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Holocene Environmental Signals from Mollusk Assemblages in Burgundy (France)

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The malacofaunas of Burgundy, France, reflect changes in climate and the activities of man during the Holocene. Statistical analyses based on the Shannon diversity index and correspondence analysis are used to describe the mollusk assemblages in a composite sequence based on three well-dated sites. The variation demonstrated by the mollusks suggests that a two-step warming took place between 10,000 and 9000 and 8000 and 6000 yr B.P. in relative agreement with the timing of the deglaciation in the tropical Atlantic Ocean proposed by Mix and Ruddiman (1985, *Quaternary Science Reviews* 4, 59–108). High humidity, partly associated with widespread inundations of the valleys between 10,000 and 8000 yr B.P., may be related to estimated variations in the rate of freshwater discharge to the Atlantic Ocean reported by Fairbanks (1989, *Nature* 342, 637–642). The increasing impact of human activities on the environment during the past 2000 yr is indicated by the low diversity of the mollusk assemblages, demonstrating the need for careful interpretation of the youngest Holocene sediments in this region.

INTRODUCTION

The complexity of malacological assemblages permits a precise reconstruction of the past Quaternary environments to be drawn, as most of the fossil taxa are still extant. Because of the specific ecological tolerances of many mollusk species, the assemblages indicate the type of vegetation and climate during the time the species lived. In the classical climatic interpretation for Europe, forest taxa indicate a temperate climate and open vegetation taxa a cooler regime (Lozek, 1964; Puisségur, 1976; Kerney, 1963; Meijer, 1984). Generally, the maximum cooling is evidenced by the occurrence of cold species that currently live in tundra or steppe environments. These climatic differences roughly correspond to the broad categories of arboreal pollen (AP) versus nonarboreal pollen (NAP).

Recently, a new analysis of terrestrial mollusks in loess sequences has shown that the assemblages can provide additional information pertaining to the time of eolian sedimentation (Rousseau, 1992). In this case, the interpretation is not based on the occurrence of characteristic species but on the statistical dispersion of the assemblages, as described by the Shannon diversity index. For example, when eolian sedimentation is high, mollusk communities show lower values of diversity. The low values may be the result of harsh climatic conditions which put stress on the snails. Calculated from modern mollusk assemblages covering western Europe (Rousseau, 1991), the diversity index H' ranges between values of 0 and 4. In Burgundy, for modern mollusk assemblages with dominant forest species which are the modern analogs of the interglacial faunas, H' shows high values of ca. 3.0 or higher (Rousseau, 1992). In the northern mountain environments of Sweden and Norway, the index value is very low, ca. 1.5 or less. This reflects the latitudinal gradient in the number of species going from south to north in western Europe (Kerney and Cameron, 1979). This difference in diversity indicates the general climatic impact corresponding to the latitudinal succession of the classical biomes.

Elevation can also affect species diversity. In the Abisko area of northern Sweden we calculated H' for recent assemblages sampled on the same slope but at different elevations (Nilson, 1968). The plot of the H' index shows a decrease with elevation. As the Abisko region is remote and apparently free from human impact (biosphere reserve of the Union for Conservation of Nature—IUCN), the variation in the diversity

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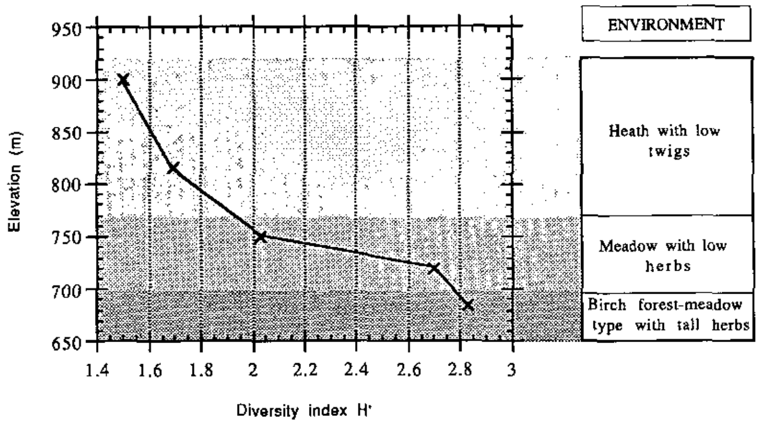

FIG. 1. Variations of the diversity index H' for terrestrial assemblages in Abisko area plotted against elevation. Vegetation according to the vegetation map of the Abisko National Park (von Sydow and Forshed, 1986).

index is due only to natural factors. Here, the effects of elevation, temperature, vegetation, and latitude on the mollusk assemblages must then be taken into account (Fig. 1).

Other samples of recent mollusk assemblages from Poland clearly show that if the substratum is also considered an influential factor, another factor affects the mollusks (Dyduch-Falniowska, 1988). Areas recently under cultivation and now abandoned to the natural vegetation were investigated in the Tatra Mountains. The diversity of the mollusk assemblages is low with values of H' ranging between 1.15 and 2.53. This strongly suggests that human impacts can be characterized by this index (Dyduch-Falniowska, 1988).

In addition, human activities also clearly contribute to the present distribution of the species (Kerney and Cameron, 1979). Establishing the degree to which this factor has affected Holocene geological sequences is important. As we demonstrate for the Burgundy region in France, the impacts of both climate and man on mollusk assemblages during the Holocene are evident. Burgundy, in central France (Fig. 2), is a region in which mollusk assemblages have been extensively investigated (Puisségur, 1976). During the last glacial age this area belonged to the periglacial belt that surrounded the Scandinavian ice sheet. With deglaciation, forests invaded former open-ground environment (Puisségur, 1976).

In the present study a relatively continuous composite faunal sequence is reconstructed from sections at three close localities. The mollusk faunas were analyzed statistically in order to propose a reliable climatic reconstruction of the Holocene and to characterize the indirect human impact on the snail communities.

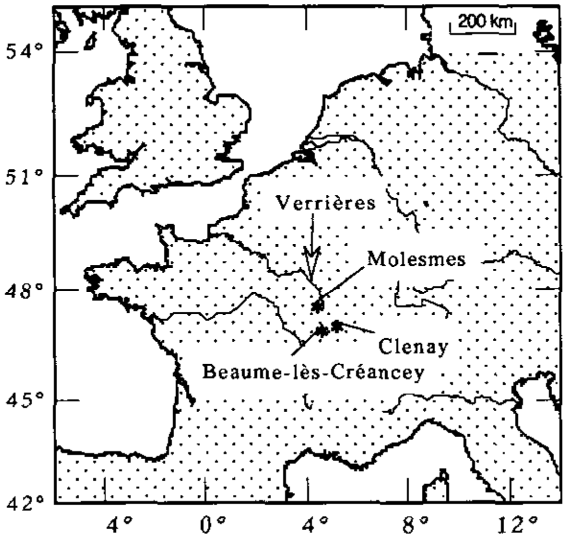

FIG. 2. Map showing location of the localities in Burgundy, France, cited in the text.

STRATIGRAPHY AND CHRONOLOGY OF THE SEQUENCES

Among the numerous sequences available, three especially well-dated ones have been selected to define more precisely the Holocene sequence in this area: Molesmes (Younger Dryas to Subatlantic), Clenay (Younger Dryas to Subatlantic), and Beaume-lès-Créancey (Boreal to Subatlantic) (Fig. 3). The lithologic successions at these localities are mainly peat, tufa, and clay in which humic horizons and shales intercalate. Each of the three series overlies coarse gravels of late-glacial age (Puisségur, 1976) that cover the bottom of the valleys. In order to define the composite sequence, the selection of horizons was based primarily on ^{14}C ages and on the quality of the molluscan records (the three selected sections provided rich and well-preserved assemblages). In some cases, the maximum thickness of the deposits was also taken into account. Using the dates related to archeological remains

