Tappan, H. and Loeblich, A. R., Jr., 1972. Fluctuation rates of protistan evolution, diversification and extinction. In: 24th Int. Geol. Congr., Montreal, Section 7, Palaeontology, pp. 205—213.

Tappan, H. and Loeblich, A. R., Jr., 1973. Evolution of the oceanic plankton. Earth-Sci. Rev., 9: 207—240.

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QUATERNARY MAMMALS AND THE "END-VILLAFRANCHIAN" DISPERSAL EVENT — A TURNING POINT IN THE HISTORY OF EURASIA

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ABSTRACT

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The history of land mammals is characterized by "dispersal events", i.e. short periods of rapid intercontinental migrations and faunal replacements. One of these, the Elephant—*Equus* event of Lindsay et al., may be dated somewhere between 3 and 2.5 Ma. A second event, the "Wolf" event, may fall near 1.7 Ma. The "end-Villafranchian" event is discussed in detail. It may be dated between 1.0 and 0.9 Ma and is marked by a practically total rejuvenation of the fauna, with the appearance of new types of adaptation, unknown in the Villafranchian. This faunal revolution is easily recognized all over Eurasia and is accompanied by wide-ranging changes in climate and vegetation. This whole sequence of phenomena may have been triggered by extensive tectonic movements in the mountain belts of central and southern Asia.

MAMMALIAN FAUNAS AND DISPERSAL EVENTS IN THE PLIOCENE AND EARLY PLEISTOCENE

The history of mammalian faunas is characterized by discontinuities that were initially interpreted as hiatuses in the record but which, in fact, are due to brief periods of rapid intercontinental dispersal. "Mammalian ages of continental scope tend to begin with an episode of intercontinental faunal dispersal" (Repenning, 1967). The concept of "dispersal events" so introduced by Repenning was developed further by the same author (1978, 1980) for Asia and North America and applied by Lindsay et al. (1980) to Asia and Europe. In the latter paper three dispersal events were recognized in the Pliocene and early Pleistocene of Asia and Europe, dated respectively at 3.4, 2.6 and 1.9 Ma. Some of these dates may possibly be revised (see below), but the main purpose of this paper is to show that after these a fourth event took place, of much wider range than the older ones. It was a really revolutionary event, with the extinction of an archaic fauna which still retained Pliocene affinities and the emergence of a new assemblage of modern appearance. No

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wonder that this event corresponds to the Pliocene/Pleistocene boundary as was currently intended by anthropologists and vertebrate palaeontologists (see the authoritative synthesis in Zeuner, 1945) before the International Geological Congress of London (1948), at which this boundary was fixed at the base of the marine Calabrian (now renamed Santernian: Ruggieri and Sprovieri, 1977) and shifted round one million years back in time. This also corresponds to the Pliocene/Pleistocene boundary as proposed by E. Bonifay (1977) and to the Eopleistocene/Pleistocene s.str. boundary of Russian authors (Schanzer, 1982), and has been called the "end-Villafranchian event" (Azzaroli and Napoleone, 1982). Its characters, age and links with floral, physiographic and climatic changes will be discussed here.

Table I summarizes the distribution of Italian mammals during the Villafranchian and early middle Pleistocene. These are taken here as a starting point for discussion because faunas are rich and varied, their stratigraphic distribution has been worked out in detail and at several sites terrestrial mammalian faunas have been correlated with marine stratigraphy, radiometric dates and sea-level fluctuations. For comprehensive reports on the stratigraphy of Italian mammals, reference is made to Ambrosetti et al. (1972), Azzaroli (1977a), Arias et al. (1979, 1980) and Azzaroli et al. (1982). Large and small mammals have been plotted separately in Table I because the record of small mammals is altogether meagre in Italy and has not the same documentary value as the record of large mammals. The record of the latter, on the other hand, is good and apart from few exceptions — obviously linked to climatic factors — it contains all the most significant taxa represented in the faunas of Western, Central and Eastern Europe. Italian faunas are not provincial and do not contain endemic taxa. Faunas of other areas are also rich, but their stratigraphic succession has not been worked out with the necessary detail for the time interval considered here and the stratigraphic allocations of some sites are still uncertain, or seem inconsistent with published lists of their faunas.

THE "ELEPHANT—*EQUUS*" DISPERSAL EVENT

This dispersal event, dated about 2.6 Ma by Lindsay et al. (1980), is clearly apparent in Table I. It marks the disappearance of a warm forest assemblage — a somewhat modified holdover of Ruscinian faunas — with the extinction of *Mammut borsoni*, *Tapirus arvernensis*, *Sus minor* and *Ursus minimus* and its replacement with an assemblage indicative of a more open, parkland or savannah landscape, with the immigration of a primitive elephant (*Archidiskodon gromovi*), gazelle (*Gazella borbonica*) and a monodactyl equid (*Equus* cf. *livenzovensis*). This is the transition from the Triversa to the Montopoli faunal unit (Azzaroli, 1977a). Lindsay et al. (1980) suggested an age of 2.6 Ma for it, which is certainly plausible but needs closer investigation. The immigration of the elephant is in any case older than the Montopoli local fauna: the skeleton from Laiatico was found interbedded in marine and brackish clays underlying the sands that cap the local Pliocene sequence and which represent the level of the Montopoli local fauna. Studies to date more exactly the position of the Laiatico elephant in the marine sequence are now under way.

Two climatic changes are known to have occurred during the middle Pliocene in Western Europe: one around, or shortly before 3 Ma, marking a transition from warm to temperate climate (beginning of Reuverian) and one around 2.5 Ma, marking a change from temperate to cooler climate (beginning of Pretiglian: Bessedik and Suc, 1983; Zagwijn and Suc, 1983). The second climatic change seems to mark the beginning of the Acquatraversan erosional phase; the former might perhaps correspond to the Elephant—*Equus* event, which would thus be 0.3—0.4 Ma older than the date assumed by Lindsay et al. An "*Equus stenonis*" of unusually large size (possibly *E. livenzovensis*) associated with *Gazella borbonica*, *Nyctereutes megamastoides*, *Mimomys* cf. *cappettai*, etc., has been recorded in the Rincòn 1 local fauna in the Júcar Valley, eastern Spain, dated about 2.6—2.7 Ma (Alberdi et al., 1982).

THE "WOLF" EVENT AND THE LATE VILLAFRANCHIAN

The faunal break of the following event is overemphasized in the Italian record by the lack of middle Villafranchian faunas. The faunal turnover was largely the result of evolutionary changes, and there is no very sharp transition from early to late Villafranchian faunas. The only outstanding facts seem to be the arrivals of *Leptobos etruscus* (which replaces *L. stenometopon*), *Sus strozzii*, *Pachycrocuta brevirostris* and *Canis etruscus*, a primitive wolf (Torre, 1967). The date of 1.9 Ma assumed by Lindsay et al. (1980) for this event is somewhat older than the age proposed by Haq et al. (1977) and by Berggren et al. (1980) for the Neogene/Quaternary boundary in marine sequences (1.7 Ma), which is also the age of the Blancan—Irvingtonian boundary in mammalian faunas of North America, as proposed by Lindsay et al. (1976). The Neogene/Quaternary boundary proposed in the Vrica section, Calabria, southern Italy, also approximates this age and seems to lie near the top of the Olduvai palaeomagnetic event (Pasini and Colalongo, 1982); unfortunately the palaeomagnetic record of this section is not fully satisfactory (Tauxe et al., 1983).

