

LATE PLIOCENE TO EARLY MID-PLEISTOCENE MAMMALS IN EURASIA: FAUNAL SUCCESSION AND DISPERSAL EVENTS

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Abstract

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Four major dispersal events mark European Villafranchian and Galerian faunas (about 3.2–0.4 Ma). The beginning of the Villafranchian is evidenced by the arrival of *Leptobos* and of large cervids and felids; the fauna still retains typical forest elements: *Mammot*, *Tapirus*, etc. The Elephant–*Equus* event (about 2.5–2.6 Ma) brought in grassland elements (elephant, horse) while several forest dwellers disappeared. The massive arrival of a primitive wolf, a large hyaena and *Leptobos etruscus* approximately marks the Plio-Pleistocene boundary (Wolf event, about 1.7 Ma). This was followed by a new wave of prairie fauna: *Praeovibos*, “*Leptobos*” *vallisarni*, *Allophaiomys*, *Canis arnensis* (a coyote), *Canis falconeri* (possibly a lycaonid); *Cervalces* and *Hippopotamus* also arrived at this time. The Villafranchian–Galerian transition saw a total faunal turnover, with massive extinctions and new, previously unknown adaptations (end-Villafranchian event, 1.0–0.9 Ma). The late Pleistocene and living fauna of Eurasia took its origin at this time. Mammalian stratigraphy of Asia is more poorly known but faunas are easily correlated with European ones and the end-Villafranchian event is clearly recognised. Faunal events are correlated with climatic and physiographic changes (late Himalayan orogeny).

Introduction

In the palaeontological record the succession of mammalian faunas is not characterised throughout their history by steady, gradually progressing evolution but is interspersed with sudden, abrupt changes: extinctions, rapid evolutionary progress, appearance of new adaptations, migrations. Such discontinuities were once interpreted as artifacts due to incompleteness of the record; but as knowledge progressed and gaps were being filled in it became apparent that they represent real revolutions of the faunal assemblages, “faunal events” of continental scope (Repenning, 1980). Calibration of faunal succession with pollen sequences, isotopic and palaeomagnetic scales

provided evidence that major faunal events tend to coincide with good approximation with changes in vegetation, in climate, sea level fluctuations, temperature changes in sea and ocean waters.

The time interval examined here spans the late Pliocene, the early Pleistocene and part of the middle Pleistocene, i.e. the Villafranchian and Galerian stages of European vertebrate stratigraphy: in terms of absolute chronology, from little before 3 Ma to approximately 0.4 Ma.

Villafranchian

The term Villafranchian was introduced by Pareto (1865) for a fauna collected from lacus-

trine deposits near Villafranca d'Asti, Piedmont, northwestern Italy; the term was extended by its author to include mammalian faunas of the upper and lower valley of the Arno in Tuscany, central Italy. Since then the term Villafranchian has been used rather loosely, mainly by Italian, French and Swiss authors to designate faunal assemblages, mostly from Italy and from southern France, which share some features: occurrence of proboscideans associated with large bovids, deer and equids, and above all the fact that they are entirely composed of taxa now extinct.

The Villafranchian was initially believed to correspond to the late Pliocene: Gignoux (1916) correlated it with his Calabrian stage. At the 18th International Geological Congress (London, 1948) it was agreed to place the Calabrian at the base of the marine Pleistocene. Several years passed before it was realised that the so-called Villafranchian faunas are far from uniform and actually span a large part of the Pliocene and the early Pleistocene (Azzaroli, 1963, 1970, 1977; Heintz, 1967). As a matter of fact the term Villafranchian survives now for traditional reasons more than for its intrinsic value, and is practically meaningless if not used with some qualification (early, middle, later Villafranchian). Azzaroli (1977) divided the Villafranchian into six more or less well defined faunal units. The beginning of the Villafranchian itself, of some of its units and its end are characterised by pronounced dispersal events; other units were distinguished on the basis of minor events or more gradual changes.

Galerian

The name Galerian was introduced by Ambrosetti et al. (1972) to designate a distinct faunal assemblage in Europe; the same assemblage, with minor changes, is found to characterise the same time interval in Asia.

The Galerian spans a much shorter time than the Villafranchian, of the order of 0.5 Ma, and is faunistically much more uniform. Its beginning has been dated with good approxi-

mation; its end has not been established with the same accuracy, but will not be dealt with in this paper. Unlike the Villafranchian, the Galerian fauna includes several taxa still living today, or taxa differing from present ones only at specific or subspecific level. In fact the present faunal assemblage of Eurasia took its origin in this time interval. The Galerian is also characterised by the appearance of new, previously unknown adaptations.

The beginning of the Villafranchian — The "Leptobos" event

The transition from Ruscinian (early Pliocene) to early Villafranchian faunas (Triversa faunal unit: Azzaroli, 1977) is marked by several changes. The Ruscinian antelopes *Parabos* and *Alephis* are replaced by the more advanced *Leptobos*. Ruscinian deer are of small size and only *Croizetoceros ramosus* has long, branched antlers. The early Villafranchian deer fauna is richer and is represented by several advanced taxa of large size: *Cervus pardinensis* and a similar deer, more derived in the development of its antlers, in western Tuscany; *Cervus perrieri*, *Arvernoceros ardei*. *Croizetoceros ramosus* survived from the Ruscinian, with more progressive subspecies (Heintz, 1970, 1974). Another immigrant among ruminants is the caprine *Pliotragus*; among perissodactyls, the slender *Dicerorhinus miguelcrusafonti*, and then *jeanvireti*, replaced the more massive *D. megarhinus* and among canids *Nyctereutes megamastoides* replaced *N. donnezani*. *Tapirus*, a survivor from the Ruscinian, is a common element of the fauna, whereas *Hipparion* was now rare in France and possibly extinct in Italy; it survived in larger numbers in Spain, at Villaroya. The large carnivores made their first appearance: *Chasmaporthetes*, *Acinonyx*, *Megantereon*, *Homotherium*. *Ursus minimus* may be a progressive descendant of *U. ruscinensis*: it has no relationships with later Villafranchian bears and its skeleton suggests a partly arboreal adaptation (Berzi, 1966). "*Lepus*" seems to have made now its first appearance in Europe. Proboscideans on the

other hand do not show significant changes from the Ruscinian: *Anancus arvernensis*, *Mammot borsoni*. In Spain the first signs of the transition can be detected in the Layna local fauna where *Chasmaporthetes*, *Leptobos* and "*Lepus*" are recorded for the first time.

The immigration of so many taxa points to some environmental change, possibly the establishment of a less dense forest cover (appearance of *Acinonyx*, *Pliotragus* etc.). Faunal assemblages of this type occur in various

sites in Italy, in the French Central Massif and in Spain (Fig.1).

The accompanying flora is rich and is indicative of a warm climate (Lona and Bertoldi, 1973; Suc and Zagwijn, 1983).

The lacustrine beds of the type localities around Villafranca d'Asti represent the deposit of a shallow coastal lake. To the east they are replaced by littoral facies with terrestrial vertebrates and marine fossils, in which the Triversa unit may be correlated, somewhat indirectly, with the *Globorotalia puncticulata*-

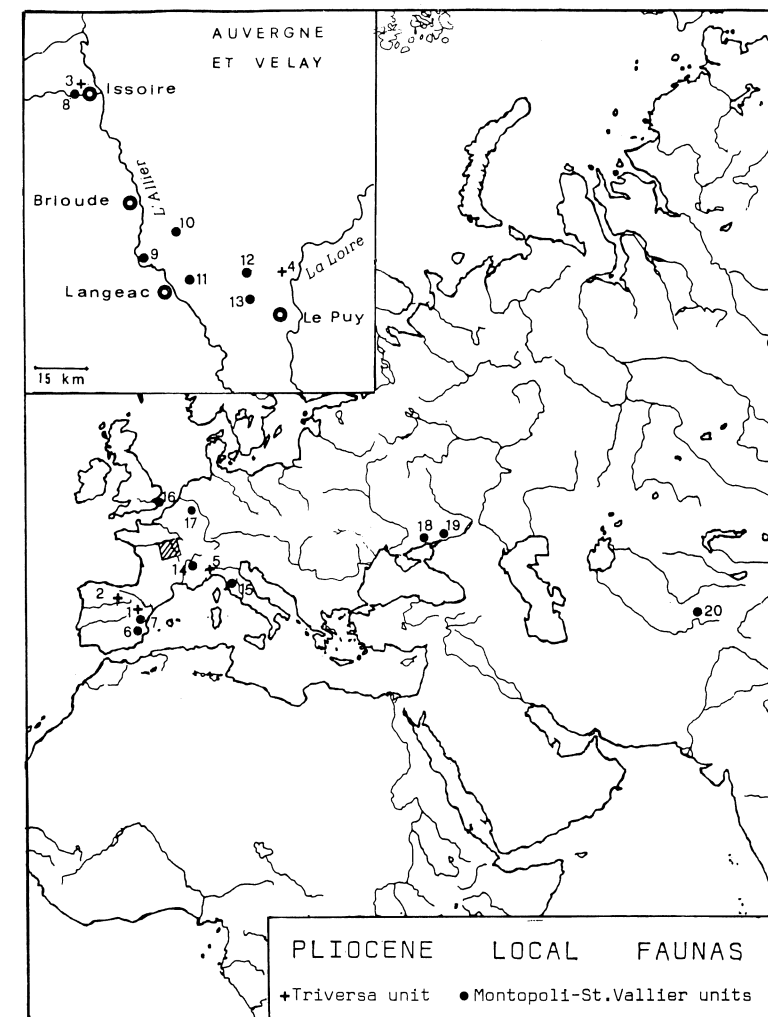


Fig.1. Pliocene local faunas, discussed in text. Triversa unit (+): 1=Layna; 2=Villaroya; 3=Les Etouaires; 4=Vialette; 5=Villafranca d'Asti. Montopoli-St. Vallier units (●): 6=Rincón; 7=La Puebla de Valverde; 8=Rocaneyra; 9=Chilhac; 10=Senèze; 11=Le Coupet; 12=La Roche Lambert; 13=St. Vidal; 14=St. Vallier; 15=Montopoli; 16=Red Crag; 17=Tegelen; 18=Khapy; 19=Livenzovka; 20=Kurksay.