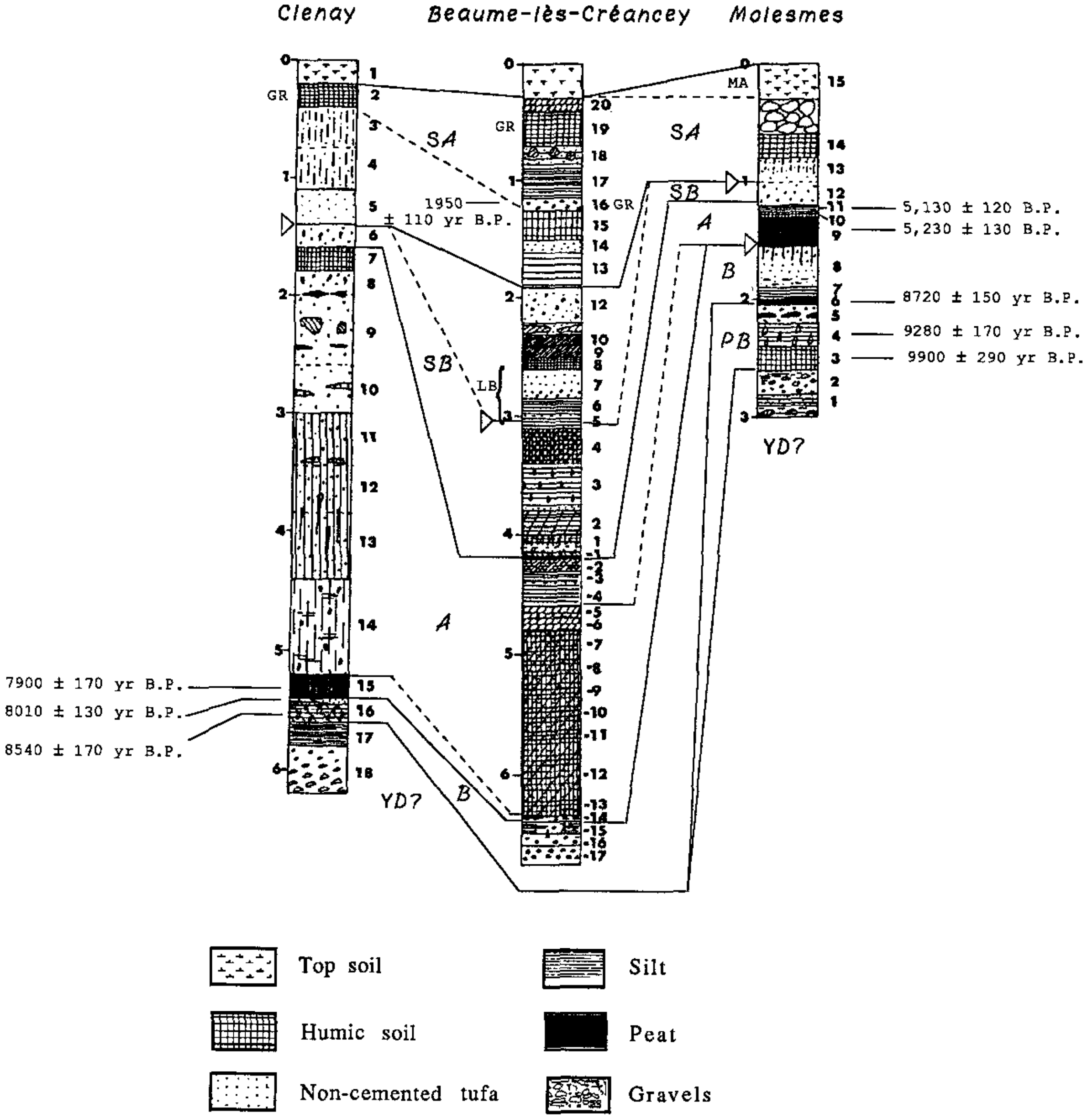

FIG. 3. Stratigraphic sections of the three sequences. Location of the different malacological samples and associated ^{14}C dates of organic matter (modified from Puisségur, 1976). Bio- and lithostratigraphic correlations used to determine the composite Holocene sequence for Burgundy, France.

in the sections, we were able to make a good stratigraphic correlation with the Holocene chronozones defined by Mangerud *et al.* (1974) (Fig. 4). The chronostratigraphic assignments of Puisségur (1976) have been revised according to this nomenclature.

The Younger Dryas chronozone is not clearly recognized in any of the sections. At Molesmes, a ^{14}C date of 9900 ± 290 yr B.P. places the MO3 horizon at the boundary between the Younger Dryas and the Preboreal. Moreover, horizons MO1 and MO2, previously assigned to the flooding at the end of the last glacial maximum (Puisségur, 1976), could also be interpreted as belonging to the Younger Dryas event, as the composition of the three mollusk assemblages shows a regular evolution (Figs. 3 and 4).

The Preboreal chronozone occurs only in the Molesmes section. A ^{14}C date from the base of horizon MO4 (9280 ± 170 yr B.P.) is of late Preboreal age (Figs. 3 and 4).

All three sections record the Boreal chronozone (Figs.

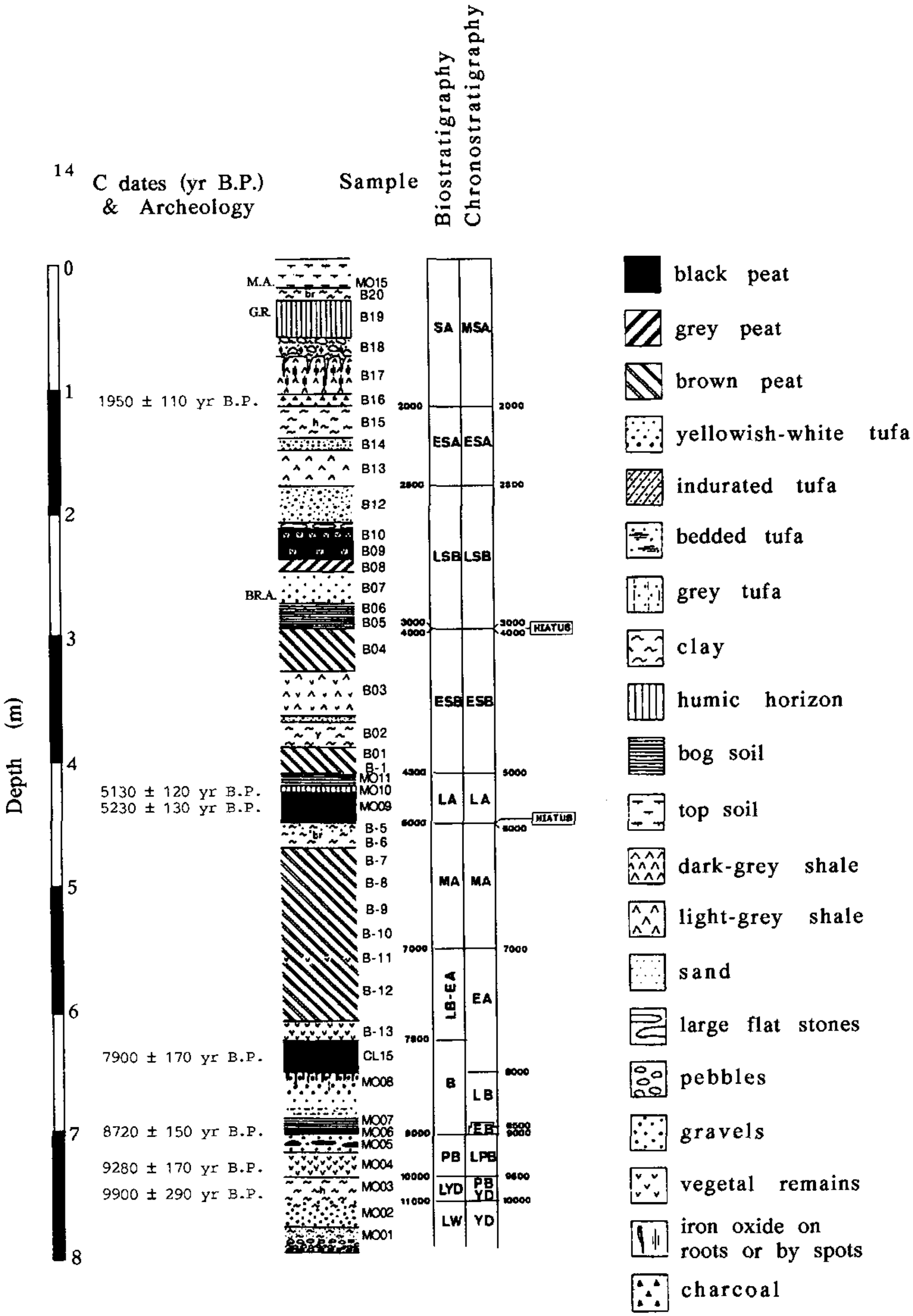

FIG. 4. Composite Holocene sequence in Burgundy, after Puisségur (1976), with the bio- and chronostratigraphic assignments according to Puisségur (1976) and Mangerud *et al.* (1974). M.A., Middle Age; G.R. Gallo-Roman; BR.A., Bronze Age; LW, Late Glacial; LYD, Late Younger Dryas; PB, Preboreal; LPB, Late Preboreal; EB, Early Boreal; B, Boreal; LB-EA, Late Boreal–Early Atlantic; MA, Middle Atlantic; LA, Late Atlantic; ESB, Early Subboreal; LSB, Late Subboreal; ESA, Early Subatlantic; SA, Subatlantic; MSA, Middle Subatlantic.

3 and 4); however, the undated Beaume sequence is not considered. In the Clenay section the CL16 horizon is dated 8540 ± 170 yr B.P. at its base and 8010 ± 130 yr B.P. at its top; thus, it spans the entire chronozone (Figs. 3 and 4). The Molesmes sequence, however, shows three horizons, with one ^{14}C date for the MO6 layer of 8720 ± 150 yr B.P. Accordingly, the MO6 horizon is assigned to the early Boreal, following the chronology of Mangerud *et al.* (1974). The following two horizons, MO7 and MO8, differ faunistically and lithologically from the former and are assigned to the late Boreal (Figs. 3 and 4).

The Clenay CL15 horizon corresponds to the early Atlantic according to a ^{14}C date of 7900 ± 170 yr B.P. (Figs. 3 and 4). The thicker horizons B − 13 to B − 5 of the Beaume section are taken into account here because, although they lack any radiocarbon age control, the horizons provide mollusk assemblages of mainly terrestrial species which are very sensitive to climate. On the contrary, the Clenay section provides five horizons yielding mollusk assemblages of numerous fresh-water taxa, which poorly characterize the climatic variations. This is also true for the late Atlantic horizons in Clenay (Figs. 3 and 4). Moreover, Puisségur (1976) indicates that samples CL8 and CL9 in Clenay come from older reworked sediments. In the Beaume section, the late Atlantic horizons are thinner than in Molesmes. The Molesmes samples, which provide ^{14}C ages of 5230 ± 130 yr B.P. for MO9 and 5130 ± 120 yr B.P. for MO10 (Figs. 3 and 4), are used here.

For the beginning of the Subboreal chronozone we have used the Beaume section which provides five samples compared to only one for each the Molesmes and Clenay sequences (Figs. 3 and 4). The middle Subboreal is not recorded in any of the sections. The late Subboreal is only recorded in the Beaume section (horizons B + 5 to B + 12; figs. 3 and 4). Based on late Bronze Age remains of human settlements, these deposits have an estimated age between 3000 and 2700 yr B.P. (Figs. 3 and 4).

