MAMMALS AND STRATIGRAPHY : THE PALEOGENE OF EUROPE

by

Donald E. RUSSELL[1], Jean-Louis HARTENBERGER[2], Charles POMEROL[3], Sevket SEN[1], Norbert SCHMIDT-KITTLER[4] and Monique VIANEY-LIAUD[2]

SUMMARY

page
Abstract, Résumé 2
Avant-propos 2
Introduction 3
  The Stratigraphic Scale 4
  The Marker Levels 4
The Paleocene Epoch 7
  The Montian Fauna 8
  The Thanetian Stage 9
  Thanetian Characterizing Assemblages 10
The Early Eocene 11
  The Ypresian Stage 11
  The Sparnacian Substage 13
  The Cuisian Substage 16
  Ypresian Characterizing Assemblages 19
The Middle Eocene 23
  The Lutetian Stage 23
  Lutetian Characterizing Assemblages 26
The Middle or Late Eocene 28
  The Bartonian Stage 28
  The Auversian Substage 32
  The Marinesian Substage 33
  Bartonian Characterizing Assemblages 35
The Late Eocene 37
  The Priabonian Stage — The Ludian Substage 37
  Priabonian Characterizing Assemblages 41
The Oligocene Epoch 44
  Regional Groups of Localities 46
  The Fauna 60
  Oligocene Characterizing Assemblages 62
Conclusion — Radiometric Datation 67
Bibliography 70

---

[1] Institut de Paléontologie (LA 12), 8 rue Buffon, Paris, France.
[2] Institut des Sciences de l'Evolution (LA 327), Université des Sciences et Techniques du Languedoc, place Eugène Bataillon, 34060 Montpellier, France.
[3] Laboratoire de Géologie des Bassins Sédimentaires, Université Pierre et Marie Curie, 4 place Jussieu, Paris, France.
[4] Institut für Geowissenschaften, Johannes Gutenberg-Universität, Saarstrasse 21, 6500 Mainz, West Germany.

Palaeovertebrata, Montpellier, Mémoire extraordinaire 1982, 1-77, 23 fig.
(Accepté le 15 Septembre 1982, publié le 1er Décembre 1982)

ABSTRACT

The mammalian faunas of the Paleogene of Europe and their localities are reviewed with comments on problems of European stratigraphy (epoch, stage and substage limits) and on the possibilities of faunal migrations. Radiometric dating is discussed. A stratigraphic scale for the Paleogene is presented, as well as a refined system of sequential faunal levels.

RÉSUMÉ

Les faunes de mammifères du Paléogène d'Europe et leurs gisements sont passés en revue et l'on fait des commentaires sur les problèmes de stratigraphie propres à la région européenne (limites d'étage et de sous-étage). On aborde aussi les problèmes de migrations de faunes. Les données radiométriques sont discutées. Une échelle stratigraphique du Paléogène est proposée ainsi que la succession des gisements repères.

AVANT-PROPOS

Le travail que nous publions aujourd'hui a été entrepris en 1975. A ce moment-là W.O. Woodburne (Riverside, University of California) demanda à D.E. Russell une revue de l'état des connaissances sur le Paléogène d'Europe et sur celui d'Asie mettant l'accent sur les Mammifères fossiles, leurs gisements et leur apport à la stratigraphie. A un tel article devaient s'ajouter des mises au point pour les autres régions et les autres périodes. S'étant entouré de spécialistes requis, D.E. Russell avait préparé une première version consacrée au Paléogène d'Europe dès décembre 1976. Depuis lors le manuscrit initial subit les modifications que commande l'accroissement des données, attendant vainement que les autres parties de l'ouvrage soient rédigées. Dans cet état, il a déjà été communiqué à de nombreux chercheurs, de telle sorte qu'il est cité avant que d'être publié. A la fin de l'année 1981, l'ensemble des auteurs qui avaient rédigé et amendé l'article consacré au Paléogène d'Europe ont demandé à W.O. Woodburne l'autorisation de le publier dans l'état, désespérant que les autres articles de ce qui aurait été un bel ouvrage soient jamais écrits.

Très compréhensif, celui-ci a accepté, et la rédaction de Palaeovertebrata, de son côté, accueille aujourd'hui ce travail longtemps balloté à travers bien des aléas.

Initialement rédigé en français il avait été ensuite traduit en anglais, puisque destiné à être publié dans un ouvrage nord-américain. C'est dans la langue anglaise qu'il fut par la suite constamment amendé, de telle sorte qu'il eût fallu le traduire à nouveau en français, la version originale ayant disparu depuis longtemps. Les auteurs francophones ont renoncé à ce nouvel effort qui risquait de retarder encore sa parution : leurs lecteurs français auxquels d'ailleurs un tel travail ne s'adresse pas au premier chef, les en excuseront peut-être.

INTRODUCTION

Geologists have studied the Tertiary formations of Western Europe for nearly 150 years. As a result, based on their observations, most of the major principles of stratigraphy have been developed in this region. The Paleogene of England, Belgium and northern France has constituted a favored field of investigation for many of our scientific predecessors of the last century ; research in the area has not abated and the accumulation of bibliographic references has reached impressive proportions. At the present time, a much more global view of geologic phenomena prevails wherein it is often difficult to preserve intact concepts that were created during the epoch of the pioneers. For example, a number of stages have acquired over the years a usage extending far beyond the limits of the area in which they were conceived ; this circumstance, coupled with the continuous evolution of local opinion, has led to numerous points of view and differences in the meaning of terms. In fact, there is hardly a stage or a formation in the Franco-Anglo-Belgian Basin that is not still subject to some incertitude or disagreement as to its precise position or limits. In an effort at simplification, Blondeau, Cavelier, Feugeur and Pomerol (1965) have suggested that the stages Sparnacian, Cuisian, Auversian, Marinesian, Ludian and Sannoisian be eliminated from the international terminology and be considered as substages or facies of only regional value. The same can be applied to the Tongrian, Lattorfian, Chattian and Rupelian. The stage names retained for the Eocene and the Oligocene would be the Ypresian, Lutetian, Bartonian and Stampian, although recent discoveries indicate that the Priabonian occupies an independent place between the Bartonian and the Stampian ; also, it is known that the Stampian does not comprise all of the Oligocene.

Further complications have arisen with the discovery that the Belgian Ypresian stage does not correspond to the combined Sparnacian and Cuisian of France, as was believed by Feugueur (1963). The base of the Sables de Cuise (type Cuisian) is now considered to be stratigraphically above the Ypres Clay (type Ypresian), and the equivalent of the latter in France is a body informally termed the « Sables de Cuise inférieur » (the Sables de Laon of Châteauneuf and Gruas-Cavagnetto, 1978) ; the Sparnacien beds underlie these sands.

An excellent, and recent, review of Paris Basin biostratigraphy is to be found in the synthesis published under the direction of Mégnien (1980).

Perhaps it should be noted in passing that the concept of a unified Franco-Anglo-Belgian Basin has been considerably exaggerated. In fact, stratigraphic continuity hardly ever existed except during the Cuisian substage and the Lutetian, when the Atlantic and the North Sea communicated by way of the English Channel. At other times, the facies of the English basins are quite different from those of the Paris Basin and indicate the presence of a deeper and colder sea ; it should be emphasized as well that the English sequence is not as complete as it is on the continent. Furthermore, uplift of the Artois anticline in the middle Lutetian interrupted communications between the Paris and Belgian basins throughout the rest of the Paleogene.

While France is particularly rich in Paleogene fossiliferous deposits, Spain also represents a tremendous potential (as is indicated by the initial explorations of Crusafont-Pairó), and the Oligocene collections from southern Germany have made, and will continue to make, an invaluable contribution. Mammalian assemblages from Belgium and England profitably fill in certain time intervals, less well known from elsewhere, and offer advantageous opportunities for correlation with the marine section. The Paleogene of Turkey has been developed here to an extent that is justified principally by the interest this country will certainly offer in the future. But whatever the paleontologic richness of other regions, referal to the Paleogene stratotypes of England, Belgium and northern France, due to their importance, is inescapable and will remain necessary despite the establishment elsewhere of marine (or continental) reference sequences endowed with richer faunas or more complete sections.

Before proceeding to the details, two basic tools should be introduced : the first is the stratigraphic scale of the Paleogene as it is presently viewed by stratigraphers, and the second is a refined series of levels, or horizons, based principally on rapidly evolving micromammals. While this sequence of levels can be integrated into that of epochs and stages, it retains an independance that permits the evolutionary history of mammals to be followed without the obstacle posed by boundary problems.

THE STRATIGRAPHIC SCALE

A recent effort to stabilize the stratigraphic scale for the Paleogene has been presented by Cavelier and Pomerol (1977). Their proposition is based on :

a/ the choice of strictly marine stratotypes, containing stratigraphically useful fossils ;

b/ the possibility of defining stratotypic limits, as well as those of parastratotypes or hypostratotypes, in continuous series of the Mesogean domaine (in particular, in Spain and Italy) ;

c/ the respect, in as much as it is possible, of tradition consecrated by usage.

The correlation of these stages (fig. 1) with those used in other regions of the world is based on the biozones nannoplankton (NP) and planktonic Foraminifera (P) figured on the chart, and on isotopic ages. However, the following reservations should be kept in mind : specific determination of microorganisms is sometimes uncertain ; most pelagic organisms are affected by ecologic conditions and are found only in a specific climatic domaine ; comparative stratigraphic scales of spores and pollen, dinoflagellates and charophytes, still under study, are not yet included ; isotopic ages should be accepted with prudence.

THE MARKER LEVELS

The marine stages of the Cenozoic epoch have been used by paleomammalogists as a stratigraphic framework in which to place the events observed in the course of mammalian faunal history with more or less happy results. One of the most charac-

AGE in MY	SERIES		STAGES		BIOZONES	
22 - 24 12 MY	OLIGOCENE		LATE OLIGOCENE (CHATTIAN)		P22 / N3 P21 / N2 P20 / N1	NP25 NP24 NP 23
			STAMPIAN		P 19 P 18	NP 22 NP 21
34 - 36 5 MY	EOCENE	Late	PRIABONIAN		P 17 P 16 P 15	NP 20 NP 19 NP 18
39 - 41 3 MY		Middle	BARTONIAN		P 14 P 13 P 12	NP 17 NP 16
42 - 44 5 MY			LUTETIAN		P 11 P 10	NP 15 NP 14
47 - 49 6 MY		Early	YPRESIAN	CUISIAN	P9 P 8 P 7	NP 13 NP 12
				ILERDIAN	P 6 P5	NP 11 NP 10 NP 9
53 - 55 10 MY	PALEOCENE		THANETIAN		P 4 P 3	NP 8 NP 7 NP 6 NP 5 NP 4
63 - 65			DANIAN		P2 P 1	NP3 NP2 NP 1

P = Planktonic Foraminifera
NP = Nannoplankton

Fig. 1. — The stratigraphic scale for the Paleogene. Modified from Cavelier and Pomerol, 1977.

teristic instances of this usage in France is furnished by Richard (1946) in her study of the mammals of the Aquitaine Basin. She attempted to locate the mammal localities of this region within the classic sequence of the Paris Basin. Thus, for example, one locality is qualified as « Lutetian » and another as « Stampian », but since the relationships between continental and marine formations are difficult to determine in the Aquitaine area, these stratigraphic attributions are founded on slender evidence. In the years since then, paleomammalogists began to search for a more practical and more accurate way of presenting their data. Thaler (1966) proposed a chronologic framework reserved for and based entirely on mammals in the form of a scale of biochronologic zones. In the initial project 23 zones subdivided the Tertiary. Each zone was provided with a type locality but neither a top nor a bottom limit was included. Later (1972), the same author refined the original definition of the zones, especially in order to remove the ambiguity that could result from the absence of upper and lower limits.

But in fact, several other workers had advocated, in the interval between his publications, abandoning the notion of zones in favor of that of marker levels (« niveaux-repères » ; Franzen, 1968 ; Hartenberger, 1969). With an aim to clarify, these authors proposed as the unit for the mammalian chronologic scale, points in time, rather than zones (see figs 6 and 15). The use of such units offers the possibility of greater sensitivity in the perception of biologic and geologic events ; the method has in recent years quite adequately proved itself in the studies made by the « Montpellier School ». Jaeger and Hartenberger (1975), expressing the wish that the system become generalized, listed some of its advantages :

« — a marker level is a single moment in faunal history.
— by definition, no problem of limits is posed.
— the marker levels can be multiplied as progress in our knowledge permits without confining this knowledge to a dogmatic system, as in the case of zones ».

The marker level is thus a point ; its definition rests on an association of species actually observed in one locality and on the evolutionary stage of the different lineages of mammals represented at this spot in time and space. On this basis it is thereby possible to avoid a major inconvenience of a « Mammal Age », whose definition (in support of a different concept) is much more vague. A « Mammal Age » combines micro- and macrofaunal elements from a variety of paleo-environments to represent a time interval ; precision is obligatorily less. The marker level method, as it is ideally conceived, avoids associations of species from different localities that tend to confuse differential evolution and phenomena of geographic isolation. In fact, a marker-level is equivalent to a biohorizon whose use is recommended by the International Stratigraphic Guide (Hedberg ed., 1976).

It is evident that each marker level chosen to be introduced in the scale should be a « classic » locality, one that is well studied, recently revised and well documented by a fauna as diverse as possible, including both the micro- and the macrofauna. Also, stratified localities should be chosen in preference to karst deposits. It should finally be emphasized that paleobiogeographic factors should be taken into account in constructing such a scale ; that is, the recognition of coherent biogeographic regions according to their particular geologic and paleobiologic conditions should precede the establishment of scales valid for each of these regions.

The use of such a scale requires that each new fauna be situated with respect to a marker level ; if not equivalent, one is obliged to place it either slightly above, or below, or in any case to explain the degree of imprecision when its relationship is not evident.

If chronological scales of this type were available for each important biogeographic entity, refined inter-regional correlations would be possible and of fundamental value. It is evident that, in the immediate future, a number of serious problems would be raised, but it is better that the questions be clearly stated than that they be masked by a language favoring misinterpretation.

THE PALEOCENE EPOCH

The individuality of Paleocene faunas and floras, in addition to the richness and the wide distribution of deposits (both marine and continental) that are referable to this epoch, have resulted in world wide usage of the term and its concept, but the Paleocene remains the only one of the Tertiary epochs that still needs to be defended.

Typologists argue that there is no concrete basis for its existence for, as Pomerol (1969, 1977), among others, has pointed out, Schimper's (1874) definition of the Paleocene was indeed both inaccurate and contradictory so that, according to the beds that one includes, the upper boundary could be placed at the top of the Thanetian or the top of the Cuisian. The lower boundary was for a long time confused by the uncertain nature of the Danian. Nevertheless, extensive mapable Paleocene beds, representing a duration of time (approximately 10 million years) comparable to other Tertiary epochs do exist. Many of us feel that the term is useful and represents a distinctive segment in geologic history.

Professional isolation by specialists of the various disciplines is a great detriment to comprehension. Thus it is that a paleontologist may say « the Paleocene is widely recognized and accepted as a valid epoch », while a stratigrapher could add that the term should be abandoned « as most of the researchers in the Paris Basin have done » ; or, while there is hardly a student of Paleocene mammals that would question the Thanetian as representing the last part of that epoch ; Curry (1975, p. 222), a specialist of marine invertebrates, remarks « ...the Thanetian is universally regarded, I believe, as Middle Paleocene ». And so the confusion continues.

We shall follow here the proposition of the « Colloque sur l'Eocène » (Mém. B.R.G.M., n° 69, 1969, p. 465) and that adopted by an international study group of the Ilerdian marine stage [Bull. S.G.F. (7), XVII, n° 2, 1975, p. 223], wherein the Paleocene is retained and its limit with the Eocene is drawn between the Thanetian and the Ilerdian (or the Sparnacien in the Paris Basin). The arguments for the placing of this limit are developed by Pomerol (1977, p. 215). In general it is possible to say that, from the practical point of view of a marine invertebrate paleontologist, the Eocene begins with the appearance of true nummulites and true alveolines, as well as with the appearance of associations of benthic foraminifera and mulluscs that differ greatly with respect to those of the Paleocene Thanetian[1].

The lower limit of the Paleocene (or, for that matter, the Tertiary) has been the subject of much controversy for many years. A gradually accruing consensus now admits the Danian as being more Tertiary in character than late Cretaceous. Unfortunately, in Western Europe, there is no known continental counterpart of the marine Danian beds that has yielded mammalian remains, that is, unless the Montian stage is included in it. Deposits attribued to the Montian overlap in faunal content with those referred to the Danian, so that frequently one sees in the literature, Dano-Montian. Just as frequently, the Montian is ignored and the Danian is presented as underlying the Thanetian (as in Berggren and Van Couvering, 1974, p. 13-16).

A pluridisciplinary symposium on the Cretaceous-Tertiary boundary event, held in Copenhagen in 1979, has eliminated definitively any remaining doubt as to the placement of the Mesozoic-Cenozoic limit and firmly established the Tertiary nature of the Danian stage (see Christensen and Birkelund, eds, 1979).

The marine aspect of Paleogene correlation problems should include mention of the extraordinary sequence in the Crimean Peninsula at Bakhchisaray. This section, practically complete for the Paleogene, is continuous from the Maestrichtian to the lower Oligocene (see Veselov, Grigorovitch and Savenko, 1973 ; Kapellos, 1973). Another remarkable marine sedimentary series is found in the El Kef section (El Haria Formation) of Tunisia (Salaj *et al.*, 1974), extending from the Cretaceous into the Eocene. The evidence provided by these marine sediments should aid considerably in reducing the validity of the arguments aimed at ignoring the Paleocene as an epoch.

THE MONTIAN FAUNA

With the discovery (Godfriaux and Thaler, 1972) of a rich mammalian fauna in the type area of Mons at Hainin (Belgium), the Montian (Dewalque, 1968) may acquire full acceptance as at least a substage, especially among mammalian paleontologists. This fauna is particularly important for understanding the evolutionary history of European mammals. Until now, the beginning of the Paleocene here has been devoid of such information, in strong contrast to the situation in North America. The Hainin assemblage will provide a more accurate picture of what was happening in Europe before Cernaysian time and during the period of difficult migration between the North Atlantic continents. Fossil material is being extracted from a vertical shaft that has traversed 15 meters of vertebrate bearing lacustrine sediments ; a total of 30 meters is shown by well-cores to be present. This sequence of Continental Montian is the result of the superposition of two lacustrine cycles ; the sediments are composed of marls, limestones, sands, and clay, underlain by marine Dano-Montian limestones and overlain by the glauconitic sands of the marine Landenian. A detailed examination of the lithology has been made by Godfriaux and Robaszynski (1974). These authors cite the recovery of wood fragments, of charophytes and other seeds and spores, and of gastropods and ostracods ; preliminary identifications are presented.

---

[1] For the point of view of a paleomammalogist, see p. 15.

Description of the vertebrate material has only begun (Vianey-Liaud, 1979), but one can cite among the mammals : several new genera of multituberculates, including the largest and most specialized of the known Ptilodontoidea ; hyopsodont and arctocyonid condylarths, adapisoricids, and perhaps nyctitheriids are also represented.

THE THANETIAN STAGE

Essentially, the Paleocene mammalian faunas of Europe are today represented by the approximately late middle Paleocene material from Walbeck (G.D.R.) and the late Paleocene (Thanetian[2]) Cernaysian localities of France. Since these localities and their contents have been discussed in detail in several recent publications (for example, Russell, 1964, 1975, 1980), they will be treated here in a more summary fashion.

Judging from its unusual composition, the Walbeck assemblage (collected from a fissure in the Muschelkalk limestone) is clearly incomplete : 50-60 % of the specimens represent two species of arctocyonid condylarth and 15-20 % belong to an adapisoricid insectivore. A few primates and even fewer condylarths (non-arctocyonid) constitute the rest. This fauna cannot be taken as representative of an age ; in fact, its age assignment is based purely on the stage of evolution of its members ; no stratigraphic control is possible.

On the other hand, the Cernaysian sediments are well situated stratigraphically and the fauna is among those that are directly correlated with the marine section (the Sables de Bracheux). In its mammalian constituents the Cernaysian assemblage is very like those of a similar age in the North American Rocky Mountain area, although they differ in proportions. Multituberculates are common (2 families, 7 species), insectivores are relatively rare but varied (7 families, 9 species), primates are dominated by 2 species of *Plesiadapis* that constitute a major element (although 3 or 4 other species are present), and condylarths, with 5 families and 24 species, make up the largest part of the fauna. This dominance of condylarths in a relatively balanced fauna is unusual and peculiar to the late Thanetian of Europe ; equally striking is the absence of large animals, like the pantodonts, which commonly occur in North American localities. Along with *Plesiadapis*, the taxon most frequently found is the meniscotheriid condylarth *Pleuraspidotherium*. Its complete absence in North America is surprising, as is the absence of meniscotheriids in Europe during the early Eocene. Apparently this group did little traveling.

The Cernaysian assemblage provides the last glimpse of typical Paleocene life in Europe. With the beginning of the Eocene a change in terrestrial mammalian constituents occurred that is the most dramatic known during the Tertiary : ten of the fourteen Eocene mammalian orders are unrepresented in the Thanetian.

Paleogeographically, we must await an analysis of the Montian fauna for information on the degree of migrational freedom that existed between North America and Europe at approximately middle Paleocene time. Already, the aberrant fissure-filling assemblage of Walbeck has indicated that, at about that time, some faunal exchange

---

[2] Thanetian : Renevier, 1873 ; type locality : Isle of Thanet, England.

had taken place. Rather unexpectedly, the Cernaysian fauna is surprising endemic and contrasts with the largely homogeneous Wasatchian-Sparnacian faunas. It is apparent that the intercontinental displacement of mammals was reduced in the late Paleocene, with respect to an acme to come in the early Eocene. Concerning Asia, Szalay and McKenna (1971) thought that the late Paleocene faunas from Gashato and the Nemegt Valley in Mongolia exhibited nothing that implies an exchange with Europe, but these faunas could well be early Eocene in age, and a few elements do indicate communication with Europe. Although some geologic evidence suggests that the Russian platform was relatively emergent at the time (Dewey *et al.*, 1973), it is necessary to conclude, for the moment, that Europe and Asia were nearly completely isolated.

The climate of Europe during the middle to late Paleocene, as indicated by the floras, was dominantly temperate or warm temperate. On the whole, and excepting an increase in tropicality during the middle of the epoch, the Paleocene was cooler than the succeeding Eocene.

THANETIAN CHARACTERIZING ASSEMBLAGES

The marker horizons discussed at the beginning of the chapter are each designated by the name of a marker locality containing a marker fauna. Ideally, for making comparisons it is preferable to use only the marker as a reference point, but, based on the evolutionary degree attained by the mammals, it is possible to assemble a certain number of localities for each marker level. The term, combined faunal association, is used in this general presentation of the Paleogene of Europe for the list of those mammals encountered in the ensemble of these localities. Even in this form, it can be regarded as a particularly refined characterizing assemblage.

Level of Cernay-lès-Reims.
Referred locality : Berru.
Combined faunal association (as it consistent with the nature of a characterizing assemblage, neither this faunal list nor those that follow are exhaustive) :

Multituberculata : *Neoplagiaulax eocaenus, N. copei, Liotomus marshi.*
Insectivora : *Adapisoriculus minimus, Adapisorex gaudryi, Pagomomus dionysi, Remiculus deutschi.*
Primates : *Plesiadapis tricuspidens, P. remensis, Chiromyoides campanicus, Berruvius lasseroni.*
Condylarthra : *Arctocyon primaevus, Arctocyonides trouessarti, A. arenae, Landenodon lavocati, Dissacus europaeus, Tricuspiodon rutimeyeri, T. magistrae, Louisina mirabilis, Pleuraspidotherium aumonieri, Orthaspidotherium edwardsi.*

THE EARLY EOCENE

THE YPRESIAN STAGE

The Ypresian[3] has been studied in monographic form by Feugueur (1963). His work was intended initially to be a revision of the Cuisian[4] as a stage in the Paris Basin, but intermeshing complications soon led him to consider supposed equivalents in England, in the Bracklesham Beds and the London Clay, and their relations to the Argiles d'Ypres in Belgium. The London Clay contains a mammalian fauna similar to that of French Sparnacian[5] beds and the latter were included at one time in the Belgian Late Landenian[6], along with Belgian sand deposits of Thanetian age. The study thus encompassed not only the Cuisian, but the Sparnacian as well, and necessitated consideration of the Thanetian as a possible lower limit of the Ypresian Stage.

The unity of the Ypresian is uncontested in Belgium, where a continuity exists in the stratigraphic sequence from top to bottom. The lower Argiles d'Ypres becomes progressively arenaceous as one goes up in the section, at the same time as marine fossils of Cuisian affinity appear. As noted earlier, the Argiles d'Ypres are no longer considered as equivalent to the combined Sparnacian and Cuisian stages ; these clays have now been shown to be stratigraphically intermediate between type Sparnacian and type Cuisian sediments. We retain, however, the term Ypresian to include the time and the rocks represented by both substages [a similar case is found in the Thanetian stage : the Thanet sands have been shown to be older than the Sables de Bracheux (Costa *et al.*, 1978), but the latter are still considered Thanetian]. The laguno-continental series in France, typifying the Sparnacian, is sharply separated lithologically from the essentially marine Cuisian. The lower limit of the Sparnacian, of which the Conglomérat de Meudon is the oldest deposit, was proposed by Feugueur as the lower limit of the Ypresian Stage.

The upper limit of Ypresian is clearly indicated in the Paris Basin ; the Lutetian generally begins by a gullying action of the transgressing sea and the sediments of the two stages are quite different. In the north eastern region of the basin the Cuisian terminates with clay beds which become sandy toward the west, finally giving way to the marine sands of the Hérouval horizon.

The fauna of the Ypresian is of exceptional importance ; coming at the end of the Paleocene, the early Eocene mammals mark a truly epoch-making transition between the primitive forms of the first Tertiary mammalian radiation and the installation of the basic corps that gave rise to the fauna of today.

In Europe, the mammals that appear with the opening of the Eocene have been collected from localities that are concentrated in southern England, Belgium, and France. In England, the London Clay has yielded specimens that won early reknown in the last century, but in fact, a relatively small total represents all that exists from this formation. The principal Sparnacian site is Abbey Wood (presently under study);

[3] Dumont, 1849 ; type locality at Ypres, Belgium.

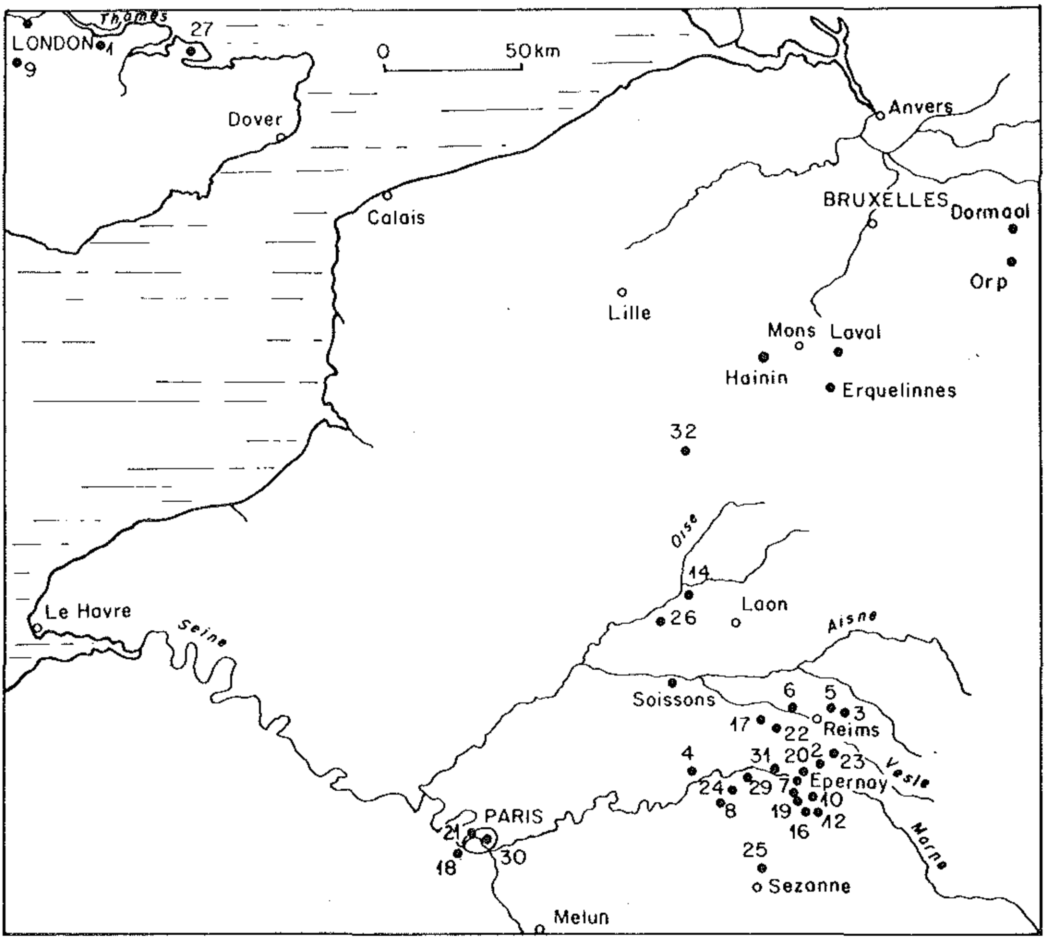
[4] Dollfus, 1877 ; type locality at Cuise-la-Motte, France.

[5] Dollfus, 1877 ; type locality at Epernay (*Sparnacum* in latin), France.

[6] Dumont, 1839 ; type locality at Landen, Belgium.

other localities (also in the area of London) offer the possibility of a least a 3-fold sequence for this stage (Hooker, 1980). In Belgium a few mammalian remains have been found at Erquelinnes (just across the border and in an extension of the same beds at Jeumont, France) and Leval ; from Dormaal a large collection has been amassed by professionals and dedicated amateurs and merits the thorough review that is currently underway. In France more than 50 localities of early Eocene age are known ; most are in the Paris Basin, but Rians and Mas de Gimel occur far to the south. Spain and Turkey are as yet mostly rich in potential, with faunules of isolated occurences constituting the present collections.

In addition to the wealth of vertebrate material that is available, an unusually well documented Ypresian flora has contributed greatly to reconstructions of the environment of the time as well as to speculations concerning the climate. While opinions differ as to the degree of tropicality that existed, there seems to be agreement on a general rise in temperature during the early Eocene.



THE SPARNACIAN SUBSTAGE

As could be expected, the Sparnacian begins with several problems, but first of all, we will reiterate our acceptance of the Sparnacian as representing the first Eocene stage. The validity of the Sparnacian as a stage, or substage, it should be noted however, has been contested since the time it was proposed, and continues to be (Bignot and Moorkens, 1975). Moreover, founded partly on continental and partly on laguno-marine deposits, it has been considered as Thanetian, included in an enlarged Landenian, or thought to be Cuisian ; the Paleocene-Eocene boundary problem has been a central and complicating issue.

In the Paris Basin it is generally true that the Thanetian terminates by a continental formation (arenaceous or calcareous) that is clearly distinct from the Sparnacian wherever fossils, either molluscs or vertebrates, are found. The limit with the Cuisian is rendered more uncertain by the presence of probable reworked molluscs in the continental sands that succeed the laguno-marine shell-marls in some areas.

The Franco-Anglo-Belgian Basin

Vertebrate material from Meudon being quite limited, the earliest significant mammalian assemblage from this region is that of Dormaal in Belgium. An analysis of the fauna, refuting its attribution to the Paleocene, has been given by Russell (1975) and by Godinot *et al.*, (1978). Succeeding localities have yielded typically Eocene faunas that permit a fairly clear concept of mammalian evolution during this time. In the Champagne district, containing the richly fossiliferous regions of Reims and Epernay, the localities of Pourcy, Mutigny, and Avenay are the most important for the Sparnacian. Mutigny was discovered in 1961 and quarried until the bone producing layer was found to be cut off by a slump fault ; the assemblage is varied and several complete mandibles were found. At Avenay, a thick exposure of sandy to lignitic-brackish water coquina contains mammals that can only be recovered by screen-washing ; very few dentitions are known, although the total assemblage is rather rich. A sand quarry near the village of Pourcy has been yielding sparse mammalian remains for nearly a century, but the present total collection numbers only a few hundred isolated teeth. Much discussion has concerned the age of the Pourcy locality, the sediments of which are difficult to locate stratigraphically. At the moment, opinions are divided as to its placement above or below the level of Mutigny.

← Fig. 2. — Thanetian and Ypresian Mammal localities in France, England and Belgium : 1. Abbey Wood; 2. Avenay ; 3. Berru ; 4. Brasles ; 5. Cernay-les-Reims ; 6. Chalons-sur-Vesle ; 7. Chavot ; 8. Condé-en-Brie ; 9. Croydon ; 10. Cuis ; 11. Epernay (Mont Bernon) ; 12. Grauves ; 13. Kyson (situated just outside the map, north of the Thames estuary) ; 14. La Fère ; 15. London ; 16. Mancy ; 17. Marfaux ; 18. Meudon ; 19. Monthelon ; 20. Mutigny ; 21. Passy ; 22. Pourcy ; 23. Rilly ; 24. Saint-Agnan ; 25. Sézanne-Broyes ; 26. Sinceny ; 27. Sheppey ; 28. Soissons ; 29. Try ; 30. Vaugirard ; 31. Venteuil ; 32. Vertain. Approximately middle Paleocene localities : Hainin (Belgium) ; Walbeck is shown on fig. 18.

