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West-European terrestrial molluscs assemblages of isotopic stage 11 (Middle Pleistocene): climatic implications

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ABSTRACT

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Tufa deposits in the Seine and the Avelasse Valleys have yielded numerous molluscs assemblages belonging to the *Lyrodiscus* Biome. These malacofaunas, primilarily indicative of forest which developed under a warm climate, have no present-day counterpart. The biostratigraphical study of several localities based on new investigations at Vernon (Seine Valley) and Arrest (Avelasse Valley) and a reexamination of the faunas from St Pierre-lès-Elbeuf suggests the allocation of a Holsteinian age. This is supported by U/Th dates for Vernon and the stratigraphy of the loess sequence of St Pierre-lès-Elbeuf. Similar assemblages yielded by tufas of the same age in England and Germany indicate that the *Lyrodiscus* Biome was widespread. The warm climate recorded by the molluscs of the tufa deposits is in agreement with pollen and marine analyses for the isotopic stage 11 (362–423 kyr B.P.). In this way, the *Lyrodiscus* Biome appears as an interesting marker for the continental Quaternary in Western Europe. If the occurrence of these particular molluscan assemblages is due to climate, refuges from the declined Tertiary biota, from which i.e *R. (Lyrodiscus)* could have emigrated, also needed to exist.

Introduction

Among biological remains which occur in continental deposits, pollen are frequently used to reconstruct paleoenvironments. Numerous studies demonstrate that climatic changes occurred at roughly the same times in the oceans and on the continents (Peteet et al., 1990; Rossignol-Strick, 1983; Woillard, 1978; Van der Hammen et al., 1972). In other geological contexts, molluscs also provide good ecological data which complement the botanical data (Kerney, 1963; Lozek, 1964; Puisségur, 1976). In the Achenheim loess series (Rousseau and Puisségur, 1990a), variations in the components of the molluscan associations are similar to the isotopic $\delta^{18}O$ curve provided by SPECMAP (Imbrie et al., 1984). Here we report the results of a malacological investigation made in terrestrial tufas, from the Seine and the Somme valleys in northern France (Fig. 1). A comparison is made with continental pollen and marine records.

New malacological records

Vernon

The Vernon tufa is a complex deposit, located in the Seine Valley, about 70 km west of Paris (Fig. 1) which shows two different stages of development (Lécolle et al., 1990) (Fig. 2):

(a) A thick travertine, well indurated in places or showing alternating discontinuous smooth-indurated levels, constitutes the base of the upper part. The travertine is one to several meters thick,

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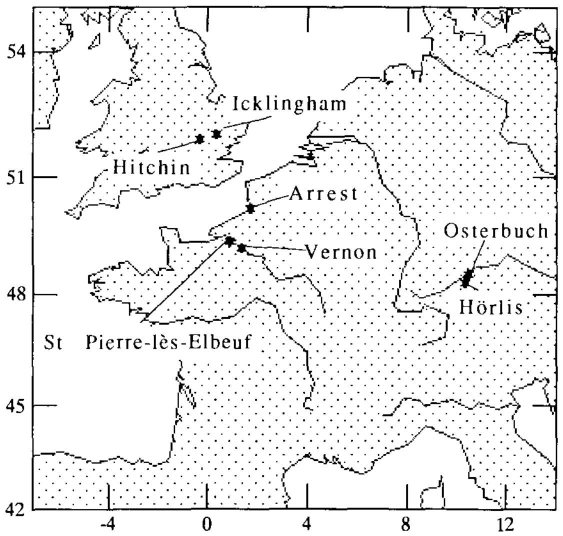

Fig. 1. Location of the different sites discussed in the text.

and consists of a so-called slab, rich in molded plant remains such as roots, branches or leaves. A two meter or so thick, smooth tufa overlays the travertine and is locally indurated. Sediment was taken for malacological investigation from this smooth unit. All these horizons are light in color. The morphology and position of the bed-rock are unknown.

(b) The lower part is dissociated from the previous one because it corresponds to the colluviation of upper part of the tufa and its rubefaction. According to a geological and geomorphological study (Lécolle, 1989), this second part corresponds to another time of deposition, clearly distinct from the upper one.

Determination of the species, present from a previous sampling in the upper non-cemented tufa, indicates that the assemblages are unique in their composition (Table 1). They do not correspond to any classical association as determined by Puisségur (1976) for northern France, but seem to be the western equivalent of the eastern European Banatica fauna (Rousseau, 1992). Four taxa are extinct: *Retinella (Lyrodiscus) skertchlyi* (Rousseau and Puisségur, 1990b), *Aegopinella bourdieri* (Rousseau and Puisségur, 1989), *Succinea joinvillensis* and *Catinella antiqua*. Six species no longer live in northern France: *Leiostyla anglica*, endemic in the British Islands, *Hygromia cinctella* present in Southern Europe, and *Discus ruderatus*, *Acicula polita*, *Aegopis verticillus* and *Ruthenica filograna* from Central Europe (Kerney et al., 1983) (Fig. 3). The other species still live in northern France, and a few aquatic taxa are also present.

In addition to this apparent heterogeneity of the assemblage, the occurrence of *Retinella (Lyrodiscus) skertchlyi* is another peculiarity. This species

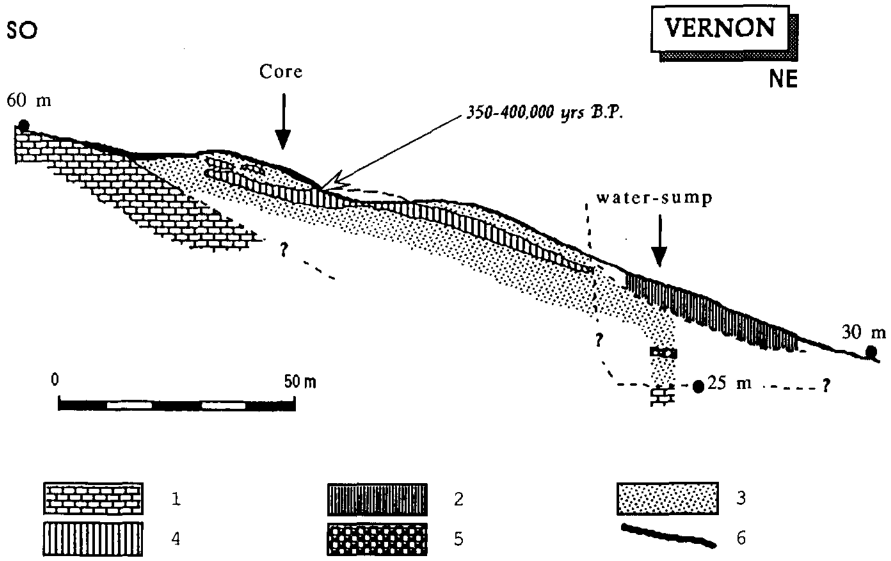

Fig. 2. Geomorphological and stratigraphical interpretation of the tufaceous formation in Vernon. *1* = substratum (chalk); *2* = rubefaction; *3* = smooth facies tufa; *4* = travertine; *5* = "sugar-plum" facies tufa; *6* = colluvium (from Lécolle et al., 1990 modified).

