

Ciências da Terra (UNL)	Lisboa	Nº 12	pp.167-179 2 figs.	1993
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Palaeontological data about the climatic trends from Chattian to present along the Northeastern Atlantic frontage

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SUMMARY

Key words: Climatic changes; Northeastern Atlantic; Chattian, Neogene, Quaternary; Faunas, Floras.

Climatic changes that affected the Northeastern Atlantic frontage are analyzed on the basis of the evolution of faunas and floras from the late Oligocene onwards. The study deals with calcareous nannoplankton, marine micro- and macrofaunas, some terrestrial vertebrates and vegetal assemblages. The climate, first tropical, underwent a progressive cooling (North-South thermic gradient). Notable climatic deteriorations (withdrawal towards the South or disappearance of taxa indicative of warm climate and appearance of "cold" taxa) are evidenced mainly during the Middle Miocene and the late Pliocene. Faunas and floras of modern pattern have regained, after the Pleistocene glaciations, a new climatic ranging of a temperate type in the northern part.

INTRODUCTION

This study presents palaeoclimatic data provided by faunas and floras from the late Oligocene onwards, on the Northeastern Atlantic frontage¹. It is based on groups which come from the oceanic domain (calcareous nannoplankton), the neritic realm (benthic foraminifers, ostracods, scleractinians, bryozoans, bivalves, gastropods, echinoids), and the continental realm (reptiles, mammals, vegetal associations). The evolution of the climate has been analyzed for the following stages: Chattian, Aquitanian, Burdigalian, Langhian-Serravallian, Tortonian, Messinian, "Pliocene, Pleistocene, Holocene. The stratigraphic frame and the retained palaeogeographic data have been previously presented (Alvinerie *et al.*, 1992). The main basins of reference are the Aquitaine Basin (Chattian-Serravallian interval) and the Loire Basin-Normandy as a whole (Langhian-Pleistocene interval).

The calcareous nannoplankton comes from continental slopes (DSDP/ODP drillings from Arctic to Equator) (Fig. 1); the information it provides does not always fit with those afforded by benthic groups. Therefore, it is necessary to take into account problems that deal mainly with long distance transportation, with frequent reworkings, with alterations of assemblages during fossilization, and with life of nannoplankton species that is generally shorter (about 100,000 years) compared to that of benthic species (several m.y.).

Groups from the neritic realm studied on the Northeastern Atlantic frontage are distributed, from North to South, in the following areas: Normandy (dependancy of the Channel), peri-Armorican regions, Ligerian Gulf (=Loire Basin), Aquitaine, North of Lisbon and Lower Tagus region, Algarve, Huelva area, western coasts of Morocco up to the Agadir latitude (Fig. 2).

Figure 2 mainly corresponds to the palaeogeography of

1 - This project results from the cooperation of the "Groupe Français d'Etude du Néogène" (GFEN) and the Centro de Estratigrafia e Paleobiologia da UNL, Faculdade de Ciências e Tecnologia, Lisboa, within the framework of the Regional Committee of the Atlantic Neogene Stratigraphy (RCANS).

the period which appears as the most transgressive (Middle Miocene) but the outline of the Channel area represents that of the Pliocene, this in order to place the main considered marine basins. As a simplification, the present latitudinal and longitudinal frame has been kept (Alvinerie *et al.*, 1992, Fig. 4). The present West-African province is used as a reference concerning the interpretation of tropical faunas. According to stages and regions, most information is provided by the study of some groups (benthic foraminifers, scleractinians, molluscs, echinoids ...) especially owing to their frequency and/or their climatic significance.

As far as the continental realm is concerned, some groups especially sensitive to climatic changes have been selected among vertebrates of Europe. Besides, detailed studies of pollens and vegetal remains dealing with Portugal (located in the middle of the studied area) have evidenced climatic fluctuations and have allowed, along with vertebrates, to observe correlations between marine and continental realms.

LATE OLIGOCENE

In the neritic realm, with which the present study mainly deals, the late Oligocene faunas, which belong to the West-Tethyan tropical province, are affected by a significant change. These faunas will act as the base from which the tropical province will form and spread along the Northeastern Atlantic frontage during the early Miocene.

Indicators of warm climate

The Chattian of the neritic realm is of a tropical type as demonstrated by the whole invertebrate fauna. Studies of benthic foraminifers, ostracods, scleractinian corals, bryozoans, molluscs and echinoids provide consistent results.

The larger foraminifers of Mesogean affinities (*Nummulites*, *Operculina*, *Miogypsinoides* ...) are, for the last time, present as large assemblages at the most northern latitude concerned by this study (i.e. peri-Armorican regions). There, smaller foraminifers indicating warm climate, such as *Pararotalia viennoti*, are part of these assemblages (Delanoë *et al.*, 1976). Southward, in Aquitaine (Chevalier, 1961; Cahuzac & Chaix, this issue), the abundance of corals should be stressed. Numerous species took part in building coral reefs. Since that time, such an abundance (140 species) has never been matched in this basin. The microfauna is rich in larger foraminifers (the same as in the peri-Armorican regions, to which are added several other genera including *Spirochlypeus*, *Cyclochlypeus*, *Heterostegina*...). Besides, numerous smaller foraminifers are often connected with reefs. The presence of *Discorbis mira* should be noted (Cahuzac & Poignant, 1988); this species is presently living in the intertropical zone. The ostracofauna is very diversified. It also displays

tropical affinities and comprises genera connected with reefs (for example, *Schuleridea*, *Cnestocythere*, and the thermophile species *Pokornyyella calix*) (Bekaert, 1990; Bekaert *et al.*, 1991). Among bryozoans (Reuss, 1869; Labracherie, 1972), assemblages include numerous genera with strict tropical affinities (*Poricellaria*, *Nellia* ...) or with broader distributions (*Margaretta*, *Onychocella* ...); mediterranean forms and cosmopolitan boreo-mauritanian genera appear. Faunal characteristics are similar in echinoids which comprise the tropical genus *Maretia*, living today in the Indo-Pacific province, along with several taxa indicative of warm climate (*Echinolampas*, *Scutella*, *Amphiope* ...). Molluscs also include numerous forms with intertropical affinities of the West-Tethyan province. Their diversity is similar to that of the present Caribbean and Indo-West-Pacific provinces. Various tropical taxa appear among bivalves (*Trisidos*, *Paradonax* ...) and gastropods (diversity of Cypraeidae, Olividae, Conidae ...); several groups show a West-African pattern (Turridae, Terebridae, Nassariidae) (Lozouet, 1986). Farther to the South (Spain, Morocco), the Chattian deposits correspond to shelf facies. They are rich in Tethyan larger foraminifers.

