Climatic Transfer Function from Quaternary Molluscs in European Loess Deposits

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Correspondence and multiple regression analysis of terrestrial molluscs in the loess sections of Achenheim (Alsace, France) has permitted the reconstruction of climatic variations during the last three glacial–interglacial cycles back to 339,000 yr B.P. The sequence has been dated according to the SPECMAP chronology of Imbrie *et al.* (1984) and the fossil faunas have been calibrated in relation to recent assemblages sampled in defined ecological conditions in Sweden and France. Transfer functions that relate the abundances of different species to climate allow the reconstruction of temperature and precipitation. Estimates for the coldest (February) and warmest (August) months in present-day Alsace were obtained and variations in temperature between $-13°$ and 2°C in winter and 10° and 17°C in summer were determined. These results are consistent with those yielded by transfer functions using other continental fossils. Estimates differ for past precipitation. Summer precipitation is always less than present (with values between 50 and 78 mm, while modern August values are 76 mm higher). Winter estimates are always higher than the present mean (between 76 and 33 mm, while the recent February value is 34 mm). Comparisons between cycles show that the climatic patterns described for one cycle cannot be strictly applied to the others. Comparisons have been made with the pollen stratigraphy of La Grande Pile, the nearest quantified sequence to Achenheim, and with some Atlantic cores in order to study the magnitude of deviations from modern mean values of the climatic parameters. © 1991 University of Washington.

INTRODUCTION

A main topic in paleoclimatology is the understanding of the mechanisms which control the climate, using the responses to insolation, the major external constraint. Observations, mainly of isotopic and biological evidence, have to be quantified in terms of climatic parameters to make advances in such a program.

Since the first publication of Imbrie and Kipp (1971), numerous workers have attempted to quantify the relationship between biological data and environment. In continental sequences pollen, tree rings, and insects have already been used (Bartlein *et al.*, 1984; Coope, 1987; Fritts *et al.*, 1971; Guiot, 1990; Howe and Webb, 1983; Overpeck *et al.*, 1985). Application of the so-called transfer functions approach is now general in Quaternary paleoclimatic studies. The organisms mentioned above are so numerous in sediments that transfer functions can be readily applied. As molluscs are abundant and well preserved in Quaternary sediment, it is surprising that this technique has not yet been applied. In loess, land snails are often the sole biological remains. Because their present occurrence is closely connected with their environment, they can potentially provide precise paleoecologic information, and they have been used in this respect by the small number of malacological workers.

The classical ecological groups determined by Lozek (1964) and Puisségur (1976) are well known and defined in accordance with the characteristics of each species. In the same way, climatic interpretations can be proposed by taking into account the variations in species abundance as a function of temperature and moisture, which are the main limiting factors. For ex-

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ample, Sparks (1961) divided molluscs into four groups on the basis of their distribution, and from the development of faunal assemblages through time made climatic conclusions. These semiquantitative analyses have, up to now, dominated land snail studies.

Molluscs are generally numerous as fossils. They have two advantages over pollen for paleoclimate work: first, they can be identified to the specific level and therefore can be used as precise paleoecological indicators, and second, they are less likely to suffer from taphonomical problems such as long-distance transport or reworking. Consequently, they are suitable for multivariate analyses and can provide precise paleoenvironmental conclusions (Rousseau, 1987). The applicability of the results have been tested at different sites by comparison with pollen analyses, and generally the evidence from both fossil groups is in good agreement (Rousseau and Puisségur, 1989; Sommé et al., 1989).

DATA

Recent Malacofaunas

Modern assemblages of terrestrial molluscs provide close similarities with the fossil communities from which transfer functions have been calculated. All the late Quaternary species used are still live today in western Europe in the same ecological conditions, and in the same species assemblages. The one exception is *Pupilla loessica* which is only known as a fossil. In northwestern Europe, a major problem is to find natural ecological sites without any human impact to provide the basic information for analysis. If we consider the scattered outcrops of chalk and limestone in western Europe because of the molluscs' need for lime, the land area which is slightly affected by human activities is very small (Fig. 1). On the other hand, because modern analog assemblages for glacial time live in the tundra and for interglacial time in the woodlands, opportunities for getting nu-

merous reliable references are reduced. I have therefore selected two particular areas: the Abisko National Park, in northern Sweden, and Burgundy, France. The former area, a UNESCO protected area, was used to study modern assemblages providing *Columella columella* and *Vertigo genesii;* the latter area was used to recover interglacial assemblages which are similar to those now found in Burgundy (Fig. 2). The data come from published and unpublished information of A. Nilsson (1968, 1987), J. J. Puisségur (Burgundy), and myself (Burgundy and Abisko). The sampling of molluscs was conducted close to meteorological stations so that the extrapolation of climatic parameters could be precisely made. Seventy-seven assemblages selected for this first attempt correspond to tundra, open land, and forest environments.

Fossil Malacofaunas

For a first application of this transfer function method it was important to work on sections already studied in detail. The Achenheim sequence (Fig. 1) has been analyzed in a semiquantitative manner (Rousseau, 1987) and its age is well calibrated (Rousseau and Puisségur, 1990) according to the SPECMAP chronology (Imbrie et al., 1984). The site has the last three climatic cycles preserved, with 123 fossil assemblages showing climatic variations between interglacial and pleniglacial periods.