TABLE I

Vernon, first malacological investigations. List of different species recognized in the samples and individuals counted.

Species \ Levels	1	2	3	4	5	/ Ecol. Groups
Acanthinula aculeata	23	31	6	4	4	
Acicula polita	3			1		
Azeca goodalli	2	15	2	3	3	
Aegopinella nitidula	47	90	12	33	35	
Aegopinella pura	38	96	15	15	18	
Aegopinella bourdieri	1					
R. (Lyrodiscus) skertchlyi	1	23	4	18	30	
Helicodonta obvoluta	22	5	3	7	5	1
Clausilia bidentata	20	8	1	1	13	
Cochlodina laminata	7	6	3		3	
Perforatella incarnata		8	3	10	8	
Orcula doliolum		25	2	4	45	
Aegopis verticillus		1			1	
Ena montana				3	2	
Ruthenica filograna				19	36	
Discus ruderatus					6	
Discus rotundatus	53	95	24	70	1	
Acicula dupuyi	11					
Cepaea sp.	35	50	18	15	50	
Bradybaena fruticum	4	15	6	4	7	
Hygromia cinctella	12					
Pomatias elegans	45	60	18			2
Laciniaria biplicata	2	4	1	10	30	
Vitrea crystallina	67	130	20			
Arianta arbustorum		12	4	5	6	
Macrogastra ventricosa	9	1		1	1	3
Cecilioides acicula	4					4
Vallonia costata			1	2	29	5
Trichia hispida	6	43	6	40	70	
Helicigona lapicida	2	4	4	1	2	
Euconulus fulvus	1	2				
Punctum pygmaeum	2					
Vitrina pellucida	6	6	1	4		7
Oxychilus alliarius	21					
Clausilia parvula	7	5		4		
Vitrea contracta	23	49	8	20	3	
Cochlicopa lubrica		31	7	14	7	
Limax sp.	10	16	4	2	25	7'
Carychium tridentatum	2	20	2		3	
Succinea joinvillensis	13	4	3		5	
Succinea oblonga	1					8
Catinella antiqua		1	1			
Columella edentula	1					
Leiostyla anglica		3	1	1		
Succinea putris		10	3	6		9
Zonitoides nitidus				1		
Belgrandia sp.	1	2		1		
Galba truncatula		7	1	2		10
Pisidium sp.		1				

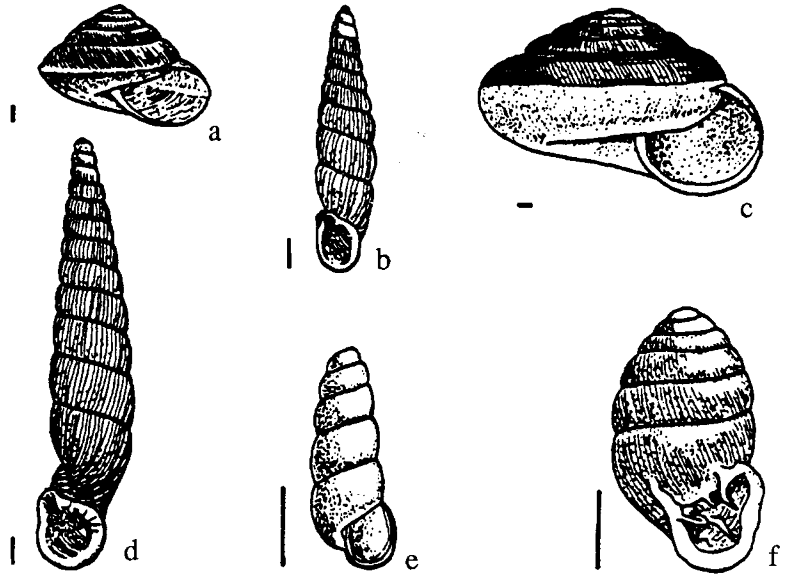

Fig. 3. Some of the allochthonous species, according to their present distribution, occurring in tufa assemblages. a. *Hygromia cinctella*; b. *Ruthenica filograna*; c. *Aegopis verticillus*; d. *Laminifera pauli*; e. *Acicula polita*; f. *Leiostyla anglica*. The scale represents 1 mm.

has related endemic species in the Canary archipelago (Kerney, 1976; Rousseau and Puissègur, 1990b).

The assemblages show a high dominance of forest species (Fig. 4a, b). This implies a forest environment that developed under a climate with warmer and drier summers than today in the same area. The occurrence of fossil leaves and seeds, including *Ficus*, which today has a more southern natural distribution, confirms the climatic interpretation.

A new investigation provides more detailed data from these pulverent deposits (Fig. 2 and 5). Above the travertine, 9 samples were taken corresponding to different recognized horizons according to color and induration of the sediment. Two additional samples were taken to control the base of the core and correlated on the basis of lithology, with the first two samples of the main core.

