buried Yarmouth soil profile (Frye and Leonard, 1952, 1954) reflects development under a grasslands cover.

Following the Kansan, a strong, distinctive, but oscillating trend toward increasing aridity in the Great Plains continued into Recent time. During the Yarmouthian, branchiate gastropods disappeared from the plains, and terrestrial gastropods declined in number, kinds, and population density (Leonard, 1952). These faunal changes support the strong physical evidence of pronounced climatic deterioration by Illinoian time.

The extensive upland deposits of early Wisconsinan sediments have preserved the buried Sangamon soil that has been studied at several hundred localities throughout much of the region. This buried soil furnishes a type of regional data not available at other stratigraphic positions in the late Cenozoic. When it is compared with the present surface soils in the central Great Plains, from positions of similar drainage conditions and parent material it becomes clear that the belts of the great soil groups are offset to the west by as much as 100 miles, which verifies the conclusion that the Sangamonian interval was more moist than the present. The thick and massive zones of caliche accumulation in the southern part of the region, however, make a regional westward offset in soil groups less clear, raising the possibility that here climatic conditions in the Sangamonian approached those of the present.

In pre-Bradyan Wisconsinan (Scandian) time the trend toward an arid climate halted temporarily. The aquatic pulmonate snails *Physa, Helisoma,* and *Gyraulus* were widespread, and the most common terrestrial snails were species of *Vallonia, Pupilla, Gastrocopta, Pupoides,* and *Succinea.*

The climax of the climatic trend toward the present semiarid condition of the plains was reached during the Bradyan interval or in the early part of succeeding Almenan time. The Brady buried soil shows no westward offset from the present surface soil, and Almenan molluscan faunas are comparable to those living in the region today. In Almenan deposits, only *Hawaiia minuscula, Succinea avara,* and *Pupoides albilabris* are widely distributed. These hardy species, capable of enduring extremes of summer heat and winter cold, together with the aquatic pulmonate snails *Helisoma trivolvis, Physa anatina,* and a few *Gyraulus,* are all that remain to form the general molluscan fauna of the Great Plains. Other species do occur but always in extremely local and abnormal ecological situations. It is obvious that the present rigorous climate of the Great Plains was initiated during the Bradyan interval.

Although the climate of the Recent is judged to approach that of latest Tertiary time, there are certain significant differences between the gross ecological situations. Now there exists a distinct and sharp topographic relief along major valleys, and although the water table under the uplands may be much lower than in latest Tertiary times, it is nevertheless sufficiently high to maintain as perennial the streams in these deeply incised through valleys. Furthermore, existing physiographic conditions produce relatively strong local variations in ecological conditions that could not have existed on the almost featureless plain of alluviation in latest Tertiary time.

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