Precise correlation in the Paris Basin between Sparnacian localities is extremely hazardous ; facies changes are frequent, outcrops few, and it is impossible to trace the beds laterally over an appreciable distance. Slight differences in the mammalian assemblages, particularly among the rodents and primates, furnish clues permitting a sequential arrangement. Of interest for correlating with sediments containing marine invertebrates has been the detection in the Sables de Sinceny and the Argiles de Sarron of an episode that is more clearly marine than is usual in this region.

Turkey

The mammals of the Paleogene of Turkey are very poorly known, both because the fossiliferous deposits offer few exposures and because sufficient time and effort have not yet been expended in collecting vertebrate material. Every discovery of pre-Miocene mammals has been made, so far, in lignite quarries.

Three localities, dated as early Eocene, have yielded remains of a large mammal attributed by Ozansoy (1966, 1969) to the Chalicotheriidae. This taxon, *Palaeoamasia kansui* OZANSOY, is now recognized as an embrithopod (Sen and Heintz, 1979). It was described from a mandible found in the lignites of Eski Çeltek (province of Amasya) in the northwest part of Anatolia. Later, more complete material from Eski Çeltek, a maxillary fragment from the lignites of Fakili (province of Çorum) and a lower jaw fragment from Boyabat (province of Sinop) were recovered. The two latter localities are situated northeast of Ankara and are dated with respect to Eski Çeltek. The formation overlying the Eski Çeltek vertebrate horizon is characterized by *Nummulites uranensis* DE LA HARPE and is considered to be early Lutetian in age. The deduction was made from this that the beds yielding *Palaeoamasia* could be attributed to the lower part of the early Lutetian or to the Ypresian. *Palaeoamasia*, now well known by its upper and lower dentition, is very close to *Crivadiatherium* from Roumania and they are grouped in a new subfamily, Palaeoamasinae Sen and Heintz, 1979.

Ozansoy (1966) has mentioned the occurrence of *Coryphodon* in the province of Sivas, but the precise locality was not given and the material not described.

Until 1979 there were only two regions in Europe, France (and the neighboring parts of England and Belgium) and Turkey, that had produced Sparnacian mammals and, as will be seen in the following section on the Cuisian, the great majority of all early Eocene localities are also concentrated in France. But a recently discovered locality (near Silveirinha) in central Portugal has yielded an unusually rich and diverse mammalian fauna (Antunes and Russell, 1981). Furthermore, its age is apparently earliest Sparnacian, even older that the faunas of Dormaal and Rians ; it is not directly comparable with the small assemblage known from Meudon.

The Sparnacian fauna is characterized by the predominance of forms new, at an ordinal level, to Europe. Artiodactyls, perissodactyls, rodents and chiropterans, heralding the creation of the modern mammalian world, appeared simultaneously with an invasion of orders known earlier in North America or Asia, but previously unrecorded in Europe — tillodonts, pantodonts, carnivores, marsupials and dermopterans. Those forms that persisted from the preceding Cernaysian assemblage represent, for the most part, terminal members of sterile lineages.

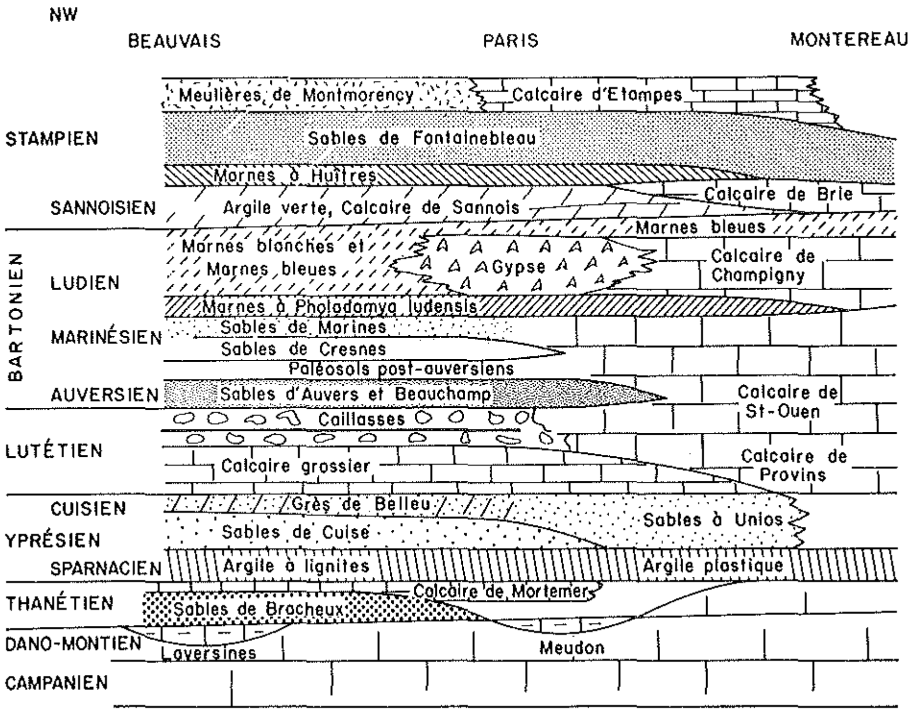


Fig. 3. — Diagram of the Paleogene transgression in the Paris Basin. The purpose of this sketch is to show the lateral variations, with continental tendencies towards the S.E. The right hand part of the sketch is approximate : in particular, the thicknesses are greatly exaggerated with respect to those of the marine formations to the left. The Thanetian transgression did not reach the level of Paris, though the latter was nearly attained by the Cuisan sea. The other transgressions extend beyond, except for that (Marinesian) of the Sables de Cresnes. The greatest extension, and the last, was that of the Sables de Fontainebleau (Stampian). The lacustrine limestone, Calcaire de Beauce (Aquitanian) which overlies the Calcaire d'Etampes (late Stampian), has not been figured. From Pomerol, 1973.

Apart from *Coryphodon*, very few large animals inhabited the Sparnacian Paris Basin, which sedimentary evidence suggests was a flat-lying country, established at the shores of the retreating Thanetian Sea and characterized by an abundance of lagoons, deltas, lakes and rivers. Rodents, on the other hand, were already diversified and numerous, accounting for 25 % of the mammalian remains during recent excavations. Often next in abundance are primates ; the appearance of the tarsioid-like *Teilhardina* and the adapid *Protoadapis* (Gingerich, 1977) is of particular significance to enthusiasts of primate phylogeny. Insectivores are fairly common, dispersed in six families of which adapisoricids are the most numerous. Didelphid marsupials appear (Crochet, 1979, 1980). Condylarths, greatly reduced from their Thanetian heyday, rarely occur, except for a relative abundance of arctocyonids at Dormaal ; the multituberculates follow a similar evolution. The first bats and dermopterans of Europe appear here, the former in rather surprising number and variety, and frequently in beds (deltaic) that indicate no affinity with the usual habitat of bats. Creodonts and carnivores are normally present, with the latter in greater abundance and variety. These two groups show a particularly high degree of identity to those of North America by a quantity of genera that exceeds that of any other order. In contrast to their late dominance, Sparnacian ungulates form but a minor part of the fauna, with only 2 or 3 small to middle-size genera in each of the orders Perissodactyla and Artiodactyla.

THE CUISIAN SUBSTAGE

The stratotype of the Cuisian, being properly marine, offers more possibilities for correlation than the preceding substage. Moreover, the paleontological content of a recent borehole at Cuise-la-Motte, near the quarry containing the type section, has been studied in detail by a pluridisciplinary group (Blondeau *et al.*, 1976). Much of the microfauna is similar to that of the Ypresian stratotype, although palynologically, the dinoflagellates indicate that, in fact the Cuisian (type) and the Ypresian (type) overlap extremely little in time (Châteauneuf and Gruas-Cavagnetto, 1978).

France

Like so many boundaries, the limit between the Sparnacian and the Cuisian also has its problematic aspects and distinction on the basis of mammals is troubled by the fact, as shown by Louis (1970), that the Sparnacian fauna of the Paris Basin remained relatively unchanged up into Cuisian deposits (exemplified by the localities of Condé-en-Brie and Sézanne-Broyes, both discovered in recent years by Louis). But, unlike that of the Sparnacian, the Cuisian fauna benefits from a direct lateral correlation with the marine section : the fluviatile Sables à Unios et Térédines (localities of Grauves, Cuis, Monthelon, Mancy and Chavot, clustered southwest of Epernay), long known for their terrestrial vertebrate content, have recently been shown to grade into marine sands at Venteuil. Also, a small collection of mammals is now known from this site.

Between the Cuisian and the overlying Lutetian deposits a hiatus exists. As a consequence, correlation between different outcrops is hindered by the uncertainty of how much is missing. The mammals from the locality at Venteuil (situated in the Sables de Brasles, according to Plaziat ; pers. comm., 1976) resemble those from Grauves, which strengthens the supposition that the fauna of the Sables à Unios et Térédines is at least of middle Cuisian age, if not later.

Mention must be made of the locality of Mas de Gimel, in the south of France near Montpellier. This site, of recent discovery, has furnished a particularly rich microfauna, which permits the supposition that it dates from late in the Cuisian (Cappetta *et al.*, 1969 ; Hartenberger, 1975).

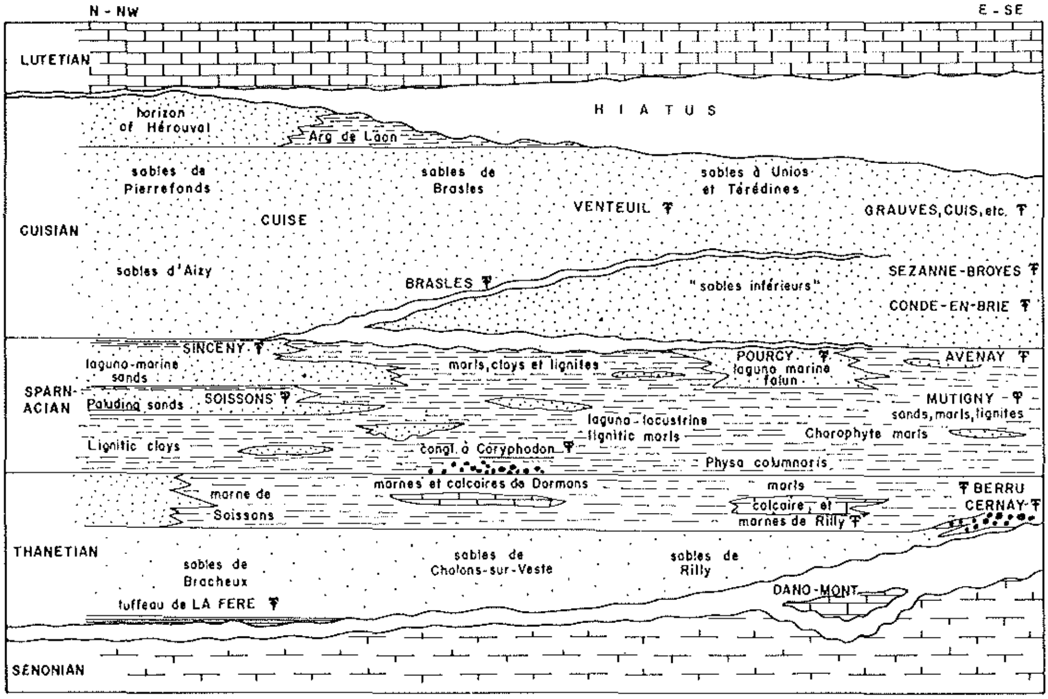


Fig. 4. — Schematic representation of the relationships between successive facies and faunas in the early Paleogene of the Paris Basin. The amount of time represented by the hiatuses is difficult to evaluate ; according to Plaziat, it is better to consider just that they become reduced toward the north, rather than to regard their local thicknesses as depicted above. Modified from Plaziat, 1975.
Note that the exact situation of several of the above localities is still uncertain Grauves, Cuis, etc., are the youngest of the Cuisian localities ; Sézanne-Broyes is the next oldest of the sequence, but its fauna shows closer affinity to that of Condé-en-Brie than to that of the Sables à Unios et Térédines. The «sables inférieurs» de Cuise are older than the type Sables de Cuise (at Cuise-la-Motte). This would place Condé-en-Brie approximately still opposite the Sables d'Aizy, but not in the «sables inférieurs». Avenay is for the moment considered as late Sparnacian, but the decision is not final. The mammalian assemblage of Pourcy indicates an age that is older than that of Mutigny, but the Sables de Pourcy are held to be lateral equivalents to the Sables de Sinceny of late Sparnacian age.

Spain

Our knowledge of the Paleogene mammals of Spain has been greatly increased during the last decade by the efforts of Prof. Crusafont-Pairó and his staff at the Museum of Sabadell. Numerous new localities have been discovered, for the most part in the sub-Pyrenean region (Provinces of Huesca and Lerida). Preliminary studies have demonstrated the particularities of these Spanish faunas with respect to those of France (Crusafont-Pairó, 1961, 1966).

It is with the Cuisian Substage that Spanish assemblages begin to appear in the European history of mammals ; for the present account we will limit our references to those Iberian localities that have already furnished a significant faunal representation.

In the region of the Tremp Basin, marine formations exist that were deposited early in the Tertiary. Studies of their faunal content led to the creation of an Ilerdian Stage[7]. Far from enjoying an immediate acceptance, this stage has been the subject of intense discussion centering around its relationships to other, more classic, stages of the early Tertiary. While the Ilerdian was at first thought to represent the Mesogean equivalent of the Paris Basin Sparnacian, further research has now extended its upper range to include the lower part of the Cuisian. With the London Clay and the Argiles d'Ypres now considered to intervene between the Sparnacian and the Cuisian, the Ilerdian covers a greater time span than was originally supposed. In any case, its importance for mammalian paleontology in Spain is its usefulness as a marker horizon. In the continental sedimentation that succeeded the marine Ilerdian episode in the sub-Pyrenean region have been discovered the oldest mammal localities of Spain ; these are grouped in the Rio Noguera (Province of Lerida) Basin and that of La Cuenca de Isabena (Province of Huesca). While relatively little material has as yet been recovered in these areas, the latter appear to hold great promise.

As demonstrated principally in the Paris Basin, the later Cuisian fauna (that collected from the Sables à Unios et Térédines) does differ from those typifying the Sparnacian, but not to a marked extent.

Although fewer localities are known, the fact that more of its constituants exhibit a larger size is not entirely an artifact of collecting. The large *Lophiodon* replaced *Coryphodon*, and the middle-size *Propachynolophus* became the prevalent perissodactyl, a group that was beginning to diversify. Among the primates *Platychoerops* became rare and *Protoadapis* dominant ; *Palaeochiropteryx* shows the influence of the approaching Lutetian in its resemblance to bats from Messel, and the rodent *Ailuravus* also announces this faunal change. Altogether, however, the Cuisian demonstrated a stabilization of the Sparnacian fauna. Condylarths diminished even more in variety, as did, somewhat surprisingly, the carnivores.

Only by migration it is possible to account for the abrupt appearance of the early Eocene fauna. The time interval between it and the Cernaysian assemblage is inadequate to have included such a degree of evolution and ancestral elements for most of the Eocene groups are lacking in the European Paleocene. The calculation of paleolatitudes, substantiated by paleobotanical evidence, indicates that the climate of northern Europe and North America was propitious for the distribution of terrestrial forms. This factor, coupled with the existence of a continous land mass in the area of the present North Atlantic, permitted an intensive exchange of terrestrial mammals that was never again equaled during the Tertiary. More than half of the Sparnacian genera occur in Wasatchian localities ; in comparison, the Thanetian fauna achieved an identity of only about 1/3 of its members with those of the Tiffanian. Apparently the faunal exchange involved only North America and Europe ; although little is yet known of the early Eocene mammals of Asia, McKenna (1975) has suggested that the Turgai Straits constituted a north-south marine barrier across the Asian continent from Jurassic time to the late Eocene. According to this hypothesis if any communication

---

[7] Hottinger and Schaub, 1960. Type locality : Tremp, Province of Lerida (*Ilerda* in latin), Spain.

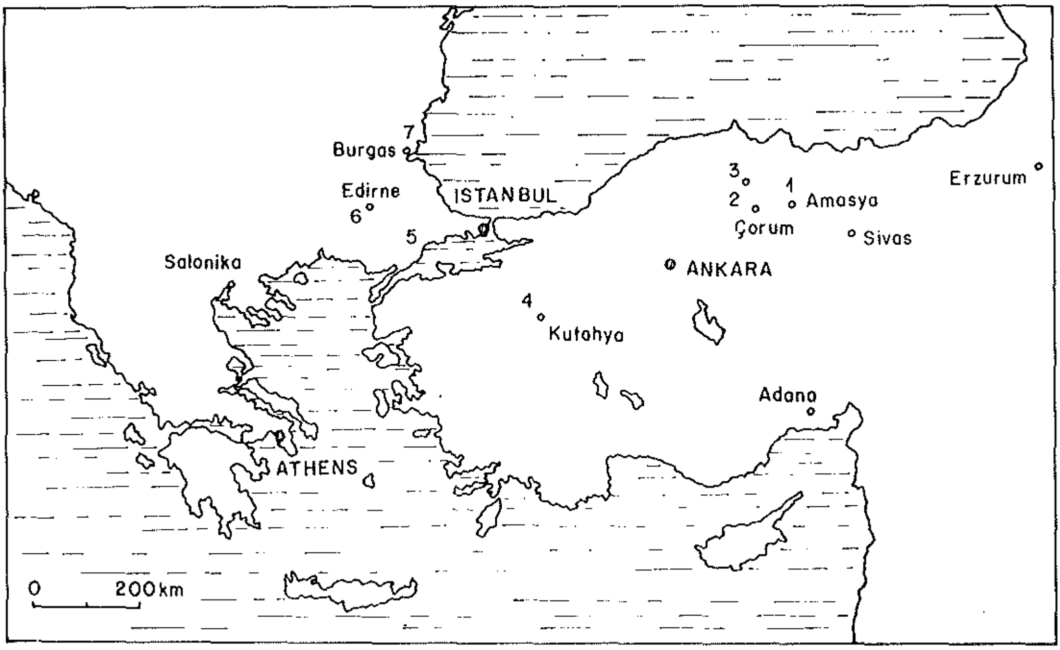


Fig. 5. — Paleogene mammal localities in Turkey, Greece and Bulgaria : 1. Eski Çeltek (Amasya Province) ; 2. Fakili (Çorum Province) ; 3. Boyabat (Sinop Province) ; 4. Tavsanli (Kütahya Province) ; 5. The localities in Turkish Thrace ; 6. Chantras (Greece) ; 7. Tscherno More (Bulgaria).

occurred between Asia and Europe it was by way of northern Canada. Such Cuisian forms as *Propachynolophus* and *Hyrachyus* may have profited by this route. The analysis of the early Sparnacian fauna of Rians by Godinot (1981) suggests that much of the migration across the North Atlantic terrestrial passage occurred in an east to west direction. Final connection of the North Atlantic Ocean with the Arctic Basin involved the separation of Greenland and Norway and was accomplished when Greenland slid by the last European land mass, as represented by Svalbard and the emerged Barents shelf. Estimating the age of the rupture at about 49 million years ago is consistent with the marked dissimilarity that exists between Cuisian and Lutetian mammals.

YPRESIAN CHARACTERIZING ASSEMBLAGES

1. Level of Dormaal.

Referred localities : Meudon, Erquelinnes, Pourcy, Kyson, Rians.

Combined faunal association :

Multituberculata : *Ectypodus* sp.
Marsupialia : *Peratherium constans, Peratherium matronense, Amphiperatherium dormaalense, Amphiperatherium goethei, Peradectes louisi.*

Insectivora : *Entomolestes* cf. *nitens, Dormaalius vandebroeki, Neomatronella luciannae, Palaeosinopa* sp., cf. *Leptacodon* sp., *Didelphodus* sp., *Apatemys sigogneaui, Eochiromys landenensis.*
Chiroptera : *Icaronycteris*? sp., cf. *Archaeonyctery* sp.
Primates : *Teilhardina belgica, Platychoerops daubrei, Platychoerops russelli, Plesiadapis* cf. *tricuspidens, Phenacolemur* sp., *Cantius* sp., *Donrussellia provincialis.*
Tillodontia : *Esthonyx* sp.
Pantodonta : *Coryphodon oweni.*
Rodentia : *Paramys* cf. *woodi, Paramys pourcyensis, Meldimys* sp., *Microparamys nanus, Microparamys* aff. *russelli, Microparamys* aff. *chandoni.*
Creodonta : *Palaeonyctis gigantea, Prototomus* cf. *mordax, Proviverra eisenmanni,* cf. *Prodissopsalis* sp., cf. *Prolimnocyon atavus.*
Carnivora : *Miacis latouri,* cf. *Vulpavus* sp.
Condylarthra : *Phenacodus teilhardi, Paschatherium dolloi, Paschatherium russelli, Hyopsodus itinerans, Microhyus musculus, Dissacus* sp., *Landenodon woutersi.*
Perissodactyla : *Hyracotherium* cf. *leporinum, Hyracotherium cuniculum.*
Artiodactyla : *Protodichobune* sp., *Diacodexis gazini.*

2. Level of Mutigny.

Referred locality : Abbey Wood.
Combined faunal association :

Multituberculata : *Ectypodus* sp., *Parectypodus childei.*
Marsupialia : *Peratherium constans, Peradectes mutigniense, Amphiperatherium maximum.*
Insectivora : *Entomolestes* cf. *nitens, Neomatronella luciannae, Macrocranion* sp., *Palaeosinopa* sp., cf. *Leptacodon, Apatemys mutiniacus, Heterohyus* sp., *Didelphodus* sp.
Chiroptera : *Icaronycteris ? menui, Archaeonycteris brailloni, Ageina tobieni.*
Dermoptera : *Placentidens lotus.*
Primates : *Berruvius* cf. *lasseroni, Phenacolemur fusculus, Cantius savagei, Cantius eppsi, Platycheorops daubrei, Donrussellia gallica.*
Tillodontia : *Esthonyx* sp.
Pantodonta : *Coryphodon eocaenus.*
Rodentia : *Paramys ageiensis, Paramys woodi, Meldimys louisi, Pseudoparamys teilhardi, Microparamys (Pantrogna)* sp., *Microparamys (Sparnacomys)* sp.
Creodonta : *Oxyaena* sp., *Palaeonyctis* ? sp., *Prototomus* or *Proviverra* sp., *Prodissopsalis* sp.
Carnivora : *Miacis* sp., cf. *Viverravus* sp., *Didymictis* sp., cf. *Vulpavus* sp.
Condylarthra : *Hyopsodus wardi, Lessnessina packmani, Phenacodus* cf. *teilhardi, Paschatherium* sp.
Perissodactyla : *Hyracotherium* sp., *Lophiaspis mauretti.*
Artiodactyla : *Protodichobune* sp., cf. *Bunophorus* sp., *Diacodexis* sp.

3. Level of Avenay.

Referred localities : Sinceny, London Clay, Condé-en-Brie, Sézanne-Broyes.
Combined faunal association :

Multituberculata : *Parectypodus* sp., *Ectypodus* sp.
Marsupialia : *Peratherium matronense, Peradectes louisi, Amphiperatherium goethei.*
Insectivora : *Entomolestes* cf. *nitens, Neomatronella luciannae, Macrocranion* sp., *Palaeosinopa* sp., cf. *Leptacodon* sp., *Apatemys* sp., *Heterohyus* sp., *Didelphodus* sp.
Chiroptera : *Icaronycteris ? menui, Archaeonycteris brailloni, Ageina* sp.
Dermoptera : *Placentidens lotus.*
Primates : *Donrussellia gallica, Platychoerops richardsoni, Platycheorops daubrei, Phenacolemur lapparenti, Cantius savagei, Protoadapis louisi.*

Tillodontia : *Esthonyx* sp.
Pantodonta : *Coryphodon eocaenus.*
Rodentia : *Paramys ageiensis, Paramys woodi, Meldimys louisi, Pseudoparamys teilhardi, Microparamys* cf. *russelli, Microparamys chandoni.*
Creodonta : *Oxyaena* sp., *Prodissopsalis* sp., *Prototomus* or *Proviverra* sp., cf. *Tritemnodon.*
Carnivora : *Miacis* sp., cf. *Viverravus* sp., cf. *Uintacyon* sp., cf. *Vulpavus* sp.
Condylarthra : *Phenacodus* sp., *Paschatherium* sp.
Perissodactyla : *Hyracotherium leporinum, Hyracotherium vulpiceps, Lophiaspis* sp., Propachynolophus sp., *Lophiodon tapirotherium.*
Artiodactyla : *Protodichobune* sp., cf. *Bunophorus* sp.

4. Level of Grauves.

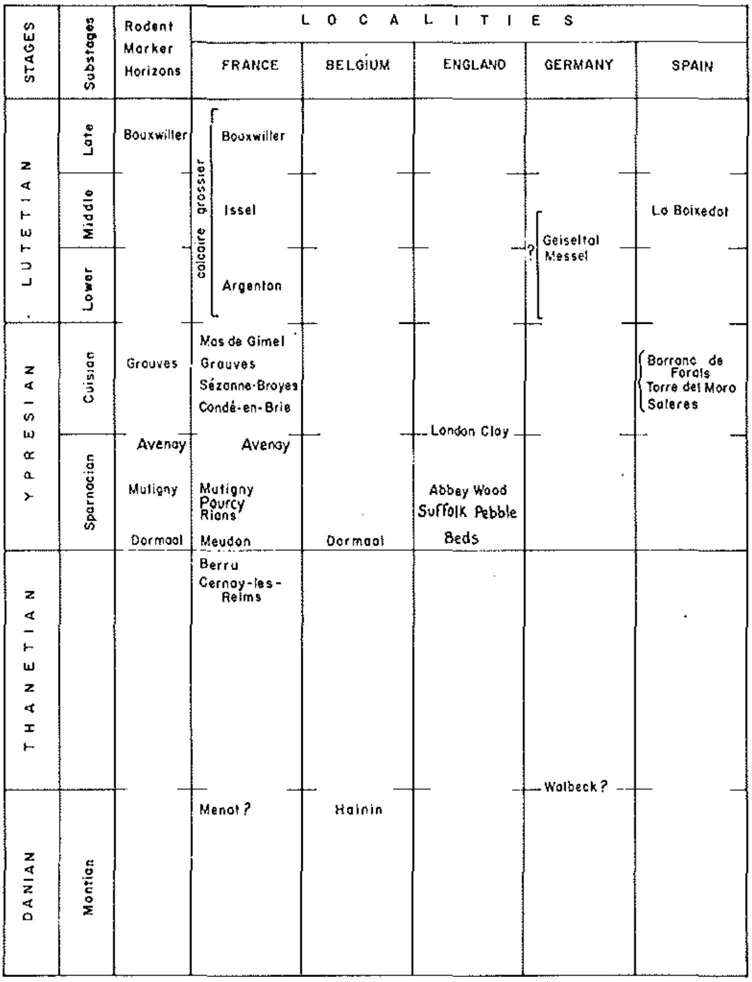
Referred localities : Mancy, Monthelon, Chavot, Cuis, Venteuil, Mas de Gimel.
Combined faunal association :

Marsupialia : *Peratherium monspeliense, Peradectes louisi, Amphiperatherium goethei.*
Insectivora : *Entomolestes* sp., *Macrocranion* sp., *Palaeosinopa* sp., cf. *Leptacodon* sp., *Heterohyus* sp., *Didelphodus* sp., *Saturninia* sp.
Chiroptera : *Archaeonycteris* ? sp., *Palaeochiropteryx* cf. *tupaidon.*
Dermoptera : *Placentidens* ? sp.
Primates : *Teilhardina* sp., *Phenacolemur* sp., *Cantius savagei, Platychoerops daubrei, Protoadapis recticuspidens, Protoadapis* cf. *klatti, Pericodon lemoinei, Anchomomys* aff. *gaillardi.*
Tillodontia : *Esthonyx* sp.
Rodentia : *Paramys savagei, Pseudoparamys* sp., *Microparamys (Patrogna)* cf. *mattaueri, Microparamys* cf. *chandoni, Ailuravus michauxi, Ailuravus remensis, Eogliravus wildi, Protadelomys* ? sp.
Creodonta : *Prototomus* cf. *palaeonictides,* cf. *Prodissopsalis* sp., *Oxyaena menui, Francotherium lindgreni.*
Carnivora : *Miacis* sp., cf. *Vulpavus* sp.
Condylarthra : *Phenacodus* sp., *Paschatherium* sp.
Perissodactyla : *Propachynolophus gaudryi, Propachynolophus maldani,* cf. *Lophiaspis* sp., *Hyrachyus modestus, Hyrachyus minimus, Propalaeotherium* sp., *Lophiodon tapirotherium.*
Artiodactyla : *Protodichobune oweni, «Protodichobune» lydekkeri.*

5. Cuisian of Spain.

Referred localities : Barranc de Forals, Los Saleres (= Ager XIII), La Roca, Las Las Badias, Torre del Moro, Castigalen.
Combined faunal association :

Marsupialia : *Peratherium* sp.
Primates : *Periconodon roselli, Periconodon lemoinei.*
Condylarthra : *Spaniella carezi, Phenacodus villaltae, Dissacus* aff. *blayaci.*
Perissodactyla : *Propachynolophus* sp., *Chasmotherium* sp., *Lophiodon?* sp.



STAGES	Substages	Rodent Marker Horizons	LOCALITIES				
			FRANCE	BELGIUM	ENGLAND	GERMANY	SPAIN
LUTETIAN	Late	Bouxwiller	calcaire grossier Bouxwiller				
	Middle		Issel			? Geiseltal Messel	La Baixedat
	Lower		Argenton				
YPRESIAN	Cuisian	Grauves	Mas de Gimel Grauves Sézanne-Broyes Condé-en-Brie				Barranc de Forals Torre del Moro Saleres
	Sparnacian	Avenay Mutigny Dormaal	Avenay Mutigny Pourcy Rians Meudon	Dormaal	London Clay Abbey Wood Suffolk Pebble Beds		
THANETIAN			Berru Cernay-les-Reims			Walbeck ?	
DANIAN	Montian		Menat ?	Hainin			

Fig. 6. — Stratigraphic distribution of principal mammal localities in the early Paleogene of Western Europe.

THE MIDDLE EOCENE

THE LUTETIAN STAGE

The middle Eocene, until recently, has been restricted to the Lutetian Stage which, somehow, escaped substage division more complex than lower, middle and upper. Moreover, the Lutetian represents the rare stage concept that has suffered little evolution in meaning since its creation[8]. Its definition is easy and exceptionnaly clear ; essentially, it is the stage of the Calcaire grossier. However, facies variations within this formation render a detailed stratigraphic analysis rather difficult and, furthermore, mammalian fossils from this stage are conspicuously lacking[9].

As was noted above, the lower limit of the Lutetian in the Paris Basin is formed by sediments of a sea that transgressed from north to south over an eroded land surface ; a continuous section from Cuisian to Lutetian deposits is not present. For the upper limit a similar problem occurs in that the terminal part of the formation is regressive and presents marked continental characteristics, rendering difficult correlation with marine deposits in neighboring basins.

Considerably altering the classic concept of European middle Eocene, Hardenbol and Berggren (1978) have proposed that the traditional late Eocene Bartonian Stage be included in the middle Eocene ; this opinion is based on the presence, in its type locality, of planktonic microfossils generally regarded as indicative of a middle Eocene age. The problem was presented by Cavelier and Pomerol (1976), who indicated that a choice was possible.

France

In France there is really only one major Lutetian site, Bouxwiller in Alsace. This locality, situated in lacustrine sediments, was especially investigated by the personnel of the Natural History Museum of Basel (Switzerland), between 1900 and 1940, who succeeded in constituting a remarkable collection. Two levels appear to be present in the principal quarry, but differing only slightly in age. The chronologic situation of Bouxwiller was determined on the basis of palaeotheres which could be correlated with the upper part of the Calcaire grossier.

Several very minor localities in the Paris Basin (Dampleux, Aizy-Jouy, Jaulgonne, for example) partly compensate for their poverty by their occurrence in the marine Calcaire grossier. *Lophiodon, Palaeotherium* and a few rodent teeth are known, and the search for more material continues.

Argenton, in central France, has furnished a meager assemblage representing the macrofauna. Its age could be early Lutetian, as indicated by the lophiodons, or late Lutetian as proposed by Blondeau *et al.* (*in* Mégnien, 1980). The locality of Issel, in the south of France is also correlated by lophiodons ; the fossiliferous level being in an indurated conglomerate, the microfauna is also unknown.

---

[8] de Lapparent, 1883 ; type locality : Paris (*Lutetia*, in latin).

[9] A mammalian fauna from a horizon within the Calcaire grossier, located in a suburb west of Paris, La Défense, has recently been described by Ginsburg *et al.*, 1977.