Given the rather gradual character of the faunal turnover, the age of the "Wolf" event is not easily defined. Two radiometric dates are available for the fairly rich fauna of Chilhac in the French Central Massif: 1.85 Ma (Bonadonna, in Azzaroli, 1977a) and 1.8 Ma (Guth, 1982). The Chilhac fauna is somewhat intermediate in composition between the St. Vallier and the Olivola faunal units as defined by Azzaroli (1977a): it contains progressive elements like *Gazellospira* and *Gallogoral* but also a holdover of the middle Villafranchian, *Nyctereutes megamastoides*, and lacks *Leptobos etruscus*, *Canis etruscus* and *Sus strozzii* (Guth, 1982; the hyaena has not been identified specifically) (see note 1 on p. 139). This might imply a some-

TABLE I

Stratigraphic distribution of Villafranchian and Galerian mammals in Italy

Abbreviations: Tr = Triversa faunal unit; Mo = Montopoli faunal unit; SV = Saint Vallier faunal unit (not recorded in Italy); Ol = Olivola faunal unit; Ta = Tasso faunal unit; Fa = Farneta faunal unit; Do = transitional Villafranchian—Galerian faunas (Domegliara, Viatelle); PG = early Galerian (Ponte Galeria and Isernia local faunas); Ra = late Galerian (Ranuccio local fauna)

	Tr	Mo	SV	Ol	Ta	Fa	Do	PG
Mammut borsoni (Hays)	+							
Tapirus arvernensis Croizet et Jobert	+							
Sus minor Dépéret	+							
Semnopithecus monspessulanus Gervais	+							
Ursus minimus Devèze et Bouillet	+							
Viverra cf. *pepratxi* Dépéret	+							
Dicerorhinus jeanvireti Guérin	+	+						
Cervus pardinensis Croizet et Jobert	+	+						
Leptobos stenometopon (Sismonda)	+	+						
Anancus arvernensis (Croizet et Jobert)	+	+	—	+				
Euryboas lunensis (Del Campana)	+	—	—	+				
Lynx issiodorensis (Croizet et Jobert)	+	—	—	+	+			
Acynonyx pardinensis (Croizet et Jobert)	+	+	—	+	+			
Homotherium crenatidens (Fabrini)	+	+	—	+	+	+	+	+
Archidiskodon gromovi Alekseeva and Garutt		+						
Equus cf. *livenzovensis* Bajgusheva		+						
Croizetoceros ramosus (Croizet et Jobert)		+						
Eucladoceros (?) sp.		+						
Gazella borbonica Dépéret		+						
Nyctereutes megamastoides (Pomel)		+						
Pachycrocuta perrieri		+	—	+	+			
Enhydrictis ardea (Bravard)				+				
Felis lunensis Del Campana				+				
Gallogoral meneghinii (Rütimeyer)				+				
Sus strozzii Forsyth Major				+	+			
Eucladoceros dicranios (Nesti)				+	+			
Archidiskodon meridionalis meridionalis (Nesti)				+	+			
Canis etruscus Forsyth Major				+	+			
Megantereon cultridens (Cuvier)				+	+			
Dicerorhinus etruscus (Falconer)				+	+	+		
Equus stenonis Cocchi				+	+	+		
Dama nestii (Forsyth Major)				+	+	+		
Leptobos etruscus (Falconer)				+	+	+		
Panthera toscana (Schaub)				+	+	—	—	+
Pachycrocuta brevirostris (Aymard)				+	+	—	—	—
Canis arnensis Del Campana					+			
Canis falconeri Forsyth Major					+			
Pannonictis nestii (Martelli)					+			
Martes sp.					+			
cf. *Bison* (see note 2 on p. 139)					+			
Equus stehlini Azzaroli					+	+		
Leptobos vallisarni Merla					+	+		

TABLE I (*continued*)

	Tr	Mo	SV	Ol	Ta	Fa	Do	PG	Ra
Macaca florentina (Cocchi)					+	+			
Hippopotamus antiquus Desmarest					+	+	+	+	+
Archidiskodon meridionalis vestinus Azzaroli						+			
Eucladoceros sp.						+			
Cervalces gallicus (Azzaroli)						?			
Leptobos sp.						+	+		
Eucladoceros tetraceros (Dawkins)							+		
Crocuta crocuta (Erxleben)							+	—	—
Ursus deningeri v. Reichenau							+	+	—
Equus süssenbornensis Wüst								+	
Equus altidens v. Reichenau								+	
Megaceros savini (Dawkins)								+	
Canis lupus cf. *mosbachensis* v. Reichenau								+	
Mammuthus armeniacus (Falconer)								+	
Bison schoetensacki Freudenberg								+	
Dama dama (?) (L.)								+	
Equus caballus L.								+	+
Dicerorhinus hemitoechus (Falconer)								+	+
Elephas namadicus Falconer and Cautley								+	+
Cervus elaphus acoronatus Beninde								+	+
Megaceros verticornis (Newton)								+	+
Bos primigenius Bojanus								+	+
Cervalces latifrons (Johnson)								?	?
Megaceros solilhacus (Robert)								?	?
Sus scrofa L.									+
Capreolus capreolus (L.)									+
Ursus arctos L.									+
Cuon cf. *alpinus* Pallas									+
Prolagus savagei Berzi	+								
Apodemus elsomyoides Schaub	+								
Mimomys polonicus Kowalski	+								
Mimomys gracilis Kretzoi	+								
Glirulus pusillus Heller	+								
Mimomys stehlini Kormos		+							
Hystrix etrusca Bosco				+					
Lepus valdarnensis Bosco					+				
Mimomys pliocaenicus (Forsyth Major)					+				
Castor plicidens Bosco					+	+			
Allophaiomys ruffoi Pasa						+			
Mimomys reidi Hinton							+		
Mimomys blanci Van der Meulen							+		
Allophaiomys sp.							+		
Pliomys episcopalis Méheny							+		
Beremendia fissidens (Petényi)							+		
Mimomys savini Hinton								+	
Pitymys sp.								+	
Microtus dentatus								+	
Allocricetus bursae Schaub								+	
Sorex runtonensis Hinton								+	

TABLE I (*continued*)

	Tr	Mo	SV	Ol	Ta	Fa	Do	PG	Ra
Lepus sp.									+
Castor cf. *fiber* L.									+
Pitymys hintoni Kretzoi									+
Arvicola cantiana (Miller)									+

The Table has been adapted from Azzaroli et al. (1982), with minor alterations. The name *Equus marxi* has been suppressed and is considered here a synonym of *E. caballus*. The name *Libralces* is considered a synonym of *Cervalces* (Azzaroli, 1983). The antler of *Cervalces* from the Crostolo river (Azzaroli, 1979b) does not come from the level of the late Villafranchian fauna but from higher beds (Cremaschi, private information, 1982); it is not known whether the specimen belongs to *Cervalces gallicus* or to a juvenile individual of *C. latifrons*. Cf. *Bison* is a single metacarpal of massive proportions referred to *Megalovis* sp. by Borselli et al. (1980, quoted in Azzaroli et al., 1982).

The exact position of *Cervalces latifrons* and *Megaceros solilhacus* within the Galerian is not known. A dash indicates inferred stratigraphic distribution.

what younger age for the Olivola fauna and for this unit as a whole, so that the age of the "Wolf" event may actually lie near 1.7 Ma.

The transition from the Olivola to the Tasso faunal unit seems to correspond with a deterioration in climate evidenced in Italy by the Aulla erosional phase (Arias et al., 1979, 1980), which may correspond with the Eburon cold phase of The Netherlands and to the Baventian of East Anglia, and perhaps to a cold episode of North America dated at 1.5 Ma by Boellstorff (1978). It was characterized by the arrival of *Canis arnensis*, a primitive jackal (Torre, 1967) or more probably a coyote (Kurtén, 1974); of *Canis falconeri*, a large dog of uncertain affinities; of *Hippopotamus antiquus*, an African immigrant (Blandamura and Azzaroli, 1977; for nomenclature see Caloi et al., 1980) and of "*Leptobos*" *vallisarni* (Merla, 1949). In the diagram the break between the Olivola and Tasso units is perhaps overemphasized by the incompleteness of the record, in particular of carnivores and primates.

In Central Europe, the massive immigration of the rodent *Allophaiomys* represents a good datum plane and has been correlated with the Eburon cold phase, dated around 1.6 Ma (Chaline, 1977). This genus has not been recorded from Italy at this stage and occurs only in faunas of latest Villafranchian age or belonging to the Villafranchian—Galerian transition. In Table I *Allophaiomys ruffoi* is tentatively referred to the Farneta faunal unit (latest Villafranchian).

THE "END-VILLAFRANCHIAN" DISPERSAL EVENT

The dispersal event which took place at the end of the Villafranchian differs from the older events both quantitatively, because of the much larger number of extinctions and replacements, and qualitatively, inasmuch as it witnessed the development, all over Eurasia, of new adaptations which brought about body structures unknown in the Villafranchian or earlier times. The most apparent of these are the emergence of heavy bovids: *Bos*, *Bison*, *Ovibos* (including *Praeovibos*) and perhaps also the large *Bubalus* in the Indian subcontinent, and of the giant deer of the genus *Megaceros* (for the taxonomy of giant deer see Azzaroli, 1979a).