Data are apparently different in the oceanic province, where the calcareous nannoplankton is poorly diversified. Significant event occurred in the Northeastern Atlantic (establishment of the North-South oceanic circulation and climatic control following on the opening of the Northern Atlantic). On the continent (Middle Europe), the evolution of the size and frequency in accordance with temperature of a castorid mammal (*Steneofiber*) will be followed. During the Oligocene, it is small.

THE OLIGOCENE/MIOCENE TRANSITION

The transition between the Oligocene and Miocene is characterized by extinctions, in the neritic realm as well as in the oceanic domain. Numerous thermophile species died out. At the same time, a significant phase of replacement occurs.

AQUITANIAN

At the outset of the Miocene, assemblages characteristic of the West-African province appear. A replacement of numerous species is noticed. However, in every group, it is not so marked than that which occurred during the Chattian. Special attention should be paid to the evolution of corals because of their sensitivity to temperature changes. The decrease in the number of scleractinian species (about half the species during the Aquitanian in comparison with the Chattian) could indicate a slight drop of the temperature at the beginning of the Neogene. However, the assemblage remains practically only comprised of hermatypic forms, characteristic of a warm climate (Cahuzac & Chaix, this issue).

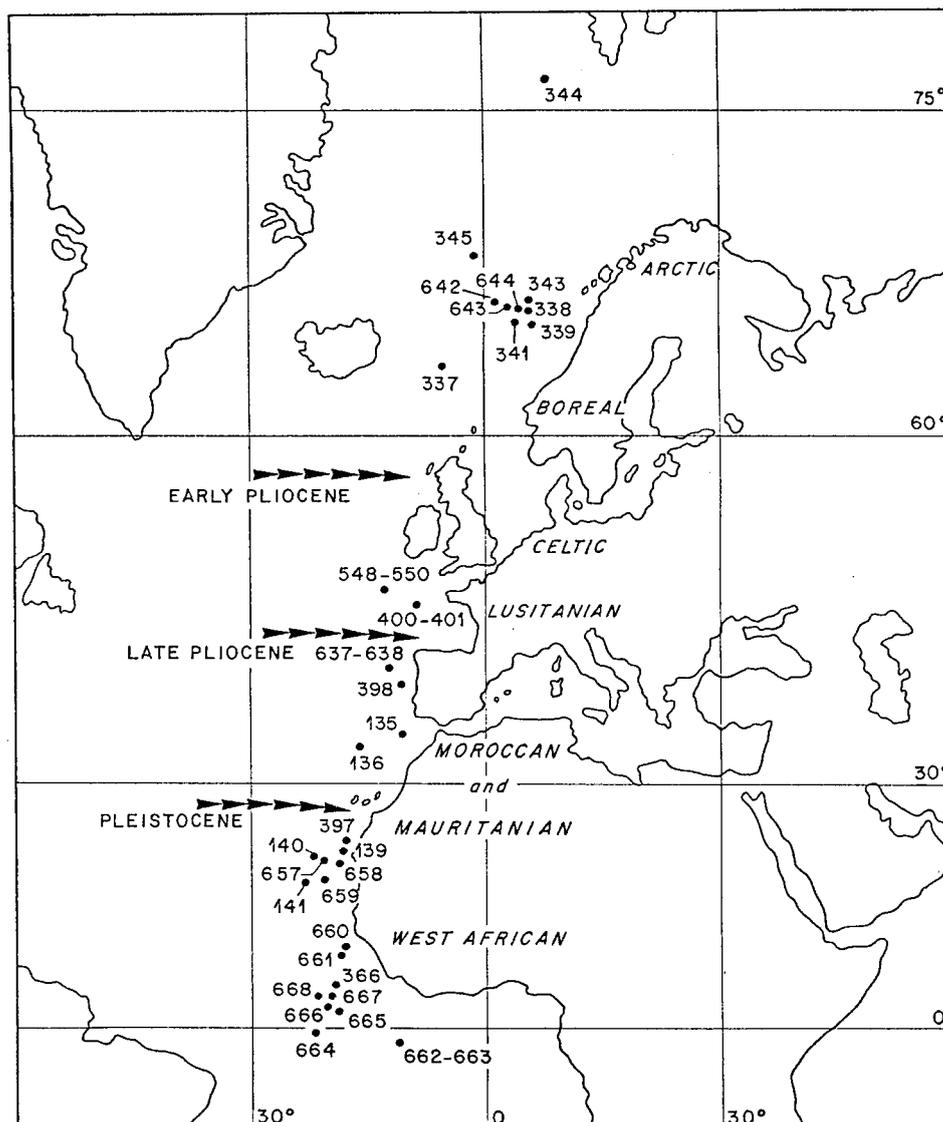


Fig. 1 — General map of the Northeastern Atlantic frontage with calcareous nannofossil data (after Roth & Thierstein, 1972; Müller, 1976; Samtleben, 1977; Blechschmidt, 1979; Cepek & Wind, 1979; Müller, 1979; Müller, 1985; Pujos, 1985; Wei *et al.*, 1988; Donally, 1989; Manivit, 1989) and indication of the northern boundary of the Ceratolithaceae range at early and late Pliocene, and Pleistocene. Marine biogeographical provinces (Hall, 1964).

Indicators of warm climate

As a whole, the climate remains warm as demonstrated mainly by: the presence of larger benthic foraminifers as far as in the peri-Armorican regions (*Miogypsina*, *Nephrolepidina* ...) (Andreieff *et al.*, 1973); the frequent presence, in Aquitaine and Portugal, of bryozoans, the range of which extends today from the Equator to the subtropical zone (*Nellia oculata*, several species of *Steginoporella* and *Thalamoporella* ...) (Vigneaux, 1949; Galopim de Carvalho, 1971); the global persistence of Tethyan mollusc groups (*Alectryonia*, *Sunetta* ..., among bivalves); the beginning of a large diversification within some groups of Tethyan gastropods (*Nassariidae*,

Turridae ...) (Lozouet, 1986); the predominance in continental areas (Portugal) of plants corresponding to a subtropical to tropical climate (ferns, *Magnolia*, *Bombax*, *Sapotaceae*, *Nyssa*) (Pais, 1981; 1986; Antunes & Pais, 1983); the presence in Europe, since the Eocene, of *Diplocynodon*, alligatorid crocodylian which indicates a comparatively high temperature.