G. crassaformis transition of marine Pliocene stratigraphy (beginning of the late Pliocene) (De Giuli et al., 1984). Radiometric ages are available for two French localities: Vialette (between 3.3 and 2.6 Ma: Bandet et al., 1978) and les Etouaires. For this site Couthures and Pastre (1983) gave an age between 3.3 and 2.6 Ma; on the other hand Ly et al. (1983) proposed an age younger than 2.6–2.5 Ma. The latter date was not obtained directly from the fossil bearing beds but by indirect correlation. The error limits are rather broad, especially for the les Etouaires date (for this site, Savage and Curtis, 1970, reported a date of 3.4–3.5 Ma in an ash underlying the fossil bed). In spite of the great discrepancy between datings, ages proposed are not incompatible with the attribution of the Etouaires fauna to an assemblage older than the elephant–*Equus* event. Lindsay et al. (1980) calibrated with the palaeomagnetic scale a section in the type area of Villafranca d'Asti and proposed an age of 3.01–3.05 Ma (a short episode of normal polarity between the Mammoth and Kaena reversed episodes).

The faunas of the Triversa unit are enriched by several taxa as compared with Ruscinian faunas and appear more advanced in their composition (occurrence of large carnivores and antlered deer). From the point of view of environment they do not show any great change from the previous situation and still keep the character of warm climate, predominantly forest assemblages. Isotopic analyses in marine and lacustrine series provide evidence of a moderate climatic deterioration between 3.2 and 3.1 Ma, followed by a return to higher temperatures, with mean values only slightly below those of the Ruscinian (Shackleton et al., 1984; Leone, 1985).

The elephant–*Equus* event

A sharp break marks the end of the Triversa fauna, and the onset of a new assemblage, typified by the later early Villafranchian faunas. The Montopoli local fauna in the Lower Valdarno basin, Tuscany, has been

selected as the type of the Montopoli faunal unit (Azzaroli, 1977).

The fauna was collected from a single pocket. It is rich and is characterised by the arrival of highly significant elements: a primitive elephant, *Archidiskodon gromovi*, a monodactyl equid of large size, *Equus* cf. *livenzovens*, closely related to *Equus stenois* and to the North American *E. simplicidens*. The cervid *Eucladoceros* appeared at this time, but is poorly represented at Montopoli. At the same time the most typical forest elements disappeared from the fauna: *Mammut*, *Tapirus*, *Sus minor*, *Ursus minimus*.

The faunal change from the Triversa to the Montopoli assemblage is sharp and from the ecological viewpoint much more significant than the change from the late Ruscinian (Perpignan) to the Triversa assemblages. The fauna is indicative of a more open, parkland and savannah landscape. The Montopoli fauna comes from littoral deposits capping a marine sequence of the *Globorotalia crassaformis* zone (De Giuli et al., 1984). Lindsay et al. (1980) tentatively calibrated it with the transition from the Gauss (normal) to the Matuyama (reversed) palaeomagnetic epochs, about 2.46 Ma. An elephant skeleton was however collected in marine and brackish beds at Laiatico, to the south west and downsection of Montopoli, so that the faunal event may be somewhat older.

An assemblage referable to the Montopoli unit is represented by the Rincòn 1 local fauna in the Júcar valley, eastern Spain (Alberdi et al., 1983; Leone, 1985). The fauna is characterised by abundant *Gazella borbonica* and an *Equus* of large size, attributed to *E. stenois* but possibly identifiable with *E. livenzovens*. This fauna occurs in the late Gauss epoch and may be dated to approximately 2.6 Ma. The appearance of this fauna corresponds to a climatic deterioration evidenced by isotopic oxygen and carbon analysis in the lacustrine beds (Leone, 1985).

Another fauna which may be referred to the Montopoli unit is Roca Neyra in the French Central Massif, dated 2.5 Ma (K–Ar date,

Savage and Curtis, 1970). The fauna, which unfortunately is rather poor, provides the oldest record of *Equus* and the last record of *Hipparion* in France (Eisenmann and Brunet, 1973).

The Dutch Praetiglian has yielded rather poor vertebrate remains, which however seem to fit in the Montopoli unit; *Anancus arvernensis*, *Archidiskodon* cf. *gromovi* (referred to as *Archidiskodon planifrons* by Van der Vlerk and Florschütz, 1950); *Eucladoceros falconeri*, the most primitive species of this genus; *Equus* sp. ind. is also present, alongside *Odoabaenus* and *Choneziphius*. The pollen flora of the Praetiglian characterizes a cold interval spanning approximately from 2.5 to 2.2 Ma (Zagwijn, 1974; Zagwijn and Suc, 1984).

The English Red Crag has a similar fauna: *Odoabaenus*, *Anancus*, *Eucladoceros falconeri*, a large *Equus* referred to as *E. robustus* by Hopwood (1937) but possibly belonging to *E. livenzovens* (several teeth, partly undescribed, in the British Museum (Nat. Hist.); an elephant, referred to as *Elephas meridionalis* by Leith Adams (1881, pl.26, fig.2), seems to fit better in *Archidiskodon gromovi* (a fragmental molar, with a very thick enamel). The molluscan fauna of the late Red Crag is rich in *Arctica islandica*, which clearly indicates a cold climate. It should be remembered however that the Red Crag mammalian fauna is mixed. Besides Pliocene elements it includes post-Villafranchian elements (Azzaroli, 1970; *Megaceros verticornis*, *Equus* cf. *caballus*), which obviously come from a younger deposit, possibly some channel filling.

In southern Russia the elephant–*Equus* event is also recognized and corresponds to the transition from the Moldavian to the Khaprovian "complex". The latter is typified by the faunas of Khapry near the Azov Sea and of Livenzovka near Rostov on Don, with *Archidiskodon gromovi*, *Equus livenzovens* etc. (Bajgusheva, 1971, 1978). The boundary between Moldavian and Khaprovian is placed at approximately 2.5 Ma by Russian authors (Schanzer, 1982); the Moldavian may be

equated with the Triversa faunal unit, the Khaprovian with the Montopoli and St. Vallier units.

In China a rather sharp break in mammalian faunas and in vegetation occurred approximately at the Gauss–Matuyama transition (Liu Tung-sheng and Ding Meng-Lin, 1982; Song Zhi-Chen et al., 1982; Wang Fu-bao and Li Bing-yuan, 1982).

In the Indian subcontinent the arrival of *Equus*, *Rhinoceros*, *Elephas hysudricus* and *Stegodon insignis* at the Gauss–Matuyama transition marks the boundary between the Tatrot and Pinjor faunal complexes (Lindsay et al., 1980; Azzaroli, 1985b).

The middle Villafranchian

The Montopoli faunal assemblage is followed without sharp break by faunas containing similar taxa, but generally showing more derived features. *Archidiskodon gromovi* is succeeded by an elephant resembling *A. meridionalis* in dental features (Boeuf, 1983) but more primitive in its skull. *Cervus pardinensis* was replaced by *C. rhenanus* Dubois, 1905 [= *C. philisi* Schaub, 1941, according to one of us (A.A.)], *Croizetoceros ramosus ramosus* by *C. r. medius* and possibly *C. r. minor* in France and *C. ramosus pueblensis* in Spain (Heintz, 1974). *Dicerorhinus jeanvireti* was superseded by the smaller *D. etruscus*. *Cervus perrieri* and *Arvernoceros ardei* are no longer recorded while the more derived *Eucladoceros tegulensis* Dubois, 1905 [= *E. senezensis* Dèpèret and Mayet, 1910, according to one of us (A.A.)] may be a descendant of the more primitive *E. falconeri*. Immigrants are few, among these the uncommon, medium sized felid *Viretailurus schaubi* from St. Vallier (Viret, 1954), and the bovids *Gallogoral meneghinii* and *Gazellospira torticornis*, which both survive into the late Villafranchian.

The limits and duration of the middle Villafranchian have not been defined in detail and will be discussed below.

The richest site of the middle Villafranchian is St. Vallier in the Rhone valley, which is also

the type local fauna of the St. Vallier unit. Other local faunas referable to this unit are Chilhac, St. Vidal, La Roche Lambert, Le Coupet (younger fauna), in the French Central Massif; La Puebla de Valverde in Spain.

Boeuf (1983) reported several, partly discordant radiometric ages for a basalt flow overlying the Chilhac fauna, which is reversely magnetised, and concluded for a probable age of 1.9 Ma for the basalt.

The fauna of Senèze, in the French Central Massif, poses a definite problem. The site is a maar surrounded by a partly eroded volcanic apparatus. Bout (1960, 1972) made reference to lacustrine beds of the maar and to superposed slope deposits as sources of the fossils and Elhay (1969) described the pollen association from the cores of a 175 m deep well drilled in the maar. The floral association is characterised by a long interval with temperate flora at the base, followed by a shorter cool interval and then by a succession of oscillations from temperate to cool. It recalls the floral spectrum of St. Vidal, a typical middle Villafranchian site, and of the Dutch Tiglian. The beds of the maar are reversely magnetized, with a short normal episode 20 m below the surface and about 10 m below the main fossil bearing horizon. Bout interpreted this as the Gilsa event and inferred an age of 1.6 Ma for the Senèze fauna. According to Ehrlich (quoted by Bout, 1972) the filling of the lake may have taken 0.2–0.3 Ma.

Thouveny and Bonifay (1984) interpret in a different way the palaeomagnetic record and correlate the short normal interval with the older Réunion event (2.12–2.14 Ma).

The mammalian association of Senèze shows some anomalies which do not allow a satisfactory correlation with other faunas and clearly point to a mixed assemblage. The deer: *Croizetoceros ramosus*, *Cervus rhenanus* (= *philisi*), *Eucladoceros tegulensis*, point to a correlation with middle Villafranchian faunas; *Nyctereutes* and *Dolichopithecus* also point to a Pliocene age. *Leptobos etruscus* was reported with a question mark by Schaub (1943) and has not been identified satisfactorily at species level.

