

# Biogeography of the Pleistocene pleniglacial malacofaunas in Europe. Stratigraphic and climatic implications

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## ABSTRACT

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As determined by Lozek, malacological associations are significant of a particular vegetal environment. In Quaternary sequences, different types of associations are recognized which can be assimilated to the present types of malacofaunas. There are associations of grass group, of forest group and of the ecotone of these two biogeographical entities. On the European scale, in Pleistocene sequences, the interglacial faunas indicate similarly the same differences as today, being of stratigraphic interest. On the contrary, pleniglacial faunas, which are mainly preserved in the loess belt, seemed not interesting for stratigraphy since they indicate more generalized and more homogeneous conditions. Moreover they are composed of few species which, for the most part, had their distribution area destroyed by the ice-cap advance. Yet, the global analysis of pleniglacial biome faunas, by ecological biogeographical approach, provides a particular stratigraphic element which allows to determine stratigraphic entities, provinces or domains in accordance with sedimentary interpretations. So, for Quaternary pleniglacial faunas, the biozone concept is efficiently supplied by ecostratigraphy. Consequently to a review of European localities, it appears that the distribution of pleniglacial malacofaunas is mainly controlled by precipitations. So the variations which are recorded in some privileged deposits, as the Achenheim sequence in Alsace (France), indicate variations through time of eastern limit of oceanic facies and western limit of continental facies of the climate.

## Introduction

Distribution of communities in stratigraphy is the topic of biostratigraphy. It is based on the widely used concept of biozone where the main useful tool to approach the real chronology is defined by the appearance and disappearance of taxa (the extension zone of taxa, Hedberg 1976). In other words it is mainly defined by taking into account high evolutive taxa and refuting

(a) the too generalist organisms, widely distributed, which are in stasis and which consequently are insufficiently informative,

(b) the high environmental influenced organisms (ecophenotypes) as their occurrence can be repeated within a sequence.

The typical case of such biostratigraphy is Mesozoic biozonation by ammonites. That point of view, though it gives good results in purely

dating studies, puts aside the causal aspect of the distribution of life which cannot be analyzed in this way. Taxa, communities are constrained by limiting factors such as temperature, hygrometry, insolation, salinity, depth of water which can vary so that the biosphere and the geosphere record these variations. These considerations originated the ecostratigraphic concept, defined by Martinsson (1973), to react against the rigid scope of biozone. He proposes to integrate the ecological aspect of community distribution in stratigraphy using "the constructions of time-planes with the greatest possible precision and frequency through environmentally defined stratigraphic units" (Martinsson, 1973). Integrated by Krassilov (1974) among the causal biostratigraphy this concept implies to notice that, like in present time, the successions of paleoecosystems are mainly controlled by climatic cycles.

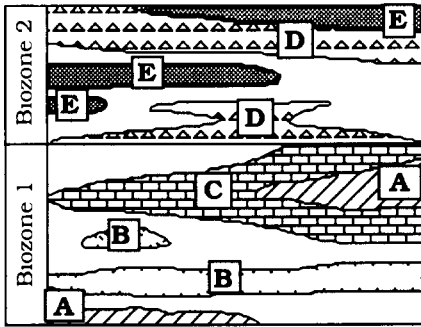


Fig 1 Theoretical succession of two biozones Spatial and temporal distribution of communities (A-E) in each of the biozones Time axis is vertical The horizontal scale is comprised between 10 and 1000 km (from Waterhouse, 1976, modified)

Following Krassilov, Waterhouse (1976) proposes to clarify the nomenclature and the relations between chronostratigraphic, lithostratigraphic, biostratigraphic and ecostratigraphic units In this scope, a biozone includes several communities

(Fig 1) and corresponds roughly to a floral or faunal province, knowing that communities are distributed following a climatic gradient So he associates communities to species, provinces to genera and biomes to families levels Then, studying these entities through time could be relevant to *Stratigraphy* But by integrating the ecological aspect, it also corresponds to *Biogeography* Once more, from this correspondence, confusions can appear in the sense of the terms used as ecological and historical factors are not precisely discriminated The biome concept illustrates such confusion

The biome concept (Clements, 1949) has been created to evoke that animal populations are associated with formations of wide vegetal complexes, a biome is thus a community of plants and animals, usually of the rank of a formation In other words it represents a climatic vegetal and animal community From this point of view the

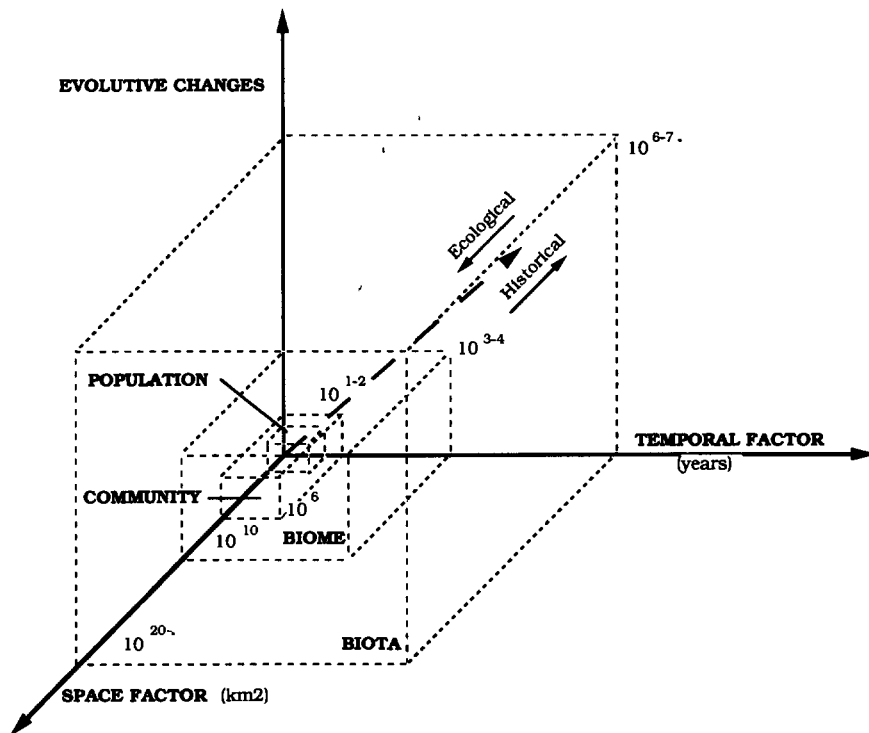


Fig 2 Spatiotemporal representation of the main biological assemblages according to evolutive changes The dotted lines indicate that the limit for each entity can be moved over or under the proposed boundary as expressed by the exposure of 10 Ecological and historical factors have reversed arrows to represent the weighting of each factor with regards to the type of approach (from Rousseau, in press, modified)

ecological factor is a major one as it can be observed in present time. The historical (i.e. evolutive) factor has to be taken into account only when the history of the biome has to be analyzed. Thus applied to the past, speaking about biomes reveals the necessary weighting between ecological and historical factors (Fig 2). In a determined area, the occurrence of successive different and opposed biomes will correspond (a) to the occurrences of major climatic changes through time due to climatic cyclicality or orogenic phases, (b) also to the history of floral and faunal stocks. In fact, what Waterhouse calls biome referring to families does not correspond to the original definition given by Clements (1949). The confusing biome of Waterhouse is the so-called biota, the historical community (at family or genus level) commonly used in historical biogeography (Croizat, 1958, Nelson and Platnick, 1981).