Meteorological Data

Climatic parameters are derived from observations provided by local meteorological stations close to the sampling sites. Present-day February and August temperatures and precipitation in the Abisko valley were obtained from B. Holmgren, those in Burgundy from the Commission Météorologique de Bourgogne, and those in Alsace from Strasbourg, which is 5 km east of Achenheim (Garnier, 1974; Sanson, 1961). These four parameters were selected because August conditions correspond to the growth and active life period of mol-

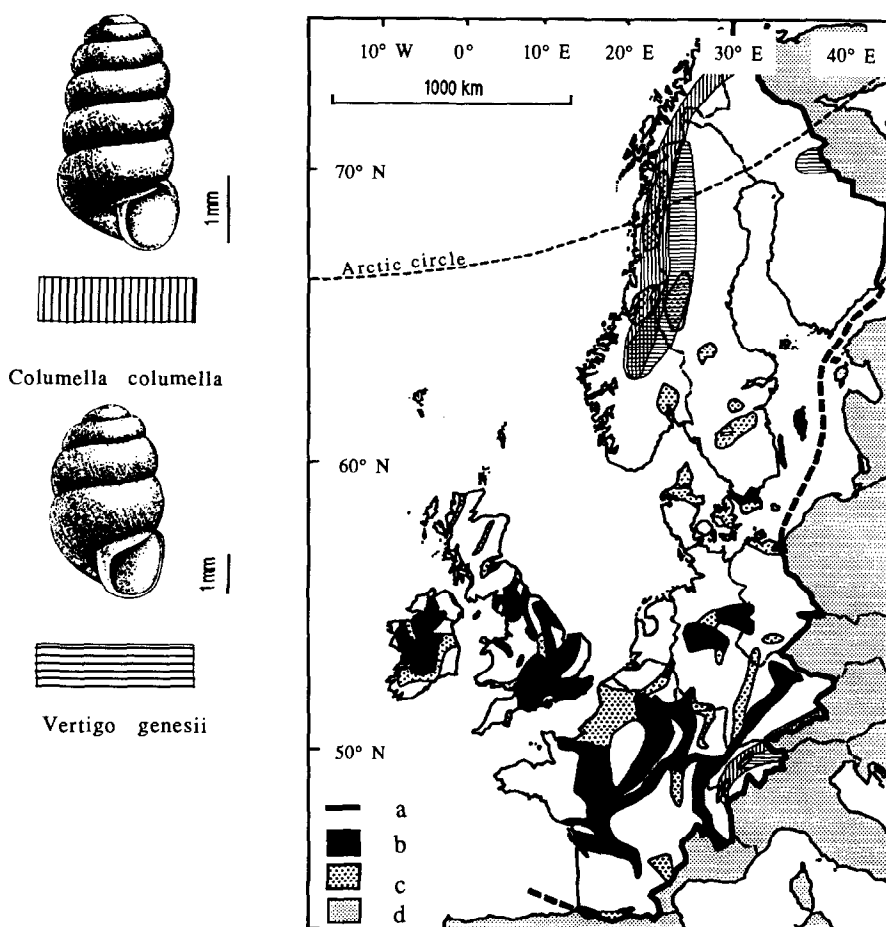Columella columella

Vertigo genesii

FIG. 1. Map of northwest Europe showing the distribution of *Columella columella* and *Vertigo genesii*. This map indicates that the opportunities to collect perfect modern analogs outside of areas affected by human activities are relatively limited, although all the taxa are still present in the study area. (a) Limit of the northwest European region; (b) major outcrops of chalk and limestone; (c) scattered outcrops of chalk and limestone (from Kerney and Cameron, 1979).

luscs, while February corresponds to the period of maximum stress caused by frost.

Choice of a Multivariate Analysis

A natural assemblage groups together species which in their occurrence correspond to the interaction between limiting factors and ecological tolerance. The limiting factor determines the possibility of success an organism has in its attempts to invade an environment, when the conditions are appropriate. It affects the general metabolism of the organism, allowing it to subsist effectively in the biotope. In extreme environments, such as tundra or desert, the limiting factors play the dominant role and strongly contribute to the definition of the biological style of the environment, determining a limiting value to all groups of organisms. In tundra, for example, the limiting factor groups the temperature and duration of the warm season, factors that allow the development of faunas. A reduction in the temperature or in the duration of summer implies an alteration in the development of the colonizing of an environment and, if intensities are too extreme, their disappearance. The inverse effect leads to important faunal changes caused by the immi-
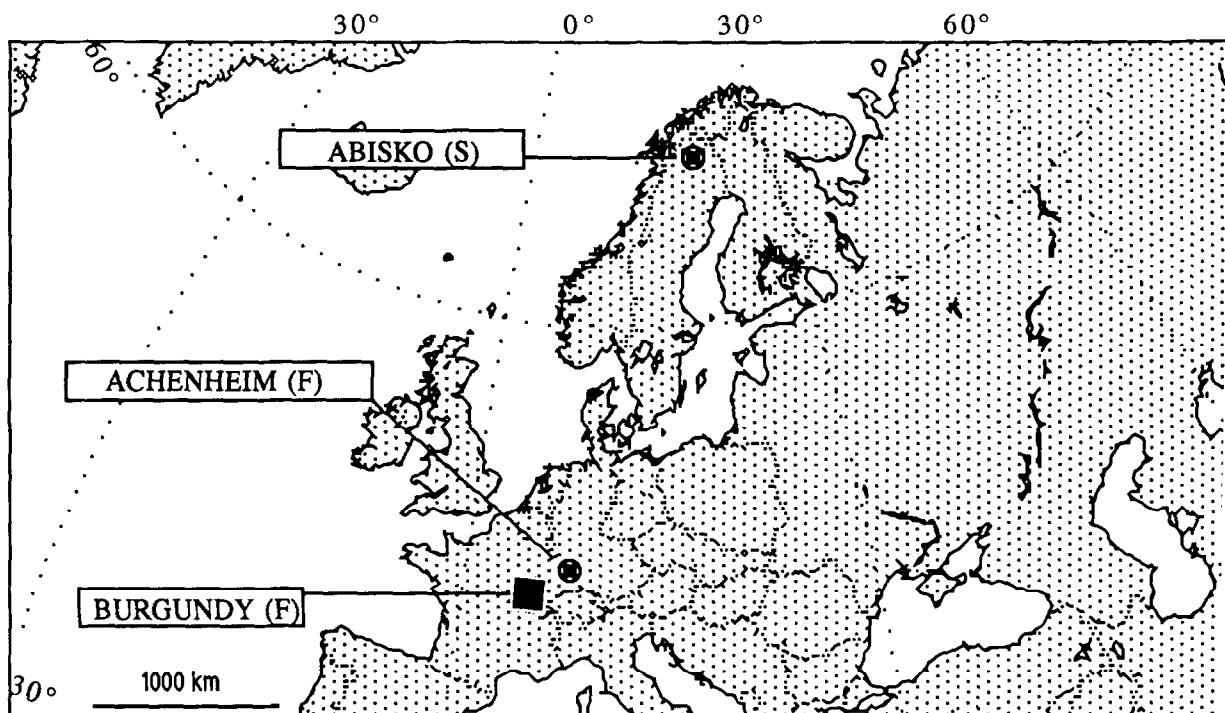
Fig. 2. Map showing the location of the Achenheim sequence relative to other sampled areas. F: France, S: Sweden.

