The Buzzard’s Roost and Eustis mollusc sequences: comparison between the paleoenvironments of two sites in the Wisconsinan loess of Nebraska, USA

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We investigated the Upper Pleistocene mollusc sequence in the loess deposit of Buzzard’s Roost, Nebraska, and compared the results with those obtained for Eustis, 50 km to the west. Both sequences show similarities in: (i) stratigraphy and magnetic susceptibility implying identical fluctuations in loess deposition, (ii) biostratigraphy which indicates a succession of cold-and-moist to cold-and-dry conditions, and (iii) an increasing trend in mollusc abundance and diversity of species characterizing a climatic and/or environmental improvement. We interpret the variations in both sequences as related to the advance of the James and Des Moines ice lobes towards both sites, which was synchronous with the retreat of the Laurentide Ice Sheet. The occurrence of hygrophilous species in the mollusc record, from the upper sequences of Buzzard’s Roost, suggests a moister environment than in Eustis. Our preliminary comparison of both malacological sequences suggests that regional or local, rather than global, influence prevailed over the Great Plains between 20 and 12 kyr BP.

Material and methods

Lithostratigraphy

The Upper Pleistocene loess deposits in the US Great Plains are directly linked to the extent of the former Laurentide Ice Sheet maximum (Fig. 1). The associated terminal moraines contain fine-grained material which, transported by strong winds, formed the sand dune fields in northwest Nebraska, and the loess deposits whose main unit is the Peoria loess. Ruhe (1983), studying the thickness variation of this deposit over the Great Plains, showed that the origin of the eolian dust is associated with northwest winds. Nebraska therefore, is an appropriate area for a detailed study of this unit. The Buzzard’s Roost sequence is located 50 km west of
Eustis (Fig. 1). Both sites have a similar stratigraphy (Feng et al. 1994; Frankel 1956a).

The Upper Pleistocene at Buzzard’s Roost yields the same succession as described in Eustis (Rousseau & Kukla 1994). The Sangamon (last interglacial) paleosol, is overlain by the black Gilman Canyon soil dated by 14C to 20 870 ± 1280 BP (May & Holen 1993). The Peoria loess is composed of three main subunits. At the base, a 7.5 m thick light colored loess is overlain by a 1.4 m thick gley soil, followed by laminations corresponding to the alternation of gley-loess layers. In Eustis, a second loess layer occurs (1 m thick) overlain by the present soil (Fig. 2). In Buzzard’s Roost, the base of the main gley is 14C AMS dated to 22 060 ± 200 BP (Beta-169529), while the top of the studied sequence is 14C AMS dated to 17 610 ± 80 BP (Beta-169530). Feng et al. (1994) obtained similar dates that they rejected because organic-coagulated aggregates occurring in a significant proportion of the sediment producing dates which may be too old. Furthermore, new optically stimulated luminescence (OSL) dates indicate that the Peoria loess deposition in Eustis started at about 20 kyr and ended after 14 kyr (Roberts et al. 2003). In Buzzard’s Roost, the top of the sequence is not exposed, thus using the Eustis depth-scale as a reference we estimated the top of the accessible part to be at about 5.7 m deep. The Buzzard’s Roost sequence also shows gley horizons at depths of 8.7 m and 5.9 m. The light colored basal loess subunit in Buzzard’s Roost contains a layer with black dots, probably manganese, at 15 m, and a slightly gleyed one at 14 m (Fig. 2).

Low field magnetic susceptibility

The low field magnetic susceptibility (MS) has been measured using a portable Bartington susceptibility meter. Ten readings were taken for each foot (30.5 cm) of depth and averaged. The climatic and environmental significance of this signal has been debated in numerous studies (Heller et al. 1991, 1993; Maher et al. 2002) and will not be repeated here. Low field magnetic susceptibility has been used to support the correlation between the two sequences with complementary lithostratigraphy. The MS was measured directly in the field and also in cubes of sediment in the laboratory.

Mollusc analysis

The sequence has been sampled every foot (30.5 cm) for mollusc content. As at Eustis (Rousseau & Kukla 1994), 10 liters of sediment per sample were taken and wet-
sieved using a 0.5 mm mesh (Fig. 2). The collected mollusc shells were identified under a binocular microscope and counted following Puisségur’s method (1976) for broken individuals. In Buzzard’s Roost, one in two samples (a resolution of 0.6 m) was analyzed, and the results compared to those from Eustis published by Rousseau & Kukla (1994). For each studied sample, the Shannon-Weaver diversity (H) and the equitability (E) indices were calculated (Dyduch-Falniowska 1988). These indices permit a better understanding of the evolution of the mollusc communities evolution through time (Dyduch-Falniowska 1988; Limondin 1995; Limondin & Rousseau 1991; Rousseau et al. 1993 1994; Rousseau & Puisségur 1999). They are computed as follows: \( H = \sum_{i} p_i \log_2 p_i \), and \( E = H / \log_2 n \), where \( p_i \) is the relative frequency of the species \( i \), and \( n \) is the total number of identified species in the community. The diversity index \( H \) represents the complexity and the biological richness of the studied mollusc assemblage, whereas equitability \( E \) measures the homogeneity of this assemblage: the lower the number, the more differences in the species counts.

