IS CAUSAL ECOLOGICAL BIOGEOGRAPHY A PROGRESSIVE RESEARCH PROGRAM?

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Various spacial and temporal time scales need to be taken into account in the interpretation of biological events. Omission of these aspects can lead to purely descriptive studies of changes in faunal assemblages, which are severely limited in scope. Terrestrial molluscs, which are very sensitive to environmental and climatic changes, provide a good example to illustrate this problem. Using an ecological biogeographic approach, a review of mollusc assemblages from holsteinian tufas in western Europe is presented. The analysis permits the definition of the *Lyrodiscus* biome, which corresponds to a temperate mixed forest community which developed under a particularly warm oceanic climate, and never occurred in Western Europe since that time.

INTRODUCTION

The new concept of biogeography, by Croizat (1958), associates the evolution of the Earth with that of life. Croizat replaces a purely descriptive biogeographical approach with a dynamic, analytical, causal process. Biogeographical works applying Croizat's methodology (pan-biogeography), or others inspired by it (e.g. vicariance biogeography — Rosen, 1978) are numerous, but they favour the historical causal approach which led to the recognition and to the analysis of biotas (historical biological communities). This paper attempts to see if it may be possible to conceive a causal biogeography during a shorter period, at the scale of 'ecological time', and to see if it is possible to integrate this approach with others. To adapt the title of the paper by Craw and Weston (1984) to the present discussion: is causal ecological (palaeo)biogeography possible and can it underpin research methodology? Hitherto examples of such an approach based on invertebrates, and more precisely land snails, are rare despite the endeavour of Solem (1984). Nevertheless, because they are well adapted to their environment, land snails are appropriate for illustrating ecological (palaeo)biogeography. Examples are presented from the global review of malacology by Solem and van Bruggen (1984).

AIMS AND SCOPES OF BIOGEOGRAPHY

An analysis of the biogeographical literature, shows two major philosophical approaches: one is essentially descriptive, the other causal. A brief review of biogeography is desirable to distinguish between them, using the summary of Dommergues and Marchand (*in press*).

Descriptive Biogeography

Descriptive biogeography is the approach that was widely used by Darwin and his followers. Its main aims are to recognize the diversity of life and to establish the hierarchical organization of living organisms. The principle has been much used by botanists and some palaeontologists, and it has allowed the recognition of floral and faunal provinces. But within it, two different concepts can be distinguished (Table 1): ecological (ecological descriptive biogeography) and phenetic (phenetic descriptive biogeography).

First, ecological descriptive biogeography. The process is eclectic and there are two approaches. The former makes an inventory of the communities, analyzed against environmental controls, and mapped. This results in a hierarchical organization of communities (a synecological approach). The latter makes an inventory of the taxa, case by case, and then maps them. Their distribution is also analyzed against environmental controls. This results in an identification of morpho-functional stresses in relation to ecological conditions (autecological approach) (Table 1).

In southern and western Finland, Aho (1984) explained the local diversity of freshwater gastropods by variation in water quality. In another context, Shikov (1984) demonstrated that human activities in the central part of European U.S.S.R. have influenced the distribution of land snails. The decrease in forest cover leads to some extinction of shade-demanding taxa and to the spread of snails adapted to open habitats.

Second, phenetic biogeography may be quantitative or qualitative. In the former case, similarity indices are calculated to compare data, to determine a hierarchical organization of distributions, and to determine (bio)geographical units. In the latter the census of taxa distributions is mapped, and leads to a definition of (bio)geographical areas (Table 1).

André (1984) described 829 stations in Mediterranean Spain and France. Computer analysis of 125 species allowed him to distinguish thirteen geographical groups on the basis of biotic and abiotic variables such as: provinces or departments, chorological and ecological sectors and vegetation series.

TABLE 1. Synthetic description of biogeography from the approaches to the aims of studies. Comparison between the descriptive and the causal biogeographies (modified from Dommergues and Marchand, 1988)

| | DESCRIPTIVE BIOGEOGRAPHY | | | | CAUSAL OR EVOLUTIVE BIOGEOGRAPHY | | | |
	PHENETIC B.		ECOLOGICAL B.		ECOLOGICALB.		HISTORICAL B.	
APPROACH	no ecological or historical approach		synecological	autecological	morpho-functional		narrative	analytical
PROCES-SES	Quantitative	Qualitative	Eclectic		Eclectic	Hypothetico-deductive	Eclectic	Hypothetico-deductive
METHODS	automatical treatments similarity indexes expert systems	Mapping and inventory of index taxa	Mapping and inventory of communities	Mapping and inventory of taxa case by case	Inventory of taxa with similar morpho-functional adaptations (morphology, biology, physiology, ecology)		Inventory of taxa connected — by eclectic systematic	by eclectic or cladistic systematic
ANALYTIC WAY	Comparison and hierarchical of distributions	analyses of congruent distributions	distribution of communities in	distribution of taxa in — relation with environmental stresses	Hierarchical organization and comparison with the environmental data		study case by case of the pat- Dispersal center hypothesis	compared study of the patterns of distribution. Vicariant hypothesis
AIM OF STUDIES	Comparison between (bio) geographical units	Definition of (bio)geographical areas	Hierarchical organization of the communities and the ecological stresses	Research of the morphofunctional stresses in relation with ecological conditions	BIOMES RECOGNITION recognition and definition of communities with a similar morpho-functional adaptations — spatio-temporal factor taken into account		BIOTAS RECOGNITION recognition and definition of communities with a similar geological and evolutionary history — partly by vicariant and dispersal events	only by vicariant events :pan- or phylogenetic biogeography

