

Late Pleistocene Climate Record in the Eustis Loess Section, Nebraska, Based on Land Snail Assemblages and Magnetic Susceptibility

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Based on multivariate analysis of mollusk assemblages and magnetic susceptibility of the Eustis section in western Nebraska, the climate of the Peoria loess steppe was relatively mild and, in terms of annual precipitation, relatively moist during the advance stages of Woodfordian ice. It was cold and dry during ice retreat. The diversity and composition of mollusk species indicates that the extreme cold and dry climate was reached during the late phase of Peoria time, in mollusk zone MZ3. Although soil moisture during the growing season at that time was high, the growing season was short and annual precipitation totals were low. Low values of magnetic susceptibility imply relatively rapid dust deposition during this interval. Judging from the current ecological tolerance of the species, no closed forest existed in the area. Only scattered shrubs or isolated tree stands may have been present. The late Peoria MZ3 assemblage compares favorably with the *Columella* fauna of Europe. In contrast, the early Peoria mollusk assemblages MZ1 and MZ2 compare well with the European pleniglacial *Pupilla* associations. Based on available ^{14}C dates from the studied region and on assumed relation of magnetic susceptibility to sedimentation rates, the estimated age of the MZ1 and MZ2 zones is 24,000 to 16,000 yr, whereas that of MZ3 is 16,000 to 12,000 yr. ©1994 University of Washington.

INTRODUCTION

Loess sections in the Northern Great Plains have been extensively studied, and the Late Pleistocene stratigraphic framework in this periglacial belt that lay beyond the Laurentide ice sheet is well defined (Wayne *et al.*, 1991). However, detailed paleoenvironmental and paleoclimatic reconstructions are rare and in part controversial. This is because the pollen records from this area cover only short time spans or reflect anomalous local environments. Micromammals, charcoal, grass-opal phytoliths, and snail assemblages have been studied locally, but mostly with a focus on biostratigraphy (Frankel, 1956; Frye *et al.*, 1974; Johnson, 1965; Leonard, 1952; Wells and Stewart, 1987).

Schematically, the stratigraphy of the Late Pleistocene in the western Nebraska loess hills is defined from base to the top as follows: (1) a reddish-brown, partly decalcified soil, the Sangamon soil, which is thought to correspond approximately to isotopic stage 5 (Wayne *et al.*, 1991). Above it (2) lies a black humus-rich horizon, the so-called "Gilman Canyon Formation." Wayne *et al.* (1991) report several dates from this dark-grey humic steppe soil ranging from 34,000 to ca. 20,000 yr B.P. At Buzzard's Roost, in Lincoln county near Eustis, conventional radiocarbon dates of soil humus are 26,900 (+1000/-900) to 32,000 (+2100/-1700) yr B.P. for the uppermost and lowermost few inches of the Gilman Canyon soil, respectively (Souders *et al.*, 1971). In central Nebraska, the top of the soil has a radiocarbon age of 20,900 ± 1280 yr B.P. (May and Holen, 1993). The Gilman Canyon soil is overlain by the Peoria Loess. The loess unit is generally thicker near the suspected source areas, identified as the valleys of the Platte and Missouri rivers and the outcrops of the Ogallala Formation of eastern Colorado (Wayne *et al.*, 1991; Welch and Hale, 1987). The loess is overlain in places by the dark humus-rich Brady Soil associated with human artifacts (Schultz *et al.*, 1965) and dated 10,000 to 9000 ^{14}C yr B.P. (Schultz and Stout, 1961; Wayne *et al.*, 1991). This soil developed in a warm, moist period immediately after deposition of the late-glacial upper Peoria Loess. Taking in account the current revision of the ^{14}C chronology, the Peoria Loess in the study area thus spans an interval from more than 20,000 to about 10,000 yr B.P. The age of the Gilman Canyon soil in Eustis is 20,000 yr based on a conventional ^{14}C date of soil humus of 25,090 ± 590 yr B.P. from the middle of this unit (Johnson *et al.*, 1990). May and Holen (1993) report a conventional ^{14}C age of 20,870 ± 1280 yr B.P. from the top of the Gilman Canyon Formation at another Nebraskan locality, La Sena, about 35 km southwest of Eustis. In the same section, another conventional ^{14}C date from

a layer above a buried Bt horizon, not recognized at Eustis, provided an age of $18,860 \pm 360$ yr B.P. Snail shells occur abundantly in the Peoria and Bignell loesses (Leonard, 1952). Results of the malacological study of the Peoria Loess at the nearby Buzzard's Roost section in south-central Nebraska by Frankel (1956) are the most detailed available from the United States (Figs. 1 and 2).

The stratigraphy of the Eustis Ash Pit, the object of our study (Fig. 1), is similar to that at Buzzard's Roost but the upper part of the sequence appears more complete and the sampling access is easier. At the bottom of the Eustis excavation pit lies the Pearlette "O" volcanic ash, dated to about 0.6 myr (Naeser *et al.*, 1971). The ash was also reported at Buzzard's Roost. Soils and loess units supposed to represent the Kansan, Yarmouth, Illinoian, Sangamon, and Wisconsin stages follow in a succession that is closely similar at both localities, suggesting that the sequences are reasonably continuous for the last 600,000 yr (Schultz and Stout, 1961).

In order to reconstruct the Late Pleistocene paleoclimatic history of the Peoria Loess at the Eustis section, we decided to investigate, in parallel, the magnetic susceptibility and the mollusk assemblages.

Previous investigations of magnetic susceptibility (MS) in loess demonstrated that it reflects variation of fine-grained magnetite and maghemite (Heller and Liu 1988) and can serve as an indicator of regional environmental changes through time. In China and most other Asian and European localities, the susceptibility of soils is considerably higher than that of loess. According to Kukla *et al.* (1988, 1991) and An *et al.* (1991), the magnetic susceptibility in the Chinese Loess Plateau responded to changing ratio of subaerial input of magnetite and of nonmagnetic mineral dust controlled by the intensity of the Asian monsoon. An alternative interpretation proposes that the susceptibility is controlled by the pedogenic *in situ* production of magnetite in the soils, which increased during mild and wet climates (Maher and Thompson, 1988, 1991; Zhou *et al.*, 1990; Verosub *et al.*, 1993). In Alaska, on the contrary, magnetic susceptibility responds to weathering in swampy environments, which tends to destroy magnetite and maghemite in interglacial soils (Begét *et al.*, 1991). In most cases, the concentration of magnetite or maghemite reflected by the magnetic susceptibility is lower in the loess than in the soil and lowest in the rapidly deposited eolian sediments. It is also low in gleyed hori-