Results

The measured values of the low field magnetic susceptibility in Buzzard’s Roost vary between 28 and 14·10^{-8} m^3 kg^-1. MS variation in Buzzard’s Roost through the Peoria loess is similar to that observed in Eustis except at the base. The difference is mostly related to the occurrence of concretions in this zone. MS variation in both Eustis and Buzzard’s Roost showed a similar pattern (Feng et al. 1994) suggesting that both sequences are comparable as already indicated by the lithostratigraphy. Use of Eustis thickness scale (Fig. 2) for Buzzard’s Roost facilitates comparison of the mollusc record in both sequences.

Eleven mollusc species were identified in Buzzard’s Roost (Fig. 3): Columella columella (Martens, 1830), Discus shimekii (Pilsbry, 1890), D. whitneyi (Newcomb, 1864), Deroceras laeve (Müller, 1774), Euconulus fulvus (Müller, 1774), Pupilla muscorum (L., 1758), Vallonia gracilicosta (Reinhardt, 1883), Vertigo modesta (Say, 1824), Succinea avara (Say, 1817) and Physa anatina (Lea, 1869). Succinea ovalis (Say, 1817) and S. grosvenieri (Lea, 1864) were also identified but consist of numerous intermediate morphotypes and juvenile individuals which could lead to important count errors. We therefore grouped these two species within Succinea sp. High counts of Physa anatina are found through the Buzzard’s Roost sequence although this species is absent at Eustis. Loess is generally deposited in arid environments, thus the occurrence of this freshwater mollusc is anomalous. However, the presence of small ponds could have allowed this species to live. We did not take this species into account in our interpretation of the composition of the mollusc assemblages instead focusing only on the terrestrial species.

The mollusc zones defined by Leonard (1952) and identified by Rousseau & Kukla (1994) are also recognized in Buzzard’s Roost (Figs 4–7). Mollusc zone (MZ) 1 or ‘lowan’ corresponds to the interval between the Gilman Canyon soil, at about 18.5 m, and 15.3 m deep, within the light colored loess. It has a low abundance and a low species richness. It is characterized by the occurrence of numerous individuals of Pupilla muscorum and Vallonia gracilicosta, and the absence of Columella columella, Discus shimekii, D. whitneyi, Succinea sp., and Vertigo modesta. The diversity is low. MZ 2 or the ‘transitional zone’ shows average diversity and species richness, and contains species of the other two mollusc zones. In both sequences, MZ 2 lies between 15.3 m and 11.4 m. Finally, MZ 3 or ‘Tazewellian’ shows high abundance and species richness characterized by the occurrence of Columella columella and Vertigo modesta. The diversity index is high. This mollusc zone corresponds to the interval starting from the main gley at 11.4 m, and continues upward to the top of the series located at 5.7 m in the Buzzard’s Roost sequence.

Compared to Eustis, two taxa are absent in Buzzard’s Roost: Helicodiscus singleyanus (Say, 1821) and Retinella sp. Mollusc eggs were observed at both localities. Two sizes were noted, although we were not able to allocate them to any species at Buzzard’s Roost. Despite the processing of the fragile samples, the eggs are found complete and empty which, as in Eustis, can imply that the sediment has not been reworked (Rousseau & Kukla 1994). The terrestrial mollusc species show a similar pattern to that of Eustis (Figs 4, 5). Pupilla muscorum, Succinea avara and Vallonia gracilicosta mainly occur at the lower part (18.0–10.8 m) of the sequence (Fig. 3), and are in smaller proportions in its upper part (10.8–5.7 m). Vertigo modesta, Columella columella and Euconulus fulvus primarily occur in the upper part of Buzzard’s Roost sequence. Deroceras laeve is present throughout the series without any particular distribution.