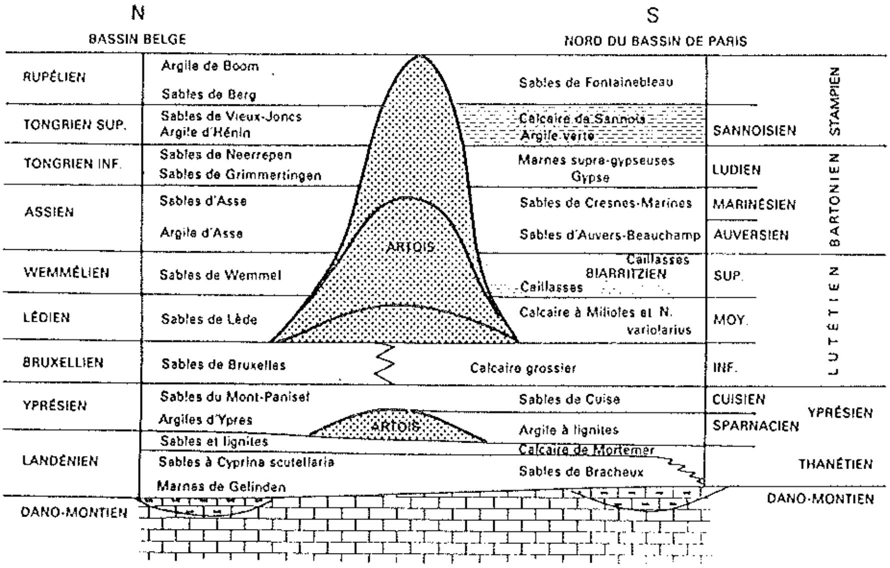


Fig. 7. — Schematic disposition of the Paleogene formations on either side of the Artois anticline. Note that nearly all of the series is marine in Belgium (and the briel lagunal or continental episodes have been omitted), whereas thick lagunal or continental formations exist even in the north of the Paris Basin. Note also the role of a barrier played by the Artois anticline during the early Ypresian and again afterwards, from the middle Lutetian on. The dominantly marine formations are in grey : dashed lines indicate dominantly lagunal formations ; in white are the dominantly continental formations. From Pomerol, 1973.

England

A few mammals have been collected from the Bracklesham Beds of Lutetian age (at Bracklesham and Lee-on-Solent) that offer a rather tenuous means of correlation.

Germany

All of Europe, in fact, is poor in middle Eocene localities ; Messel, located near Darmstadt (in West Germany), and Geiseltal near Halle (G.D.R.) are of reknown, although more for the state of preservation encountered than for the variety of the included mammals. Other German sites have furnished a few specimens but, with the exception of Heidenheim am Hahnenkann, they are not mentioned on Fig. 20. The age of the fossil bearing bituminous freshwater pelites («oil shales») of Messel was discussed at length by Tobien (1968) ; evidence from the rodents and equids indicate the fauna to be of early Lutetian age. In the same publication Tobien showed that there was reason to believe that Messel could be stratigraphically situated between the two principal coal layers of Geiseltal. Hartenberger (1973) ranged both localities between the levels of Grauves and Bouxwiller and referred them to the middle Lutetian, but his present opinion is that they should be rather loosely assigned to the early half of the Lutetian[10]. The continuing excavations at Messel will hopefully produce a more diversified fauna for further precision in its correlation. One of the most exciting new finds was reported by Storch (1981) who described a myrmecophagid (Xenarthra), the only record of this group outside of South America. Reports of new artiodactyls by Tobien (1980) and Franzen (1981) have focused attention on the site as well as description of a Pholidota (Storch, 1978). Comparative studies between *Messelobunodon* species found in Messel and Geiseltal confirmed the hypothesis that Geiseltal is younger than Messel (Franzen and Krumbiegel, 1980).

Spain

Most of the localities of this age (Montllobar and La Boixedat, for example) seem to be slightly older than that of Bouxwiller and rather comparable in their faunal composition to the locality of Argenton. A distinctive element, however, resides in the presence of the condylarths *Dissacus, Phenacodus* and *Almogaver*, which, at this time, have disappeared from the mammalian assemblage of France. Differences of this sort have led Crusafont-Pairó to envisage a certain degree of endemism in the Spanish fauna with respect to the rest of Europe, beginning in the Lutetian and based on the functioning of the Pyrenees as a geographic barrier. This factor is helpful in explaining the difficulties often met with in attempting to establish rigorous parallels between Spanish and French localities.

Portugal

Mammalian remains have been found north of Nazaré (Ginsburg and Zbyszewski, 1965), but few taxa have been identified.

Whereas the Cuisian fauna was constituted in large part by a continuation of Sparnacian forms, the same is not true with respect to the succeeding Lutetian ; endemic diversification, coupled with the probable introduction of at least a certain number of foreign genera, produced a fauna of a quite different aspect. By Lutetian time multituberculates seem to have nearly disappeared from Europe. Insectivores continue to occupy a place of modest importance, but primates expand slightly in diversity, with adapids and microchoerine tarsioids dominating. Bats are known by many specimens from Messel and others from Geiseltal, but only 2 of the 4 Cuisian genera are present ; dermopterans may be presumed to be absent from Europe. Among the condylarths, *Phenacodus* persists and the group is amplified by 3 genera of paroxyclaenids. Creodonts and carnivores diminish in diversity while rodents increase. Theridomyids appear timidly (at Bouxwiller a single species is present : *Protadelomys alsaticus*), but by rapid diversification they will dominate all other groups during the late Eocene and Oligocene. Another family, the Gliridae, has been recognized in the middle Eocene, and seems to be derived directly from autochthonous genera (such as *Microparamys*). In fact, an autochthonous origin can be envisaged for all the new forms, even if definitive proof for some is still lacking.

---

[10] Krumbiegel (Geiseltalmuseum, Halle ; pers. comm., 1975) confirms the opinion that there is no justification for considering the lower Geiseltal fauna as being of Cuisian age as it was for many years ; it too would be Lutetian.

Pholidota and Xenarthra have been recently reported from the Messel locality. The former are known from old collections made in the Quercy, but the myrmecophagids were, until now, restricted to South America.

The most spectacular phenomenon of this age is the explosion of perissodactyls and artiodactyls ; from 2 Cuisian genera of the latter, its ranks are suddenly increased to 11. Out of 9 genera of perissodactyls, 4 represent Cuisian forms that continue into the Lutetian, but 5 are new. For the artiodactyls, the appearance of *Cebochoerus, Dichobune, Hyperdichobune, Catodontherium, Dacrytherium* and *Tapirulus* heralds the extraordinary flowering of the group in the succeeding late Eocene. The most noteworthy of the new perissodactyls are *Palaeotherium* and *Paraplagiolophus*, which also undergo a wide diversification in the last part of the Eocene.

Despite the suggestion by McKenna (1975) that Europe was isolated from both Asia and North America from the beginning of the Lutetian until the beginning of the Oligocene, it seems difficult to account for the tremendous increase in the ungulate population other than by immigration. If indeed there was isolation of Europe at this time, it appears doubful that this was total, or, if such was really the case, an alternative explanation may be that a wave of immigrants arrived immediately before the rupture. But the rupture at this moment was between North America and Europe, and there appears to be little reason to doubt its definitiveness. The new taxa shows little affinity to North America forms (cf. the Bridger faunal list ; Gazin, 1976) and if they filtered through from Asia before the North Atlantic separation, it is unlikely that so many arrived in Europe without leaving a notable trace of their Canadian passage. An African origin for these forms is equally unlikely, due to basic differences in the faunal constituents of the continent, in so far as they are known. The newcomers, then, would seem to indicate that exchange between Asia and Europe was not entirely interrupted by the Turgai marine barrier during Eocene times. In fact, it is probable that the Turgai straits functioned only intermittantly. Of uncertain relation to these speculative migrations, although surely important, is the fact that climatically the peak of Eocene temperature occurred during the Lutetian.

LUTETIAN CHARACTERIZING ASSEMBLAGES

1. Combined faunal associations of Messel and Geiseltal :

Marsupialia : *Amphiperatherium giselense.*
Insectivora : *Macrocranion tupaiodon, Macrocranion tenerum, Leptictidium auderiense, Heterohyus heufelderi, Buxolestes piscator.*
Chiroptera : *Palaeochiropteryx tupaiodon, Palaeochiropteryx spiegeli, Archaeonycteris trigonodon, Archaeonycteris revilliodi, Cecilionycteris prisca, Matthesia germanicus, Matthesia ? insolita.*
Primates : *Protoadapis klatti, Protadapis weigelti, Nannopithex raabi, Amphilemur eocaenicus.*
Rodentia : *Paramys* sp., *Ailuravus picteti, Ailuravus macrurus, Masillamys beegeri, Masillamys krugi, Microparamys parvus, Plesiarctomys* sp.
Creodonta : *Prodissopsalis eocaenicus, Prodissopsalis voigti, Allopterodon theriodes, Proviverra gracilis, Oxyaenoides bicuspidens, Geiselotherium robustum.*
Carnivora : *Quercygale* (= *Tapocyon*?) *macintyri, Paroodectes feisti.*

Condylarthra : *Kopidodon macrognathus, Pugiodens mirus.*
Perissodactyla : *Propalaeotherium isselanum, Propalaeotherium messelense, Lophiodon tapirotherium, Lophiodon cuvieri, Paralophiodon buchsowillanum.*
Artiodactyla : *Haplobunodon* cf. *mulleri, Anthracobunodon weigelti, Rhagatherium* cf. *kowalevskyi, Messelobunodon ceciliensis, Massilabune martini.*
Xenarthra : *Eurotamandua joresi.*
Pholidota : *Eomanis waldi.*

2. *The Lutetian of Spain.*

Referred localities : Sierra de Montllobar, La Boixedat, San Miguel, Mas de Faro, Pont de Montanana, Corsa II, Can Camperol, Zamora.

Combined faunal associations :

Rodentia : *Plesiarctomys* sp.
Condylarthra : *Almogaver condali, Phenacodus* aff. *teilhardi.*
Perissodactyla : *Pachynolophus boixedatensis, Achilophus depereti,* ? *Anchilophus simpsoni, Hyrachyus minimus, Lophiaspis occitanicus, Lophiodon leptorhynchum.*
Artiodactyla : *Haplobunodon solodurense, Dacrytherium* sp.

3. *Level of Bouxwiller*

Referred localities : Aumelas, Calcaire grossier sites.

Combined faunal associations :

Marsupialia : *Peratherium* sp. *Amphiperatherium goethei, Amphiperatherium bastergense.*
Insectivora : *Saturninia* sp., *Buxolestes hammeli, Heterohyus armatus, Heterohyus gracilis.*
Chiroptera : *Palaeochiropteryx* sp.
Primates : *Nannopithex filholi, Periconodon huerzeleri, Amphilemur leemanni, Phenacolemur* sp.
Rodentia : cf. *Paramys* sp., *Ailuravus picteti, Plesiarctomys hartenbergeri, Eogliravus hammeli, Protadelomys alsaticus.*
Creodonta : *Proviverra typica, Alienetherium buxwilleri, Praecopsalis acutus, Allopterodon* cf. *therioides.*
Carnivora : *Quercygale helvetica.*
Perissodactyla : *Pachynolophus duvali, Propalaeotherium* cf. *parvulum, Propalaeotherium* cf. *argentonicum, Anchilophus* cf. *depereti, Lophiotherium pygmaeum, Plagiolophus cartieri, Paraplagiolophus codiciensis, Palaeotherium eocaenum, Lophiodon medium, Lophiodon medium, Lophiodon parisiensis, Lophiodon cuvieri, Lophiodon tapirotherium, Lophiodon tapiroides, Paralophiodon leptorhynchus, Paralophiodon buchsowillanum*[11], *Chasmotherium cartieri, Hyrachyus minimus.*
Artiodactyla : *Dichobune robertiana, Buxobune daubreei, Hyperdichobune hammeli, Meniscodon europaeum, Aumelasia gabineaudi, Catodontherium* cf. *fallax, Catodontherium* sp., *Catodontherium* cf. *argentonicum, Tapirulus* cf. *majori, Cebochoerus dawsoni, Cebochoerus jaegeri, Cebochoerus suillus, Cebochoerus ruetimeyeri, Mixtotherium* cf. *prisca, Dacrytherium* cf. *elegans, Leptotheridium* cf. *traguloides.*

---

[11] There is a problem of synonymy between the genera *Paralophiodon* DEDIEU, 1977 and *Rhinocerolophiodon* FISCHER, 1977.

THE MIDDLE OR LATE EOCENE

THE BARTONIAN STAGE *S. l.*

The late Eocene presents a formidable complex of difficulties. Until recently the classic subdivision of the Eocene into three units, early, middle and late, corresponded to the three most widely used stages : Ypresian, Lutetian and Bartonian *sensu lato*[12]. The Mesogean equivalent of the latter was considered to be the Priabonian[13] ; but recent work in marine stratigraphy (Cavelier and Pomerol, 1977) has shown that in fact the Priabonian can be situated between the Bartonian *sensu stricto* (the early part of the late Eocene) and the Stampian *sensu stricto* (the early part of the Oligocene). Thus, as pointed out by Cavelier and Pomerol (1976), the limit between the middle and the late Eocene could be placed either at the base of the Bartonian, as was usual in northern Europe, or at the base of the Priabonian, as had been done in the Mesogean region. But, as noted above, this choice has been eliminated by Hardenbol and Berggren (1978) who showed that there is reason to include the Bartonian in the middle Eocene.

For several generations of geologists, the Bartonian (in a sense that included the present Priabonian) was divided into three substages : Auversian, Marinesian and Ludian[14]. Much confusion was involved in the latter : while the authors of the term intended to designate only the *Pholadomya ludensis* marls (Marnes à *Pholadomya ludensis*) and the gypsum beds above and below these marls, many later workers extended the definition of the Ludian to include the Gypse de Montmartre. This diversity of opinion contributed little towards clarifying the problem of the Eocene-Oligocene limit, since an equivalence had been demonstrated between the Gypse de Montmartre and the Lattorfian beds[15]. But this Lattorfian stage was for a long time (and still is for many workers) considered in northern Europe as the base of the Oligocene. The Eocene-Oligocene limit thus passed through the middle of the Paris Basin Ludian, a concept to which a number of workers objected. Denizot (1957) noted the successive incoherencies contained in the definition of stages, or substages, created to describe the formations of the late Eocene. Moreover many authors worked independently and at times with an inadequate knowledge of the faunal contents of the beds in question, which aggravated the situation. The recent synthesis of Cavelier (1979) on the subject of the Eocene-Oligocene limit has shed considerable light on the problem and, among other things, has demonstrated the equivalence that exists between the Ludian, the Priabonian and the Lattorfian. The limit would therefore pass between the top of these stages and the bottom of the Stampian.

It should be stated that there is not yet complete assurance that the summit of the Priabonian and the base of the Stampian coincide exactly ; a hiatus may intervene.

---

[12] Mayer-Eymar, 1857 ; type locality at Barton, England.

[13] Munier-Chalmas and de Lapparent, 1893 ; type locality at Priabona, Italy.

[14] Auversian, Dollfus, 1877 ; type locality at Auvers-sur-Oise, France ; Marinesain, Dollfus, 1905 ; type locality at Marines, France ; Ludian, Munier Chalmas and de Lapparent, 1893 ; type locality at Ludes, France.

[15] Mayer-Eymar, 1893 ; type locality at Latdorf, Germany.

For paleomammalogists the solution often adopted before the publications of Cavelier and Pomerol, was to follow the « Lexique stratigraphique international » (Denizot, 1957) ; the summit of the Eocene was considered to be above the level of Euzet (see Fig. 15). Since then, the proposition of Cavelier and Pomerol has been gradually gaining acceptance ; it must be admitted that it has the merit (and the satisfaction) of superimposing the Eocene-Oligocene limit and the « Grande Coupure » of Stehlin (1909). The latter is a major phenomenon in the history of Paleogene mammals of Europe and corresponds to the striking interruption in faunal continuity that

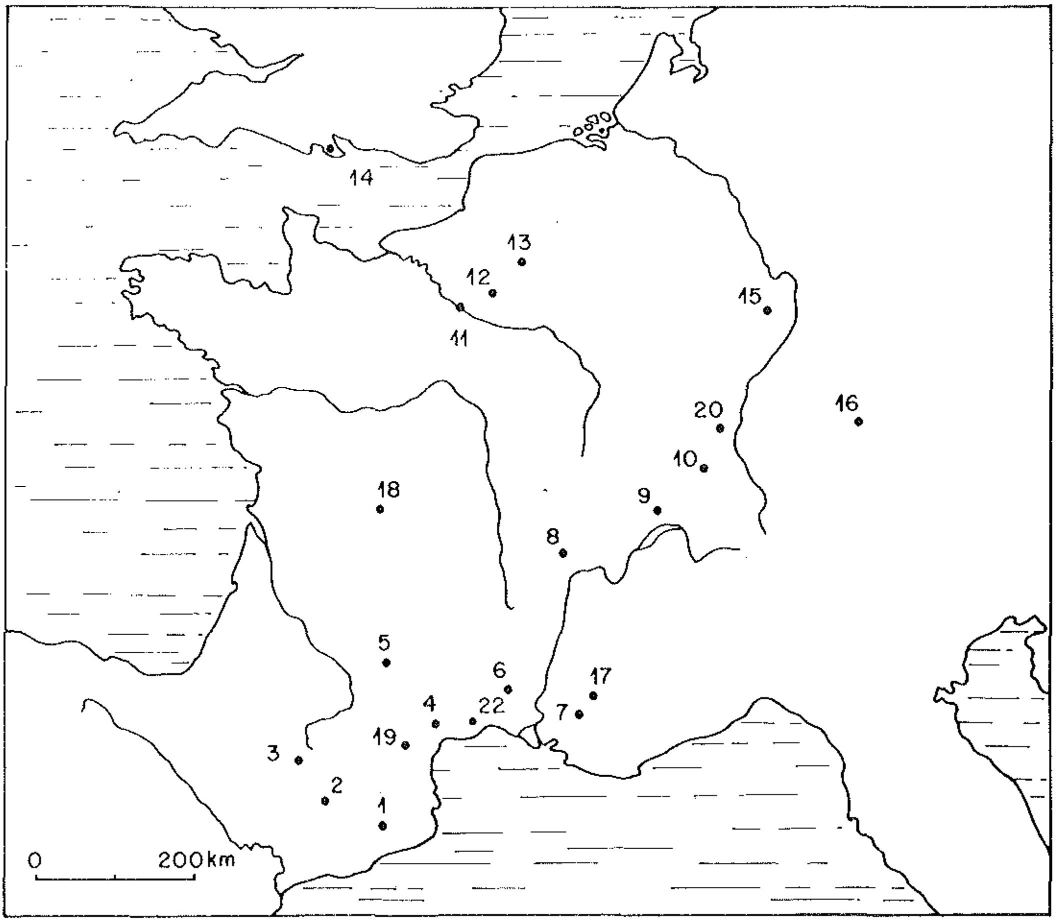


Fig. 8. — Geographic distribution of Bartonian and Priabonian mammal localities of Western Europe : 1. San Cugat ; 2. Laguarrès, Cappella ; 3. Sosis ; 4. La Livinière ; 5. (Quercy) Escamps, Rosières, Coanac, Sainte-Néboule ; Célarié, Gousnat, Perrière, Malpérié ; La Bouffie, Les Pradigues, Le Bretou ; 6. Fons, Robiac, Euzet, Lascours ; 7. La Débruge, Mormoiron ; 8. Lissieu ; 9. Mormont ; 10. Egerkingen ; 11. Montmartre, Pantin ; 12. Le Guépelle ; 13. Grisolles ; 14. Headon Hill, Hordle ; 15. Neustadt, Nordshausen ; 16. Ehrenstein 1 A ; Möhren, Frohnstetten. Other Eocene localities of France ; 17. Rians (Sparnacian) ; 18. Argenton (early Lutetian) ; 19. Issel (middle Lutetian) ; 20. Bouxwiller (Late Lutetian) ; 21. Creechbarrow. 22. Mas de Gimel (Cuisian).

occurred when paleogeographic conditions permitted Asian mammals to extend into Europe ; the event has been documented with increasing precision in such works as those of Thaler, 1966 ; Hartenberger, 1973 ; Lopez and Thaler, 1974 ; Sigé, 1975 a, 1975 b, 1976 ; Brunet, 1979 ; Vianey-Liaud, 1976, 1979 ; Lange-Badré, 1980.

Recent studies (Sigé *et al.*, 1977 ; Sudre, 1978 ; Heissig, 1979 ; Sigé and Vianey-Liaud, 1979) indicate that more endemic evolution nevertheless took place in Europe preceeding the «Grande Coupure» than has here tofore been suspected. The hypothesis of Heissig holds that immigration from Asia through southeastern Europe was possible during the middle Eocene, but the route was then broken in several places with the result that a number of isolated centers of evolution developed. A marine regression next permitted some forms to enter western Europe from these southern centers. In the Priabonian, new land connections through the Balkans to southern Asia and Anatolia (as well as to North Africa) were developed. With the «Grande Coupure» unrestricted movement across the site of the former Turgai Strait was possible but of little importance for western Europe since the latter was isolated by a branch of the sea extending from the north across Poland to the region of the Black Sea. However, considerable exchange took place between the Balkans and France through an alpine bridge. It is only with the middle Oligocene that northern Asian forms began to cross the Polish lowlands and to penetrate into western Europe, although the marine Rhine graben still presented a barrier.

Bartonian (*s.l*) mammal localities are numerous and most of them are situated in the south of France ; moreover, many karst localities can be added to those occurring in stratified sediments, such as the celebrated fissure filling assemblages of Egerkingen and Mormont, in Switzerland (Fig. 8) and, especially, the localities in Quercy : the oldest of the Quercy sites dates from the late Eocene and others in the region furnish a continuity that extends to the late Oligocene (de Bonis *et al.*, 1978 ; Crochet *et al.*, 1981).

→

Fig. 9. — Proposed stratigraphic correlations between the Paleogene basins of London, Hampshire, Belgium and Paris. Of particular interest to the paleomammalogist are those mammal localities that are situated in marine beds or in littoral deposits that can be directly correlated with them. Modified from Curry, Gulinck and Pomerol, 1969.

		PARIS BASIN	Mammal localities in Marine Beds	BELGIUM W	BELGIUM E	ENGLAND HAMPSHIRE BASIN	ENGLAND LONDON BASIN
STAMPIAN Oligocene		Calcaires d'Etampes Sables de Fontainebleau Falun de Jeurre Marnes à Huîtres Calcaire de Sannois Argile verte	La Ferté-Alais Etampes	Sables de Voort Argile de Boom S. de Berg / Arg. à *Nucula comta* Complexe Argilo-sableux de Kallo	S. de Kerkom / S. de Vieux Joncs S. de Boutersem \ Arg. de Henis Niv. d'Hoogbutsel	Hamstead Beds	
Eocene PRIABONIAN	LUDIAN	Marnes blanches Marnes bleues Gypse Marnes à *Pholadomya lud.*	Montmortre		Sables de Neerrepen Sables de Grimmertingen	Bembridge Beds Osborne Beds Headon Beds	
BARTONIAN	MAR.	S. de Marines S. de Cresnes	Grisolles Lotilly	Sables d'Asse Argile d'Asse		Barton Beds	
	AUV.	S. d'Auvers-Beauchamp	Arcis-le-Ponsart Le Guépelle	Sables de Wemmel		Upper Brack. Beds	
LUTETIAN	UPPER	Calc. grossier sup. (caillasses)	Jaulgonne Dampleux Jumencourt Damery	S. de Lède ▨		Brack. B IX à XV	
	MIDDLE	Calc. grossier à *Orb. compl.*	La Défense Aizy-Jouy	Sables de Bruxelles		Bracklesham B. VI à VIII	
	LOW.	Calc. grossier à *Num. laev.*					
YPRESIAN	CUISIAN	S. d'Hérouval S. de Pierrefonds S. d'Aizy		S. d'Aalter S. de Vlierzele et du Mont Panisel S. de Mons en Pévèle		Lower Brack. Beds I à V	Bagshot Beds Bagshot Beds London Clay
Eocene	SPARNACIAN or ILERDIAN	Arg. à *Ostrea* Sables de Sinceny Arg. à Lignites Arg. plastique Cong. de Meudon	Sinceny	Argile d'Ypres ou des Flandres Couches de Dormaal et d'Erquelinnes		Abbey Wood	Blackheath B. Woolwich et Reading B.
Paleocene THANETIAN		Cong. de Cernay Sables de Bracheux Tuffeau de la Fère ▨	Cernay-les-Reims	Sables à *Cyprina scutellaria* Tuff. de Lincent (*Phol. oblitterata*) Marnes de Gelinden à *Cypr. morrisi* sables d'Orp ▨			Thanet Beds ▨
DANIAN		Marnes de Meudon Calcaire de Vigny		Calc. de Mons Tuffeau de Ciply			

THE AUVERSIAN SUBSTAGE

France

This period is nearly as poor in mammal localities as was the Lutetian. But happily the karst fillings of Egerkingen (Switzerland), studied essentially by Stehlin at the beginning of this century, has yielded a rich assemblage providing a fairly exact image of the Auversian fauna. Nearly 50 genera are known, of which most are perissodactyls and artiodactyls. Although the collections were made from different fissures, analysis of the assemblages shows that there was apparently not much difference in age between them. The correlation that is possible between Egerkingen and Le Guépelle, a locality considerably less rich but situated in a marine section of the Auversian (Ginsburg *et al.*, 1965), demonstrates the attribution of the former to this substage. The assemblage from Arcis-le-Ponsart (Paris Basin), greatly enlarged by the excavations of Louis, has recently been described by the latter (Louis, 1976). In the south of France, a few localities containing *Lophiodon* can also be referred to the Auversian. Finally, Lissieu (near Lyon), another karst filling, has furnished an interesting assemblage for this period (Hartenberger, 1969 ; Sudre, 1972).

England

An important new locality of this age has been briefly described by Hooker (1977) from the Creechbarrow freshwater limestone at Creechbarrow Hill in Dorset. The large collection being studied by Hooker represents about 35 species and has been amassed since 1975. A small assemblage of mammals is known from the Barton Clays at Hengistbury Head and at Barton Cliff (fig. 11).

The Auversian fauna represents a direct derivation from the Lutetian and in it a great diversification of ceratomorphs took place ; the artiodactyls, extremely varied at Egerkingen, show even greater development in this respect and to a somewhat lesser degree the phenomenon is repeated by the primates, represented by several lineages. Among the rodents, information is still incomplete, but the theridomyids are already present in the form of several genera, ancestors of lineages destined to diversify later (*Paradelomys, Sciuroides* and *Elfomys*).

Spain

Two localities, Laguarrès and Cappella (fig. 8), are referable to the lower part of the Bartonian. Other than *Lophiodon* specimens, they have yielded two primate genera of particular interest : *Arisella* and *Pseudoloris*. Rodents are rather diversified and ressemble closely those known at La Livinière II (Hartenberger *et al.*, 1968). Recently, a new locality with rodents and charophytes of the same age as La Livinière and Laguarrès was found in the Ebre Basin. A marine horizon with nannoplankton of the NP 17 sone is situated at the top of the sequence (Anadon *et al.*, 1982).

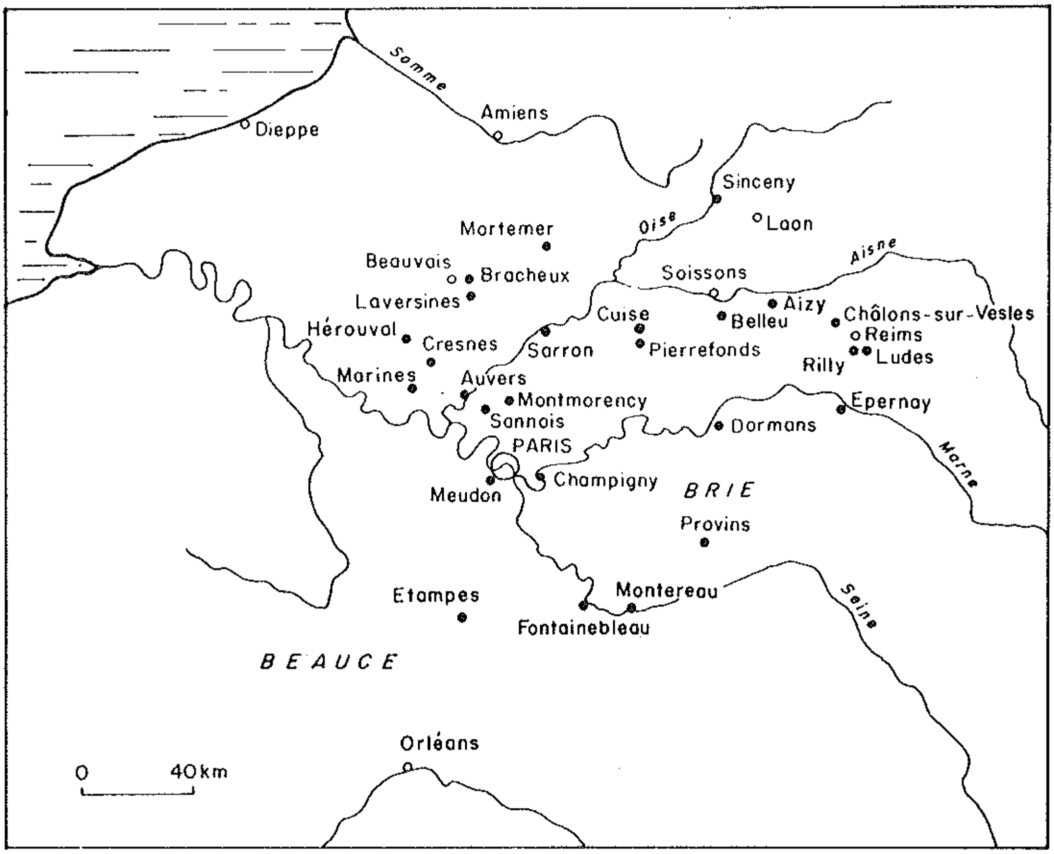


Fig. 10. — Paris Basin type localities of principal Paleogene formations.

THE MARINESIAN SUBSTAGE

France

Most of the localities are situated in the south of France ; Robiac and Le Castrais, for example, are among those found in stratified sediments, and within the Castrais the most important site is that of Lautrec (with *Lophiodon lautricense*). The oldest of the Quercy karst sites is referable to this period, Le Bretou (Hartenberger *et al.*, 1974), as well as certain karst localities of Switzerland (Mormont — Eclépens). The recent discovery of the stratified locality of Grisolles in the Calcaire de Saint-Ouen of the Paris Basin (Louis and Sudre, 1975 ; Hartenberger and Louis, 1976 ; Louis, 1976) has permitted a precise correlation to be established with the classic sedimentary formations of the region.

England

The Huntingbridge division of the Bracklesham group has yielded two taxa of mammals of rather minor significance.

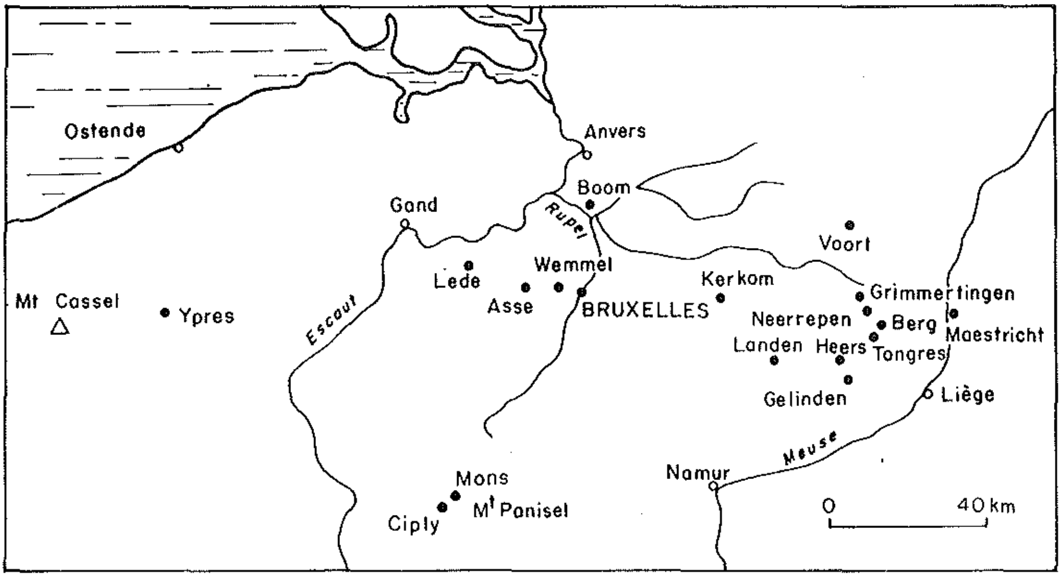


Fig. 11. — Belgian Paleogene type localities of stages and principal formations.