The lack of *Pachycrocuta brevirostris*, *Panthera toscana* and *Canis etruscus*, all common elements in late Villafranchian faunas, is surprising. *Sus strozzi* is alien to the St. Vallier and other mid-Villafranchian assemblages but is recorded at Tegelen: in Senèze it is represented by a single specimen, with somewhat primitive marks (retention of the third upper incisors: Azzaroli, 1954). The fauna fits well in a mid-Villafranchian (late Pliocene) assemblage.

On the other hand, faunal lists include some elements that do not fit in such an old context and clearly point to a late Villafranchian age: *Cervalces gallicus*, *Canis arvensis*, *Equus bressanus* and a small equid which may possibly be *Equus stehlini*. *Megalovis* may also be a member of this younger fauna.

Associating these remarks with Bout's description of two fossil bearing horizons the idea comes quite naturally that Senèze contains in fact two faunas of very different age: one, which is also the richest in species and individuals, representing the middle Villafranchian and is about 2 Ma old, we assume the palaeomagnetic interpretation to be correct (it is supported by the pollen record, see below); the second representing the latest Villafranchian, about 1 Ma younger.

The fauna of Tegelen in Limburg, The Netherlands, is more difficult to evaluate because of its fragmentary state. Freudenthal et al. (1976) gave the following list: *Mammuthus meridionalis*, *Anancus arvernensis*, *Tapirus arvernensis*, *Dicerorhinus etruscus*, *Equus bressanus*, *Leptobos* sp., *Eucladoceros ctenoides*, *Sus strozzi*, *Ursus etruscus*, *Enhydriactis ardea*, *Pannonictis pliocaenica*, *Pachycrocuta perrieri*, *Panthera gombaszogensis*, *Castor fiber*, *Trogotherium cuvieri*, *Miomys pliocaenicus*, *M. newtoni*, *Macaca sylvana florentina*. Some comments may be made on the stratigraphy and fauna of the site. The pollen diagram of the Tiglian shows in its lower part a pronounced temperate episode (TA) followed by a shorter cool period (TB) and then a series of more rapid oscillations from temperate to cool (TC1 to TC6). The agreement of this succession with

the one observed in Senèze is remarkably good. The mammalian fauna seems to come from the TC1–TC6 interval (Zagwijn, 1974); however, most fossils were collected by quarry workers in old times and their stratigraphic location was not exactly recorded. Freudenthal et al. (1976) retrieved a rich assemblage of molluscs and small mammals from level TC5 (temperate) in the Egypte quarry. This is clearly a homogeneous assemblage; on the other hand the list of large vertebrates raises some problem. The occurrence of *Tapirus* is surprising and, to us, suspect; this genus was not recorded in former papers (Schreuder, 1945; Van der Vlerk and Florschütz, 1950).

The elephant was reported as "*Archidiskodon meridionalis*, archaic form" by Van der Vlerk and Florschütz; it is based on fragmental molars to which the thick enamel gives a rather archaic appearance; it may possibly represent *A. gromovi* or some transitional form. The remains of the large deer, called *Eucladoceros ctenoides* by Freudenthal et al. (1976), were referred to *Cervus dicranios* and to *C. teguliensis* by Bernsen (1930), and to *Eucladoceros teguliensis* by Kunst (1937). Comparison with deer from other sites is not easy. Only two nearly complete antlers are known, and antlers of *Eucladoceros* are highly variable. The specimen figured by Bernsen, pl.2, fig.1, fits well with *E. senezensis*; the other specimen is juvenile and less characteristic. Freudenthal et al. omitted to mention *Cervus rhenanus*. This is a species of small size, with two bifurcations in the adult antlers, and according to Kunst conforms very well with the small deer from Senèze, *Cervus philisi*, which in 1937 had not yet received a scientific name.

We consider the two species synonyms, and *Cervus rhenanus* Dubois 1905 has priority. More important, we have here a species typical of the middle Villafranchian. *Eucladoceros tegulensis* (Dubois) 1905 also has priority over *E. senezensis* (Dépéret) 1910.

The record of *Trogotherium cuvieri* is probably incorrect: Van der Vlerk and Florschütz record *T. boisvilletti*. The rest of the fauna is composed of species less characteristic because

of their rather broad stratigraphic distribution, or of doubtful identification. Only the panther calls for attention. It was described as *Felis (Panthera) schreuderi* by Von Koenigswald (1960); Ficcarelli and Torre (1968) consider it a synonym of *Panthera toscana* Schaub, a species typical of the late Villafranchian (the name *gombaszogensis* Kretzoi has time priority over *toscana* but was based on mixed material and is represented by a rather poor type: the meaning of the term *gombaszogensis* is ambiguous: Ambrosetti et al., 1979). Von Koenigswald's sample consists of dentitions and fragments of skulls, representing at least three individuals. The specimens were collected between 1943 and 1948; unfortunately the exact stratigraphic position was not recorded. It may be presumed that they were derived from the uppermost part of the section, where the pollen diagram marks a trend to a climatic deterioration forestalling the Eburonian cold phase.

The time span of the Tiglian is roughly between 2.2 and 1.7 Ma (Zagwijn, 1974), its mammalian fauna belongs to the middle Villafranchian and may possibly reach the beginning of the late Villafranchian in the highest part of the section. Correlations of the Tiglian with marine sequences have not been established but Nilsson (1983) proposes a correlation with the Icenian.

A mid-Villafranchian fauna was also recorded from San Giacomo near Anagni, Central Italy (Biddittu et al., 1979). The fauna has not been fully studied but shares several elements with the faunas of St. Vallier, Senèze (older fauna) and Tegelen. Among the most diagnostic species for its age are *Cervus rhenanus*, *Croizetoceros ramosus*, *Gazella borbonica*, *Equus stenonis*, *Archidiskodon meridionalis*.

The "Wolf" event and the beginning of the late Villafranchian

A pronounced faunal break marks the transition to the following unit; this was called the "wolf" event (Azzaroli, 1983). The most characteristic faunal changes are: the disappearance

of *Nyctereutes*, *Gazella*, *Leptobos stenometopon*, and the massive expansion in Europe of *Canis etruscus* (the "wolf"), *Pachycrocuta brevirostris*, *Panthera toscana*, *Leptobos etruscus*. *Eucladoceros tegulensis* is replaced by *E. dicranios* and *Cervus rhenanus* by *Dama nestii*; both are possibly evolutionary changes. *Ananacus* survived for a short time in the late Villafranchian but soon disappeared; elephants are represented by *Archidiskodon meridionalis meridionalis* (Azzaroli, 1977a).

A first dispersal of *Canis* in Europe and Africa took place between the late Miocene and the early Pliocene. At the beginning of the Villafranchian *Canis* disappeared from Europe, where it immigrated again at the beginning of the late Villafranchian. It survived during the Pliocene in Asia, where the wolf event has not been recognized.

The wolf event marks the beginning of the Olivola faunal unit, the oldest unit of the late Villafranchian. The name was derived from a site in NW Tuscany and the local fauna was retrieved from a pocket near the top of a fluvial section of calcareous loam interspersed with lenses of coarse conglomerate. This fluvial complex overlies lacustrine clays with lignites at their base; the clays yielded some teeth of *Sus strozzi* at Quercia, a short distance W of Olivola (Azzaroli, 1950). The fluvial complex provides evidence of intensive erosion which may have been due to two, possibly concomitant causes: an increase in rainfall and a lowering of sea level, which led to the downcutting of the sill that separated the basin from the sea and rejuvenated the streams. This was called the Aullan erosional phase (Arias et al., 1980), and in the light of mammalian stratigraphy may be correlated with the Eburonian cold phase of the North Sea basin (De Giuli et al., 1984). This begins approximately around the end of the Olduvai palaeomagnetic episode, that is, in coincidence with the beginning of the Pleistocene.

The Olivola faunal unit is followed without sharp breaks by two other units, all belonging to the late Villafranchian.

The fauna of the Tasso unit is mainly

represented in the Upper Valdarno basin, where it overlies faunas of the Olivola unit (Azzaroli and Lazzeri, 1977; Borselli et al., 1980; De Giuli and Masini, 1987). It retains practically all the elements of the Olivola fauna, with the only notable exception of *Ananacus*, but is enriched by the arrival of new species: *Canis arnensis*, a primitive coyote (Kurtèn, 1974); *Canis falconeri*, possibly a primitive lycaon-like form; *Hippopotamus antiquus*, a relative of the East African *H. gorgops* (Blandamura and Azzaroli, 1977); "*Leptobos*" *vallisarni*, closely related to bisons but still retaining slender limbs; a ovicaprine, represented only by limb bones of possibly a single individual (De Giuli and Masini, 1984). De Giuli and Masini (1987) point out the occurrence of an *Eucladoceros* of rather small size as well as of some peculiar characters of *Dama*. The small *Equus stehlini* seems to be a descendant of the larger *E. stenorhinus*. *Mimomys savini* occurs in some sites near the centre of the basin, and may belong to the Tasso faunal unit (Torre, 1985).

The assemblages of the latest Villafranchian, except Selvella in Umbria (De Giuli, 1987) and Pirro Nord in Apulia (De Giuli et al., 1987) are more poorly known. The following features may be pointed out: *Archidiskodon meridionalis* evolves towards an extremely large size, a short deep skull, an increase in number of tooth plates: *A.m. vestinus* in Italy, *A.m. cromerensis* in England, *A.m. tamanensis* in southern Russia. The extreme specialisation of the skull does not provide evidence of an evolutionary trend directly leading to *Mammuthus* (Azzaroli, 1977a), but rather seems to represent a side branch, ending without descendants.