The analysis of Puisségur (1976) indicated a high occurrence of aquatic mollusks during the early Subatlantic due to inundations. While the horizons are also numerous in the Clenay section (Figs. 3 and 4), we have selected those of the Beaume sequence, as it has the highest percentage of terrestrial species.

Finally, the middle Subatlantic is mainly developed in the Beaume section, which has a ^{14}C date for horizon B + 16 of 1950 ± 110 yr B.P. and the remains of a Gallo-Roman settlement (second to third century A.D.). Horizon MO15 of the Molesmes section, which yields the most recent archaeological remains (Middle Age), is used for the end of the composite sequence (Figs. 3 and 4).

The composite section based on the three Holocene sections from valley bottoms in Burgundy provides a chronology of an 8-m-thick sequence spanning the interval 10,000 to 1000 yr B.P., with two main hiatuses, one during the late Atlantic and the other in the middle Subboreal (Fig. 4).

METHODS

All samples that contained the mollusk assemblages were collected in the same way. They correspond to samples of sediment (about 10 kg) that were washed and sieved to extract the shells. Then the different taxa were identified and counted, applying the method of Lozek (1964) for broken shells.

Diversity Index

The structure of the molluscan communities can be described in terms of diversity. We use the Shannon index H' (Magurran, 1988) calculated as

$$H' = -\sum_{1}^{n} p_k \log_2 p_k,$$

where n equals the number of species and p_k the frequency of the k species (k varying between 1 and n).

Correspondence Analysis

Correspondence analysis (Benzecri and Benzecri, 1980; Greenacre, 1984), used to characterize the climatic impact on snails, has been previously applied to mollusk assemblages (Rousseau, 1987) and was described by Rousseau and Puisségur (1990) and Rousseau (1991). The data are initially coded using abundance classes based on a logarithmic scale (Rousseau, 1987). This analysis permits study of both the species and the assemblages using the same statistical technique. The results for both these elements are plotted in a single diagram that takes into account the present ecology of the species, thereby making the interpretation easier. Generally, the first two factors are interpreted as gradients corresponding to "temperature" (ranging from temperate to cold) and humidity (ranging from dry to moist) according to the modern ecology of the mollusk species. Plotting the corresponding loadings of the assemblages in stratigraphic position makes it possible to propose a climatic scenario based on the mollusks.

RESULTS

Diversity Index H′

Values of H' vary between 0.6 and 4.1 (Fig. 5). From the base of the sequence to the top, the variation of H'

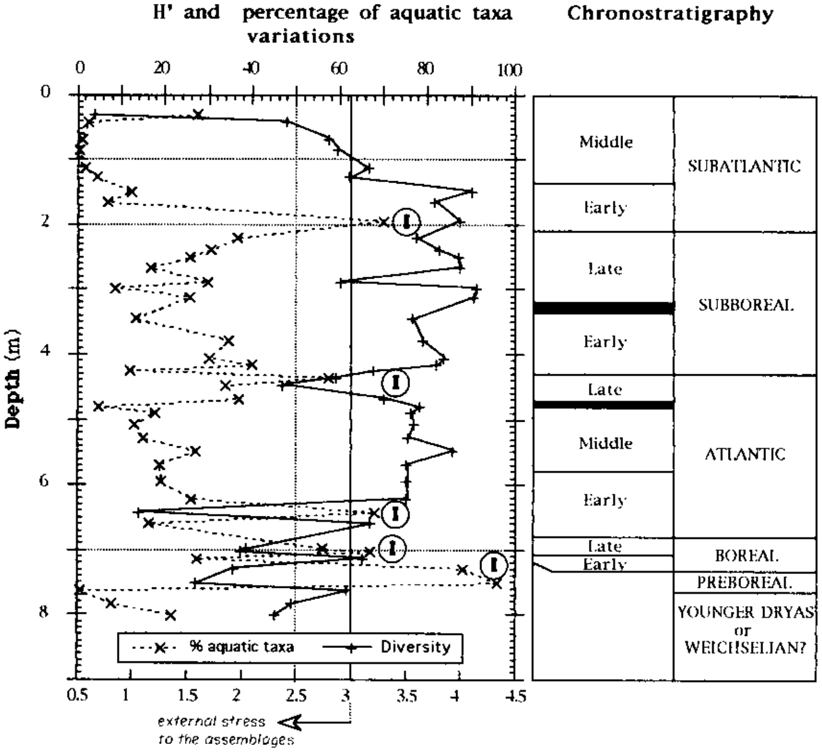

FIG. 5. Variations of the diversity index *H'* for terrestrial assemblages and percentage of aquatic taxa versus terrestrial ones plotted against depth. High percentages of freshwater species indicate inundations of the valleys (I).

can be described in five parts indicating a particular trend.

(a) Between 8 and 6.2 m (Younger Dryas–early Atlantic), *H'* shows large variations in the values (Fig. 5) and no trend is evident. Three minimum values, lower than 2, are interspersed between peaks higher than 3. The lowest values are a sign that some type of stress affected the communities.

(b) Between 6.2 and 4.5 m (Atlantic) the values are all around 3.5, except for a peak around 4 (Fig. 5). The mollusk communities are well developed during this interval. The high value of *H'* indicates a temperate environment (although a stratigraphic hiatus may be present) compared to the modern values (Rousseau, 1992).

(c) Low *H'* values are found between 4.5 and 2.9 m (Subboreal), followed by a trend toward high values and a slight decrease at the end (Fig. 5). A stratigraphic hiatus, as previously described, is present.

(d) Between 2.9 and 1.3 m (late subboreal–early Subatlantic), the variation is not regular although the values remain high between 2.9 and 4 (Fig. 5); however, the low value at the base (2.9 m) should be noted.

(e) Between 1.3 m and the top (Subatlantic), the values of *H'* decrease quite regularly to the lowest one (0.6) of the sequence (Fig. 5).

Taking *H'* = 3 as a threshold, based on the values calculated for modern mollusk assemblages in Burgundy forests, we conclude that the sequence recorded several important stresses in the mollusk communities (Fig. 5). These occurred mainly at the bottom of the sequence, at the end of the Atlantic and at the end of the Subatlantic chronozones (Fig. 5). These episodes could correspond to times of changes in habitat resulting from vegetation changes. However, in the diversity analysis, the freshwater species, which correspond to another type of assemblage, were not taken into account.

Plotting the percentage of aquatic taxa (*A%*) against terrestrial diversity allows us to propose one interpretation concerning the stress indicated by some communities (Fig. 5). Indeed, it can be assumed that inundations of the valley, i.e., the occurrence of marsh or stream, are likely to have had an impact on the terrestrial assemblages that lived there. Such an interpretation is suggested for the lower part of the sequence between its base and 6.4 m (Fig. 5). During this period, the lowest values of *H'* are found with high percentages of the aquatic taxa (*A%*), indicating that species diversity and floodings are inversely correlated. However, between 6.4 m and the top, the lowest values of *H'* do not correspond to higher percentages of aquatic species (Fig. 5). In the uppermost part of the sequence the percentage of aquatic species remains close to zero (Fig. 5) resulting in no correspondence between the percentage of aquatic taxa and the diversity index. Another factor apparently stressed the mollusk assemblages from 1.2 m to the top, which is not related to inundation (Fig. 5).

From these results, we can conclude that inundations may have affected the malacofaunas at the base of the sequence (Younger Dryas to early Atlantic chronozones) to a greater extent than in the remainder. However, the magnitude of *H'* and the percentage of aquatic taxa do not match, indicating that the mollusk communities were already destabilized by other environmental factors. The occurrence of archeological remains in the top levels of the sequence lead us to interpret the decreasing values of *H'* as a response to human impact on the malacofaunas.

Correspondence Analysis

A data set based on terrestrial species was analyzed using correspondence analysis. The data matrix was composed of 55 species and 42 samples, each corresponding to one stratigraphic horizon. The total number of individuals is 46,261.

The first two factors together, 20.15 and 19.66%, respectively, explain 39.71% of the total variability. The theoretical contribution of each species to the total variability is 1/55 = 0.018. All of the species that show values higher than 0.018 are considered in the interpretation of variability. For the mollusk samples the theoretical value is 0.024.

The first axis discriminates *Vallonia pulchella, Abida secale, Cecilioides acicula, Pupilla muscorum, Helicella sp., Helix pomatia, Cochlostoma septemspirale, Trichia hispida, Vallonia costata,* and *Vertigo pygmaea* on the negative side (Fig. 6; Table 1). These species characterize open-ground environments, primarily grassland with mostly dry conditions. The positive side of the axis groups together *Euconulus fulvus, Zonitoides nitidus, Carychium tridentatum, Vallonia enniensis, Vertigo substriata, Clausilia bidentata, Vitrea crystallina,* and *Columella edentula*. These species indicate the occurrence of various types of arboreal vegetation, from bushes in meadows to open forest (Fig. 6; Table 1).

The second axis gathers *Vertigo genesii, Vertigo antivertigo, Vertigo angustior, Vertigo pygmaea, Vallonia pulchella, Succinea putris,* and *Carychium minimum* on the positive side and together indicate the occurrence of a relatively moist, open environment (Fig. 6; Table 1). The other group on the negative side includes *Vertigo alpestris, Columella edentula, Vitrea crystallina, Discus rotundatus, Pomatias elegans, Aegopinella pura, Aegopinella nitidula, Azeca goodalli, Discus rotundatus,* and *Oxychilus sp*. These species indicate less humidity in an arboreal environment (Fig. 6; Table 1).