In this case, integrating ecosystems in stratigraphy seems to be a too difficult challenge because, apart from the Quaternary, the fossil ecosystems have little in common with recent conditions. Nevertheless, it is correct to assume that mainly causal biogeographical studies can provide precise scopes of life evolution for stratigraphic interpretations. But the reverse assumption is really less valid, in a global point of view, because of a too rigid scope. This is the reason why, as proposed by Rousseau (in press), the integration of ecology is suitable within causal biogeography, which provides a better scope than biostratigraphy.

How can causal ecological biogeography supplant biostratigraphy? In other words, what is the evolution of biomes through time? According to Braque (1988), two main aspects have to be analyzed.

The first is that biomes are factual. In recent time, the distribution of biomes can appear to approximate a latitudinal gradient, in accordance with vegetal formations (Fig 3). But in fossil deposits, the succession of biomes through time has to be parallel with the occurrences of global climatic events groups together within cycles.

The second is that the composition of the biomes reveals structural changes. The composition of a biome is representative of the area where it occurs. According to the geomorphology, to the geogra-

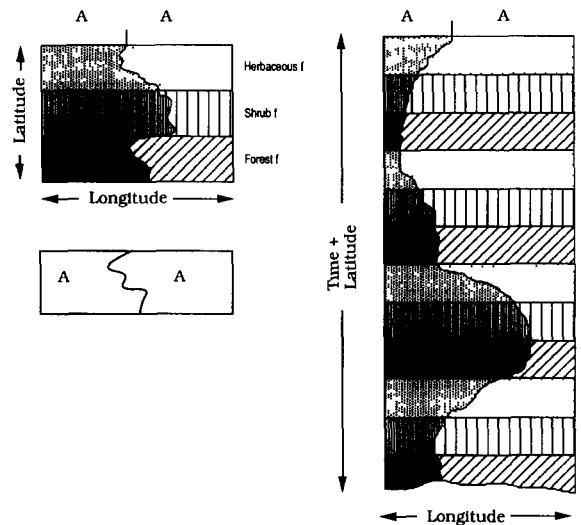


Fig 3 Biotic entities *A* and *A'* characterize two biological assemblages among one biome. At present, such splitting occurs in the three main types of vegetal covering with regard to latitude and longitude. In the fossil record, similar discriminations can be observed in Quaternary deposits where latitude factor is assimilated to time.

phy of the country, different domains or provinces can be determined with reference to the occurrence of particular taxa (biological entities *A* and *A'* in Fig 3). The different biomes saw their distribution changed through time as for example during the Quaternary, in front of advances and retreats of ice caps, with direct implications in their composition (Rousseau, 1989).

The causal biogeography, hypothetic-deductive, consists to follow the spatiotemporal evolution of the recognized biomes, their relation and to propose a hypothetical sketch which will be confirmed or not with regard to other biological, morphosedimentary or climate data. In the case of the pleniglacial biomes in Europe, their evolution during the Middle and the Upper Pleistocene provides new stratigraphic information.

### The European Pleistocene Pleniglacial biomes

#### The faunal concept

Two major trends appear referring to the main malacological works in Europe. Sparks' and Lozek's approaches. They both analyze malaco-

faunas by the recognition of different ecological groups but paleoclimatic interpretations are based on different elements. For Sparks, 4 main groups are determined according to the latitudinal distribution of the taxa: (A) Species reaching to or almost to the Arctic Circle in Sweden, (B) Species reaching roughly 63°N in Sweden, (C) Species reaching roughly 60–61°N in Sweden, i.e. the approximate limit of the oak, (D) Species only found in the very southern of Scandinavia or confined to the European mainland (Sparks, 1961, 1964). Use of these groups can be found in different analyses (Furhmann, 1973, Mejer, 1985).

Lozek (1964), and Puisségur (1976) determined associations which correspond to climatic conditions: glacial, interglacial and transitional. Such a distinction recalls the three main ecological entities recognized by biogeographers: grass, forest and their ecotone. For example within glacial faunas, Lozek recognizes *Pupilla* and *Columella* faunas. Their composition is different as in richness as in abundance. The *Pupilla* fauna is mainly composed by the *Pupilla* species *P. muscorum*, *P. alpicola*, *P. loessica*, *P. sterri*, but *Trichia hispida*, *Succinea oblonga* are also present. Sometimes few *Vallonia tenuilabris* and *Helicopsis striata* can occur. The *Columella* assemblage groups *Columella columella*, *Vertigo parcedentata*, *Pupilla muscorum*, *Pupilla alpicola*, *Vertigo genesu*, *Vertigo alpestris*, *Eucobresia nivalis*, and sometimes *Arianta arbustorum alpicola*, *Euconulus fulvus*, *Nesovitrea hammonis*, *Clausilia dubia* and *Orcula dolium*. While a *Columella* fauna is quite present in Scandinavia (Swedish and Norwegian tundra area), the *Pupilla* fauna is a heterogeneous assemblage, with regard to present ecological characteristics of the included species, which does not occur in present time. The important fact in Lozek's nomenclature is that these faunas correspond to specific environments: i.e. tundra-like for *Columella* and loess steppe for *Pupilla*. As they represent different types of vegetal covering, they have to be assimilated to different biomes.

So the biome approach which takes into account the global dynamic of life, is more appropriate for the analysis of the distribution of pleniglacial malacofauna with regards to Quaternary cyclicality and thus allows to define a good stratigraphic scheme.

### Published data

In Quaternary deposits, loess is the best sediment for analysis of the historical distribution of these pleniglacial biomes because it is widespread in Europe, mainly in longitude, the time record being roughly continuous and because a lot of informative molluscs have been well preserved. Many studies have been made on the large European loess belt (Fig. 4). The varied outcrops have different importance yielding one or several climatic cycles. It is not the place here to list in detail all the sites but for Czechoslovakia we have to refer to Lozek (1964, 1976), Horacek and Lozek (1988), for East Germany to Furhmann (1973) (Pegau, Grimma, Golzern, Altenburg, Klosterbuch), for West Germany to Lozek (Karlich, in Brunnacker et al., 1971, Puisségur (Ariendorf), in Brunnacker et al., 1975, for Poland to Alexandrowicz (1986) (Odonov), for Austria to Lozek (1976) (Krems), for France to Puisségur (1976) (Schiltigheim), Longpré-les-Corps-Saints (in Sommé et al., 1984), Tancarville (in Lebret et al., 1983), Achenheim (1978), to Rousseau (1987) (Achenheim) for Channel Islands to Keen (1978) (Jersey), and Rousseau and Keen (1989) (Portelet Bay). In all these sites one or the two biomes have been recognized in good stratigraphic position.