Three kinds of deposits, from bottom to top (Fig. 5), overlay the travertine:

—a relatively non-cemented tufa, with weakly indurated levels of various colors (−3.6 to −2 m),

—deposits with a loamy facies which seem to

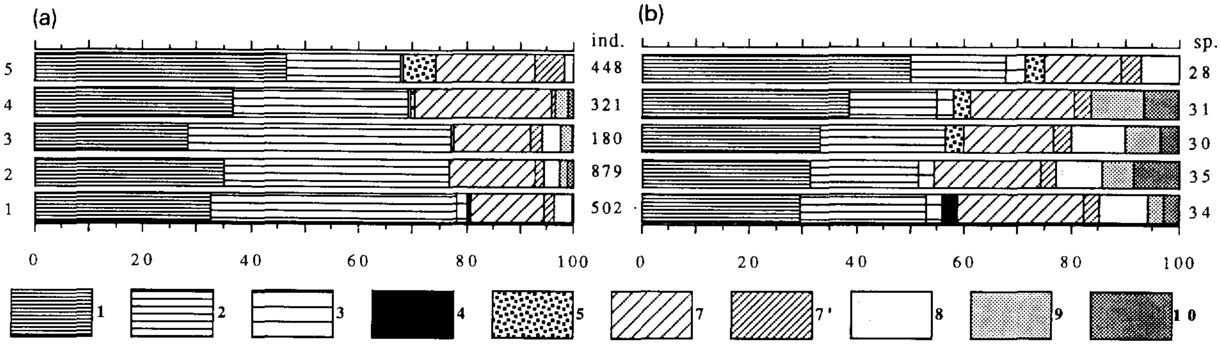

Fig. 4. Vernon. First malacological investigations. Variation of the percentage in (a) individuals (*ind.*) and (b) species (*sp.*) within each ecological group, according to Puissègur (1976). Signification of the groups: *1* = forest, *2* = open forest, *3* = damp forest, *4* = steppe, *5* = open ground, *7* = mesophilous taxa, *7'* = slugs, *8* = hygrophilous taxa, *9* = paludal, *10* = fresh water.

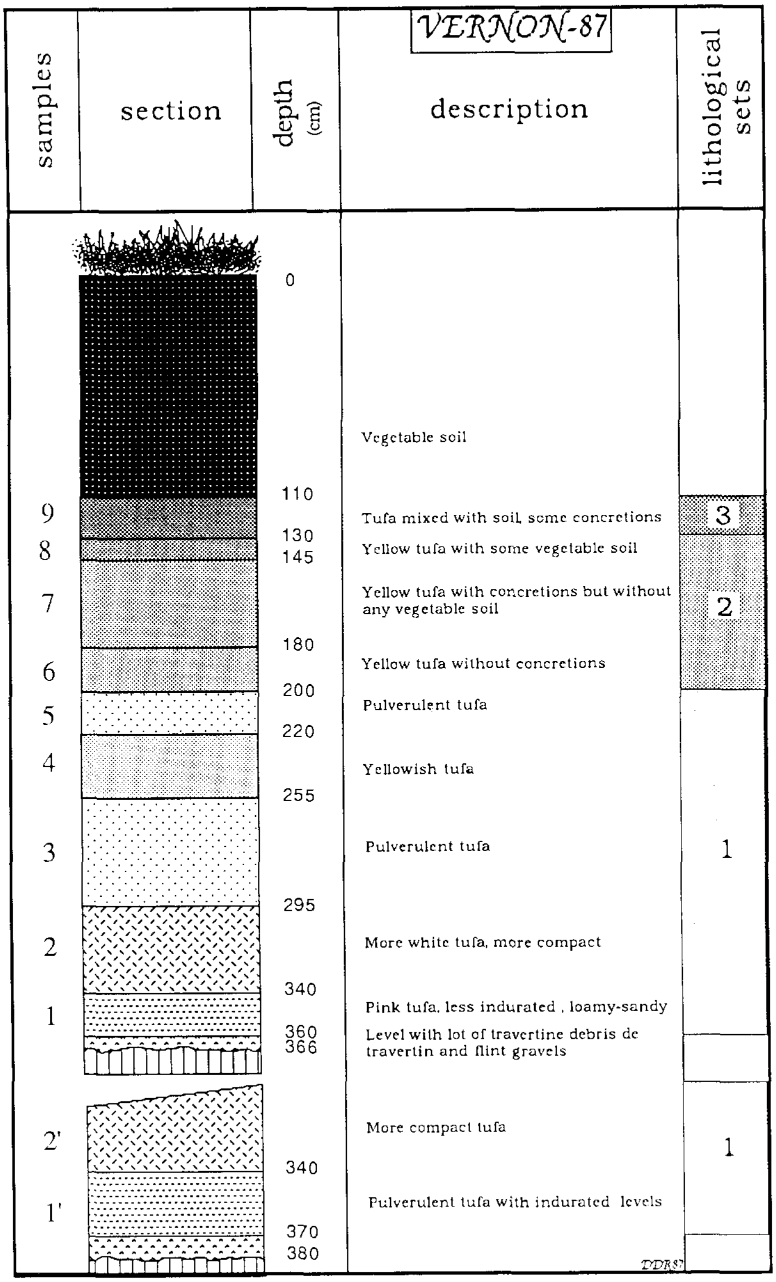

Fig. 5. Vernon. New malacological investigations. Location of the different malacological samples and schematic lithological description of the levels. *1–3* correspond to the different groups recognized.

correspond to a degradation of the tufa (−2 to −1.3 m)

—a composite of tufa and soil under the modern soil.

The list of the recognized species shows high diversity and abundance (Table 2). Moreover, the variations in the total number of individuals occurring in each ecological group, sensu Puisségur (1976), is in agreement with the three previously defined units based on lithology (Fig. 6).

TABLE 2

Vernon, new malacological investigations. List of different species recognized in the samples and individuals counted.