Leptobos etruscus and "*L.*" *vallisarni* are recorded from Farneta, Tuscany; in other sites *Leptobos* is represented by a species morphologically similar to *L. etruscus* but of larger size: Selvella, Mugello, and also in assemblages transitional from late Villafranchian to Galerian at Domegliara, (Selva Vecchia), northern Italy. The bovid occurring in the more recent Pirro Nord fauna according to De

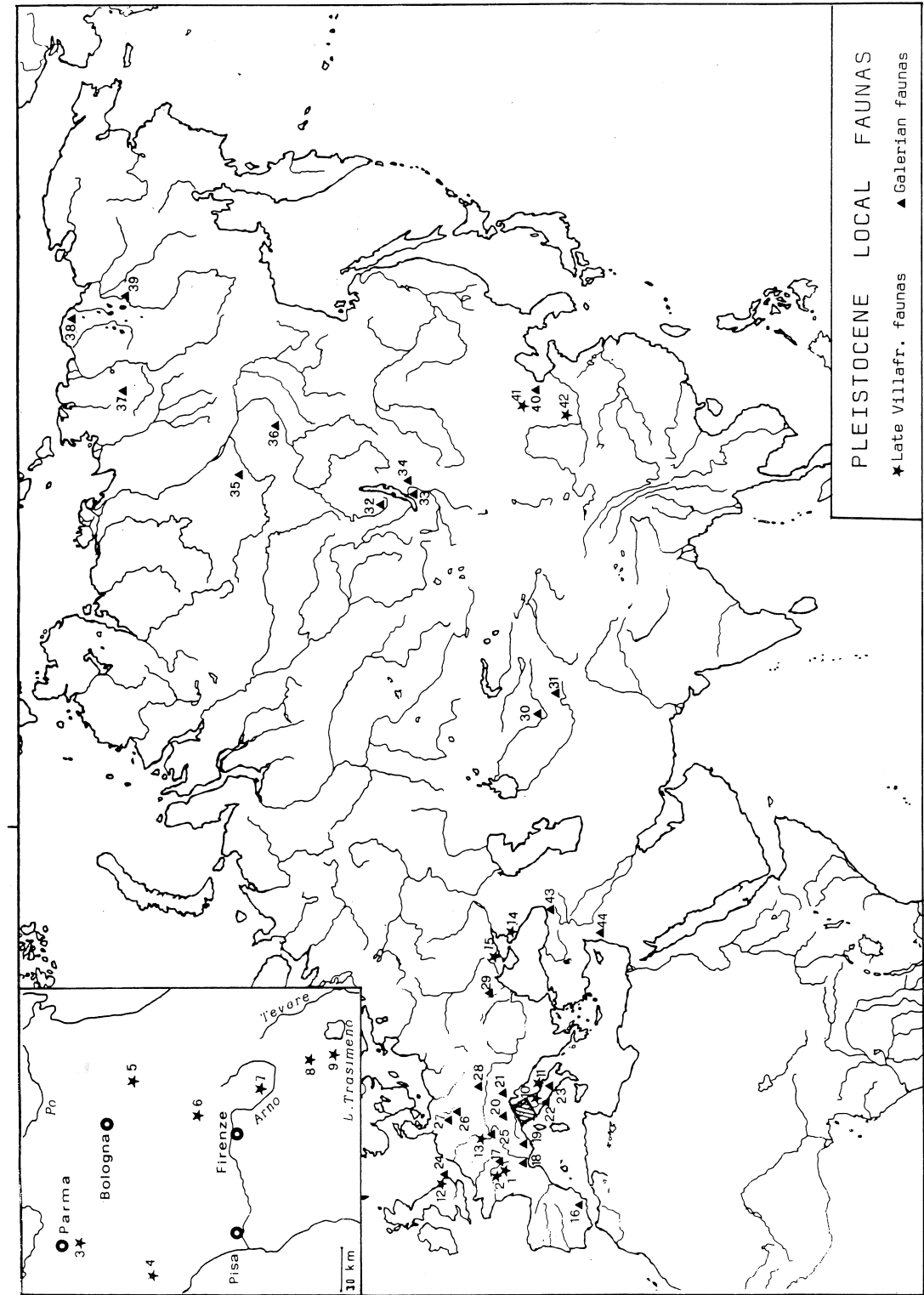


Fig. 2. Pleistocene local faunas, discussed in text. Late Villafranchian faunas (★): 1 = Sinzelles; 2 = Peyrolles; 3 = Crostolo; 4 = Olivola; 5 = Imola; 6 = Mugello; 7 = Upper Valdarno; 8 = Farneta; 9 = Salvella; 10 = Scoppito; 11 = Apricena; 12 = Erpfingen; 13 = Taman; 14 = Nogausk; 15 = Nogausk; 16 = Tai Ku. Galerian faunas (▲): 16 = Venta Micena; 17 = Solihac; 18 = L'Escale; 19 = Vallonet; 20 = Domegliara; 21 = Slivica; 22 = P. te Galeria; 23 = Isernia; 24 = Forest Bed; 25 = Moshbach; 26 = Süßenborn; 27 = Voigtstedt; 28 = Stranska Skala; 29 = Tiraspol; 30 = Koshkurgan; 31 = Lakhtui; 32 = Anga; 33 = Dodogol; 34 = Ulan Ude; 35 = Chebede; 36 = Olyokminsk; 37 = Bereliakh; 38 = Olyor; 39 = Krestovka; 40 = Chou Kou Tien; 43 = Akhalkalaki; 44 = Latamne.

Giuli et al. (1987) is closer to *Eobison* than to *Leptobos*.

Eucladoceros dicranios also shows a tendency to increase in size and antler complexity, but is poorly known because remains are scanty and fragmentary. In the Pirro Nord and Selvella faunas a large *Eucladoceros* occurs, considered to be a species different from *E. dicranios* (De Giuli, 1987; De Giuli et al., 1987). Outside Italy some faunas of very late Villafranchian age (Creux de Peyrolles, central France; East Runton, England: Bout and Azzaroli, 1953; Azzaroli, 1953) are characterised by *Eucladoceros tetracerus*; this is recorded in Italy from beds transitional from Villafranchian to Galerian (Selva Vecchia).

Another typical element of the latest Villafranchian is *Cervalces gallicus* (Azzaroli, 1983), which is common in the late Villafranchian of England, has been recorded from Senèze (Azzaroli, 1952, 1953) and also from Italy, in the Crostolo river near Parma (Ambrosetti and Cremaschi, 1976). The latter diagnosis however rests on a rather poor antler fragment.

Equus bressanus is a species of large size and distinct from the much older *E. livenzovensis*, with which it was sometimes confused; it is somewhat transitional between *E. stenorhis* and *E. süssenbornensis* and seems to characterize some late Villafranchian assemblages (Azzaroli, 1984).

Latest Villafranchian fossil assemblages may be referred to the marine Emilian and at least part of the Sicilian stages and in the Rome area underlie the Cassian erosional phase, which was dated approximately 1 Ma (Ambrosetti and Bonadonna, 1967; Ambrosetti et al., 1972) but seems now to have had its peak around 0.8 Ma (Shackleton and Opdyke, 1976; Thunell and Williams, 1983).

Latest Villafranchian faunas are known in Tuscany; in the Chiana valley around Farneta, the type locality of the Farneta faunal unit, and in the Mugello lacustrine basin (Azzaroli, 1977a; Azzaroli et al., 1982; De Giuli et al., 1984); at Imola in the Po valley, the site where Gignoux established his correlation between Calabrian and Villafranchian (Azzaroli and

Berzi, 1970); at Pirro Nord (Apricena) in the Gargano peninsula (De Giuli and Torre, 1984; De Giuli et al., 1987); at Scoppito (Aquila) in Abruzzo; at the Creux de Peyrolles in the French Central Massif (Bout and Azzaroli, 1953).

The Galerian fauna and the "end-Villafranchian" dispersal event

The Galerian is characterized by a highly distinctive faunal assemblage which ranges, with some local variation, throughout Eurasia, from the Iberian peninsula and Great Britain to eastern Siberia. It was not recorded however from the Indian subcontinent, where faunas are highly endemic.

The most common species, restricted to the Galerian, are:

Cervalces latifrons
Megaceros (Megaceros) savini
Megaceros (Megaceroides) verticornis
Megaceros (Megaceroides) solihacus
Cervus elaphus acoronatus
Soergelia sp.
Praeovibos priscus
Bison schoetensacki
Equus altidens
Equus süssenbornensis
Equus verae
Ursus deningeri
Canis lupus mosbachensis
Xenocyon lycaonoides
Gulo schlosseri
Homotherium latidens
Arvicola cantiana
Trogontherium cuvieri

These species, or subspecies, are confined to the Galerian or to part of it.

Other common species that made their first appearance in the Galerian and survived into later stages are:

Elephas antiquus
Mammuthus armeniacus
Saiga tatarica
Bos primigenius
Rangifer tarandus
Capreolus capreolus
Sus scrofa
Equus caballus

Dicerorhinus aff. *hemitoechus*
Dicerorhinus kirchbergensis
Crocota crocuta
Panthera leo
Panthera pardus
Acinonyx jubatus (= *Acinonyx intermedius*)

Cuon priscus was recorded by Thenius from localities of possibly Galerian age (fide Kurtèn, 1968). *Hippopotamus antiquus* is recorded from the late Villafranchian and from the Galerian. *Dicerorhinus etruscus* was reported by several authors from Galerian deposits: Mosbach, Voigtstedt and Süssenborn (Schroeder, 1903; Kahlke, 1961), Tiraspol (Nikiforova, 1971). One of us (A.A.) considers all records of this species to be based on erroneous identifications: according to him the specimens do not correspond to *D. etruscus*, which is restricted to the middle and late Villafranchian. *Ovibos* was recorded by Kahlke (1969) on fragmentary remains from Süssenborn.