Beside loess outcrops, cryoclastic deposits can also provide well preserved malacofauna: see Lozek (1964), Puisségur (1976, 1974), Kerney (1963, 1977), which complete the data set.

### New data

Since several years, the stratigraphy of Quaternary loess deposits has been greatly developed in Western France mainly by J. P. Lauridou and J. L. Monnier, providing new data. Generally the sequences have been published in details contrary to the malacological contents. This is the reason why they are presented here (Fig. 4).

In Brittany, loess sections have been investigated by Monnier (1980). The few fossiliferous sequences are mainly located in St. Brieuc Bay, north of Brittany. They provided Weichselian molluscan faunas according to stratigraphic correlations with

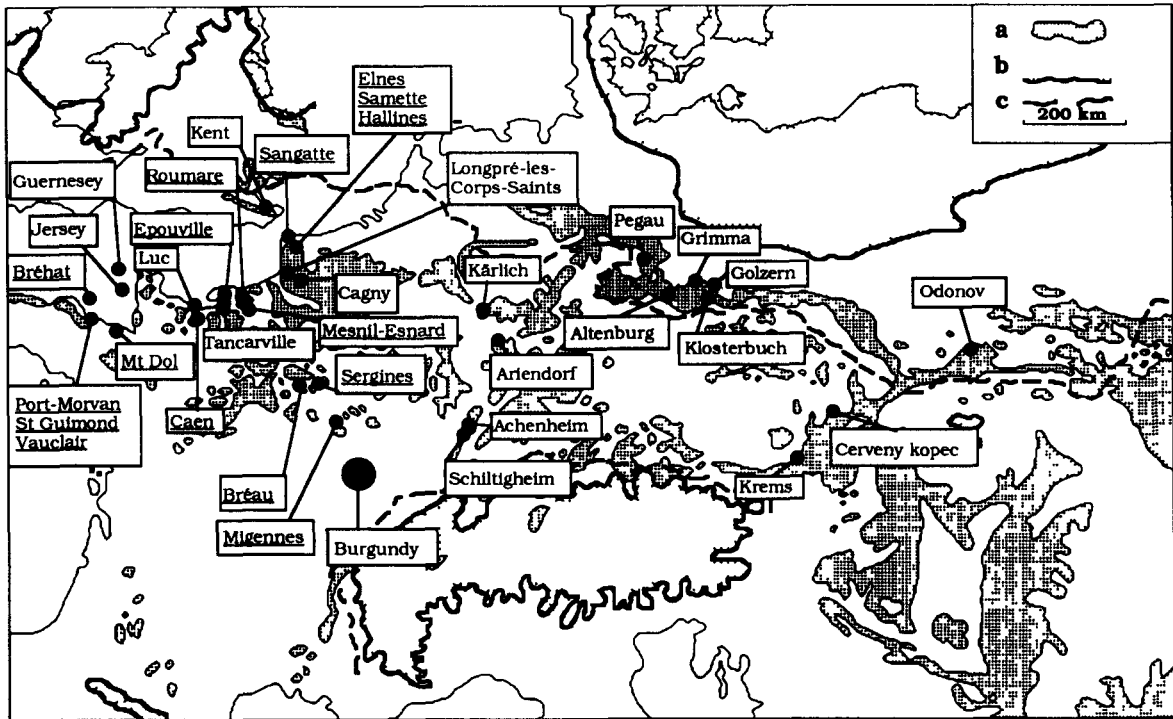


Fig 4 Map of the European loess belt. Location of the different sites discussed in the text. Unpublished ones are underlined. a = loess b = last glacial advance c = maximum glacial advance

the north of France and Normandy (Lautridou et al., 1983, 1986)

(a) Port-Morvan (Fig 4, 5) near St Briec is a loess section where Upper Saalian and Weichselian levels have been preserved. This is a complete reference sequence for Brittany. In lower Weichselian levels, the malacofauna seems mixed (glacial and reworked interglacial faunas). But the Weichselian pleniglacial fauna is represented by *Pupilla muscorum* with some intrusive individuals of *Ceciloides acicula*.

(b) St Guimond and Vauclair (Fig 4) are two loess sections correlated with Port-Morvan. But molluscs have been recognized in only one level. The association is composed by *Pupilla muscorum* and *Trichia hispida*.

(c) Ot Ar Villiec (Fig 4, 5) sequence is on Bréhat island, located in the western part of St Briec Bay. Following Monnier, the fossiliferous level where *Columella columella* occurs is correlated with pleniglacial deposits in Port-Morvan with only *Pupilla muscorum*. There is a double interest

for the Bréhat fauna. First, this pleniglacial fauna is the far western pleniglacial malacofauna where *Columella columella* occurs. Second, the composition of the association with *Columella columella*, *Pupilla muscorum*, *Succinea oblonga* and *Limax* sp. is similar to that observed at Portelet Bay in Jersey (Rousseau and Keen, 1989).

(d) Mont Dol (Fig 4, 5) is a granitic rock which stands in a large low plain close to Mt St Michel. In one level occurs a pleniglacial fauna composed by *Pupilla muscorum* and *Trichia hispida* with few *Galba truncatula*.

Loess sections in Normandy and Paris Basin have been mainly investigated by Lautridou (1985) but as in Brittany, few of them are fossiliferous.

(a) Mesnil-Esnard (Fig 4, 6) is a Weichselian loess sequence truncated at its basis (lack of the Eemian interglacial soil) overlaying Saalian loam and paleosoils. Pleniglacial fauna is composed by *Pupilla muscorum*, *Trichia hispida* and *Succinea oblonga* while below only *Pupilla muscorum* occurs in the fossiliferous levels.