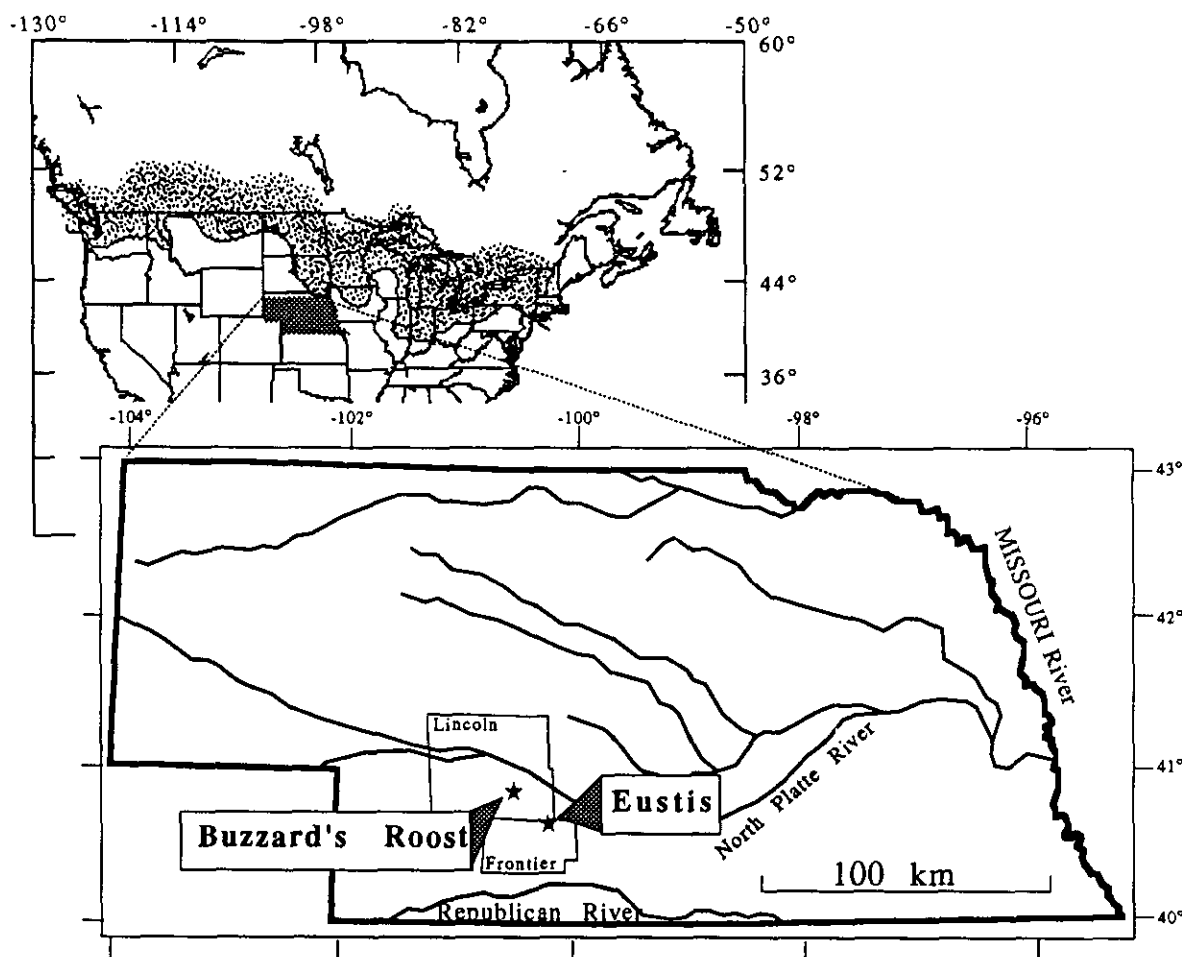


FIG. 1. Map showing location of Eustis Ash Pit and Buzzard's Roost localities in Nebraska. Maximum (Woodfordian) ice extent is dotted.

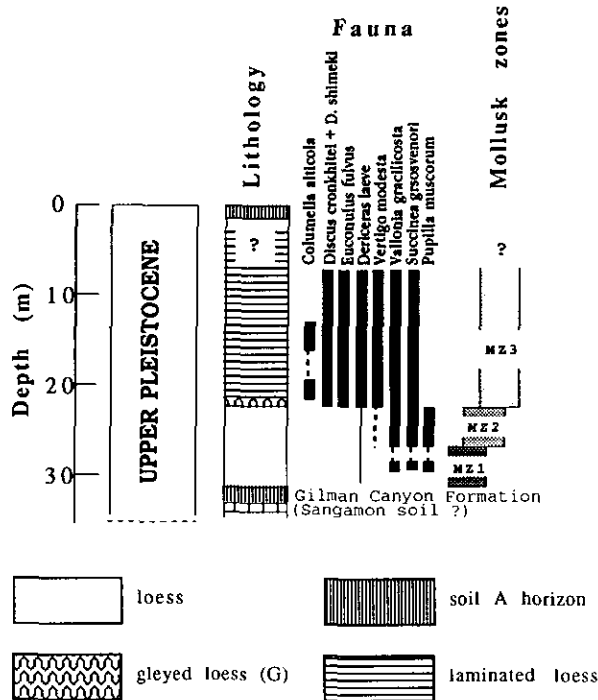


FIG. 2. Scheme of the Upper Pleistocene sequence in Buzzard's Roost according to Kukla (1978) and Frankel (1957), modified. Also shown is the distribution of the main snail species and correlation with the three mollusk zones in Eustis (this work). Lithologic symbols same as in Figure 3. Depth scale according to Kukla (1978).

zons affected by redox weathering. The variations of magnetic susceptibility through time in China are in broad agreement with variations of oxygen isotopes in the ocean sediments (Kukla, 1987; Hovan *et al.*, 1989, 1991; An *et al.*, 1991; Kukla *et al.*, 1990).

MATERIALS AND METHODS

After cleaning the Eustis section, we took and averaged 10 magnetic susceptibility measurements each at levels half a foot (15 cm) apart. We used a Bartington MS2 portable susceptibility meter with an MS2F probe operating at the frequency of 0.58 kHz. Measurements were made from the base of the Gilman Canyon Formation to the Holocene soil (Fig. 3).

In parallel with the magnetic susceptibility measurements, about 10 to 12 liters of sediment were taken at 1-foot (30.5 cm) intervals to study the mollusks. The samples were washed and sieved on a 0.5-mm mesh and the mollusk shells sorted and counted. The minimum count was 1 shell at the base of MZ1, and the maximum was several hundred in upper Peoria (Table 1).

For each mollusk assemblage, corresponding to one sample, a species count was made and the Shannon index H' computed. Shannon index describes the diversity of a biological community after the formula

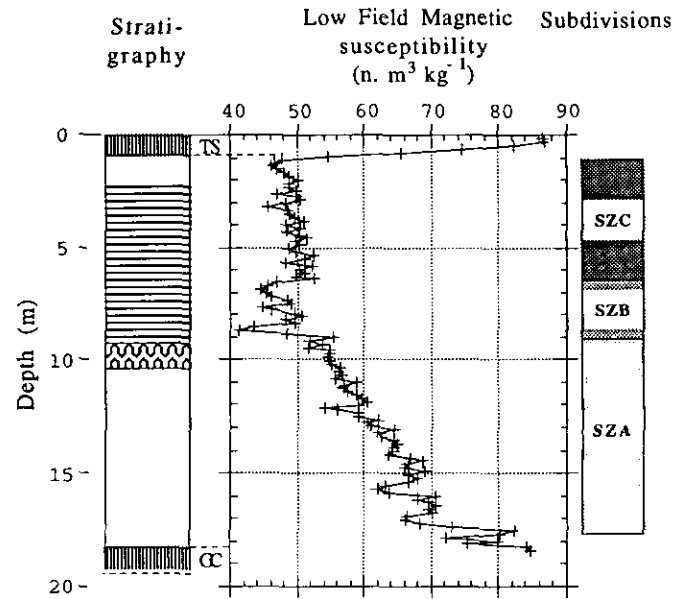


FIG. 3. Variation of the low-field magnetic susceptibility (MS) with depth showing the three MS units recognized within the Peoria Loess. TS, top soil; GC, Gilman Canyon; SN, Sangamon. Lithological symbols same as in Figure 4.