Most Galerian taxa have their forerunners, and immediate ancestors in late Villafranchian faunas of Eurasia. Only a part of these is however known and the roots of a large part of the middle and late Pleistocene fauna should be looked for in the largely unexplored melting pot of inner Asia. *Cervalces latifrons* is a gigantic descendant of *C. gallicus* (Azzaroli, 1983a); Galerian giant deer (*Megaceros*) seem to have their ancestors among medium sized Villafranchian megacerids of eastern Europe. *Bison* may have evolved from a "Leptobos-Bison" group of the late Villafranchian of Eurasia; it is interesting to remark that giant deer, bison and musk ox brought about for the first time the characteristic adaptation, respectively, of gigantic antlers and of heavy body forms, two kinds of structures that were unknown before.

Equus süssenbornensis seem to have been derived from *E. stenorhis*, while *Equus caballus* and probably *Equus altidens* are immigrants from North America. *Ursus deningeri* may safely be assumed to be a descendant of *U. etruscus*, *Canis lupus mosbachensis* of *Canis etruscus* and *Xenocyon* of *C. falconeri*. *Dicerorhinus* aff. *hemitoechus* is closely related to

D. etruscus and may well be its direct descendant. *Panthera leo*, *P. pardus*, *Acinonyx jubatus* and *Crocota crocuta* are most likely immigrants from Africa. The origin of other taxa is not known.

The late Villafranchian taxa which did not develop new adaptations: *Eucladoceros*, *Dama nestii*, *Leptobos etruscus* and other bovids, *Sus strozzi*, *Archidiskodon meridionalis* and several carnivores became extinct at the end of the Villafranchian or in the early Galerian.

Obviously the transition from late Villafranchian to Galerian did not take place at once. Localities are known with mixed and somewhat transitional faunas: Villafranchian assemblages with few Galerian elements or vice versa have been recorded from Italy, France, Germany and Spain (Bonifay, 1978; Brüning, 1978; Azzaroli et al., 1982; Azzaroli, 1983a; De Giuli and Torre, 1984; De Giuli et al., 1983). Sites with naturally mixed, i.e. not reworked assemblages are in any case few and the transitional phase seems to have been of geologically short duration.

The result of the dispersal event was a total rejuvenation of the fauna: not only new adaptations were developed, but the faunal assemblage took a modern appearance: the late Pleistocene and present day faunas are composed of species that appeared in the Galerian, or by their direct, slightly modified descendants.

In the literature faunas of early Mid-Pleistocene age and similar in composition to the Galerian fauna of western Europe are often referred to as Cromerian, but this term was introduced to designate a stage based on pollen and of much shorter duration than the Galerian. Russian authors speak of a Tiraspolian complex (Gromov, 1948; Schanzer, 1982), typified by a fauna in Moldavia, and this term was also applied to Siberian faunas (Vangengeim and Sher, 1970). According to recent papers (Nikiforova, 1971; Schanzer, 1982) this term seems to refer only to the younger part of the Galerian, comprised in the Brunhes palaeo-

magnetic epoch, i.e. younger than 0.7 Ma. Sher (1971) introduced the term of Olyorian suite, more a lithostratigraphic term, for a sequence in the Kolyma lowland of western Siberia with a faunal assemblage of Galerian type, and straddling the late Matuyama and early Brunhes epochs (Sher and Kaplina, 1979); on another occasion Sher writes of a "Mindel" fauna (Sher, 1975). New details on the Olyorian faunal complex were added recently by Sher (1984), and the fossil bearing sections of the Kolyma lowland were calibrated with the palaeomagnetic scale by Virina et al. (1984). The fauna may be divided into an older, Chukochian, and a younger, Akanian unit. Characteristic of the former are *Praedicrostonyx capitalis*, *Allophaiomys pliocaenicus*, *Gulo* cf. *schlosseri*, *Praeovibos beringiensis*, possibly *Cromeromys intermedius* and an elephant, provisionally indicated as *Elephantidae* gen. nov. sp. 1. The Akanian is characterised by *Elephantidae* gen. nov. sp. 2 (more derived than sp. 1), *Dicrostonyx renidens*, *Microtus* spp., and in a correlated section at Ulakhan-Sudar on the Adych river *Equus* (*Equus*) *mosbachensis* (= *Equus caballus mosbachensis*). *Allophaiomys pliocaenicus* is restricted to the base of this unit. Other species, characteristic of the entire Olyorian complex, are: *Clethrionomys* ex gr. *rutillus*, *Trogotherium* cf. *cuvieri*, *Canis lupus* cf. *mosbachensis*, *Xenocyon* cf. *lycaonoides*, *Homotherium* sp., *Equus* (*Plesippus*) *verae*, *Cervalces* aff. *latifrons*, *Soergelia* sp., *Praeovibos* cf. *priscus*, *Bison* ex gr. *schoeten-sacki* and others.

The Chukochian unit begins in the Matuyama reversed epoch, at an estimated date of approximately 1.2 Ma. The transition to the Akanian has been dated more accurately and falls near the top of the late Matuyama, at a date of approximately 0.80–0.78 Ma. The Olyorian complex is followed by a gap and its upper limit cannot be exactly dated.

It will be noticed here that the onset of the Olyorian faunal complex in eastern Siberia would predate the end-Villafranchian event by approximately 0.2 Ma; although the date of the beginning of the Chukochian is a rather broad

estimate, the difference in time is probably real.

The Galerian fauna spread over Europe and the middle and high latitudes of Asia and also extended to the Near East in Syria. Maps of the distribution of some of its typical representatives were published by Kahlke (1969, 1971: large cervids; the Italian localities were unfortunately omitted), Vangengeim and Sher (1970: several species in Siberia), Sher (1975: elk, *Soergelia*, *Praeovibos*, *Equus*, in Russian Asia, eastern and central Europe and Great Britain), Vangengeim (1977: several species in Siberia).

In such a vast area local variations are to be expected. *Cervalces* has not been recorded from Spain but was recently recorded from Italy; *Megaceros* on the other hand does not seem to extend east of Tadjikistan; *Bos* is lacking in the high latitudes, *Praeovibos* is rare in Europe and common in Siberia, while *Equus* appears to have been extremely adaptable and is practically ubiquitous.

It was stated in a previous section that the Galerian witnessed new body adaptations, unknown in previous times. These are represented by the heavy, massively built bovids *Bison*, *Bos*, *Ovibos*, which developed from ancestors of smaller size and more slender build; of the giant deer of the genus *Megaceros*, which also evolved from smaller, still poorly known ancestors and equalled in the Galerian the body size and antler span of the late Pleistocene *Megaceros giganteus*; of the gigantic *Cervalces latifrons*, which stood about 2 m at the shoulder, with antlers spanning well over 2.00 m, supported by 40-mm thick frontals of solid bone. Rhinoceroses and bears also evolved to larger size during the Galerian and continued their evolution in the later Pleistocene. Equids on the other hand reacted in a different way. They seem to have reached their largest size at a somewhat earlier date, in the latest Villafranchian, with *Equus bressanus*, the stature of which may be evaluated between 170 and 180 cm at the withers. But *Equus bressanus* is a zebra (subgenus *Dolichohippus*), closely related to almost equally large *Equus süssenbornensis* (Azzaroli, 1984), which became

extinct before the end of the Galerian; the two immigrant species, horse (*Equus caballus*) and the hemione-like *Equus altidens*, represent different lineages, better adapted to highly seasonal and even very cold climates.

Age of the end-Villafranchian event

Late Villafranchian mammals were recorded from the top of a Calabrian (Santernian) sequence in a position immediately underlying the Cassian erosional phase (Ambrosetti and Bonadonna, 1967; Ambrosetti et al., 1972) in the Rome area, and in a position immediately below the Jaramillo event in the Danube valley (Kukla, 1977). The Lakhuti 2 fauna of Tadjikistan is a Galerian assemblage with few late Villafranchian holdovers (Azzaroli, 1983a) and is situated at the top of the Jaramillo (Dodonov, 1980).

The fauna of Ponte Galeria in the Tiber delta is comprised between the Cassian and the Flaminian erosional phases (Ambrosetti et al., 1972); the fauna of Isernia La Pineta in central Italy, also a typically Galerian assemblage, falls in the late Matuyama reversed epoch and is dated by volcanics to 0.73 ± 0.04 and 0.73 ± 0.07 Ma (Coltorti et al., 1982); the Galerian fauna of Solilhac in the French Central Massif has been calibrated with the Jaramillo episode (Thouveny and Bonifay, 1984).

The stratigraphic position of the Isernia fauna is in contrast with calibrations proposed for some classic sites, as Stranska Skala 2, Voigtstedt and Süssenborn. Biostratigraphically Isernia should be younger than these because of the occurrence of *Arvicola*; on the other hand the normal magnetic polarities observed at Stranska Skala 2 and Voigtstedt were referred to the Brunhes, thus indicating an age younger than Isernia. In as much as paleomagnetic and radiometric dates of Isernia seem reliable, and assuming that *Arvicola* is a valid marker of continental scope, the sites of central Europe referred to above should be older, and their normal magnetic fields

should correspond to the Jaramillo or possibly to some minor fluctuation within the late Matuyama.

The pre-glacial Pleistocene of England

Correlation of vertebrate bearing deposits of the English North Sea coast and of continental Europe were discussed in a previous paper (Azzaroli, 1983a: p. 127). The picture in its broad lines is now fairly clear but some minor problems still await for a final solution.

The Red Crag is readily correlated with the Praetiglian, i.e. the Montopoli faunal unit of Villafranchian stratigraphy (not with the middle Villafranchian, as in Azzaroli, 1970). Equivalents of the Tegelen fauna are possibly represented by rather scanty remains from the cliffs at Easton Bavents, reported by Stuart (1982: pp. 104–105). West (1980) correlates the Antian stage of Easton Bavents with the Olduvai event, in agreement with this view, while a correlation with the Olivola faunal unit, proposed by Azzaroli (1983a: p. 127) seems incorrect in as much as Olivola is of younger age (Eburonian). Some identifications reported by Stuart do not fit however in this picture and may perhaps need a revision: *Eucladoceros falconeri* belongs to an older stage, *Mimomys blanci* to a younger one.