gration of allochthonous species to tundra and the occurrence of new biocenoses (Rousseau, 1989). The presence of species in an assemblage also depends on its ecological tolerance, which represents its capacity to colonize different environments, i.e., to survive and to proliferate under various ecological conditions. A species with a low valency tolerates a low variability of the environment and is qualified as stenoecious. On the other hand, if the species is able to populate numerous environments, it is qualified as euryecious (Knight, 1965).

All of these characteristics which constrain the distribution and the development of the species imply that the multivariate cloud of a data set will not be spherical but will have nonlinear shape that factor analysis will characterize and explain.

The factor analysis of biological assemblages requires homogeneous data. The initial table is constituted by rows (malacological associations = stratigraphic levels) and columns (strengths of recognized species) which are used in this status causing a great disturbance to the analysis. The abundance coding of classes adopted here is based on a logarithm transformation with a base 2 (Rousseau, 1987).

As the coded strengths vary between 0 and 12, they constitute sets of homogeneous data which comprise the recent and the fossil assemblages.

Various methods allow the analysis of such a table (e.g., Q or R mode factor analysis, principal component analysis, correspondence analysis), and numerous applications which refer to them have been published. The method used here, correspondence analysis (Benzecri et al., 1973), allows the analysis of both columns and rows without any a priori assumptions concerning the structure of the data. This is contrary to principal components analysis. Each element (point) I is represented in a J dimension space by its coordinates on each J variable (kij, and $\Sigma kij = ki$) but is also allocated a weight ($= ki/k$, $k = \Sigma ki$, $\Sigma k = 1$).

For example, three assemblages yield the following counts for three species a, b, and c:

assemblage 1: $a = 2 - b = 4 - c = 8 - ki = 14$,

assemblage 2: $a = 4 - b = 8 - c = 16 - ki = 28$,

assemblage 3: $a = 3 - b = 10 - c = 0 - ki = 13$; $k = 55$.

The coordinates (kij) of each assemblage are: 2/14, 4/14, and 8/14 for the first two examples and 3/13, 10/13, and 0 for the latter. The weightings are 14/55, 28/55, and 13/55.

This procedure is available for both rows and columns, and yields superimposable factors (reference axes of the hyperspace) that allow the simultaneous plotting of both variables and individuals (rows). This makes the interpretation of the results easy by underlining the species and the assemblages that are ecologically significant, and by determining relative evaluations of temperature, moisture (temperature and moisture gradients), evolution of environments, and thus climate. Taking into account these gradients, the assemblages, considered in their stratigraphic position, provide precise data on the variations in climate.

The general table is elaborated with the modern assemblage sets linked to the fossil ones.

Processes

Analogs. A first correspondence analysis allows the rejection of the columns (species) which do not contribute to the global sample. If each species V has the same influence on the variability of the total set, its theoretical contribution equals $1/p$, p being the total number of species. Consequently, all species which have a lower contribution than this theoretical threshold have to be rejected. Then, a second analysis is made on the new table. The general variability of the sample is approached by taking into account the factors when the cumulative sum of the expressed variance equals 90 (which is 90% of the open information).

Estimations. The estimates of the recent climatic parameters (Pa) are realized with stepwise regressions of their real value as a function of the loadings on the retained factors. Various analyses are performed by varying the threshold of rejection and agreement of the null hypothesis and thus the independence of the climatic parameters with regard to factor loadings. The retained coefficient corresponds to the analysis which provides the highest multiple correlation coefficient and the lowest standard error. The analysis of the residuals (Real values Pa – Estimated values $P'a$) allows the agreement or rejection of the results.

Reconstructions. The estimation of former climatic parameters $(P'f)$ is thus calculated by applying the equations of the stepwise regressions for the present compared to the loadings of the fossil assemblages on the selected factors.

This kind of approach, which uses correspondence analysis and multiple regression, is similar to that used by Gasse and Tekaia (1983) on diatoms.