Indicators of temperate or "cold" climate

However, a North-South thermic gradient takes form from that time onwards. This gradient tends to cool marine waters of northern regions. It is demonstrated either by

progressive withdrawal, toward the South, of certain taxa according to the latitude, or the appearance of taxa with northern affinities.

For example, among the ostracods of Aquitaine, the tropical genus *Pokornyella* becomes scarce (only one species instead of 7 previously) (Bekaert *et al.*, 1991), whereas to the South, is known the richest ostracofauna of the Portuguese Neogene; it should be noticed that, among them, *Neonesidea* characterizes today the tropical and subtropical zones and develops near reefs (Nascimento, 1988).

Some species, with rather northern affinities, such as *Elphidiella arctica angulata* and *Globocassidulina*

(*Islandiella crassa* appear among smaller benthic foraminifers from Northwestern France (Curry *et al.*, 1965).

In the oceanic domain, the calcareous nannofossils are still poorly diversified.

BURDIGALIAN

The climate is of a warm tropical type in the whole studied area. The Burdigalian thermic optimum is marked; since that time, such an optimum probably never occurred on the Northeastern Atlantic frontage.

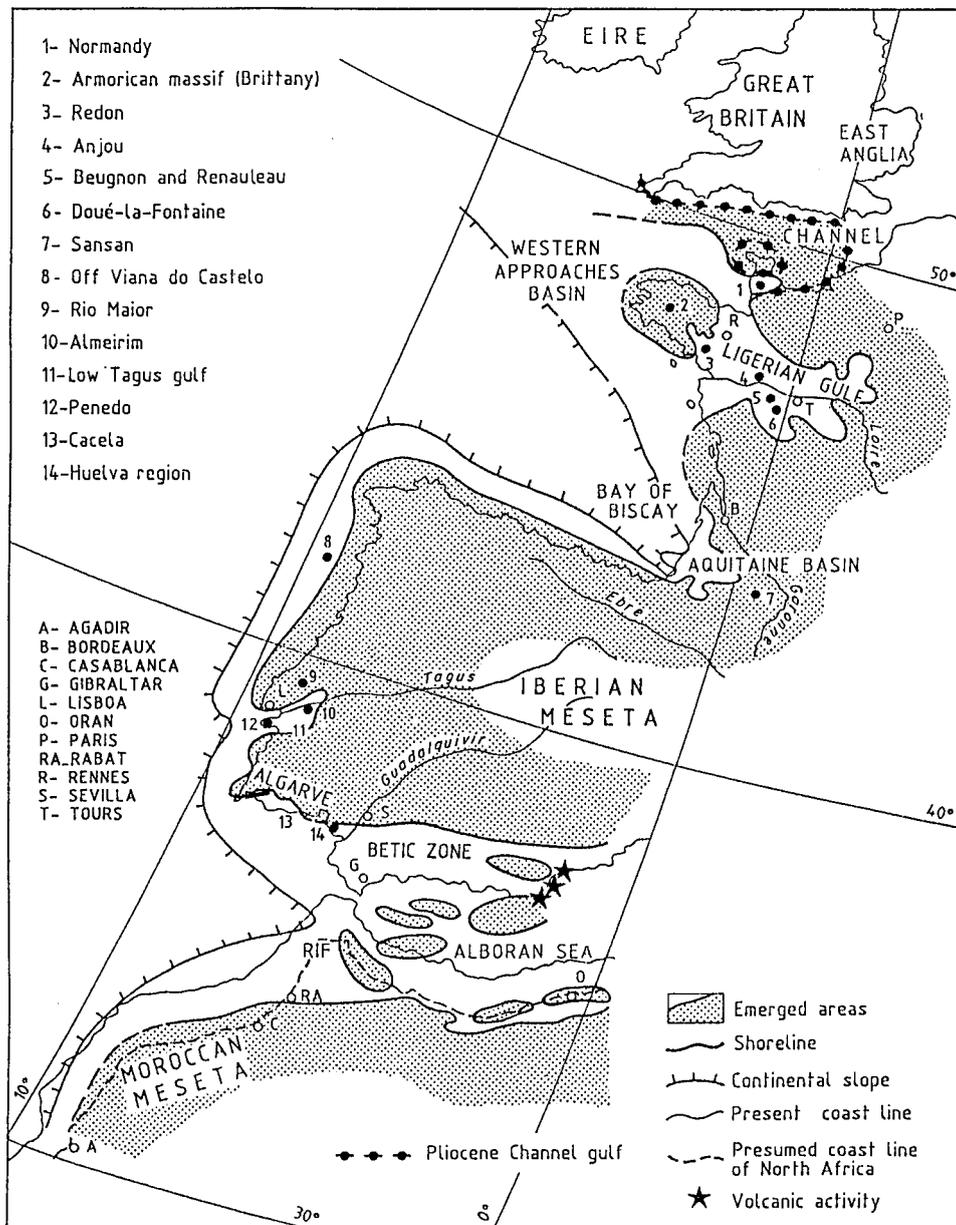


Fig. 2 - Map of the Middle Miocene, which is the most transgressive time on the Northeastern Atlantic frontage (Alvierie *et al.*, 1992, fig. 4); however, the outline of the Channel is the Pliocene presumed one.

Indicators of warm climate

In the neritic province, the development of reefs is continuing in Aquitaine during at least the first half of the Burdigalian (Cahuzac, 1980). Comparatively to the Aquitanian, the number of scleractinians increases (almost 90 species, most of them being hermatypic); this could be indicative of a warming, reminiscent of that of the late Oligocene (Cahuzac & Chaix, this issue). According to molluscs, the Burdigalian is a time of warm climate; an intense evolution affects numerous gastropods and Pectinidae, among bivalves, for example *Gigantopecten*. Portuguese malacofaunas are very rich (Zbyszewski, 1957). French and Portuguese malacofaunas are similar. Affinities are also noticed between the Lusitanian and the Mediterranean provinces (numerous common Pectinidae for example). Among echinoids, tropical genera (*Clypeaster*, *Maretia*) reach the Aquitaine to the North. Among benthic microfaunas, some thermophile ostracod genera are still present, but they are scarce; larger foraminifers seem rather frequent, from Aquitaine to Morocco, at least during the first part of the stage (Cahuzac & Poignant, this issue).