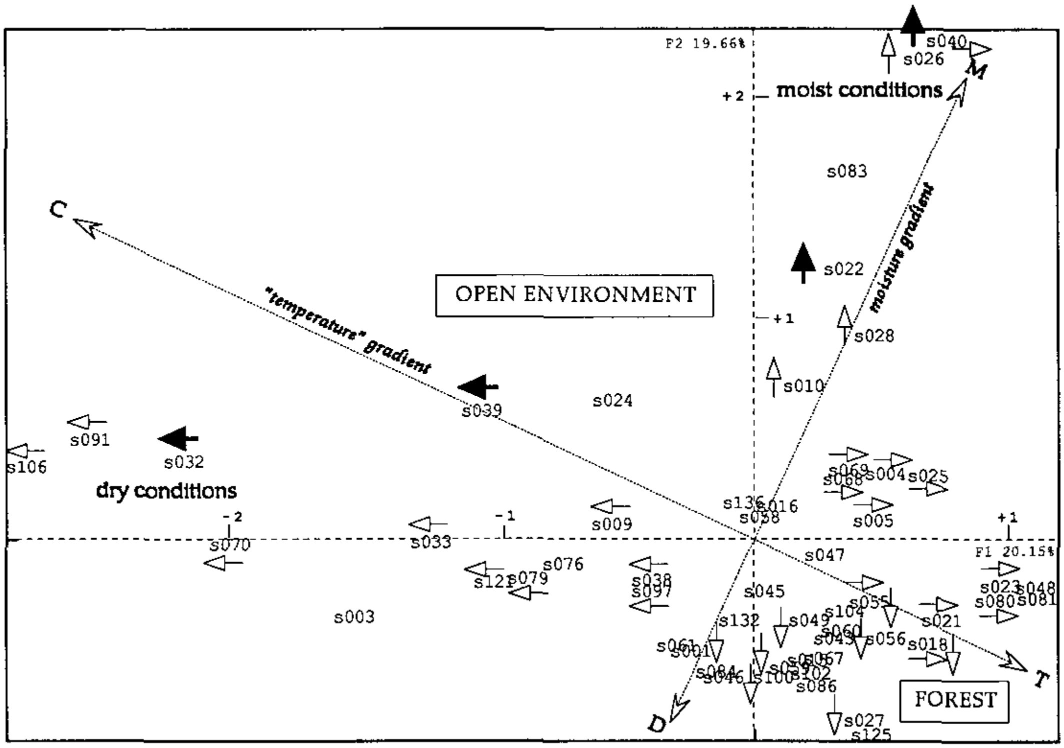

FIG. 6. Correspondence analysis of Holocene malacofaunas in Burgundy. Plot of the species on the first factor plane (axes 1–2). The arrows indicate how the species explain the variability of the general data set. Black arrows indicate highest contributions while white ones show high ones. Determination of temperature and moisture gradients by 25° rotation.

TABLE 1
Correspondence Analysis of the Holocene Malacological Samples in Burgundy

Code species	Species	Factor 1	Factor 2
s001	*Pomatias elegans*	−0.072	−0.224
s003	*Acicula dupuyi*	−0.026	
s004	*Carychium minimum*	0.358	0.157
s005	*Carychium tridentatum*	0.26	
s009	*Succinea oblonga*	−0.218	
s010	*Succinea putris*	0.019	0.706
s015	*Azeca goodalli*		−0.197
s016	*Cochlicopa lubrica*		0.032
s018	*Columella edentula*	0.187	−0.147
s021	*Vertigo pusilla*	0.178	0.073
s022	*Vertigo antivertigo*	0.074	1.612
s023	*Vertigo substriata*	0.123	
s024	*Vertigo pygmaea*	−0.261	0.273
s025	*Vertigo moulinsiana*	0.235	0.05
s026	*Vertigo genesii*	0.046	0.707
s027	*Vertigo alpestris*		−0.101
s028	*Vertigo angustior*	0.086	0.514
s032	*Abida secale*	−1.035	0.023
s033	*Pupilla muscorum*	−0.614	
s038	*Vallonia costata*	−0.377	−0.086
s039	*Vallonia pulchella*	−1.808	0.477
s040	*Vallonia enniensis*	0.124	1.521
s043	*Acanthinula aculeata*	0.05	−0.238
s046	*Ena obscura*		−0.077
s047	*Punctum pygmaeum*	0.055	
s049	*Discus rotundatus*	0.034	−0.333
s055	*Vitrea crystallina*	0.218	−0.177
s056	*Vitrea contracta*	0.074	−0.099
s059	*Aegopinella pura*		−0.243
s060	*Aegopinella nitidula*	0.081	−0.277
s061	*Aegopinella minor*	−0.095	−0.191
s067	*Oxychilus sp.*	0.029	−0.311
s068	*Zonitoides nitidus*	0.105	0.106
s069	*Euconulus fulvus*	0.132	0.129
s070	*Ceciloides acicula*	−0.925	
s079	*Clausilia parvula*	−0.358	
s080	*Clausilia bidentata*	0.23	−0.033
s083	*Clausilia sp.*		0.118
s084	forest *Clausilia*	−0.019	−0.172
s086	*Bradybaenum fruticum*		−0.085
s091	*Helicella sp.*	−0.418	
s097	*Trichia hispida*	−0.412	−0.142
s100	*Helicodonta obvoluta*		−0.041
s102	*Helicigona lapicida*		−0.073
s104	*Cepaea sp.*	0.047	−0.092
s106	*Helix pomatia*	−0.25	
s121	*Cochlostoma septemspirale*	−0.257	
s132	*Phenacolimax major*		−0.022
s136	*Limax sp.*	−0.023	0.027
Percentage of variance		20.15	19.66

Note. Significant contributions (higher than the theoretical threshold = 1/55) of species to the explanation of the variability of the data set according to the first two factors. Positive or negative signs indicate the location on the axes.

The first factor plane (axes 1–2) shows a typical "Guttman effect" (Benzecri and Benzecri, 1980) for the distribution of the species. This means that a particular relation exists between the first two axes. Indeed, the distribution of the species suggests a change from dry grassland to a moderately humid forest environment and then to a moist grassland (Fig. 6; Table 1). In France, temperate conditions were represented during the Quaternary by forest environments. The forest part of the distribution can also be interpreted as representing temperate climatic conditions, as opposed to cold-dry or humid ones (Puisségur, 1976).

The distribution of the mollusk assemblages in this diagram is similar to that of the species distribution, so a similar interpretation can be proposed (Fig. 7; Table 2). There is a gradient between dry and cold assemblages to moderately humid forest assemblages. There is no progression to assemblages representative of cold, moist conditions. Taking into account the stratigraphic assignment of the assemblages, Younger Dryas or late-glacial communities indicate dry, cold conditions (MO1-2). For Preboreal communities, cold, humid (MO4–5) conditions predominate, except for MO3 at the YD-PB boundary, which characterizes a dry environment. This result suggests that the terrestrial malacofaunas also recorded the inundation (determined by the high percentages of aquatic taxa) which occurred during the Preboreal in Burgundy. Assemblages of the Boreal chronozone are concentrated in the cold and humid quadrant (Fig. 7; Table 2). Again the assemblages recorded the inundations indicated by high values of the fresh-water individuals (Fig. 4). Except for the first assemblage which is cold and humid, all the assemblages of early and middle Atlantic age are plotted in the moderately humid temperate zone (Fig. 7; Table 2). The late Atlantic malacofaunas indicate cold, humid conditions. The Subboreal assemblages are distributed along the mid-humid forest gradient. The Subatlantic chronozone communities are also plotted on the same gradient but with a trend toward open, dry environments. For these assemblages, the "thermal" interpretation is questionable because of the magnitude observed for this interval, which should be equivalent to that of the Younger Dryas. We interpret these variations as the result of the intensification of human activities and the impact of post-Neolithic deforestation. In this case, human impact on the environment has had the same result as climatic change.

INTERPRETATION

Multivariate analysis of the mollusk communities indicates variations between temperate, cold, dry, and moist conditions. This distribution is classical in mollusk investigations which interpret the mollusk time

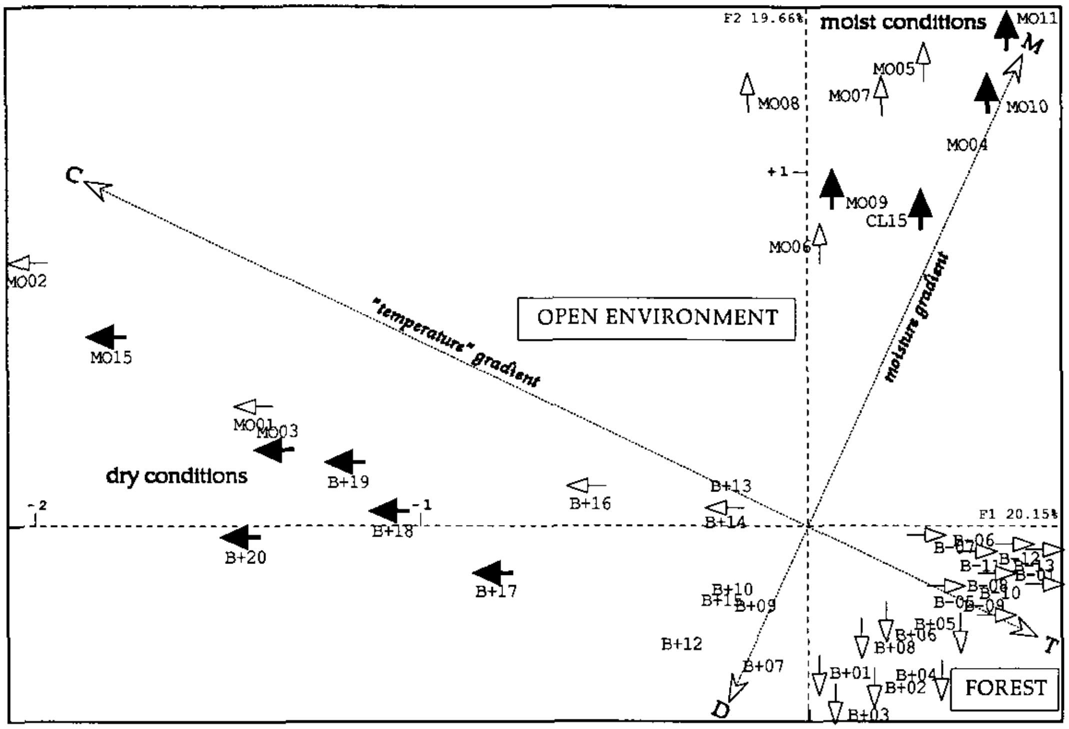

FIG. 7. Correspondence analysis of Holocene malacofaunas in Burgundy. Plot of the mollusk assemblages on the first factor plane (axes 1–2). Determination of temperature and moisture gradients by a 25° rotation of the factors. Same legend as Figure 5.