It is during the Marinesian that the first important modifications occur within the mammalian assemblages, announcing the impoverishment of the terminal Eocene just preceding the « Grande Coupure ». As an indication, above the Robiac level the large perissodactyl *Lophiodon* is no longer found and even at this locality it is represented by only a single species ; previously several commonly occurred in the same site. The genera *Palaeotherium* and *Plagiolophus* clearly show a tendency to acquire hypsodont characters and, among the rodents also, the first forms with hypsodont tendencies appear (*Theridomys, Pseudoltinomys* and *Elfomys*) ; not long after, the latter became more numerous than the brachyodont forms.

In general, one can say that the Bartonian mammalian assemblages are the direct descendant of those of the Lutetian ; a long period of isolation began with the Lutetian and the fauna knew no important allochthonous additions before the « Grande Coupure ». The last half of the Eocene history of western European mammals can be divided into two epochs : a period of intense diversification at the beginning of the Bartonian, followed by a period of improverishment just before the « Grande Coupure » at the end of the Ludian. This impoverishment is especially marked in the large mammals ; apart from the disapearance of the lophiodons, the perissodactyls as a whole are less diverse at the end of the late Eocene, and this phenomenon is still more striking in the artiodactyls. Also, it must be added that the Primates do not survive in Europe beyond the end of the Eocene.

This history of the mammals has been paralleled by the paleoclimatic history of western Europe ; a decrease in mean annual temperature, with lower humidity, led to a general degradation of the climate at the end of the Eocene. It is not yet possible to describe precisely what type of climate it was, but it is certain that it was rather far from the humid, tropical climate of the middle Eocene. Palynological studies (Gruas-Cavagnetto, 1978) give some indication of the evolution of these floras.

BARTONIAN CHARACTERIZING ASSEMBLAGES

Auversian

1. Level of Egerkingen.

Referred localities : Le Guépelle; Les Echelles, Chamblon.
Combined faunal association :

Marsupialia : *Amphiperatherium bastbergense.*
Insectivora : *Heterohyus europaeus, Heterohyus gracilis.*
Chiroptera : *Hipposideros egerkingensis, Stehlinia ruetimeyeri, Stehlinia pusilla.*
Primates : *Caenopithecus lemuroides, Periconodon pygmaeus, Anchomomys stehlini, Adapis priscus, Adapis sciureus, Adapis ruetimeyeri.*
Rodentia : *Protadelomys cartieri, Ailuravus picteti, Plesiarctomys spectabilis.*
Creodonta : *Proviverra typica, Allopterodon phonax, Prodissopsalis theriodis, Cynohyaenodon trux, Cynohyaenodon ruetimeyeri, Propterodon magnum, Oxyaenoides schlosseri.*
Carnivora : *Quercygale helvetica.*
Perissodactyla : *Chasmotherium cartieri, Lophiodon rhinocerodes, Palaeotherium eocaenum, Palaeotherium ruetimeyeri, Plagiolophus cartieri, Propalaeotherium helveticum, Anchilophus depereti.*
Artiodactyla : *Hyperdichobune langi, Hyperdichobune nobilis, Meniscodon europaeum, Mouillacitherium cartieri, Cebochoerus ruetimeyeri, Cebochoerus jurensis, Mixtotherium gresslyi, Mixtotherium priscum, Mixtotherium infans; Haplobunodon solodurense, Haplobunodon mulleri, Rhagatherium kowalevskyi, Catodontherium buxgovianum, Catodontherium fallax, Dacrytherium priscum, Leptotheridium traguloides, Tapirulus depereti, Tapirulus majori, Dichodon ruetimeyeri, Haplomeryx egerkingensis, Pseudamphimeryx schlosseri.*

2. Level of Lissieu.

Marsupialia : Didelphidae indet.
Insectivora : *Leptictidium auderiense.*
Primates : *Anchomomys gaillardi, Nannopithex filholi, Necrolemur* sp.
Rodentia : *Protadelomys lugdunensis.*
Creodonta : *Prodissopsalis theriodis, Prodissopsalis ginsburgi.*
Carnivora : *Quercygale helvetica.*
Perissodactyla : *Propalaeotherium isselanum, Propalaeotherium parvulum, Lophiotherium pygmaeum, Plagiolophus cartieri, Anchilophus depereti, Palaeotherium castrense, Lophiodon tapirotherium, Lophiodon glandicus, Lophiodon rhinocerodes, Lophiodon* aff. *thomasi, Paralophiodon isselensis, Hyrachyus minimus, Chasmotherium cartieri.*
Artiodactyla : *Dichobune robertiana, Hyperdichobune langi, Hyperdichobune nobilis, Meniscodon europeaum, Mixtotherium priscum, Mixtotherium gresslyi, Lophiobunodon rhodanicum, Haplobunodon mulleri, Dacrytherium priscum, Catodontherium fallax, Catodontherium buxgovianum, Tapirulus depereti, Dichodon lugdunensis, Pseudamphimeryx schlosseri.*

3. Level of La Livinière.

Referred locality : Cesseras.
Combined faunal association :

Marsupialia : *Peratherium sudrei, Amphiperatherium bourdellense.*
Rodentia : *Paradelomys* sp., *Elfomys* sp., *Sciuroides* sp., *Gliravus* sp.
Perissodactyla : *Lophiodon leptorhynchum, Lophiaspis occitanicus, Pachynolophus duvali, Pachynolophus cesserasicus, Propalaeotherium parvulum, Propalaeotherium isselanum.*
Artiodactyla : *Lophiobunodon minervoisensis.*

4. Bartonian of Spain.

Referred localities : Cappella, Laguarrès, Pontils.
Combined faunal association :

Marsupialia : *Peratherium* sp.
Insectivora : Leptictidae indet.
Primates : *Adapis priscus, Arisella capellae, Pseudoloris isabenae.*
Rodentia : *Paradelomys* sp., *Sciuroides* sp., *Gliravus* sp., *Pseudoltinomys cosetanus.*
Perissodactyla : *Lophiodon rhinocerodes, Anchilophus desmaresti, Pachynolophus* cf. *dumasi.*
Artiodactyla : *Pseudamphimeryx* ? sp., *Cebochoerus suillus.*

Marinesian

1. Level of Robiac.

Referred locality : Castrais (Lautrec).
Combined faunal association :

Marsupialia : *Peratherium sudrei, Amphiperatherium bourdellense, Amphiperatherium fontense.*
Chiroptera : *Archaeonycteris* sp., *Stehlinia* sp., cf. *Palaeochiropteryx* sp., Rhinolophoide indet.
Insectivora : *Saturninia mamertensis, Saturninia hartenbergeri, Heterohyus sudrei.*
Primates : *Necrolemur antiquus, Adapis sudrei, Pseudoloris parvulus, Gesneropithex* sp.
Rodentia : *Psesiarctomys hurzeleri, Gliravus robiacensis, Paradelomys crusafonti, Elfomys tobieni, Remys minimus, Suevosciurus romani.*
Creodonta : *Pterodon dasyuroides.*
Carnivora : *Quercygale angustidens, Simamphicyon helveticus.*
Perissodactyla : *Plagiolophus annectens, Palaeotherium castrense, Palaeotherium siderolithicum, Palaeotherium ruetimeyeri, Palaeotherium pomeli, Leptolophus stehlini, Anchilophus duasi, Anchilophus gaudini, Anchilophus desmaresti, Lophiotherium robiacensis, Lophiodon lautricensis, Chasmotherium carteri.*
Artiodactyla : *Mouillacitherium elegans, Cebochoerus campichii, Cebochoerus* ? *helveticus, Choeropotamus lautricensis, Catodontherium robiacensis, Catodontherium* ? *paquieri, Tapirulus schlosseri, Robiacina minuta, Haplomeryx picteti, Xiphodon castrense, Paraxiphodon cournovense, Leptotheridium* cf. *traguloides, Haplomeryx* cf. *picteti, Pseudamphimerix renevieri.*

2. Level of Grisolles.

Referred localities : Le Bretou, Paris (Batignolles, parc Monceau, Gare du Nord), Creechbarrow, Barton Cliff, Hengistbury Head.
Combined faunal association :

Marsupialia : *Peratherium bretouense, Peratherium lavergnense, Amphiperatherium bourdellense, Amphiperatherium minutum, Amphiperatherium giselense.*

Chiroptera : *Rhinolophus* sp., *Vespertiliavus gracilis, Vespertiliavus* sp., Rhinolophoïde indet.

Insectivora : *Saturninia grisollensis, Saturninia grandis, Saturninia intermedia, Scraeva* sp. *Heterohyus sudrei.*

Primates : *Adapis* cf. *sudrei, Adapis* aff. *magnus, «Anchomomys» grisollensis, Necrolemur zitteli, Microchoerus erinaceus, Nannopithex filholi, Pseudoloris crusafonti, Amphilemur* sp.

Rodentia : *Plesiarctomys* sp., *Ailuravus stehlinischaubi, Theridomys varleti, Suevosciurus russelli, Treposciurus* sp., *Pseudoltinomys* sp., *Paradelomys crusafonti.*

Carnivora : Miacidae indet.

Condylarthra : *Pugiodens* sp.

Perissodactyla : *Lophiodon lautricense* var. *franconicum, Propalaeotherium* cf. *parvulum, Lophiotherium robiacense, Plagiolophus* sp., *Anchilophus desmaresti, Palaeotherium castrense.*

Artiodactyla : *Anthracobunodon louisi, Choeropotamus* sp., *Cebochoerus campichii, Cebochoerus helveticus, Cebochoerus* cf. *ruetimeyeri, Mixtotherium priscum, Haplobunodon* sp., *Rhagatherium* sp., *Dacrytherium* cf. *elegans, Robiacina minuta, Leptotheridium* cf. *traguloides, Xiphodon* cf. *castrense, Dichodon cuspidatus, Haplomeryx* cf. *picteti, Pseudamphimeryx pavloviae.*

THE LATE EOCENE

THE PRIABONIAN STAGE — THE LUDIAN SUBSTAGE

The series of historical events leading up to the present consideration of the Priabonian as the stage representing the late Eocene have been discussed earlier (p. 28, 29, 30).

As noted above, the Ludian is a time of particular significance. Apart from the polemic that surrounded it in the boundary problem, its fauna has a distinctive character. It is possible to summarize in four categories the tendancies that are apparent in this fauna :

- impoverishment by the extinction of certain lineages ;
- a few appearances, of speculative origin, by groups of a modern type ;
- the frequent presence of hypsodonty in several groups ;
- the individualization of biogeographic subprovinces, or fragmentation of the insular European region.

These evolutionary facts, documented by mammalian assemblages, seem related on one hand to the strong degree of endemism that was caused by the relative isolation of Europe during more than 10 million years (since the last major faunal exchange in the Sparnacian), and on the other hand to climatic modifications which led to a pronounced degradation of the previous climate. These negative climatic oscillations were accentuated on two occasion towards the end of the Eocene (Cavelier, 1979 ; Savin *et al.*, 1975) ; it is quite likely that they were manifestations of general conditions prevailing on a global scale (Frakes and Kemp, 1973). The importance of the climatic crisis has been recently underscored by Berggren *et al.* (1980) who call it the «Terminal Eocene Event» (for a recent bibliography on the problem, see Cavalier *et al.*. 1981).

The phenomenon of the «Grande Coupure», formerly regarded as a brutal immigration of an ensemble of Asia forms, now can be seen instead as more a consequence of late Eocene environment and geography.

Many European artiodactyl lineages disappeared ; they and primates are notably less numerous in Ludian assemblages than before. As an example, the locality of Frohnstetten (Dehm, 1937) has yielded an abundant fauna, but one that is significantly little varied. These disappearences are not compensated by the few appearances that can be ascertained. For some of the latter the possibility could be raised that they heralded to a small extent the flood of allochthonous immigrants that arrived at the «Grande Coupure». Certain elements (*Anoplotherium*) allow this eventuality to persist, but others, like cainotheriids (*Oxacron*), are the result of autochthonous evolution (Sudre, 1978). Evolutionary modifications in rodent communities have been recently summarized (Vianey-Liaud and Hartenberger, 1982).

The existence of biogeographic subprovinces seems clearly indicated by the minor differences in faunal composition observed in diverse groups for localities situated, for example, south of the Pyrenees (Hartenberger, 1973), in England (Sudre, 1974) or in southern Germany (Schmidt-Kittler, 1971 ; Hartenberger, 1973 ; Schmidt-Kittler and Vianey-Liaud, 1975). Differences at a specific or subspecific level exist within rodent populations from these regions ; Sudre made comparable observations with respect to the artiodactyls and primates in southern England and in southern France. Related to this phenomenon and à propos of the «Grande Coupure», Schmidt-Kittler and Vianey-Liaud (1975) have demonstrated that the wave of immigrants that appeared in France at the Hoogbutsel level made a more precocious appearance in southern Germany, where cricetids are known as early as the level of Frohnstetten.

France

The numerous Quercy sites (La Bouffie, Les Pradigues, Célarié, Escamps, Perrière and Malpérié : see Crochet *et al.*, 1981) and the wide geographic distribution of other localities have produced an adequate material for demonstrating the interest of this period in the history of Paleogene mammals, preceeding the dramatic crisis of the «Grande Coupure». The best localities of this period are Euzet-les-Bains (= Saint-Hyppolyte-de-Caton), Fons and La Débruge in the south of France, and Montmartre in Paris ; studies of the mammals from the latter site by Cuvier early in the 19th century were of considerable importance in launching the sciences of comparative anatomy and vertebrate paleontology.

England

The Ludian faunas of England are comprised of those from the Lower, Middle and Upper Headon Beds, the Osborn Beds, the Bembridge limestones and marls and the lower part of the Hamstead Beds. This represents an important sequence which has provided a large assemblage of fossil mammals. The most extensive collection is that from Headon Hill, Hordle Cliff, Totland Bay and Whitecliff Bay out of the Lower Headon Beds (HH 1). The Middle Headon Beds (the *Microchoerus* Beds), also at Headon Hill, and the Brockenhurst Beds at Roydon have produced the smallest variety of mammals, while the fauna from the Upper Headons, again at Headon Hill (HH 2-4), is of intermediate size. Unfortunately, there is not much from the continental side of the France-Anglo-Belgian basin with which to compare or correlate these assemblages.

From the Osborne Beds, at Headon Hill (HH 5) and other localities, a rather important fauna is known that has long been considered as equivalent to that from the Gypse at Montmartre.

Another diversified fauna has been collected from the Bembridge limestones, next in the Isle of Wight section, at Headon Hill (HH 6-7) as well as number of other sites. The overlying Bembridge marls have also furnished an interesting fauna.

For an excellent analysis of the Tertiary beds in the British Isles and their correlation with the rest of Europe, see Curry *et al.*, 1978. For a different treatment of the correlation problem, based on vertebrate fossils, the reader is directed to Russell *et al.*, 1982.

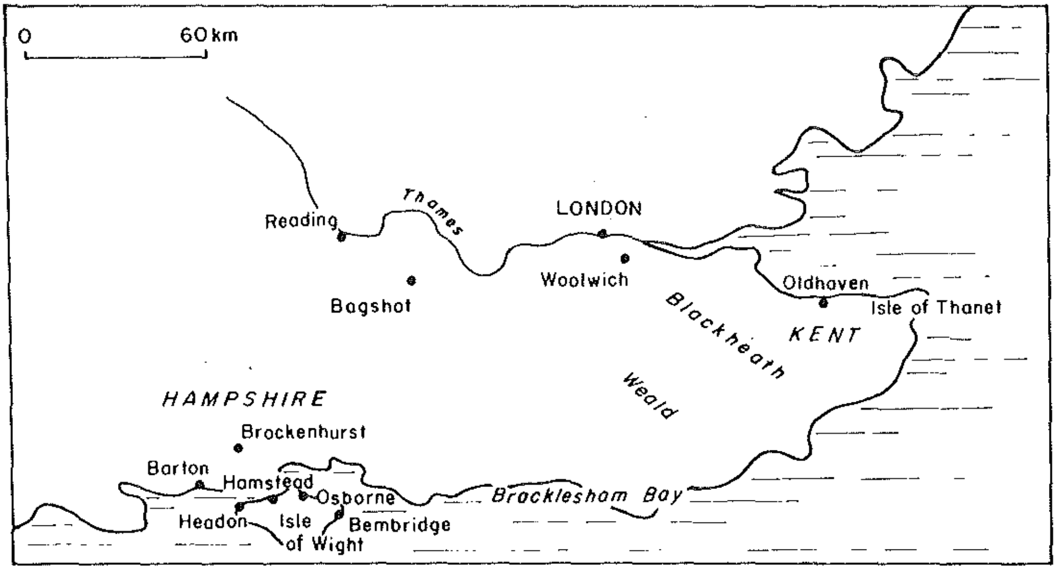


Fig. 12. — English Paleogene type localities of principal formations.

West Germany

Mammal sites that correspond to the levels of La Débruge, Montmartre and Escamps-Frohnstetten have been found in the south of Germany and in northern Hesse. Because of difficulties concerning the placement of the Eocene-Oligocene boundary, these localities are here regarded to be of late Eocene age, whereas German paleontologists have until now ranged them in the early Oligocene ; they will be treated in that part of the text.

Spain

The important localities in Spain are Sosis (in the Tremp Basin) and Llamaquique (Oviedo). The fauna is comparable to that of Euzet (early Ludian)[16] and the few sites known in Spain are the richest yet known from the Paleogene of that country. On the generic level there are essentially no differences from the fauna of Languedoc or of the Quercy, but species particularities are apparent which evoke segregation of a geographic order (Casanovas Cladellas, 1975 ; Crusafont-Pairó, 1961 ; Crusafont-Pairó *et al.*, 1963 ; Crusafont-Pairó and Golpe-Posse, 1968 ; Hartenberger, 1973).

Geographically originating differences with respect to the contemporaneous fauna of the rest of Europe are quite clear in the late Ludian and well documented (Vianey-Liaud, 1979 b). Unfortunately, localities of this age are very rare in Spain.

Portugal

In Portugal only a few localities (Côja, in particular), of late Eocene age, have been made known (Antunes, 1967 ; Antunes *in* Ribeiro *et al.*, 1979), but they are of considerable local importance for the classification of the stratigraphy of continental formations.

Turkey and Bulgaria

Ozansoy (1966) has figured an upper molar of an erinaceid that was found in the provinces of Çorum, at Yaglit. He gave its age as late Eocene, but presented no evidence for this assignement.

A lignitic locality in Bulgaria, Tscherno More (north of Burgas), is dated by stratigraphic means and by palynology as late Eocene. This site, with two species of *Elomeryx* (Nikolov, 1967) represents an extension of the environmental conditions that prevailed in parts of neighboring Turkey apparently throughout the Eocene and Oligocene.

Yugoslavia

A single specimen of anthracothere, *Prominatherium dalmatinum* (MEYER, 1854) (generic name : Teller, 1884) from the Promina beds of Dalmatia, bears mentioning. The fact that its age could well be late Eocene (an element of uncertainty does exist) would make this form perhaps the first in the anthracothere invasion of Europe.

---

[16] Concerning the age of Euzet, it has been correlated with certain levels of the Headon Beds (in southern England) by means of mammals, but an equivalence between the brackish water sediments in the Headon Beds and the Marnes de Ludes (of the type section near Reims, France) cannot be considered as definitely proven ; Euzet could belong to the late Marinesian.

PRIABONIAN CHARACTERIZING ASSEMBLAGES

Ludian

1. *Level of Fons 4.*

Referred localities : Fons 1, Fons 2, Fons 3, Fons 5, Fons 6, Euzet. Aubrelong 2, La Bouffie, Les Clapiers.

Combined faunal association :

Marsupialia : *Peratherium lavergnense, Amphiperatherium fontense, Amphiperatherium bourdellense, Amphiperatherium minutum, Amphiperatherium giselense.*
Chiroptera : *Stehlinia* sp.
Insectivora : *Saturninia* sp.
Primates : *Microchoerus erinaceus, Adapis magnus, Huerzeleris quercyi.*
Rodentia : *Plesiarctomys* sp., *Gliravus meridionalis, Sciuroides intermedius, Paradelomys crusafonti, Suevosciurus (Treposciurus) mutabilis, Microsuevosciurus minimus, Theridomys euzetensis, Estellomys cansouni, Pseudoltinomys mamertensis, Elfomys parvulus, Remys garimondi.*
Creodonta : *Quercytherium tenebrosum, Hyaenodon requieni, Hyaenodon minor, Paroxyaena galliae.*
Perissodactyla : *Plagiolophus annectens, Palaeotherium siderolithicum, Palaeotherium medium, Palaeotherium curtum, Anchilophus* cf. *dumasi, Anchilophus* cf. *gaudini, Pachynolophus garimondi, Propalaeotherium* sp.
Artiodactyla : *Mouillacitherium elegans, Cebochoerus minor, Cebochoerus fontensis, Cebochoerus* cf. *lacustris, Cheoropotamus sudrei, Choeropotamus depereti, Leptotheridium lugeoni, Dacrytherium ovinum, Dichodon cervinum, Haplomeryx euzetensis, Xiphodon intermedium, Paraxiphodon teulonensis, Pseudamphimeryx renevieri.*

2. *Level of Perrière.*

Referred localities : Malpérié, Lavergne, Headon Hill(HH 1-2), Rosières 5, Saleme, Les Sorcières.

Combined faunal association :

Marsupialia : *Peratherium perrierense, Peratherium lavergnense, Peratherium cuvieri, Amphiperatherium minutum, Amphiperatherium fontense.*
Insectivora : *Saturninia gracilis, Saturninia beata, Scraeva woodi, Scraeva hatherwoodensis, Eotalpa anglica, Cryptopithecus major, Heterohyus nanus, Pseudorhyncocyon cayluxi.*
Chiroptera : *Hipposideros schlosseri,* Rhinolophoid indet., *Stehlinia gracilis, Stehlinia quercyi,* cf. *Tadarida* sp., *Vespertiliavus gracilis, Vespertiliavus* sp., *Paraphyllophora quercyi, Necromantis adiohaster.*
Primates : *Pseudoloris parvulus, Microchoerus erinaceus, Adapis magnus, «Anchomomys»* cf. *grisollensis, Amphilemur* sp., *Necrolemur antiquus.*
Rodentia : *Plesiarctomys* sp., *Gliravus priscus, Gliravus meridionalis, Sciuroides ehrensteinensis, Treposciurus mutabilis helveticus, Treposciurus intermedius, Suevosciurus mutabilis, Suevosciurus palustris, Thalerimys fordi, Theridomys pseudosiderolithicus, Theridomys euzetensis, Paradelomys quercyi, Pseudoltinomys phosphoricus, Elfomys parluvus, Microsuevosciurus minimus.*
Creodonta : *Prototomus ? minor, Hyaenodon requieni, Hyaenodon brachyrhynchus, Hyaenodon minor, Paroxyaena galliae.*
Carnivora : *Quercygale angustidens, Miacis exilis.*
Perissodactyla : *Anchilophus* sp., *Plagiolophus annectens, Palaeotherium magnum stehlini, Palaeotherium muehlbergi praecursum, Palaeotherium duvali priscum.*

Artiodactyla : *Mouillacitherium elegans, Acotherulum pumilum, Mixtotherium cuspidatum, Dacrytherium ovinum, Leptotheridium lugeoni, Robiacina quercyi, Tapirulus perrierensis, Haplomeryx picteti, Pseudamphimeryx pavloviae, Pseudamphimeryx renevieri, Pseudamphimeryx hantonensis, Dichodon cervinum, Dichodon cuspidatus, Diplopus aymardi, Robiacina lavergnensis.*

3. Level of La Débruge.

Referred localities : Cregols, Mas de Labat, Sainte-Néboule, Gousnat, Headon Hill (HH 5), Ehrenstein 1 A, Gösgen Kanal, Dielsdorf.

Combined faunal association :

Marsupialia : *Peratherium cuvieri, Peratherium cayluxi, Amphiperatherium minutum, A. lamandini.*

Insectivora : *Saturninia gracilis, S. beata, Scraeva woodi, Scraeva hatherwoodensis, Dyspterna hopwoodi, Heterohyus* sp., *Pseudorhyncocyon cayluxi.*

Chiroptera : *Hipposideros schlosseri, Palaeophyllophora oltina, P. quercyi, Rhinolophus* cf. *priscus.*

Primates : *Adapis stintoni, Adapis magnus, A. parisiensis, Protoadapis ulmensis, Necrolemur antiquus, Pseudoloris parvulus, Microchoerus erinaceus edwardsi.*

Rodentia : *Pseudosciurus praecedens, Paradelomys spelaeus, Microsuevosciurus minimus, Sciuroides quercyi, Treposciurus mutabilis, Ectropomys exiguus, Thalerimys headonensis, Patriotheridomys* sp., *Pseudoltinomys gousnatensis, Elfomys* aff. *parvulus, Archaeomys (Blainvillimys)* sp., *Theridomys pseudosiderolithicus, Theridomys perrealensis, Plesiarctomys gervaisi, Gliravus* cf. *priscus.*

Creodonta : *Pterodon dasyuroides, Hyaenodon requieni, Hyaenodon heberti, Hyaenodon minor, Hyaenodon brachyrhynchus.*

Carnivora : *Cynodyctis lacustris,* cf. *Palaeoprionodon* sp.

Perissodactyla : *Palaeotherium duvali duvali, Palaeotherium magnum girondicum, Palaeotherium medium perrealense, Palaeotherium crassum robustum, Palaeotherium siderolithicum, Palaeotherium muehlbergi muehlbergi, Palaeotherium curtum villerealense, Plagiolophus minor, Plagiolophus annectens, Anchilophus radegondense.*

Artiodactyla : *Dichobune leporina, Dichobune* cf. *fraasi, Choeropotamus parisiensis, Xiphodon gracile, Dichodon* cf. *frohnstettense, Dichodon stehlini, Dichodon cervinum, Dichodon cuspidatum, Dacrytherium saturnini, Tapirulus hyracinus, Anoplotherium commune, Anoplotherium latipes, Anoplotherium laurillardi, Diplobune secundaria, Haplomeryx zitteli, Elomeryx crispus, Oxacron courtoisi, Amphimeryx murinus, Pseudamphimeryx* sp., *Acotherulum pumilum, Haplobunodon lydekkeri, Acotherulum saturninum, Dacrytherium lugroni.*

4. Level of Montmartre.

Referred localities : Mormoiron, Headon Hill (HH 6, HH 7), Möhren 6, Mormont-Entreroches, St-Etienne de l'Olm, Escamps, Coanac, Lostange, Palembert, Rosières 1, 2 et 4, Sindou D, Tabarly.

Combined faunal association :

Marsupialia : *Peratherium cuvieri, Peratherium laurillardi, Amphiperatherium minutum, A. lamandini, A. antiquum, A. exile.*

Insectivora : *Scraeva woodi, Scraeva hatherwoodensis, Pseudorhyncocyon cayluxi, Saturninia gracilis, S. tobieni, Amphidozotherium cayluxi.*

Primates : *Adapis parisiensis, Adapis duvernoyi, Microchoerus ornatus, Microchoerus erinaceus, Pseudoloris parvulus.*

Chiroptera : *« Vespertilio » cerotinoides, Stehlinia gracilis, Hipposideros morloti, H. schlosseri, Palaeophyllophora oltina, P. quercyi, Rhinolophus priscus.*

Rodentia : *Theridomys* aff. *siderolithicus, Blainvillimys rotundidens, Patriotheridomys altus, Pseudoltinomys cuvieri, Elfomys parvulus, Ectropomys exiguus, Sciuroides* sp., *Suevosciurus fraasi, Suevosciurus ehingensis, Pseudosciurus suevicus, Gliravus priscus, Plesiarctomys* sp., *Paradelomys spelaeus, Oltinomys platyceps.*
Creodonta : *Hyaenodon brachyrhynchus, Pterodon dasyuroides, Galethylax blainvillei, Parapterodon lostangensis.*
Carnivora : *Cynodictis parisiensis, Cephalogale parisiensis, Cynodictis compronideus.*
Perissodactyla : *Palaeotherium magnum magnum, Palaeotherium crassum crassum, Palaeotherium medium medium, Palaeotherium siderolithicum, Palaeotherium muelhbergi muelhbergi, Palaeotherium curtum curtum, Palaeotherium duvali duvali, Plagiolophus minor, Plagiolophus annectens, Anchilophus radegondensis.*
Artiodactyla : *Diplobune secundaria, Xiphodon gracile, Dichobune leporina, Amphimeryx murinus, Haplomeryx obliquus, Choeropotamus parisiensis, Choeropotamus depereti, Anoplotherium commune, Anoplotherium laurillardi, Haplobunodon lydekkeri, Hyperdichobune spinifera, Hyperdichobune spectabilis, Acotherulum pumilum, Acotherulum saturninum, Rhagatherium valdense, Gelocus minor.*

5. Level of Frohnstetten.

Referred localities : Saint-Capraise-d'Eymet, Lascours, Neustadt, Nordshausen, Möhren 19, Ehrenstein 1 B, Baby, ? Pantin, Bembridge limestones, Bembridge marls.

Combined faunal association :

Marsupialia : *Peratherium cuvieri, Amphiperatherium ambiguum, Amphiperatherium exile.*
Insectivora : *Stehlinia minor, Stehlinia* sp., *Tadarida* sp., *Amphidozotherium cayluxi, Saturninia gracilis, Scraeva woodi, Scraeva hatherwoodensis.*
Chiroptera : *Palaeophyllophora* aff. *oltina, Hipposideros* cf. *morloti, Hipposideros* cf. *schlosseri, Rhinolophus* cf. *priscus, Vespertiliavus* sp.
Primates : *Adapis parisiensis, Microchoerus erinaceus, Pseudoloris parvulus, Pseudoloris* cf. *reguanti.*
Rodentia : *Patriotheridomys altus, Blainvillimys rotundidens, Pseudoltinomys cuvieri, Theridomys golpei, Theridomys* sp., *Theridomys* aff. *aquatilis, Oltinomys platyceps, Paradelomys spelaeus, Microsuevosciurus* cf. *minimus, Thalerimys fordi, Scuevosciurus fraasi, Sciuroides* sp., *Pseudosciurus suevicus, Ectropomys exiguus, Gliravus priscus, Gliravus* aff. *meridionalis, Plesiarctomys* cf. *gervaisi.*
Lagomorpha : *Shamolagus franconicus.*
Creodonta : *Pterodon dasyuroides, Hyaenodon gervaisi, Hyaenodon brachyrhynchus.*
Carnivora : *Cynodyctis compressidens* var. *viverroide, Cynodyctis* sp.
Perissodactyla : *Palaeotherium curtum frohnstettense, Palaeotherium medium medium, Palaeotherium medium suevicum, Palaeotherium muelhbergi muelhbergi, Palaeotherium curtum curtum, Palaeotherium duvali duvali, Palaeotherium magnum magnum, Plagiolophus annectens, Plagiolophus minor, Plagiolophus fraasi, Anchilophus radegondensis.*
Artiodactyla : *Diplobune secondaria, Dichobune leporina, Choeropotamus parisiensis, Oxacron courtoisi, Anoplotherium laurillardi, Anoplotherium commune, Tapirulus hyracinus, Dacrytherium ovinum, Dichodon frohnstettense, Haplobunodon lydekkeri, Xiphodon gracile, Haplomeryx zitteli, Pseudamphimeryx renevieri, Acotherulum saturninum, Amphimeryx murinus, Amphirhagatherium frohnstettense, Paragelocus suevicus, Elomeryx* sp.

Ludian of Spain

1. Early Ludian.

Referred localities : Sosis, Roc de Santa, Llamaquique.

Combined faunal association :

Marsupialia : *Peratherium perrierense, Peratherium lavergnense.*
Insectivora : *Leptictis* sp., *Saturninia* sp.
Primates : *Adapis magnus, Necrolemur antiquus, Necrolemur erinaceus, Pseudoloris parvulus.*
Rodentia : *Theridomys euzetensis, Suevosciurus mutabilis, Estellomys ibericus, Pseudoltinomys* sp., *Gliravus* aff. *priscus.*
Creodonta : *Hyaenodon minor, Hyaenodon heberti.*
Carnivora : *Miacis exilis, Viverravus* sp.
Perissodactyla : *Palaeotherium magnum, Palaeotherium medium, Palaeotherium crusafonti, Palaeotherium curtum, Plagiolophus annectens, Anchilophus dumasi, Anchilophus gaudini.*
Artiodactyla : *Choeropotamus sudrei, Dacrytherium ovinum, Leptotheridium lugeoni, Dichodon cervinum, Xiphodon intermedium, Haplomeryx euzetensis.*

2. Late Ludian.

Referred localities : San Cugat de Gavadons, Huermeces del Cerro.

Combined faunal association :

Marsupialia : Didelphidae indet.
Primates : *Pseudoloris reguanti, Microchoerus ornatus, Necrolemur* sp.
Rodentia : *Pairomys crusafonti, Theridomys golpei, Pseudoltinomys cuvieri, Elfomys nanus, Gliravus* sp.
Perissodactyla : *Palaeotherium magnum, Palaeotherium medium.*
Artiodactyla : *Moiachoerus simpsoni, Dichodon* cf. *frohnstettense, Dichodon cervinum, Acotherulum simpsoni, Xiphodon gracile.*

THE OLIGOCENE EPOCH

The definition of the beginning of the Oligocene has been the subject of numerous controversies [Colloque sur le Paléogène, Bordeaux, 1962 (Mém. B.R.G.M. n° 28, 1964) ; Colloque sur l'Eocène, Paris, 1968 (Mém. B.R.G.M. n° 58, 1968, and 69, 1969) ; Cavelier, 1972, 1979]. One contradiction in the historical sense of the term is that the important «Oligocene» marine transgression, that Beyrich intended to emphasize, actually begins, in Northern Germany, early in the late Lutetian (Martini and Ritskowski, 1969). But without going further into the argument, it is of interest to note that despite the work of Stehlin (1909), which showed the importance of the faunal renewal after the late Ludian, most European paleomammalogists followed the definitions in the «Lexique stratigraphique international» (Denizot, 1957) wherein the Oligocene included the late Ludian. At present many stratigraphers (Cavelier and Pomerol, 1977, for example) place the deposits of the Lattorfian s.s. (= late Ludian) in the late Eocene, in which case the Oligocene would begin after the last Priabonian deposits, with the base of the Stampian[17], and after the «Grande Coupure».