In the continental province, the presence of the crocodylians *Diplocynodon* (Europe) and *Tomistoma* (Portugal, France, Mediterranean areas) clearly argues for a warm climate. It may be admitted also that the increase both in number and size of *Steneofiber* (Castoridae) during the whole stage in France, results from favourable climatic conditions: importance of continental water (lakes, rivers) and thermic increase (Ginsburg, 1968). In Spain, the relative abundances of Burdigalian rodent families (Eomyidae, Gliridae, Cricetidae, Sciuridae, Zapodidae, Castoridae) the ecological requirements of which are known or have been inferred, indicate a rise in temperature up to the Langhian (Daams & van der Meulen, 1983). Vegetal associations provide regional information. Thus, in Portugal, successive climatic changes are evidenced: cooling during the early and late Burdigalian, warming during the middle and latest Burdigalian. During the coolest phases, tropical and subtropical species are nevertheless present but they are mixed with taxa indicative of a temperate climate. Warmings correspond to a climate of tropical type: Bryophyta, numerous ferns, climax of *Bombax* and Sapotaceae during the middle Burdigalian; ferns and numerous angiosperms (including *Magnolia*, *Bombax*, *Myrica*, *Engelhardtia*, Sapotaceae) during the latest Burdigalian, suggesting a variation of moisture and a thermic maximum (Pais, 1981; 1986; Antunes & Pais, 1983).

The latest Burdigalian warming noted in the continental province coincides with the beginning of a renewal of the calcareous nannoplankton (especially by Coccolithaceae and Helicosphaeraceae) in the oceanic domain.

Indicators of temperate or "cold" climate

Nevertheless, the Burdigalian climate is not uniformly optimal in the neritic realm. The North-South thermic

gradient, initiated during the Aquitanian, is strengthened. Moreover, the climate slightly evolved during the Burdigalian. Larger benthic foraminifers clearly evidence this. During the Burdigalian, larger benthic foraminifers are absent from peri-Armorian regions, but, to the South, they persist along the whole Northeastern Atlantic frontage. During the late Burdigalian (ca. 18 Ma/16,5 Ma), the Miogypsinidae disappear from Aquitaine but are still developed from Portugal to Morocco. At the same time, several tropical ostracods become rare (*Nestocythere*, *Pokornyella*, *Neonesidea* ...) in Aquitaine or in Portugal (Nascimento, 1988; Bekaert *et al.*, 1991). In the same way, the echinoid *Agassizia* (today strictly confined to the intertropical zone) does not extend northward beyond the latitude of Algarve and the Huelva region, whereas it reached the Almeirim region (Ribatejo) during the Aquitanian (Zbyszewski, 1954; Veiga Ferreira, 1962).

On the other hand, some groups are characterized by the arrival of northern taxa, which is probably locally connected to cold currents: within bryozoan assemblages (Vigneaux, 1949; Galopim de Carvalho, 1971) indicative of warm climate (abundance of *Cupuladria*, *Discoporella* in Aquitaine) appear several forms with temperate affinities, or even with northern affinities (*Calloporella lineata*, *Sertella beaniana* ...); among bivalves, some invaders indicative of "cold" climate (*Cyprina*, *Yoldia*) appear in Aquitaine.

These data, when scrutinized, argue for a warm global climate tending towards a tropical type, with however signs of an incipient deterioration already perceptible north of the Algarve latitude.

LANGHIAN-SERRAVALLIAN

In the Northeastern Atlantic frontage, the Langhian is generally considered as a warm period following the Burdigalian thermic optimum. However, as early as the beginning of the Middle Miocene, coral reefs no longer exist in the studied area.

Indicators of warm climate

In the neritic province, the still warm climate enables the persistence of a large diversity of organisms. A very abundant fauna of bryozoans (Buge, 1957) characterizes the Savignean and Pontilevian facies in the Ligerian Gulf; it presents a subtropical pattern, with taxa living in warm waters (*Crisia elongata*, *Tremopora radificera*, *Steginoporella*, *Thalamoporella* ...), and numerous forms indicative of temperate waters. Locally, large *Cellopora* colonies correspond to bryozoan reef episodes. Among the abundant molluscs, certain genera are reported for the last time at this latitude (*Linga* ... among bivalves; *Strombus*, *Galeodes*, *Subula* ..., among gastropods) (Brébion, 1974). Among echinoids, the genera *Echinolampas* (subtropical) and *Tripneustes* (tropical) reached the Ligerian Gulf during

the Langhian. At the same time, in Aquitaine and Portugal south to Lisbon (Penedo), the presence of the tropical genus *Clypeaster* is noticed; another tropical form, *Plagiobrissus s. str.*, is also present in the Penedo only (Kotchetoff *et al.*, 1975).

On the continent, the thermic conditions are favourable everywhere during the Langhian. This is demonstrated by the presence, in Europe, of the crocodylians *Diplocynodon* and *Tomistoma* (Antunes & Ginsburg, 1989), and by the abundance in France of the castorid *Steneofiber*. because of its continuous growth, initiated in the early Miocene, *Steneofiber* has become the giant of the group by the Burdigalian-Langhian boundary; this genus is lacking in Spain because of the drought. In Spain, relative frequencies of rodent families indicate a regular decrease in temperature up to the end of the Vallesian (Daams & van der Meulen, 1983). During the Langhian in Portugal, the vegetation of tropical and temperate type (last *Magnolia* and gallerie forests with *Terminalia*) has turned to a vegetation of rather warm and very dry climate evidenced by the appearance of woods such as *Rutoxylon* with a traumatic structure indicative of a sudden environmental change. The presence of *Tamaricoxylon* and the foliar physiognomy are characteristic of such a climate (Pais, 1979; 1981; 1986; Antunes & Pais, 1983). The presence (Portugal, Spain, scarce in France) of *Hispanotherium*, a savanna rhinocerotid, also indicates adaptation to drought during the Langhian (Antunes, 1979, Antunes & Pais, 1983).