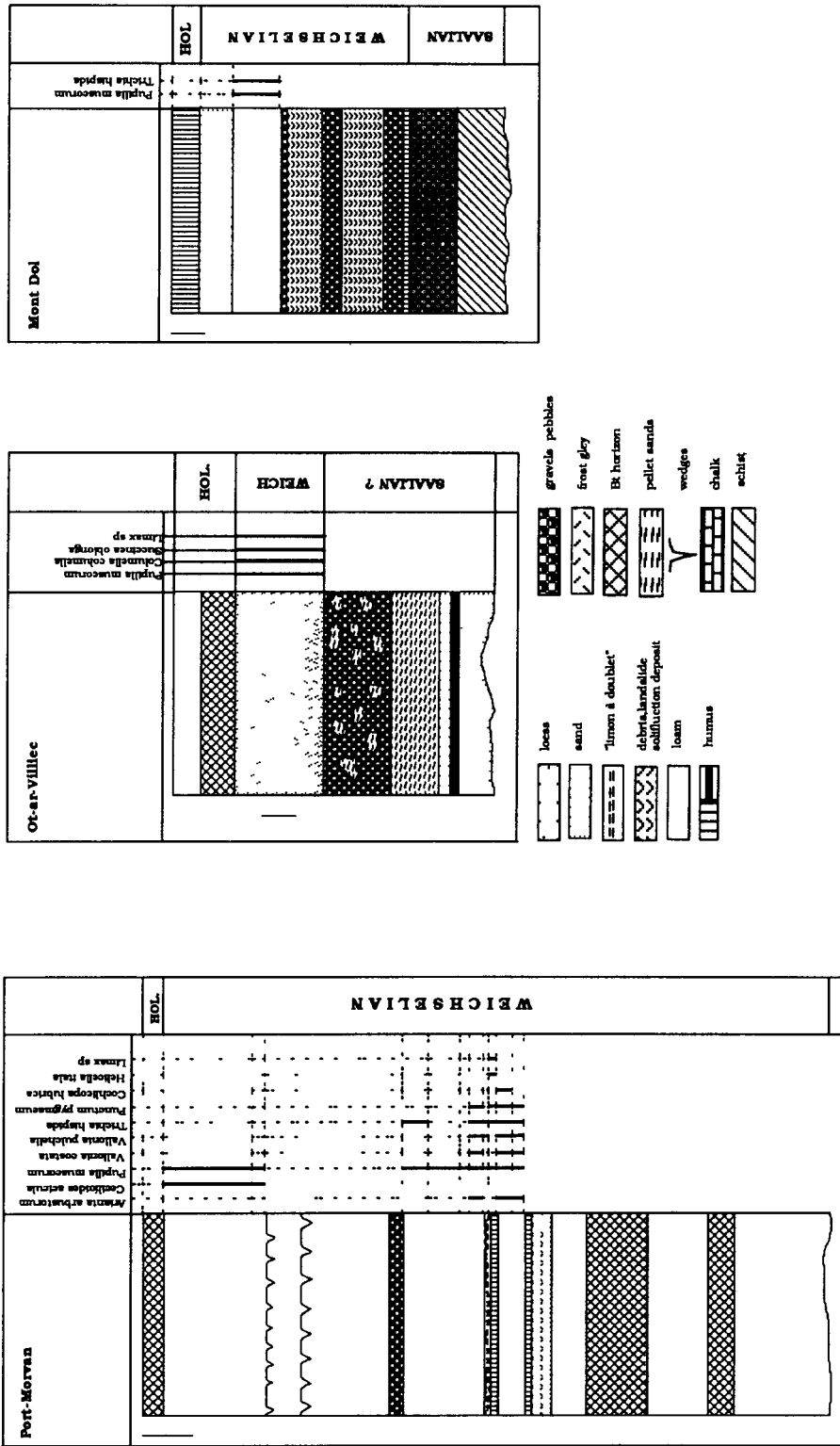


Fig 5 Outcrops in Brittany and occurrence of the mollusc species in the Port-Morvan, Ot-Ar-Villicc and Mont Dol sections *HOL* = Holocene, *WEICH* = Weichselian The vertical scale is 1 m h

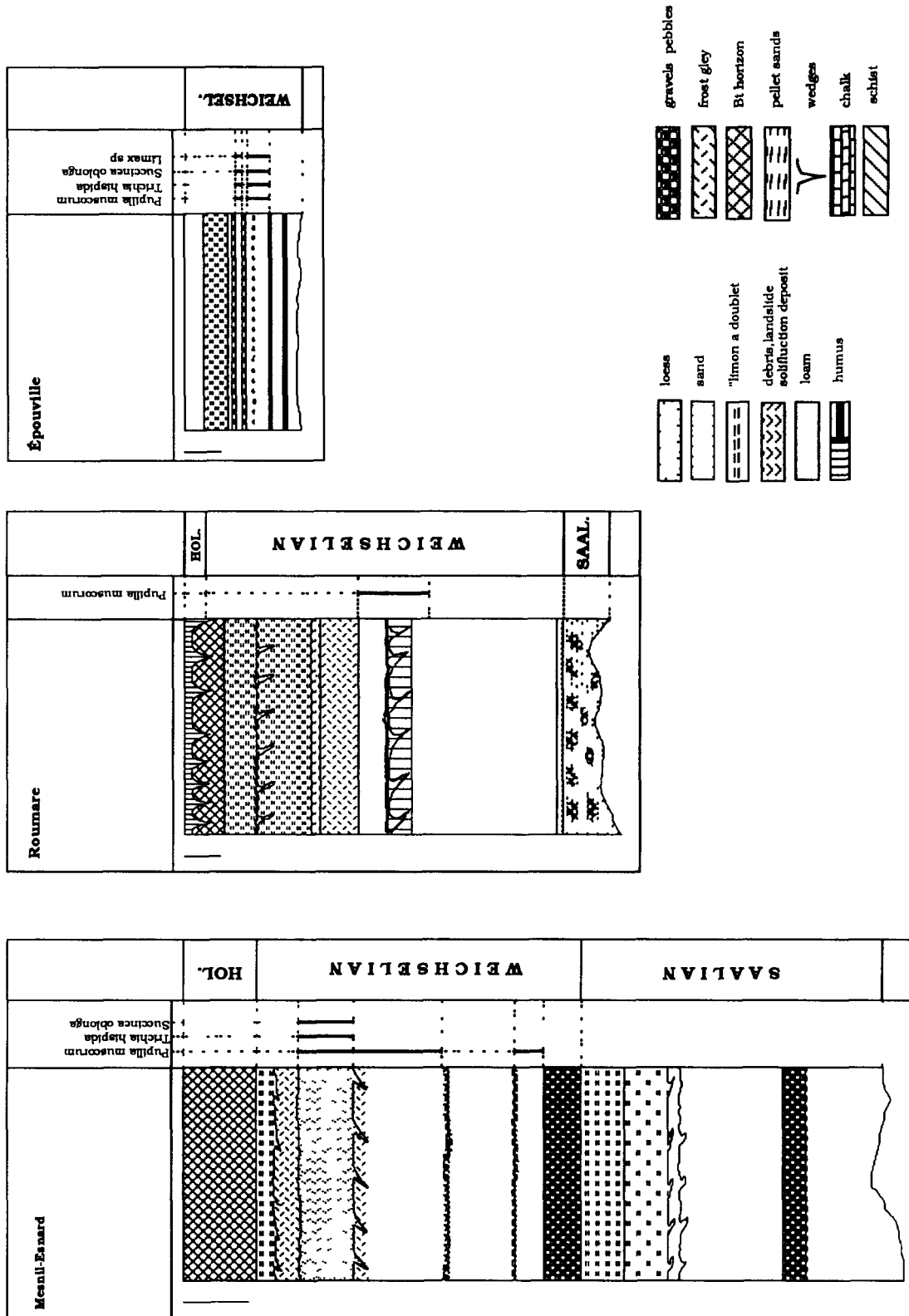


Fig 6 Outcrops in Normandy and occurrence of the mollusc species at the Mesnil-Esnard, Roumare and Épouville sections





(b) Roumare (Fig 4, 6) is a Weichselian section overlaying altered red clays. The malacofauna is only concentrated in pleniglacial levels and is composed by *Pupilla muscorum*.