[17] A. d'Orbigny, 1852 ; type locality at Etampes, France.

Some paleomammalogists (for example, Sigé and Vianey-Liaud, 1979 ; Hartenberger, 1979) feel that the mammalian fossil record is even inapplicable to the problem of the Eocene-Oligocene boundary ; the latter is, in their opinion, marine in nature and the paleomammalogist in consequence should follow the results of stratigraphers and micropaleontologists, and not the contrary. However, good correlations by any means can be of value ; between parallel biochronologic sequences, one based on marine and the other on terrestrial organisms, links have frequently been established.

The type section of the Stampian was defined by A. d'Orbigny in the Paris Basin for the beds included between the base of the Argile verte de Romainville to the Calcaire supérieur d'Etampes. The early Stampian (= early Oligocene) is represented, locally, by a time-rock division of facies value only, the Sannoisian. Between the late Stampian (= middle Oligocene) and the Aquitanian a relatively thick group of deposits represents the late Oligocene. They do not correspond exactly to the Chattian Stage, whose definition is still subject to discussion.

			Micromammal Marker Horizons (Vianey-Liaud, 1976)	Macromammal Marker Horizons (Brunet, 1975)
OLIGOCENE	UPPER	OLIGOCENE	Coderet Rickenbach Boningen Mas de Pauffié	Coderet La Milloque Rabastens
	STAMPIAN	Upper	Antoingt Heimersheim Les Chapelins Montalban	Etampes La Ferté-Alais Montalban
		Lower	Villebramar Hoogbutsel	Villebramar Ronzon Soumailles

Fig. 13. — Comparison of marker horizons of the Oligocene based on micromammals (left) and on macromammals (right).

The Oligocene, then, is made up of three divisions :

— the early Oligocene = early Stampian ;

— the middle Oligocene = late Stampian ;

— the late Oligocene = an as yet undefined, or undecided upon, stage (Cavelier and Pomerol, 1977) (opinion at present appears to be deciding in favor of using the stage name Chattian).

Within the above framework many successive localities occur and the unfolding of mammalian history can be viewed as a continuous phenomenon. Within this continuum it is possible to observe considerable detail in faunal renewal and in evolutionary changes. In the late Stampian, for example, four distinct horizons are discernable in certain rodent lineages. The greatest precision for correlating such paleofaunas will not be made at the level of combined faunal assemblages (grouping all the elements of a stratigraphic stage or substage), but with assemblages from single points in time, that is, those corresponding to marker levels.

REGIONAL GROUPS OF LOCALITIES

The disproportionate size of this section on the localities of the Oligocene, with respect to those of the preceding stages, is dictated by the great number of sites, by their concentration in scattered regions, and by the richness and variety of their included assemblages.

France : Aquitanian Basin

The Oligocene begins here with the Castillon Formation from which has been collected the rich fauna of Soumailles. Apart from the forms inherited from the Ludian, such immigrants as *Entelodon magnum antiquum* and *Eusmilus bidentatus* are also found. The upper part of this formation contains a few localities at Sainte-Marthe.

The Molasses de l'Agenais, which continue throughout most of the duration of the Oligocene, contain in their lower part the localities of Puylaurens and Villebramar. The latter has furnished a fine assemblage (Brunet, 1970, 1979) with perissodactyls, artiodactyls, creodonts, carnivores and a few rodents. In the middle part of the Molasses de l'Agenais are known two localities : Saint-Martin-de-Casselvi (= Saint-Martin-de-Briatexte) and Rabastens. Finally, the upper levels of this formation have yielded abundant mammals in the locality of La Milloque (Brunet, 1979). The association of a small anthracothere (*Microbunodon minimum*) with a primitive brachypothere (*Brachypotherium* aff. *lemanense*), a middle-sized acerathere (*Mesaceratherium* aff. *paulhiacensis*) and the rodents *Archaeomys laurillardi, Issiodoromys pseudanaema* and *Eucricetodon praecursor* indicates a position late in the late Oligocene of this site ; it is nevertheless a little older than that of Coderet, the last level of the Oligocene.

→

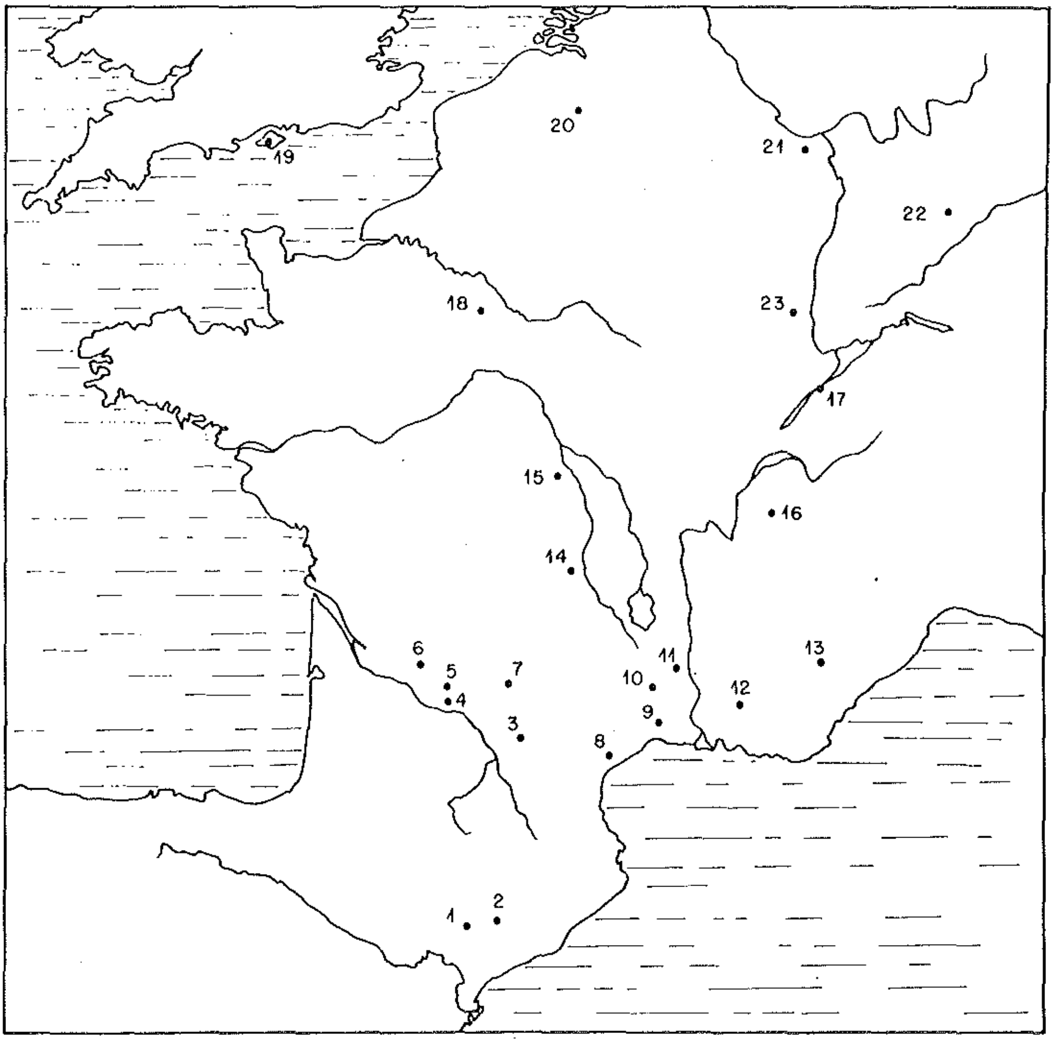
Fig. 14. — Geographic distribution of Oligocene localities of Western Europe : 1. Montalban ; 2. Campins ; 3. Saint-Martin-de-Briatexte, Rabastens ; 4. La Milloque ; 5. Villebramar, Soumailles ; 6. Sainte-Marthe ; 7. (Quercy) Aubrelong 1, Ravet, Mas de Got, La Plante 2, Roqueprune 2, La Garouilles, Les Bories, Itardies, Mège, Pech-Crabit, Genebrières, Belgarric, Rigal-Jouet, Espeyrasse, La Devèze, Mas de Pauffié, Pech Desse, Pech du Fraysse ; 8. Le Portel ; 9. Les Matelles, Saint-Vincent-de-Barbeyrargues, Assas, La Colombière ; 10. Boujac, Sarèle ; 11. Saint-Victor-La-Coste ; 12. Saint-Henri, Les Chapelins, Fontaines-de-Vaucluse, Mazan, Saint-Martin-de-Castillon, Aubenas-les-Alpes ; 13. La Tuilière ; 14. Antoingt, Cournon ; 15. Coderet ; 16. Lovagny ; 17. Balm, Oensingen-Ravellen, Mumliswyl, Boningen, Aarwangen, La-Fabrique-près-Boudry, Rickenbach, Nant d'Avril, Küttingen ; 18. Etampes ; 19. Isle of Wight (see Bosma, 1974, for locality details) ; 20. Hoogbutsel, Hoeleden ; 21. Heimersheim ; 22. Ehrenstein 1B, Ehingen 1, 2, Ronheim 1, Schelklingen, Herrlingen, Bernloch 1B, Burgmagerbein 1, 2 ; Ehrenstein 4, Gaimersheim ; 23. Lobsann.

Quercy

Sixteen localities occur in this region distributed throughout eight successive biochronologic levels, from the « Grande Coupure » to the beginning of the late Oligocene (level of Boningen). The terminal Oligocene (level of Rickenbach and Coderet) is not represented in the phosphate pockets of Quercy (de Bonis *et al.*, 1973).

The first Oligocene localities, Aubrelong 1 and Ravet (with 32 mammalian species) contain, beside the persistant lineages from the Eocene, immigrants of the « Grande Coupure ».

The fauna of the beginning of the middle Oligocene, the level of Villebramar, (from the localities of Mas de Got, La Plante 2 and Roquebrune 2) is known by nearly 50 species. It differs from the following level, that of Montalban (with the localities of



Pech Crabit, Mège and Itardies), only by the more archaïc character of certain lineages (*Blainvillimys gregarius* and *Eucricetodon atavus*) and by the absence of *Pseudocricetodon.*

Only a single locality corresponds to the level of Chapelins ; the site (Genebrière 1) is represented by a small remnant of sediment on the wall of a phosphate pocket that has yielded rodents and chiropterans.

It is possible to distinguish two levels in the interval of the late middle Oligocene by the use of rodents (in particular), Belgarric and Rigal-Jouet. In the same manner, one can distinguish two levels at the beginning of the late Oligocene, that of Mas de Pauffié and that of Pech Desse-Pech du Fraysse (level of Boningen) ; this last level is characterized by *Issiodoromys quercyi, Archaeomys intermedius* and *Blainvillimys geminatus.*

Basins of the south and southeast of France

(Synclines to the north and northwest of Montpellier (Hérault) ;
the Alès Basin (Gard) ; the synclines of Provence).

The sedimentation in the Oligocene basins of the Montpellier region took place in two phases. One of them resulted in the deposition of the Lez Formation and the second gave rise to the Assas Formation. These two episodes are separated by a phase of tectonic movements and fracturing. It is the second that has furnished the mammal localities : Assas, Les Matelles and Saint-Vincent-de-Barbeyrargues, the fauna of which indicates a position high in the middle Oligocene, at the level of Antoingt.

The terminal Oligocene (level of Coderet) is represented by fissure fillings in the quarries of La Colombière, north of Montpellier (see Thaler, 1966 ; Vianey-Liaud, 1979 b).

The localities of the Alès Basin have been found in the large detrital ensemble that is limited to the west by the Cévennes fault (direction NE-SW) : Boujac, very close to the fault, and Sarèle, more to the north at the eastern edge of the formation (see Hartenberger *et al.*, 1970). These two localities, from their fauna, seem close to the level of Boningen. The terminal Oligocene is represented by the karst filling of Saint-Victor-la-Coste (see Remy and Thaler, 1967 ; Hugueney, 1968 ; Vianey-Liaud, 1972).

The Argiles de Marseille contain the locality of Saint-Henri ; this assemblage (and notably the rodents) is similar to that of the level of Mas de Pauffié (Vianey-Liaud, 1976).

The oldest Oligocene localities in the Provence basins are those of Fontaines-de-Vaucluse and Mazan of the Hoogbutsel level. The localities of Murs and Les Chapelins, of the middle Oligocene, have furnished specimens of *Blainvillimys helmeri.* Saint-Martin-de-Castillon contains a fauna that is more evolved than the preceding (Hugueney, 1971). Aubenas-les-Alpes is known by a fauna of the Antoingt level (Helmer and Vianey-Liaud, 1971).

In the Castellane syncline, one of the youngest beds has produced (northeast of

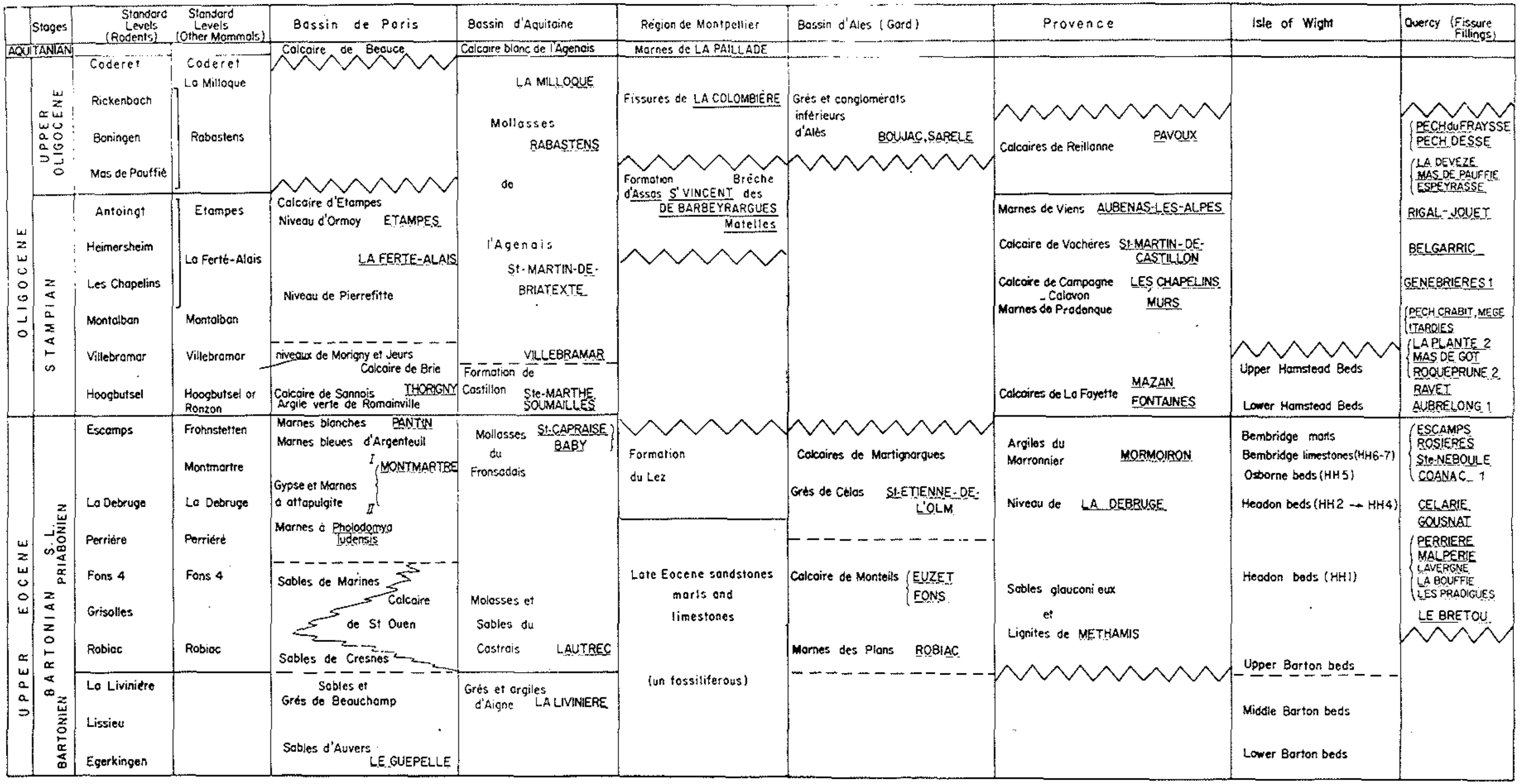


Fig. 15. — Stratigraphic distribution of late Paleogene formations and principal mammal localities of Western Europe. Underlined names are mammal localities.

Forcalquier, near the Pavoux farm) a fauna of the Boningen level. The youngest molasse beds of the Barrême syncline, attributed to the Aquitanian by Depéret (1895), then to the middle Oligocene by Rey (1967), would appear to occupy a position close to the Boningen level from the indications of the rodents, in particular those from the locality of La Tuilière (Carbonnel *et al.*, 1972).

Auvergne

The Oligocene begins here with the classic site of Ronzon. Revision of the material from other such often cited localities as Cournon and La Sauvetat has revealed the presence of a mixture in the old collections (Vianey-Liaud, 1972). Only the fauna of Antoingt, of the end of the middle Oligocene, appears homogeneous. A new fossiliferous locality, Cournon-les-Soumeroux, on the hill of Cournon, has been recently discovered (Brunet *et al.*, 1981). It permits the precise placement of Cournon among the late Oligocene localities : it is slightly younger than Pech du Fraysse, and older than Coderet.

The late Oligocene has yielded a few fossiliferous localities, like the Mine des Roys and, especially, Coderet (Hugueney, 1969).

Paris Basin and Alsace

In the late Stampian, two localities are known, one at La Ferté Alais and the other at Etampes (Ginsburg, 1969).

In Alsace the few mammals that have been found in the Pechelbronn beds and the Calcaire de Lobsann permit these formations to be situated close to the level of Ronzon - Hoogbutsel.

Isle of Wight and Belgium

On the Isle of Wight the Oligocene begins in the Hamstead Beds with the arrival of the cricetids and *Entelodon magnum*, accompagnied by other artiodactyls, mostly anthracotheres. These Hamstead Beds have been correlated with the Sables de Boutersem of the late Tongrian[18] of Belgium which contain the localities of Hoogbutsel and Hoeleden. The fauna of these localities contains immigrants of the « Grande Coupure ». As Glibert and de Heinzelin (1952) have pointed out, the fauna of Hoogbutsel, which is clearly younger than the « Grande Coupure », was found in the section at Butsel rather far below the Sables de Berg which define the base of the middle Oligocene.

A single other Oligocene locality is known in Belgium : a few mammalian remains have been noted at Burght in the Argile de Boom (*Aceratherium albigense*).

---

[18] Dumont, 1839 ; type locality near Tongres, Belgium.

Basins of Switzerland and of Savoy

No localities are known from the beginning of the Oligocene. The oldest, Balm (Switzerland) and Lovagny (Savoy), have been considered as close to the level of Montalban (see Schaub, *in* Erni, 1941 ; Vianey-Liaud, 1972-1979 b). The end of the middle Oligocene and the late Oligocene are represented by many localities, certain of which have played an important role in the biozonation of this period (Thaler, 1964, 1966) : Oensingen-Ravellen (level of Mas de Pauffié), Boningen-Aarwangen (level of Boningen), Rickenbach and Küttingen (level of Coderet).

West Germany

The recently published proposition (by Cavelier and Pomerol, 1977) of a stratigraphic scale for the Paleogene (see p. 37) including, in particular, the placement of the Eocene-Oligocene limit (fig. 1), renders necessary an explanation of the countercurrent of thought regarding this boundary as it is particularly expressed in West Germany. This opposition cites the rules applying to stratigraphic terms, which state that the lower Oligocene is bound to the glauconitic sands of Westeregeln (northern Germany), designated by Beyrich, 1854 (the author of the Oligocene) as the lowest part of his newly created epoch. The same beds later furnished the type section of the Lattorfian (Mayer-Eymar, 1893). Recent investigations have revealed that the Oligocene, and consequently the Lattorfian, of the type area begins with sediments corresponding to the nannoplancton zone NP 21, thus permitting an international resolution of the Eocene-Oligocene limit (see Berggren, 1972 ; Steininger, Rögl and Martini, 1976). However, the Lattorfian nannoplancton zones are treated in some detail by Cavelier (1979), which did not prevent him from considering the Eocene-Oligocene limit as being earlier than this stage. The synthesis presented by Cavelier combines data from the disciplines of invertebrate and vertebrate paleontology, stratigraphy, paleoclimatology, isotopic radiometry and the multiple aspects of paleobotany in an attempt to establish this limit on the broadest possible basis of facts. It is to be hoped that differences in interpretation, and hence of opinion, can soon be reduced or even eliminated.

Although Paleogene mammals have long been known in Germany, investigations especially concerned with their geochronology are of rather recent date. Dehm (1935, 1950) was the first to explore German mammal localities not only for their paleontological interest, but also from a stratigraphical point of view. In the upper Rhine graben and in northern Hesse, work on the stratigraphical position of sites has been mainly done by Tobien (1949, 1968, 1972). Localities in the Lower Freshwater Molasse of southern Germany, possessing a high potential for new geochronological study, were first made known by the studies of Vollmayr (1966). Additional contributions to the subject have been made by Franzen (1968), Schmidt-Kittler (1971), Bahlo (1975), and Schmidt-Kittler and Vianey-Liaud (1975).

Paleogene mammal localities in Germany are mainly concentrated in the Oligocene. Their frequency, and vertical distribution, is such that a stratigraphic scale,

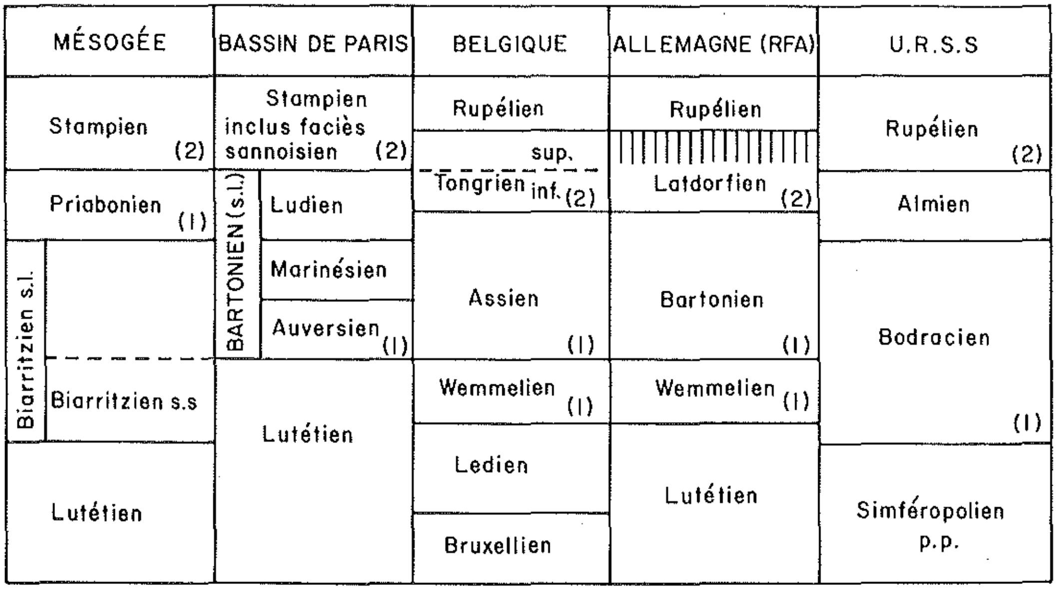


Fig. 16. — Chart showing the relationships between the different stage names presently used in certain regions of Europe. The lines marked by (1) indicate the limit generally used to separate the middle Eocene and the late Eocene ; those with (2) indicate the Eocene-Oligocene limit. In Belgium and Germany the Wemmelian more or less straddles the middle Eocene late Eocene limit. The term Assian in Belgium is becoming less used and is now often replaced by « Bartonian », associated or not with the Wemmelian. From Cavelier, 1979.

practically without gaps, can be constructed. The sites mentioned in fig. 19 are important partly because of the abundant vertebrate remains they contain, or the high correlative value of certain faunal elements, and partly because of their intercalation with well defined sections. The lithostratigraphic chart of fig. 18 presents only an approximation of the sections ; the details of lateral variations in the upper Rhine graben and the Mainz Basin, for instance, are omitted.

Most of the German Oligocene collections have been made from fissure fillings in the Jurassic limestones in the southern part of the country. A small number of localities occur in continental beds or in sediments that are transitional between marine and continental environments.

Figuring among the principal sites, Möhren 19 and Ehrenstein 1B, the oldest localities with cricetids, contain *Palaeotherium duvali* and *Palaeotherium medium*. These perissodactyls indicate a level approximately equal to that of Frohnstetten. Ronheim 1 and Möhren 13, with *Theridomys aquatilis*, are contemporary with the horizon of Ronzon and Hoogbtusel. Schelklingen 1, with the primitive *Blainvillimys gregarius*, is close to the Villebramar horizon. Bernloch 1 has furnished an evolutionary stage of *Suevosciurus ehingensis* similar to that found at Itardies (Quercy), at the level of Montalban. Burgmagerbein 2 contains *Archaeomys gracilis*, which is indicative of the Heimersheim - Antoingt horizon. The rodent assemblage of Gaimersheim is very

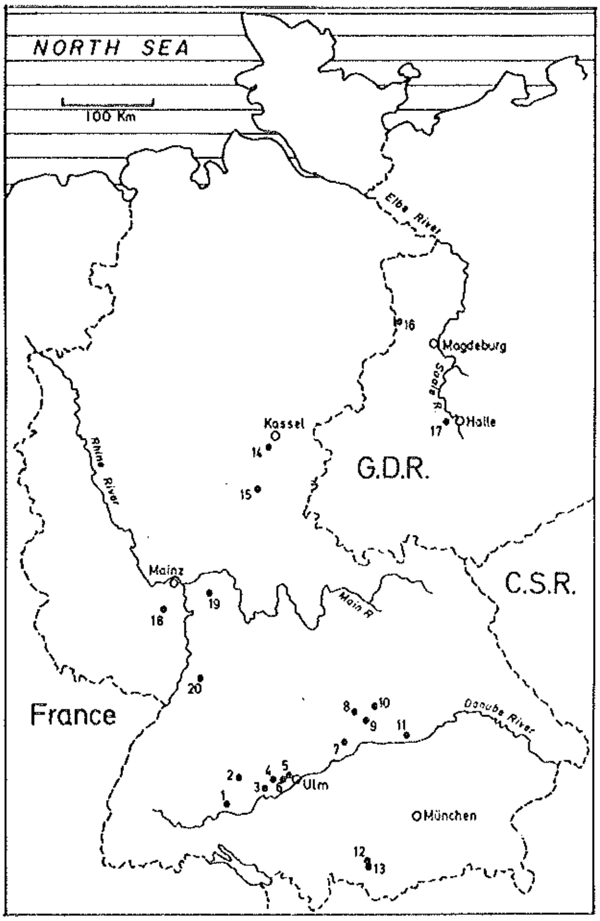


Fig. 17. — Distribution of the principal localities for mammalian geochronology in Germany : 1. Frohnstetten ; 2. Bernloch ; 3. Ehingen 1 ; 4. Schelklingen 1 ; 5. Ehrenstein 1 (A), 4 ; 6. Herrlingen 1 ; 7. Burgmagerbein 2 ; 8. Heidenheim am Hahnenkamm ; 9. Möhren 6, 13, 19 ; 10. Weissenburg 8 ; 11. Gaimersheim ; 12. Echelsbacher Brucke ; 13. Schleifmuhle 1 ; 14. Nordshausen ; 15. Neistadt ; 16. Walbeck ; 17. Geiseltal ; 18. Heimersheim ; 19. Messel ; 20. Rot-Malsch. G.D.R., German Democratic Republic ; G.F.R. German Federal Republic ; C.S.R. Czechoslovakian Socialist Republic.

similar to that of Pech du Fraysse and, consequently, to that of Boningen horizon. The Ehrenstein 4 fauna cannot be differentiated from that of Coderet.

Correlation problems are caused however by the presence of the upper Rhine graben, which has presented a marine or brackish barrier during most of the early and middle Oligocene ; this ecologic filter was probably especially effective for rodents, forming a wet lowland between the French Quercy region and the rather dry, high Jura plains of southern Germany. Relatively strong endemism in the rodent faunas of the two regions has been demonstrated by Schmidt-Kittler and Vianey-Liaud (1975). Nevertheless, the German sites can be correlated with French localities and with those on the Isle of Wight in southern England (the latter are conveniently intercalated with marine sediments). A biostratigraphic history of the numerous karst faunas of southern Germany can be created from the evolutionary steps of the theridomyid *Pseudosciurus*, which occurs from the end of the Priabonian to the middle Stampian (called respectively early Oligocene and middle Oligocene in Schmidt-Kittler, 1971). The faunas of the latter part of the Oligocene can be correlated mainly using the theridomyids *Blainvillimys* and *Archaeomys* (Schmidt-Kittler and Vianey-Liaud, 1975).

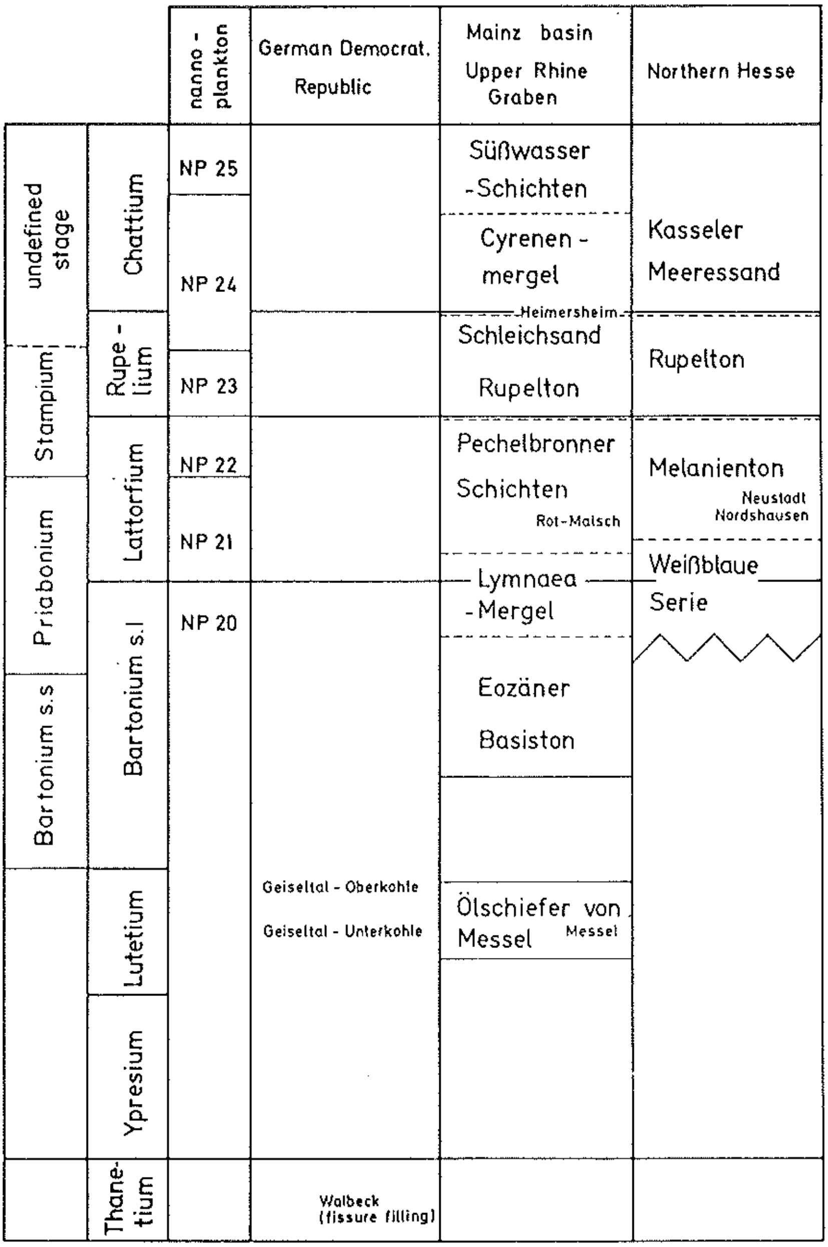


Fig. 18. — Correlation chart of mammal sites and geologic sections important for mammalian geochronology in Germany. The sections of the Main basin and Northern Hesse are simplified after Anderson *et al.*, 1969. Concerning the mammalian reference localities see Fahlbusch, 1967.