In the oceanic domain, the calcareous nannoplankton of the Langhian indicates a mild global climate as suggested by the occurrence of the warm water group *Sphenolithus* as far as in the Arctic sites. The North-South thermic gradient is indicated by a southward abundance decrease in *Coccolithus pelagicus* (cold water species) and a southward increase in *Sphenolithus heteromorphus* (warm water species). The climate of the Serravallian appears similar, but smaller variations in the assemblages from a site to another may reflect climatic conditions less stable than during the Langhian.

Indicators of temperate or "cold" climate

Compared with the early Miocene, new signs of cooling still appear: disappearances of taxa of warm climate and appearances of indicators of "cold" temperatures. Concerning scleractinians, it should be noted (see above) that reefs definitively disappear, on the Northeastern Atlantic frontage, as early as the beginning of the Langhian. Moreover, corals show a considerable decrease in both number of species and proportion of hermatypic forms (Chevalier, 1961, Chevalier & Nascimento, 1975). Besides, the diversity strongly drops during the Middle Miocene: during the Langhian, about 40 species, about half of them being hermatypic, are known in Aquitaine (whereas in Northwestern France, the Pontilevian comprises a subreefal fauna of some 30 species, and in Portugal less than 10 species are known); only 6 species have been identified in

the Serravallian of Aquitaine, and they are ahermatypic and little abundant (Cahuzac & Chaix, this issue).

The North-South thermic gradient becomes more pronounced, chiefly during the Serravallian: absence (Ligerian Gulf) and decrease (Aquitaine, Portugal, Spain, Morocco) in larger benthic foraminifers (*Operculina* and *Heterostegina* persist); progressive impoverishment in smaller foraminifers (Ligerian Gulf, Aquitaine, where the tropical *Discorbis* is now lacking); low diversity of Langhian ostracods (the thermophile *Cnestocythere* and *Pokornyyella* have disappeared at the top of the Burdigalian) (Moyes, 1965). Among gastropods, three phases of withdrawal of tropical taxa are noticed. In the studied area, Arcidae, Chamidae ..., among bivalves, are less abundant than during the early Miocene, and Carditidae are more numerous in Aquitaine than in the Ligerian Gulf; numerous Pectinidae are common to Portugal and to the Mediterranean province. The accentuation of the thermic gradient is linked to the initiation of the important cooling evidenced in the world ocean since the middle Serravallian, this later being connected to the increase in the Antarctic glaciation (Savin *et al.*, 1981).

Several groups are concerned by faunal turns. Among smaller benthic foraminifers, new assemblages herald those of the Pliocene; in the Ligerian Gulf, they comprise a large population of the Miocene form of the *Aubignyana mariei* lineage (Margérel, 1988). Ostracods assemblages include northern and mediterranean newcomers in Portugal where the ostracofauna is slightly more diversified during the Serravallian than during the Langhian (Nascimento, 1988). In the Ligerian Gulf, progressively appear echinoids indicative of a temperate climate during the Langhian (*Arbacina*) followed by marsupiate echinoids of northern affinities (*Coptechinus*, *Temnotrema*) during the Serravallian (Roman, 1983).

On the continental areas, the cooling leads, during the Serravallian, to the sudden decrease in size and abundance of the castorid *Steneofiber* (Ginsburg, 1968), to the diminution in number of rodents, to the extinction (Sansan, Aquitaine) of the crocodylian *Diplocynodon*, and the withdrawal of the longirostral crocodylian *Tomistoma* towards the South (Algarve, Portugal) where it is known up to the end of the Middle Miocene. In Portugal, vegetation indicative of a moist tropical climate (*Toddalia*, *Spirematospermum*, *Taxodium*) is back, which indicates a cooler and mainly moister climate than the previous one in this area (Pais, 1978; 1981; 1986; Antunes & Pais, 1983).

Comparison with the Western Mediterranean

During the early Miocene, the conditions seem similar in the West-Mesogean and East-Atlantic areas. During the Middle Miocene, in the Mediterranean, where coral reefs and tropical Alveolinidae (*Borelis* ...) persist, the Langhian thermic maximum, which is a continuation of the Burdigalian one, occurs during the first part of the stage only (Bizon & Müller, 1977; Bizon, 1981; Demarcq & Pouyet, 1990); but in the Atlantic neritic realm such a

maximum cannot be evidenced in the Langhian, which suggests a certain decrease in temperature as early as the beginning of the stage.

TORTONIAN

The fauna, as a whole, retains a warm pattern. Nevertheless, the North-South thermic gradient is more marked.

Indicators of warm climate

In every group of the neritic realm, one still notices indicators of tropical climate mixed with faunas of a subtropical to warm temperate type. All these forms, indicative of warm climate, are still present up to the Ligerian Gulf which is, however, a comparatively northern area. For example, *Dakaria* (3 species) and *Trematopora radificifera* among bryozoans (Buge, 1957), as well as *Tripneustes* and *Plagiobrissus s. str.* among echinoids, which are all restricted today to the equatorial and tropical zones of the Atlantic and Pacific oceans, have been recorded at Doué-la-Fontaine.

However, the faunas from the southern basins (Portugal, Spain, Morocco) show a more pronounced tropical pattern. Thus, among bivalves, species living today in the West-African province (*Linga columbella* ...) occur in the Tortonian of the Atlantic coasts of Morocco (latitude of Rabat) and in Portugal. These faunas, west of Gibraltar, mainly display similarities with the contemporaneous warm fauna of the Mediterranean (Pectinidae, *Paphia vetula* ...). Gastropods show a clear tropical pattern there: *Peristernia* at Cacela (Algarve), *Persicula* and large *Marginella* at Lisbon, forms which are unknown at higher latitudes.

Indicators of temperate or "cold" climate

In spite of the predominance of taxa indicative of warm climate, the climatic deterioration continues. As a result, thermophile groups withdraw southward or disappear, allowing the installation of taxa of northern origin.

On the oceanic domain, a global cooling is apparently demonstrated by the calcareous nannoplankton. The range of some *Discoaster* (*D. variabilis* and *D. brouweri*) and of *Sphenolithus* (*S. abies*) shifts southward; they are no longer evenly present north of Gibraltar (probable stress of seasonal/secular variations).