series in terms of "temperature" and moisture. However, because of the absence of typical pleniglacial assemblages, the lower extremes for the "temperature" gradient are not located on the negative side of the first axis. Such distribution has been observed in the analysis of the mollusk sequence of Verrières (France), another Holocene deposit (Limondin and Rousseau, 1991). Because of the fan shape of the distribution, and using the forest-temperate taxa and assemblages as a reference, a climatic gradient, corresponding to an arbitrary 25° rotation of the first axis, can be drawn from temperate forest conditions (quadrant 1+2−) to cool and then cold, open-ground environments. Perpendicular to this gradient is one linking dry, moderately humid to moist environments. Plots of the loadings of each assemblage on these gradients permit us to propose a climatic history for this time span, as recorded by the malacofaunas.

Taking into account the stratigraphic allocation of each mollusk assemblage, the climatic interpretation of this composite sequence is shown in Figure 8.

The Younger Dryas associations indicate a cold, dry environment. This is in agreement with the generally inferred conditions for this time span as described in other kinds of records of terrestrial mollusks (Limondin and Rousseau, 1991), insects (Coope, 1987), and pollen (Peteet *et al.*, 1990) (Fig. 8).

The Preboreal chronozone was cool, but with moister conditions (Fig. 8), in agreement with the inundation indicated by the aquatic taxa.

The Boreal chronozone shows a cold humid peak preceded and followed by cool events, the first one dry and the second one moist (Fig. 8).

The Atlantic chronozone shows a long interval of warm conditions, with no indication of very moist conditions (Fig. 8). This corresponds to the warm interval interpreted as the climatic optimum of the Holocene. The end of this chronozone is marked by a moist cooling, corresponding to another inundation.

The climatic trend of the Subboreal chronozone seems to be similar to the Atlantic one (Fig. 8). First a warm, dry interval occurs, followed by cool but continued-dry conditions.

Based on multivariate analysis, the Subatlantic chronozone could be interpreted as showing a cooling trend with colder and drier conditions similar to those of the Younger Dryas chronozone (Fig. 8). However, these results are contradicted by the diversity index which shows that the mollusk assemblages were seriously stressed with increasing intensity during this period. In fact, the occurrence of archeological artifacts in this part of the sequence suggests that there was increasing human impact on the environment and consequently on the mollusk assemblages. Temperature and inundations are important during the late-glacial transition, while the impact of man, involving an increase in settlements and defor-

TABLE 2

Correspondence Analysis of the Holocene Malacological Samples in Burgundy

Code	CTR F1	CTR F2	Thickness	F1	F2	rF1	rF2
M015	−0.787	0.056	0.31	−1.775	0.467	−1.806	−0.327
B+20	−0.859		0.42	−1.448	−0.100	−1.270	−0.703
B+19	−0.779		0.69	−1.190	0.108	−1.124	−0.405
B+18	−0.720		0.85	−1.078	−0.027	−0.966	−0.480
B+17	−1.004	−0.060	1.14	−0.824	−0.199	−0.663	−0.529
B+16	−0.329		1.28	−0.592	0.048	−0.557	−0.207
B+15	−0.094	−0.071	1.50	−0.264	−0.227	−0.143	−0.317
B+14	−0.102		1.66	−0.258	−0.004	−0.232	−0.113
B+13	−0.033		1.94	−0.243	0.100	−0.262	−0.012
B+12	−0.077	−0.074	2.22	−0.363	−0.352	−0.180	−0.472
B+10	−0.070	−0.050	2.40	−0.236	−0.198	−0.130	−0.279
B+9	−0.037	−0.060	2.52	−0.186	−0.236	−0.069	−0.292
B+8	0.028	−0.139	2.67	0.163	−0.361	0.300	−0.258
B+7		−0.073	2.89	−0.163	−0.411	0.026	−0.441
B+6	0.043	−0.099	2.98	0.216	−0.322	0.332	−0.201
B+5	0.086	−0.107	3.12	0.264	−0.291	0.362	−0.152
B+4	0.086	−0.357	3.46	0.218	−0.438	0.383	−0.305
B+3		−0.424	3.79	0.096	−0.554	0.321	−0.462
B+2	0.047	−0.301	4.06	0.189	−0.475	0.372	−0.351
B+1		−0.312	4.17	0.054	−0.434	0.232	−0.371
B−1	0.331	−0.026	4.26	0.515	−0.144	0.528	0.087
MO11	0.249	1.913	4.36	0.523	1.432	−0.131	1.519
MO10	0.255	1.470	4.48	0.497	1.180	−0.048	1.279
MO9		−0.991	4.69	0.098	0.905	−0.294	0.862
B−5	0.120	−0.068	4.81	0.313	−0.232	0.382	−0.078
B−6	0.079		4.89	0.362	−0.074	0.359	0.086
B−7	0.113		5.09	0.312	−0.076	0.315	0.063
B−8	0.196	−0.046	5.29	0.398	−0.190	0.441	−0.004
B−9	0.139	−0.054	5.49	0.388	−0.239	0.453	−0.053
B−10	0.183	−0.040	5.69	0.428	−0.198	0.472	0.001
B−11	0.145		5.96	0.377	−1.280	0.396	0.043
B−12	0.281		6.22	0.474	−0.114	0.478	0.097
B−13	0.350	−0.022	6.43	0.513	−0.128	0.519	0.101
CL15	0.026	0.925	6.60	0.145	0.853	−0.229	0.834
MO8		0.481	6.99	−0.119	1.193	−0.612	1.031
MO7		0.632	7.04	0.057	1.212	−0.461	1.123
MO6		0.497	7.14	−0.091	0.783	−0.107	0.013
MO5		0.426	7.30	1.660	1.290	−0.395	1.239
MO4		0.035	7.52	0.348	1.073	−0.138	1.120
MO3	−1.348	0.051	7.64	−1.368	0.262	−1.351	−0.341
MO2	−0.475	0.058	7.84	−1.990	0.686	−2.093	−0.219
MO1	−0.466		8.01	−1.423	0.272	−1.405	−0.355

Note. Significant contributions (higher than the theoretical threshold = 1/42) of assemblages to the explanation of the variability of the data set according to the first two factors. Positive or negative signs indicate the location on the axes. Coordinates of the assemblages on the first two factors, and on the two climatic gradients after a rotation of 25°.

estation, is of increasing importance in the upper part of the sequence (i.e., the Subatlantic).

As reported for the Verrières Holocene sequence (Limondin and Rousseau, 1991) or for the long-term sequence of the Achenheim loess (Rousseau and Puisségur, 1990), variations through time of the "temperature" and moisture gradients are not parallel. For example, the Younger Dryas appears to have been a cold, dry interval, whereas the Boreal cold event is interpreted as moist.

DISCUSSION AND CONCLUSION

The mollusk sequence at Verrières, north of the Burgundy region, show variations during the Holocene that are attributed to climatic change (Fig. 2). All the chronozones occur and are well-preserved (Limondin and Rousseau, 1991). The Preboreal, however, is represented by only one level, and a stratigraphic hiatus during the Atlantic chronozone has been recognized. The climatic variation determined from the mollusk analysis and

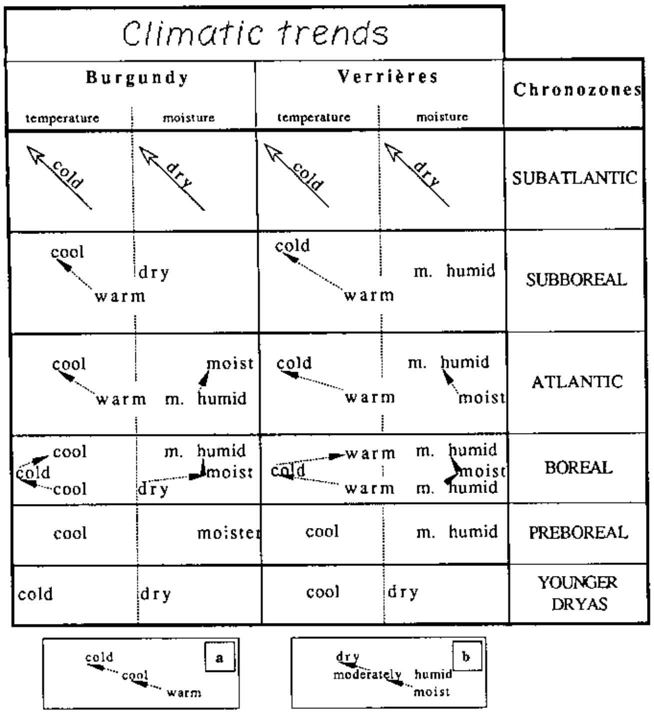

FIG. 8. Comparison of the results from the multivariate analyses of snail assemblages in Burgundy (present study) and the Paris Basin (after Limondin and Rousseau, 1991). General trends for temperature and moisture (respectively, on the left and on the right of each box) are indicated for each chronozone in both the Verrières and Burgundy composite series.

other nearby pollen sequences has been shown to be in good agreement (Limondin and Rousseau, 1991). The good correspondence between the Verrières sequence and the composite one from Burgundy (Fig. 9) lends support for the climatic sequence that we have defined, but comparisons with other mollusk sequence can be proposed.