Comparison of the Buzzard’s Roost and Eustis records shows clear differences. Pupilla muscorum, Vallonia gracilicosta, Succinea avara, Euconulus fulvus and Discus shimekii occur later in Buzzard’s Roost. Pupilla muscorum disappears in the upper part of the Buzzard’s Roost series, whereas it is present all through the sequence in Eustis. Vallonia gracilicosta is much more abundant in the lower part of Buzzard’s Roost than in Eustis, as is Pupilla muscorum and Succinea avara (Figs 4, 5). Vertigo modesta is much more abundant in Buzzard’s Roost than in Eustis (Fig. 4).

Variations in abundance (total count of individuals) and in species richness (total count of species) are synchronous in both sequences implying that similar general environmental conditions prevailed through time (Fig. 6). The maximum abundance is at 8.7 m,
Fig. 3. Identified species in the Buzzard’s Roost sequence. A = Columnella columella; B = Discus shimeki; C = D. whitneyi; D = Vertigo modesta; E = Euconulus fulvus; F = Vallonia gracilicosta; G = Succinea sp.
with counts higher than 2000 individuals per sample in both localities. In Buzzard’s Roost, a second maximum occurs at 13.7 m (Fig. 6), which corresponds to another maximum in species richness and is associated with the top of a gley subunit. Similar results have been described in Europe in the Nussloch loess sequence (Moine et al. 2002). After the main gley, at about 10.8 m, the species richness is stable in Buzzard’s Roost, whereas it shows fluctuations in Eustis. These fluctuations occur based on the sporadic presence of Helicodiscus singleyanus and Retinella sp. in the upper sequence in Eustis. The diversity index (H) increases upward in both sequences, although it is not synchronous. In Buzzard’s Roost, the first decrease in diversity at 16 m is due to the lack of any individual of Succinea avara. The strong decrease at 13 m in both indices corresponds to the abrupt dominance of 90% Vallonia gracilicosta (Figs 4, 7). In Eustis, a similar decrease in both indices occurs at 8.7 m, which also corresponds to the strong dominance of Vallonia gracilicosta.

**Interpretation**

Most of the species identified in both Buzzard’s Roost and Eustis do not currently live in Nebraska even if they still exist in some North American regions (Leonard 1959; Rousseau & Kukla 1994). The identified species indicate particular climatic and environmental characteristics (Table 1) and the mollusc assemblages have been shown to react closely to environmental variations (Rousseau 1989). The variations in time of their relative abundance and diversity of species provide clues to the climatic evolution of the studied area. First, considering the relative frequencies within the Buzzard’s Roost sequence, two main phases can be determined.

(a) From the base to 10.8 m, biozones MZ 1 + MZ 2. This first phase is dominated by two open-ground species indicating cold and dry conditions: Pupilla muscorum and Vallonia gracilicosta. They appear to be in ecological competition. As one increases in abundance the other decreases or, alternatively, is favored by cyclic climatic/environmental changes. These species are associated with Succinea avara, which has a broad ecological fitness. The cold and moist indicative species like Columella columella and Vertigo modesta are lacking. The cold and dry conditions of this first phase are in agreement with last-glacial maximum climatic conditions, and matches the nature of the sediment, light-colored loess. The dryness varied as marked by
alternations of *Pupilla muscorum* and *Vallonia gracilicosta*, the driest conditions marked by the latter.

(b) From 10.8 m to the top, MZ 3. The second phase is dominated by *Vertigo modesta*. *Columella columella*, which today lives at high latitudes and elevations, also occurs. Both are species of cold and moist habitats. *Succinea ovalis* and *S. grosvenerii*, species which were not differentiated, *Discus shimekii*, *D. whitneyi* and *Euconulus fulvus*, species which usually prefer the humus of arboreal environments (Frankel 1956a, b; Pilsbry 1946), imply the presence of shrubs. *Vertigo modesta* is correlated with *Columella columella* (Fig. 8), and thus no ecological competition prevailed between them. In Buzzard’s Roost, this second zone should have been cold but moister than the previous one.

Rousseau & Kukla (1994) interpreted the mollusc assemblages from Eustis as indicating a cooling and increased aridity trend for the interval from 18 to 14 kyr. This was recently supported by the δ^13^C study of shells of *Vertigo modesta* from Eustis (Labonne et al. 2002) also showing an aridity trend characterized by the record of the occurrence of plants showing C₄ photosynthetic pathway on top of the sequence. This appears to contradict the results for Buzzard’s Roost, whose similar trend has been interrupted by moister intervals corresponding to gley layers. The discrepancy between the interpretation of Eustis and Buzzard’s Roost mollusc fauna is tenuous. In the former sequence, the interpretation is based on the multivariate analysis of the mollusc counts which integrated all the components of the environment. In the present study, the interpretation focuses on particular species. Furthermore, modern mollusc faunas in the Abisko valley in northern Sweden indicate the occurrence of the moist loving species *Columella columella* or *Vertigo genesii* (Nilsson 1968, 1987). However, the annual precipitation in this rain-shadowed area is about 360 mm, which, in other places, could be interpreted as dry and semi-desert. In fact, the occurrence of these particular species relies first on their location in high latitudes but also on the presence of a scarce arboreal vegetation associated with streams and small ponds which maintain sufficient moisture for the freshwater or moisture-loving molluscs to grow. Similar conditions could have prevailed during MZ 3 in Buzzard’s Roost, indicating this apparent increase in moisture. Another study supports this interpretation. Reviewing the full glacial mollusc assemblages of the