The origins of these taxa are not known in detail — a *Megaceros* sp., not described, has been reported from the middle (?) Villafranchian of Kuruksay—Navrukho, Tadzhikistan (Vislobokova, 1980) — but since no taxa of similar body structure were observed in the now fairly well known Villafranchian faunas of Europe and Asia, there is every reason to believe that these adaptations developed rapidly at the end of this stage. Possible ancestors of the heavy bisons are the medium-sized *Bison sivalensis* of northern India (Lydekker, 1878; Pilgrim, 1939), *Bison palaeosinensis* of China (Teilhard de Chardin and Piveteau, 1930) and "*Leptobos*" *vallisarni* of central Italy (Merla, 1949), a species closely similar to *Bison sivalensis*: but neither this nor *Bison palaeosinensis* attain the large size nor the massive limb structure of the heavy bovids of the middle and late Pleistocene (the limbs of *Bison sivalensis* are not known).

More than one half of the late Villafranchian fauna disappeared without descent at the end of the Villafranchian. Few species survived without apparent change but did so only for a short time in the early middle Pleistocene. Other lineages survived at the cost of marked evolutionary changes. Admittedly, this point is to a large extent conjectural, nevertheless some phyletic relationships appear fairly well established, or at least highly probable. The rhinoceros *Dicerorhinus etruscus* grew to large size and heavy build, giving rise to primitive subspecies of *D. hemitoechus* (Azzaroli, in press); *Equus stenonis*, or some closely related species, evolved to the large *E. süssenbornensis*, which did not survive the early middle Pleistocene. *Cervalces gallicus* grew to gigantic size with *C. latifrons*, persisted in the late Pleistocene with the somewhat smaller *C. latifrons postremus*, and ended in the Holocene of North America with *C. scotti* (Azzaroli, 1983). *Ursus etruscus* gave rise to *U. deningeri* and eventually to *U. spelaeus*, and possibly also to *U. arctos*. *Canis etruscus* may be the ancestor of later wolves, *C. lupus mosbachensis* and then *C. lupus lupus* and other local subspecies. The red deer, with the primitive *Cervus elaphus acoronatus*, is a new element of the fauna, of still unknown origin. Other immigrants of uncertain origin are the roe (*Capreolus*), the wild boar (*Sus scrofa*) — which is not a descendant of *Sus strozzii* — the spotted hyaena (*Crocuta crocuta*) and some species that appeared in central Europe in the early middle Pleistocene but reached Italy only later: the wolverine (*Gulo*), the reindeer (*Rangifer*), the heavy rhinoceros *Dicerorhinus mercki* (or *kirchbergensis*: the nomenclature of this species is controversial). *Elephas namadicus* (= *antiquus*) and *Mammuthus armeniacus* (= *trogontherii*, = *wüsti*) are other immigrants; the latter, although related to the late Villafranchian advanced *Archidiskodon meridionalis*, does not seem to be its direct descendant (Azzaroli, 1977b). True horses (*Equus caballus*, or *Equus* *ferus*) and a primitive ass (*Equus altidens*) immigrated from North America and dispersed rapidly over Eurasia (Azzaroli, 1979b, 1982).

In Table I the rodent *Allophaiomys ruffoi* has been tentatively referred to the Farneta faunal unit (see above). The early middle Pleistocene is characterized by *Mimomys savini* and *Mimomys intermedius*, presumably evolved from some late Villafranchian species. *Arvicola* appeared as an immigrant after the Villafranchian.

The result of all this faunal turnover was an association of modern appearance. Whereas no Villafranchian species survives now, about three quarters of the early post-Villafranchian fauna survived unchanged, or with minor changes, until the late Pleistocene—Holocene, and many of its components survive in the present fauna.

THE GALERIAN FAUNA AND ITS AGE

In Western Europe the mammalian assemblages of the early middle Pleistocene are often designated by the terms Cromerian, or Biharian. Neither is however appropriate. The Biharian was based on small mammals and is currently assumed to begin with the immigration of *Allophaiomys*, considered to coincide with the Eburon cold phase (Fejfar, 1976; Chaline, 1977). If this correlation is correct, the Biharian overlaps the latest Villafranchian, i.e. approximately the Farneta faunal unit. The Cromerian is based on pollen and corresponds to a short time interval prior to the Cromer Till, or Anglian glaciation (West and Wilson, 1966; West, 1980). The meaning of the Cromerian has sometimes been stretched to cover a wider range of time (Zagwijn et al., 1971) but its definition still rests on palynological data. For these reasons, Ambrosetti et al. (1972) introduced the term Galerian for early middle Pleistocene faunas; the name was derived from the locality Ponte Galeria in the Tiber delta west of Rome. Taking into account information collected in recent years, the most typical representatives of Galerian assemblages may be considered to be: *Megaceros* (*Megaceroides*) *verticornis*, *M.* (*Megaceroides*) *solilhacus*, *M.* (*Megaceros*) *savini*, *Cervus elaphus acoronatus*, *Cervus elaphoides* (not yet recorded from Italy), *Cervalces latifrons*, *Bison schoetensacki*, *Equus süssenbornensis*, *E. altidens*, *Ursus deningeri*. These species did not outlive the Galerian. *Hippopotamus antiquus* seems also to have disappeared at the end of the Galerian but immigrated earlier, in the late Villafranchian.

The date of the end of the Galerian does not concern us here; it may be mentioned however that a late Galerian site at Ranuccio in Latium is bracketed between two volcanite levels dated respectively 0.487 ± 0.0075 and 0.365 ± 0.0045 Ma (K/Ar dates by Radicati di Brozolo and Villa, in Biddittu et al., 1979).

The date of the end-Villafranchian dispersal event will now be discussed. In central Italy late Villafranchian and early Galerian deposits are divided by an unconformity corresponding to the Cassian erosional phase, caused by an extensive negative oscillation of sea level (Ambrosetti et al., 1972). The Cassian has been placed at the Matuyama—Brunhes palaeomagnetic reversal (0.7 Ma) in a recent synthesis by Russian geologists (Schanzer, 1982) but Ambrosetti et al. (1972) dated it, on indirect evidence, at around 1 Ma. Late Villafranchian faunas extend to beds immediately underlying the Cassian unconformity. A characteristic molar of the elephant *Archidiskodon meridionalis* was retrieved near the top of the late Calabrian (Santernian) sequence at Monte Mario near Rome, in the Tiber delta area. The late Villafranchian fauna of Sainzelles in the French Central Massif has been dated radiometrically at 1.3 Ma (Méon et al., 1979). Fink (quoted by Kukla, 1977) reported typical late Villafranchian rodents *Mimomys hungaricus* and *Mimomys pliocaenicus* from the Krems loess in the Danube Valley, in levels immediately underlying the Jaramillo palaeomagnetic episode.

The Galerian beds overlying the Cassian unconformity are capped by volcanites dated 0.706 ± 0.070 and 0.680 ± 0.070 Ma; the mammalian fauna occurs in deltaic beds interfingering with marine deposits called Portuensian (Ambrosetti et al., 1972).

At Isernia, in the southern part of central Italy, a Galerian fauna has been calibrated with the late Matuyama reversed epoch and is immediately overlain by volcanic beds for which two dates were obtained independently: 0.73 ± 0.04 in a laboratory in Rome and 0.73 ± 0.07 in a laboratory at Amsterdam (Coltorti et al., 1982; Cremaschi et al., 1982).

Circumstantial evidence for dating the end-Villafranchian event comes from western Germany and southern France. In the well-known quarries of Mosbach in Rhineland, Brüning (1978) distinguished two fossil-bearing horizons. The younger horizon ("Graues Mosbach") contains the main fauna and falls in the Brunhes magnetic epoch. Its fauna is rich and lacks Villafranchian holdovers: it may be correlated with good approximation with the Ranuccio fauna. The older horizon ("Grobes Mosbach") is separated from the former by barren beds and has been calibrated with the Jaramillo episode (0.90—0.97 Ma). Its fauna is not very rich but contains the most typical markers of the Galerian: *Ursus deningeri*, *Megaceros verticornis*, *Cervus elaphus acoronatus*, *Cervus elaphoides*, *Cervalces latifrons*, as well as more long-lived species that immigrated in the Galerian: *Elephas namadicus*, *Mammuthus armeniacus*, *Capreolus capreolus*, *Sus scrofa*. There are, however, two holdovers from the late Villafranchian: *Archidiskodon meridionalis* and, if the identification is correct, *Dicerorhinus etruscus*. The assemblage is thus somewhat transitional between late Villafranchian and Galerian.