$$H' = -\sum_1^n p_k \log_2 p_k,$$

where p_k is the frequency of one species in one determined assemblage. Each count was also coded for multivariate analysis by transforming the values into abundance classes on a logarithmic scale following the method described by Rousseau (1987). This method retains the information on environmental variations while suppressing the impact of poorly represented or overabundant species. Correspondence analysis (Benzecri and Benzecri, 1980) applied to the mollusk data (Rousseau, 1991; Rousseau *et al.*, 1993) allows the parallel study of mollusk assemblages (represented by rows) and mollusk species (represented by columns). Consequently, results from rows and columns can be plotted in a single diagram facilitating environmental interpretation. This method has already been successfully applied to European sites (Rousseau, 1986, 1987, 1991; Rousseau and Puisségur, 1989, 1990; Rousseau *et al.*, 1993; Limondin and Rousseau, 1991). The interpretation of environmental significance of the Eustis mollusks is based on the current ecological tolerance of living species which includes their thermal and hygrometric requirements, and vegetation association (Frankel, 1956; Leonard, 1952; Johnson, 1965). For example, the occurrence in Eustis of *Columella alticola*, which at present lives only at elevations above 2400 m in the arctic-alpine Cordillera (Johnson, 1965), implies that colder climatic conditions occurred during the second part of Peoria Loess deposition.

It is important to realize that in our analyses the link of molluscan species with their preferred climate type is

TABLE 1
Table of Basic Counts

Samp	Pm	Ef	Vm	Vsp	Vg	Sg	Cav	Ds	Dc	DI	Ca	Hs	So	Gsp	Hm	Hp	Pa	Eggs	Depth (m)	Mollusk zones
00	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	18.1	
02	55	0	0	0	18	5	0	0	0	0	0	0	0	0	0	0	0	0	17.5	
03	23	0	0	0	11	19	0	0	0	0	0	0	0	0	0	0	0	0	17.2	
04	54	0	0	0	12	81	0	0	0	0	0	0	0	0	0	0	0	0	16.9	
05	5	0	0	0	2	7	0	0	0	0	0	0	0	0	0	0	0	0	16.6	
06	21	0	0	0	23	15	0	0	0	0	0	0	0	0	0	0	0	0	16.3	
07	37	0	0	0	67	23	0	0	0	0	0	0	0	0	0	0	0	0	16.0	MZ1
08	2	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	15.7	
10	2	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	15.1	
11	330	1	1	0	186	71	0	0	0	2	0	0	0	0	0	0	0	0	14.8	
12	172	0	0	0	95	69	0	0	0	0	0	0	0	0	0	0	0	0	14.5	
13	205	0	0	0	160	69	11	0	0	0	0	0	0	0	0	0	0	0	14.2	
14	137	6	27	0	277	47	26	3	0	0	0	0	0	0	0	0	0	0	13.9	
15	104	0	10	0	133	32	13	3	0	2	0	0	0	0	0	0	0	0	13.6	
16	53	1	5	0	150	19	10	5	0	0	0	0	0	0	0	0	0	0	13.3	
17	125	11	35	0	158	36	19	6	2	1	0	0	0	0	0	0	0	X	13.0	
18	2	17	176	0	83	19	4	24	10	0	0	0	1	0	0	0	0	0	12.6	
19	7	16	76	0	49	6	5	11	4	0	0	0	0	0	0	0	1	0	12.8	MZ2
20	3	8	57	0	69	21	2	11	7	0	0	0	0	0	0	0	0	0	12.0	
21	5	23	66	0	58	16	16	14	10	0	10	0	0	0	0	0	0	0	11.7	
22	0	2	30	0	6	9	7	10	0	0	0	0	0	0	0	0	0	0	11.4	
23	7	7	45	0	48	24	18	4	3	0	5	0	0	0	0	0	0	0	11.1	
24	4	2	6	0	27	25	15	4	0	0	0	0	0	0	0	0	0	0	10.8	
25	13	30	67	0	137	48	33	8	9	0	3	0	0	0	0	0	0	0	10.5	
26	42	15	105	0	399	41	27	33	26	7	22	8	10	0	0	0	0	X	10.2	
27	26	21	85	0	240	55	76	21	13	2	4	2	13	0	0	0	0	X	9.9	
28	6	31	281	0	24	12	21	37	7	1	12	0	2	0	0	0	0	X	9.6	
29	1	50	313	0	47	48	67	43	11	7	48	0	13	0	0	0	0	X	9.3	
30	0	37	199	0	25	42	0	24	30	0	18	0	3	4	0	0	0	X	9.0	
31	0	64	531	0	17	43	11	33	6	1	114	0	3	0	0	0	0	X	8.7	
32	2	59	321	0	173	151	66	44	30	5	37	0	27	1	0	0	0	X	8.4	
33	5	15	237	0	197	84	71	64	11	4	43	0	24	0	0	0	0	X	8.1	
34	81	52	247	0	1483	137	20	50	17	12	21	4	19	0	0	0	0	0	7.8	
35	49	60	426	0	250	156	183	18	10	7	146	0	26	0	0	0	0	X	7.5	
36	12	58	296	0	536	100	135	102	12	7	44	5	13	3	0	0	0	X	7.2	
37	0	23	148	0	28	17	33	54	5	4	21	0	0	0	0	0	0	X	6.9	
38	1	20	154	0	306	64	81	28	6	11	14	0	13	0	0	0	0	X	6.6	
39	64	27	246	0	647	74	99	38	8	4	22	0	26	0	0	0	0	X	6.2	
40	1	36	341	0	226	116	105	86	30	4	58	0	29	11	0	0	0	X	5.9	
41	2	50	418	0	120	126	120	138	17	8	251	0	38	3	0	0	0	X	5.6	
42	38	13	210	0	289	34	39	28	2	4	26	1	20	0	0	0	0	X	5.3	MZ3
43	58	44	372	0	375	134	93	44	9	9	29	4	26	5	0	0	0	X	5.0	
44	63	87	379	0	478	80	45	110	27	5	118	1	17	0	0	0	0	X	4.7	
45	0	43	250	0	321	128	69	66	31	7	66	0	20	5	0	0	0	X	4.4	
46	0	28	248	0	81	40	7	38	6	1	59	0	8	0	0	0	0	X	4.1	
47	20	38	219	0	165	57	28	78	19	7	159	0	14	0	0	0	0	X	3.8	
48	0	49	221	0	134	117	47	30	15	3	59	0	26	0	0	0	0	X	3.5	
49	5	61	316	0	117	107	15	16	8	8	148	0	14	0	0	0	0	X	3.2	
50	0	29	80	0	41	22	5	16	14	2	10	0	2	0	0	0	0	X	2.9	
51	0	60	259	0	325	84	12	55	40	3	57	0	19	0	0	0	0	X	2.6	
52	0	38	301	0	91	203	0	89	32	3	84	0	25	0	0	0	1	X	2.3	
53	0	88	204	2	330	150	0	138	64	10	116	0	40	0	0	0	1	X	2.0	
54	0	37	231	0	243	150	0	54	51	3	87	0	28	0	0	0	0	X	1.7	
55	0	14	204	0	67	119	0	24	11	6	83	0	20	0	1	1	0	X	1.4	
56	0	4	78	0	65	77	0	29	6	1	19	0	4	0	0	0	0	0	1.1	
57	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0.8	

Note. Coding procedure was done according to Rousseau (1987). Samp, Sample number, same as in Figure 4. Species codes: Pm, *Pupilla muscorum*; Ef, *Euconulus fulvus*; Vm, *Vertigo modesta*; Vsp, *Vertigo sp.*; Vg, *Vallonia gracilicosta*; Sg, *Succinea grosvenori*; Cav, *C. avara*; Ds, *Discus shimeki*; Dc, *D. cronkhitei*; DI, *Deroceras laeve*; Ca, *Columella alticola*; Hs, *Helicodiscus singleyanus*; So, *Succinea ovalis*; Gsp, *Glyphalinia sp.*; Hm, *Hawaiiia minuscula*; Hp, *Helicodiscus parallelus*; Pa, *Physa anatina*.

made in terms of annual mean temperature and annual total precipitation. Thus, species living today in places with a wet but short growing season and cold but dry winter may be classified as of dry climate type (i.e., because annual precipitation is low). This is frequently the case with *Columella* faunas.