![Fig. 5. Relative frequencies (percentages) of the different species identified in both sequences of Buzzard’s Roost (black line) and Eustis (gray line). Lithology symbols as in Figs 2 and 4.](image-url)
European Upper Pleistocene, Rousseau et al. (1990) interpreted the low diversity of the western mollusc communities, mostly constituted by *Pupilla muscorum* and *Succinea oblonga*, resulting from a higher precipitation regime in western compared to central Europe. In full glacial deposits in Czech Republic, the mollusc assemblages show a higher diversity and abundance of *Columella columella* and other cold indicator species (Lozek 1964). The comparison of the European glacial mollusc assemblages indicates that the *Pupilla* fauna appears to be associated with precipitation amounts to a higher degree than *Columella* fauna (Rousseau 2001).

In addition to these general trends, the molluscs from Buzzard’s Roost indicate several particular events. MZ 1 (upward 15.5 m) is characterized by very few individuals and species, the first two samples yielding no shells. The lack of shells can be explained by several non-exclusive hypotheses: (i) Occurrence of too cold temperature and too little moisture. Molluscs require a minimum of water to survive and cannot endure too low temperature thresholds. Their absence could indicate strong aridity with very low temperatures representing the ecological characteristics of the species (*Vallonia gracilicosta* and *Pupilla muscorum*). This would point to the coldest and driest conditions, which should have prevailed during the Last Glacial Maximum interval. (ii) Bad preservation of the fossils in the sediment leading to the dissolution or the destruction of the shells. This generally occurs in paleosols. (iii) A high sedimentation rate, which would dilute the number of shells within a sample. The two last hypotheses cannot be supported stratigraphically. MZ 1 and MZ 2, which show differences in their mollusc content, occur within the same basal light loess deposit. This subunit shows a level with black dots at about 15 m depth containing a high number of individuals, and a high species diversity. This also corresponds to the first occurrence of the cold and moist species *Columella columella* and *Vertigo modesta*. An increase in moisture and a possible change in the vegetation cover could explain the occurrence of these hygrophilous taxa. This is a local event, as it is not reported in Eustis. As indicated previously, a water supply other than direct precipitation could be considered (i.e. the presence of local ponds). However, the sediment is loess without any freshwater or fluvial facies, which could support such a hypothesis. In Eustis, while this layer is not reported, at the same depth, the total of individuals (abundance) also increases. This moist event, documented in Buzzard’s
Roost, was also recorded eastward showing at least its regional significance.