(c) Épouville (Fig 4, 6) was investigated by C. Lechevallier. Above a gravel nappe is a red loam overlaid with different loess ("limon à doublet") levels of Weichselian age. The pleniglacial fauna is composed by *Pupilla muscorum*, *Trichia hispida*, *Succinea oblonga* and few *Limax* sp.

(d) Caen (Fig 4), during the building of the new railway station, a Weichselian loess has provided a pleniglacial fauna which is only composed by *Succinea oblonga*.

(e) Bréau (Fig 4, 7). Above a periglacial alluvial nappe lays an humiferous complex, a lower loess and an upper loam. The pleniglacial fauna is mainly composed by *Pupilla muscorum* and *Trichia hispida*.

(f) Sergines (Fig 4, 7). Once more these deposits have a Weichselian age. The sequence is similar to the previous one. The malacofauna is richer as *Vertigo pygmaea*, *Vallonia costata* are present among *Pupilla muscorum* and *Trichia hispida* individuals.

(g) Migennes and Champley (Fig 4, 7). The outcrops are located in the valley of Yonne river. Several sections have been studied corresponding to Weichselian and at the basis Saalian slope deposits. Pleniglacial faunas occur which are mainly composed by *Pupilla muscorum* and *Trichia hispida*.

In Normandy, Weichselian deposits Mesnil-Esnard, Épouville, Roumare, Caen (only *Succinea oblonga*) yield always the same associations, poor in species.

The north of France also provides loam or loess sections where occur molluscan faunas.

(a) Elnes and Samette (Fig 4, 8) were investigated by Boutry et al (1968). In Weichselian deposits, a loam overlays altered gravels and has been attributed to the basis of the Weichselian pleniglacial. As previously mentioned the malacofauna is mainly composed by *Pupilla muscorum*, *Trichia hispida*, *Succinea oblonga* and few individuals of *Columella columella* have been recognized. In the same way this composition recalls the Bréhat and Portelet faunas.

(b) Hallines (Fig 4, 8). In Weichselian deposits dated by radiometric measures (Tuffreau, 1987, Fagnart, 1988) and rodents (Chaline, pers comm, 1989), a loam has provided pleniglacial fauna where occurs abundantly *Pupilla alpicola*. On the contrary to the previous sequence, no *Columella columella* occurs.

(c) Sangatte (Fig 4, 8). At "Fond Pignon", a new and more complete section of the Weichselian deposits of Sangatte has been observed (Antoine, 1989). From bottom to top, the succession is a chalk substratum, a slope deposit, a Bt horizon, an humiferous level, a lenticular basin of chalky mud provided molluscs and finally the present soil. The molluscan fauna is typical of pleniglacial environment and is composed by *Pupilla muscorum* and *Trichia hispida*.

These new data come from sites which cover a large part of Northwestern Europe. They provide complementary elements which allow to compare more precisely the distribution of pleniglacial faunas in both western and central Europe and to determine stratigraphic interpretations.

### Stratigraphical implications

The new data confirm the previous results between central and western Europe. The pleniglacial faunas seem similar in western and in central Europe (Lozek, 1969, Puisségur, 1976). Westwards, the malacofaunas are poorer than eastwards. In several outcrops in Normandy, for example, the association is exclusively composed by *Pupilla muscorum*. Is this phenomena regular in time or are variations in the distribution able to be observed?

In this favorable context, the Achenheim sequence appears as a key for biogeographical analysis (Rousseau, 1987). Its location in the loess belt is just at the boundary between the corridor expressed by the Scandinavian ice cap and the Alpine glaciers to the east and the open plain in northern France and, Belgium to the west (Fig 4). The location of this site is also fundamental as the core of *Columella* and *Pupilla* faunas were in central Europe. So the emigrations of these faunas if they reached the western European open mainland can easily be recognized in the Achenheim