These concepts correspond to a special approach which does not take into account the temporal factor but favours an instantaneous ecological one. Such works have always had a descriptive hard core, but in the view of Craw and Weston (1984) they are not an appropriate basis for research.

Causal or Evolutionary Biogeography

Unlike the methods previously discussed, this approach seeks to establish the distribution of living organisms, but also to understand it from an historical point of view, proposing hypotheses which may be confirmed by data provided by other sciences: for example tectonics or climatology. Data sets can be considered according to an ecological (Blondel, 1986) or historical time perspective (Table 1).

First, ecological causal biogeography. Although the approach is morpho-functional, the process can be an eclectic or hypothetical-deductive one. The methods are similar: the establishment of an inventory of taxa showing one or more similar morpho-functional adaptations (morphology, biology, physiology, ecology), which are compared with environmental data. The aim in the former case (eclectic) is to recognize and define communities and their variations through time according to known data about the environment. In the latter case, the environment does not explain the communities. Using spatial and temporal factors, the aim is to determine biomes (ecological biogeographical communities), and afterwards to propose hypotheses about

controls, such as environment, climatology, or connections between land masses, which may be confirmed by other earth sciences (Table 1).

This approach is well developed in a recent faunistic and systematic review by Solem (1984). He proposed a generalized world model of land snail diversity and abundance. First he cited the example of the highest diversity of land snails in the mid-North island of New Zealand and proposed arguments to explain such diversity. Then using that example, he attempted to explain the diversity of land snails in the major recent biomes. He illustrated the temporal aspect of diversity with, for example, the Miocene of Kenya and the Pleistocene of Europe.

Second, historical causal biogeography. The approach is either narrative or analytical, that is to say that the process is eclectic in the former case and hypothetico-deductive in the latter. Differentiation exists in the method used: in the former case, an inventory of taxa is related to Simpsonian systematics; in the latter, the taxa are related to phylogenetic systematics. The analysis by the narrative process consists of a case by case study of the patterns of distribution compared with a dispersal centre hypothesis. In the analytical processes, the analysis is made by a congruent study of the patterns of distribution with the vicariance hypothesis. In the two cases the result is the recognition of biotas defined in the former case partly by vicariance and dispersal, and in the latter case essentially by vicariant events, in accordance with the

concept of pan-biogeography of Croizat (1958), or phylogenetic biogeography of Rosen (1978) and his followers (Table 1).

Meier-Brook (1984) reviewed the tribe *Planorbini* of the Planorbidae, on the basis of cladistic analysis: the distribution of the freshwater pulmonate gastropods is explained by vicariant events at different levels of family, species, genus or sub-genus. In another example, Gittenberger (1984) revised the land snails of the sub-family Chondrinidae, and gave prominence to two patterns of distribution in the western Palaearctic region. In this example members of *Granaria* show evidence of vicariant patterns, while species of *Chondrina* indicate a dispersal pattern; other genera show a combination of vicariant and dispersal events.

If we consider causal ecological and causal historical biogeographies, we notice that the differentiation between biotas and biomes reflects the divergence of integration levels between, on one hand, extensive areas over a relatively long time scale (historical communities: biotas), and on the other hand, 'local' situations over an instantaneous geological time scale (ecological communities: biomes) (Fig. 1).

From the definition of Lémée (1967), following Clements (1949), a biome is a biogeographical entity characterized by biological individuals, and the dominant species which constitute it. Therefore, the biome concept defines a major biological community which is in equilibrium (that is to say at its climax), and is composed of plants and animals having homologous morpho-functional adaptations (Table 1). In other words a biome can be understood as the association, for a determined geographical entity, of the plant and animal populations adapted to particular ecological conditions, but nevertheless susceptible to small spatial variations. Thus, the ecological community can be associated with an ecological sector or area corresponding with a climatic sector or area.

The question of the association of plant and animal groupings needs addressing. A group of vertebrates could easily be found, during a migratory cycle, among two or more distinct vegetational associations. On the other hand, with their low mobility, small animals like land snails constitute communities superimposed on plant associations, and like them are characterized by a dominant species.