RESULTS

Stratigraphy of Peoria Loess in Eustis

The Peoria Loess in Eustis is 17.4 m thick. It can be subdivided into three units: a brownish homogenous loess at the base, a series of gleyed horizons in the middle, and a laminated yellowish-grey and whitish upper loess (Fig. 4). The topsoil, about 1 m thick, is in part artificially reworked. The Bignell Loess is missing, as on most platform sites, so that the Brady soil and the recent soil have merged into a single unit (Souders *et al.*, 1971).

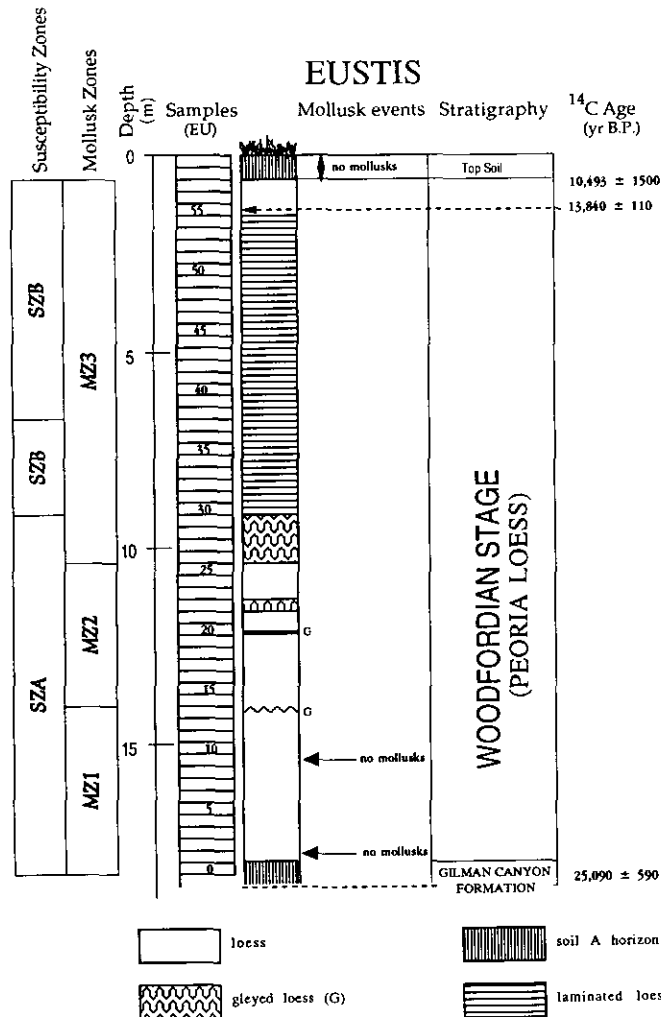


FIG. 4. Upper Pleistocene section in the Eustis Ash Pit. The ^{14}C date for the Gilman Canyon unit is from Johnson *et al.* (1990). Also shown is the position of samples EU 0 to EU 59 taken for malacological analysis.

Vallonia gracilicosta shells at a depth of 1.5 m have a ^{14}C AMS age of $13,840 \pm 110$ yr B.P. This age determination, however, must be regarded with precaution, since we did not determine the apparent ^{14}C age of living *Vallonia gracilicosta* which lives along the Republican River (Fig. 1) in the vicinity of the study area (T. B. Miller, written communication, 1993). Such a test would have enabled us to correct for anomalies due to the source of carbon in the shell. Mollusks build their shells from atmospheric CO_2 and also from the calcium carbonate contained in plant liquids. Since the carbonate available to land snails via soil and plants is generally old, the reported living shell age anomalies range between few centuries and about 5000 yr (Goodfriend, 1987). The bias varies depending on the ecology of different snail groups. Snails living on plants show the largest anomalies.

Magnetic Susceptibility (MS)

Magnetic susceptibility varies between 41.2 and 86.8 n kg m^{-3} (Fig. 3). Highest values come from the recent soil and from the Gilman Canyon humus soil horizon (87 and 84 n kg m^{-3} , respectively) (Fig. 3). From the base of the studied Peoria section, about 18.5 m below the surface, to about 9 m below surface, the MS gradually decreases from >70 to ca. 50 units (Fig. 3). Between depths of 9 and 6 m, in an ochre and greenish-grey-mottled pseudogleyed horizon, low values of 41, 44.6, and 44.5 were obtained (Fig. 3). Between 6 and 1 m below the surface, the MS oscillates between about 52 and 46 n kg m^{-3} . Finally, in the uppermost meter in the top soil, MS shows a rapid increase from 48 to ca. 87 n kg m^{-3} .

Based on its magnetic susceptibility, the Peoria Loess in Eustis has been divided into three lithologic subzones SZ A, SZ B, and SZ C. In SZ A, susceptibility decreases from 84 to 55, with several secondary minor oscillations. In SZ B, the magnetic susceptibility varies between 40 and 50 n kg m^{-3} , with large and frequent variations. In the third zone, SZ C, the magnetic susceptibility remains stable, with minor oscillations around the mean value of 50 n kg m^{-3} .

The interpretation of the results can best be made in terms of changing sedimentation rates of nonmagnetic dust and pedogenic destruction of previously present magnetite. The deposition of SZ C is likely to have proceeded at a relatively high but uniform rate, whereas SZ A indicates the gradual increase of an originally low dust-deposition rate and a gradual wetting of the climate, leading to partial destruction of magnetite in redox type of weathering in the upper part of SZ A and in SZ B.

Snail assemblages

Sixteen species of terrestrial mollusk were identified: *Columella*, *alticola*, *Deroceras laeve*, *Discus shimiki*, *D. cronkhitei*, *Euconulus fulvus*, *Hawaiiia minuscula*, *Heli-*

codiscus singleyanus, *H. parallelus*, *Pupilla muscorum*, *Catinella avara*, *Succinea grosvenori*, *S. ovalis*, *Vallonia gracilicosta*, *Vertigo modesta*, *Glyphalinia sp.*, and *Vertigo sp.* (Table 1). Unbroken land snail eggs often occurred in the samples, indicating that secondary reworking of the shells, if any, was minimal. The freshwater species *Physa anatina* was found at three levels, represented by only one individual each. This species can live in ephemeral pools that dry up seasonally (Leonard, 1959). Microvertebrate bones, as yet unidentified, were also recovered. The number of species increases from the Gilman Canyon unit to the top of the section (Fig. 5). The biostratigraphic sequence is in good agreement with the results of Frankel (1956) in Buzzard's Roost (Figs. 2 and 5).

Three main mollusk zones (MZ) were distinguished: MZ1 between 18 and 14 m depth, MZ2 between 14 and 10 m, and MZ3 between 10 and 1 m.