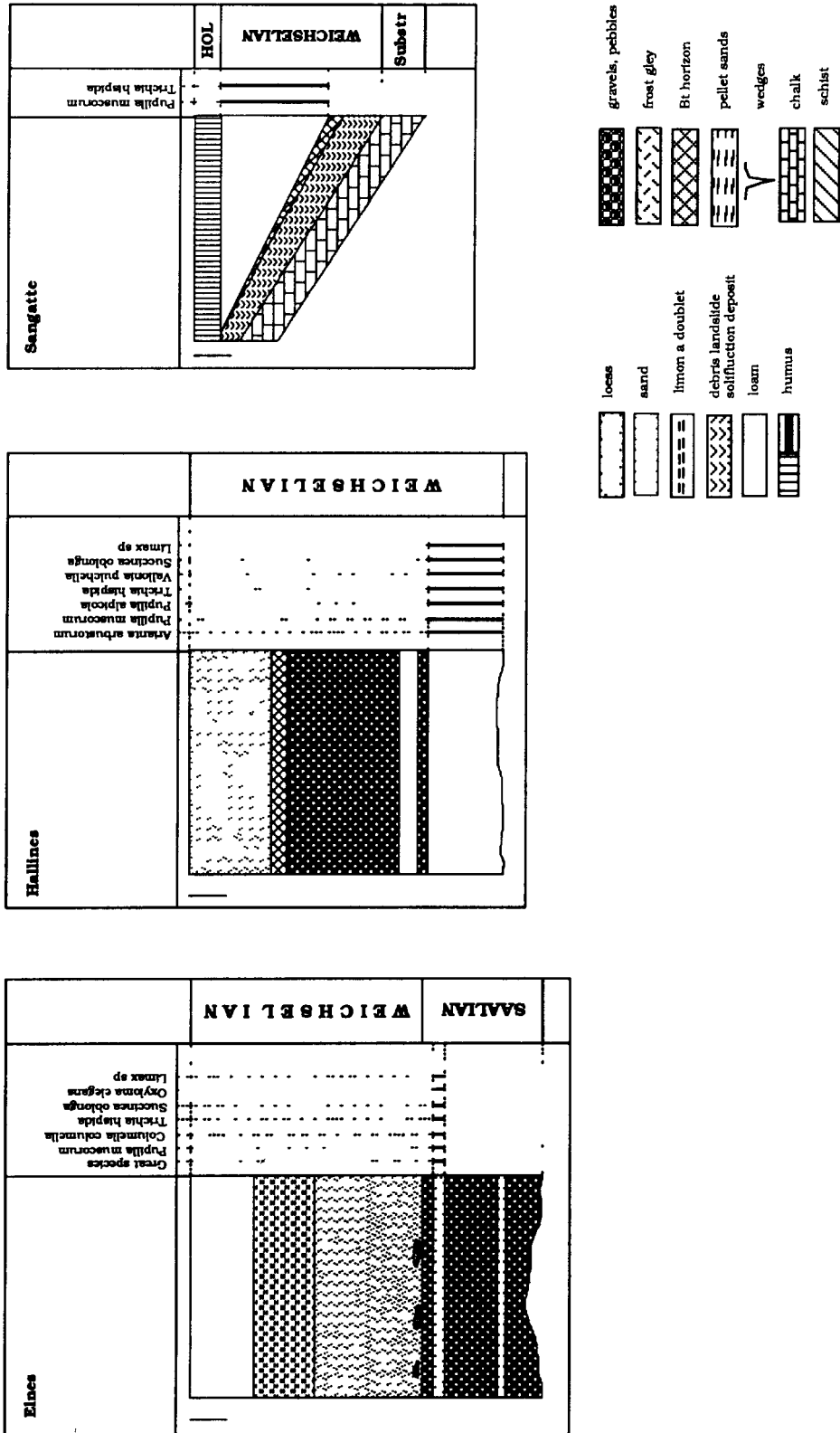


Fig 8 Outcrops in the north of France and occurrence of the mollusc species at the Elnes, Hallines and Sangatte sections (see legends in Fig 5)

record For comparison Cerveny Kopec is able to provide perfect data as several cycles are recorded

The last five climatic cycles (*sensu* Kukla, 1977) are preserved in the Achenheim deposits (Heim et al., 1982, Lautridou et al., 1983, 1985, Sommé et al., 1986, Rousseau, 1987) (Fig 9) The record is considered as being roughly continuous, especially for the last three cycles, each one containing various malacological associations Variations in pleniglacial faunas observed at Achenheim have been compared with those from Cerveny Kopec

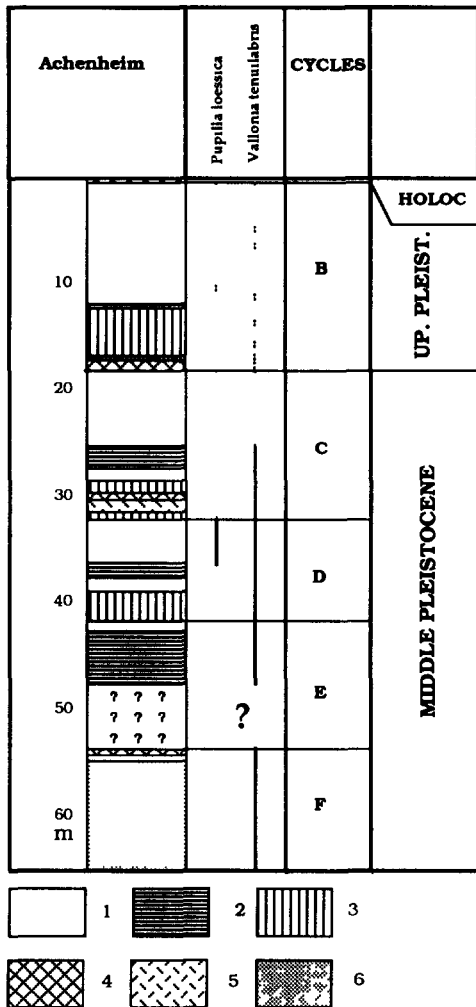


Fig 9 Achenheim section and occurrence of *Pupilla loessica* and *Vallonia tenuilabris* in the sequence 1=loess 2=bedded formations (pellet sands) 3=humiferous soils 4=Bt horizon 5=colluvium 6=fluvial sands of the Terrace sequence

which represents the reference sequence in central European loesses (Kukla 1977)

Up to cycles E and F (524,000–339,000 yr B P), correlations are not possible between these two outcrops They belong to two different biogeographical domains The sedimentary facies are completely different In Alsace, there is no typical loess as in Czechoslovakia, thus the pleniglacial faunas are not homologous (Fig 9)

In cycle D (339,000–245,000 yr B P) the sequences show several analogies In Achenheim it begins with a pedocomplex followed by bedded pellet sands and then a typical loess, some of them corresponding to stratigraphic elements of the classical central European sequence bedded pellet sands overlaid by loess Also in the Achenheim sequence, the pleniglacial biome fauna is a *Pupilla* fauna where *P loessica* is the fundamental element This occurrence has been recognized only in that stage in all the French sequences (Fig 9) In central Europe, the same malacological event, *Pupilla* fauna, occurs in a similar chronological place (Lozek, 1964, Kukla 1977) but this assemblage has been recognized in the following cycles

The pleniglacial biomes faunas of cycle C (245,000–128,000 yr B P) are *Columella* faunas Among the species contributing to the association, *Vallonia tenuilabris* does not occur until the top of the Achenheim sequence contrary to central Europe (Fig 9) Nevertheless, the sedimentary sequence of this cycle is completely similar to its central European homologous The pedosedimentary balance sheet is the same flood loam, Bt horizon, humiferous brownish soil, marker, bedded pellet sands and loess

With the last cycle, corresponding to Eemian + Weichselian (128,000–10,000 yr B P), new conditions appear which imply differences between the two reference sections (Fig 9) If the new data of western Europe are integrated, a clear gradient of richness is observed from west to east In western countries *Columella columella* occurs only in protect sites (Bréhat, Jersey, North of France, Kent), the pleniglacial fauna is mainly composed by *Pupilla muscorum*, *Succinea oblonga* and *Trichia hispida* In Alsace, the pleniglacial fauna comprises *Columella columella*, some *Vertigo parcedentata*, *Pupilla alpicola*, *Pupilla muscorum*, *Trichia hispida*