In Norfolk, on the coast between Happisburgh and Weybourn, the oldest vertebrate bearing sediments contain an early Pleistocene (late Villafranchian) fauna and directly overlie the chalk. Their age ranges through Pre-Pastonian and Pastonian in the pollen scale (West, 1980). These are overlain by Cromerian deposits and by glacial till. The series is extremely condensed, formations vary in thickness from a few meters to less than one meter and are discontinuous, the sequence being cut by gaps and erosion channels. Most fossils were collected on the beach after storms had eroded the cliffs and their provenance may be reconstructed on indirect evidence. It is however clear that two distinct faunas are present, one late Villafranchian, the second Cromerian

(Azzaroli, 1953), or better Galerian; a younger fauna, recorded by Azzaroli, may be present but is poorly documented.

A purely late Villafranchian fauna occurs at East Runton: here only Pre-Pastonian and Pastonian deposits were recorded (West, 1980: fig.51). At West Runton the exposed sequence ranges from Pre-Pastonian to Cromerian: Azzaroli (1953) recorded only Cromerian (Galerian) vertebrates but more recently late Villafranchian elements were reported: *Archidiskodon meridionalis*, *Cervalces gallicus* (Stuart, 1982: p.106). At other sites: Bacton, Mundesley, Sidestrand, Overstrand, both late Villafranchian and Galerian elements were collected.

The older fauna includes elements characteristic of the latest Villafranchian (Farneta unit): *Archidiskodon meridionalis cromerensis*, *Eucladoceros tetraceros*, *Cervalces gallicus*, *Equus bressanus*, *Canis arnensis*; other elements are only broadly indicative of a late Villafranchian age: *Dama nestii*, *Eucladoceros dicranios*, (incl. *E. ctenoides*), *Leptobos etruscus*, *Equus stenorhinus*, *Dicerorhinus etruscus*. The evidence provided by small mammals is partly contradictory. Stuart (1982: pp.106-107) reported *Mimomys pliocaenicus*, *M. reidi* and *M. blanci* from the Pre-Pastonian and the same species plus *M. newtoni* from the Pastonian. This is partly in contrast with the date offered by large mammals, as *M. pliocaenicus* seems to be restricted to the older part of the late Villafranchian (Olivola unit).

Assuming that identifications are accurate, two possibilities remain open: either the Pre-Pastonian and Pastonian encompass more or less all the late Villafranchian, from the Olivola to the Farneta units; or alternatively some of the small mammals were reworked.

The Beestonian, the cold phase dividing the Pastonian from the Cromerian, may be correlated with the Menap or the Linge glacial of central Europe and with the Cassian erosional phase of the Mediterranean.

A final remark may be made: there are reasons to believe that England may have witnessed a period of insularity during the Pleistocene. The giant deer *Megaceros daw-*

kinsi is a typically Galerian species closely related to *Megaceros verticornis*, of which it represents a stunted variant. It is not primitive; the dentition is relatively hypsodont, but the small size, the reduction of the antlers, the occasionally observed disproportion between the thick pedicles and burrs and the slender beams (Azzaroli, 1953; fig.33D, E, fig.34E) may indicate an incipient evolution towards the reduction in size that characterizes large mammals in insular environments.

Vegetation and climate

The Menapian cold phase entrained changes of great moment. The pollen sequences of the Pannonian plain, analysed in deep boreholes, reveal the series of oscillations from warm to cool and even cold climate that characterise the whole late Pliocene and Pleistocene, but cold dry assemblages appear for the first time at the top of the Jaramillo (Cooke, 1981).

The pollen sequence of The Netherlands was worked out in great detail. Zagwijn and De Jong (1984) correlated the Menapian cold (glacial) phase with a reversed paleomagnetic interval immediately predating the Jaramillo episode. This was followed in rapid succession by the Bavel interglacial, corresponding to the Jaramillo, and then in the late Matuyama by the Linge glacial, the Leerdam interglacial, the Dorst glacial, the interglacial I. Glacial A of Dutch geologists corresponds with the beginning of the Brunhes Epoch and is followed by Interglacial II. Zagwijn and De Jong point out that in the Bavel and Leerdam interglacials the return of warm floral elements did not happen suddenly as in older interglacials, but in a definite succession of migrations, and this pattern of migration was repeated in younger interglacials; they conclude that this may have been due to the fact that the Menap and later glacials pushed the warm floral elements farther away to the south than the older cold periods. The Menapian glacial appears thus to have caused the greatest vegetational change in the Pleistocene of western Europe.

In Japan a spectacular change took place in the vegetation, with the appearance of an alpine type flora, at the base of the Jaramillo, i.e. round 0.1 Ma earlier than in the Pannonian plain (Suzuki and Manabe, 1982). Sedimentation of loess, a typical product of a cold dry climate, generally began during the late Matuyama in central Asia: Uzbekistan, Tadzhikistan (Dodonov, 1980, 1982); in northern China it started somewhat earlier, but still after 1.2 Ma (Derbyshire, 1983). In central Europe the loess sequence is more complex and scattered loess horizons were recorded since the Olduvai event in the Krems section on the Danube, but loess became more frequent and abundant during the Jaramillo (Kukla, 1977).

Physiographic evolution

Azzaroli and Napoleone (1982) showed that strong tectonic movements set in in the Himalayan belt around 1 Ma ago. A mountain belt dividing the Indian subcontinent from central Asia had been in existence since the Miocene and had already given rise to highly endemic Indian faunas (Heintz and Brunet, 1982; Brunet and Heintz, 1983; Azzaroli, 1985b). The sediments derived from these mountains, the richly fossiliferous Sivalik series of northern India and Pakistan, were at this time generally fine grained molasse deposits. Stronger tectonic movements are revealed by the onset of coarse conglomeratic sedimentation near the top of the series. Scattered beds of coarse conglomerates occur interbedded in the molasse in levels calibrated with the Olduvai event near Pinjor, northern India, and during the Jaramillo event sedimentation became entirely conglomeratic (Azzaroli and Napoleone, 1982), until the late Sivalik sequence was closed by the overthrusting of older Siwalik molasse and then by a series of overthrusts of increasingly older formations.

The strong upheaval of the Himalayas during the Pleistocene may have been the primary

cause of the whole sequence of climatic, vegetational and faunal changes. The rising mountain barrier caused the onset of a monsoon climate to the south and of increasingly drier and more continental conditions in central Asia; this was presumably the area in which most of the faunal evolution took place and from which migratory waves spread to Europe and possibly also to the Far East.

The elephant-*Equus* event of Europe has a counterpart in the transition between the so-called Tatrot and Pinjor faunal complexes of India and Pakistan, marked by the virtual disappearance of hipparions, of *Merycopotamus* and of several other species and the arrival of *Equus*, *Rhinoceros*, *Punjabitherium* (a two-horned rhinoceros), *Elephas hysudricus* and *Pachycrocuta felina*. No counterpart of the Pleistocene faunal events could be detected in the Sivalik sequence as the fossil record becomes scanty at the beginning of the Pleistocene and almost everywhere comes to an end within the early Pleistocene.

On the other hand the rather marked faunal migration that took place in the Tasso faunal unit does not correlate with any obvious climatic crisis. Maybe western Europe was only the point of arrival of wide ranging dispersals prompted by increasingly continental, strongly seasonal conditions that were developing in central Asia.

The climatic record in the marine environment

Palaeotemperature records in marine sequences indicate a succession of climatic changes, some of which can probably be correlated with dispersal events of terrestrial faunas. Synchronicity in some cases seems however to be only approximate, and time lags exceeding the range of random errors may be observed between the events detected in the two series of phenomena.

In the north Atlantic and north Pacific, analysis of DSDP Sites (Thunell and Williams, 1983; Shackleton et al., 1984; Rea and Schrader,