In late Devensian and Flandrian deposits in Kent, Kerney *et al.* (1980) determined six Holocene mollusk zones (A to F). They do not correspond strictly with the European Holocene chronostratigraphy, but radiocarbon dates permit stratigraphic correlations. Mollusks zones A to C, which correspond to Preboreal and Boreal, provide more details than in Burgundy. However, the climatic trends are similar. The Preboreal chronozone begins with dry, open environment but ends with the appearance of woodland species. The Boreal chronozone is marked by swamp conditions, but with the occurrence of some cold species like *C. columella* or *V. genesii*. The Atlantic chronozone is indicated by woodland species. This is the forest optimum which is followed by an open-ground environment during the Subboreal and Subatlantic chronozones.

In Poland, Alexandrowicz (1984) presents the mollusk succession of the Malopolska Upland. In the lower Holocene deposits, few forest snails occur, but large valley floors were occupied by swamps and marshes. The middle part of the climatic optimum is characterized by forest snails. In small valleys and gorges, similar to those studied in Burgundy, human impact is first recognized indirectly, but since the Subatlantic it is distinct through the snail assemblages.

Finally, in Czechoslovakia, the mollusk zones of Lozek (1982) indicate increasing temperature and moisture during the Preboreal and Boreal chronozones. The Atlantic optimum is clearly marked by closed forest.

These different results from both French and northwest or central European localities are in good agreement with our results from Burgundy. Some differences occur, however, which are mainly characteristic of local conditions.

Some other indications can be obtained from pollen analyses. In his study of the compositional changes of the European postglacial forests, Huntley (1990) points to a sharp disruption of the tundra or shrub pattern which prevailed during late-glacial time over an area north of the Alps to a woodland steppe about 10,000 yr B.P. He also mentions forest vegetation over the European mainland about 8000 yr B.P. Finally, in a compilation of the variation of treeline, Richard (1988) infers several oscillations during the Holocene: a rise during the Preboreal and lowering during the Boreal. At the end of the Boreal and during most of the Atlantic a more important extension of the forest occurred to >2400 m altitude. At the Atlantic/Subboreal transition, the treeline again lowered. Finally, the beetle record from Great Britain (Atkinson *et al.*, 1987) shows an important warming just after the Younger Dryas chronozone that is also shown by the mollusks in Burgundy. Despite the temperature trends, which are similar, the increase in moisture before the Atlantic chronozone also seems generally to be consistent, although de Beaulieu *et al.* (1988) indicate particularly dry conditions in the French Massif Central between 9000 and 8000 yr B.P.

In order to compare these results with other terrestrial and marine records, we linearly interpolated ages between available ^{14}C dates, also taking into account the occurrence of archeological artifacts and main sedimentological hiatuses recognized in the sequence (Fig. 10).

Using this chronology, the climate in Burgundy was cold and dry before 10,000 yr B.P., in agreement with the classical interpretation of the Younger Dryas. After this event, the general climatic trend was toward temperate conditions which were established after 8000 yr B.P. (Fig. 11). This change is not continuous but shows two steps, interrupted by a cool event between 8500 and 8000 yr B.P. (Fig. 11). The interval between 10,000 and 8000 yr B.P. also shows two main moist events associated with large inundations (Fig. 11). The classical Holocene optimum (8000–5000 yr B.P.) was warm and moderately humid. About 5000 yr B.P. a cool event occurred followed by a temperate and moist one in conjunction with another inundation of the valleys (Fig. 11). The climate then became warm and dry (Fig. 11). Because of the stratigraphic hiatus, no information is available for the middle Subboreal. However, the end of that chronozone was warm and was followed by cool, dry conditions. Until ca. 2100 yr B.P., the climate remained cool but the moisture alternated from dry to moderately humid and then back to dry again (Fig. 11). The remainder of the sequence cannot be interpreted simply in terms of climate, as anthropogenic impacts are evident (Fig. 10).

Changes in the isotopic values of marine foraminifera are likely to reflect changes in the volume of land-based ice. The transition between the last glacial maximum and the Holocene recorded an important melting of the northern ice sheets which implies drastic climatic changes during a relatively short interval. The analyses of foraminifera from the Bay of Biscay and a correlative study of pollen provided the basis for Duplessy *et al.* (1981) to define a two-step deglaciation (Terminations Ia and Ib) model. This model, in agreement with Fairbank's (1989) results on sea-level fluctuation from an analysis of the isotopic composition of the Barbados corals, was improved by Mix and Ruddiman (1985). Oxygen isotopes of foraminifera in tropical Atlantic cores indicated that the isotopic transition after the late-glacial maximum occurred between 14,000 and 6000 yr B.P. They characterized three steps in the last deglaciation which they placed at 14,000–12,000, 10,000–9000, and 8000–6000 yr B.P., respectively, and named Terminations 1a, 1b, and 1c. The last step, which was tentatively identified, seems to correspond to the final outflow of the Laurentide ice sheet in Hudson Bay and in Hudson Strait (Paterson and Hammer, 1987).

Considering these records of $\delta^{18}O$ changes measured in Atlantic Ocean sediments, the results of the mollusk assemblages in Burgundy indicate a two-step warming trend following the cold Younger Dryas event (Fig. 11). In our chronology, the two steps are separated by a pause corresponding to a small cooling ca. 8300 yrs B.P. (Fig. 11). From this comparison, and except that Termination 1a occurred earlier than in the sequence of Burgundy, good agreement is seen between the marine isotope and continental "temperature" gradient. This interpretation is also in agreement with the synchrony of last deglaciation events in land and marine records demonstrated by Rind *et al.* (1986) and Broecker and Denton (1989).

Our results are also compared with the proposed rate of glacial meltwater discharge to the Atlantic Ocean during the last deglaciation. The sea-level record provided by corals in Barbados (Fairbanks, 1989) clearly indicates two major peaks, occurring before and after the Younger

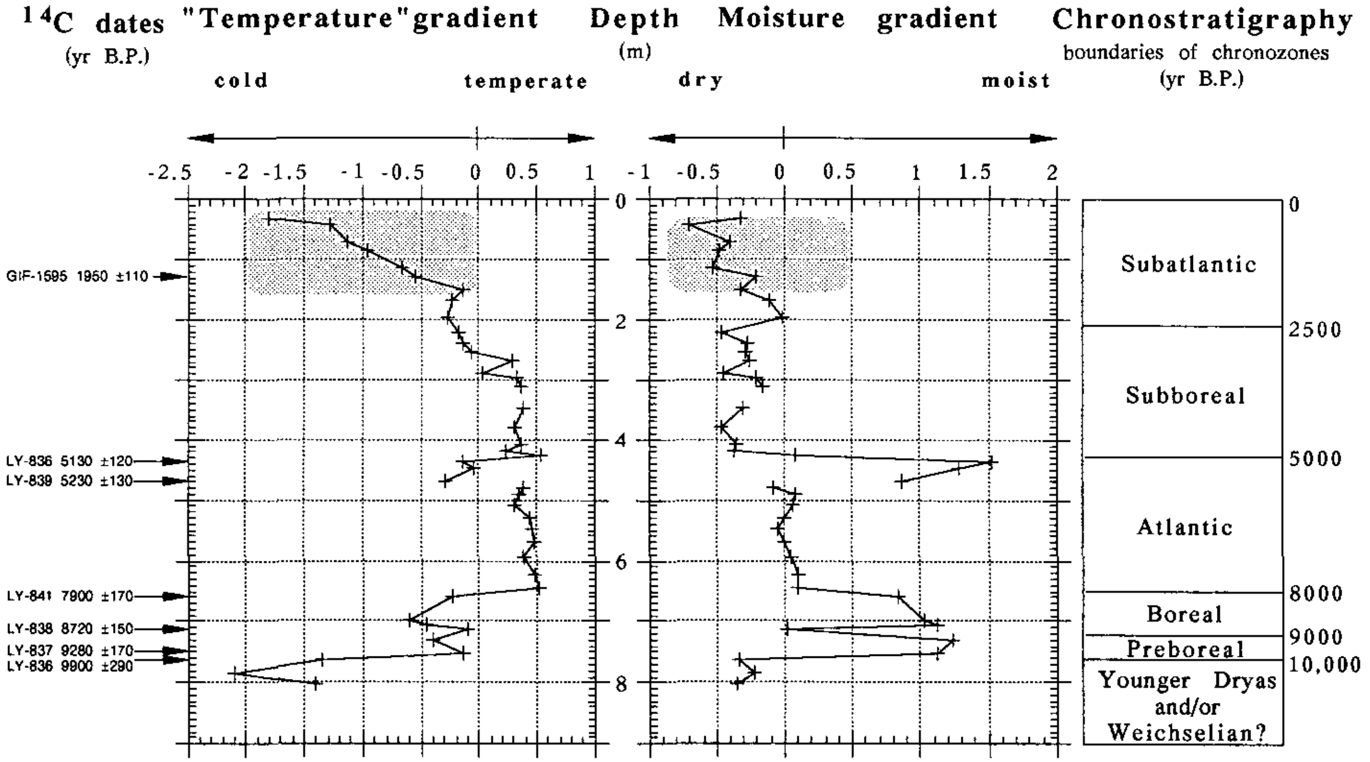

FIG. 9. Time series of mollusks from Holocene assemblages in Burgundy on the temperature and moisture gradient against depth. The values correspond to the variability of the general data set along the axes. The white parts in the curves correspond to the major breaks recognized in the stratigraphy. The gray area underlines the assumed anthropogenic effects on environment.