In the neritic realm, the progressive southward withdrawal of some taxa is also noticed. During the Late Miocene, the ostracod *Krithe papillosa* is known in Morocco only, whereas it was present in Aquitaine during the Chattian and during the early Miocene; in Portugal, it was abundant during the early Miocene but rare in the Middle Miocene (Nascimento, 1988; Benson *et al.*, 1991). In the same way, the echinoid *Clypeaster* is no longer recorded at the latitude of Lisbon, but it is present in the Guadalquivir Basin (Huelva) where large species (*C. insignis* and *C.*

pyramidalis) thrive as they do in Western Mediterranean (Betic basins). Besides, larger benthic foraminifers do not occur in Aquitaine (the last died out during the Serravallian) where an assemblage of small forms indicative of warm temperate climate develops (Caralp *et al.*, 1963).

Among the indicators of "cold" climate, the marsupiate echinoids *Coptechinus* and *Temnotrema*, which were present in the Serravallian of the Ligerian Gulf, are still reported from the same area. The first witnesses of a significant northern lineage, the bivalve *Astarte omalii* (Lauriat-Rage, 1981), occur there. Some forms of northern affinities (*Celtia* ...) also appear within the ostracofauna of Aquitaine and Portugal; the latter region includes several mediterranean species too (Nascimento, 1988). At least, the reduced number of scleractinians (among which non-reefal forms predominate) recorded in France (9 species) and in Portugal and Azores (8 species), argues for a cooling of waters in the Atlantic, whereas at the same time the reefal phenomenon develops in the Mediterranean.

On the continent, the disappearance of the last crocodylian (*Tomistoma*) and the relative abundances of various rodent families, the ecological requirements of which have been reconstituted, are accounted for by a decrease in temperature, initiated during the Serravallian, which has continued up to the end of the Vallesian (early Tortonian). At the latitude of Portugal, the climate of the early Tortonian appears milder than that of the Serravallian on the continent. The vegetation is composed of temperate taxa (Oleaceae, *Quercus* ... near the sea; *Populus*, *Salix* ... inland) along with some subtropical to tropical forms (*Engelhardtia*, *Myrica*) which are still present. Inland, the climate is dryer with contrasted seasons (Pais, 1981; 1986; 1989; Antunes & Pais, 1983).

MESSINIAN

The Messinian is poorly documented on the Northeastern Atlantic frontage, at least from Brittany to Southern Spain. The regressive trend is conspicuous and a secure allocation of deposits to the Messinian is a difficult problem (Alvinerie *et al.*, 1992). On the whole, no major faunal nor nannofloral change apparently occurred between the Tortonian and the Messinian.

In the Loire Basin, a small gulf (Beugnon, Renauleau) could have persisted during the Messinian, but this is subject to the establishment of the age of these localities. Their malacofaunas are of a warm or temperate pattern, and a small decrease affects tropical families. Other groups also indicate waters of a warm temperate type: genus *Arbacina* among echinoids, association of little diversified benthic foraminifers with species which herald Pliocene faunas, poor small fauna of scleractinians that is entirely ahermatypic and that shows no major change since the previous stages.

In the oceanic domain, the global cooling recorded in the Tortonian persists. The distribution of the calcareous nannoplankton shows little variations in the studied localities which suggests that the climate did not undergo drastic variations during that period.

On the Morocco Atlantic frontage, the neritic realm indicates a warm climate as demonstrated by several gastropod taxa which make up abundant associations (*Amalda*, *Cymbium* ...). The coral fauna is more diversified there than in the European Atlantic: more than 30 species that are, however, non-reefal. The presence of rather important coral reefs in Madere Island requires a corroboration concerning their age (Tortonian or Messinian).

In deeper realm, the South-Rifian Basin is rather well documented (Benson *et al.*, 1991). During the early Messinian, the ostracofauna becomes impoverished, and 2 psychrospheric forms (*Agrenocythere* and *Oblitacythereis*) appear. At that time, a current of cold deep water apparently occurs in the Rifian passage from Atlantic to Mediterranean; this phenomenon seems connected to the global oceanic cooling and to the end of warm mediterranean water supplying into the Atlantic (beginning of the water deficit in Western Mediterranean). Afterwards, this "siphon" no longer acts, which has caused the initiation of the evaporitic phenomenon in the Mediterranean, whereas, western to the South-Rifian Basin, thermospheric and well oxygenated conditions are back.

Remark

It is apparently during the Messinian that the climatic differences between Atlantic ocean and Mediterranean are the most perceptible. In this last region (Maghreb, Southeastern Spain ...), the early Messinian, with a tropical climate, is well represented (Alvinerie *et al.*, 1992), yielding well developed coral reefs, rich faunas of molluscs (Ben Moussa *et al.*, 1987 and 1988), echinoids (Lachkhem, 1982)... Relations with the Atlantic are evidenced by the neritic association of this period. In the Gibraltar area, the above noticed cold current from the Atlantic brings a group of bryozoans of temperate or "cold" pattern in the neritic realm of Northeastern Morocco (El Hajjaji, 1988 and 1982), and *Orania* (Moissette, 1988), where it is mixed with other bryozoans, the affinities of which are tropical or warm temperate. Bryozoans of Southeastern Spain show clear affinities with those of North Africa; these assemblages express the intervening position of the Alboran Sea subjected to both atlantic and mediterranean influences.

THE MIOCENE/PLIOCENE TRANSITION

The transition between the Miocene and the Pliocene is characterized by numerous extinctions or southward withdrawals, affecting tropical and subtropical taxa belonging to most groups. On the other hand, a faunal replacement is noticed, that represents an important step towards the recent fauna and flora establishment.

PLIOCENE

The earliest Pliocene climate is somewhat warmer than the Messinian one. In spite of the arrival of northern taxa,

mainly in the most northern areas, thermophile taxa are still present in many groups. Successive intra-Pliocene coolings (ca. 3 Ma, and ca. 2.4 Ma) are connected to the advance of the Arctic ice cap; they progressively eliminated the remaining taxa indicative of warm climate and caused the southward dispersal of northern forms indicative of a climate colder than the previous one up to Portugal. At the same time, marked changes occurred on the continent.