Species \ Levels	9	8	7	6	5	4	3	2	1	2'	1'	/ Ecol. Groups
Aegopinella nitidula	3		4	4	34	25	35	12	20	18	6	
Aegopinella pura		1		1	14	21	12	3	2	6	3	
Helicodonta obvoluta		1	3	2	31	10	8	6	6	8	8	
Ena obscura			1									
Azeka goodalli			1	2	2	2	5		1	3		
Aegopinella bourdieri					5	4						
Cochlodina laminata					2	3	6	2		1	1	1
Perforatella incarnata					3	1		1		1		
Acanthinula aculeata					3	1	4	4	4	5	1	
Aegopis verticillus					3	5	1		2		1	
Clausilia bidentata					4	5	3	2	4	2		
Pomatias elegans	20	4	3		9	30	17	18	9	5	4	
Discus rotundatus	7	1	3	5	17	22	8	31	12	8	1	
Cepaea sp.	7	3	2	5	35	35	30	28	27	10	16	
Hygromia cinctella			1	2	6	2	1	2	1	1	2	
Laciniaria biplicata			1		2	2						2
Arianta-Bradybaena					1	1	2		1		1	
Acicula dupuyi						3	1			15		
Vitrea crystallina							1		7	1	2	
Acicula polita										1		
Macrogastra ventricosa					1	2	2	1	1		1	3
Cecilioides acicula	37	6	2	3								
Helicella sp.	12	7	3	1								4
Vallonia costata	200	16	15	2								
Vallonia pulchella	50	3										5
Pupilla muscorum	3	1	2	1								
Helix aspersa		1	1	1								
Trichia hispida	213	16	17	1	3	3	5			1		
Cochlicopa lubrica	43	1	1									
Oxychilus sp.	5	1	3	1	3							
Nesovitrea hammonis	5											
Vitrea contracta	1	1	1	2	7	3	1	1	1	1		7
Clausilia parvula	3			1								
Helicigona lapicida					4	4	2	1	1	1	1	
Vitrina pellucida				1	13	3	3	2	2	2		
Punctum pygmaeum									1			
Limax sp.	13		1		1	2	2	1		1	3	7'
Succinea oblonga	71	3	1	2							1	
Carychium tridentatum									1			8
Succinea putris	12					2						
Zonitoides nitidus	10		2	2	6	3	3	4	4	5		9
Carychium minimum	3											
Planorbis planorbis	5											
Galba truncatula	4											
Belgrandia sp.						1	1					10
Ancylus fluviatilis							1					

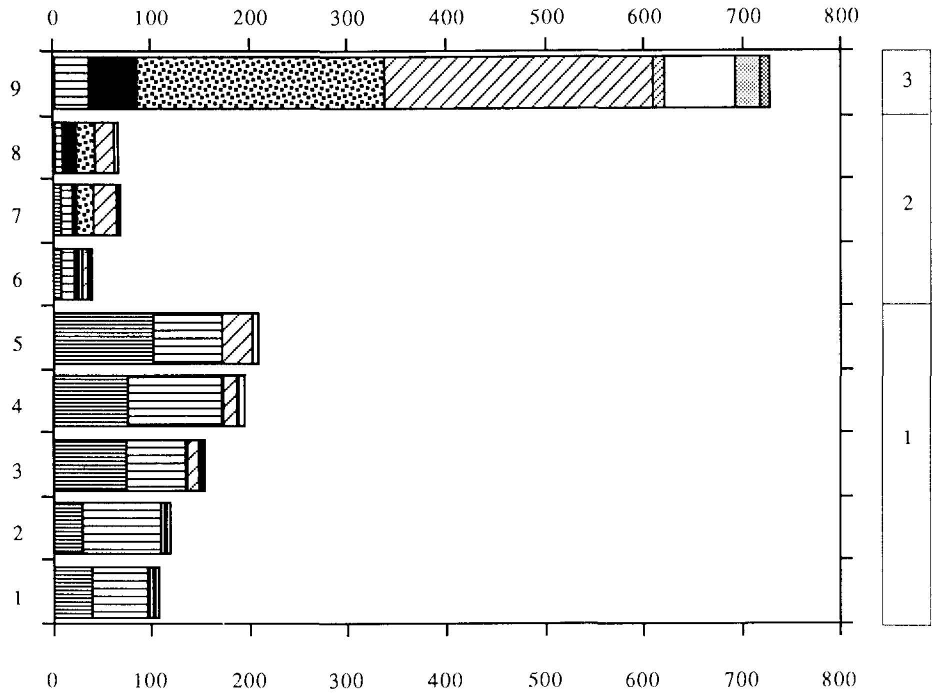

Fig. 6. Vernon. New malacological investigations. Variation of individual numbers in each ecological group (see legends in Fig. 4).

An increasing number of individuals from bottom to top and a high percentage of forest taxa characterize the malacofauna of the first unit. The second unit shows a generally decreasing number of individuals, a decrease in forest species, and the occurrence of steppe and open ground taxa. Finally the number of individuals increases sharply again in the top sample. This increase does not correspond to a bias in the sampling as this is a 20 cm sample taken under conditions roughly similar to the others.

This tripartition occurs when the different assemblages are compared, using species and individuals spectra of the following ecological groups: (1) forest, (2) semi-forest, (3) moist forest, (4) steppe, (5) open ground, (7) mesophilous, (7)' slugs, (8) hygrophilous, (9) paludal and (10) aquatic species (Fig. 7a, b). These ecological groups are defined according to the ecology of each mollusc species (Lozek, 1964; Puisségur, 1976).

The first unit reflects the high dominance of forest taxa, especially in the number of individuals, and has a small aquatic component (three individuals in samples 3 and 4 (fig. 7). However, moisture is indicated by the occurrence of *Macrogastra ventricosa* (Table 2). The lack of aquatic species agrees with the occurrence of a non-permanent spring, an interpretation previously suggested by Puisségur (Puisségur in Lécolle, 1989). At the top of this unit (sample 5; Table 2), the proportion of mesophilous species increases. The species *Helicigona lapicida*, which has a preference for a slight forest covering, does not occur above sample 5. This development agrees with the general evolution of the malacofaunas.

Variations in group 7 permit the definition of the second unit (Fig. 7), which represents a more open environment. In this unit the progressive decrease of the forest taxa occurs from bottom to top (fig. 7), corresponding to increasing steppe and open ground species. The forest component gradually decreases after sample 5 and is replaced by a grassland in which still occur some trees or bushes.

The last sample, corresponding to the third unit, shows a completely open environment in which few bushes remain.