A further question is, how is a biome integrated in a biota? A biota represents a biological superstructure at the geological time scale (Fig. 1). It groups together phylogenetic systems having a closely similar history, and in which the pattern of distribution is identical. Within a biota, it is thus possible to determine and to characterize one or several sub-systems, each apparently less complex, which are instantaneous because their existence is brief (Fig. 1). Biomes can be exclusive for a long time. In such cases, the biome merges into the biota, as is probably the case with insular communities. In another way, the distinction between biota and biome expresses the difference between the ecological and the historical weights which are characteristic of the scale of the approach (Fig. 1). At the regional scale, ecological factors are always dominant. But if the scale is changed, for example to a continental one, historical factors become dominant. Ecological factors have less importance at this scale. On the other hand, all the history of the continent, and consequently of the biological elements, may become important in explaining the observed distributions (Fig. 1).

The applications of these concepts in palaeontology are relatively new (Janvier, 1982, 1986) but they are worth extending. Nevertheless, it is nearly always the historical approaches which are developed, that is to say those corresponding to an evolutionary time-scale. Because of the relative precision of its records, with
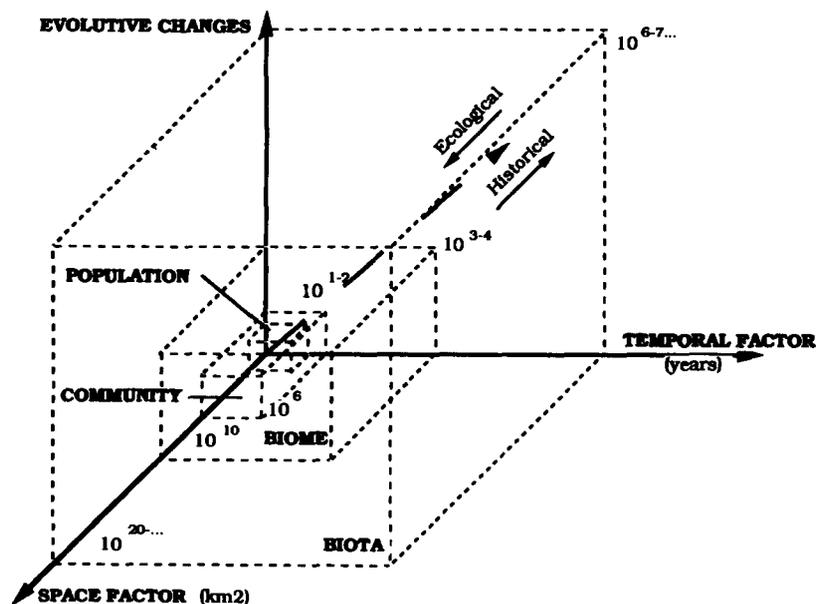

FIG. 1. Spatio-temporal representation of the main biological assemblages according to the evolutionary changes. The dotted lines indicate the limit that each entity can move over or under the proposed boundary as expressed by the exposure of 10.

numerous horizons yielding high chronostratigraphical
resolution, the Quaternary is a period for this analysis.
Among the invertebrates, which are susceptible to this
method, Pleistocene land snails appear to be appropri-
ate because they show less evolution than other animal
groups, such as, for example the rodents, during this
period.

THE FOREST MALACOLOGICAL ASSOCIATIONS
OF THE 'HOLSTEINIAN' TUFAS: AN EXAMPLE OF
THE BIOME CONCEPT

The Problem

The climatic optima of interglacials in central Europe
are characterized by a malacofauna which is rich in
thermophilous and forest species, whose present distri-
bution is south-eastern Europe: *Helicigona banatica*
(south-Carpathians), *Soosia diodonta* (north-Balkans),
Iphigena densetriata (east-Alpine), *Aegopinella ress-
manni* (southeastern-Alpine), and *Mastus bielzi* (east-
Carpathians). In addition, some taxa belonging to these
malacofaunas are fossil, such as *Helicigona capeki*, or
they have radically changed their distribution, like
Gastrocopta theeli (presently east-Asiatic) (Lozek,
1964). This *H. banatica* malacological association
(Lozek, op. cit.) did not come farther west than
southern and central Germany in the Middle Pleisto-
cene (Lozek, 1969; Kukla, 1977).

In western Europe, taxa occur in some interglacials
which have modified their distribution as compared
with the present for example: *Ruthenica filograna* ('last
interglacial' in Burgundy; Puisségur, 1976 — now
mainly in central Europe), *Aegopis verticillus* ('third'
interglacial before the Holocene in Normandy and in
Alsace; Puisségur, 1978; Lautridou *et al.*, 1985, 1986).
These species do not indicate the southern component
of the central-European species previously cited. In
England, numerous taxa, are found in interglacial
deposits, but they always indicate an immigration from
central Europe: e.g. *Discus ruderatus*, *Clausilia
pumila*, *Helicigona striata*, *Acicula polita*, *Macrogastra
ventricosa*, *Truncatellina callicratis*, *Vitrinobrachium
breve*, *Ruthenica filograna* (Kerney, 1977; Holyoak and
Preece, 1986). *Laminifera pauli* which now lives in the
region of Bayonne (Pyrénées atlantiques, France) has
also been found in England (Kerney, 1959; Holyoak *et
al.*, 1983). But the lack of some taxa, which have a
south-western European distribution today, in the
interglacial fauna in western Europe was surprising to
Lozek (1969).