Indicators of warm climate

Warm climate indicators are mainly recorded in the early Pliocene but only certain persist in the late Pliocene up to the North (Pliocene of Western and Northwestern France = "Redonian"). Among benthic foraminifers of the early Pliocene from Normandy and Ligerian Gulf, assemblages characteristic of warm temperate waters develop (abundance of *Polymorphina*). Among bryozoans (Buge, 1957), *Cupuladria canariensis* (tropical), as well as *Hornera frondiculata* and *Discoporella umbellata* (tropical to subtropical) may be cited. Among bivalves (from the Ligerian Gulf), some tropical to subtropical forms, such as *Plicatula* and *Crassatina s. str.* (early Pliocene, Anjou), and *Circomphalus plicatus* (late Pliocene, South of the gulf) are mixed with numerous taxa indicative of warm temperate climate (of mediterranean type) including *Spondylus*, *Chama*, Carditidae (Lauriat-Rage, 1981). On the other hand, among gastropods, the whole fauna of the Ligerian Gulf seems subtropical as well as that of the Miocene one of the same gulf; it includes numerous indo-pacific, west-indian and west-african representatives in the early Redonian of Anjou (*Clavatula*, *Ficus*, *Protoma* ...). The fauna is still subtropical (holding a Miocene pattern) in the late Redonian of the southern part of the Ligerian Gulf: *Clavatula* and *Amalda* persist, but weak northern influences are noticed (*Calliostoma subexcavatum* and *Nassarius reticosus*); at last, a true Pliocene fauna is noticed at Redon and in Normandy with a few genera (*Latirus* and *Amalda*) still present today in the Mediterranean (Brébion, 1974). A marked difference is noticed between the climatic significance suggested by Redonian gastropods (with numerous taxa that are tropical today) and by bivalves (with less numerous tropical taxa). A similar problem arises in Portugal, Southwestern Spain and Morocco.

Indicators of temperate or "cold" climate

The isotopic palaeotemperature method ($^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$) applied to bivalves (Astartidae) from the Ligerian Gulf and Normandy (Lauriat-Rage & Vergnaud-Grazzini, 1977) has evidenced a cooling in the early Pliocene, at about 3 Ma, and has enabled the establishment of a climatic scale for the localities: the coldest ones are the most recent localities. This cooling stressed the North-South thermic gradient.

In the oceanic domain, the decrease, or even the disappearance, in some groups of calcareous nannoplankton

is noticed chiefly since the Piacenzian (full disappearance of Sphenolithaceae and considerable rarefaction of Discoasteraceae north of Gibraltar). Among taxa indicative of "cold" climate, *Coccolithus pelagicus* is present up to the Equator and the *Gephyrocapsa* group expands. Differences between the composition of assemblages from north and south to Gibraltar become more pronounced; this probably results from a more marked seasonality in temperate latitudes.

In the neritic realm, among benthic foraminifers, a biozonation from North to South appears during the Pliocene (Marguerel in Anonymous, 1989): A cooling occurs in Belgium during the early Pliocene (*Buccella frigida*, associated to the sinistral planktonic foraminifer *Globigerina pachyderma*) and warm temperate waters persist in Normandy (*Elphidium*, *Discorbitura* and *Polymorphina* biozones); during the middle Pliocene, a cooling affects Normandy (*Buccella frigida*, *Aubignyana mariei*, *Faujasina*) and, to a lesser degree the Ligerian Gulf (rare *A. mariei*); at last, during the late Pliocene, a marked cooling is noticed in the whole Western France; *Elphidiella hannai* appears in Normandy (Le Calvez, 1987) and *A. mariei* is abundant south of the Armorican Massif (Marguerel, 1988). Southward, in Aquitaine (drillings), the northern influences apparently do not affect the assemblages of benthic foraminifers, which rather indicates a warm temperate climate (Caralp et Julius, 1965).

The ostracofaunas become impoverished. In Aquitaine, numerous Miocene taxa disappear and the replacement is reduced. In Portugal, the increase in cooling is mainly noticeable in, maybe, the latest Pliocene with *Bythocythere constricta* (boreo-arctic form of the Atlantic) and *Bythoceratinamediterranea* (arctic psychrospheric waters) (Nascimento, 1983 and 1990). In Northwestern Morocco (Gharb), the climate is markedly warmer with a variation in the upper part of the Pliocene: semi-arid during the early and middle Pliocene, less arid during the late Pliocene (Carbonel, 1980; Carbonel et al., 1981). Echinoids also evidence this climatic gradient: Marsupiate forms (Pliocene of East Anglia) reach Normandy and the Ligerian Gulf, which indicates a cooling; south to the gulf, influences are mixed (persistence of tropical *Plagiobrissus s. str.*) (Roman in Anonymous, 1989). Southward, the strictly tropical *Rotuloidea* extends up to the Casa blanca latitude (Roman, 1972). The scleractinians (all ahermatypic) are more numerous than during the Late Miocene. In France, they occurred during the early and middle Pliocene, and then disappeared as a result of the late Pliocene cooling (Chaix, 1989; Chaix in Anonymous, 1989). In Portugal, they persisted in small number till the end of the Pliocene (Chevalier, 1965). The bryozoans from Normandy (*Cellopora compressa* ...) show some affinities with those from northern areas (East Anglia, the Netherlands). Besides cold water currents in the Ligerian Gulf may explain the presence of a few boreal species such as *Sertella*. In Portugal (Galopim de Carvalho, 1971), taxa with tropical affinities remain (*Tremopora radificera*, *Cupuladria*, 4 species of *Metrarabdotos*), but species with boreal affinities expand. Among the bivalves from the Ligerian Gulf,

northern taxa include some Nuculidae, *Pecten maximus*, most of Astartidae ... Other cold invaders (*Nuculana minuta*, *Yoldia oblongoides*) appear in the most recent levels of the late Pliocene (Lauriat-Rage, 1986). Among gastropods, the first encountered northern forms are labelled as warm (*Terebra exilis*, *Asthenotoma ornata*). The first "cold" boreal forms (*Buccinum*, *Nucella* ...) are reported from the late Pliocene (Brébion, 1988).