At 14 m depth, a light gley is reported in the Buzzard’s Roost sequence, less marked than those in the upper sequence. However, a maximum abundance in mollusc diversity is observed, which contrasts with the general trend of this part of the sequence. Species like Discus shimekii, D. whitneyi and Euconulus fulvus, requiring some arboreal vegetation, occur and remain present up the sequence. The species characteristic of drier conditions, Vallonia gracilicosta, decreases, as does Pupilla muscorum, which nearly disappears. The gley, which is interpreted as a tundra soil, indicates increasing moisture, and is well characterized by the mollusc fauna. The next gley lying between 10.8 m and 9.4 m deep is, as indicated previously, an important stratigraphical marker and is present in both Buzzard’s Roost and Eustis. This subunit corresponds to an important change in the vegetation cover and probably in the climatic regime. A first estimate of its age was made by Rousseau & Kukla (1994), who proposed a date of about 16000 yr BP, in agreement with reconstruction of the Laurentide Ice Sheet deglaciation (Hughes 1987). The $^{13}$C AMS dates from loess sediment in Buzzard’s Roost indicate 17610 ± 80 yr BP (21-460–20440 cal. yr BP Beta-169530). At the Last Glacial Maximum (LGM), the Laurentide Ice Sheet expanded southward in South Dakota, some hundreds of kilometers from the studied localities. However, at about 16000 yr BP, the Des Moines (DML) and James (JL) lobes moved southward close to both sites (Fig. 1). The maximum advance of the Wisconsinan Laurentide Ice Sheet would have implied climatic conditions in Nebraska leading to deposition of the MZ 1 and 2 loess (Rousseau 2001). The climatic conditions improved following the general retreat of the ice sheet, but remained cold enough to prevent the development of a large mollusc community. This interval might also have experienced a high degree of seasonality, which could have permitted ecological competition between the two main mollusc species: Pupilla muscorum and Vallonia gracilicosta. During this interval, another climatic regime favoring the occurrence of another mollusc assemblage would have prevailed (Rousseau 2001). The main gley episode, associated with the advance of the two Laurentide lobes, corresponds to an important change in the environmental conditions. Relatively more moisture was available, which modified the type of vegetation cover and then allowed another mollusc community to evolve. Again by reference to modern observations in northern Europe, the environmental conditions in MZ 3 can be classified as a cold semi-desert (tundra-like), although the $^{13}$C analyses from the shells in Eustis clearly indicate a change in the trend of this signal since the main gley (Labonne et al. 2002). The appearance of C4 plants, characteristic of arid and dry environments, at the end of the aridity trend in MZ 3, is indicated by the $^{13}$C measured on the shells in MZ 3. It is also measured on the organic matter preserved in the sediment in the Beecher Island loess sequence in Colorado (Muhs et al. 1999). However, the $^{13}$C from the molluscs in Eustis show that this trend was not linear (Labonne et al. 2002). Moister intervals, corresponding to a seasonality in the precipitation regime associated with the reduced ice sheet and new patterns of air-mass circulation are indicated (Kirby et al. 2002; Labonne et al. 2002; Wang et al. 2000).

**Conclusion**

Our preliminary study of the Buzzard’s Roost mollusc record indicates a continuous history of past climate changes in mid-continenental North America during the 20000–14000 yr BP interval. The mollusc assemblages

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**Table 1. Ecological characteristics of the mollusc species identified in Buzzard’s Roost (from Kerney & Cameron (1979) and Leonard (1952, 1959)).**

<table>
<thead>
<tr>
<th>Species</th>
<th>Living temperature</th>
<th>Environment</th>
<th>Ecology</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Columella columella</em></td>
<td>Very cold</td>
<td>Moist</td>
<td>Limited to very cold environments at high elevation</td>
</tr>
<tr>
<td><em>Deroceras laeve</em></td>
<td>Eurytherm</td>
<td>Moist</td>
<td>Broad variety of environments, like herbaceous chlorophyll vegetation</td>
</tr>
<tr>
<td><em>Discus whitneyi</em></td>
<td>Relatively cold</td>
<td>All environments from relatively dry to moist</td>
<td>Forests, around lakes, but also in open and dry environment, catholic species</td>
</tr>
<tr>
<td><em>D. shimekii</em></td>
<td>Colder than <em>D. whitneyi</em></td>
<td>All environments: relatively dry to moist</td>
<td>More often found at 2000–3000 m high in mountains</td>
</tr>
<tr>
<td><em>Euconulus fulvus</em></td>
<td>Eurytherm</td>
<td>All environments from relatively dry to moist</td>
<td>In all environments (woods, meadows, swamps)</td>
</tr>
<tr>
<td><em>Pupilla muscorum</em></td>
<td>Slightly cold</td>
<td>Dry</td>
<td>Dry and sunny calcareous and open environments (meadows, grasslands)</td>
</tr>
<tr>
<td><em>Succinea sp.</em></td>
<td>Eurytherm</td>
<td>Moist</td>
<td>Swamps, banks, diversely moist environments depending of the species</td>
</tr>
<tr>
<td><em>Vallonia gracilicosta</em></td>
<td>Cold</td>
<td>Dry</td>
<td>Dry and open environments (meadows and grasslands)</td>
</tr>
<tr>
<td><em>Vertigo modesta</em></td>
<td>Cold</td>
<td>Moist</td>
<td>Calcareous mountains, moist and shadowed environments</td>
</tr>
<tr>
<td><em>Vitrea aff. crystallina</em></td>
<td>Eurytherm</td>
<td>Moist</td>
<td>Catholic but prefers swamps or moist meadows</td>
</tr>
</tbody>
</table>
indicate a cooling trend similar to that observed in the nearby (50 km) Eustis sequence. Comparison of the mollusc assemblages from both sequences indicates that the observed variations are at least regional because of the similarity in the response of these organisms to the variation in the environmental conditions. The mollusc assemblages suggest changes in the seasonality of temperature and precipitation regimes, which affected the vegetation cover. This preliminary analysis supports a trend toward more continentality upward through the sequence although moister conditions are indicated than at Eustis.

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