In MZ1, only few species (1 to 3) were present, with the exception of the top assemblage which contained 6 species (Table 1). The assemblages do not include any individuals of *Discus* or *Columella alticola*. The diversity index increases from 1 at the bottom to 1.5 at the top (Fig. 6). The second zone, MZ2, is characterized by more species and individuals and by the presence of *Discus*. The diversity index increases from 1.5 to 2.5. The third zone, MZ3, has the highest number (9 to 13) of recognized species in each sample. *Helicodiscus singleyanus* is present only in this zone. MZ3 is characterized by abundant *Succinea ovalis*, which occurred in zone 2 only as a few individuals and eggs (Table 1).

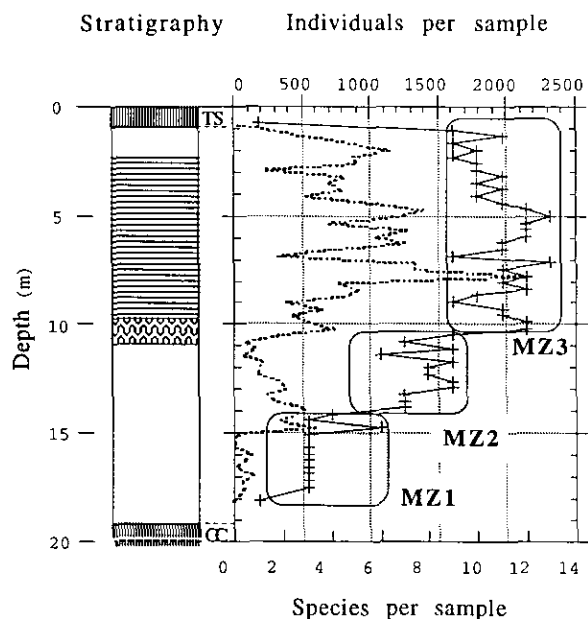


FIG. 5. Variations of the total number of mollusk species (solid curve) and individuals (dashed curve) in Eustis as a function of depth. Three mollusk zones MZ1–MZ3 are also shown. Lithological symbols same as in Figure 4. The base and top of the section are sterile.

The diversity, expressed by the Shannon index (Fig. 6), indicates that the snail assemblages reflect significant climatic variation during the interval encompassing the deposition of Peoria Loess. Diversity increases gradually from the bottom to about 12 m depth. It is at this level, within MZ2, where the Cordilleran–boreal species *Columella alticola* (Fig. 6) first appears. The gradual increase of diversity is accompanied by a decrease in the total number of individuals observed. This trend is particularly apparent between the level with the first occurrence of Cordilleran–boreal *Vertigo modesta*, at about 15 m depth, and the *Columella* appearance, at 12 m depth (Fig. 6). Then, between 12 and 6 m, the diversity varies greatly, reflecting changes in the composition of the assemblages dominated by abundant Cordilleran–boreal *Vallonia gracilicosta*, *V. modesta*, and *C. alticola* (Fig. 7). Only a few *V. gracilicosta* abundance peaks are paralleled by those of *V. modesta* or *C. alticola* during this interval. Instead, they are out of phase. No statistically significant correlation exists between *C. alticola* and *V. gracilicosta* counts ($r = 0.13$) or between *V. modesta* and *V. gracilicosta* ones ($r = 0.33$). In contrast, *V. modesta* and *C. alticola* peaks occur in parallel, with a significant correlation coefficient of $r = 0.80$. The best example is in a layer at 8 m depth which is due to the large number of individuals of *V. gracilicosta*. By comparison, populations of *V. modesta* and *C. alticola* in this assemblage are low (Fig. 7). As a result, the ecological characteristics of *V. gracilicosta* dominate in the environmental interpretation of the assemblages. *V. gracilicosta* favors a generally dry environment such as that expected at times of the high dust deposition, interpreted from the low magnetic susceptibility values between 9 and 6 m depth. Finally, between 6 and 1 m, diversity shows little variation around the mean of 2.5 (Fig. 6). The number of individuals is irregular, with peak abundance corresponding to frequent *V. gracilicosta* and *C. alticola* (Figs. 6 and 7). Another interesting feature is the apparent intensification of cold climate indicated by the upward increasing abundance of *V. gracilicosta*, *V. modesta*, and *C. alticola* in the lower part of MZ 3 (Fig. 7). This trend is paralleled by a decrease of magnetic susceptibility (Fig. 6).

The Eustis sequence roughly agrees with the zonation described by Leonard (1952) in the Peoria Loess of Kansas. He recognized two main malacological zones characterized by different species, diversity, and abundance. In the lower zone (Iowan), *Catinella avara*, *Helicodiscus parallelus*, *Lymnaea parva*, *Pupilla muscorum*, *Pupilla blandi*, *Hawaiiia minuscula*, *Vallonia gracilicosta*, and *Deroceras laeve* are present. In the upper zone (Tazewellian), *Succinea ovalis*, *Discus shimaki*, *Hendersonia occulta*, *V. gracilicosta*, *P. muscorum*, *D. laeve*, *Columella alticola*, *V. modesta*, *Helicodiscus singleyanus*, *Cionella lubrica*, *Succinea grosvenori*, *Discus cronkhitei*, *Helicodiscus parallelus*, *Pupilla blandi*, *Retinella electrina*, *Ha-*

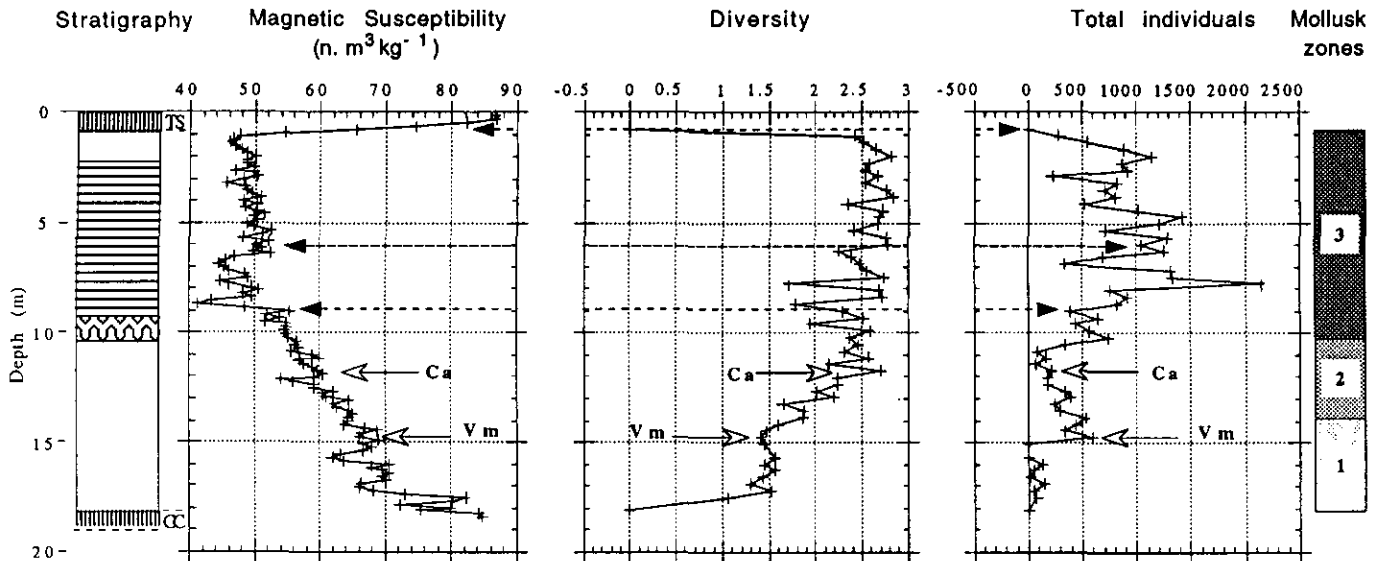


FIG. 6. Low-field magnetic susceptibility, mollusk diversity, and total number of individuals in Eustis versus depth. Arrows and dashed lines show the boundaries of SZ1, SZ2, and SZ3. Ca and Vm correspond to the first occurrences of *Columella alticola* and *Vertigo modesta*. Lithological symbols same as in Figure 4.

waiia minuscula, and *Striatura milium* occur. He also mentioned a transitional zone separating the two units, considered to be of local significance. Judging from the composition of the assemblages, this transitional zone may correspond to our MZ2.