In the cave of Vallonnet, in the French Maritime Alps, a mixed fauna, with late Villafranchian elements (*Leptobos*, a caprid of Villafranchian affinities, *Equus stenonis*, *Archidiskodon meridionalis*, *Pachycrocuta perrieri*) and post-Villafranchian elements (*Cervus elaphoides*), occurs at the top of a marine Calabrian transgression and has also been correlated with the Jaramillo episode (De Lumley et al., 1976).

Mixed faunas are known from other sites in France. One of the best known is Saint Prest, a filling of a karst cavity with *Equus stenonis* and

Archidiskodon meridionalis associated with *Bos* or *Bison*, *Megaceros*, *Elephas namadicus* and an elk, *Alces carnutorum*, of uncertain affinities (M. F. Bonifay, 1973; Heintz and Poplin, 1981; the latter authors remark that the fauna, dispersed in several collections, needs a thorough revision). M. F. Bonifay listed thirteen localities considered of transitional age between early and middle Pleistocene, but not all faunal lists are consistent with this dating. The lists given for La Malouteyre and Peyrolles, in the Central Massif, contain only late Villafranchian elements. Sainzelles is another site in the Central Massif often quoted as transitional from early to Middle Pleistocene; the faunal list of M. F. Bonifay includes however seven late Villafranchian species and, in addition, *Cervus pardinensis*, a typical early Villafranchian (Pliocene) species. To make things more complicated, two fossil-bearing horizons have been distinguished and the younger one has been referred to the early Mindel. A radiometric age of 1.3 Ma (Méon et al., 1979), presumably relating to the older horizon, clearly speaks for a late Villafranchian age. Still in the Central Massif, Solilhac (also written Soleilhac, Soleihac; the spelling adopted here is derived from the original account by Robert, 1829) has yielded a typical Galerian fauna, in accordance with a radiometric age of 0.7 Ma (Méon et al., 1979). E. Bonifay (1977) distinguished several fossiliferous horizons but they seem to span a short time.

In Italy there are also assemblages in which late Villafranchian and Galerian elements are associated. Unfortunately they all come from bone breccias filling karst cavities so that the risk of contamination of faunas cannot be fully ruled out. Domegliara (Selva Vecchia) near Verona has yielded a large *Leptobos* and the cervid *Eucladoceros tetraceros*, representing late Villafranchian faunal elements, together with *Crocuta crocuta*, *Ursus deningeri* and *Cervus elaphus* ssp. ind.

Assemblages of similar type have been recorded from Spain. The fauna of Cueva Victoria in eastern Spain (Carbonell et al., 1981) contains *Archidiskodon meridionalis*, *Equus stenonis* and *Canis etruscus* associated with *Cervus elaphoides*, *Megaceros savini*, *Ovibos* and others. At Venta Micena and Bagur 2, Moyà Solà et al. (1981) recorded similar assemblages. In the Granada area Ruiz Bustos (1976) described a fairly rich, though very fragmentary fauna from Çullar de Baza 1, with *Equus* cf. *stenonis*, *E.* cf. *süssenbornensis*, *Dicerorhinus etruscus*, *Megaceros savini* (described as *verticornis*), *Cervus* cf. *acoronatus*, *Bison* sp., *Canis etruscus*, *Crocuta* sp., *Microtus breccensis*, *Arvicola mosbachensis* and others.

The series of terraces of the Tagus west of Toledo is interesting (Alferez, 1977). Scanty but characteristic late Villafranchian species (*Archidiskodon meridionalis*, *Equus stenonis*) were retrieved from the fourth and third terraces (respectively 72—85 m and 50—65 m above the present talweg), while the second terrace (32—45 m) has yielded a typical Galerian fauna with *Megaceros savini*, *Hippopotamus antiquus*, *Mammuthus armeniacus* and an early Palaeolithic industry. A similar fauna and industry occur in the Pinedo terrace east of Toledo.

It is seen thus that late Villafranchian faunas lived during the Matuyama reversed epoch more or less up to the beginning of the Jaramillo normal episode. In the late Matuyama, between the end of the Jaramillo and the beginning of the Brunhes normal epoch, the faunal revolution that led to the formation of Galerian assemblages was already accomplished. The scarcity of intermediate faunas seems to indicate that the process of transition was rapid and its date may be equated with good approximation with the Jaramillo episode, that is, with the Cassian erosional phase.

The Pleistocene stratigraphy of Great Britain has been worked out in detail, mainly on palynological data, but its correlation with the mammalian stratigraphy of continental Europe is not yet fully satisfactory. This may be due in part to the fact that fossils were collected mostly loose on the shore, at the foot of cliffs in which several superposed horizons are exposed, so that their exact position in the sequence could not be determined. The Cromerian falls in the earlier part of the Brunhes epoch but there are also Villafranchian assemblages which have not been properly placed, or have been placed only in a tentative way. One of these occurs in the Norwich Crag series at Easton Bavents and nearby localities; on palaeontological grounds it may be equated with the Olivola faunal unit and with the Tegelen fauna of The Netherlands and presumably comes from beds of Antian age; West (1980) correlates the Antian with the Olduvai event, in good agreement with this view. A second assemblage is characteristic of the latest Villafranchian (Farneta faunal unit), with *Equus stenonis*, *Leptobos etruscus*, *Dama nestii*, *Eucladoceros dicranios* (= *ctenoides*), *E. tetraceros*, *Cervalces gallicus*, *Canis arnensis*, *Mimomys pliocaenicus*, possibly also *Equus major* (= *bressanus*) etc. (Azzaroli, 1953; Stuart, 1974; and unpublished observations by the author). It occurs at several sites in the Forest Bed series of Norfolk: East Runton, Sidestrand, Overstrand, Mundesley. This is not a case of a transitional fauna, with predominantly Cromerian elements joined to scattered Villafranchian holdovers, or vice versa, as in the case of the Grobes Mosbach or of the cave of Vallonnet: on the contrary, rich and varied late Villafranchian and Galerian assemblages occur side by side at these sites, except perhaps at East Runton, where the present writer detected only late Villafranchian elements (West Runton, on the other hand, has a purely Galerian fauna). In any case, even transitional faunas should not be significantly younger than 0.9 Ma. In a former study (Azzaroli, 1953) the present writer assumed that the late Villafranchian fauna came from the Weybourn Crag. In fact, it is not clear whether the fossils were derived from beds of Pastonian or pre-Pastonian age. West (1980, fig.54) suggested a possible correlation of these levels with the Jaramillo episode.

GALERIAN FAUNAS IN EASTERN EUROPE AND ASIA

Faunal assemblages of Galerian affinity are easily recognizable in Eastern Europe and also in Asia, where they keep their distinctive features in spite of local variations.

In southern Russia two faunal units have been distinguished in the early middle Pleistocene (early Pleistocene in the terminology of Russian authors). These are the Karaj Dubin and the overlying Tiraspol complexes. The latter is typified by the rich fauna of the fifth terrace of the Dnestr, a fauna practically identical to those of Western and Central Europe, with the only addition of a camel and of the antelope *Pontoceras ambiguus*; the fossil-bearing beds fall in the Brunhes magnetic epoch (Nikiforova, 1971). The Karaj Dubin fauna is poorer and consists of few rodents (Vangengeim, 1982, p. 273); it cannot be dated precisely, the occurrence of *Allophaiomys* may indicate a pre-Galerian or early Galerian age.

Typical Galerian faunas occur at Akhalkalaki in Georgia, with *Equus süssenbornensis*, *Megaceros solilhacus*, *Bos* sp., *Hippopotamus georgicus*, *Panthera* cf. *tigris* (Vekua, 1962: identification of *Megaceros* revised by the present author) and at Latamne in Syria, with *Stegodon* cf. *trigonocephalus*, *Mammuthus armeniacus*, *Dicerorhinus* cf. *hemitoechus*, *Megaceros verticornis*, *Bison* cf. *priscus* (Hooijer, 1961).