RESULTS

In the first analysis, the first seven factors explain 44.77% of the total variability of the global sample. The 51 taxa which do not contribute to the variability of the data set were removed from the initial table. Another problem is *Pupilla loessica,* which is the only fossil species. It is typical of certain loess horizons and generally appears only in the *Pupilla* fauna, which has no modern analog (Lozek, 1964). It is an association dominated by *Pupilla* species: *P. muscorum, P. alpicola, P. sterri,* and *P. loessica.* If *Pupilla muscorum* is a eurytope, the other species have strong ecological characteristics: *P. alpicola* lives in moist grassland, while *P. sterri* prefers dry conditions in steppe or rocks (Kerney *et al.,* 1983). As *P. loessica* and *P. sterri* are only present in three levels and nevertheless mask the variability of the other spe-

cies by their high contribution, they also are rejected for the second analysis.

In the second analysis, 89.98% of the total variance of the global sample is explained by the first 24 factors. The contribution of variables (species) to the factors is described using the first seven factors (56.19% of the global variance), the theoretical contribution of the variables being of $1/49 = 0.0204$ (Table 1).

The first axis shows the discrimination between species which are mainly represented in both fossil and Swedish assemblages and species which are mainly represented in Burgundian and fossil assemblages. The second axis discriminates the species with regard to their geographical occurrence whether Swedish or Burgundian. The third axis discriminates species which characterize moist conditions from species indicating lower moisture in an environment with mainly arboreal vegetation. The fourth axis shows the difference between species indicating a cold, marshy open environment, and species characteristic of a relatively moist environment with little arboreal vegetation. The fifth axis discriminates cold open conditions with little moisture from a more temperate environment with forests. The sixth axis divides marshy from less moist environments. As observed in Table 1, some axes seem to discriminate the same poles, yet if we consider the species which originate these factors, they are not always the same.

Transfer Functions

The stepwise regressions of the assemblages: 49 + 4 columns (species + February and August temperatures and precipitations) × 77 rows (modern assemblages) have been calculated with various partial F ratios. Finally, the largest part of the variance of each dependent predicted variable (high correlation and low standard error) has been obtained with partial F corresponding to 50%. Because it only discriminates the modern assemblages, the first

axis cannot be taken into account in the regressions, while the other 23 will be used.

Mean Temperatures (Table 2).

February. Among the 23 factors, 13 were selected. The transfer function has a low standard error of estimate of $\pm 1.045°C$ and a multiple correlation coefficient of 0.98.

August. Among the 23 factors, 11 were selected. The standard error of estimate is lower than that for the February temperature, $\pm 0.82°C$, with a multiple correlation coefficient equal to 0.968. The analyses of the residuals, the difference between observed and estimated parameters, imply that the assumptions underlying application of regression analysis are not violated.

Mean Precipitation (Table 2).

February. The regression implies 12 factors. The transfer function indicates a standard error of 9.0 mm and a multiple correlation coefficient of 0.811.

August. Twelve factors which contribute to the explanation of this parameter were selected. The standard error of estimate is 5.9 mm and the multiple correlation coefficient 0.889. The analysis of residuals allows the application of the transfer function.

It is evident that land molluscs are mainly and directly affected by temperature. As the mollusc's main period of activity comprises a part of spring, summer, and the beginning of autumn, the climatic parameters act directly in summer. In winter molluscs hibernate; thus, climatic controls are indirect. Precipitation is not a direct effect, except through surface soil moisture.

What are the limitations of the reduced modern data set? While Abisko and Burgundy cannot represent the entire range of climates in Europe, nevertheless, they correspond on the basis of the mollusc assemblages to the climatic extremes that are recognized in the Quaternary record. This implies that intermediate fauna are not well recorded in the modern data set and that care should be taken in using their estimates. In this way, the western European

TABLE 1. Taxa Used in the Second Correspondence Analysis

Species	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
C. lubrica	227	414	42		103	498	377
C. columella		573		118	2663	38	
V. genesii	30	395		226	2895	1146	32
N. petronella	339	563	70	31	443		454
V. pellucida	371	637	59	41	570		144
E. fulvus	800	618	105				90
A. arbustorum	202				82	662	99
D. agreste		36			249	70	
V. modesta	379	848	74			187	732
P. pygmaeum	620				97	53	61
V. lilljeborgi	61	262	2382		62		
E. alderi	33	78			32	74	82
O. sarsi		136	1660	7098	353	40	
V. extima	48	102			32	331	6455
V. ronnebyensis	130	213	28		262	223	
Succinea sp.		126	5362	2348	116		
D. ruderatus	53	76			200		107
V. geyeri					26	27	46
V. subrimata	26						48
Vertigo sp.	31	64					27
C. edentula	40						48
V. alpestris		46				29	51
Z. harpa	143	228	50		369	395	
Limax sp.	411				66		
A. nitidula	90	229				58	
V. crystallina	303	477					
V. contracta	333	470				39	
D. rotundatus	248	596				32	
H. lapicida	51	119				22	
H. obvoluta		54			24	181	35
C. bidentata	389	575			28	35	
V. pulchella	77				104	471	81
V. costata	503				138	104	52
C. tridens	74				68	185	58
A. aculeata	394	585			26	37	
P. muscorum	1190					208	
V. pygmaea	67				48	72	22
S. oblonga	1087				46	1150	154
P. elegans	333	567			28		
C. septemspirale	481	791			36	26	
S. doliolum		25				101	
B. fruticum	27				156	1028	122
V. tenuilabris	39						
V. parcedentata						47	
P. alpicola	187				489	1834	420
S. putris	28					337	
Helicella sp.	66				49	143	52
Percentage of variance	12.82	11.20	9.25	7.67	5.72	4.95	4.60

Note. Higher contributions to the variability of the data set than the theoretical threshold ($1/49 = 0.020$) are indicated (values in thousandths) and percentage of the total variance is expressed by the factors.