Correspondence Analysis

Correspondence analysis (Benzecri and Benzecri, 1980) was done on 56 assemblages and 16 species. The first two axes explain about 61% of the total variability of the data (49 and 12%, respectively). Assuming that each species or each assemblage contributes equally to the variability, the significant thresholds are, respectively, $1/16 = 0.063$ and $1/56 = 0.018$. Each species or assemblage showing higher contribution than the threshold values has to be considered significant for the climatic in-

terpretation of the results (Table 2). The distribution of the species on the first factor plane (axes 1 and 2) shows a hyperbolic pattern (Fig. 8). Most of the species appear plotted close to the origin. Plots of *Hawaiiia minuscula* and *Helicodiscus parallelus*, the only two species now living in the Great Plains (Leonard, 1952), and *P. muscorum* are on the opposite extremes of the hyperbole (Fig. 8). Indeed, *P. muscorum* shows a large contribution to the variability on the first axis while *H. minuscula* and *H. parallelus* indicate a large contribution to the variability on the second one (Fig. 8). Such a plot is mainly due to the relatively high occurrence of *P. muscorum* in MZ1 and the single occurrence of *H. minuscula* and *H. parallelus* on top of MZ3 in sample EU 55 (Fig. 9). The distribution of the assemblages shows the same pattern (Fig. 9). However, two main groups can be identified: one

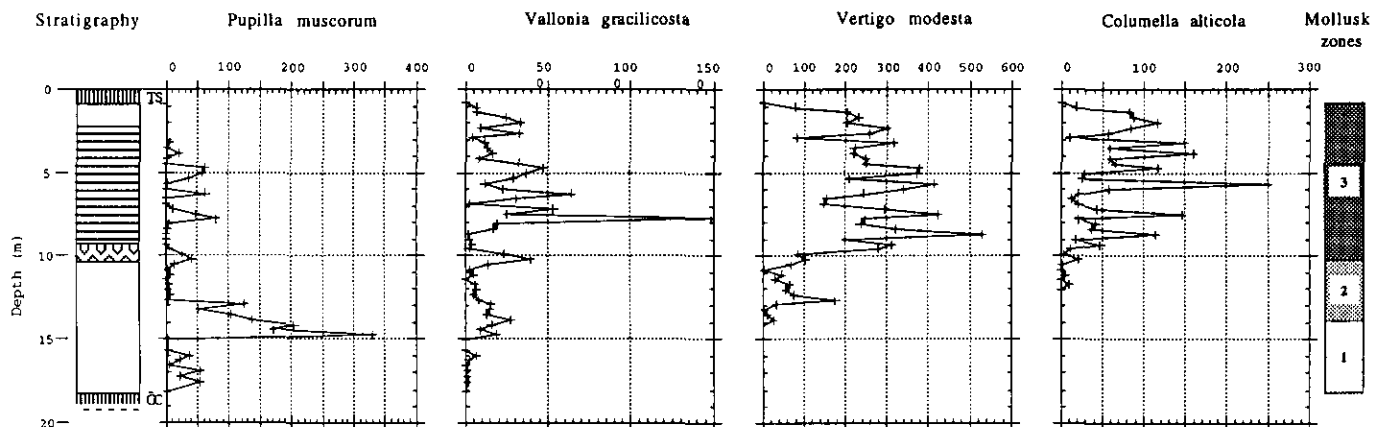


FIG. 7. Variation through depth of counted individuals of *Pupilla muscorum*, *Vallonia gracilicosta*, *Vertigo modesta*, and *Columella alticola*. Lithological symbols same as in Figure 4.

TABLE 2
Correspondence Analysis of the Malacofaunas from the
Eustis Section

Code	Species	Factor 1	Factor 2
Pm	<i>Pupilla muscorum</i> (Linné)	5.450	
Ef	<i>Euconulus fulvus</i> (Müller)	-0.345	
Vm	<i>Vertigo modesta</i> (Say)	-0.388	
Vsp	<i>Vertigo</i> sp.		0.187
Vg	<i>Vallonia gracilicosta</i> Reinhardt	0.716	
Sg	<i>Succinea grosvenori</i> Lea	0.764	0.579
Cav	<i>Catinella avara</i> (Say)		-2.729
Ds	<i>Discus shimiki</i> (Pilsbry)	-0.379	
Dc	<i>D. cronkhitei</i> (Newcomb)	-0.446	
Di	<i>Deroceras laeve</i> (Müller)	-0.157	
Ca	<i>Columella alticola</i> (Ingersoll)	-0.739	0.303
Hs	<i>Helicodiscus singleyanus</i> (Pilsbry)		-0.553
So	<i>Succinea ovalis</i> Say	-0.451	0.198
Gsp	<i>Glyphalina</i> sp.	-0.114	-0.798
Hm	<i>Hawaii minuscula</i> (Binney)		2.213
Hp	<i>Helicodiscus parallelus</i> (Say)		2.213
Percentage of variance		49.25%	11.78%

close to the origin of the axes, and another on the positive pole of the first axis (Fig. 9).

The usual interpretation of the correspondence analysis on mollusk assemblages associates temperature gradients with the first axis and moisture with the second axis (Rousseau, 1986, 1987, 1989). This is valid for data sets comprising interglacial and pleniglacial assemblages.

In the present study, this is not the case. The assemblages and species which are assumed to correspond to the extreme climatic conditions plot outside the axes. Subarctic grassland species (i.e., *C. alticola*) and assemblages fall into the third quadrant of the factorial plane (1-; 2-). Species still living in the area (*H. parallelus* and *H. minuscula*) are in the second quadrant (1-; 2+) and the dominant species of MZ1, *P. muscorum*, is in the first quadrant. Consequently, one has to rotate the first two axes in order to interpret the results. This procedure was already applied previously (Limondin and Rousseau, 1991; Rousseau *et al.*, 1993).