Characteristic taxa, *Hygromia cinctella*, *A. bourdieri*, *A. verticillus* and *A. polita* (Fig. 3), occur only in the first unit (Table 2) confirming its interglacial allocation, followed by unit two repre-

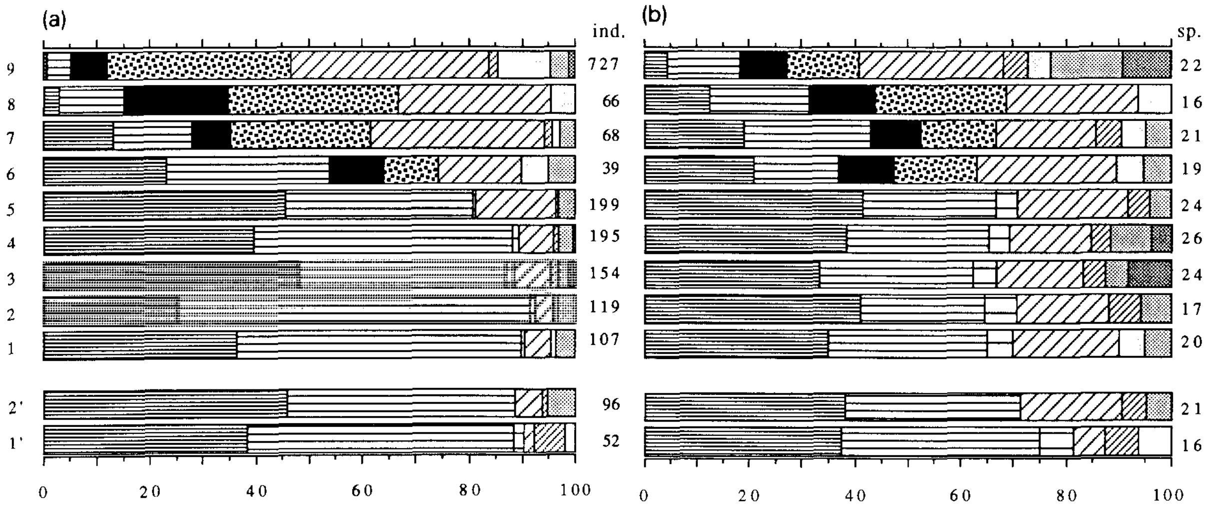

Fig. 7. Vernon. New malacological investigations. Variation of the percentage in (a) individuals (*ind.*) and (b) species (*sp.*) within each ecological group, according to Puisségur (1976) (see legends in Fig. 4).

senting the degradation phase. Under these conditions the correlation with the previous samples (Table 1), a few meters away, is proposed as follows.

1972	new study
Sample 5	sample 6
Sample 4	sample 5
	sample 4
Sample 3	sample 3
Sample 2	sample 2
Sample 1	sample 1

The travertine samples were dated using the ^{230}Th/^{234}U method. The measurements indicate a radioactive equilibrium implying an age equal to or older than 350,000–400,000 yr B.P. (Lécolle et al., 1990). We suggest a correlation with isotopic stage 11, in agreement with the geomorphological and stratigraphical context of this area (Lécolle, 1989).

The composition of the malacofaunas, provided by the two series of samples in Vernon, confirms the biostratigraphic correlation proposed between Vernon and La Celle-sous-Moret (Bourdier et al., 1969). In these two sites, the tufaceous sedimentation is connected with a biological association which gathers both plant and molluscs associations. According to Clement's (1949) definition of a biome, which evokes that animal populations are associated with formations of wide vegetal complexes, a biome being thus a community of plants and animals usually of the rank of a formation which in other words represents a climatic vegetal and animal community, we can determine the *Lyrodiscus* Biome for this particular Pleistocene community (Rousseau, 1992). Its malacological and botanical composition (occurrence of the fig tree, the laurel of the Canary islands, *Buxus*, *Celtis*) is clearly heterogenous compared to the present time.

St Pierre-lès-Elbeuf

In the Seine Valley, 42 km west of Vernon (Fig. 1), the St Pierre-lès-Elbeuf deposits yield an important continental record of the Middle and Upper Pleistocene (Lautridou et al., 1974). This locality is a key loess section for Western Europe (Lautridou, 1985). Five non-calcareous loess units were recognized, separated by four interglacial Bt soils: Elbeuf I = Eemian, Elbeuf II, III = intra-Saalian, and Elbeuf IV (more weathered than the others) of Holsteinian age (Lautridou et al., 1974). A calcareous tufa, which yielded a rich malacofauna, overlays this soil (Fig. 8).

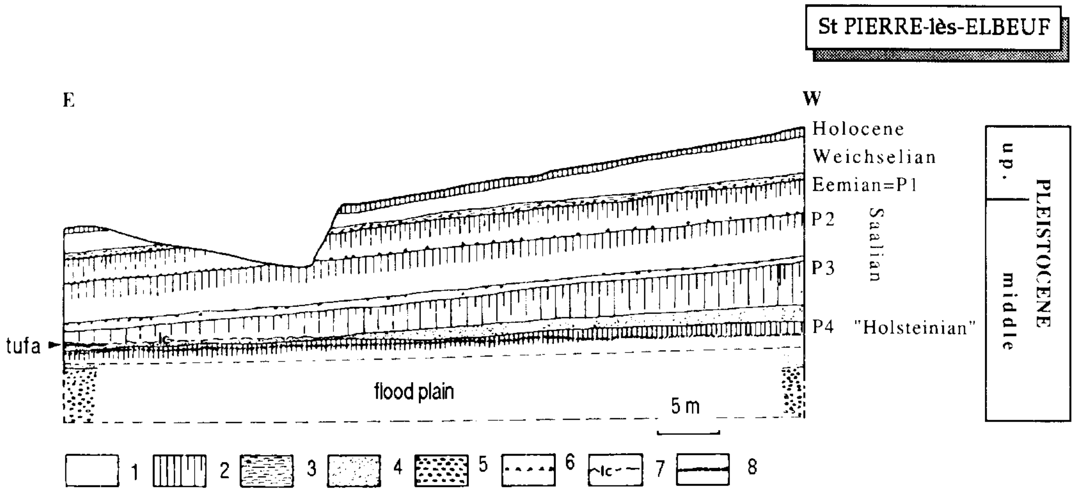

Fig. 8. St. Pierre-lès-Elbeuf. Main outcrop showing the stratigraphic sequence. *1* = loess, *2* = paleosol, *3* = humiferous soils, *4* = fluviatile sands, *5* = fluviatile gravels, *6* = stone line, *7* = "liseré chocolat", *8* = base of the quarry. The "liseré chocolat" corresponds to a thin brown layer of argilans (paleosol III) fixed upon the calcareous tufa (*Bt*) (from Lautridou et al., 1983, modified).