TABLE 2. Statistics of Transfer Functions

	Temperature (°C)		Precipitation (mm)	
	February	August	February	August
Multiple correlation coefficient	0.98	0.966	0.811	0.889
Standard error of estimates	±1.045	±0.82	±9.024	±5.296
Intercept	−3.081	14.123	46.183	65.873
F2	5.18	3.012	12.037	11.488
F3	−0.792	−0.474	−1.268	−1.398
F4		0.049		
F5	−1.401			−0.999
F6	−2.194	0.728		
F7	1.459			0.697
F8	1.006			
F9			−1.619	−1.219
F10	−0.661			
F11			2.15	1.838
F13			4.111	13.026
F14	−0.031	−0.29		3.433
F15		0.154	−2.273	
F16	−0.946	−1.912	19.774	
F17			2.384	2.05
F18				−2.879
F19	−0.439	−0.18	3.755	
F20				−6.989
F21		0.19	−2.223	−1.887
F22	0.432	0.222	−2.628	
F23	−2.374	−1.599		
F24	0.471		−3.087	

location of Abisko and Burgundy could introduce some bias in the climatic reconstructions, i.e., overestimating winter precipitation. In fact, considering this meteorological point of view, at low altitudes in Abisko the average annual temperature is −1°C and the annual precipitation is 300 mm, with a maximum in summer of (July) 40 mm. These values are lower than those obtained in Poland, e.g., at Chelm (23.47°E, 51.13°N; 7.33°C and 563.88 mm) or Zabkowice (16.88°E, 50.35°E; 6.89°C and 668.02 mm). Burgundy has an average annual temperature of 10.61°C and annual precipitation of 695.96 mm. The present-day climate of Burgundy and Abisko is not typically oceanic, as could be expected for this area. However, even in the absence of perfect analogs for intermediate fauna, the two regions represent well the extremes of a glacial plus interglacial climate for Achen-heim, and do not invalidate the method and the results obtained.

APPLICATION OF THE TRANSFER FUNCTIONS TO THE FOSSIL ASSEMBLAGES OF ACHENHEIM

The Achenheim sequence has been time-calibrated according to the SPECMAP chronology and with regard to the rate of sedimentation and radiometric dates yielded by TL and ^{14}C measurements (Rousseau and Puisségur, 1990) (Fig. 3). The equation used for the calibration is

$$Tm = T1 + \frac{\sum_{i=1}^{m} ai\,(T2 - T1)}{\sum_{i=1}^{n} ai},$$

where a_i is the thickness of a level i, Tm is the calibration of level m between two boundary dates $T1$, and $T2$, and n is the total number of surrounded levels. This process does not ensure the independence of the chronology of this continental sequence, but the successively recognized climatic phases—supported by geomorphology, soil micromorphology, palynology, and the relatively good correspondence between radiometric dates and the marine isotopic chronology—allow the confirmation of the proposed time scale of the Achenheim sequence (Fig. 3).

Description

Temperatures. February estimates are generally lower than mean present values except for the Holocene, and during stage 7. Minima reach −11°C about 20,000 yr B.P. (stage 2) and 280,000 yr B.P. (stage 8). Stage 6 minimum values are close to −5°C. Estimates of winter temperatures greater than 0°C are obtained for the Holocene, in stages 7 and 9 and for event 5.1 (Fig. 4).

In the summer estimates, an important minimum (between 9° and 10°C) appears about 245,000 yr B.P. Higher estimates are obtained for the Holocene, with a value close to 17°C. Stages 7 and 9 have lower values than at present, with stage 9 ranging between 12° and 16°C, and stage 7 between 10° and 15°C. Estimates of past summer temperatures are always lower than the mean modern value in Achenheim (Fig. 4).
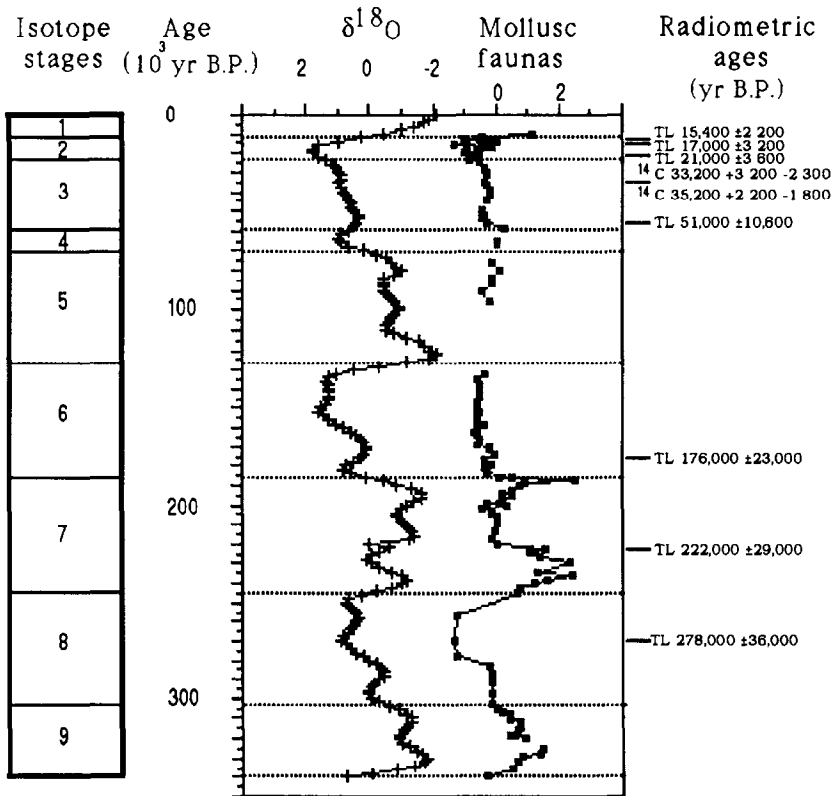
The evolution of summer and winter tem-