More circumstantial information comes from Tadzhikistan. The Lakhuti fauna of the Tadzhik depression has been correlated with the Karaj Dubin complex by Vangengeim (1982, p. 274). As a matter of fact, there are two fossil-bearing horizons, both calibrated in the palaeomagnetic scale. Lakhuti 2 lies in the late Matuyama reversed epoch, a short distance above the end of the Jaramillo episode: Lakhuti 1 lies at the base of the Jaramillo (Dodonov, 1980). The faunas are still under study and only provisional identifications are available at present. Combining data from various authors (in Nikiforova and Dodonov, 1980) with observations by D. Torre on the collections of Moscow and by the present writer in Moscow and Dushanbe, the following list may be proposed for Lakhuti 2: *Canis lupus* cf. *mosbachensis*, *Pachycrocuta brevirostris*, *Homotherium latidens*, *Panthera* cf. *gombaszogensis*, *Equus caballus* ssp. ind., *Bison* cf. *palaeosinensis*, *Pontoceras* sp., *Eucladoceros* sp., *Megaceros* sp., *Paracamelus* or *Gigantocamelus* sp., *Archidiskodon* (?) sp. and *Allophaiomys* (?) sp. The assemblage is essentially of Galerian type, with only *Eucladoceros* and the doubtful *Archidiskodon* as survivors from older faunas. In the collection of Lakhuti 1 in Dushanbe, the present writer identified *Equus* cf. *altidens*, also a component of Galerian faunas in Europe. The two Lakhuti faunas thus define the date of immigration of advanced equids in central Asia.

Koshkurgan, in eastern Kazakhstan on the right bank of the Syr Dar'ya, is another assemblage of Galerian type. The faunal list (Kozhamkulova, 1969; Vangengeim, 1982) includes *Elephas namadicus*, *Equus caballus* cf. *mosbachensis*, an ass identified as *E. hydruntinus* (possibly *E. altidens*?), *Dicerorhinus kirchbergensis*, *Praeovibos* sp., *Cervalces latifrons*, *Mimomys intermedius* and several more endemic species: *Elasmotherium sibiricum*, *Paracamelus gigas*, various rodents. The Koshkurgan complex is considered equivalent of the Karaj Dubin and Tiraspol complexes (Vangengeim, 1982, table 32); so are other faunal complexes of Western Siberia and of Transbaikalia, and the

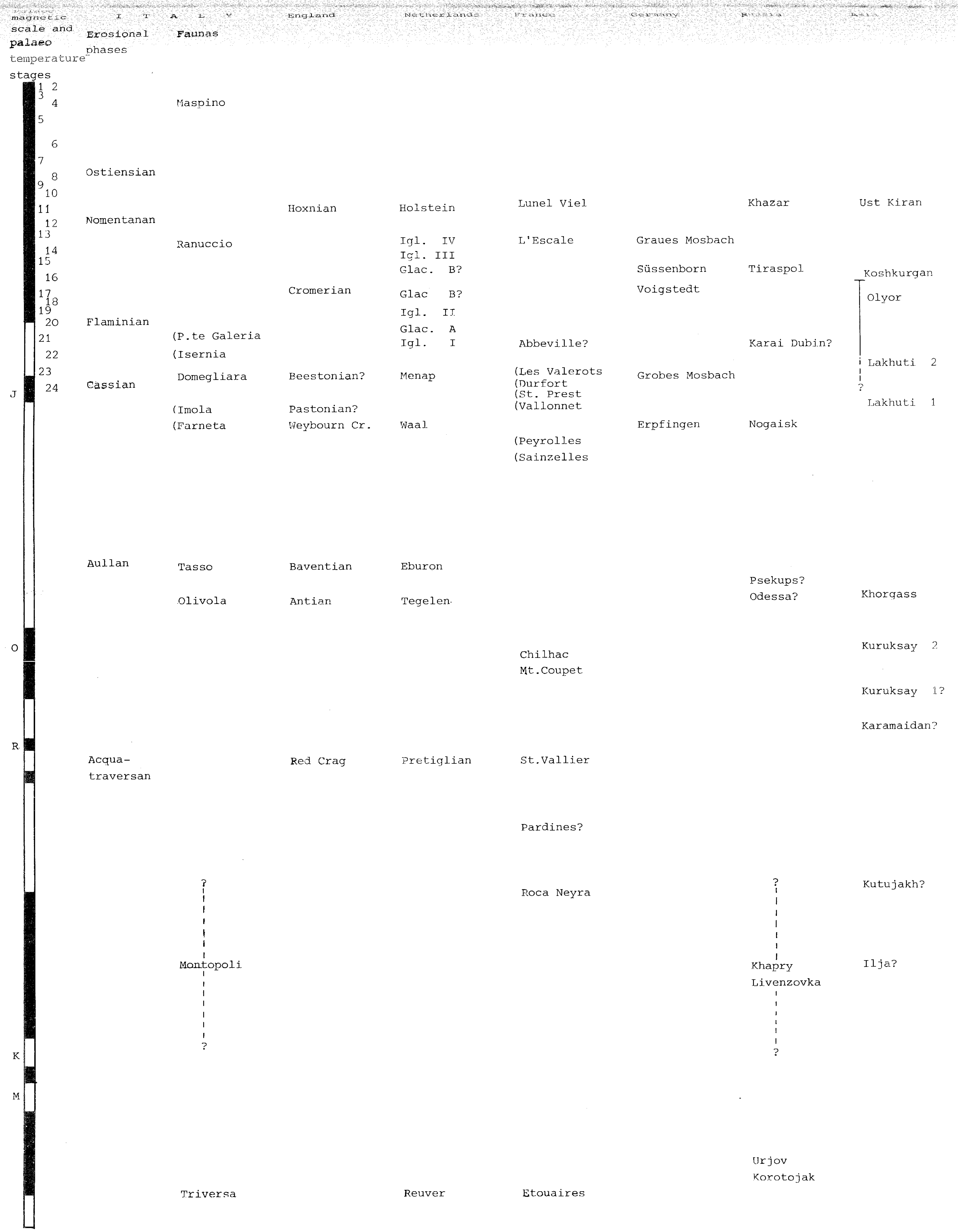


Fig.1. Eurasian fossil sites mentioned in the text, and other Villafranchian and post-Galerian sites, plotted against the palaeomagnetic and palaeotemperature scales.

Olyor complex of the Kolyma lowland in Eastern Siberia (Sher, 1971; Sher and Kaplina, 1979). The latter is of particular interest as it represents the easternmost extension of a faunal assemblage of Galerian type and has been calibrated with the palaeomagnetic scale. The fauna includes *Allophaiomys* cf. *pliocaenicus*, *Xenocyon lycaonoides*, *Gulo* cf. *schlosseri*, *Equus verae* (closely related to *E. süssenbornensis*), *Cervalces latifrons*, *Praeovibos beringensis*, *P.* cf. *priscus* and an unidentified elephant. The fossil-bearing beds, in the interpretation of Russian authors, straddle the Matuyama—Brunhes boundary. Although the beginning of the Olyor fauna is not dated, it appears that a typical Galerian assemblage had already formed in the late Matuyama.