During the early Pliocene, on the continent (Rio Maior, Portugal) (Diniz, 1984), palustrine (*Typha*, *Potamogeton* ...) and arboreal associations (*Magnolia*, *Palmae* ...) are rich and diversified whereas gymnosperms are predominant in altitude. Several climatic fluctuations are recorded during this stage; a first temperature decline is noticed at the beginning of the Piacenzian (development of *Salix*) followed, later, by a second one (most of thermophilous taxa disappear or become rare at that time). In France, have been distinguished the Reuverian (temperate climate), the Pretiglian (marked cooling) and the beginning of the Tiglian.

THE PLIOCENE/QUATERNARY TRANSITION

Numerous species die out near the Pliocene-Quaternary boundary. Since that time, northern influences increase.

PLEISTOCENE

During the Pleistocene, the glaciations considerably alter faunas and floras of the Northeastern Atlantic frontage, mainly in its northern part. The various phases of warming do not succeed compensating for the effects of cooling. In the oceanic domain, the calcareous nannoplankton is characterized by assemblages close to that of present deposits, except some variations which affect relative abundances of species (development of Gephyrocapsaceae, and especially of *Emiliana huxleyi* that becomes preponderant during the latest Pleistocene). Besides, *Discoaster* definitively disappears, even in the equatorial zone (which can partly result from the global climatic degradation).

In the neritic realm, among foraminifers, the low temperatures cause the development of *Elphidiella hannai* in Normandy, and the disappearance of *Aubignyana mariei* (Le Calvez, 1987). The advance of the cold front reaches Southern Brittany (sinistra *Globigerina pachyderma*). The cooling that affects the ostracofaunas in Aquitaine (Bay of Biscay) causes the arrival of boreo-arctic taxa (*Elofsonella*, *Robertsonites*, *Heterocyprideis* ...) during and after the first glaciations; these taxa are added to the previously present east-atlantic and mediterranean species (Carbonel, 1980). In Portugal (off Viana do Castelo, continental shelf), the ostracod assemblages show similar characteristics with, however, a higher proportion of mediterranean species (Silva & Nascimento, 1989).

In Normandy (drillings), numerous molluscs are of Tiglian age (warming). Mediterranean taxa remaining or reappearing in the Channel characterize this malacofauna

of French-Iberian type ; these taxa are no longer in this area today (abundant *Cardita calyculata* among bivalves, *Seila*, *Petalococonchus*, *Gyroscala*, among gastropods). To this fauna are mixed temporary northern newcomers such as *Acila cobboldiae* ... among bivalves (Lauriat-Rage, 1986), and *Boreotrophon*, *Searlesia* ... among gastropods (Brébion, 1988). This fauna is very different from the present one of the North Sea which displays a celto-boreal pattern ; this is the result of the closure of the Straits of Dover. Two Eemian malacofaunas (Southern England and Northern Brittany) evidence the last warming of the Quaternary, as demonstrated by the southern species *Eastonia rugosa* (bivalve) and *Astraea rugosa* (gastropod). The Eemian (=Tyrrhenian) has been recorded south to the Armorican Massif with *Cerithium vulgatum* and in Portugal with *Patella safiana*. Southward, a rather complete series of terraces is known in the Moroccan Atlantic frontage; they evidence the climatic alternations of the Pleistocene, from a semi-tropical climate to a climate cooler than today (Brébion, 1980). Southward, the range of the tropical echinoid *Rotula* does not spread, to the North, beyond the Atlantic Sahara.

HOLOCENE

During the Holocene, the modern bioprovinces become established with characteristics common to the various groups.

For example, modern ostracofaunas of the Northeastern Atlantic frontage are rather homogenous ; they present a decreasing gradient of boreal species from the North to the South on the one hand, and of guinean forms from the South to the North on the other hand. On the Moroccan shelf, the ostracofauna is typically atlantic and it is practically devoid of boreo-arctic forms; it is marked by the presence of a notable stock of mediterranean species and by the appearance of some guinean forms. At the Mauritanian and Senegal latitude, the fauna becomes mainly of guinean pattern with a stock of mediterranean species (Llano, 1981).

Among corals, after the disappearance of the fauna during the Pleistocene, a Boreo-Atlantic province emerges during the outset of the Holocene, owing to the arrival of 80 species, all ahermatypic, in the Northeastern Atlantic (Zibrowius, 1980).

ACKNOWLEDGEMENTS

We are indebted to Françoise Pilard for the illustrations and Didier Molin for typing and formatting the text.

CONCLUSIONS

The trends evidenced in this paper are involved in the continuous climatic degradation observed since the Eocene in marine domain. The late Oligocene seems the warmest period in the neritic realm of the studied area.

An important renewal of the species takes place during the early Miocene, characterized by a persistent tropical climate with a thermic optimum in the Burdigalian. At the same date, a North-South thermic gradient is established, leading to a cooler sea-water temperature in the northern areas.

The Langhian climate remains generally warm (tropical to subtropical type) in spite of the increasing North-South thermic gradient. It is noteworthy that the reefal buildings definitively disappeared from the Northeastern Atlantic frontage, whereas they continuously developed in the Mediterranean area, where a thermic maximum is indicated at this time. The climatic degradation becomes more pronounced during the Serravallian, giving rise to a marked decrease in the species number as well as to the appearance of "cold" taxa. In the Late Miocene, the latitudinal gradient corresponds to the establishment of a climate varying from a warm temperate type northward to a tropical one southward.

The earliest Pliocene is also warm. The faunas are partly renewed, and the main elements of the extant assemblages develop. As a result of the intra-Pliocene coolings, the remaining species indicative of warm conditions are driven to the South, and the arrival of new northern taxa is favoured.

Finally, after the Pleistocene (marked by considerable glacial episodes in Europe), it is during the Holocene that the present-day bioprovinces are definitively constituted.

Apart from biological evolution, the faunal changes which occurred between the late Oligocene and the Middle Miocene result from the main palaeoclimatic (appearance and accentuation of a latitudinal thermic gradient) as also palaeogeographical (break of the connections between Western and Eastern Tethys and formation of a broad Euro-West-African province) events. Variations of the climate during the Neogene and Pleistocene have considerably restricted this broad tropical province to a West-African province, leaving space to the North, to several other provinces climatically ranged (Fig. 1). It can also be suggested that the Equator was situated farther North, for example during the Middle Miocene, as evidenced by the location of ecoclimatic belts in connection with a pole displacement (Pickford, 1992).

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