FIG. 3. Time series of molluscs from the Achenheim sequence. The variations of smoothed and stacked $\delta^{18}O$ (crosses) during the last three climatic cycles (0–339,000 yr B.P.) are from Imbrie *et al.* (1984). Plot of the variations of malacological associations (dark squares) on the climatic factor (first factor of the multivariate analysis) against the proposed calibration of the levels (sedimentation rate/ age) and the isotopic stratigraphy. The factor values are scaled for comparison to have similar amplitudes as the $\delta^{18}O$ variations (modified from Rousseau and Puisségur, 1990).
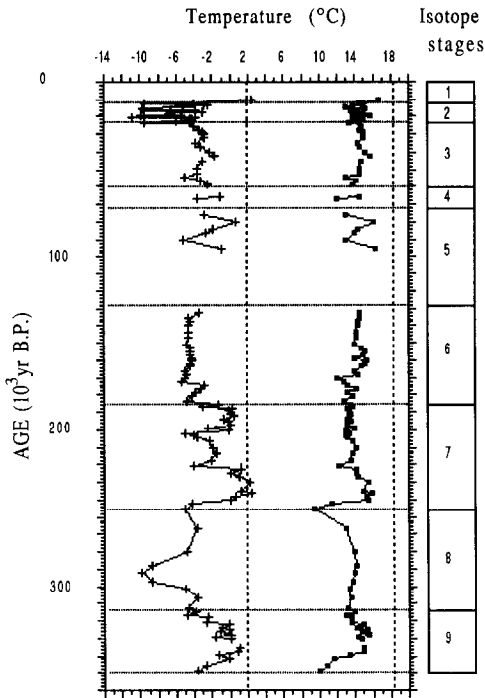
Temperature (°C)   Isotope
stages

FIG. 4. Reconstructions (analog climate) of the mean February (crosses) and August temperatures in the Achenheim sequence. Dotted lines indicate the present mean temperatures (1.8°C for February and 18.3°C for August). Blank parts in the curves correspond to barren levels.

peratures during the last three cycles indicates different patterns which can be considered as characteristic of the phases concerned. During glacial stages, 2–3, 6, and 8, winter estimates provide a higher variation from the modern mean value than do summer estimates. During interglacial stages 7 and 9 and event 5.1, there is evidence of the contrary, with cold summers. Nevertheless, among such trends a few small inversions occur, as during stages 5 and 7.

Precipitation. Estimates of past winter precipitation are always higher than the modern mean value, while summer estimates are always less than present. Winter estimates indicate two maxima at about 335,000 and 245,000 yr B.P. (close to 77 mm; present reference = 34 mm) and a third maximum at about 170,000 yr B.P. (65 mm). At about 80,000 yr B.P. (event 5.1),

winter estimates are less than present for the only time in the record (Fig. 5). Summer estimates are higher than the modern value (76 mm) only to about 335,000 yr B.P. Three estimates equal the reference value at about 240,000, 230,000, and 59,000 yr B.P. A minimum value of 50 mm is observed about 20,000 yr B.P. and several estimates between 186,000 and 200,000 yr B.P. are close to 50 mm (Fig. 5).

In contrast to the temperatures, the course of winter and summer estimates cannot be summarized in the distinction between pleniglacial and interglacial stages. Diminished summer precipitation does not always correspond to high winter values and vice versa. Similarly, when winter precipitation rises, summer rainfall does not also rise each time.

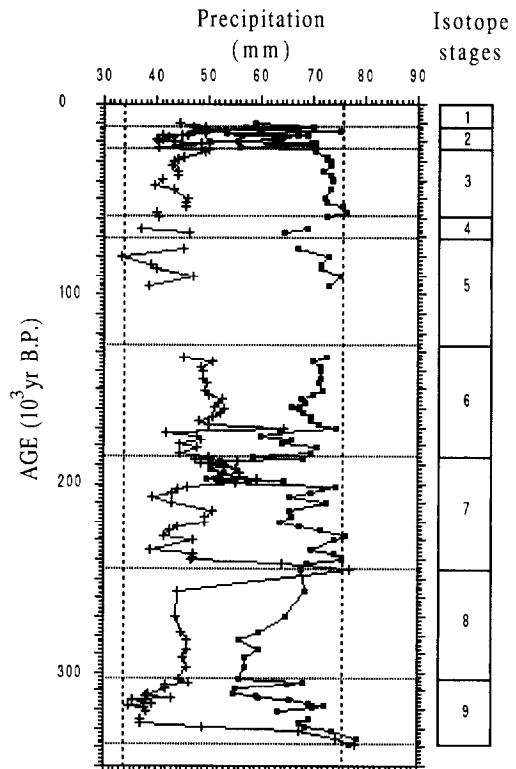Precipitation   Isotope
(mm)   stages

FIG. 5. Reconstructions (analog climate) of the mean February (crosses) and August precipitation for the Achenheim sequence. Dotted lines indicate the present mean values (34 mm for February and 76 mm for August).