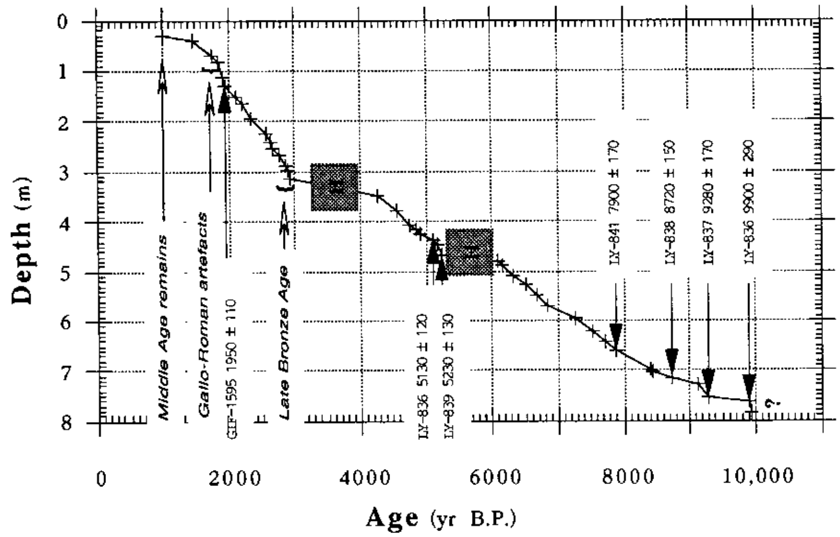

FIG. 10. The relation of depth to age, used for the interpolation of the ages of the different stratigraphical horizons. Locations of ^{14}C-dated horizons are shown.

Dryas event. The younger peak, which is smaller in magnitude, occurs between 10,000 and 9000 yr B.P. (Fig. 11), with decreasing values to 5000 yr B.P. The occurrence of a freshwater discharge to the North Atlantic Ocean coupled with a temperature increase may have led to an increase in the evaporation–precipitation balance. In Europe, this mechanism is associated with a westerly atmospheric flow (COHMAP, 1988) which could have resulted in increased precipitation contributing to the observed inundations of the valleys in Burgundy (Fig. 11). This change in the precipitation pattern over Burgundy is in agreement with reconstructions from pollen data in northwest Europe (Huntley, 1990) which suggests the occurrence of increased precipitation between 10,000 and 8000 yr B.P., decreased precipitation between 8000 and 5000 yr B.P., and increased precipitation after 5000 yr B.P. This pattern of precipitation is in agreement with the results of the analysis of mollusk assemblages in Burgundy (Fig. 11).

Similarities between the mollusk record and records reflecting a larger-scale response to climatic variations suggest that teleconnections between ocean, atmosphere, and continent need to be developed further over the European continent. Human activities in the late Holocene considerably reduce the reliability of the climatic signal recorded by the mollusk assemblages.

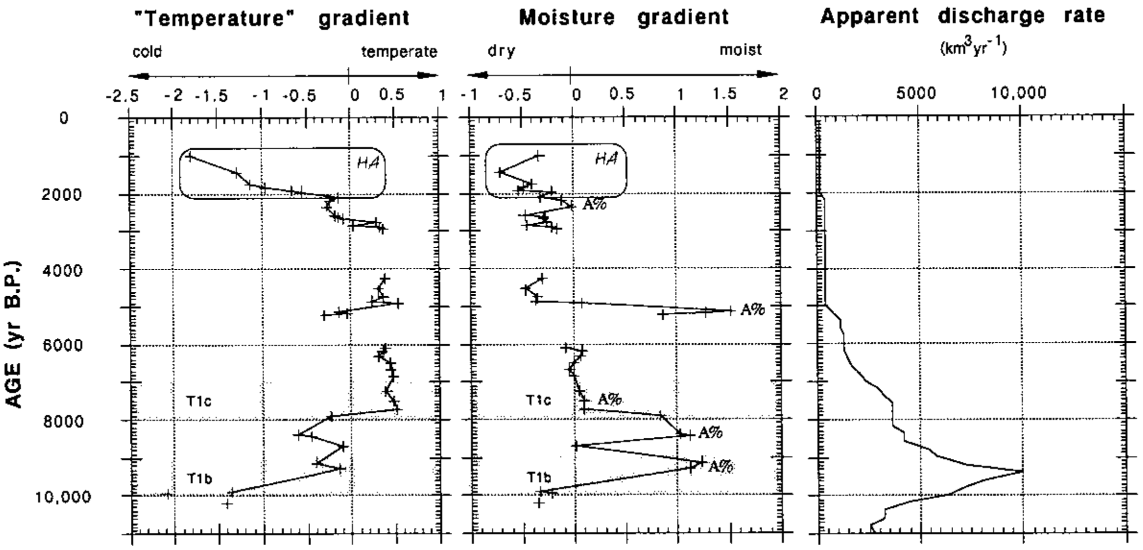

FIG. 11. Time series of Holocene malacofaunas in Burgundy. Location of Termination 1b and 1c events (gray areas) according to Mix and Ruddiman (1985). Comparison with meltwater discharge curve according to Fairbanks (1989), relieving impacts of both climate and human factors (circled HA area) on the mollusk communities. *A%*, inundations events as recorded by aquatic taxa.

APPENDIX 1

Coded Data Set Used for the Correspondence Analysis

Samp.	m1	m2	m3	m4	m5	m6	m7	m8	m9	m10	m11	m12	m13	m14	m15	m16	m17	m18	m19	m20
MO01	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	3	1	4
MO02	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	3	0	1
MO03	0	0	1	0	3	1	0	4	0	0	0	0	4	0	0	0	0	8	0	7
MO04	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
MO05	0	0	1	0	0	5	0	0	0	0	7	0	0	3	0	0	0	0	0	0
MO06	0	0	7	4	7	8	0	6	0	0	8	0	5	4	0	0	0	0	0	0
MO07	0	0	5	1	0	9	0	0	0	0	8	0	0	0	1	0	0	0	0	1
MO08	0	0	1	0	1	7	0	2	0	0	7	0	0	0	0	0	1	0	0	0
MO09	0	0	10	8	4	7	0	8	0	0	8	0	6	0	2	0	8	0	0	3
MO10	0	0	12	9	0	8	0	9	0	0	8	0	3	5	1	0	6	0	0	0
MO11	0	0	10	7	0	9	0	6	0	0	8	0	5	5	5	0	6	0	0	0
MO15	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3	2
CL15	0	0	10	8	0	6	0	8	0	1	9	0	5	0	5	0	7	0	1	0
B-13	0	0	8	9	0	0	0	6	4	5	4	5	0	3	0	0	6	0	0	7
B-12	1	0	9	9	0	0	0	6	2	3	1	4	0	3	0	0	8	0	0	7
B-11	0	0	8	7	0	3	0	5	3	2	0	4	0	3	0	0	2	1	1	4
B-10	0	0	8	7	0	3	0	5	1	3	0	1	0	3	0	0	0	0	0	5
B-09	1	0	5	6	0	3	1	5	3	2	0	0	0	4	0	0	0	0	0	5
B-08	1	0	8	9	0	3	0	7	5	5	1	1	1	4	0	0	0	0	0	7
B-07	0	0	9	7	0	3	0	6	3	2	5	0	0	3	0	1	0	0	0	7
B-06	2	0	5	3	0	4	1	5	0	1	1	1	0	3	0	0	0	0	0	2
B-05	1	0	9	8	2	4	4	8	5	3	0	0	0	4	0	0	0	0	0	6
B-01	0	0	9	9	0	4	5	6	5	2	5	0	0	4	0	0	0	0	0	0
B+01	7	0	5	6	2	4	5	7	3	2	3	0	1	3	0	1	0	2	1	7
B+02	5	0	7	7	3	5	4	6	3	1	0	0	0	1	0	4	0	0	0	4
B+03	6	0	5	7	3	1	4	6	2	2	0	0	1	1	0	3	0	0	0	5
B+04	6	0	10	9	3	3	6	8	5	1	2	0	1	4	0	3	0	0	0	4
B+05	1	0	7	6	4	5	2	5	4	5	0	0	2	3	0	0	0	0	0	0
B+06	1	0	4	4	3	3	2	5	3	2	2	0	0	0	0	1	0	0	0	1
B+07	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4
B+08	3	0	5	4	0	3	3	5	1	0	2	0	0	1	0	0	0	0	0	1
B+09	2	0	5	6	1	3	1	5	0	0	2	0	3	0	0	0	0	0	3	7
B+10	5	0	4	0	2	4	3	6	2	0	1	0	4	1	0	0	5	0	2	8
B+12	4	0	0	1	0	1	2	0	0	0	1	0	2	0	0	0	0	0	0	5
B+13	1	0	2	2	0	4	0	3	0	0	1	0	0	2	0	0	2	0	1	5
B+14	4	0	6	7	0	6	4	7	0	0	4	0	5	0	0	0	6	0	4	9
B+15	5	0	5	5	1	4	4	5	0	1	2	0	3	1	0	0	0	0	2	8
B+16	3	0	3	0	0	7	1	5	0	0	1	0	4	0	0	0	0	0	3	8
B+17	3	1	0	8	7	1	1	8	0	0	0	0	7	0	0	0	1	3	7	9
B+18	2	0	0	1	5	1	0	5	0	0	0	0	1	0	0	0	0	0	3	6
B+19	1	0	1	0	3	3	0	4	0	0	0	0	0	0	0	0	0	0	2	5
B+20	3	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	5