The relatively rich fauna of Heimersheim corresponds to the middle Oligocene - late Oligocene boundary (Tobien, 1955 ; Bahlo, 1975). It was found in sediments transitional between the Schleichsand and the overlying Cyrenenmergel (*Cyrena* marls) ; the latter are equivalent in age to the Kasseler Meeressand, the type deposit of the late Oligocene. The Heimersheim assemblage is older than that of Antoingt.

The Oligocene part of the Lower Freshwater Molasse of southern Germany contains many localities that are still far from adequately explored. At the beginning of the continental sedimentary cycle there occurs in a coal bed (at Echelsbacher Brücke) a

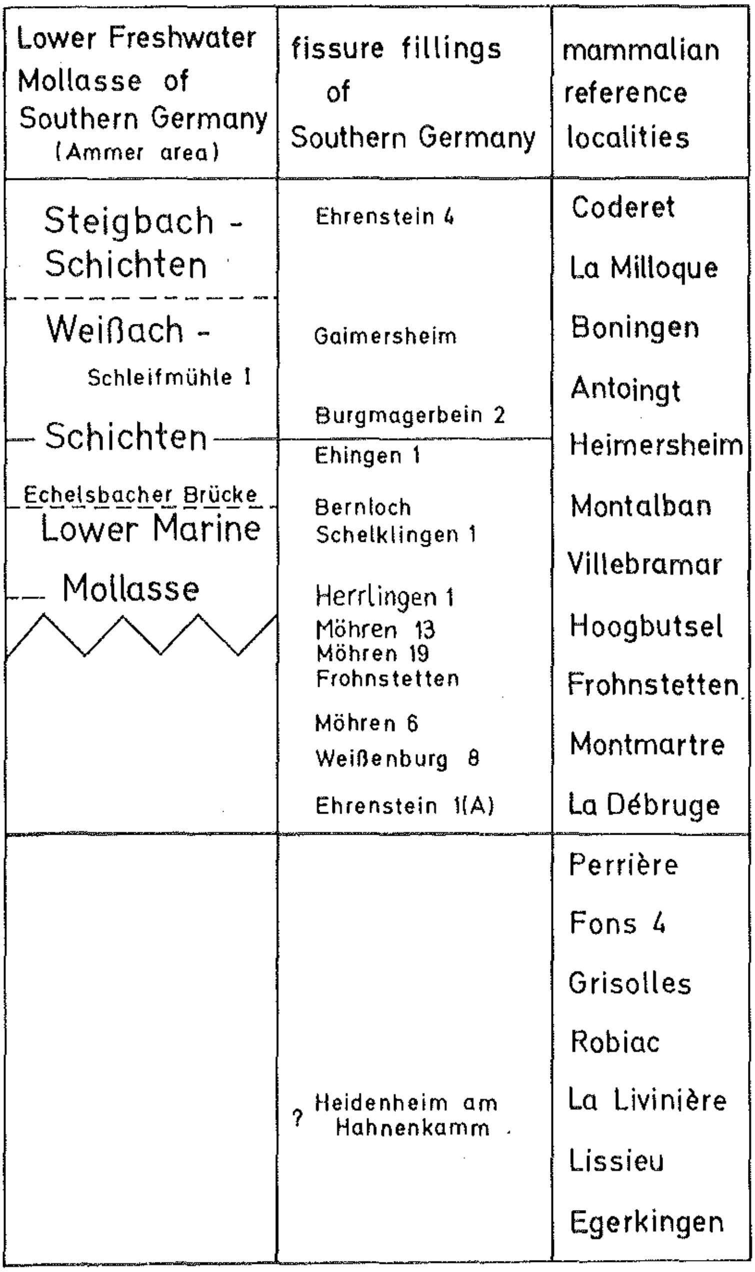


Fig. 19. — Stratigraphie distribution of principal mammal localities in the late Paleogene of Germany.

theridomyid (*Suevosciurus*) which shows a degree of evolution typical of those also occurring in the middle Oligocene karst faunas of the same region. It is hoped that additional material from this horizon, combined with investigations of nannoplankton from the underlying sediments, will be an aid in correlating with marine chronostratigraphy.

In the Austrian part of the Molasse (the Vorarlberg region), littoral beds (the Linzer Sande) have yielded a few large mammals (*Halitherium abeli, Diceratherium minutum kuntneri, Ronzotherium velaunum, Anthracotherium* cf. *alsaticum, A.* cf. *magnum, Elomeryx* sp.) which indicate a middle Oligocene age. A single form, *Microbunodon minus*, known only from the end of the Oligocene in Western Europe, seems to indicate a younger age, but it is possibly reworked from the overlying formation (Sickenberg, 1934 ; Semes, 1975).

Future work in West Germany will continue exploitation of its rich Oligocene deposits, and emphasis will be put on direct or indirect correlations with marine sediments in the Mainz Basin and the upper Rhine graben, as well as in the Lower Freshwater Molasse in the south. Although correlation between mammal localities depends mainly on rodents, their strongly marked endemism during most of the Oligocene requires that future investigations consider palaeoecological differences between German and more western European regions. At present it can be shown that the rodents of the lowland sites (the upper Rhine graben, Mainz Basin, Rhône Valley, Isle of Wight, etc.) resemble each other more than they do assemblages of the high plains, like the karst region of Quercy (France) and the Jura of southern Germany. Concentration, therefore, on the lowland faunas is necessary in future because these have the greatest potential for refining correlations.

Spain

The localities of the early Oligocene in Spain are few ; Espinosa de Henares (Guadalajara), and Rocallaura (La Segarra) have yielded only *Entelodon magnum* (Crusafont-Pairó *et al.*, 1962 ; Golpe-Posse, 1974). Calaf has furnished *Peratherium leptognathus, Theridomys major*?, *Diplobune minor, Ephelcomenus* sp. and *Bothriodon aymardi.* As in the rest of Europe, the arrival of *Bothriodon* and *Entelodon* marks the « Grande Coupure ».

In Majorca, the age of the lacustrine series extends from the early Ludian to the middle Oligocene. Several localities (Selva, Lloseta, Manacor and Sineu), with rather short faunal lists, have produced in particular *Plagiolophus fraasi, Diplobune secundaria, Anoplotherium commune* and *Anthracotherium magnum* or *A. alsaticum* (Colom, 1961, 1972 ; Golpe-Posse, 1974).

The richest localities are those of Montalban (Aragon) and El Talladell (Tarrega, Barcelona). Their fauna is characteristic of the middle Oligocene (Montalban horizon) and includes in particular *Plagiolophus* cf. *fraasi* and the rodents *Theridomys major, Blainvillimys gregarius, Elfomys nanus, Pseudoltinomys major* and *Pseudocricetodon montalbanensis* (Crusafont-Pairó, 1967 ; Thaler, 1969 ; Vianey-Liaud, 1979 b).

The more recent localities are Campins (Barcelona) and Cerro Arenosa (Carrascosa) (*Cadurcotherium nouleti*). The presence of the rodent *Issiodoromys minor* establishes a relationship to the horizon of Antoingt (end of the middle Oligocene).

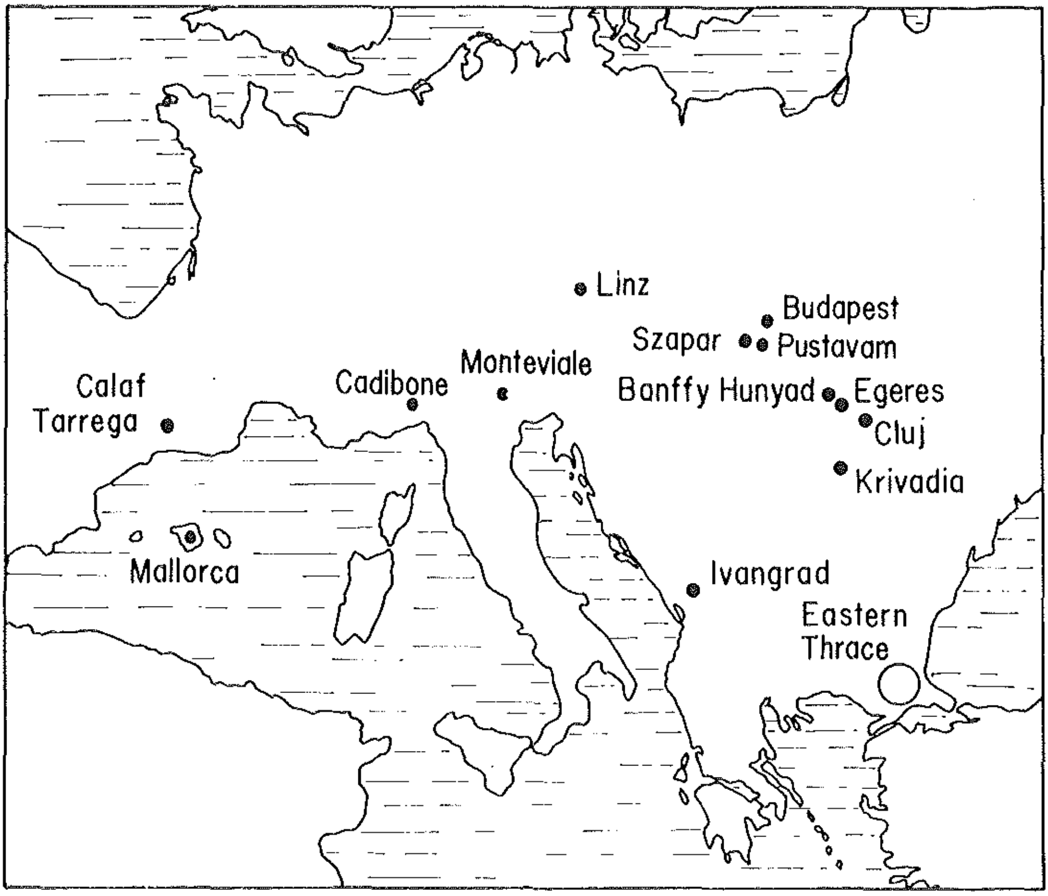


Fig. 20. — Geographic distribution of Oligocene mammal localities in south and central Europe.

Hungary

Mammal localities of the transdanubian region have been found in the Szapar Formation and in the Cstakaï complex. The lignites of Szapar and Vertessomlya have yielded *Anthracotherium magnum* (Jámbor *et al.*, 1969). A bore-hole at Ganna (in the Bakony Mountains) has furnished a single eomyid tooth : *Meteomys noskyi* (Kretzoï, 1951). Another tooth of a primitive eomyid has been recovered from the locality of Sür : *Pseudotheridomys* (*Anomegodus*) *baconicus* (Jámbor *et al.*, 1969) and the skull of a new cricetid : *Heterocricetodon* (*Alsocricetodon*) *telonii* (Jámbor *et al.*, 1969) has been collected from a bore-hole in Cstakaï complex at Pustavam.

Apart from these rare finds from stratified formations, two karstic fillings have produced mammals. In one, only *Protaceratherium albigense* (Kretzoï, 1940) has been found, but the other, Bodajk Kajmat, is richer, and especially in micromammals. A complete and accurate faunal list of this site has not yet been established. Jámbor *et al.* note the presence of «squirrels, dormice», *Diplobune, Sciuroides* and the absence of lagomorphs.

The few fossils chronologically useful (*Anthracotherium, Protaceratherium* and *Diplobune*) indicate a middle Oligocene age for the ensemble of the localities. In the present state of our knowledge it is difficult to be more precise.

Romania

Most of the few remains of Paleogene mammals described from this country come from the region west of Cluj ; from Andrashaza, *Prohyracodon orientale* and *Brachydiastematherium transylvanicum*, from Egeres is known *Allacerops kochi, Anthracotherium magnum* and *Kochictis centenii*, and from Banffy Hunyad, *Entelodon* aff. *deguilhemi*. Indricotheriid remains have also been described from the area near Cluj. Further south, from Krivadia, *Entelodon magnum* has been cited and *Crivadiatherium mackennai* has recently been described (see Kretzoï, 1940, 1943 ; Thenius, 1959 ; Gabounia and Iliescu, 1960 ; Crusafont-Pairó and Russell, 1967 ; Brunet, 1979 ; Radulesco *et al.*, 1976).

With the exception of *Kochictis* (a paroxyclaenid), *Brachydiastematherium* (a brontothere) and *Crivadiatherium* (an embrithopod), unknown outside of this area, these mammals seem to indicate an age equivalent to an interval between the summit of the early Stampian and the middle Stampian. *Prohyracodon orientale*, however, was originally described as being from the middle Eocene ; Radinsky (1967), finding it precocious, suggested it was of late Eocene age. Radulesco regarded the level in which *Crivadiatherium* was found to be questionably late Eocene or, more probably, early Oligocene. The beds (characterized by the presence of *Corbula*) that yielded the unique specimen of *Kochictis* are considered to be late Oligocene in age.

Yugoslavia

Of particular interest is the occurrence of indricotheriids in the Oligo-Miocene basin of Ivangrad (Montenegro). The remains were found in lignite deposits similar to those yielding Oligocene fossils in Transylvania and the Caucasus (at Benara). The age of the locality was considered to be late Oligocene or early Miocene by Petronijevic and Thenius (1957).

Turkey

Oligocene mammals in Turkey are more numerous than those from the preceding part of the Paleogene and the localities that produced them, concentrated in Thrace (European Turkey) and western Anatolia, are better situated stratigraphically. Their age assignements are principally due to the work of Lebküchner (1974), based on ver-

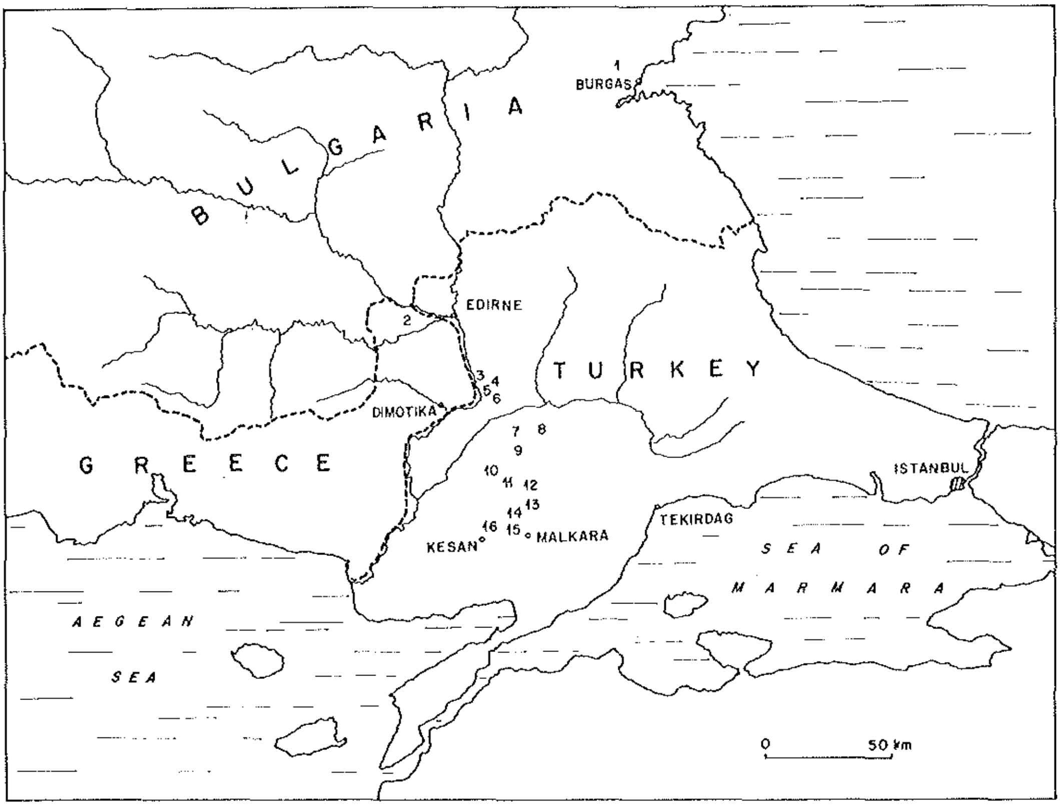


Fig. 21. — Oligocene mammal localities in Turkish Thrace, Greece and Bulgaria : 1. Tscherno More (Bulgaria) ; 2. Chantras (Greece) ; 3. Sigircili : 4. Meseliköy ; 5. Kurttepe ; 6. Hamitli ; 7. Sipahi ; 8. Karabürçek ; 9. Elmali ; 10. Harmanli ; 11. Çavuslu ; 12. Tatarcedit ; 13. Ibrice ; 14. Hask ; 15. Yaylagöne ; 16. Karakaya.

tebrate and stratigraphic studies, and on pollen analysis by Nakoman (1966). These sites (see Fig. 21) have yielded only the remains of anthracotheres. The first discovery, that of *Elomeryx woodi*, was described by English (1904) ; Yalçinlar (1954) and Ozansoy (1962) dealt in more detail with material from other localities. The species is the same as that found at Chantras in the Greek part of Thrace (Lüttig and Thenius, 1961), and ranges in time from early to late Oligocene. *Anthracotherium prealsaticum* Ozansoy (1963) is represented by a maxillary from the lignites of Karakaya (northeast of Kesan, in eastern Thrace), dated as early Oligocene. A few dental fragments (described by Ozansoy, 1964) from Karakaya and Çavuslu (from the same region) belong to a form close to *Anthracotherium monsvialense* Dal Piaz (1932). Widely distributed in more than a dozen localities in Turkish Thrace, *Anthracotherium magnum* is represented by relatively abundant material. Yalçinlar (1954) noted the existence of a large anthracothere (*Anthracotherium* sp.) in the lignites of Tavsanli (western Anatolia), at a level that is apparently late Oligocene.

The rare faunal elements of oriental Thrace are similar to those of western Europe, which indicates paleogeographic continuity between the two areas. However, the Paleogene faunas of Turkey, and of its neighbors to the north and west, are still essentially unknown. Moreover, the chronologic position of the localities that have produced sparse mammalian remains, particularly those of the Eocene, still lack precision.

THE FAUNA

The European Oligocene mammal fauna is, to a minor degree, made up of forms derived from endemic Eocene groups and, for the major part, of allochthonous forms, early immigrants of the «Grande Coupure», or later ones whose appearances were distributed throughout of Oligocene.

Among the rodents, the Theridomyidae, with 14 genera, represented the dominant family at the end of the Eocene, but lost this hegemony with the massive arrival of immigrants and the extinctions marking the «Grande Coupure». In the early Oligocene only 8 species are represented. A renewal of theridomyine importance character-

			THRACE		ANATOLIA		ADJACENT AREAS	
			localities	mammals	localities	mammals	localities	mammals
OLIGOCENE	LATE	X	Elmali Sipahi	Elomeryx woodi E. sp.	Tavşonli	Anthracotherium sp.	Chantras (Greece)	Elomeryx woodi
		IX	Karabürçek Sipahi Tatarcedit	Anthracotherium magnum A. sp				
		VIII	—	—				
		VII	Karabürçek	Elomeryx woddi Anthracotherium cf. magnum				
	EARLY	VI	Yaylagöne Hasköy Ibrice	Elomeryx woodi				
		V	—	—				
		IV	Harmanli Çavuşlu	E. woodi E. cf. porcinus Anthracotherium cf. monsvialense A. sp				
		III	Karakaya Kirikali	Elomeryx woodi Anthracotherium cf. monsvialense A. prealsaticum				
		II	—	—				
		I	—	—				
EOCENE	LATE				Yaglit	Erinaceidae indet.	Tscherno More (Bulgaria)	Elomeryx spp.
	MIDDLE							
	EARLY				Eski Çeltek Fakili Boyabat	Palaeoamasia kansui		

Fig. 22. — Stratigraphic distribution of the Paleogene mammal localities of Turkey, Greece and Bulgaria. The roman numerals refer to stratal zones as arranged by Lebküchner, 1974.

ized the middle Oligocene since 11 species coexist at this level ; but this second apex is of short duration : with the beginning of the late Oligocene, 6 species persist and only 3 at the end of the Oligocene.

This evolution of the Theridomyidae has been related to the progressive aridification of the Oligocene climate (Vianey-Liaud, 1979 b). The forms that were probably aquatic, like the *Theridomys aquatilis* — *T. lembronicus* lineage, disappear rapidly. Moreover, the disappearance of tropical vegetation, the installation of new forests (cupulifers and conifers), and perhaps, in correlation with the increasing aridity, the extension of open and steppe regions, all contributed to the creation of new biotopes favoring the differentiation of new species. This could be one of the causes for the cladogenesis of *Archaeomys* in the middle Oligocene and also for the realization of hypsodont and taeniodont teeth in the Theridomyinae. In a hot and dry environment, only the three well adapted lines of theridomyines (*Blainvillimys geminatus, Archaeomys laurillardi* and *Issiodoromys pseudanaema*) persisted until the end of the Oligocene.

Glirids evolved from autochthonous lineages and without great diversification up to the beginning of the late Oligocene. At that time an adaptative explosion began : 6 species of Gliridae occur in the late Oligocene and, in the Aquitanian, at least 12 lineages are represented.

The families of Oligocene Chiroptera differentiated from Eocene autochthonous forms. Alone, the vespertilionids appear after the «Grande Coupure» and still it is not impossible that they derived from the Eocene Kerivoulidae (Sigé, 1975).

Among the perissodactyls, the last Palaeotheriidae became extinct in the middle Oligocene (*Plagiolophus fraasi* and *P. minor* of the Villebramar horizon).

In nearly all of the mammalian groups, the forms that arrived at the time of the «Grande Coupure» were supplemented by immigrants that followed in successive waves throughout the Oligocene. The Dimylidae, whose date of arrival is still indefinite (middle or late Oligocene), continue until the Aquitanian.

Among the Rhinocerotidae, *Epiceratherium* is known with certitude only in the early Oligocene of Venetia (Monteviale) and *Aceratherium* in the middle Oligocene (above the Villebramar level). *Brachypotherium* appears at the end of the Oligocene (La Milloque) and persists into the Neogene.

The change in character of the creodonts, due to the replacement by immigrants of persistent archaic elements or endemic species, is documented by Lange-Badré (1979).

For the Carnivora, according to de Bonis (1974), the sudden appearance of most, if not all the genera, evokes the idea of successive migrations more than that of indigeneous evolution. The most important wave seems to have been that of the middle Oligocene, which introduced *Stenoplesictis, Nimravus, Pachycynodon, Cephalogale, Plesictis, Stenogale* and *Paleogale.* In the late Oligocene only the genus *Amphictis* makes itself known for the first time.

Among the artiodactyls, after the arrival of *Entelodon* at the «Grande Coupure», the Tayassuidae and the Anthracotheriidae appear successively during the middle (*Palaeochoerus* and *Anthracotherium*) and the late Oligocene (*Doliochoerus*). The first Gelocidae are known in middle Oligocene localities (*Bachitherium, Prodremothe-*

rium, Gelocus) and the appearance of the Cervidae occurs in the late Oligocene (*Amphitragulus*).

The rodent fauna of the late Oligocene presents a great diversity (Gliridae, Theridomyidae, Rhizospalacidae, Castoridae, Zapodidae, Sciuridae, Cricetidae, Eomyidae and Aplodontidae). At the end of that period the extinction of specialized forms, like *Archaeomys* and *Issiodoromys*, adapted to a rather arid environment, is related to the climatic modifications of the beginning Miocene and probably also to the development of the lagomorphs, possible competitors in their ecologic niche.

The faunal renewal for most of the mammals manifested itself essentially by the disappearance of several lineages, such as those of the Hyaenodontidae or the Theridomyidae already cited, and by the transformation and, occasionally, the diversification of autochthonous groups (Gliridae, for example). No massive immigrations can be detected. Due to these combined circumstances, the Aquitanian fauna is an impoverished one. It is only with the Burdigalian that it will again diversify, this time particularly by the arrival of the Equidae (*Anchitherium*), the primates and the proboscideans.

OLIGOCENE CHARACTERIZING ASSEMBLAGES

Early Oligocene

Two levels can be distinguished on the basis of rodents : that of Ronzon — Hoogbutsel and that of Villebramar. According to the evolutionary stages of *Entelodon* (*E. antiquum — E. magnum*) Brunet (1979) believes it is possible to differentiate a level immediately preceeding Ronzon, referred to as Soumailles. The rest of the fauna, as it is presently known, does not permit such a distinction. *Palaeotherium medium*, which, according to Brunet, does not extend above the level of Soumailles, is also found at Aubrelong 1 in association with *Entelodon magnum* (de Bonis *et al.*, 1973). It is nevertheless true that the two evolutionary stages of *Entelodon* demonstrate a chronologic difference between Soumailles and Ronzon. But in the relatively generalized framework under consideration here, it seems simpler to utilize only one faunal association.

1. Level of Hoogbutsel.

Referred localities : Soumailles, Ronzon, Sainte-Marthe, Aubrelong 1, Ravet, Mazan, Fontaines-de-Vaucluse, Lower Hamstead Beds, Möhren 13, Ronheim 1, Thorigny.

Combined faunal association :

Marsupialia : *Peratherium elegans, Peratherium lavergnense, Amphiperatherium exile, Amphiperatherium ambiguum, Amphiperatherium lamandini.*

Insectivora : *Cryptopithecus siderolithicus, Tetracus nanus, Dyspterna woodi, Butselia bieveri, Darbonetus aubrelongensis.*

Chiroptera : *Palaeophyllophora* cf. *quercyi, Hipposideros* cf. *morloti, Vespertilianus* cf. *gracilis.*

Rodentia : *Microsuevosciurus palustris, Tarnomys quercinus, Theridomys aquatilis, Steneofiber butselensis, Blainvillimys langei, Pseudoltinomys gaillardi, Suevosciurus ehingensis, Suevosciurus fraasi, Pseudosciurus suevicus* (subterminal stage), *Sciuromys* sp. *Gliravus* aff. *priscus, Gliravus* cf. *majori, Peridyromys micio, Paracitellus cingulatum, Paracitellus marmoreus, Oligopetes radialis, Oligopetes lophulus, Oligopetes obtusus, Trigonomys simplex, Palaeosciurus* sp., *Sciurodon cadurcensis, Eomys antiquus, Eucricetodon atavus,* (*Pseudocricetodon montalbanensis* and *Paracricetodon dehmi,* east of the Rhine graben).

Lagomorpha : *Shamolagus* sp., *Shamolagus franconicus.*

Creodonta : *Hyaenodon dubius.*

Carnivora : *Cynodon velaunus, Eusmilus bidentatus, Pseudocyonopsis antiquus, Brachycyon gaudryi.*

Perissodactyla : *Palaeotherium medium, Pseudopalaeotherium longirostrum, Plagiolophus minor, Ronzotherium velaunum, Eggysodon* sp.

Artiodactyla : *Entelodon antiquum* (Soumailles), *Entelodon magnum* (other localities), *Bothriodon velaunum, Bothriodon aymardi, Bothriodon leptorhynchum, Dichobune leporina, Cebochoerus* sp., *Paroxacron* sp., *Amphimeryx riparius, Gelocus communis, Tapirulus* cf. *hyracinus, Elomeryx woodi.*

2. Level of Villebramar.

Referred localities : Mas d'Agenais, Roqueprune 2, Mas de Got, La Plante 2, Schelklingen 1, Lobsann, ? Monteviale, upper Hamstead Beds.

Combined faunal association :

Marsupialia : *Peratherium elegans, Amphiperatherium minutum, Amphiperatherium lamandini, Amphiperatherium ambiguum, Amphiperatherium exile.*

Insectivora : *Tetracus nanus.*

Chiroptera : *Palaeophyllophora* cf. *quercyi, Hipposideros* cf. *morloti, Hipposideros* aff. *schlosseri.*

Rodentia : *Blainvillimys gregarius* (primitive stage), *Elfomys medius, Pseudoltinomys major, Sciuromys cayluxi, Suevosciurus fraasi, Suevosciurus ehingensis, Pseudosciurus suevicus* (terminal stage), *Eucricetodon atavus* (*Pseudocricetodon montalbanensis* and *Melissiodon* aff. *schaubi,* east of the Rhine graben), *Gliravus majori, Gliravus priscus, Peridyromys* aff. *micio, Plesispermophilus angustidens, Palaeosciurus goti.*

Creodonta : *Hyaenodon dubius, Hyaenodon leptorhynchus, Apterodon gaudryi.*

Carnivora : *Pseudocyonopsis quercyensis, Pseudocyonopsis landesquei, Pseudoambiguus, Cynelos crassidens, Cynelos piveteaui, Brachycyon gaudryi, Symplectocyon praecursor, Harpagophagus sanguineus, Pseudamphicyon lupinus, Sarcocyon ferox, Haplocyon robustus, Haplocyon elegans.*

Perissodactyla : *Plagiolophus fraasi, Eggysodon* sp., *Ronzotherium filholi,* (*Epiaceratherium*).

Artiodactyla : *Dichobune jehennei, Entelodon deguilhemi, Anthracotherium alsaticum,* (*Anthracotherium monsvialense*), *Gelocus* sp., *Lophiomeryx chalaniati, Prodremotherium elongatum, Plesiomeryx cadursensis,* (*Anthracochoerus stehlini, Palaeochoerus paronae*), *Metriotherium minutum.*

Early Oligocene of Spain

Referred localities : Rocallaura, Espinosa de Henares, Calaf.

Combined faunal association :

Marsupialia : *Amphiperatherium frequens.*

Rodentia : *Theridomys crusafonti.*
Artiodactyla : *Entelodon magnum, Bothriodon aymardi, Diplobune minor, Ephelcomenus* sp.

Middle Oligocene

In the middle Oligocene, the evolutionary stages of the rodents permit four marker horizons to be distinguished. The indications based on the macrofauna are less precise as only three successive assemblages are discernable. In order to make use of as many mammals as possible, the three latter levels are presented.

1. Level of Montalban.

Referred localities : Itardies, Pech-Crabit, Mège, Lovagny, Balm, Tarréga, Bernloch 1.
Combined faunal associations :

Marsupialia : *Peratherium elegans.*
Insectivora : *Tetracus nanus, Neurogymnurus* ? sp.
Chiroptera : *Palaeophyllophora oltina, Rhinolophus* cf. *priscus, Vespertiliavus* sp., *Stehlinia minor, Stehlinia* sp.
Rodentia : *Blainvillimys gregarius* (evolved), *Theridomys major, Pseudoltinomys major, Elfomys nanus, Elfomys medius, Sciuromys cayluxi, Taeniodus curvistriatus, Suevosciurus fraasi, Suevosciurus ehingensis, Pseudosciurus suevicus* (terminal stage), *Eucricetodon atavus, Eucricetodon huerzeleri, Pseudocricetodon montalbanensis, Paracricetodon cadurcensis,* (*Paracricetodon dehmi* and *Melissiodon schaubi* east of the Rhine graben), *Eomys zitteli, Palaeosciurus goti, Heteroxerus* aff. *paulhiacensis, Plesispermophilus angustidens, Gliravus* sp., *Peridyromys* sp.
Creodonta : *Thereutherium thylacoïdes, Hyaenodon dubius, Hyaenodon exiguus.*
Carnivora : *Stenoplesictis minor, Nimravus intermedius, Stenogale gracilis, Plesictis* sp., *Amphicynodon leptorhynchus, Amphicynodon* cf. *speciosus, Pachycynodon tenuis, Pachycynodon dubius, Cynodictis* sp.
Perissodactyla : *Plagiolophus fraasi, Hyrachyus minimus*?, *Aceratherium albigense, Ronzotherium filholi*?.
Artiodactyla : *Metriotherium* sp., *Elomeryx* sp., *Anthracotherium monsvialense, Gelocus communis, Bachitherium medium, Diplobune minor, Caenomeryx procommunis, Propalaeochoerus* sp., *Cainotherium* sp.

2. Level of La Ferté-Alais = ? Les Chapelins + Heimersheim.

Referred localities : Les Chapelins, Heimersheim, Saint-Martin de Briatexte, Saint-Martin de Castillon, Murs, Genebrière 1, Belgarric, Ehingen 1, Burgmagerbein.
Combined faunal association :

Marsupialia : *Peratherium elegans.*
Rodentia : *Blainvillimys helmeri, Blainvillimys heimersheimensis, Taeniodus hexalophodus, Taeniodus curvistriatus, Archaeomys gracilis* and *Archaeomys gervaisi,* primitive stage (level of Heimersheim) *Suevosciurus ehingensis,* terminal stage, *Pseudoltinomys* aff. *major, Elfomys* cf. *medius* (*Issiodoromys* aff. *minor,* level of Heimersheim), *Eucricetodon* cf. *atavus-huberi, Pseudocricetodon philippi, Pseudocricetodon moguntiacus, Paracricetodon dehmi, Paracricetodon walgeri, Paracricetodon spectabile, Melissio-*

don schaubi schaubi, Sciurodon sp., *Heteroxerus* sp., *Gliravus tenuis, Oligodyromys planus, Glirudinus* cf. *praemurinus, Plesiosminthus* aff. *promyarion.*
Perissodactyla : *Ronzotherium romani, Eggysodon gaudryi.*
Artiodactyla : *Anthracotherium* sp., *Entelodon* sp., *Bachitherium* sp., *Lophiomeryx* sp.