DISCUSSION

An initial comparison of temperature estimates has to be made with peat cores from La Grande Pile which is the nearest site to Achenheim investigated in detail (Woillard, 1978). Guiot's (1990) results compared La Grande Pile and Les Echets for the last climatic cycle, but they differed from molluscan estimates. The pollen assemblages from these sites correspond with Achenheim in indicating summer temperatures always lower than the mean modern value, with a deviation equal to −5°C, while in Alsace the reduced values vary between −6° and −2°C, the latter characterizing the more temperate periods (Fig. 4). In winter, the magnitudes of the oscillations are completely different between pollen and mollusc records. During pleniglacial stages 4, 3, and 2, the former provides great temperature variations with reduced values between −22° and −10°C. Temperate periods have values closer to modern ones, but higher ones during the Eemian. In the Achenheim record, reduced winter estimates vary between −12.8° and −3.5°C during pleniglacial times and −6° and 0.5°C in interglacial times (Fig. 4). A disagreement seems to exist between the two winter estimates, while a deviation between −13° and −6°C is similar to published results from oceanic-core studies. Again, Guiot (1990) observes the same deviation of −20° and −5°C for reduced winter and summer values, respectively, at the end of stage 6. Contemporaneous Achenheim results provide lower values of between −7° and −5°C in February and between −3.8° and −4.4°C in August (Fig. 4).

Reduced values for La Grande Pile indicate variations in summer precipitation between −60 mm (66,000 yr B.P.) and +30 mm (13,000 yr B.P.) and between −40 mm (46,000 and 26,000 yr B.P.) and +60 mm (3000 yr B.P.) in winter precipitation (Guiot, 1990). For January, Guiot's values are always less than present values except

for the Eemian and the beginning and end of event 5.1. For July, the reduced precipitation is less than present during stages 2, 3, and 4, during the 5.1, and 5.3 events, and during the transition 5.4–5.3. Achenheim also shows a summer deficit with the same magnitude as in pollen records (Fig. 5), but February estimates disagree with the pollen estimate; as in the loess sequence, winter precipitation is higher than the modern value (Fig. 5).

The knowledge of the modern precipitation regime allows an explanation of these differing values. At present, mean annual temperature and precipitation at La Grande Pile are 9.5°C and 1080 mm while those for Achenheim are 10°C and 696 mm. The former site is located on the western side of Les Vosges mountains which dominate the Rhine valley near Achenheim. The precipitation difference between the two sites is 384 mm, so that the modern precipitation regime is completely different. In Alsace, precipitation is abundant in summer (June–July–August, with a positive peak at about 80 mm) and in winter the lowest precipitation is recorded in February, with a minimum of about 30 mm (Pagney, 1976) (Fig. 6). This implies that during several of the periods recorded in the Achenheim sequence, February and August precipitation was similar with values around 50 mm, nevertheless, a small precipitation peak occurred in summer. If we consider the results from La Grande Pile, the variation in the precipitation leads to a change in the regime similar to that of Achenheim, with a maximum in summer and minimum in winter, but with values slightly higher than in Alsace because of the effects of the west wind circulation.

Such a profile of precipitation, with a summer maximum and winter minimum, is characteristic of continental interiors in cold temperate climates and is in agreement with the winter temperatures expected. In fact, summer temperatures are similar (around 13°C) but winter values are some-
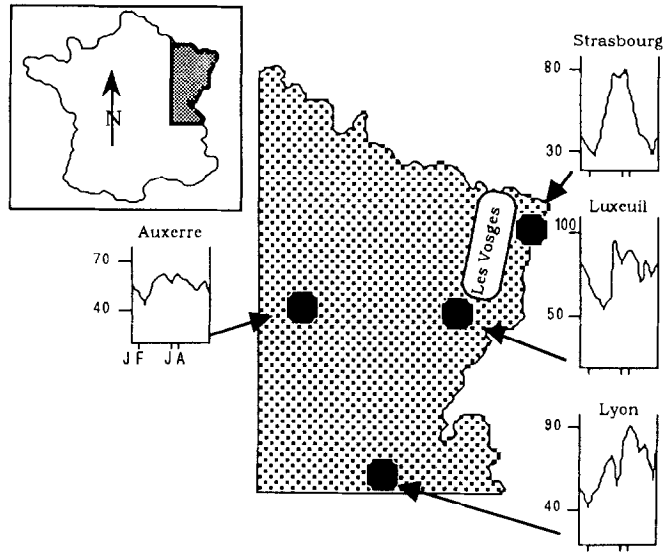
FIG. 6. Modern pluviometric regime of sites close to Achenheim (Strasbourg), La Grande Pile (Luxeuil) and Les Echets (Lyon). The comparison of the regimes between western and eastern sides of Les Vosges mountains characterizes the westerly circulation. Note the differences between Luxeuil and Lyon. J, F, J, A: January, February, July, and August. Also note the differences between January and February, or July and August values. (modified from Pagney, 1976).

what different (about −19°C in La Grande Pile and −11°C in Achenheim). This difference perhaps is due to the occurrence of glaciers on the western side of Les Vosges mountains, but also perhaps results because of the different months taken into account.