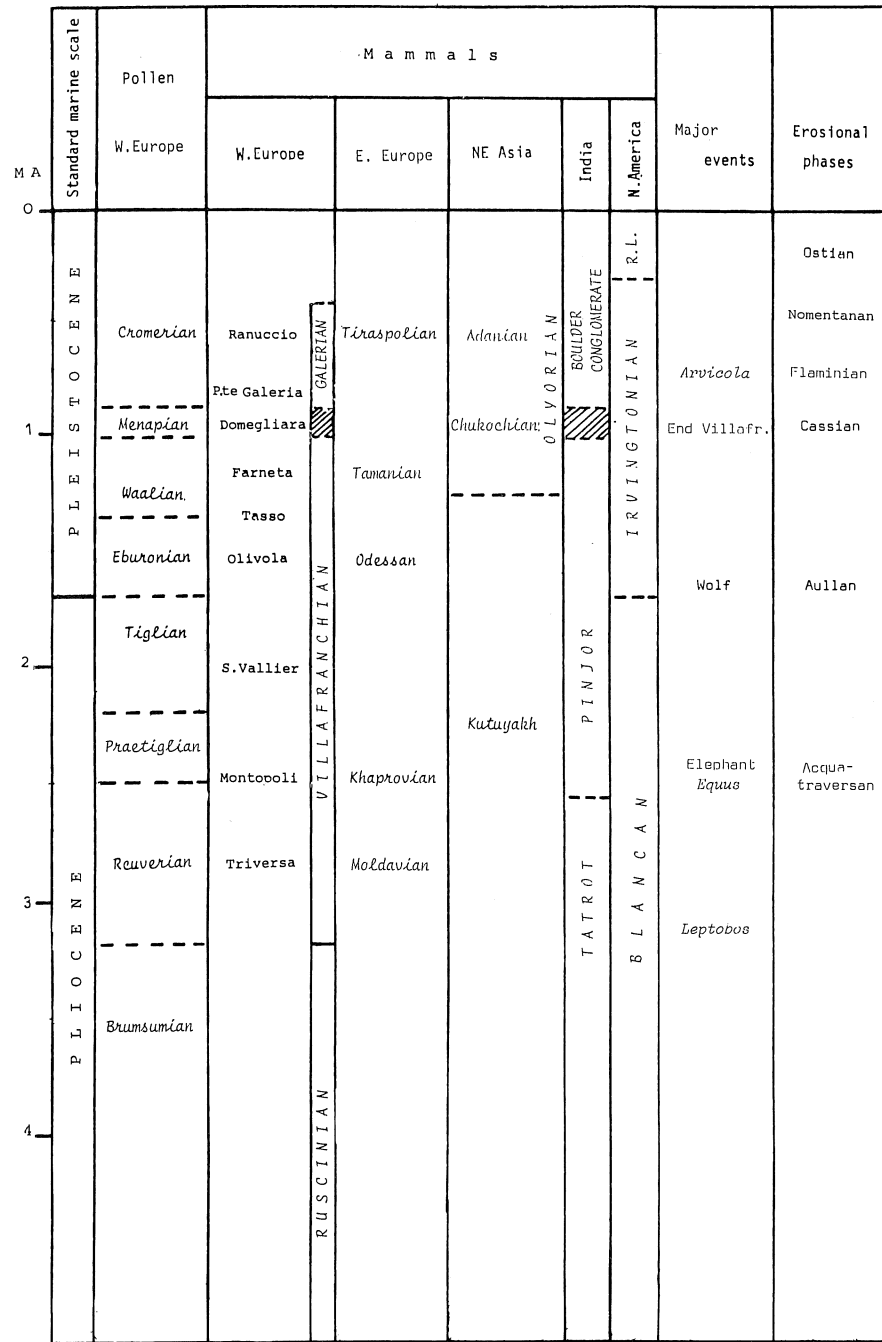


Fig.3. Correlation chart of continental stages, faunal units, major faunal events and erosional phases (negative eustatic oscillations of sea level).

1985) shows a sharp fall in deep water temperature and a sudden increase of ice rafted debris at 2.4–2.5 Ma. There is a time difference of at least 0.1 and possibly as much as 0.3 Ma

between the temperature falls of the north Atlantic and of the lacustrine beds of the Jucar basin of Spain. The lowering of temperature in Atlantic deep water corresponds to a wide

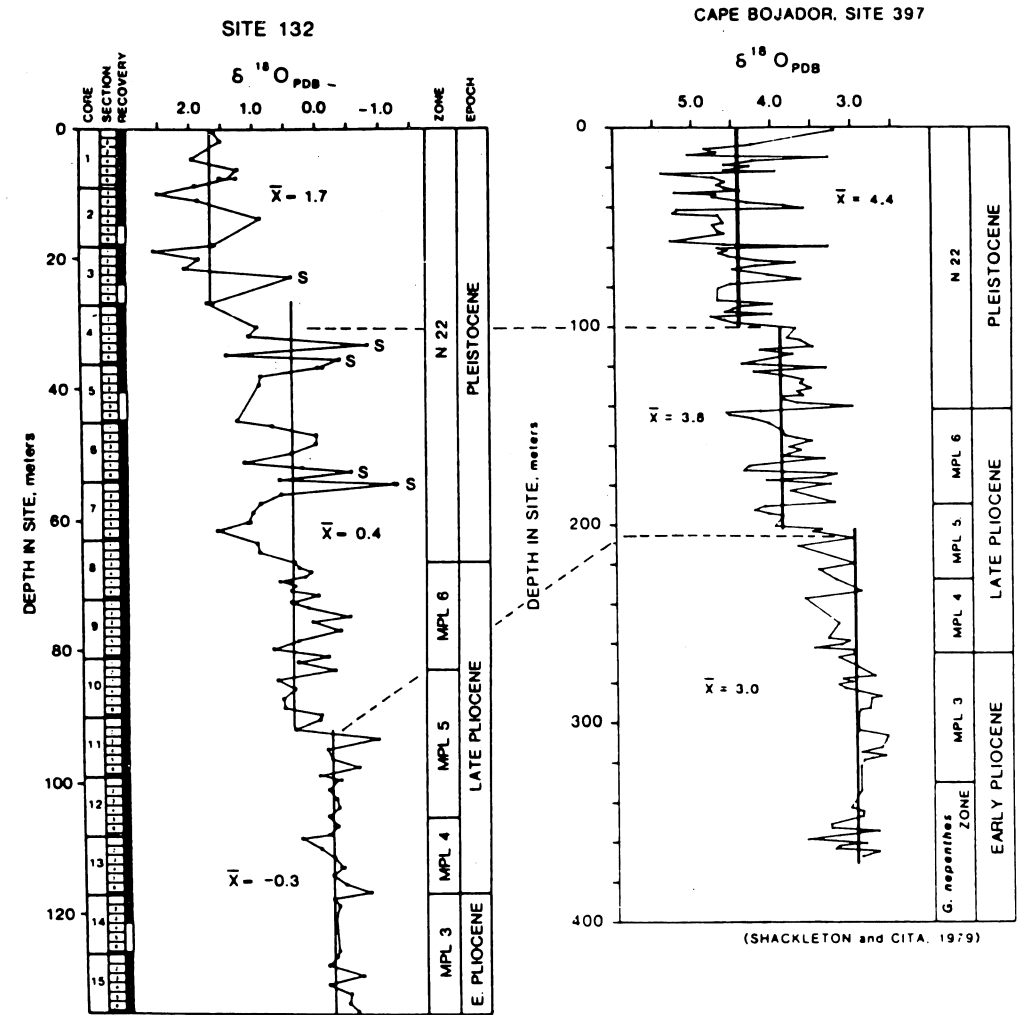


Fig.4. Major shifts in ocean water temperatures in the late Pliocene and early Pleistocene (after Vergnaud Grazzini, 1984).

ranging crisis of extinction in the marine mollusc fauna. An earlier extinction crisis of molluscs in the northern Atlantic was variously dated between 3.5 Ma (Stanley, 1982) and 3.2–3.1 Ma (Raffi and Marasti, 1982); the latter date agrees with a temporary temperature drop recorded in DSDP 552A (3.3–3.1 Ma) and in the Jucar basin (3.2–3.1 Ma).

The crisis dated 2.4 Ma on DSDP 552A is considered the greatest climatic crisis in the Plio-Pleistocene marine record (Shackleton et al., 1984). It coincides with a world wide drop of sea level: the Acqua-traversa erosional phase

of Blanc (Ambrosetti et al., 1972), the Moulouyan of the Atlantic coast of Marocco (Biberson, 1971), the marked drop in sea level described by Stipp et al. (1967) in New Zealand. Agreement is less satisfactory with the picture of global cycles of sea level provided by Vail et al. (1977: fig.3): these authors show sharp drops of sea level in the Pliocene at approximately 3 or 2.9 Ma and at 2.0 Ma. The discrepancies, in our opinion, are due to inaccurate datings of sea level fluctuation in the synthesis of Vail et al. A closer agreement with the interpretation adopted in this paper is found in an article on

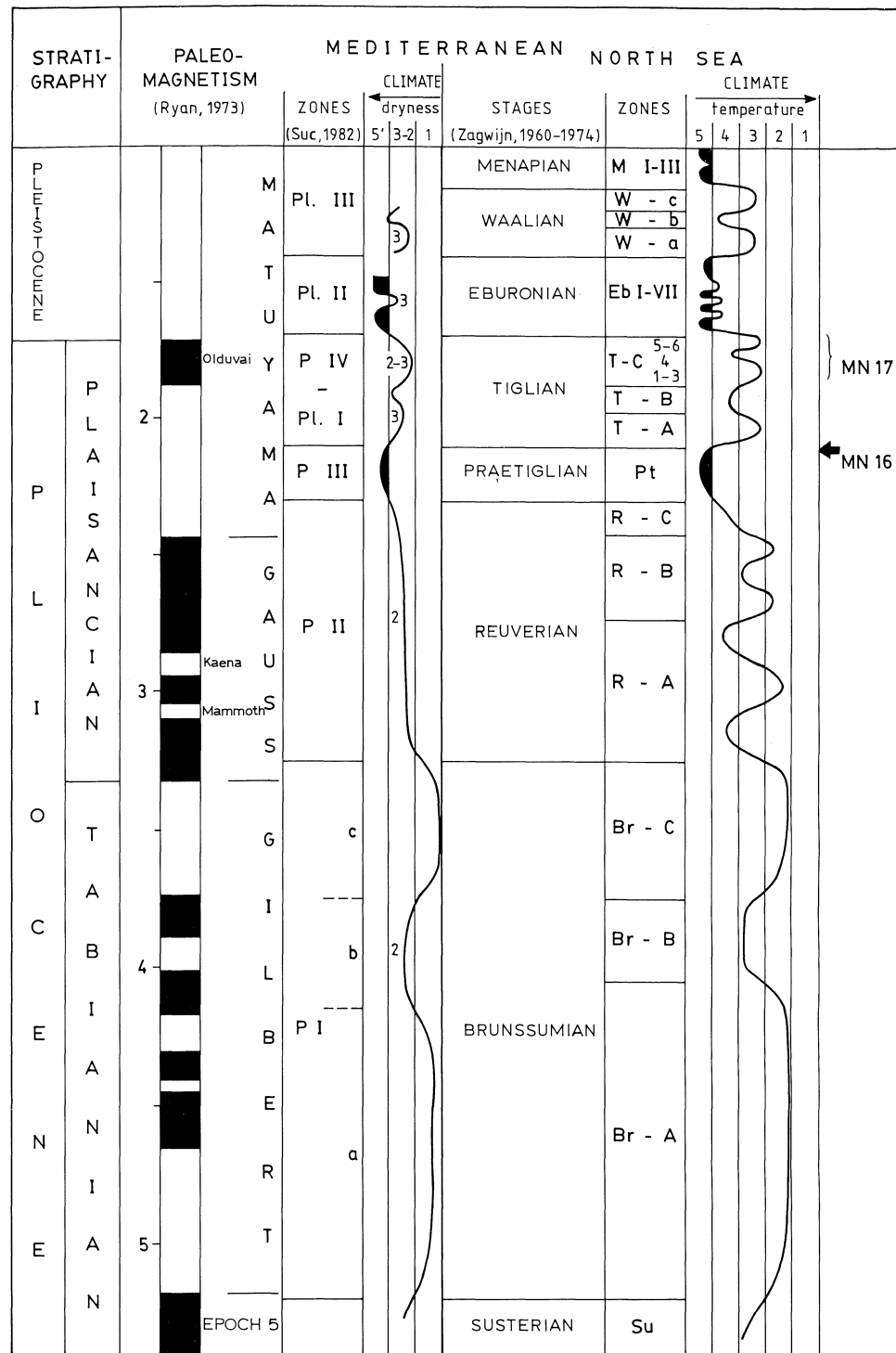


Fig.5. Pollen climatic curves for the Mediterranean and North Sea, Pliocene to Pleistocene, plotted against the palaeomagnetic scale. Adapted from Zagwijn and Suc (1984).