Why did this mixing of the interglacial malacofauna,
with the occurrence of 'foreign taxa', only take place in
central Europe, although favourable environmental
conditions existed in western Europe (Fig. 2)? This
reveals on the one hand, the lack of complementary
data about France and England at the time of Lozek's
(1969) review, and on the other hand, conceptual
differences, previously mentioned, about the
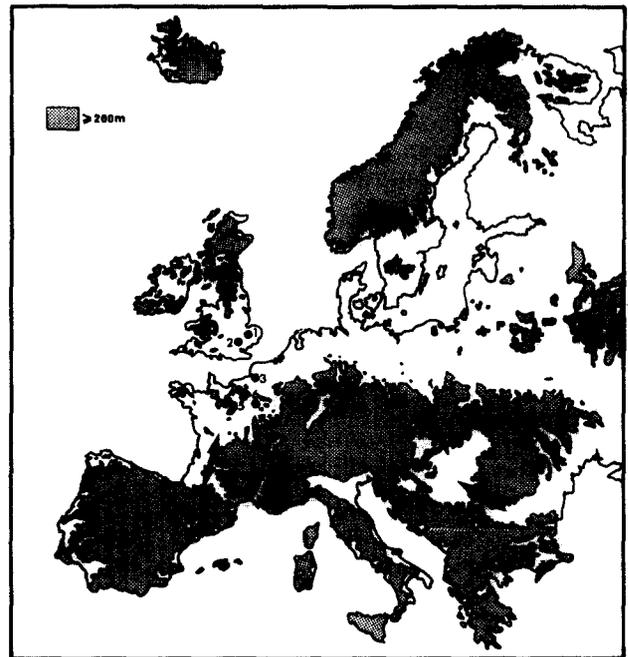palaeobiogeographical processes.

FIG. 2. Map of west and central Europe with shading showing land
over 200 m. The arrows show the main emigration routes in
interglacials (arrows: oceanic coast, Saône–Rhone and Danubian
corridors). The location of the sites in the text is indicated by the
numbers: 1-Icklingham, 2-Hitchin, 3-Arrest, 4-St Pierre-lès-Elbeuf,
5-Vernon, 6-La Celle-sous-Moret.

Materials

In Europe, two pleniglacial biomes have been recog-
nized (Rousseau, 1986). They represent two ecological
classes: cold steppe and tundra. The latter is charac-
terized by a richer malacological association with
greater specific diversity. Analysis of the Achenheim
deposits (Rousseau, 1986, 1987) has demonstrated that
during the last five interglacial–glacial cycles, the
glacial phases in west and central Europe have been
characterized by the sharing of only one biome or by
the occurrence of two biomes. This is partly due to the
geomorphology of Europe, notably the northern plain
and the central Alpine mountains, which allows a
dispersal from east to west for taxa living in periglacial
environments (Fig. 2).

In the interglacials, the topography of southern
Europe limited potential immigration routes to only
three, the Atlantic littoral, the Saône–Rhône valley
and the Danubian corridor (Fig. 2). The use of the
latter by the *H. banatica* fauna has been demonstrated
by Lozek (1964, 1969). Up to now, the emigration
along the Rhodanian corridor has not been given
prominence because the interglacial faunas found in
Burgundy and Alsace do not reveal the occurrence of
southern immigrants (Puisségur, 1976, 1978). On the
other hand, revisions of the malacofauna of Normandy
show interglacial taxa with a clear southern distribu-
tion.

In western Europe, during the 'Holsteinian' or the
British 'Hoxnian', tufa sedimentation developed in a
moist forest context under interglacial conditions. Such

deposits occur at: Hitchin and Icklingham (England); Saint-Pierre-lès-Elbeuf, Vernon and Arrest (France). There are some doubts about the age of the latter, because correlation is based on the malacofauna only (Fig. 2). Another site which might also be included is La Celle-sous-Moret, but the collection of Munier-Chalmas has been lost. Besides the common forest species typical of deciduous temperate forest (determined by the forest and semi-forest species *sensu*; Puisségur, 1976), these deposits yield several taxa with a distinctive recent distribution (Puisségur, 1983).

Botanical data

The site of La Celle-sous-Moret has provided plant macro-fossils and pollen, among which occur *Laurus canariensis* (*L. azorica*), Canary laurel *Ficus carica* (fig), *Cercis siliquastrum* (Judas tree), *Buxus sempervirens* (box), *Cerasus mahaleb* (the St Lucy cherry), and *Viburnum tinus* (Viburnum). All these taxa are now Mediterranean, with *Laurus canariensis* now being confirmed to the Canaries (Bourdier, 1969; Guyot, 1969). In the Vernon tufa, Bourdier (1969) mentions the occurrence of the same species, which, with the malacofauna allows him to correlate the two sites.