The malacofauna is typically interglacial (Table 3). Thirteen forest species correspond to 33.8% and 9 semi-forest species to 32.3% of the total amount. The occurrence of species representative of steppe, open ground, xerophilous ecological groups seems to be accidental. Aquatic species are well represented, but the St Pierre malacofauna cannot be an aquatic dominant fauna since it typically characterizes a moist forest where intermittent streams supply semi-permanent pools (Fig. 9a: *A*, *B*).

Fossil species, *Retinella (Lyrodiscus) skertchlyi*, *Aegopinella bourdieri*, as well as *Laminifera pauli* (endemic in the Bayonne neighborhood) and *Hygromia cinctella* (Fig. 3), a mediterranean taxon (Table 3) occur as well.

The proximity of both Vernon and St Pierre-lès-Elbeuf permits a correlation to be made based on geomorphological (Lécolle, 1989) and biostratigraphical evidence. Holsteinian age is suggested for the Vernon upper tufa, in agreement with the radiometric age reported by Lécolle et al., 1990.

Arrest

The Arrest site is located in a small valley of the Avalasse river, 8 km south of the Somme estuary (Fig. 1). Tufas occur 22 m above the present-day river level (Fig. 10). These tufas impregnated the underlaying chalk which is consolidated. The following succession was observed from the base to the top (Bourdier, pers. comm.): a silty tufa with white concretions providing malacofaunas, a non-cemented level, an indurated level in which one meter thick pedological pockets are present, and finally a colluvium layer. A level of rounded flint gravel occurs between the indurated chalk and the tufas.

As determined in the previous sites, the malaco-

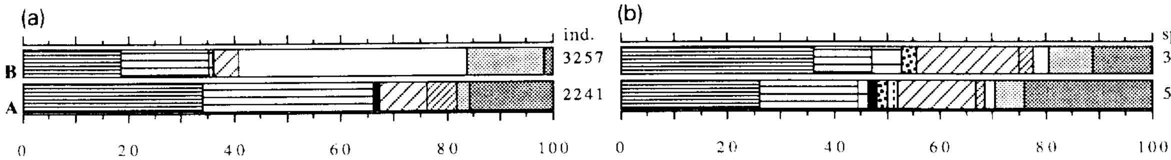

Fig. 9. Variation of the percentage in (a) individuals (*ind.*) and (b) species (*sp.*) within each ecological group, according to Puisségur (1976). *A* = St Pierre-lès-Elbeuf. *B* = Arrest (see legends in Fig. 4).

TABLE 3

St. Pierre-lès-Elbeuf. List of different species recognized in the samples and individuals counted.

Species	/	Ecol. Groups
Ena montana	25	1
Acicula polita	5	
Acanthinula aculeata	57	
Helicodonta obvoluta	60	
Aegopinella pura	212	
Aegopinella nitidula	192	
Cochlodina laminata	35	
Macrogastra rolphii	2	
Clausilia bidentata	100	
Macrogastra plicatula	4	
Perforatella incarnata	2	
Aegopinella bourdieri	52	
Aegopis acieformis	16	
R. (Lyrodiscus) skertchlyi	1	
Discus rotundatus	345	2
Acicula dupuyi	17	
Vitrea crystallina	63	
Laciniaria biplicata	25	
Laminifera pauli	11	
Cepaea hortensis	200	
Arianta arbustorum	20	
Bradybaena chouquetiana	1	
Bradybaena fruticum	19	
Hygromia cinctella	16	
Macrogastra ventricosa	12	3
Cecilioides acicula	1	4
Vallonia costata	3	5
Monacha cartusiana	2	6
Punctum pygmaeum	25	7
Trichia hispida	28	
Vitrina pellucida	5	
Helicigona lapicida	10	
Vitrea contracta	35	
Euconulus fulvus	1	
Clausilia parvula	93	
Oxychilus sp.	16	
Limax sp.	121	7'
Carychium tridentatum	2	8
Vertigo antivertigo	10	9
Succinea putris	27	
Zonitoides nitidus	17	
Pisidium sp.	22	10
Valvata piscinalis	172	
Ancylus fluviatilis	15	
Bathyomphalus contortus	2	
Galba truncatula	5	
Galba palustric	33	
Bulimus sp.	2	
Radix ovata	9	
Limnaea stagnalis	6	
Gyraulus albus	60	
Planorbis pl. -carinatus	18	
Physa fontinalis	1	
Belgrandia sp.	8	

TABLE 4

Arrest. List of different species recognized in the samples and individuals counted.

Species	/	Ecol. Groups
Acanthinula aculeata	70	1
Aegopinella nitidula	176	
Aegopinella pura	149	
Azeca goodalli	50	
Clausilia bidentata	12	
Cochlodina orthostoma	2	
Clausilia sp.	58	
Discus ruderatus	57	
Ena montana	9	
Helicodonta obvoluta	4	
R. (Lyrodiscus) skertchlyi	11	
Vertigo pusilla	1	
Vitrea subrimata	7	
Arianta + Bradybaena	7	2
Cepaea sp.	30	
Discus rotundatus	224	
Vitrea crystallina	284	
Perforatella bidentata	15	3
Macrogastra ventricosa	2	
Vallonia costata	8	5
Clausilia dubia	15	7
Cochlicopa lubrica	14	
Euconulus fulvus	5	
Helicigona lapicida	1	
Nesovitrea hammonis	3	
Trichia hispida	80	
Vitrea contracta	36	
Limax sp.	1	7'
Carychium tridentatum	1399	8
Carychium minimum	466	9
Succinea putris	4	
Vertigo antivertigo	2	
Anisus leucostomus	24	10
Galba palustris	4	
Galba truncatula	5	
Pisidium sp.	22	

fauna is typically interglacial (Table 4). Forest and semi-forest species represent 52.78% of the total number of species and 35.86% of the total number of individuals (Fig. 9b: *A*, *B*). The environment is the same as that of St Pierre-lès-Elbeuf. A moister forest accompanied the occurrence of *Perforatella bidentata*, *Macrogastra ventricosa* and a high number of *Carychium tridentatum* (Table 4). Contrary to the two previous sites, few allochtonous species occur. Only the fossil *Retinella (Lyrodis-*