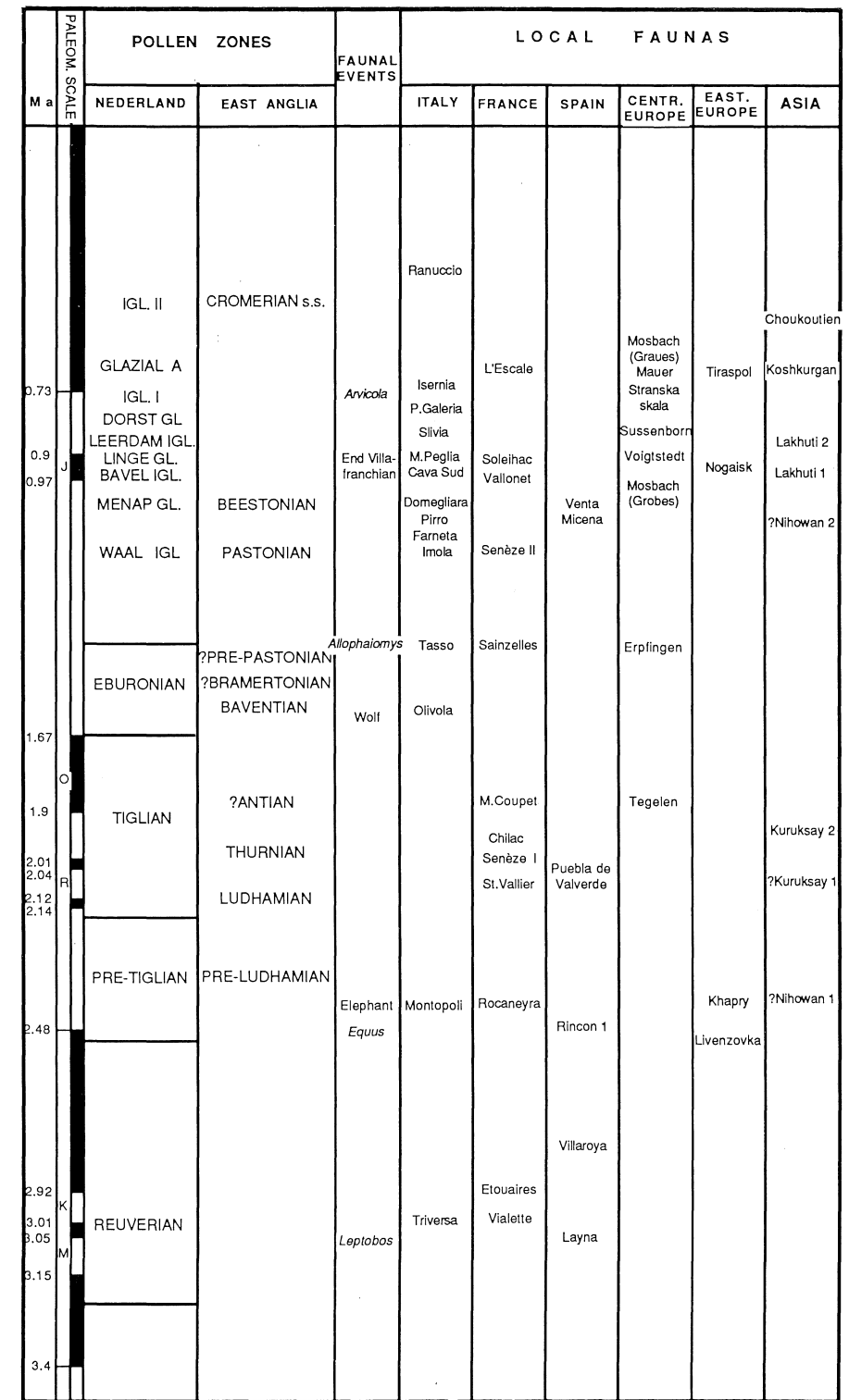


Fig.6. Correlation chart of local faunas, Pliocene to early middle Pleistocene, for Europe and Eastern Asia.

quaternary eustatic cycles, mainly based on evidence from the west Atlantic, by Beard et al. (1982).

The carbon isotope curve of DSDP Site 552A shows an increase in water temperature between 2.1 and 1.7 Ma (the Tiglian of Zagwijn) followed by a new minimum between 1.7 and 1.6, which may mark the beginning of the Eburon phase of the North Sea, the Aullan erosional phase of central Italy, the Baventian cold period of East England and the beginning of the Pleistocene-Late Villafranchian.

Temperature of the north Atlantic at this time was no less severe than during the previous cold interval: if the impact on the marine fauna was less dramatic this may have been because the fauna had already been selected for cold waters, warm water dwellers having been eliminated earlier.

This is the cold period during which *Arctica islandica* entered the Mediterranean, or at least of its first record in Italy, slightly preceding the first appearance of the nannofossil *Gephyrocapsa oceanica* in the Stirone section near Parma (Pelosio et al., 1980; Raffi, 1982, 1986), although the climate was not really cold at this time in the Mediterranean area (Raffi, 1982).

The climatic crisis of the end-Villafranchian event was much more severe than the previous ones. If this was not observed in subaerial exposures of marine sequences, this is because continuous marine sedimentation almost everywhere came to an end in the presently emerged areas and from now on was largely restricted to raised beaches and terraces.

Pleistocene paleotemperatures in deep sea cores show characteristic features. A cold phase immediately above the Olduvai event is clearly recognised in a core from the tropical Atlantic, V 16-205 (Kukla, 1977: fig.2). This is followed by a period of minor oscillations, then by a sequence of more marked oscillations which have been numbered, starting from the top, from 1 to 23: even numbers stand for cold phases, odd ones for warm intervals. The oldest marked cold stage, no. 22, falls in the late Matuyama, about half way between the end

of the Jaramillo and the beginning of the Brunhes, i.e. around 0.8 Ma.

Ruggieri et al. (1984) showed a marked increase in cold water pteropods in a sandy bed, possibly evidencing a drop in sea level, at Ficarazzi near Palermo, in the type section of the Sicilian, and date it again to 0.8 Ma. The date was obtained through detailed correlation with nannofossil sequences (Di Stefano and Rio, 1981; Ruggieri et al., 1984). Here not only the temperature drop but also the eustatic oscillation of sea level turns out to be 0.1 to 0.2 Ma younger than the end-Villafranchian event. The difference in time between major changes in continental faunas and floras and events in the marine environment is a challenging theme for future investigations. Unfortunately the Ficarazzi section was not calibrated in the palaeomagnetic scale. We hope the discrepancy may be solved through more accurate datings of the Cassian erosional phase in the Rome area and of the Ficarazzi series of northern Sicily. The point is not without relevance because Ruggieri et al. propose the Ficarazzi section as the stratotype for the boundary between early and middle Pleistocene: the boundary should be represented by the sandy bed rich in cold water pteropods.

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PALAEOGEOGRAPHIC SIGNIFICANCE OF STROMATOLITIC BUILDUPS ON LATE PROTEROZOIC PLATFORMS: THE EXAMPLE OF THE WEST CONGO BASIN

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Abstract

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The West Congo Basin, equatorial Africa, is filled with a Late Proterozoic sedimentary succession. Its middle part is made up of the "Schisto-calcaire" (shale–limestone) Group. A study of the lower part of this group has resulted in a model of carbonate sedimentation. A stromatolite buildup, very similar to the present barrier reefs and cut by tidal and/or swell channels, separates an intertidal and supratidal inner platform from a subtidal outer one. The inner platform is characterized by deposition of dolomitic limestones containing gypsum crystals epigenetically replaced by calcite and chalcedony. The outer platform is made up of stromatolite biostromes arranged in elongate domes parallel to marine currents alternating with limestones with thin shale stringers.

In Proterozoic basins, stromatolitic barrier reefs mark transitions either between inner and outer platforms, or between platform and deep basin. Subtidal stromatolite biostromes, with an elongation of ten to hundreds of meters, locally encroached upon some of the slowly subsiding, flat-bottomed epicontinental basins.

Introduction

The West Congo Basin is a vast synclorium, referred to as the Niari or Nyanga Synclitorium, which trends NNW–SSE and parallels the Atlantic coast from Gabon to Angola. The present study is concerned with the Congo part of this basin. The northeastern flank of the basin is monoclinical and rests unconformably on the basement of the Chaillu Massif. The steepened and folded southwestern flank makes up the external structural units of the West Congo Belt (Fig.1A). The underlying Mayombian succession, which probably is Middle Proterozoic in age, together with the

reactivated basement constitute the internal part of this belt whose age has been much discussed. Certain workers believe it to be a paired orogen in which a Pan-African Belt, approximately 700 Ma old (Cahen et al., 1976) or 600 Ma old (Hossié and Caby, 1979), joins an older Mayombian Belt of about 1100–1200 Ma. Others think that it is a Mayombian Orogen very slightly reactivated during the Pan-African Orogenesis (Vellutini et al., 1983). Recent investigations by Hossié and Caby (1979), Hossié (1980) and Boudzouyou (1986) suggest the entire orogenic ensemble has been subjected to only a single, polyphased orogenesis of Pan-African age.