Malacological data

The following are species peculiar to each deposit.

Icklingham–Hitchin: (from Kerney, 1976; Holyoak *et al.*, 1983; Holyoak and Preece, 1986):

— *Acicula diluviana* (fossil);
— *Retinella (Lyrodiscus) skertchlyi* (fossil) (a);
— *Ruthenica filograna* (currently in central Europe; Fig. 3);
— *Acicula polita* (currently in central Europe; Fig. 4);
— *Laminifera pauli* (Pyrenean, around Bayonne at present; Fig. 5).

Arrest (Puisségur, *unpublished data*; Rousseau and Puisségur, 1990):

— *Retinella (Lyrodiscus) skertchlyi* (fossil) (a).

FIG. 4. Present distribution (shading) of *Acicula polita* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.

FIG. 5. Present distribution (shading) of *Laminifera pauli* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.

Vernon (Puisségur, *unpublished data*; Rousseau and Puisségur, 1989, 1990):

— *Aegopinella bourdieri* (fossil) (b);
— *Retinella (Lyrodiscus) skertchlyi* (fossil) (a);
— *Hygromia cinctella* (currently Mediterranean; Fig. 6);
— *Leiostyla anglica* (currently British Isles; Fig. 7);
— *Ruthenica filograna* (currently central Europe);
— *Zonites acieformis* (currently central Europe; Fig. 8).

Saint-Pierre-lès-Elbeuf (Puisségur, 1983; Rousseau and Puisségur, 1990):

— *Aegopinella bourdieri* (fossil) (b);
— *Bradybaena chouquetiana* (fossil);
— *Retinella (Lyrodiscus) skertchlyi* (fossil) (a);
— *Hygromia cinctella* (currently Mediterranean);
— *Laminifera pauli* currently Pyrenean, near Bayonne);
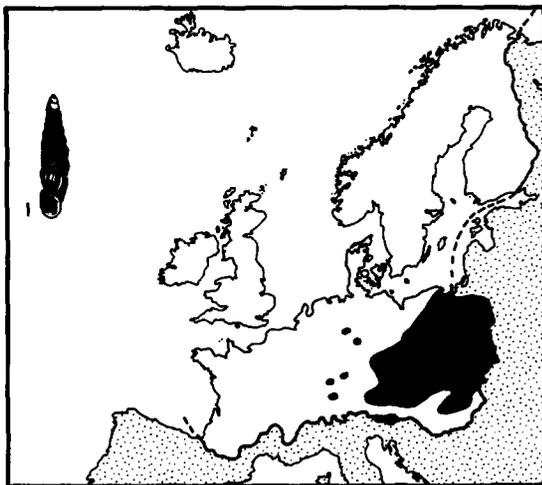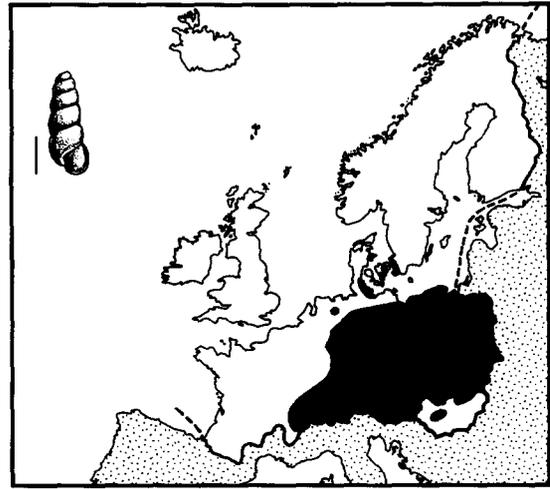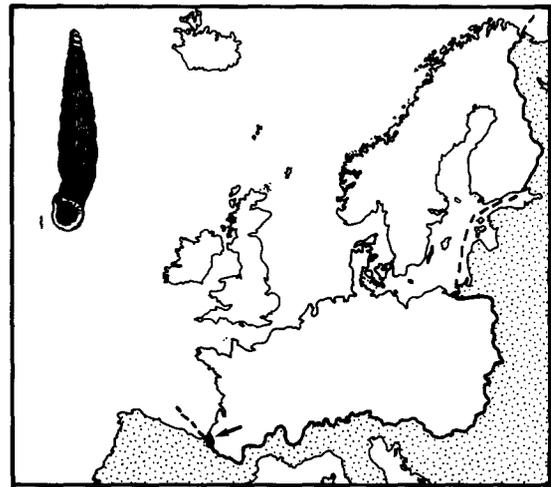— *Zonites acieformis* (currently central Europe).