The principles of correspondence analysis of Quaternary snail assemblages are described in more detail by Rousseau (1987). The first two axes determine four ecological poles, representing opposing environments. The diagram thus shows a crosslike pattern, with the forest pole opposed by the tundra-like or loess steppe pole. Forest is considered temperate, whereas tundra is interpreted as cold (first axis). The open environment is divided into relatively moist on one side or relatively dry on the opposite side (second axis). The environmental gradients are parallel (superimposed) on the factor axes. In case of either pleniglacial or interglacial conditions, the poles are not located as expected from the theory (Limondin and Rousseau, 1991; Rousseau *et al.*, 1993). Such is the case also in Eustis where true interglacial faunas are missing. As a consequence, if one still wants

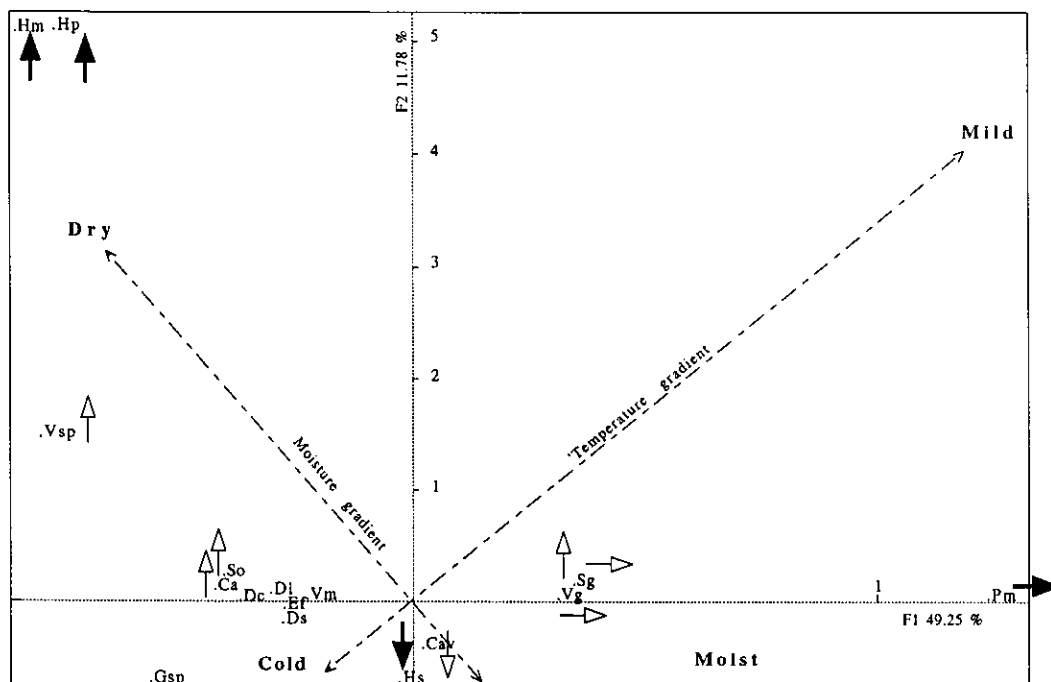


FIG. 8. Correspondence analysis of the mollusk assemblages in Eustis. Plot of the species on the first two axes. From the ecological characteristics of the species, four poles are determined: cold and mild and dry and moist. Temperature and moisture gradients are determined, after a 39° rotation of the factors (see Rousseau *et al.*, 1993, for explanation). The arrows indicate the species that contribute to the variability of the general data set. Black arrows indicate highest contributions, while the open arrows show high contributions (Table 2). Same codes as those of Table 1. The dot next to the species code designation shows the position of the element in the diagram.

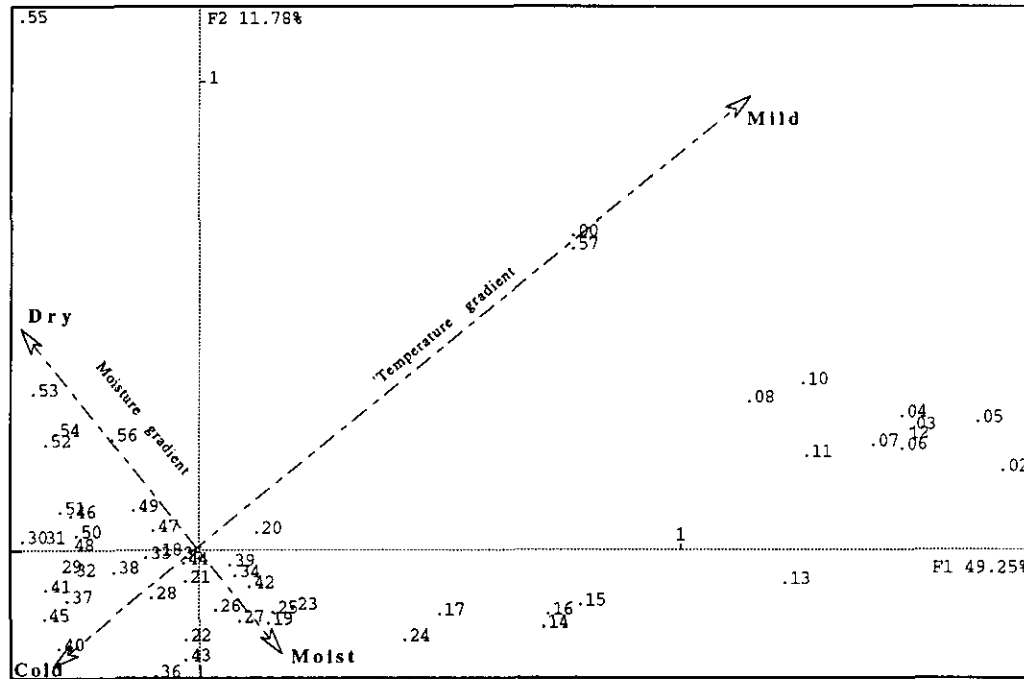


FIG. 9. Correspondence analysis of the mollusk assemblages in Eustis. Plot of the mollusk assemblages recovered from the samples EU 1-59 shown on the first factor plane (axes 1-2). From the composition of the assemblages (designated by the sample numbers; Fig. 4), the same four environmental poles are recognized as in Figure 8. Temperature and moisture gradients are identical to those determined in Figure 8 after a 39° rotation of the factors. Same legend as in Figure 8.

to interpret the snail assemblages in terms of climate variations, "environmental gradients" need to be determined, which are not parallel to the original axes. A rotation of the axes permits the definition of the environmental gradients.

We took the assemblages in samples EU00 and EU56 as reference points for the rotation by 39° because they are located about half way between the two extreme poles. The magnetic susceptibility data also show ex-

treme values at the corresponding stratigraphic levels. After recomputing the coordinates of the assemblages and taking into account their stratigraphic position, we obtained two curves, one representing estimated temperature changes and the second estimating the annual mean precipitation trends (Fig. 10).

The temperature curve shows a moderately cool interval in the lowest 3 m of the Peoria Loess (Fig. 10). The transitional interval, between 15 and 12 m, has abundant

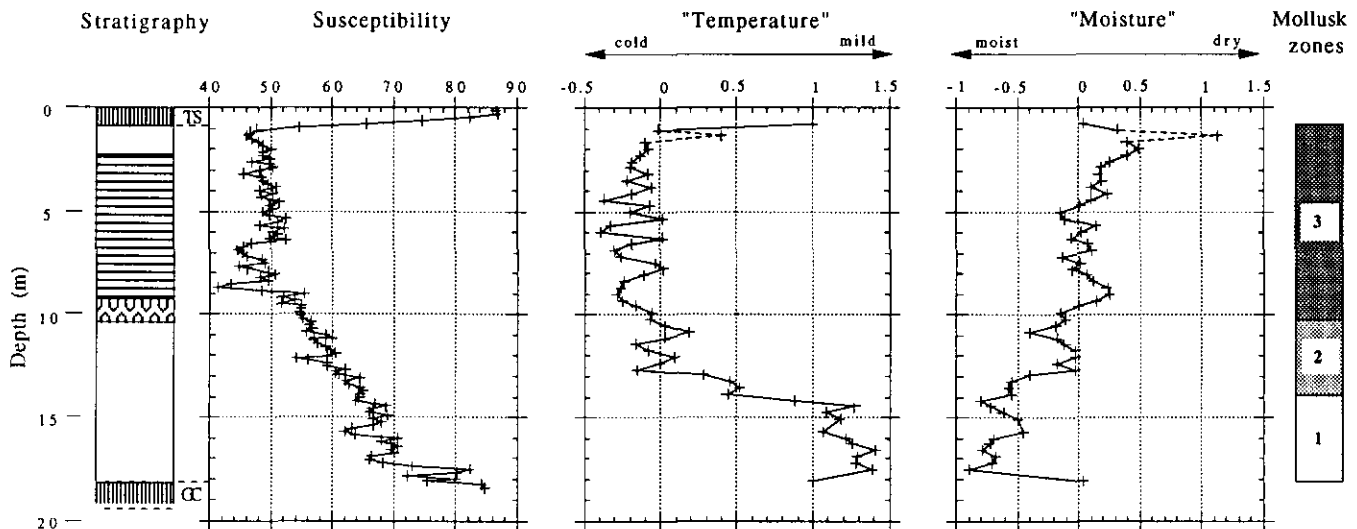


FIG. 10. Temperature and precipitation variation in Eustis as reconstructed from the mollusk assemblages as a function of depth. Comparison with the variation of the low-field magnetic susceptibility. Lithological symbols same as in Figure 4.