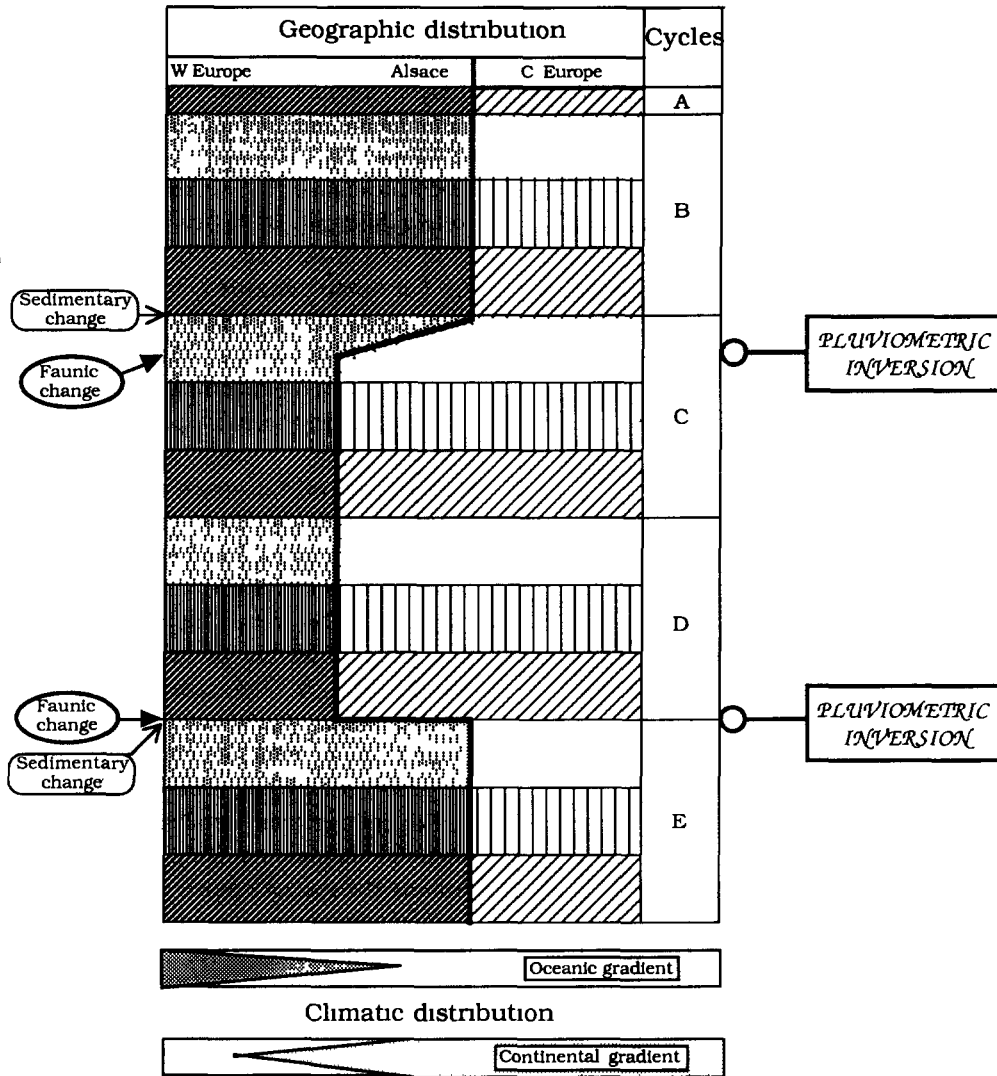


Fig 10 Schematic variations of western and eastern facies through the last four climatic cycles (A = Holocene, B = Weichselian, C-E = Saalian s 1). Pleniglacial malacofaunas (dotted areas) and sedimentary sequences variations are superimposed which determined the variations through time of the connection of Alsace to one or the other facies. Proposal of the occurrence of two pluvio-metric inversions in response to the more or less importance of oceanic gradient versus continental one.

and *Succinea oblonga*. In central Europe, pleniglacial faunas are represented by mainly *Columella* faunas with occurrence of some *Pupilla* faunas. But among them, *Vallonia tenuilabris* is not present in Alsace and in Western Europe while it still occurs in Central Europe until the Late Glacial (Krolopp, 1966, 1983, Horacek and Lozek, 1988). In the same way *Pupilla loessica* still absent in the previous cycle does not occur in Alsace and Western Europe while Lozek notes also its occurrence in Czecho-

slovakia during the beginning of the Holocene. The sedimentary evolution in Alsace also does not correspond to the classical succession determined in central Europe as discussed above. Finally the direct possibilities of correlations by lithostratigraphy (facies, mark level) allow to group Alsace within the Northwestern European domain since the pleniglacial faunas are characterized by *Columella* fauna in all European deposits.

In these conditions, the occurrence or the lack of

*Pupilla loessica* and *Vallonia tenuilabris* in the studied sections are connected with the climatic conditions which affected Europe and which implied fluctuations in the composition of the pleniglacial faunas. In Northwestern Europe, *Pupilla loessica* and *Vallonia tenuilabris* are never mentioned while *Columella columella*, *Pupilla alpicola*, *Vertigo parcedentata*, *Vertigo genesu* occurred. These different conditions, connected with both the malacofaunas and the sedimentary sequences, imply that these two pleniglacial species are biogeographic indicators.

Consequently two biogeographic domains are proposed with a varying extension during the Quaternary: the Western and Central European domains. Their limits are not always superimposable to the present ones following the climatic cycles. Alsace belongs to one or the other domain. What does it mean and how can we characterize such a history? Is there any limiting factor which discriminates between these two domains?

### Proposal for a Climatic Sketch

According to Berger's (1979, 1988) reconstructions, the general climate of the Last Pleniglacial time over the European loess belt can be assimilated to the present climate of the cold temperature latitudes: temperature contrasts are important (cold and long winter followed by a short thermic break corresponding to summer, temperatures higher than 10°C) and the pluviometric regime is continental, with distinctions between oceanic and continental facies with regards to the exposure of the country: western or eastern maritime sides, continental interior, which constraint the pluviometric regime (Frécaut and Pagny, 1983).

The Weichselian, because many records are known from this period, is thus a privileged time to propose some hypothesis. The review of the localities where cold climate molluscan faunas in western France and Britain are recorded shows that the tundra-like assemblage typified by *C. columella* spread to the extreme western parts of the continent in sheltered sites (Bréhat, Jersey, north of France, England). By comparison with central European faunas of the same type however, those of western Europe are impoverished in terms of

species numbers leading to characterize the two different domains.

Complementary explanations can be proposed for such impoverishment.

First is the "peninsula" effect. Faunas of peninsulas have always reduced numbers of species compared to the adjacent areas, due to ecological competition. As determined previously, the cores of the area of *Columella* and *Pupilla* fauna were in central Europe. In this case, the western France and southeast Britain loess deposits, limited by the Atlantic Ocean to the west and by polar desert to the north, can be considered being at the outer limit of the distribution area of these biomes with a corresponding reduction in the numbers of the species in the fauna. But among the loess belt, a particular area has been characterized which constitutes a marginal zone which represents the so-called "damp loess landscape" of Fink (1965), of which the malacofauna was characterized by Lozek (1965), and which is usually characterized by a fauna poor in species (Rousseau and Keen, 1989). The loess occurrence of Brittany and the Channel Islands are also located in such a marginal zone.

What are possibly the climatic implications? From Lozek (1968) and Kukla's (1977) investigations, loesses of the European belt originated under continental, cold, climatic conditions, at a mean annual temperature of about -3°C to -2°C rising in the warmest phases toward 0°C. The weather had a tranquil annual course. A long, severe, but relatively dry winter was succeeded by a humid and fairly warm period that became summer (July averaged more than 10°C, probably about 15°C) then a dry period persisted until winter. In fact these interpretations only concern central Europe and consequently cannot be strictly applied to all European areas according to its geographical complexity. Consequently, according to causal ecological biogeography as exposed in the first part of this paper, malacological results need to be confronted with data provided by other studies.