FIG. 3. Present distribution (shading) of *Ruthenica filograna* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.
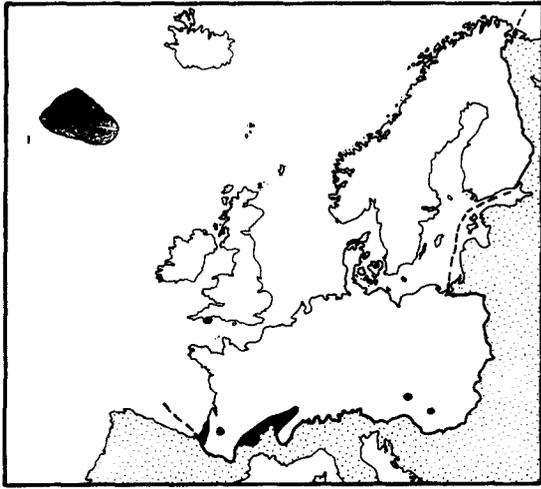
FIG. 6. Present distribution (shading) of *Hygromia cinctella* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.
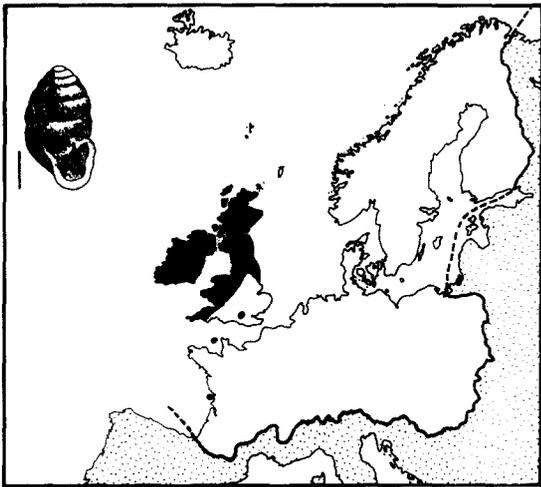

FIG. 7. Present distribution (shading) of *Leiostyla anglica* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.
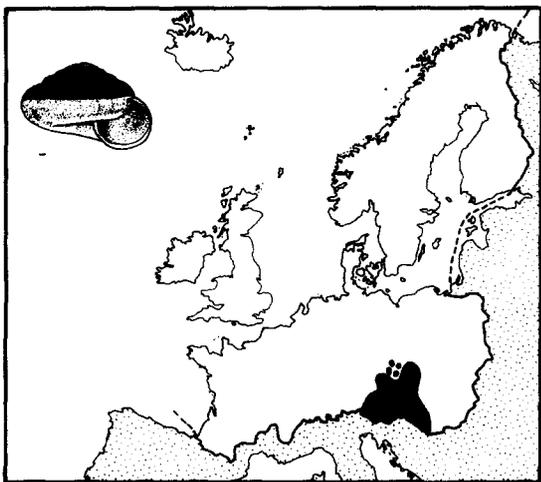

FIG. 8. Present distribution (shading) of *Aegopis verticillus* in northern and central Europe (modified from Kerney *et al.*, 1983). The scale indicates 1 mm high.

(a) *Retinella (Lyrodiscus) skertchlyi* is a zonitid described by Kerney (1976) from the tufa of Icklingham. This taxon is very interesting. It had a west-European distribution during the Plio–Pleistocene, but its related recent species are confirmed to the Canary Islands (Rousseau and Puisségur, 1990). So its occurrence, in deposits with the Canary laurel is an important biogeographical record.

(b) *Aegopinella bourdieri* is a new fossil species which has so far only been found in Normandy, at Vernon, and St Pierre-lès-Elbeuf (Rousseau and Puisségur, 1989).

The association of recent forest and semi-forest taxa, together with 'immigrant' species which have changed their distribution and their ecological peculiarities, allows us to characterize a peculiar faunal community. Taking into account the botanical data which indicate the same type of association, the fauna and flora of these tufas constitute an interesting biogeographical association. The environment in which these fossils are found is similar for each deposit, a spring tufa produced by seepage of calcareous water. Such analogies contribute to characterize a biome, a grouping together of a plant association of temperate deciduous forest with xerophilous taxa, and a particular malacological association with southern species, which reached its climax during tufa sedimentation. The currently known distributional area of the biome is from west Suffolk in England to Normandy in France.

DISCUSSION AND CONCLUSION

Do such faunal and floral associations have any links? According to the evidence of present faunas, the heterogeneous nature of the botanical and malacological associations is the limiting factor for any interpretation. No a priori argument allows us to assert or to invalidate the idea that these emigrant taxa have kept or changed their ecological affinities and peculiarities. Nevertheless, we have to consider such a biome with causal biogeography.