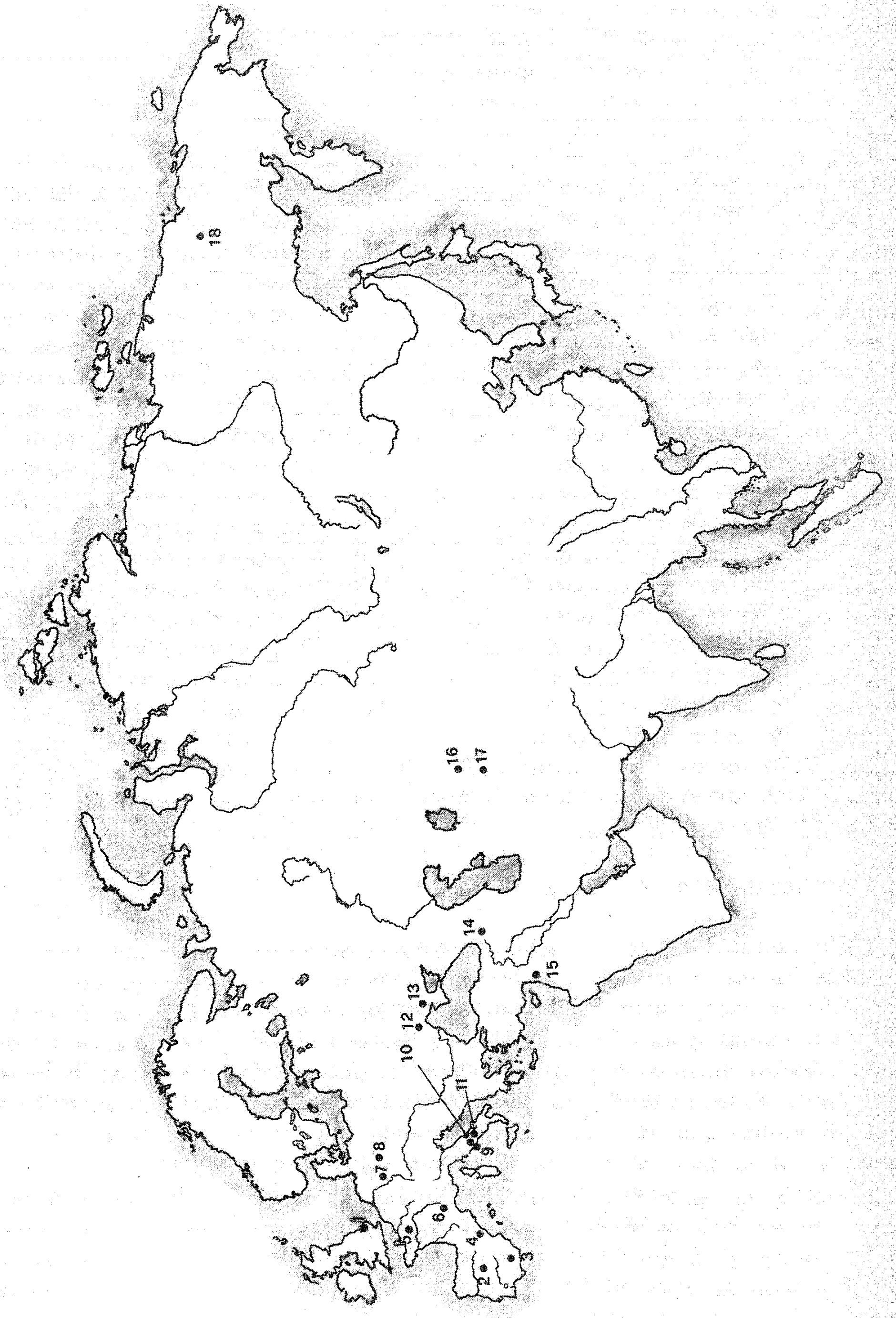
It is fair to state however that C. Repenning (private information), on the basis of small mammals, is inclined to assign an older age to the Olyor complex. It may be that the fossiliferous Olyor complex extends below the Galerian stage in its older part, but the Galerian age of the fauna of large mammals seems firmly established (see note 3 on p. 139).

In the Indian subcontinent a sharp faunal change may be recognized in the Quaternary, although its age cannot be defined at present. Indian faunas are highly endemic and are not easily correlated with those of the rest of Asia and of Europe (Azzaroli and Napoleone, 1982) but the greatest difficulty in the reconstruction of faunal history is poor resolution in the stratigraphic record, especially for the late Pliocene and Pleistocene. A marked break may however be recognized between the faunas of the Pinjor stage (late Pliocene to early Pleistocene: Azzaroli and Napoleone, 1982) of the Sivalik Hills and the middle or late Pleistocene faunas of the alluvial deposits of the large rivers in the Dekkan peninsula: Narmada, Godavari etc. (Badam, 1979), which contain typical post-Villafranchian elements. Some of these are endemic to India (*Rhinoceros*, *Hexaprotodon*, *Bubalus*) but others have a wider distribution in Galerian and later faunas: *Elephas namadicus*, *Bos namadicus* (closely related to *Bos primigenius*).

CORRELATION WITH OTHER EVENTS

In conclusion, although Galerian faunas display local variations, they are sharply distinct from late Villafranchian faunas, are easily recognizable for a set of common features and can be traced throughout Eurasia, from the Iberian peninsula and Great Britain to Eastern Siberia. The transition from late Villafranchian to Galerian faunas may be dated, in round figures, between 1.0 and 0.9 Ma: I thereby do not intend a clear-cut, artificial boundary to be placed somewhere between these extremes, but I mean that this may have been the time span during which the faunal turnover took place.

As may be expected, the spectacular faunal change of the end-Villafranchian event was no isolated phenomenon. Changes of vegetation occurred repeatedly during the Pleistocene and only continuous, or nearly continuous records over appreciable time spans can give an idea of the major features. This is the case of cores drilled in the Pannonian depression in central



Europe: the record shows many oscillations from warm to cool and cold, but cold dry climate assemblages begin to appear only at the end of the Jaramillo episode (Cooke, 1981). In Japan the picture is somewhat different: "the most significant change in floral composition took place toward the beginning of the Jaramillo event. This change is characterized by the replacement of exotic older plants by many new subalpine elements in Japan. The change possibly corresponds to the end of the age of extinctions of older plants, when the climatic deterioration became more intense than in the preceding periods" (Suzuki and Manabe, 1982). There is a time difference between east and west of the order of 0.1 Ma, which may be due to various causes, but both events fall near the Jaramillo episode.

Most of the loess sedimentation in Central Asia — Uzbekistan, Tadzhikistan — began during the late Matuyama, after the end of the Jaramillo episode (Dodonov, 1980, 1982).

In the Upper Sivaliks of northern India, sedimentation is entirely continental and of molasse type, with a tendency to increasing coarseness in the younger levels. At a normal polarity episode which has been tentatively calibrated with the Jaramillo sedimentation becomes entirely and coarsely conglomeratic (Lower Boulder Bed, of Tavi Formation), indicating the onset of strong tectonic movements in the Himalayas around 1 Ma (Azzaroli and Napoleone, 1982).

In deep ocean cores the Jaramillo episode marks the disappearance of dominant small *Gephyrocapsa* assemblages, and after this episode the palaeoclimatic curve based on ^{18}O isotopes shows an uninterrupted sequel of oscillations of great amplitude, from warm to cold. The oldest markedly cold oscillation (palaeoclimatic stage 22) occurs in the late Matuyama interval, about half way between the end of the Jaramillo episode and the beginning of the Brunhes normal epoch (Kukla, 1977; Berggren et al., 1980).

The various phenomena considered here — beginning of strong upheaval in the Himalayas, a wide-ranging revolution in floras and mammalian faunas, climatic changes which also affected deep ocean water circulation — are not strictly contemporary but they all crowd in a short time interval around the Jaramillo normal episode. This is certainly not fortuitous and perhaps also the time lag between different phenomena is significant. The chain of reactions may have been triggered by tectonic movements in the mountain area of Central and Southern Asia: these brought about extensive changes in climate and vegetation, which in turn prompted mammalian faunas to develop new adaptations and to migrate over wide distances.

Fig. 2. Location of early middle Pleistocene (Galerian) sites discussed in the text. *1* = Forest Bed Series; *2* = Toledo; *3* = Cullar de Baza, Venta Micena; *4* = Cueva Victoria; *5* = Saint Prest; *6* = Solilhac; *7* = Mosbach; *8* = Süssenborn, Voigtstedt; *9* = Ponte Galeria; *10* = Ranuccio; *11* = Isernia; *12* = Tiraspol; *13* = Karaj Dubin; *14* = Akhalkalaki; *15* = Latamne; *16* = Koshkurgan; *17* = Lakhuti; *18* = Kolyma depression (Olyorian fauna).

FINAL REMARK

The proposed chronological position of the main faunas and fossil sites of Eurasia mentioned in the text is shown in Fig.1, plotted against the palaeomagnetic and palaeotemperature scales. In order to give a more comprehensive picture, several Villafranchian and post-Galerian sites and faunas not mentioned in the text have been added.

The distribution of localities is shown in Fig.2.