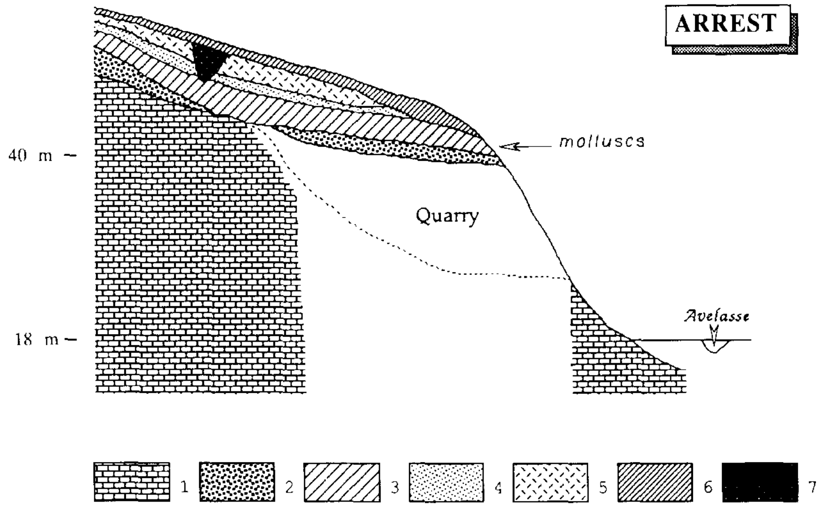

Fig. 10. Arrest. Schematic distribution of the stratigraphy. *1* = substratum (chalk); *2* = rounded flint gravels; *3* = white silty tufa with some concretions; *4* = non-cemented tufa; *5* = indurated tufa; *6* = colluvium; *7* = pedological pocket (from Bourdier, pers. comm., modified)

cus) skertchlyi and the central European *Discus ruderatus* were recognized.

The occurrence of these deposits in the Somme Valley implies that this particular assemblage is not a response to the microclimate of the Seine Valley. At least four localities, in an area of about 210 km long, recorded this ecological event. Similar assemblages in the surrounding countries of this area, already published, are examined to determine whether further evidence of this occurrence exist.

Other West-European malacological records

England

Kerney described a particular malacofauna from tufas in Icklingham (1976) and Hitchin (Kerney, 1959; Holyoak et al., 1983). These two assemblages, typifying an interglacial forest environment (fig. 11a: *a*, *b*), are characterized by the occurrence of species which have no relatives today in the British Isles (Table 5). The assemblages contain the fossil *Acicula diluviana* and *Retinella (Lyrodiscus) skertchlyi*, the central European *Semilimax semilimax*, *Clausilia parvula* and *Acicula polita*, the East European *Ruthenica filograna* and the West European *Laminifera pauli* (Fig. 3). The age allocated to these tufas is Hoxnian, the British equivalent of the Holsteinian (Kerney, 1977).

Germany

Münzig (1974) described the malacofaunas from a carbonaceous silty level in the Swabian Jura, at Hörlis, southwestern Germany (Table 6). Once more the composition is heterogeneous and seems to be similar to those already found in France and England (Fig. 11b: *A*, *B*). Apart from the extinct *R. (Lyrodiscus) skertchlyi*, the Atlantic species *Clausilia bidentata*, and *Azeca goodalli* occur

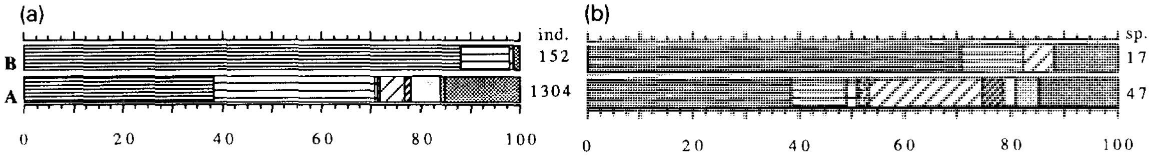

Fig. 11. Variation of the percentage in (a) individuals (*ind.*) and (b) species (*sp.*) within each ecological group, according to Puisségur (1976). *A* = Icklingham (England). *B* = Hörlis (Germany) (see legends in Fig. 4).

TABLE 5

Icklingham. List of different species recognized in the samples and individuals counted (from Kerney, 1976).

Species		/ Ecol. Groups
Acanthinula aculeata	50	1
Acicula diluviana	5	
Acicula polita	64	
Aegopinella nitidula	78	
Aegopinella pura	98	
Azeca goodalli	92	
Clausilia bidentata	2	
Cochlodina laminata	1	
Cochlodina sp.	5	
Clausilia sp.	28	
Ena montana	2	
Helicodonta obvoluta	4	
R. (Lyrodiscus) skertchlyi	37	
Ruthenica filograna	1	
Vertigo pusilla	6	
Vitrea subrimata	7	
Zenobiella subrufescens	1	
Zonitoides excavatus	20	
Arianta arbustorum	3	2
Cepaea nemoralis	3	
Discus rotundatus	289	
Pomatias elegans	25	
Vitrea crystallina	101	
Clausilia pumila	1	3
Vallonia costata	4	5
Balea perversa	1	7
Clausilia parvula	1	
Cochlicopa sp.	2	
Euconulus fulvus	10	
Helicigona lapicida	2	
Nesovitrea hammonis	3	
Oxychilus cellarius	3	
Oxychilus sp.	2	
Punctum pygmaeum	30	
Vitrea contracta	17	
Deroceras/Limax	12	7'
Milax sp.	7	
Carychium tridentatum	78	8
Carychium minimum	7	9
Leiostyla anglica	3	
Bathyomphalus contortus	1	10
Bythinia sp.	1	
Hippeutis complanatus	2	
Pisidium obtusale	7	
Planorbis planorbis	2	
Sphacrium corneum	1	
Valvata cristata	175	

TABLE 6

Hörlis. List of different species recognized in the samples and individuals counted (from Münzing, 1974).

Species		/ Ecol. Groups
Acanthinula aculeata	1	1
Aegopinella sp.	9	
Azeca goodalli	82	
Clausilia bidentata	7	
Discus perspectivus	11	
Ena montana	1	
Isognomostoma isognomostoma	6	
Orcula sp.	8	
R. (Lyrodiscus) skertchlyi	5	
Trichia edentula	1	
Vitrea subrimata	2	
Vitrea sp.	1	
Arianta arbustorum	1	2
Eucobresia diaphana	13	
Clausilia dubia	1	7
Lymnea sp.	1	10
Physa fontinalis	1	

Alpine *Isognostoma isognostoma, Eucobresia diaphana, Trichia edentula.* At Osterbuch, southern Germany, the same association is described from a silty level between two Alpine tills (Münzing and Aktas, 1987). The fauna is quite similar to the Hörlis assemblage showing that the distribution of the *Lyrodiscus* Biome reached as far as 11°E.