3. *Level of Antoingt* = ? Etampes.

Referred localities : Campins, Carrascosa, Rigal-Jouet, Saint-Vincent-de-Barbeyrargues, Les Matelles, Aubenas-les-Alpes, Mümliswyl, Etampes.
Combined faunal association :

Marsupialia : *Peratherium elegans.*
Insectivora : *Tetracus nanus, Myxomygale* sp.
Rodentia : *Blainvillimys blainvillei, Theridomys lembronicus, Archaeomys gervaisi, Archaeomys gracilis, Issiodoromys minor, Taeniodus curvistriatus, Eucricetodon huberi, Pseudocricetodon* aff. *montalbanensis, Pseudocricetodon philippi, Paracricetodon* aff. *dehmi, Heterocricetodon helbingi, Melissiodon* sp., *Gliravus* aff. *bruijni* (= *tenuis*?), *Pseudodryomys* sp., *Sciurodon* sp.
Creodonta : *Hyaenodon brachyrhynchus, Hyaenodon gervaisi, Hyaenodon exiguus.*
Carnivora : *Cynelos crassidens*?.
Perissodactyla : *Ronzotherium romani, Aceratherium albigense, Cadurcotherium cayluxi, Schizotherium modicum.*
Artiodactyla : *Palaeochoerus gergovianus, Doliochoerus quercyi, Lophiomeryx chalaniati, Anthracotherium* sp., *Bachitherium insigne, Caenomeryx procommunis, Plesiomeryx cadurcensis.*

Late Oligocene

Like the middle Oligocene, the evolutionary stages of the rodents (4 in number) allow more levels to be recognized in the chronology of the late Oligocene than do the other mammals. Since the macrofauna does not permit such refined distinction, the first two rodent horizons will be considered globally.

1. *Level of Boningen* (= Mas de Pauffié + Boningen) = ? Rabastens.

Referred localities : a/ Mas de Pauffié, Espeyrasse, La Devèze, Saint-Henri ;
b/ Boningen, Aarwangen, La Tuilière, Boujac, Sarèle, Gaimersheim, Rabastens, Cournon, Pech Desse, Pech du Fraysse, Pavoux.
Combined faunal association :

Marsupialia : *Peratherium antiquum, Peratherium elegans, Amphiperatherium exile.*
Insectivora : *Geotrypus cadurcensis, Paratalpa* sp., *Neurogymnurus mediterraneus, Plesiosorex sorinoides.*
Chiroptera : cf. *Palaeophyllophora, Rhinolophus* cf. *priscus, Stehlinia minor,* cf. *Myotis* sp.
Rodentia : *Archaeomys major* (a), *Archaeomys intermedius* (b), *Issiodoromys pauffiensis* (a), *Issiodoromys quercyi* (b), *Blainvillimys geminatus, Steneofiber dehmi, Eucricetodon quercyi, Eucricetodon huerzeleri, Pseudocricetodon* sp., *Pseudocricetodon philippi, Heterocricetodon gaimersheimense* (= *Heterocricetodon schlosseri* ?), *Heterocricetodon* cf. *helbingi, Melissiodon chatticum* (= *Melissiodon quercyi* ?), *Paracricetodon*

spectabile, Plesiosminthus promyarion, Heteroxerus costatus, Heteroxerus cf. *lavocati, Eomys zitelli, Eomys major, Pseudotheridomys pusillus, Pseudotheridomys schaubi, Glirudinus praemurinus, Peridyromys* sp., *Gliravus* aff. *bruijni.*

Creodonta : *Hyaenodon brachyrhynchus.*

Carnivora : *Stenoplesictis cayluxi, Palaeogale* sp., *Amphictis ambiguus, Plesictis* cf. *stenogalinus.*

Perissodactyla : *Ronzotherium romani, Aceratherium albigense, Protapirus* cf. *priscus.*

Artiodactyla : *Anthracotherium* sp. of large size, *Dremotherium* sp., *Elomeryx* cf. *borbonicus, Lophiomeryx chalaniati, Caenomeryx procommunis, Plesiomeryx cadurcensis, Prodremotherium elongatum, Amphitragulus* (?) *nouleti, Palaeochoerus gergovianus, Doliochoerus quercyi aquensis, Ephelcomenus filholi.*

Pholidota : cf. *Necromanis* sp.

2. *Level of Rickenbach.*

Referred localities : Nant d'Avril, Les Chauffours, Saint-Victor-la-Coste, Rickenbach.

Combined faunal association :

Rodentia : *Archaeomys laurillardi helveticus, A. laurillardi laurillardi, Issiodoromys pseudanaema* (large size), *Columbomys* sp., *Rhizospalax poirrieri, Steneofiber? eseri antiquus, Eomys* sp., «*Sciurus*» indet., *Plesiosminthus promyarion, Eucricetodon praecursor, Pseudocricetodon thaleri, Melissiodon quercyi, Gliravus? bruijni, Peridyromys murinus, Glirudinus praemurinus, Gluridinus glirulus.*

Perissodactyla : *Ronzotherium romani.*

Artiodactyla : *Microbunodon minimum.*

3. *Level of Coderet.*

Referred localities : La Milloque (a little older than Coderet), La Mine des Roys, La Colombière, Küttigen, Ehrenstein 4, Coderet.

Combined faunal association :

Marsupialia : *Peratherium antiquum, Amphiperatherium exile.*

Insectivora : *Palaeoerinaceus arvernensis, Heterosorex* sp., Dimylid indet. *Sorex* cf. *pusillus, Geotrypus cadurcensis, Mygatalpa arvernensis.*

Chiroptera : *Rhinolophus cluzeli, Hipposideros branssatensis.*

Rodentia : *Archaeomys laurillardi laurillardi* (evolved), *Issiodoromys pseudanaema* (small size), *Columbomys lavocati, Rhizospalax poirrieri, Allomys ernii, Eucricetodon collatus* (sp. *longidens* at Coderet), *Pseudocricetodon thaleri, Adelomyarion vireti, Melissiodon* aff. *quercyi, Rhodanomys schlosseri* (sp. *transiens* at Coderet), *Rhodanomys* sp., *Pseudotheridomys* aff. *schaubi* or *parvulus, Plesiosminthus schaubi, Peridyromys murinus, Gliravus bruijni, Glirudinus praemurinus, Glirudinus glirulus, Pseudodryomys fugax, Bransatoglis concavidens, Heteroxerus lavocati, Heteroxerus paulhiacensis,* «*Sciurus*» *solitarius,* ? *Paleosciurus* sp. (the size of *feignouxi*).

Lagomorpha : *Amphilagus antiquus, Piezodus branssatensis.*

Creodonta : *Hyaenodon gervaisi, Hyaenodon leptorhynchus, Hyaenodon exiguus.*

Carnivora : *Cephalogale* cf. *geoffroyi, Plesictis julieni* mut. *sicaulensis, Plesictis branssatensis, Plesictis* sp., *Amphictis borbonicus, Stenogale gaillardi, Proailurus* aff. *lemanensis.*

Perissodactyla : ? *Aceratherium albigense, Brachypotherium lemanense, Protapirus aginense, Mesaceratherium* aff. *paulhiacensis.*

Artiodactyla : *Microbunodon minimum, Anthracotherium* sp. (large size), *Palaeochoerus gergovianus elaverensis, Cainotherium* cf. *geoffroyi* (*commune* aff. *elegans*), *Amphitragulus primaevus, Amphitragulus feningrei, Prodremotherium* sp.

CONCLUSION — RADIOMETRIC DATATION

This paper started with chronologic scales based on stratigraphy and on mammalian evolution ; it seems appropriate to close the discussion with the presentation of another scale, that of radiometric calibration. Several hundred radiometric ages have been determined in Europe during the last decade on Paleogene glauconites, principally from France, Belgium and Germany. Others, fewer in number, have been obtained in the Mesogean region and Eastern Europe.

The formations of the Paleogene of Western Europe that are sufficiently rich in glauconite to be dated are :

In the late Paleocene (Thanetian to Landenian) :
- the Thanet Beds (England) ;
- the Bracheux Sands (Paris Basin) ;
- the Gelinden Marls and the Lincent Tuffeau in Belgium.

In the early Eocene (Ypresian) :
- the London Clay and the lower Bracklesham Beds (England) ;
- the Cuisian Sands (Paris Basin) ;
- the Ypres Clay and the Mons-en-Pélève Sands (Belgium).

In the middle Eocene (Lutetian and Bartonian *s.s.*) :
- the middle and upper Bracklesham Beds and the Barton Beds (England) ;
- the « Glauconie grossière » of the base of the Calcaire grossier (Paris Basin) ;
- the Bruxelles Sands and the Wemmel Sands (Belgium).

In the late Eocene :
- the Headon Beds (England) ;
- the « black band » at the base of the Asse Clay and the Neerrepen Sands (Belgium) ;
- the Gehlberg and Silberberg Beds (Germany).

The results published by numerous authors of measurements obtained from glauconites of the above formations, usually by the K-Ar method and more rarely by Rb-Sr, have been assembled in the form of geochronologic scales by Berggren (1972), Rubinstein and Gabunia (1972, 1976), Odin (1973, 1975, 1978, 1981), Cavelier and Pomerol (1976), and Hardenbol and Berggren (1978) (Fig. 23).

These average values are calculated for the K-Ar method with a disintegration constant of λ^{40}K total = 0.584. $10^{10}Y^{-1}$, except Odin (1978) who used λ_e = 0.575. $10^{10}Y^{-1}$. In 1976 the Geochronology Commission of the I.U.G.S. proposed the following constant : λ_e = 0.581. $10^{10}Y^{-1}$. The uncertaintly of the value of the so-called « constant » is evident and introduces an imprecision that can attain 5 %, if the constant utilized in the U.S.S.R. (O.557. $10^{10}Y^{-1}$) is taken into account. This represents about 2 MY for the middle Eocene.

To this uncertainty are added others that are the result of variation in chemical composition and the state of crystalinity of the glauconite and of the physical and/or chemical treatment undergone by the grains during their purification.

Furthermore, in order for a determination to be precise, the crystalline system must have been closed at the moment of mineral formation, and subsequently neither an addition nor a subtraction of radioactive or radiogenic elements resulting from the disintegration of the former should have occurred : if a glauconite dated by K-Ar is enriched in atmospheric argon (argon whose most abundant isotope is the same as that constituting radiogenic argon, that is, ^{40}Ar), especially by the action of great pressure at the time of its formation, its measured age is superior to its real age. On the other hand, a loss of this radiogenic argon (by alteration, by burial to a depth of more than 200 – 500 m, by increase in temperature to more than 100 – 200° C) leads to a diminution of the age of the specimen.

As the number of measurements increases, the specialists have become more and more prudent. But this should not conceal the problem caused by the discordance between the scales proposed by Berggren (1972, 1978) and the second version of Odin's scale (1975). For example, the Lutetian, whose duration is estimated at 5 MY, is dated from 49 – 44 MY by Berggren (1972) and from 44 – 39 by Odin (1975). Thus 44 MY markes the end of the Lutetian for Berggren and its beginning for Odin [the latter now (1981) considers it 45 MY ± 0,5].

An interesting article by Keppens, Elewaut and Pasteels (1979) has been written on the age of the « black band » at the base of the Asse Clay in Belgium (terminal Lutetian or basal Bartonian). With a maximum of experimental precaution, 9 specimens were dated by both the K-Ar and the Rb-Sr methods. In the results, a difference on the order of 1 MY appears between the two methods (K-Ar age – 40.9 MY ± 0.5 ; Rb-Sr age – 41.8 MY ± 0.8). An age of 42 MY is thus reached, in the place of 39 (Odin, 1975), increased in 1978 to 40 MY and now (1981) cited at 39 MY ± 0.5 (Fig. 23). The Rb-Sr date of Keppens *et al.* is intermediate between those of Odin and of Berggren, reducing the discordance to 2 MY instead of 4 or 5.

Another element of discussion comes from the comparison between Paleogene dating of European marine formations and dating of continental formations in North America, rich in mammalian faunas with intercalations of volcanic flows or ash. Some of these formations can even be correlated with marine beds (Berggren, McKenna, Hardenbol and Obradovich, 1978). Good correlation exists, in particular, between the terminal part of the Wasatchian and that of the Ypresian (49 MY).

The Wasatchian is overlain by the Bridgerian, which corresponds to the basal Lutetian and is situated within a range of 49 – 50 and 47 – 48 MY. This continental stage of the base of the middle Eocene can be directly correlated with the Rose Canyon Shale (Ulatisian marine stage). It belongs to the NP 14 (*Discoaster sublodoensis*) biozone, along with P 10 (*Hantkenina aragonensis*).

It seems then that the radiometric dates obtained from glauconite are younger than those from volcanic rock minerals (biotite, sanidine, hornblend). As early as 1964, Obradovich showed that radiometric data from glauconite deviated from its inferred age by more than 10 %. Berggren *et al.* (1978) also noted that glauconite generally yields ages that are anomalously young, and younger than ages obtained on biotite — sanidine from the same level (compare results in Owens and Sohl, 1973, vs. Obradovich and Cobban, 1975).

EPOCH SERIES		TIME IN MILLIONS OF YEARS								
		BERGGREN		ODIN				RUBINSTEIN GABUNIA		CAVELIER POMEROL
		1972	1978	1973	1975	1978	1981	1972	1975	1976
EARLY MIOCENE										
		22,5	22,5	24	22	23	23	25	23,5	22 -24
OLIGOCENE										
		37,5	37	37	35	35	34	37,5	35,5	34-36
EOCENE	PRIABONIAN									
			40				37			39-41
	BARTONIAN									
		44	44	43	39	40	41	45	43	42-44
	LUTETIAN									
		49	49	49	44	45	45	54	51	47-49
	YPRESIAN									
		53,5	53,5	54	51	51	51	60	57	53-55
PALEOCENE										
		65	65	65	64	65	65	68	64,5	63-65
LATE CRETACEOUS										

Fig. 23. — Paleogene geochronology — Comparison of the scales of Berggren (1972, 1978), Odin (1973, 1975, 1978), Rubinstein and Gabunia (1972, 1975) and Cavelier-Pomerol (1976).

Rubinstein and Gabunia column A shows dates published by the authors in 1972, 1975, using decay constant : 0,557 × $10^{-10}y^{-1}$; column B shows dates recalculated with the decay constant used in Western Europe (0,584 × $10^{-10}y^{-1}$). These values are in good accordance with Cavelier and Pomerol (1976) except for the early Eocene. This fact is probably due to a discrepancy in biostratigraphic correlations (i.e. the Simferopolian generally considered by the Russian authors as middle Eocene begins in fact in the early Eocene and ends in the middle part of the Lutetian (Pomerol, 1976).

The reason for this discrepancy between measurements effected with glauconite, whatever the method, and those obtained from volcanic rocks of the same age, remains to be explained ; perhaps closing of the glauconite occurs, in some cases, long after sedimentation (1 to 4 MY for the Paleogene), or perhaps leaks have occurred of argon that are difficult to detect (Pomerol *et al.*, 1980).

In conclusion, we will summarize the results of a critical review of isotopic dates in relation to Paleogene stratotypes (Pomerol, 1978) :

1. The isotopic age of some limits still depends on the choice by stratigraphers of the stratotype boundary. We need first to improve the stratigraphy. More precise isotopic dates for boundaries will follow.
2. The uncertainties of isotopic dating lead us to propose that, provisionally, each date limit be included in an interval of 2 MY. This suggestion is made to avoid a cluttering of the geochronologic literature with fluctuating dates (something concerning the same specimen and the same analysis) which leads to scepticism about glauconite K-Ar dates. It would be desirable for authors to resist the urge to publish uncertain new results immediately. Specimens utilized for the dating should be analyzed in several laboratories. Publication should then not occur until after discussion between geochronologists, sedimentologists, stratigraphers, paleontologists, and paleomagneticians.
3. It is premature to adopt, without discussion, isotopic dates that are not in agreement with biostratigraphic correlations established between marine and continental formations previously dated by several laboratories.
4. In the present state of knowledge it is obvious that, for Paleogene correlations, the precision of isotopic datings is inferior to that of classic biostratigraphic methods.

BIBLIOGRAPHY

ANADON P., FEIST-CASTEL M., HARTENBERGER J.-L., MULLER C., and de VILLALTA J.M., 1982. — Un exemple de corrélation marin-continental dans l'Eocène de Catalogne (Espagne). *Bull. Soc. géol. France* (in press).

ANDERSON H.J., GRAMANN F., RITZKOWSKI S., SONNE V., and TOBIEN H., 1969. — Führer zur Oligozän-Exkursion, Marburg : 115 p.

ANTUNES M.T., 1967. — Dépôts paléogènes de Côja : nouvelles données sur la paléontologie et la stratigraphie. Comparaison avec d'autres formations paléogènes. *Rev. Fac. Cienc.*, Lisboa, 2^e sér., C, v. XV, n° 1, p. 69-111.

ANTUNES M.T. and RUSSELL D.E., 1982. — Le gisement de Silveirinha (Bas Mondego, Portugal) : la plus ancienne faune de vertébrés éocène connue en Europe : *C.r. Acad. Sci. Paris*, t. 293, sér. 2, p. 1099-1102.

BAHLO E., 1975. — Die Nagetierfauna von Heimersheim bei Alzey (Rheinhessen, Westdeutschland) aus dem Grenzbereich Mittel-Oberoligozän und ihre stratigraphische Stellung. *Abh. hess. L. Amt. Bodenforsch.*, Wiesbaden, Bd 71, 128 p.

BERGGREN W.A., 1972. — A Cenozoic time-scale. Some implications for regional geology and paleobiogeography. *Lethaia*, Oslo, v. 5, p. 195-215.

BERGGREN W.A., and VAN COUVERING J.A., 1974. — The Late Neogene. Biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences. *Paleogeogr. Paleoclimat. Paleoecol.*, Spec. Issue, v. 16, n° 1/2, 216 p.

BERGGREN W.A., McKENNA M.C., HARDENBOL J., and OBRADOVICH J.D., 1978. — Revised Paleogene polarity time scale. *Jour. Geol.*, v. 86, p. 67-81.

BERGGREN W.A., AUBRY M.-P., BUJAK J.P., NAESER C.W., and VAN COUVERING J.A., 1980. — The Terminal Eocene Event and the Polish Connection. *26^e Congr. géol. intern.* Paris, Abstracts, v. 1, p. 204.

BEYRICH E., 1854. — Mon. Berlin Akademie, p. 640.

BIGNOT G., and MOORKENS Th., 1975. — Position relative du stratotype de l'Ilerdien et de plusieurs autres étages par rapport à quelques microbiozonations. *Bull. Soc. géol. Fr.*, 7^{e} sér., t. XVII, n° 2, p. 208-212.

BLONDEAU A., CAVELIER C., FEUGUEUR L., and POMEROL Ch., 1965. — Stratigraphie du Paléogène du Bassin de Paris en relation avec les bassins avoisinants. *Bull. Soc. géol. Fr.*, 7^{e} sér., t. VII, n° 2, p. 200-221.

BLONDEAU A., GRUAS-CAVAGNETTO C., LE CALVEZ Y., and LEZAUD L., 1976. — Etude paléontologique du sondage de Cuise (Oise). *Bull. Inform. Géologues Bassin de Paris*, v. 13, n° 2, p. 3-32.

BODELLE J., LAY Cl., and ODIN G.S., 1969. — Détermination d'âge par la méthode géochronologique « potassium-argon » de glauconies du Bassin de Paris. *C.r. Acad. Sci. Paris*, t. 268, sér. D, p. 1474-1477.

BONHOMME M., ODIN G.S., and POMEROL Ch., 1968. — Age des formations glauconieuses de l'Albien et de l'Eocène du Bassin de Paris. *Mém. B.R.G.M.*, v. 1, n° 58, Colloque sur l'Eocène, Paris 1968, p. 339-346.

BONIS L. de, 1974. — Premières données sur les Carnivores Fissipèdes provenant des fouilles récentes dans le Quercy. *Palaeovertebrata*, Montpellier, v. 6, n° 1-2, p. 27-32.

BONIS L. de, CROCHET Y., RAGE J.-Cl., SIGÉ B., SUDRE J., and VIANEY-LIAUD M., 1973. — Nouvelles faunes de Vertébrés oligocènes des phosphorites du Quercy. *Bull. Mus. natn. Hist. nat.*, Paris, 3^{e} sér., n° 174, Sci. Terre 28, p. 105-113.

BOSMA A.A., 1974. — Rodent biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. *Utrecht Micropal. Bull.*, Spec. Publ., p. 9-126.

BRUNET M., 1970. — Villebramar (Lot-et-Garonne) : très important gisement de Vertébrés du Stampien inférieur du Bassin d'Aquitaine. *C.r. Acad. Sci. Paris*, t. 270, sér. D, p. 2535-2538.

BRUNET M., 1979. — Les grands mammifères chefs de file de l'immigration oligocène et le problème de la limite Eocène-Oligocène en Europe. *Edit. Fondation Singer-Polignac*, Paris, 325 p.

BRUNET M., HUGUENEY M., JEHENNE Y., 1981. — Cournon-les-Souméroux : un nouveau site à vertébrés d'Auvergne ; sa place parmi les faunes de l'Oligocène supérieur d'Europe. *Géobios*, Lyon, n° 14 (3) : 323-359, 71 fig., 10 tabl.

CAPPETTA H., HARTENBERGER J.-L., SIGÉ B., SUDRE J., 1968. — Une faune de Vertébrés de la zone de Cuis dans l'Eocène continental du Bas-Languedoc (gisement du Mas de Gimel, Grabels, Hérault). *Bull. B.R.G.M.*, sér. 2-3, p. 45-48.

CARBONNEL G., CHATEAUNEUF J.-J., FEIST-CASTEL M., GRACIANSKY P.-C. de, and VIANEY-LIAUD M., 1972. — Les apports de la paléontologie (Spores et pollens, Charophytes, Ostracodes, Mammifères) à la stratigraphie et à la paléogéographie des molasses de l'Oligocène supérieur de Barrême (Alpes de Haute-Provence). *C.r. Acad. Sci. Paris*, t. 275, sér. D, p. 2599-2602.

CASANOVAS CLADELLAS M.L., 1975. — Estratigrafia y Paleontologia del yacimiento ludiense de Roc de Santa. *Resumen de Thesis*, Univ. de Barcelona, 16 p.

CAVELIER Cl., 1972. — L'âge Priabonien supérieur de la « zone à *Ericsonia subdisticha* » (nanno-plancton) en Italie et l'attribution des Latdorf Schichten allemands à l'Eocène supérieur. *Bull. B.R.G.M.*, v. 2, t. IV, n° 1, p. 15-24.

CAVELIER Cl., 1979. — La limite Eocène-Oligocène en Europe occidentale. Mém. n° 54, *Univ. L. Pasteur Strasbourg, Sci. géol.*, 280 p.

CAVELIER Cl., CHATEAUNEUF J.-J., POMEROL C., RABUSSIER D., RENARD M., and VERGNAUD-GRAZZINI C., 1981. — The geological events at the Eocene/Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 36 : p. 223-248.

CAVELIER Cl., and POMEROL Ch., 1976. — Les rapports entre le Bartonien et le Priabonien. Incidence sur la position de la limite Eocène moyen-Eocène supérieur. *C.r. somm. Soc. géol. Fr.*, fasc. 2, p. 49-51.

CAVELIER Cl., and POMEROL Ch., 1977. — Proposition d'une échelle stratigraphique standard pour le Paléogène. *Newsl. Stratigr.*, v. 6, n° 1, p. 56-65.

CHATEAUNEUF J.-J., and GRUAS-CAVAGNETTO C., 1978. — Les zones de Wetseliellaceae (Dinophyceae) du Bassin de Paris. *Bull. B.R.G.M.*, sect. IV, n° 2, p. 59-93.

CHRISTENSEN W.K., and BIRKELUND T., eds 1979. — Cretaceous-Tertiary boundary Events. *Symposium*. v. I, The Maestrichtian and Danian of Denmark, 210 p. ; v. II, Proceedings, 250 p., Univ. Copenhagen, Denmark.

COLLOQUE SUR LE PALÉOGÈNE, 1964. — Bordeaux 1962. *Mém. B.R.G.M.*, t. 11, n° 28, p. 547-1107.

COLLOQUE SUR L'ÉOCÈNE, 1969. — Paris 1968. *Mém. B.R.G.M.*, v. III, n° 69, propositions, p. 465.

COLLOQUE, POMEROL Ch., organisateur, 1975. — Le contenu de l'Ilerdien et sa place dans le Paléogène. *Bull. Soc. géol. Fr.*, 7^{e} sér., t. XVII, n° 2, p. 123-266.

COLOM G., 1961. — La paléoécologie des lacs du Ludien-Stampien inférieur de l'île de Majorque. *Rev. Micropal.*, v. 4, n° 1, p. 17-29.

COLOM G., 1972. — Les bassins tertiaires de l'île de Majorque (Baléares). *Rapp. Comm. Intern. Mer Méditerranée*, v. 20, n° 4, p. 535-538.

COSTA L., DENISON C., and DOWNIE C., 1978. — The Paleocene/Eocene boundary in the Anglo-Paris Basin. *Jour. Geol. Soc.*, v. 135, pt. 3, p. 261-264.

CROCHET J.-Y., 1979. — Diversité systématique des Didelphidae (Marsupialia) européens tertiaires. *Géobios*, n° 12, fasc. 3, p. 365-378.

CROCHET J.-Y., 1980. — Les Marsupiaux du Tertiaire d'Europe. *Edit. Fondation Singer-Polignac*, Paris, 279 p., 241 fig., 2 pl.

CROCHET J.-Y., HARTENBERGER J.-L., RAGE J.-C., RÉMY J.A., SIGÉ B., SUDRE J., et VIANEY-LIAUD M., 1981. — Les nouvelles faunes de vertébrés antérieurs à la « Grande Coupure » découvertes dans les phosphorites du Quercy. *Bull. Mus. natn. Hist. nat.*, 4e sér., 3, section C : p. 245-265.

CRUSAFONT-PAIRÓ M., 1961. — Traits endémiques chez les faunes de Mammifères du Lutétien d'Espagne. *Coll. Intern. Lower and non-specialized mammals*, Bruxelles, t. I, p. 201-204.

CRUSAFONT-PAIRÓ M., 1966. — Sur quelques Prosimiens de l'Eocène de la région préaxiale pyrénaïque et un essai provisoire de reclassification. *Coll. Intern. C.N.R.S.*, *« Problèmes actuels de Paléontologie »*, Paris 1966, p. 611-632.

CRUSAFONT-PAIRÓ M., 1967. — Nuevos datos sobre la edad de los sedimentos terciarios de la zona Utrillas-Montalban. *Acta geol. hisp.*, v. 2, n° 5, p. 115-116.

CRUSAFONT-PAIRÓ M., and GOLPE-POSSE J.M., 1968. — Los nuevos yacimientos de mamiferos del Eoceno español. *Bol. geol. y Min.*, t. LXXIX-IV, p. 341-353.

CRUSAFONT-PAIRÓ M., and RUSSELL D.E., 1967. — Un nouveau Paroxyclaenidé de l'Eocène d'Espagne. *Bull. Mus. natn. Hist. nat.* Paris, 3e sér., t. 38, n° 4, p. 757-773.

CRUSAFONT-PAIRÓ M., GINSBURG L., and TRUYOLS J., 1962. — Mise en évidence du Sannoisien dans la Haute Vallée du Tage (Espagne). *C.r. Acad. Sci.* Paris, t. 255, sér. D, p. 2155-2157.

CRUSAFONT-PAIRÓ M., HARTENBERGER J.-L., and THALER L., 1963. — Sur des nouveaux restes de Mammifères du gisement éocène supérieur de Sosis, au Nord de Tremp (Lerida, Espagne). *C.R. Acad. Sci.* Paris, t. 257, sér. D, p. 3014-3017.

CURRY D., 1975. — The status of the Ilerdian and its relation to the Paleocene-Eocene Boundary. *Bull. Soc. géol. Fr.*, 7e sér., t. XVII, n° 2, p. 222.

CURRY D., GULINCK M., and POMEROL Ch., 1969. — Le Paléocène et l'Eocène dans les bassins de Paris, de Belgique et d'Angleterre. *Mém. B.R.G.M.*, n° 69, Colloque sur l'Eocène, Paris 1968, p. 361-369.

CURRY D., ADAMS C.G., BOULTER M.C., DILLAY F.C., EAMES F.E., FUNNELL B.M., and WELLS M.K., 1978. — A correlation of Tertiary rocks in the British Isles. *Geol. Soc. London*, Spec. Report n° 12, 72 p.

DAL PIAZ G.B., 1932. — I mammiferi dell'Oligocene veneto. *Anthracotherium monsvialense. Mém. Ist. Geol. Univ.* Padova, v. 10, 63 p.

DEDIEU P., 1977 a. — Sur la systématique des Tapiroidea de l'Eocène européen. *C.R. Acad. Sci.* Paris, 284, p. 2219-2222.

DEDIEU P., 1977 b. — Le Tapiroïde à denture rhinocerotoïde du gisement lutétien d'Israel (Aude) : *Paralophiodon esselensis* (Fischer, 1829). *Bull. Soc. Hist. nat.* Toulouse. 113 (1-2), p. 32-39.

DEHM R., 1935. — Über tertiäre Spaltenfüllungen im Fränkischen and Süddeutschen Jura. *Zbl. Min. Geol. Paläont.*, Abt B, Bd 4, p. 113-124.

DEHM R., 1937. — Neue tertiäre Spaltenfüllungen im südlichen Fränkischen Jura. *Zbl. Min. Geol. Paläont.*, Abt. B, Bd 9, p. 349-369.

DEHM R., 1950. — Zur Eozän-Oligozän-Grenze. *N. Jb. Geol. Paläont. Mh.*, Jg. 1950, H. 7, p. 193-200.

DENIZOT G., 1957. — Lexique stratigraphique international. V. I, Europe, fasc. 4 a, France, Belgique, Pays-Bas, Luxembourg ; fasc. 4 a VII, Tertiaire.

DEPÉRET C., 1895. — Observations à propos de la note sur la nomenclature des terrains sédimentaires par MM. Munier-Chalmas et de Lapparent. *Bull. Soc. géol. Fr.*, 3e sér., t. XXIII, p. 873-883.

DEWALQUE G., 1868. — Liste des fossiles de divers étages. (Prodrome d'une description géologique de la Belgique, chap. XVII, Bruxelles, p. 313.)

DEWEY J.G.F., PITMAN W.C. III, RYAN W.B.F., and BONNIN J., 1973. — Plate tectonics and the Evolution of the Alpine systems. *Bull. Geol. Soc. America*, v. 84, p. 3137-3180.

DOLLFUS G., 1877. — Contribution à la faune des marnes blanches supérieures au gypse. *Bull. Soc. géol. Fr.*, 3e sér., t. V, p. 314-317.

DOLLFUS G., 1905. — Classification de l'Eocène moyen et supérieur. *Bull. Soc. géol. Fr.*, 4e sér., t. V, p. 6.

DUMONT A., 1839. — Rapports sur les travaux de la carte géologique pendant l'année 1839. *Bull. Acad. Roy. Sci. Lett. & Bx Arts Belgique*, t. VI, pt. 2, p. 466.

DUMONT A., 1949. — Rapport sur la carte géologique du Royaume. *Bull. Acad. Roy.* Bruxelles, t. 16, p. 351-373.

ENGLISH T., 1904. — Eocene and Later Formations surrounding the Dardanelles. *Quart. Jour. Geol. Soc.* London, v. 6, p. 243-274.

FAHLBUSH V., 1976. — Report on the International Symposium on Mammalian stratigraphy of the European Tertiary in Munich, April 11-14, 1975. *Newsl. Stratigr.*, Leiden, v. 5, n° 21, p. 160-167.

FEUGUEUR L., 1963. — L'Yprésien du Bassin de Paris. Essai de monographie stratigraphique. *Mém. Carte géol.* détail. France, 568 p.

FISCHER K.S., 1977. — Neue funde von *Rhinocerolophiodon* (n. gen.), *Lophiodon* und *Hyrachius* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle. *Z. geol. Wiss.* 5-9 : p. 1129-1152.

FRAKES L.A., and KEMP E., 1973. — Influence of continental positions on Early Tertiary climates. *Nature*, v. 240, p. 97-100.

FRANZEN J.-L., 1968. — Revision der Gattung *Palaeotherium* (Perissodactyla, Mammalia). *Thesis Univ.* Freiburg, Bd 1-2, 181 p.

FRANZEN J.-L., 1981. — Das erste skelet eines Dichobuniden (Mammalia, Artiodactyla) geborgen aus mitteleozänen Olschiefern der «Grube Messel» bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana lethaea*, 61, p. 299-353. Frankfurt.

FRANZEN J.-L., and KRUMBIEGEL G., 1980. — *Messelobunodon ceciliensis* n.sp. (Mammalia, Artiodactyla) ein neuer Dichobunide aus der mitteleozänen Fauna des Geiseltales Bei Halle (DDR). *Z. geol. Wiss.* 8 : p. 1585-1592.

GABUNIA L.K., DEVIATKIN E.V., and RUBINSTEIN M., 1975. — Données sur l'âge absolu des formations continentales cénozoïques d'Asie, et leur signification biostratigraphique. *Akad. Nauk S.S.S.R.*, t. 225, n° 4, p. 895-898 (in Russian).