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REFERENCES

Agadjanian, A. K., 1977. Quartäre Kleinsäuger aus der Russischen Ebene. Quartär, 27/28: 111—145.

Alberdi, M. T., Arias, C., Bigazzi, G., Bonadonna, F. P., Leone, G., Lopez, N., Michaux, J., Morales, J., Robles, F. and Soria, Y. D., 1982. Nuevo yacimiento de moluscos y vertebrados del Villafranquiense de la cuenca del Júcar (Albacete, España). Colloque "Le Villafranchien Méditerranéen", Lille, 9—10 Déc. 1982, pp. 255—271.

Alferez Delgado, F., 1977. Estudio del sistema de terrazas del rio Tajo al W de Toledo. Estud. Geol., 33: 223—250.

Ambrosetti, P., Azzaroli, A., Bonadonna, F. P. and Follieri, M., 1972. A scheme of Pleistocene chronology for the Tyrrhenian side of Central Italy. Boll. Soc. Geol. Ital., 91: 169—184.

Arias, C., Bigazzi, G., Bonadonna, F. P. and Urban, B., 1979. Tentative correlations among Quaternary series of Central and Southern Europe. Acta Geol. Acad. Sci. Hung., 22: 81—88.

Arias, C., Azzaroli, A., Bigazzi, G. and Bonadonna, F. P., 1980. Magnetostratigraphy and Pliocene—Pleistocene boundary in Italy. Quaternary Res., 13: 65—74.

Azzaroli, A., 1953. The Deer of the Weybourn Crag and Forest Bed of Norfolk. Bull. Br. Mus. (Nat. Hist.), Geol., 2: 1—96.

Azzaroli, A., 1977a. The Villafranchian Stage in Italy and the Plio—Pleistocene Boundary. G. Geol., 41(2): 61—79.

Azzaroli, A., 1977b. Evolutionary patterns of Villafranchian elephants in Central Italy. Atti Accad. Naz. Lincei, Mem., Cl. Sci. Fis., 14(8): 149—168.

Azzaroli, A., 1979a. Critical remarks on some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. Palaeontogr. Ital., 71: 5—16.

Azzaroli, A., 1979b. On a Late Pleistocene Ass from Tuscany; with notes on the history of Asses. Palaeontogr. Ital., 71: 27—47.

Azzaroli, A., 1982. On Villafranchian palaearctic Equids and their allies. Palaeontogr. Ital., 72: 74—97.

Azzaroli, A., 1983. On the Quaternary and Recent cervid genera *Alces*, *Cervalces*, *Libralces*. Boll. Soc. Paleontol. Ital., 20: 147—154.

Azzaroli, A., in press. Taxinomie des rhinocéros du Pléistocène inférieur et moyen de l'Italie péninsulaire. In: H. De Lumley (Editor), les Anténéandertaliens en Europe.

Azzaroli, A. and Napoleone, G., 1982. Magnetostratigraphic investigation in the Upper Sivaliks near Pinjor, India. Riv. Ital. Paleontol. Stratigr., 87: 739—762.

Azzaroli, A., De Giuli, C., Ficcarelli, G. and Torre, D., 1982. Table of the stratigraphic distribution of terrestrial mammalian faunas in Italy from the Pliocene to the early middle Pleistocene. Geogr. Fis. Dinam. Quat., 5: 55—58.

Badam, G. L., 1979. Pleistocene Fauna of India. Deccan College, Postgr. Res. Inst., Pune, 250 pp.

Berggren, W. A., Burckle, L. H., Cita, M. B., Cooke, H. B. S., Funnell, B. M., Gartner, S., Hays, J. D., Kennet, J. P., Opdyke, N. D., Pastouret, L., Shackleton, N. J. and Takayanagi, Y., 1980. Towards a Quaternary time scale. Quaternary Res., 13: 277—302.

Bessedik, M. and Suc, J. P., 1983. Les caractères du climat au Néogène en Méditerranée nord-occidentale d'après l'analyse pollinique. Interim Coll. "Mediterranean Neogene continental palaeoenvironments and palaeoclimatic evolution", Montpellier, 1983: 33—37.

Biddittu, I., Cassoli, P. F., Radicati di Brozolo, F., Segre, A. G., Segre Naldini, E. and Villa, I., 1979. Anagni, a K/Ar dated Lower and Middle Pleistocene site, Central Italy: preliminary report. Quaternaria, 21: 53—71.

Blandamura, F. and Azzaroli, A., 1977. L'"Ippopotamo Maggiore" di Filippo Nesti. Atti Accad. Naz. Lincei, Mem., Cl. Sci. Fis., 14(8): 169—188.

Boellstorff, J., 1978. North American Pleistocene Stages reconsidered in the light of probable Pliocene—Pleistocene continental glaciation. Science, 202, N. 4365: 305—307.

Bonifay, E., 1977. Les limites Tertiaire—Quaternaire et Pliocène—Pléistocène en France. G. Geol., 41(2): 39—50.

Bonifay, E., Bonifay, M. F., Panattoni, R. and Tiercelin, J. J., 1977. Soleihac (Blanzac, Haute-Loire), nouveau site préhistorique du début du Pléistocène moyen. Bull. Soc. Préhist. Fr., 73: 293—304.

Bonifay, M. F., 1973. Principaux gisements paléontologiques français du Pléistocène moyen: essai de classification. In: 9e Congr. Int. INQUA, Christchurch, 1973, Travaux Français Récents: 41—50.

Brüning, H., 1978. Zur Untergliederung der Mosbacher Terrassenabfolge und zum klimatischen Stellenwert der Mosbacher Tierwelt im Rahmen des Cromer-Komplexes. Mainzer Naturwiss. Arch., 16: 143—190.

Caloi, L., Palombo, M. R. and Petronio, C., 1980. Resti cranici di *Hippopotamus antiquus* (= *H. major*) e *Hippopotamus amphibius* conservati nel Museo di Paleontologia dell' Università de Roma. Geol. Rom., 19: 91—119.

Carbonell, E., Estevez, J., Moyà Solà, S., Pons Moyà, J., Agustì, J. and Villalta, J. F., 1981. "Cueva Victoria" (Murcia, España): lugar de ocupación humana màs antiguo de la Penìnsula Ibérica. Endins, 8: 47—57.

Chaline, J., 1977. Les évènements remarquables de l'histoire plio—pléistocène des campagnols (Arvicolidae, Rodentia) dans l'hémisphère nord, essai de corrélation de la limite plio—pléistocène établie dans les depôts marins d'Italie. G. Geol., 41(2): 123—129.

Coltorti, M., Cremaschi, M., Delitala, M. C., Esu, D., Fornaseri, M., McPherron, A., Nicoletti, M., Van Otterloo, R., Peretto, C., Sala, B., Schmidt, V. and Sevink, J., 1982. Reversed magnetic polarity in an early Lower Palaeolithic site in Central Italy. Nature, 300: 173—176.

Cooke, H. B. S., 1981. Age control of Quaternary sedimentary/climatic record from deep boreholes in the Great Hungarian plain. In: W. C. Mahaney (Editor), Quaternary Palaeoclimates. U.K. Geol. Abstr.: 1—12.

Cremaschi, M., Peretto, C. and Sala, B., 1982. A settlement of *Homo erectus* in Isernia (Central Italy) more than 700,000 years old. In: 11th INQUA Congr., Moscow 1982, Abstr., 1: 67.

De Lumley, H., De Lumley, M. A., Miskowsky, J. C., Renault-Miskowsky, J. and Girard, M., 1976. Grotte du Vallonnet. In: H. De Lumley and L. Barral (Editors), IX Congr. Int. Sci. Préhist. Protohist., Nice 1976, Livret-Guide des excursions, pp. 93—103.

Dodonov, A. E., 1980. Principles of stratigraphic subdivision of Upper Pliocene to Quaternary deposits in Tadzhikistan. In: K. V. Nikiforova and A. E. Dodonov (Editors), Boundary of Neogene and Quaternary Systems. Nauka, Moscow, pp. 22—31 (in Russian).

Dodonov, A. E. (Editor), 1982. 11th INQUA Congr., Moscow 1982. Guideb. Excursions, A-11 and C-11, 68 pp.