The Composition of the Biome

Plant and animal species reveal a temperate open forest. But the immigrant taxa yield special information (Becker *et al.*, 1982). *Buxus sempervirens* (Fig. 9) is mainly common in the south of France. It is tolerant of drought caused by summer heat, but is also hardy in winter. It is a common plant in the Holsteinian and Eemian in northwestern Europe. *Cerasus malaheb* is a species of the hills and lower slopes of southern mountains, requiring some heat but less than the typically Mediterranean species. It is tolerant of dryness, but requires good light. *Cercis siliquastrum* (Fig. 10) is spontaneous in the Mediterranean region; it lives on dry calcareous hillsides, never in forest, but in open vegetation, and is moderately hardy against the cold. *Ficus carica* (Fig. 11) lives in parts of the Mediterranean, in warm and sunny, often, rocky localities. *Viburnum tinus*, lives in the garrigue and in the scrub.
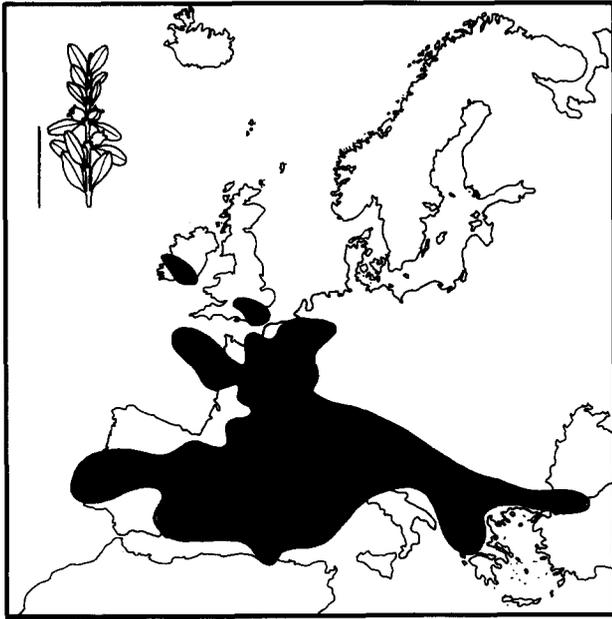
FIG. 9. Present distribution (shading) of *Buxus sempervirens* in western Europe (modified from Becker *et al.*, 1982). The scale indicates 5 cm high.
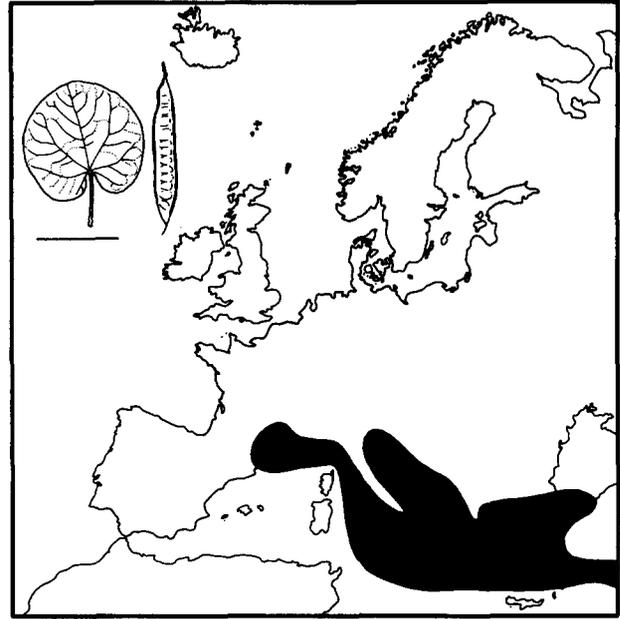

FIG. 11. Present distribution (shading) of *Cercis siliquastrum* in western Europe (modified from Becker *et al.*, 1982). The scale indicates 5 cm high.
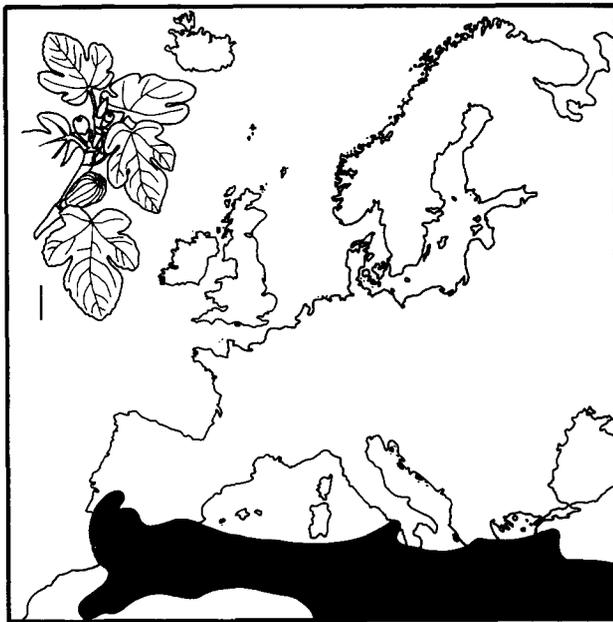

FIG. 10. Present distribution (shading) of *Ficus carica* in western Europe (modified from Becker *et al.*, 1982). The scale indicates 5 cm high.

but never in the drier localities. Finally, *Laurus canariensis* inhabits the Canary Islands laurel forest, which "is a remnant of the much richer evergreen forest that covered parts of Europe and Africa in the Tertiary" (Raven and Axelrod, 1974).