Discussion and conclusion

As determined from the multidisciplinary investigation of the Biache St Vaast site, a well-defined hierarchy seems to exist between pollen and mollusc records (Sommé et al., 1989). When both remains are in complete agreement, the event can be characterized generally as an interglacial phase. On the contrary, if disagreements occur, mainly in the amplitude of the implied climatic variations, an interstadial episode is implied.

Is this warmest stage, recorded by molluscs, also recognized in the pollen assemblages? First, some fossil leaves and seeds indicate the occurrence of a interglacial warm forest in Vernon and La Celle-sous-Moret (Bourdier et al., 1969). Secondly, based on the continental equivalent of isotopic stage 11, several pollen analyses indicated that the related stratigraphical levels indicate a warm climate.

In Great Britain, Hoxnian substages III and IV indicate an oceanic climate with forests of mainly evergreen composition. Besides the sparse mixed-oak forest elements, Lusitanian components (present-day components of the west Irish flora: *Daboecia cantabrica, Erica mackiana* and *E. ciliaris*), Hiberno-American species (*Eriocaulon septangulare*) or plants which no longer grow there (*Brasenia cf purpurea, Lysimachis punctata, Nymphoides cordata* and *Erica scoparia*) occur (Godwin, 1977).

In southwest France, Texier et al. (1983) drew attention to high temperature conditions during the "Mindel–Riss" stage. The flora contains numerous thermophilous taxa (mixed-oak), hygrophilous herbs but also Mediterranean species (*Rhododendron ponticum, Erica mediterranea*) and taxa with Lusitanian affinities (*Dabaoecia cantabrica*).

The Tenagghi Philippon sequence (41°10'N, 24°20'E), in Greece, indicates a long and warm episode at the base of the Lekanis complex during which herbs completely disappear (Van der Hammen et al., 1972).

All these continental records imply a warmer climate, deduced from the malacofaunas of the *Lyrodiscus* Biome, which occurred in Europe during the isotopic stage 11. However, other data from both continental and marine records also show evidence of a warmer climate during isotopic stage 11.

In the Hula Basin, in Northern Israel, a long pollen sequence shows a well developed episode, part of the QVI zone, correlated with stage 11. During this stage, steppe elements are highly dominant, corresponding to the interglacial extension (Fuji and Horowitz, 1989).

In the Colombian Bogota-Funza cores (4°N, 74°W), changes of the vegetation are recorded over the last 3.5 myr B.P. (Hooghiemstra, 1989). During stage 11, the altitudinal position of the forest line was higher than 3300 m, quite similar to the current position. The prevailing average temperature of the high plain of Bogota was estimated to be greater than 14.8°C, associated with a low lake level (Hooghiemstra, 1989).

Ruddiman and McIntyre (1976) showed that Atlantic Ocean cores recorded a well-developed interglacial stage 11, with high carbonate content and high $^{18}O/^{16}O$ values associated with a high sea level. More recently, DSDP 609 core (49°53'N, 24°14'W) in the Northern Atlantic, indicates the highest carbonate percentages for the last four climatic cycles during stage 11 (Ruddiman et al., 1989). Core V30-97 (41°10'N, 32°56'W) indicates that the largest differences between current and estimated paleo-sea surface temperature for summer and winter (SSTs and SSTw; +5.1°C) also occurred during stage 11 (Ruddiman et al., 1989).

The climatic signal provided by molluscs during stage 11 is in agreement with the results of various pollen analyses which confirm the interglacial characteristics of the *Lyrodiscus* Biome. Moreover, as marine records also indicate warm climatic conditions during this time span, a global warming, in order to microclimatic conditions over Western Europe, can be involved in permitting the development of this particular assemblage. However, this biological association corresponding to isotopic stage 11 never occurred in the following interglacials (i.e. isotope stages 9, 7 and 5). According to the astronomical theory of climate, climatic variations, as a function of insolation, can be explained in terms of changes in the configuration of the three orbital parameters: (1) the longitude of the perihelion, which determines in which season the insolation is maximum, (2) obliquity, which determines where more insolation is directed in summer, and (3) eccentricity, which is a measure of how elliptical the Earth's orbit about the sun is (Berger, 1978, 1982).

Kukla et al. (1981) studied the orbital configuration of each interglacial. They conclude that interglacials have a specific orbital configuration, high obliquity and an autumn perihelion but can present difference in the eccentricity. Stage 11, for example, shows high obliquity, autumn perihelion but low eccentricity. It shares the same characteristics with the Holocene, however. Although stage 11 shows differences with the other interglacials which could involve particular climatic conditions, this does not explain why such a particular assemblage occurred in Western Europe. The variation in the composition of a biome reflects regional ecological impact on the fauna (Rousseau et al., 1990). This explains the differences observed in the malacofaunas of the *Lyrodiscus* Biome between England and Germany, but does not explain, however, where it originated. Because no similar associations were recorded prior to this stage, in France and Engrecorded prior to this stage, in France and England, southern European refuge zones of the declined Tertiary biota can eventually be involved, but need to be investigated. This proposal is mainly based on *R.*(*Lyrodiscus*), the history of which seems to be closely connected to that one of the Tertiary forest (Rousseau and Puisségur, 1990b), which occurred in Europe and Africa, and declined to be restricted, for one part, to the Canary archipelago (Raven and Axelrod, 1974). A precise location of these refuge zones is, today, difficult to draw, but the Spanish Atlantic coast or Northwestern Africa can be proposed. In this way, a limitation, climatic or other, in the opportunities to extend their distribution, can explain the lack of the *Lyrodiscus* Biome during the previous stages. On the contrary, the warmer climatic conditions during stage 11 somehow permitted the molluscs and the plants to occur northward of their restrictive zone. Because such conditions never occurred afterwards and because such assemblages evolved in endemic conditions, the *Lyrodiscus* Biome appears to be a biostratigraphical as well as a biogeographical or climatic marker for the Quaternary in western Europe.

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