Fejfar, O., 1976. Plio—Pleistocene mammal sequences. In: Int. Geol. Correl. Progr., Project 73/1/24, Rep. 3 on Session 1975 in Bellingham, pp. 351—366.

Guth, C., 1982. Chilhac in der Auvergne — eine Wirbeltierfundstätte des Villafranchium in Mittelfrankreich. Z. Geol. Wiss., 10: 913—921.

Haq, B. U., Berggren, W. A. and Van Couvering, J. A., 1977. Corrected age of the Pliocene—Pleistocene boundary. Nature, 269: 483—488.

Heintz, E. and Poplin, F., 1981. *Alces carnutorum* (Laugel, 1862) du Pléistocène de Saint Prest (France). Systématique et évolution des Alcinés (Cervidae, Mammalia). Quartärpaläontologie, 4: 105—122.

Hooijer, D. A., 1961. Middle Pleistocene Mammals from Latamne, Orontes Valley, Syria. Ann. Archéol. Syrie, 11: 117—132.

Kozhamkulova, V. S., 1969. Antropogenovaja iskopaemaja teriofauna Kazakhstana. Nauka, Alma Ata, 150 pp.

Kukla, G. J., 1977. Pleistocene land—sea correlations. I — Europe. Earth-Sci. Rev., 13: 307—374.

Kurtén, B., 1974. A history of coyote-like dogs (Canidae, Mammalia). Acta Zool. Fenn., 140: 1—38.

Lindsay, E. H., Johnson, N. M. and Opdyke, N. D., 1976. Preliminary correlation of Northern American land mammal ages and geomagnetic chronology. Univ. Mich., Pap. Paleontol., 12: 111—119.

Lindsay, E. H., Opdyke, N. D. and Johnson, N. M., 1980. Pliocene dispersal of the horse *Equus* and late Cenozoic mammalian dispersal events. Nature, 287: 135—138.

Lydekker, R., 1878. Indian Tertiary and Post-Tertiary Vertebrata. Vol. 1—3. Crania of Ruminants. Mem. Geol. Surv. India (Paleontol. Indica), Ser. X.3, pp. 88—171.

Méon, H., Ballesio, R., Guérin, C. and Mein, P., 1979. Approche climatologique du Néogène supérieur (Tortonien à Pléistocène moyen) d'après les faunes et les flores d'Europe occidentale. Mém. Mus. Natl. Hist. Nat. Ser. B, 27: 182—195.

Merla, G., 1949. I *Leptobos* Rütim. italiani. Palaeontogr. Ital., 46: 41—155.

Moyà Solà, S., Agustì, J., Gibert, J. and Pons Moyà, J., 1981. El yacimiento cuaternario de Venta Micena (España) y su importancia dentro de las asociaciones faunìsticas del Pleistoceno inferior Europeo. Paleontol. Evol., 16: 39—53.

Nikiforova, K. V. (Editor), 1971. Plejstozen Tiraspolja. Akad. Nauk SSSR, Akad. Nauk Moldavsk. SSR, 118 pp.

Nikiforova, K. V. and A. E. Dodonov (Editors), 1980. Boundary of Neogene and Quaternary Systems. Collected papers. Akad. Nauk SSSR, Geol. Inst., 275 pp. (in Russian).

Pasini, G. and Colalongo, M. L., 1982. Status of Research on the Vrica section (Calabria, Italy), the Proposed Neogene/Quaternary Boundary-Stratotype Section, in 1982. Ist. Geol. Marina CNR—Ist. Geol. Pal. Univ. Bologna, 75 pp.

Pilgrim, G. E., 1939. The fossil Bovidae of India. Mem. Geol. Surv. India (Palaeontol. Indica) (N.S.) 26, 1, 355 pp.

Repenning, C. A., 1967. Nearctic mammalian dispersal in late Cenozoic. In: D. M. Hopkins (Editor), The Bering Land Bridge. Stanford University Press, Palo Alto, CA, pp. 208—311.

Repenning, C. A., 1978. Faunal exchanges between Siberia and North America. In: Am. Quaternary Ass., V Bienn. Meet., Edmonton, Alta, Abstr., pp. 40—55.

Repenning, C. A., 1980. Faunal exchanges between Siberia and North America. Can. J. Anthropol., 1: 37—44.

Robert, F., 1829. Mémoire sur les ossemens fossiles des environs de Cussac, Commune de Polignac (H. te Loire). Mém. Soc. Agric. Puy, 2: 68—88.

Ruggieri, G. and Sprovieri, R., 1977. A revision of Italian Pleistocene stratigraphy. Geol. Rom., 16: 131—139.

Ruiz Bustos, A., 1976. Estudio sistemàtico y ecològico sobre la fauna del Pleistoceno medio en las depresiones Granadinas. Thesis, Univ. Granada, Trab. Monogr. Dep. Zool., 175 pp.

Schanzer, E. V. (Editor), 1982. Chetvërtichnaja Sistema, 1. Nauka, Moscow, 442 pp.

Sher, A. V., 1971. Mlekopytajushie i Stratigrafija Plejstozena krajnego Severo-Vostoka SSSR i Severnoj Ameriki. Nauka, Moscow, 310 pp.

Sher, A. V. and Kaplina, T. N. (Editors), 1979. XIV Pacific Sci. Congr., Tour XI, Guide-Book. Khabarovsk 1979, 116 pp.

Stuart, A. J., 1974. Pleistocene history of the British vertebrate fauna. Biol. Rev., 49: 225—266.

Suzuki, K. and Manabe, K., 1982. Pliocene—Pleistocene chronology of the Yamato Group of Sizu Basin, Northeast Honshu, Japan. In: M. Itihara and Y. Kuwano (Editors), The Third Report on the Pliocene—Pleistocene Boundary in Japan. Japan. Natl. W.G. IGCP Proj. 41 and Natl. Subcomm. Plio-Pleistocene boundary, Japan Branch, INQUA, pp. 18—27.

Tauxe, L., Opdyke, N. D., Pasini, G. and Elmi, C., 1983. Age of the Plio-Pleistocene boundary in the Vrica section, southern Italy. Nature, 304: 125—129.

Teilhard de Chardin, P. and Piveteau, P., 1930. Les mammifères fossiles de Nihowan (Chine). Ann. Paléontol., 19: 134 pp.

Torre, D., 1967. I cani villafranchiani della Toscana. Palaeontogr. Ital., 63: 113—138.

Vangengeim, E. A., 1982. In: E.V. Schanzer (Editor), Chetvërtichnaja Sistema, 1. Nauka Moscow.

Vislobokova, I. A., 1980. Oleni iz mestonakhozhdenija Kuruksay. In: K. V. Nikiforova and A. E. Dodonov (Editors), Boundary of Neogene and Quaternary Systems. Akad. Nauk SSSR, Geol. Inst., pp. 256—258 (in Russian).

West, R. G., 1980. The Pre-Glacial Pleistocene of the Norfolk and Suffolk Coasts. Cambridge University Press, Cambridge, 203 pp.

West, R. G. and Wilson, D. G., 1966. Cromer Forest Bed Series. Nature, 209: 497—498.

Zagwijn, W. H. and Suc, J. P., 1983. Plio-Pleistocene correlations between the Northwestern Mediterranean region and Northwestern Europe. In: Interim Coll. "Mediterranean Continental Palaeoenvironments and Palaeoclimatic Evolution", Montpellier, 1983, pp. 111—113.

Zagwijn, W. H., Van Montfrans, F. M. and Zandstra, J. G., 1971. Subdivision of the "Cromerian" in the Netherlands: pollen analysis, palaeomagnetism and sedimentary petrology. Geol. Mijnb., 50(1): 41—58.

Zeuner, F., 1945. The Pleistocene Period. Ray Society, London, 322 pp.

NOTES ADDED IN PROOF

[1] Odile Boef (1983, Le site villafranchien de Chilhac. Thesis, University of Paris VII, 253 pp.) reports scanty remains belonging to *Pachycrocuta perrieri*.

[2] This taxon has recently been identified as a primitive ovibovine (C. de Giuli and F. Masini, Boll. Soc. Paleontol. Ital., in press).

[3] The type Olyor fauna of the Chukochya River is a characteristic Galerian assemblage, but C. Repenning (pers. commun.) points out that the fauna of the Krestovka section, also referred to the Olyorian complex by Russian authors, is actually of older age.