GABUNIA L.K., and ILIESCU O., 1960. — On the discovery of giant rhinoceros remains (family Indricotheriidae) in Romania. *Doklady Akad. Sci. U.S.S.R.*, v. 130, n° 2, p. 75-77 (in Russian).

GAZIN L., 1976. — Mammalian Faunal zones of the Bridger middle Eocene. *Smiths. Contr. Paleobiology*, n° 26, 25 p.

GINGERICH P.D., 1977. — New species of European Primates and the phylogeny of European Adapidae. *Folia Primatol.*, v. 28, p. 60-80.

GINSBURG L., 1969. — Une faune de Mammifères terrestres dans le Stampien marin d'Etampes (Essonne). *C.r. Acad. Sci.* Paris, t. 268, sér. D, p. 1266-1268.

GINSBURG L., MONTENAT Ch., and POMEROL Ch., 1965. — Découverte d'une faune de Mammifères terrestres dans les couches marines de l'Auversien (Bartonien inférieur du Guespelle (Val d'Oise). *C.r. Acad. Sci.* Paris, t. 260, sér. D, p. 3445-3446.

GINSBURG L., ARQUES J., BROIN F. de, LE CALVEZ Y., MOUTON J., OBERT D., PRIVÉ-GILL C., and ROUCAN J.-P., 1977. — Découverte d'une faune de Mammifères dans le Lutétien supérieur de La Défense à Puteaux près de Paris (Hts-de-Seine). *C.r. somm. Soc. géol. Fr.*, fasc. 6, p. 311-313.

GINSBURG L., and ZBYSZEWSKI G., 1965. — Découverte de vertébrés paléogènes dans la falaise de Feligueira Grande entre S. Pedro de Muel et Nazaré. *Comm. Serv. Géol. Portugal*, v. 48, p. 97-108.

GLIBERT M., and HEINZELIN J. de, 1952. — Le gîte des vertébrés tongriens de Hoogbutsel. *Inst. roy. Sci. nat. Belgique*, v. 28, n° 52, 22 p.

GODFRIAUX J., and ROBASZYNSKI F., 1974. — Le Montien continental et le Dano-Montien marin des sondages de Hainin (Hainaut, Belgique). *Ann. Soc. géol. Belgique*, t. 97, p. 185-200.

GODFRIAUX J., and THALER L., 1972. — Note sur la découverte de mammifères dans le Montien continental du Hainaut (Belgique). *Bull. Acad. roy. Belgique*, Cl. Sci., t. LVIII, 5e sér., n° 4, p. 536-541.

GODINOT M., 1981. — Les Mammifères de Rians (Eocène inférieur, Provence). *Palaeovertebrata*, v. 10, fasc. 2, p. 43-126.

GODINOT M., BROIN F. de, BUFFETAUT E., RAGE J.-Cl., and RUSSELL D., 1978. — Dormaal : une des plus anciennes faunes éocènes d'Europe. *C.r. Acad. Sci.* Paris, t. 287, sér. D, p. 1273-1276.

GOLPE-POSSE J.M., 1974. — Faunas de yacimientos con suiformes en el Terciario español. *Publ. Inst. Prov. Paleont. Sabadell, Paleont. y Evol.*, v. VIII, 87 p.

GRAMANN F., HARRE W., KRENZER H., LOOK E.R., and MATTIAT B., 1975. — K-Ar ages of Eocene - Oligocene glauconitic sands from Helmstedt and Lehrte (N.W. Germany). *Newsl. Stratigr.*, v. 4, n° 2, p. 71-86.

HARDENBOL J., and BERGGREN W.A., 1978. — A new Paleogene numerical time scale. *A.A.P.G. Studies in Geol.*, n° 6 : The Geologic Time Scale, p. 214-234.

HARTENBERGER J.-L., 1969. — Les Pseudosciuridae (Mammalia, Rodentia) de l'Eocène moyen de Bouxwiller, Ergerkingen et Lissieu. *Palaeovertebrata*, v. 3, n° 2, p. 27-61.

HARTENBERGER J.-L., 1971. — La systématique des Theridomyoidea (Rodentia). *C.r. Acad. Sci.* Paris, t. 273, sér. D, p. 1917-1920.

HARTENBERGER J.-L., 1973. — Les Rongeurs de l'Eocène d'Europe. Leur évolution dans leur cadre biogéographique. *Bull. Mus. natn. Hist. nat.* Paris, 3e sér., n° 132, Sci. Terre 24, p. 49-70.

HARTENBERGER J.-L., 1975. — Evolution des Rongeurs primitifs de l'Ancien Monde. *Colloque C.N.R.S.* : problèmes actuels de paléontologie (Evolution des Vertébrés), n° 218, p. 777-790, 1 pl.

HARTENBERGER J.-L., and LOUIS P., 1976. — Nouveaux Rongeurs dans l'Eocène supérieur de Grisolles (Aisne, Bassin de Paris). *Géobios*, v. 9, n° 1, p. 81-95.

HARTENBERGER J.-L., SIGÉ B., and SUDRE J., 1968. — Nouveaux gisements de Vertébrés de l'Eocène continental du Minervois. *C.r. somm. Soc. géol. Fr.*, fasc. 1, p. 22-23.

HARTENBERGER J.-L., SIGÉ B., and SUDRE J., 1974. — La plus ancienne faune de Mammifères du Quercy : le Bretou. *Palaeovertebrata*, v. 6, nos 3-4, p. 177-196.

HARTENBERGER J.-L., SIGÉ B., SUDRE J., and VIANEY-LIAUD M., 1970. — Nouveaux gisements de vertébrés dans le bassin tertiaire d'Alès (Gard). *Bull. Soc. géol. Fr.*, t. XII, 7e sér., n° 5, p. 879-885.

HEDBERG H.D. ed., 1976. — International stratigraphic guide. *Wiley and Sons publication.* 200 p.

HEISSIG K., 1979. — Die hypothetische Rolle Südosteuropas bei den Säugetierwanderungen im Eozän und Oligozän. *N. Jahr. Geol. Paläont.*, H. 2, p. 83-96.

HELMER D., and VIANEY-LIAUD M., 1970. — Nouveaux gisements de Rongeurs dans l'Oligocène moyen de Provence. *C.r. somm. Soc. géol. Fr.*, fasc. 2, p. 45-46.

HOOKER J.J., 1977. — The Creechbarrow Limestone — its biota and correlation. *Tertiary Res.*, v. 1, n° 4, p. 139-145.

HOOKER J.J., 1980. — The succession of *Hyracotherium* (Perissodactyla, Mammalia) in the English early Eocene. *Bull. Brit. Mus. Nat. Hist., Geol.*, v. 33, n° 2, p. 101-114.

HOTTINGER L., and SCHAUB H., 1960. — Zur Stufeneinteilung des Paleocaens und Eocaens Eifürhung der Stufen Ilerdien und Biarritzien. *Eclog. geol. Helvetiae*, v. 53, n° 1, p. 453-480.

HUGUENEY M., 1968. — Les Gliridés (Rodentia) de l'Oligocène supérieur de St-Victor-la-Coste (Gard). *Palaeovertebrata*, v. 2, n° 1, 16 p.

HUGUENEY M., 1969. — Les Rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Bransat (Allier). *Thèse, Univ. Lyon*, n° 596, 227 p.

HUGUENEY M., 1971. — *Pseudocricetodon philippi*, nouvelle espèce de Cricétidé (Rodentia, Mammalia) de l'Oligocène moyen de Saint-Martin-de-Castillon (Vaucluse). *C.r. Acad. Sci.* Paris, t. 272, sér. D, p. 2533-2535.

JAEGER J.-J., and HARTENBERGER J.-L., 1975. — Pour l'utilisation systématique de niveaux repères en biochronologie mammalienne. *3ᵉ Réun. ann. Sci. Terre*, Montpellier, p. 201.

JÁMBOR A., KORPÁS L., KRETZOI M., PÁLFALVY I., and RÁKOSI L., 1969. — A dunántuli oligocén képzödmények rétegtani problémai. *M. áll. földtani intézet évi jelentése az*, p. 141-154.

KAPELLOS Ch., 1973. — Biostratigraphie des Gurnigelflysches mit besonderer Berücksichtigung der Nummuliten und des Nannoplanktons, unter Einbeziehung des paläogenen Nannoplankton der Krim (USSR). *Mém. Suisses Paléont.*, v. 96, 128 p.

KEPPENS E., ELEWAUT E., and PASTEELS P., 1978. — Rubidium-Strontium and Potassium-Argon radiometric datations on glauconites of the « Bande Noire » (Base of the Asse Clay) from the Belgian Eocene. *Ann. Soc. géol. Belgique*, t. 101, p. 179-192.

KING C., 1981. — The stratigraphy of the London Clay and associated deposits. *Tert. Res. Spec. Pap.*, n° 6, pp. 1-158.

KOENIGSWALD W. von, 1980. — Fossillagerstätte Messel — Literaturübersicht der Forschungsergebnisse aus den Jahren 1969-1979. *Geol. Jb. Hessen*, 108, p. 23-38. Wiesbaden.

KRETZOI M., 1940. — Alttertertiäre Perissodactylen aus Ungarn. *Ann. Mus. Nat. Hungarici, Pars Min. Geol. Palaeont.*, v. 33, p. 87-98.

KRETZOI M., 1943. — *Kochictis centennii* n.g., n.sp., ein altertümliche Creodonte aus dem oberoligozän Siebenbürgens. *Földt. Közl.*, v. LXXIII, p. 190-195.

KRETZOI M., 1951. — Uj Eomyidae a Balkonyból (New Eomyid from the Kakomy Mountains). *Földt. Közl.*, v. 81, p. 88-89.

KREUZER H., DANIELS C.H.V., GRAMANN F., HARRE W., and MATTIAT B., 1973. — K-Ar dates of some glauconites of the N.W. German Tertiary basin. *Fortschr. Miner.*, Bd. 50, B. 3, p. 94-95.

LANGE-BADRÉ B., 1979. — Les Créodontes (Mammalia) d'Europe occidentale de l'Eocène supérieur à l'Oligocène moyen. *Mém. Mus. natn. Hist. nat.*, Paris, t. 42, sér. C, 249 p.

LAPPARENT A.F. de, 1883. — Traité de Géologie. *Savy Ed.*, Paris, 1280 p.

LEBKÜCHNER R.F., 1974. — Beitrag zur Kenntnis der Geologie des Oligozäns von Mittelthrakien (Turkei). *Bull. Min. Res. Expl. Inst. Turkey*, n° 83, 30 p.

LILLEGRAVEN J.A., 1979. — A biogeographical problem involving comparisons of later Eocene terrestrial vertebrate faunas of western North America. *In* : Historical biogeography, plate tectonics, and the changing environment, Gray, J. and Boucot, A.J., Eds. *Oregon State Univ. Press*, p. 333-347.

LOPEZ N., and THALER L., 1975. — Sur le plus ancien Lagomorphe européen et la « Grande Coupure » oligocène de Stehlin. *Palaeovertebrata*, fasc. 3-4, p. 243-251.

LOUIS P., 1970. — Note préliminaire sur un gisement de Mammifères de l'Eocène inférieur situé route de Broyes à Sézanne (Marne). *Ann. Univ. et A.R.E.R.S.* Reims, t. 8, fasc. 2, p. 48-62.

LOUIS P., 1976. — Gisements de Mammifères bartoniens du Tardenois. Remarques sur la paléogéographie de l'Auversien du sud de Fismes. *Bull. Inform. Géologues Bassin de Paris*, v. 13, n° 2, p. 41-58.

LOUIS P., and SUDRE J., 1975. — Nouvelles données sur les Primates de l'Eocène supérieur européen. *Coll. Intern. C.N.R.S.*, « Problèmes actuels de Paléontologie, Evolution des Vertébrés », Paris 1973, p. 805-828.

LÜTTIG G., and THENIUS E., 1961. — Uber einen Anthracotheriiden aus dem Alttertiär von Thrazien (Griechenland). *Paläont. Z.*, Bd 35, n° 3/4, p. 179-186.

McKENNA M.C., 1975. — Fossil mammals and early Eocene north Atlantic land continuity. *Ann. Miss. Bot. Gardens*, v. 62, n° 2, p. 335-353.

MARTINI E., and MÜLLER C., 1971. — Das marine Alttertiär in Deutschland und seine Einordnung in die Standard Nannoplankton Zonen. *Erdöl u. Kohle*, Jg. 24, p. 181-184.

MARTINI E., and RITZKOWSKI S., 1969. — Die Grenze Eozän/Oligozän in der typus-region des Unteroligozäns (Helmstedt-Egeln-Latdorf). *Mém. B.R.G.M.*, t. III, n° 69, Colloque sur l'Eocène, Paris 1969, p. 233-237.

MAYER-EYMAR C., 1857. — Tableau synchronistique des terrains tertiaires de l'Europe. Zurich (unknown pages).

MAYER-EYMAR C., 1893. — Le Ligurien et le Tongrien en Egypte. *Bull. Soc. géol. France*, v. XXI, n° 3, p. 7-43.

MÉGNIEN C., Ed., 1980. — Synthèse géologique du Bassin de Paris, stratigraphie et paléontologie, v. 1. *Mém. B.R.G.M.*, n° 101, 466 p.

MEYER H. von, 1854. — *Anthracotherium dalmatinum* aus der Braunkohle des Monte Promina in Dalmatien. *Palaeontographica*, v. IV, p. 61-66.

MUNIER CHALMAS E., and LAPPARENT A.F. de, 1839. — Note sur la nomenclature des terrains sédimentaires. *Bull. Soc. géol. France*, v. 21, 3e.sér., p. 438-488.

NAKOMAN E., 1966. — Contribution à l'étude palynologique des formations tertiaires du Bassin de Thrace. I. Etude qualitative. *Ann. Soc. géol. Nord*, t. 86, p. 65-100.

NIKOLOV I., 1967. — Neue oberoligozäne Arten der Gattung *Elomeryx*. *N. Jahrb. Geol. Palaeont. Abh.*, Bd. 128, n° 2, p. 205-214.

OBRADOVICH J.D., and COBBAN W.A., 1975. — A time scale for the late Cretaceous of the Western interior of North America. *Geol. Assoc. Canada Spec. Paper*, n° 13, p. 31-54.

ODIN G.S., 1973. — Résultats de datations radiométriques dans les zones sédimentaires du Tertiaire de l'Europe occidentale. *Rev. Geogr. phys. Geol. dyn.*, v. 15, n° 2, p. 317-330.

ODIN G.S., 1975. — Les glauconies : constitution, formation, âge. *Thèse Univ. Paris*, 250 p.

ODIN G.S., 1978. — Isotopic dates for a Paleogene time scale. *In* : Contribution to the Geologic time scale. *A.A.P.G. Studies in Geol.*, n° 6, p. 247-257.

ODIN G.S., CURRY D., and HUNZIKER J.C., 1978. — Radiometric dates from NW European glauconites and the Paleogene time scale. *Jl. Geol. Soc.* London, v. 135, p. 481-497.

ODIN G.S., BODELLE J., LAY Cl., and POMEROL Ch., 1970. — Géochronologie de niveaux glauconieux paléogènes d'Allemagne du Nord (méthode potassium-argon). Résultats préliminaires. *C.r. somm. Soc. géol. Fr.*, fasc. 6, p. 220.

ODIN G.S., GULINCK N., BODELLE J., and LAY Cl., 1969. — Géochronologie des niveaux glauconieux tertiaires du Bassin de Belgique (méthode potassium-argon). *C.r. somm. Soc. géol. Fr.*, fasc. 6, p. 198.

ODIN G.S., CURRY D., BODELLE J., LAY Cl., and POMEROL Ch., 1969. — Géochronologie de niveaux glauconieux tertiaires des Bassins de Londres et du Hampshire (méthode potassium-argon). *C.r. somm. Soc. géol. Fr.*, fasc. 8, p. 309.

ODIN G.S., and CURRY D., 1981. — L'échelle numérique des temps paléogènes en 1981. *C.r. Acad. Sci.* Paris, t. 293, sér. II, pp. 1003-1008.

ORBIGNY A. d', 1849-1852. — Cours élémentaire de paléontologie et géologie stratigraphiques. *Masson Ed.*, Paris, v. I : (1850), 394 p. ; v. II : (1850), 428 p. ; v. III : (1852), 198 p. ; table (1852), 190 p.

OWENS J.P., and SOHL N., 1973. — Glauconites from the New Jersey-Maryland coastal plain ; their K-Ar ages and application in stratigraphic studies. *Bull. Geol. Soc. Amer.*, v. 84, p. 2811-2838.

OZANSOY F., 1962. — Les Anthracothériens de l'Oligocène inférieur de la Thrace orientale (Turquie). *Bull. Min. Res. Expl. Inst. Turkey*, n° 58, p. 85-96.

OZANSOY F., 1963. — Fosil Memeli faunizon birimleri isiginda Trakya Tertier kronostratigrafisi. *Ankara Univ. D.T.C.F. Antropoloji Derg.*, v. 1, n° 1, p. 63-77.

OZANSOY F., 1964. — Le niveau du Sannoisien et sa faune mammalienne de la Thrace orientale (Turquie) dans le système de l'Oligocène d'Europe : Coll. sur le Paléogène (Bordeaux 1962). *Mém. B.R.G.M.*, t. II, n° 28, p. 991-999.

OZANSOY F., 1966. — Türkiye Senozoik çaglarinda fosil insan formu problemi ve biostratigrafik dayanaklari. *Ankara Univ. D.T.C.F. Yay.*, n° 172, 104 p.

OZANSOY F., 1969. — Yeni bir *Palaeoamasia kansui*, Boyabat (Sinop) Eosen fosil Memeli biozonu ve paleontolojik belgeleri. *Türk Tarih Kurumu, Bell.* n° 33, p. 581-585.

PETRONIJEVIC Z., and THENIUS E., 1957. — Uber den ersten Nachweis von Indricotherien (= Baluchitherien, Rhinocerotidae, Mammalia) im Tertiär von Europa. *Anz. d. math-naturw. Kl. Osterr. Akad. Wissensch.*, n° 9, p. 153-159.

PLAZIAT J.-Cl., 1975. — L'Ilerdien à l'intérieur du Paléogène languedocien ; ses relations avec le Sparnacien, l'Ilerdien sud-pyrénéen, l'Yprésien et le Paléocène. *Bull. Soc. géol. Fr.*, 7e sér., t. XVII, n° 2, p. 168-182.

POMEROL Ch., 1969. — Rapport sur la limite Paléocène-Eocène : Coll. sur l'Eocène. *Mém. B.R.G.M.*, n° 69, p. 447-449.

POMEROL Ch., 1972. — Ages radiométriques dans le Tertiaire des bassins de l'Ouest de l'Europe. *Bull. Inform. Géologues Bassin de Paris*, n° 32, p. 3-6.

POMEROL Ch., 1973. — Stratigraphie et paléogéographie, ère Cénozoïque (Tertiaire et Quaternaire). *Doin Ed.*, Paris, 269 p.

POMEROL Ch., 1975. — La signification de l'Ilerdien et l'intérêt de cet étage dans la stratigraphie du Paléogène mésogéen. *Bull. Soc. géol. Fr.*, 7e sér., t. XVII, n° 2, p. 213-217.

POMEROL Ch., 1977. — La limite Paléocène-Eocène en Europe occidentale. *C.r. somm. Soc. géol. Fr.*, fasc. 4, p. 199-202.

POMEROL Ch., 1978. — Critical review of isotopic dates in relation to Paleogene stratotypes. *In* : Contribution to the Geologic time scale. *A.A.P.G. Studies in Geol.*, n° 6, p. 235-245.

POMEROL Ch. (edit.), 1981. — Stratotypes of Paleogene Stages. *Bull. Inform. Geol. Bassin Paris*, Mém. hors sér., n° 2, pp. 1-301.

POMEROL Ch. (edit.), 1981. — Paleogene paleogeography and the geological events at the Eocene/Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 36, n° 3/4, pp. 1-364.

POMEROL Ch., BABIN Cl., LANCELOT Y., LE PICHON X., and RAT P., 1980. — Stratigraphie et paléogéographie. Principes et méthodes. *Doin Ed.*, Paris, 1 v., 212 p.

RADINSKY L., 1967. — A review of the Rhinocerotoid family Hyracodontidae (Perissodactyla). *Bull. Amer. Mus. Nat. Hist.*, v. 136, art. 1, 46 p.

RADULESCO C., ILIESCO G., and ILIESCO M., 1976. — Un Embrithopode nouveau (Mammalia) dans le Paléogène de la dépression de Hateg (Roumanie) et la géologie de la région. *N. Jahrb. Geol. Paläont., Monatsh.*, H. 11, p. 690-698.

REMY J.A., and THALER L., 1967. — Une faune de Vertébrés de l'Oligocène supérieur dans les phosphorites du groupe d'Uzès. *C.r. somm. Soc. géol. Fr.*, fasc. 4, p. 161-163.

RENEVIER E., 1873. — Tableau des terrains sédimentaires représentant les époques de la phase organique. *Bull. Soc. Vaudoise Sci. nat.*, v. 12, n° 71, p. 2-34.

REY R., 1967. — Les Gastéropodes continentaux situent les différentes formations de la «zone alpine externe» de J. Boussac, par rapport à l'Oligocène nord-européen. *C.r. Acad. Sci.* Paris, t. 265, p. 781-783.

RIBEIRO A., ANTUNES M.T., FERREIRA M.P., ROCHA R.B., SOARES A.F., ZBYSZEWSKI G., MOITINHO DE ALMEIDA F., DE CARVALHO D., and MONTEIRO J.H., 1979. — Introduction à la Géologie générale du Portugal. *Serv. Geol. Portugal.*

RICHARD M., 1946. — Contribution à l'étude du bassin d'Aquitaine. Les gisements de Mammifères tertiaires. *Mém. Soc. géol. Fr.*, t. 52, n° 24, 380 p.

RUBINSTEIN M.M., and GABUNIA L.K., 1972. — Certain aspects of Cenozoic geochronology. *Akad. Nauk. S.S.S.R.*, Izv., Ser. Geol., n° 3, p. 3-8. (In Russian.)

RUSSELL D.E., 1964. — Les Mammifères paléocènes d'Europe. *Mém. Mus. natn. Hist. nat.* Paris, sér. C, Sci. Terre, t. 13, 324 p.

RUSSELL D.E., 1975. — Paleoecology of the Paleocene-Eocene transition in Europe. *In* : Approaches to Primate Paleobiology, *Szalay. F.S. Ed.*, Contributions to Primatology, v. 5, p. 28-61.

RUSSELL D.E., 1980. — Sur les Condylarthres cernaysiens *Tricuspidon* et *Landenodon* (Paléocène supérieur de France). *Palaeovertebrata*, Mém. Jubil. R. Lavocat, p. 127-166.

RUSSELL D.E., BONÉ E., de BROIN F., BRUNET M., BUFFETAUT E., CORDY J.M., CROCHET J.-Y., DINEUR H., ESTES R., GINSBURG L., GODINOT M., GROESSENS M.C., GIGASE P., HARRISON C. J.O., HARTENBERGER J.-L., HOCH E., HOOKER J.J., INSOLE A.N., LANGE-BADRÉ B., LOUIS P., MOODY R., RAGE J.-Cl., REMY J., ROTHAUSEN K., SIGÉ B., SIGOGNEAU-RUSSELL D., SPRINGHORN R., SUDRE J., TOBIEN H., VIANEY-LIAUD M., VINKEN R., and WALKER C.A., 1982. — Tetrapods of the Tertiary Basin of North Western Europe : UNESCO, Intern. Geol. Correl. Progr., Project 124. *Geol. Jahrbuch.*

SALAJ J., BAJANIK S., BATIK P., BISMUTH H., BONNEFOUS J., FLORIDIA S., HOOYBERGHS H.J.E., LAJMI T., MAAMERI N., MAAMOURI A.L., MAAMOURI M., and MEMMI L., 1974. — Livret guide des excursions du VI^e Coll. Africain de Micropal., Tunis, 88 p.

SAVIN S.M., DOUGLAS R.G., and STEHLI F.G., 1975. — Tertiary marine paleotemperatures. *Bull. Geol. Soc. Amer.*, v. 86, p. 1499-1510.

SCHAUB S., *in* ERNI A., 1941. — Ein Tertiäraufschluss am Südfuss der Balmfluh bei Solothurn. Mit ein Beitrag von H.G. Stehlin, Basel. *Eclog. Geol. Helvetiae*, v. 34, p. 209-219.

SCHIMPER W.P., 1874. — Traité de Paléontologie végétale. *J.P. Baillière Ed.*, Paris, v. 3, 896 p.

SCHMIDT-KITTLER N., 1971. — Odontologische Untersuchungen an Pseudosciuriden (Rodentia, Mammalia) des Alttertiärs. *Abh. Bayer. Akad. Wiss., math.-naturw. Kl.*, N.F., Bd 150, 131 p.

SCHMIDT-KITTLER N., and VIANEY-LIAUD M., 1975. — Les relations entre les faunes de rongeurs d'Allemagne du Sud et de France pendant l'Oligocène. *C.r. Acad. Sci.* Paris, sér. D, t. 281, p. 511-514.

SEN S., and HEINTZ E., 1979. — *Palaeoamasia kansui* Ozansoy, 1966, Embrithopode (Mammalia) de l'Eocène d'Anatolie. *Ann. Paléont. (Vert.)*, v. 65, fasc. 1, p. 73-91.

SEMES J., 1975. — Die Wirbeltierreste (excl. Pisces) aus dem Egerien von Österreich. Chronostratigraphie und Neostratotypen Miozän OM. Egerien. Veda, Bd V, *Verl. Slowak. Akad. Wiss.*, Bratislava, E. Bresyenska Ed., p. 437-450.

SIGÉ B., 1975 a. — Données nouvelles sur le genre *Stehlinia* (Vespertilionoidea, Chiroptera) du Paléogène d'Europe. *Palaeovertebrata*, v. 6, p. 253-272.

SIGÉ B., 1975 b. — Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale : Apatemyidés et Leptictidés. *Coll. Intern. C.N.R.S.* n° 218 «Problèmes actuels de Paléontologie, Evolution des Vertébrés», Paris 1973, p. 653-673.

SIGÉ B., 1976. — Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale : Nyctithériidés. *Mém. Mus. natn. Hist. nat.* Paris, n.s., sér. C, Sci. Terre, t. 34, 140 p.

SIGÉ B., and VIANEY-LIAUD M., 1979. — Impropriété de la Grande Coupure de Stehlin comme support d'une limite Eocène-Oligocène. *Newsl. Stratigr.*, v. 8, n° 1, p. 79-82.

SIGÉ B., CROCHET J.-Y., and INSOLE A., 1977. — Les plus vieilles taupes. *Géobios*, Mém. sp. 1, p. 141-157.

SPRINGHORN R., 1980. — *Paroodectes feisti*, der erste Miacide (Carnivora, Mammalia) aus dem Mittel Eozän von Messel. *Paläont. Z.*, 54.

STEHLIN H.G., 1909. — Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bull. Soc. géol. Fr.*, sér. 4, t. IX, p. 488-520.

STEININGER F., RÖGL F., and MARTINI E., 1976. — Current Oligocene/Miocene biostratigraphic concept of the central Paratethis. *Newsl. Stratigr.*, Bd 4, n° 3, p. 174-202.

STORCH G., 1978. — *Eomanis waldi*, ein Schuppentier aus dem Mittel-Eozän der «Grube Messel» bei Darmstadt (Mammalia, Pholidota). *Senckenbergiana Lethaea*, 59, p. 503-529, Frankfurt.

STORCH G., 1981. — *Eurotomandua joresi*, ein Myrmecophagide aus dem Eozän der «Grube Messel» bei Darmstadt (Mammalia, Xenarthra). *Senckenbergiana Lethaea*, 61, 247-289, Frankfurt.

SUDRE J., 1972. — Révision des Artiodactyles de l'Eocène moyen de Lissieu (Rhône). *Palaeovertebrata*, v. 5, fasc. 4, p. 111-156.

SUDRE J., 1973. — Un *Dichodon* géant de La Débruge et une nouvelle interprétation phylétique du genre. *Bull. Mus. natn. Hist. nat.*, 3e sér., n° 133, p. 73-78.

SUDRE J., 1974. — L'endémisme des faunes de mammifères du Sud de l'Angleterre à l'Eocène supérieur. *2e Réun. ann. Sci. Terre*, Pont-à-Mousson, p. 362.

SUDRE J., 1978. — Les Artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale. Systématique et évolution. *Mém. E.P.H.E.*, Inst. Montpellier, n° 7, 229 p.

SZALAY F.S., and McKENNA M.C., 1981. — Beginning of the age of mammals in Asia : the late Paleocene Gashato fauna, Mongolia. *Bull. Amer. Mus. Nat. Hist.*, v. 144, art. 4, p. 273-317.

TELLER F., 1884. — Neue Anthracotherienreste aus Südsteiermark und Dalmatien. *Beitr. Pal. Geol. Österr.-Ung.*, v. IV, p. 45-134.

THALER L., 1964. — Sur l'utilisation des Mammifères dans la zonation du Paléogène de France : Coll. sur le Paléogène, Bordeaux 1962. *Mém. B.R.G.M.*, v. 28, n° 2, p. 985-989.

THALER L., 1965. — Une échelle des zones biochronologiques pour les Mammifères du Tertiaire d'Europe. *C.r. somm. Soc. géol. Fr.*, fasc. 4-5, p. 118.

THALER L., 1966. — Les Rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. *Mém. Mus. natn. Hist. nat.* Paris, n.s., C, v. 27, 284 p.

THALER L., 1969. — Rongeurs nouveaux de l'Oligocène moyen d'Espagne. *Palaeovertebrata*, v. 2, fasc. 5, p. 191-207.

THALER L., 1972. — Datation, zonation et Mammifères. *Mém. B.R.G.M.*, v. 77, p. 411-424.

THENIUS E., 1959. — Wirbeltierfaunen. *In* : Handbuch der stratigraphischen Geologie (F. Lotze) — Tertiär (A. Papp and E. Thenius), Bd III, t. 2, 309 p., *Enke Verl.* Stuttgart.

TOBIEN H., 1949. — Säugetierpaläontologische Daten zur Altersbestimmung des tieferen Tertiärs im Rheintalgraben. *Ber. naturforsch. Ges. Freiburg*, Bd 39, 1943/1949, p. 17-52.

TOBIEN H., 1955. — Eine stampische Kleinsäuger Fauna aus der Grenzregion Schleichland Cyrenenmergel von Heimersheim bei Alzei (Rheinhessen). *Z. deutsch. geol. Ges.*, Bd 106, p. 565.

TOBIEN H., 1968. — Das biostratigraphische Alter der mitteleozänen Fossilfundstätt Messel bei Darmstadt (Hessen). *Notizbl. hess. L.-Amt. Bodenforsch.*, Bd 96, p. 111-119.

TOBIEN H., 1972. — Mikromammalier aus dem alttertiären Melanienton von Nordhessen. T. 2 : Rodentia, biostratigraphie, biostratonomie. *Notizbl. hess. L.-Amt Bodenforsch.*, Bd 100, p. 7-40.

TOBIEN H., 1980. — Ein anthracotherioider Paarhufer (Artiodactyla, Mammalia) aus dem Eozän von Messel bei Darmstadt (Hessen). *Geol. Jahrbuch Hessen*, 108, p. 11-22.

VESELOV A.A., GRIGOROVITCH A.S., and SAVENKO N.G., 1973. — Sur la question de la subdivision en étages du Paléogène de l'U.R.S.S. *Doklady Acad. Sci. USSR*, v. 209, n° 2, p. 423 (in Russian).

VIANEY-LIAUD M., 1972. — L'évolution du genre *Theridomys* à l'Oligocène moyen. Intérêt biostratigraphique. *Bull. Mus. natn. Hist. nat.* Paris, 3e sér., t. 98, Sci. Terre 28, p. 295-372.

VIANEY-LIAUD M., 1979 a. — Les Mammifères montiens de Hainin (Paléocène moyen de Belgique) ; part I ; Multituberculés. *Palaeovertebrata*, v. 9, fasc. 4, p. 117-139.

VIANEY-LIAUD M., 1979 b. — Evolution des Rongeurs à l'Oligocène en Europe occidentale. *Palaeontographica*, Abt. 4, Bd 166, p. 136-236.

VIANEY-LIAUD M., and HARTENBERGER J.-L., 1982. — Modalités évolutives des Rongeurs du Paléogène d'Europe occidentale. *Colloque intern. C.N.R.S.* : Modalités et rythmes de l'Evolution (Dijon, 1982), p. 297-312. Prétirage.

VOLLMAYR T., 1966. — Oberoligozäne Gliridae (Rodentia, Mammalia) aus der süddeutschen Faltenmolasse. *Mitt. Bayer. Staatssamml. Paläont. hist. Geol.*, Bd 6, p. 65-107.

YALÇINLAR I., 1954. — Les gisements de Mammifères et d'autres Vertébrés fossiles de Turquie. *Congr. Géol. intern. Alger*, C.r. 19e sess., sect. XIII, 3e part., fasc. XV, p. 139-147.