APPENDIX 1—*Continued*

Samp.	m21	m22	m23	m24	m25	m26	m27	m28	m29	m30	m31	m32	m33	m34	m35	m36	m37	m38	m39	m40
MO01	3	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
MO02	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
MO03	7	0	0	0	0	6	0	0	0	0	5	0	0	0	0	3	3	0	0	5
MO04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
MO05	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0
MO06	8	0	0	0	0	2	0	0	0	0	5	0	0	0	0	6	6	0	0	0
MO07	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	6	0	0	0
MO08	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	4	0	0	0
MO09	9	6	0	0	0	5	0	0	7	0	7	0	0	0	0	7	5	0	0	0
MO10	0	11	0	0	0	4	0	0	0	0	5	0	0	0	0	8	7	0	0	0
MO11	0	9	0	0	0	2	0	0	0	0	0	0	0	0	0	7	7	0	0	0
MO15	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CL15	10	1	0	0	0	5	0	6	3	0	9	0	3	0	0	7	6	0	0	0
B-13	0	0	4	0	0	7	1	6	7	6	7	0	6	0	4	4	6	0	0	0
B-12	0	0	4	0	0	7	0	7	8	6	7	1	6	0	1	3	6	0	0	0
B-11	0	0	2	0	0	6	0	7	7	0	4	0	5	0	4	5	5	0	0	1
B-10	0	0	5	0	0	6	0	7	8	2	4	0	5	0	1	5	6	0	0	0
B-09	0	0	3	0	0	5	0	7	6	1	3	1	5	0	2	5	5	0	0	0
B-08	0	0	4	1	0	6	0	8	8	3	5	0	5	0	2	5	7	0	0	0
B-07	0	0	4	3	0	6	0	8	8	0	5	1	3	0	4	6	6	0	0	0
B-06	0	0	3	1	0	3	0	5	5	0	0	0	1	0	1	0	6	0	0	0
B-05	0	0	3	0	0	6	0	8	8	0	1	3	6	0	2	6	7	0	0	2
B-01	0	0	5	0	0	8	0	10	8	1	2	3	5	0	2	7	6	0	0	0
B+01	1	0	5	1	4	5	0	10	8	0	4	6	8	5	6	6	6	0	0	0
B+02	0	0	3	0	0	4	0	9	7	0	2	5	7	4	6	6	5	0	0	0
B+03	1	0	4	0	3	4	0	9	7	2	3	5	7	6	6	4	4	0	0	0
B+04	1	0	7	0	2	7	0	11	8	4	6	7	7	5	8	7	7	0	0	0
B+05	1	0	5	0	0	6	0	7	7	3	4	4	5	3	6	6	6	0	0	0
B+06	0	0	5	0	1	4	0	7	5	2	3	4	5	0	5	5	4	0	0	3
B+07	1	0	1	0	0	1	0	4	3	0	0	0	2	1	2	2	2	0	0	1
B+08	1	0	4	0	1	4	0	7	7	4	3	5	5	5	5	5	4	0	0	2
B+09	5	0	4	0	0	5	0	7	5	2	1	4	5	4	5	2	2	0	0	3
B+10	6	0	4	1	1	4	0	8	5	1	4	4	6	5	4	2	3	0	1	3
B+12	3	0	1	1	0	2	0	4	1	0	2	0	4	3	2	0	1	0	0	3
B+13	3	0	0	0	0	1	0	4	1	0	3	1	1	2	0	2	3	1	0	1
B+14	8	0	6	2	1	5	0	6	6	0	7	2	4	6	0	5	4	0	0	4
B+15	7	0	5	1	2	3	0	7	4	0	6	1	3	6	4	5	5	0	0	3
B+16	9	0	0	1	0	3	0	5	1	0	5	1	3	5	0	4	3	1	1	1
B+17	11	0	6	0	1	5	0	8	3	3	5	5	2	6	4	0	1	4	0	4
B+18	7	0	0	0	0	0	0	4	0	0	5	0	0	1	0	0	0	5	0	1
B+19	7	0	0	0	1	0	0	1	0	0	3	0	0	0	1	3	0	6	0	0
B+20	7	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	4	0	1

APPENDIX 1—*Continued*

Samp.	m41	m42	m43	m44	m45	m46	m47	m48	m49	m50	m51	m52	m53	m54	m55
MO01	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
MO02	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
MO03	0	0	0	0	0	4	8	0	0	0	0	0	0	0	3
MO04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MO05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
MO06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
MO07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
MO08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MO09	0	0	0	0	1	0	1	0	0	0	0	0	0	0	6
MO10	0	0	0	0	0	0	1	0	0	0	0	0	0	0	6
MO11	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4
MO15	0	0	0	2	0	1	0	0	0	1	1	0	0	0	0
CL15	0	0	4	0	0	0	0	0	0	3	0	0	0	0	7
B-13	5	0	0	0	0	0	5	0	0	4	0	0	0	0	4
B-12	4	0	0	0	0	0	3	0	0	4	0	0	0	0	5
B-11	3	0	0	0	0	0	3	0	0	2	0	0	0	0	5
B-10	3	0	0	0	0	0	4	0	1	4	0	0	0	0	3
B-09	3	0	0	0	0	0	4	0	1	3	0	0	0	0	3
B-08	4	0	0	0	0	0	6	0	0	3	0	0	0	0	5
B-07	1	0	0	0	0	0	6	0	0	3	0	0	0	0	6
B-06	1	0	0	0	0	0	3	0	0	1	0	0	0	0	2
B-05	3	0	0	0	0	0	7	0	0	3	0	0	0	0	4
B-01	5	1	0	0	0	0	3	0	1	3	0	0	0	1	5
B+01	0	0	0	7	3	0	7	0	4	5	0	0	0	0	2
B+02	0	0	0	5	3	0	7	0	1	3	0	0	1	0	2
B+03	0	0	0	5	2	0	7	0	1	4	0	0	0	2	3
B+04	0	0	0	6	4	0	5	3	2	4	0	0	0	1	5
B+05	0	0	0	4	1	0	5	0	1	1	0	0	0	0	4
B+06	0	0	0	0	0	0	4	1	0	1	0	0	0	0	3
B+07	0	0	0	0	1	0	4	0	0	1	0	0	0	0	7
B+08	0	0	0	0	0	0	6	1	0	3	0	0	0	1	3
B+09	0	0	0	0	0	0	6	1	1	1	0	1	0	1	3
B+10	0	0	0	0	0	0	8	1	1	1	0	2	0	0	4
B+12	0	0	0	0	1	0	5	1	1	1	0	0	0	0	6
B+13	0	0	0	0	0	0	5	0	0	1	0	0	0	1	3
B+14	0	0	0	0	0	0	9	0	1	2	0	4	0	4	6
B+15	0	0	0	4	1	0	7	1	1	1	0	4	0	2	5
B+16	0	0	0	1	0	0	8	0	0	0	0	3	0	0	4
B+17	0	0	0	4	0	1	8	0	0	0	0	6	0	0	5
B+18	0	0	0	0	0	0	8	0	0	2	0	0	0	0	5
B+19	0	0	0	0	0	0	6	0	0	1	1	1	0	0	5
B+20	0	0	0	0	0	0	7	0	0	0	1	1	0	0	5

Note. m1, *Pomatia elegans;* m2, *Acicula dupuyi;* m3, *Carychium minimum;* m4, *Carychium tridentatum;* m5, *Succinea oblonga;* m6, *S. putris;* m7, *Azeca goodalli;* m8, *Cochlicopa lubrica;* m9, *Columella edentula;* m10, *Vertigo pusilla;* m11, *V. antivertigo;* m12; *V. substriata;* m13, *V. pygmaea;* m14, *V. moulinsiana;* m15, *V. genesii;* m16, *V. alpestris;* m17, *V. angustior;* m18, *Abida secale;* m19, *Pupilla muscorum;* m20, *Vallonia costata;* m21, *Vallonia pulchella;* m22, *V. enniensis;* m23, *Acanthinula aculeata;* m24, *Ena montana;* m25, *E. obscura;* m26, *Punctum pygmaeum;* m27, *Discus ruderatus;* m28, *Discus rotundatus;* m29, *Vitrea crystallina;* m30, *V. contracta;* m31, *Nesovitrea hammonis;* m32, *Aegopinella pura;* m33, *A. nitidula;* m34, *A. minor;* m35, *Oxychilus* sp.; m36, *Zonitoides nitidus;* m37, *Euconulus fulvus;* m38, *Cecilioides acicula;* m39, *Macrogastra ventricosa;* m40, *Clausilia parvula;* m41, *Cl. bidentata;* m42, *Cl. dubia;* m43, *Clausilia* sp.; m44, forest *Clausilia;* m45, *Bradybaenum fruticum;* m46, *Helicella* sp.; m47, *Trichia hispida;* m48, *Helicodonta obvoluta;* m49, *Helicigona lapicida;* m50, *Cepaea* sp.; m51, *Helix pomatia;* m52, *C. septemspirale;* m53, *Zebrina detrita;* m54, *Phenacolimax major;* m55, *Limax* sp. (for the coding process, see Rousseau 1987).

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