All the mollusc species mentioned inhabit forest or semi-forest habitats. So the vegetation is a temperate, non tropical, sparse mixed forest which has existed in western Europe since the Late Miocene and in the northwestern Mediterranean region since the Reuverian (Suc and Zagwijn, 1983; Suc, 1985).

The Origin of that Biome

As indicated above, such a forest type developed during the Tertiary in Europe and in NW Africa (Raven and Axelrod, 1974). From that time the laurel forest changed progressively into a mixed forest. This change has been identified in Europe and in Africa (Raven and Axelrod, 1974). Some localities such as the Canary Islands currently show relics of that Tertiary forest. The occurrence in northwestern Europe of such a biological association during the Middle Pleistocene does not illustrate evolution on the spot, but an emigration from refugia permitted by favourable environmental conditions.

Complementary Elements

Other sites of Hoxnian age have provided data which strengthen this interpretation. In England, Godwin (1977) indicates that the Hoxnian interglacial flora is composed of plants already known in England as well as in Ireland, but also Lusitanian or Hiberno–American species. The association is an open mixed-oak forest.

In southwest France, Texier *et al.* (1983) indicate during their 'Mindel-Riss' stage, the occurrence of a flora of numerous thermophilous taxa (mixed-oak) and hygrophilous herbs. High temperature conditions are indicated by the occurrence of Mediterranean species (i.e. *Rhododendron ponticum*, *Erica mediterranea*) and by taxa with Lusitanian affinities (*Dabaoecia cantabrica*).

The deposition of tufa requires the conjunction of different influences in which the local topography, the environment, the possibility of the mobilization of calcium carbonate in the vicinity, and also the climate are important. Because the southern taxa seem to have kept their ecological character, the development of such a deposit implies the occurrence of a warmer

climate than that recently observed in Normandy or England.

The Climate

In all cases the climate indicated is highly oceanic with high summer temperatures. Such a climate is unlike the present one in this region. It seems difficult to consider such a biome as the result of a special microclimate, so changes in the oceanic and atmospheric circulations may have occurred. The sites are located in Normandy and also in eastern England. So, if we consider a modification of the oceanic circulation, this might be appropriate for Normandy and also for southwest France. But for west Suffolk, it would be necessary to propose warm waters in the North Sea.

What is the age of all these tufas? The ages of Hoxnian and of the Holsteinian are the subjects of debate. Amino acid dating based on land snail shells by Occhietti (*unpublished data*) indicate a younger age for the tufa of St Pierre-lès-Elbeuf than that proposed by Lautridou. The hypothesis of Lautridou, the immigrant episode in western Europe, is younger than that of central Europe. Following his interpretation, and using the nomenclature of Kukla, the St Pierre tufa corresponds to the interglacial of glacial Stage E. In central Europe *H. banatica* faunas occur in the interglacials of the glacial Stages B and D (Kukla, 1977). But are these immigrant episodes synchronous? Do they correspond to a response to the same physical constraints but of different ages? Where do the immigrant taxa come from? More data are necessary to establish the distribution of these taxa during both interglacials and glacials.

Two main conclusions are possible. First, the development of that biome raises again the problem of the correct stratigraphical position of the tufa of St Pierre-lès-Elbeuf. Is it part of a pedocomplex overlying the Elbeuf II palaeosol, or are they distinct? At present, it is not possible to confirm either of these possibilities without the help of complementary studies such as micromorphology. Nevertheless, the examination of the section does not allow us a priori to distinguish any erosional break between the tufa and the palaeosol. If the hypothesis of the pedocomplex was confirmed, two interglacial biomes would have occurred during the same period in western and central Europe, which show malacological communities with some southern emigrant species. For this episode, such a case would involve the occurrence of different atmospheric circulations providing a warm oceanic temperate climate in western Europe and a more Mediterranean continental temperate climate in central Europe reaching higher latitudes than at present.

Second, concerning the biogeographical relationship, the biome concept characterizes a biogeographical entity grouping the botanical and the zoological data together in a fluctuating spatio-temporal scope. According to its nature, it does not correspond to the purely stratigraphic biozone. Contrary to the biota concept, another fundamental biogeographical unit, the biome, optimizes the weight of the ecological factor to the detriment of the temporal factor. In other terms, the distinction of the biome and the biota concepts leads to an inversion of the balance of the ecological and of the temporal factors. As the integration of both botanical and zoological data allows us to better delimit the real conditions of life and thus lead to a more precise research orientation, causal ecological biogeography is certainly progressive. By its hypothetico-deductive process, this approach is a successful research programme which involves channeling approaches to a problem. From such data, only few appropriate hypotheses can be developed which will be confirmed or denied by new studies. The analysis of the biome of the Holsteinian tufas of northwestern Europe has been proposed to demonstrate this point of view. So the multidisciplinary implications of this analysis in the Life Sciences as in Earth Sciences indicates that this scientific research programme, up to now undeveloped, is particularly appropriate for Quaternary palaeontology, and seems more suitable for further development.

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