What are the implications of such an interpretation? First, responses to climatic constraints cannot be generalized because of the influence of local conditions where altitude is a dominant factor. The example of the last climatic cycle in Achenheim and La Grande Pile is significant. During pleniglacial stages, these two sites were under a cold continental–interior climate. Although summer temperature estimates for the two sites are similar, differences appear in winter. The precipitation regime also seems similar, although differences due to the exposure to westerly winds tend to appear.

Second, does interpretation of the general trends expressed by temperature and precipitation estimates during the last three cycles agree with the mechanisms described by Ruddiman and McIntyre (1981)

for ice growth and ice decay? As was recognized by Guiot from the pollen series, continental ice growth implies that the temperature decreases on the humid continent, in agreement with oceanic mechanisms, while the Atlantic Ocean remains warm between 50° and 60°N. The mollusc record suggests favorable periods for continental ice growth between 310,000 and 303,000 yr B.P., 218,000 and 204,000 yr B.P., 200,000 and 186,000 yr B.P., and 84,000 and 71,000 yr B.P. (Fig. 7). If we refer to Berger (1979), we have to pay attention to some proposed dates for the beginning of insolation signatures which occur in the different stages (315,000, 220,000, 199,000, 105,000, and 84,000 in warm stages and 290,000 yr B.P. in cold stage 8). The first dates occurring in interglacial stages are in relatively good agreement with the beginning of the proposed ice-growth phases recorded in the Achenheim sequence (Figs. 4 and 5). They indicate a period of diminished summer insolation characterized by a strong negative peak and a weak late winter insolation. Several signatures appear in stages 7 and 5
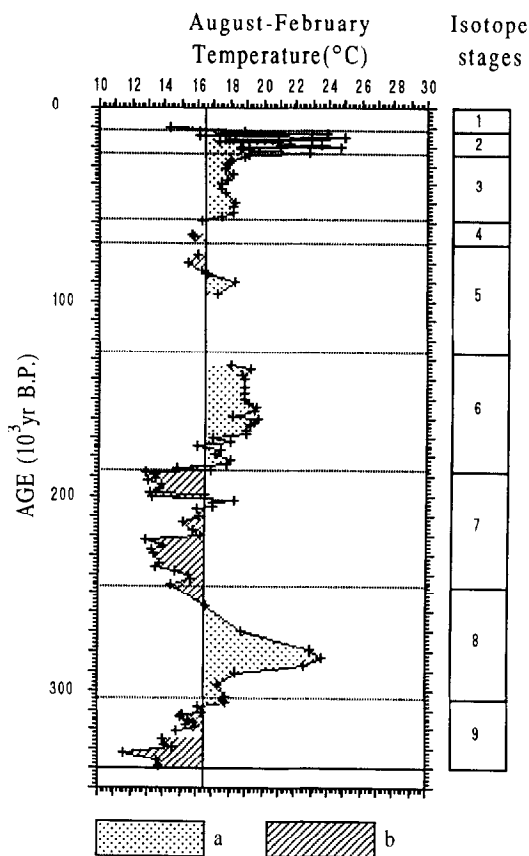
FIG. 7. Difference between August and February temperature estimates (a) Characteristic periods where winter deviations from modern values are higher than summer values, (b) periods where summer deviations are high and winter deviations are weak.

(220,000, 200,000, 105,000, and 84,000 yr B.P.), but none occurs in the cold stages that immediately follow them. On the contrary, one signature during stage 8 (290,000 yr B.P.) corresponds to one signature in stage 9 (315,000 yr B.P.) (Figs. 4 and 5).

The correspondence of the observations in the Achenheim record and the variations calculated by Berger is important. The signature occurrences during stages 9 and 8 are also singular characteristics which distinguish this pair of stages from those that succeed them. They imply that major ice growth was not complete during interglacial stages.

Decreasing winter precipitation corresponds to decreased moisture extraction by

the atmosphere from the ocean due to decreased winter insolation, which further leads to increased winter sea ice and decreased winter precipitation. Increased summer insolation increases the flow of icebergs to the ocean and decreases summer precipitation which causes ice decay. In the Achenheim record, the results of these oceanic mechanisms are recognized during periods connected with terminations I and II (Figs. 4 and 5).

The temperature and precipitation estimates obtained from the Achenheim sequence clearly indicate that the climatic course defined for each of Kukla's (1977) interglacial–glacial climatic cycles cannot be superimposed on other cycles on the continent; however, these results can also be observed in the sequences defined in Atlantic cores. In continental settings, each cycle has its own characteristics: winter and summer temperatures and precipitation evolve through time, following a particular pattern that the marine $\delta^{18}O$ curve cannot explain. For this reason, many continental investigations must be pursued and the results compared with the oceanic results. From a more dynamic point of view, if the mechanisms of Ruddiman and McIntyre can be generalized for at least the last three climatic cycles, circulation patterns were not identical, which implies that climate modeling of the last glacial age cannot be used as a general analog for earlier climatic cycles.

CONCLUSION

The results of this study indicate that transfer functions can be applied to gastropods in long terrestrial loess sequences where they generally constitute the sole biological remains present insufficient quantity for paleoclimatic analysis. The estimates achieved are generally consistent with those obtained from pollen transfer functions, but they also agree with some of the oceanic results, particularly those concerning ice volume transformations. In this way, molluscs can contribute greatly to pa-

leoclimatic reconstructions on a global scale. Molluscs are sufficiently widespread in calcareous loess as to make them of regional importance in paleoclimatic reconstructions. New sets of paleoclimatic data can likely be obtained from such deposits, especially in long sequences covering numerous climatic cycles, as in eastern Europe or in China. This prospect presents a new challenge for students of the continental Quaternary record.

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