P. muscorum and indicates severe cold conditions (Fig. 8 and 10). Up to the uppermost 1 m, the climate was generally very cold. Secondary temperature oscillations may be indicated by changing abundance of *C. alticola*, *V. modesta*, and *V. gracilicosta* (Figs. 6 and 7). The precipitation (moisture) curve indicates that the basal part of the Peoria Loess (15–13 m) was deposited under relatively humid conditions. Then, from 13 m to the top, a gradual decrease of annual precipitation is indicated by the data. Low magnetic susceptibility points to an increased rate of dust deposition expectable with such reduced precipitation.

An extreme "dry" event may be indicated in the uppermost Peoria close to the base of the Holocene soil in sample EU 55 by two species still living in this area today. This layer may have formed in an environment entirely different from any older level of the Peoria, i.e., marked by extremely dry climate and mild temperatures. However, we cannot exclude the possibility that the sample is contaminated by Holocene gastropods which burrowed or penetrated along fissures into the Peoria Loess from higher levels (Table 1).

DISCUSSION

Leonard (1959) discussed the ecologic significance of his two mollusk zones, recognized in several states in the central United States. He reported the older zone (Iowan) from Kansas, Oklahoma, northern Texas, and Nebraska, and the younger zone (Tazewellian) from Kansas, southern and central Nebraska, western Iowa, and central Illinois.

The wide distribution of the zones shows that they represent well-defined biostratigraphic units which reflect specific environmental conditions that were relatively uniform over large expanses of the Great Plains. At Eustis, our results from MZ 1, with few species and very small individuals, point to a moderately cool and relatively moist climate and to the presence of grassland. The environmental conditions changed in MZ2. Temperature and moisture both decreased, and new species immigrated. The occurrence of *Discus* in the assemblage indicates that some arboreal vegetation was present (Frankel, 1956). However, this does not imply the presence of a closed forest in the area, but rather of scattered trees or shrubs. Mollusk zone MZ3 corresponds to an interval of extreme cold, with low and gradually decreasing annual precipitation concentrated in a short growing season. Nevertheless the soil moisture was sufficient to allow the mollusks to survive, grow, and breed. Again, while some shrubs or sparse trees can be invoked, there is no evidence of any closed forest during this interval. This contrasts with the conclusion of Wells and Stewart (1987) who claimed that central Great Plains were not a "loess

steppe" during the most recent Pleistocene glaciation but were covered by a taiga-like forest.

The composition of mollusk assemblages in MZ 1 and MZ3 is strikingly reminiscent of pleniglacial assemblages of the European loess belt. The older community of a grassland environment could be compared with the European low diversity loess-steppe *Pupilla* association (Ložek 1964; Puisségur 1976). The assemblage of the younger zone (MZ3) shows more species and individuals, more diversity, and an environment in which some sparse arboreal vegetation is present. It can be compared with the European tundra-like *Columella* associations in which the boreal *Columella columella* and the boreoalpine *Vertigo genesii* among others are well represented.

The extensive distribution of the Iowan and Tazewellian faunal zones in the Great Plains implies also that our results from the Eustis section do not reflect merely a local microclimate variation. They show changes of more general, large-scale regional significance.

Interesting also is the diversity and magnetic susceptibility variation in the upper 10 m of Eustis section (Figs. 6 and 10). Most of this zone consists of laminated loess. The laminae could result from niveoelion deposition or from frequent oscillations of local microclimate. If so, the alternations of peak occurrences of *P. muscorum*, *V. gracilicosta*, *V. modesta*, and *C. alticola* in MZ3 would reflect such oscillations (Fig. 7). The ecology of mollusk zone MZ3 of the Eustis section, its laminated horizons, and the environment it reflects are closely comparable with the laminated, possibly niveoelion last-glacial loess of the Vestonice brickyard (Klima *et al.*, 1961).

The deposition of Peoria Loess in the Eustis sequence took place when both Laurentide and Cordilleran ice sheets expanded, reached their maximum extent about 18,000 yr B.P. (Hughes, 1987; Andrews, 1987), and then retreated. The increase of ice volume calls for low temperature but also a sufficient moisture supply. Both are indicated by the MZ1 and MZ2 environments in the periglacial area of the Nebraskan loess hills. Based on ¹⁴C dates available from the studied region and on the assumed relation of magnetic susceptibility to sedimentation rates, the age of MZ1 and MZ2 zones is estimated to be from 24,000 to 16,000 yr B.P., whereas the MZ3 zone lasted until ca. 12,000 yr B.P. (Souders *et al.*, 1971; Wayne *et al.*, 1991; May and Holen, 1993). Thus, while the first two molluscan zones in Eustis are indicative of relatively high annual precipitation and milder temperature, the upper MZ3, showing cold and relatively dry conditions, parallels ice retreat.

CONCLUSION

The parallel study of snails and magnetic susceptibility in the Eustis loess section in Nebraska permits the reconstruction of environmental changes during the latest

Pleistocene in the North American Great Plains. Three main mollusk assemblages (MZ) have been recognized in the Peoria Loess. MZ1 is poor in number of species and individuals, and the diversity of snail communities is low. It indicates a cool and increasingly wet environment culminating in the strongly pseudogleyed, possibly permafrost-affected zone. The overlying MZ2 shows an increase in the number of species and diversity. It is characterized by the occurrence of *Discus*. The gastropod *Columella alticola* also first occurs in this zone. MZ3 shows the highest number of species and high diversity. It is characterized by abundant *Succinea ovalis*, *Vallonia gracilicosta*, *Vertigo modesta*, and *C. alticola*. The mollusk zones in Eustis compare well with Leonard's faunal zones, with MZ1 corresponding to Leonard's Iowan, MZ2 to his unnamed transitional zone, and MZ3 to the Tazewellian. The environmental reconstruction based on mollusk assemblages points to the occurrence of a grassy loess steppe during MZ1 and MZ2, and of a cold steppe with patches of subarctic-like grassland vegetation in MZ3. No closed forest was present during Peoria time in Eustis. Only scattered shrubs and sparse trees existed during MZ3 time. Mollusk zones MZ1 and MZ3 in Eustis compare favorably with coeval European pleniglacial loess-steppe to tundralike mollusk assemblages. MZ1 and MZ2 were mild to cool and relatively moist biozones that were associated with the advance of the Laurentide and Cordilleran ice sheets between 24,000 and 16,000 yr B.P. The MZ3 zone, which was very cold but relatively dry, was associated with ice retreat.

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