#### (a) Field analyses

Lautridou's (1985) investigations in Normandy and Brittany determined that, for the last climatic

cycle, westerly winds greatly contributed to loess sedimentation in this country and he concluded to moist, cloudy summers during the pleniglacial period. Also Lautridou and Sommé's (1981) investigations concerning ice-wedges provide that the deep continuous permafrost during the Weichsel glacial age was located in western Europe. Pursuing this research, Van Vliet-Lanoé (1988) has specially investigated the Weichselian European permafrost. First of all she concludes that, taking into account her field experience in Arctic region, the physical limits available for the present-time permafrost cannot be applied in the same terms for the last western European Pleniglacial. She evokes relative moisture, low insolation to explain the occurrence of a continuous permafrost in this area (Van Vliet-Lanoé, 1988).

#### (b) Modelling analyses

Joussaume's results (1989) concerning the last glacial maximum (i.e. 18,000 yr B.P.) indicate the occurrences of (1) the strongest cooling in western Europe, (2) high precipitation during both winter and summer in western Europe according to strong westerly winds, and (3) a warming of central Europe.

This also agrees with the proposed westerly circulation of Lautridou (1985) and the occurrence of a relative humidity for the elaboration of continuous permafrost for Van Vliet-Lanoé (1988). The direct implication is the occurrence of precipitation limiting the insolation, mainly in summer. In this way the favorable period for vegetation and the development of land snails was less favorable westwards than eastwards, with more precipitation so that a selection can be made among the tolerant cold species because moisture also contributed as a limiting factor to land snails (Rousseau, 1989). That is why *Vallonia tenuilabris* never occurs in western Europe.

Thus the impoverishment of pleniglacial faunas from east to west, corresponds to an increasing atmospheric moisture. Such a proposal corresponds, during glacial stages to the occurrence of an "oceanic" gradient over an area characterized by a continental facies of a "cold" temperate-latitude climate, according to Frécaut and Pagney (1983).

These interpretations and proposal for a climatic sketch determined by the confrontation of molluscs results against field and modelling analyses, concerns the last climatic cycle. But during the course of the Quaternary, and more specially during the Middle and the Upper Pleistocene, *Vertigo parcedentata*, *Pupilla loessica*, *P. alpicola* or *Columella columella*, always present in central Europe up to the Late-Glacial, have a different distribution in western Europe.

In this way, the faunal dynamics of the last Pleniglacial can be considered as a model which can be tested for a more long time extrapolation, i.e. the four last cycles, taking into account that in the Achenheim sequence, the analysis of the malacofauna has demonstrated that each climatic cycle has its own course and characteristics (Rousseau, 1987). That is why to test the European faunal dynamics over ancient cycles needs to consider both the occurrence of climatic events and the location of the analyzed loess sites, with regards to the southern limits of Scandinavian ice cap during the past climatic cycles. Generally admitted in the literature, the Saalian s1 ice caps had a greater expansion than the Weichselian ones. Southwards the limits were, from maximum to minimum, Saalian s5 (isotopic stage 8=cycle D), Warthe (isotopic stage 6=C) and Weichselian (isotopic stages 4,3,2=cycle B). During these glacial stages, ice-cap limits were closer in central Europe while great differences occur in western Europe. In this case, the Achenheim sequence appears as a strategic site for the well understanding of European Quaternary.

Between cycles C and B, a deviation characterizes a faster response in the malacofauna than in the sedimentary sequence. While the sedimentary sequence is maintained, biological remains strongly indicate changes which occur, at around 170,000 yr B.P. in the balance sheet between "oceanic" and continental gradients (Rousseau and Pusségur, 1990). New conditions occur which allow oceanic facies to reach Alsace (Fig 10). This interpretation is in agreement with respective limits of the Scandinavian ice cap during these two climatic cycles. Biogeographical analysis indicates that after the first 10,000 yr B.P. of stage 6 course, assemblages record changes in their composition.

(Rousseau, in press) Also the paleoecologic analysis of Achenheim molluscs indicates that the maximum recorded cooling occurs during stages 2 and 8 (Rousseau, 1987) This does not correspond with the observed extension of the ice caps Nevertheless the use of the last glacial model, previously extrapolated, leads to propose an increased precipitation, mainly in summer between 170 and 128,000 yr B P in stage 6 If precipitation became more important over an always cold continent, ice attack during summer was greatly reduced and consequently ice growth could pursue

So the extension of the ice cap was stronger, in western Europe, during stage 6 than during stage 2 because of important precipitation over this country

On the contrary, between cycles E and D, sedimentary and mollusc responses are contemporaneous because the central Europe domain spreads over Alsace indicating homogeneous climatic conditions This is a consequence of the great extension of the Scandinavian ice cap over all of Europe during glacial stage of cycle D which consequently imposed that oceanic facies could not reach Alsace (Fig 10)

## Conclusions

Consequently to this review, European pleniglacial faunas are not strictly identical from one cycle to another and from one part to another part of the distributional area of the biome (longitudinal variations) Their composition characterizes both local and global climatic conditions In this way they can also contribute to characterize stratigraphical events which represent the responses of the environment to climate In one site, a local ecostratigraphy can be proposed, based on the succession of the recognized biomes, which can be connected with a more general chronostratigraphy the interglacial-glacial cycles of Kukla or the  $^{18}\text{O}$  SPECMAP chronology

For a global ecological biogeography, at the European scale, fluctuations in differences between entities of expansion are significant to define biostratigraphic domains In this way the spatial factor is not a problem for ecostratigraphy

During cycle E, Alsace belongs to the west

European domain During the following cycle D and first 10,000 yr B P of cycle C, this region belongs to the central European domain Finally after 170,000 yr B P and until the end of cycle C and cycle B Alsace is again connected with western domain

Two events can be determined with regards to this time evolution which occur during cycles C and D The first biologic event is the ubiquitous *Pupilla* biome fauna in all the area (Alsace + central Europe) during Pleniglacial of cycle D Some differences appear at the end of cycle C while globally the *Columella* biome fauna is distributed in all of this area These biologic events are underlined in cycle D by the occurrence of pure loess levels as in Alsace as in central Europe In cycle C the sedimentary sequence plays the same role Nevertheless, a slight discordance occurs which indicates that malacofaunas have immediately recorded a major event while the sedimentation yields it only in the following cycle These major events correspond to inversions in the pluviometric regime in Alsace through time during cycles E and B on oceanic facies and during cycles C and D a continental facies

The modifications in both the distribution of the pleniglacial faunas and the sedimentary sequences give to Alsace a privileged position for Quaternary climatic studies by its intermediary position between northwestern Europe and central Europe as this is the case today

In fact, if pleniglacial biome occurrence is primarily due to decreased temperature, a factor always evoked in the literature, important variations in the pleniglacial assemblages are due to different pluviometric regimes over the area where they lived

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