

## CORRELATION BETWEEN TERTIARY MAMMAL HORIZONS OF EUROPE AND AMERICA

### AN INTRODUCTION TO THE MORE EXACT INVESTIGATION OF TERTIARY ZOÖGEOGRAPHY. PRELIMINARY STUDY WITH THIRD TRIAL SHEET

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<sup>1</sup> An abstract of the second address was published in *Science*, April 13, 1900, pp. 561-574.

PART I. PARALLELS BETWEEN TERTIARY  
HORIZONS.

## INTRODUCTION.

This address is designed to reconsider an old subject in the new spirit and methods of modern palæontology. It does not pretend to cover the whole subject, but rather certain parallels between the mammalian faunæ of America and Europe and between the later Tertiary faunæ of Europe; it is introductory to a more exhaustive treatment.

The work done hitherto in this field of commanding interest and importance serves mainly to pioneer the more exact comparisons between Europe and America which are now becoming possible.

I desire to enter an urgent plea for the establishment of uniform divisions of the Tertiary and for the international usage of common terms both as to life stages and life forms. As in military disarmament, this result is easier to propose than attain, because each is willing to disarm on his own basis, each is reluctant to part with either the language or perspective belonging to the historical development of the geology and palæontology of his own land. Yet in these matters patriotism and provincialism naturally should have no weight. Palæontology knows neither the divisions formed by the English channel, the Rhine, nor the Atlantic; it does not recognize the superiority of an English system, of a French or German system, or of an American system, but like all its sister branches of science in this time of absolute scientific good will it demands an international system. As during the Tertiary period animals migrated freely by land over the entire northern hemisphere, so our ideas and methods must enjoy a free migration and fall beneath the rigid operation of the law of the survival of the fittest. Since anatomical, descriptive, taxonomic and geologic terms are mere symbols for the expression of certain facts, ideas, hypotheses and theories, we should all employ the same symbols whatever our national

sympathies. For my own part if an approximate synchronism can ever be established, I would go so far as to advocate the adoption of the standard European divisions for the American Tertiary as soon as the European stages and periods are finally determined upon. In the meantime no one can oppose the immediate adoption of the fundamental principle that the old and new world palæontology should be studied as a unit.

If we are eager to solve the great number and variety of most interesting questions still unsolved as to the source, origin, filiation, migration and extinction of the noble races of animals which passed across the stage of the Northern Hemisphere or *Ancient Holarctic Region*, during the Tertiary we must hasten to use more exact methods, to agree upon the synchronism of the Tertiary and the arbitrary limits which we shall assign to the Eocene, Oligocene, Miocene, Pliocene and Pleistocene periods and their subdivisions. The synchronism is a difficult subject, in fact it involves the main question; the limits of the periods are largely arbitrary and are capable of being settled at once. Although the *lower* Tertiary of America from the base of the Eocene to the summit of the Oligocene is infinitely more complete, in fact an unbroken historic chapter, it will probably prove best that the beautiful series of Tertiary horizons of France should be adopted as the *basis of division*, partly because of their priority and completeness throughout, but chiefly because of the remarkable alternation of marine and freshwater deposits, whereby the vertebrate is checked by the invertebrate time scale. After we pass the summit of the Oligocene our country affords a series of vistas only while Europe offers a commanding view of the later Tertiary life periods. If France furnishes the initial basis, comparison with America will serve to check and amplify—thus the final basis for the division of the Tertiary will be comparative.

**European Correlations:**—In France GERVAIS, GAUDRY, FILHOL, LEMOINE, DEPÉRET, BOULE, and others have drawn the demarcations of the typical horizons. The parallels with England have been especially set forth by PRESTWICH and DAWKINS and with Germany by SCHLOSSER, DEPÉRET and V. ZITTEL,

while the parallels between Europe and America, or the ancient Palæarctic and Nearctic Regions, have been discussed by GERVAIS, LEIDY, COPE, FILHOL, SCOTT, v. ZITTEL and SCHLOSSER. LYDEKKER has broadly covered the whole field in his *Geographical History of Mammals*.

It may seem remarkable that a nearctic palæontologist should enter the palæarctic field, as the herald of a conference and agreement upon common usage of terms, but I make no apology because the matter arose from necessity rather than choice; several years ago the discovery of some new types of rhinoceroses in this country directed my attention afresh to the study of the Tertiary fauna of Europe as parallel with that of America, in the succession of European and American types it appeared that there were most interesting similarities between rhinoceroses as widely separated as the present regions of Colorado and southern France, but upon attempting more than a general comparison I was confronted by a lack of definite time scale between the levels in which these animals occur. The available correlations by COPE, FILHOL, SCOTT, v. ZITTEL and others proved too indefinite at certain points. This difficulty became so obstructive that a more exact correlation of European and American horizons appeared to be an essential basis not only for the phylogeny of the rhinoceroses but for that of other types of mammals of Europe and North America. We need a unified old-world system as a starting point for comparison. As a matter of fact there is even at the present moment no consensus of opinion or common usage among palæarctic palæontologists as to the larger divisions of the Tertiary.

**The Trial Sheets:**—As an initial step towards a more exact correlation I offer here a provisional classification of the Tertiary of Europe with critical discussion of the reasons for placing the larger division lines at certain points, also, a comparison chiefly with the Eocene of America, both accomplished with as much aid from workers past and present as could be mustered. This classification probably contains many errors, some of them, perhaps, of a gross description. As I freely criticise and differ from some of my colleagues, I trust they will

freely criticise, correct and expand this preliminary parallel and the methods of attack here advocated. Realizing that an acceptable working basis could only be secured by coöperation I drew up in 1897 a '*Trial Sheet of the Typical and Homotaxial Tertiary Horizons of Europe*' and circulated it abroad for criticism. This proved to be a rather faulty trial; extremely valuable corrections and additions were received, especially from my friends Professor GAUDRY, Professor v. ZITTEL, Professor DEFÉRET and Doctor SCHLOSSER, Madame PAVLOW, Doctor BOULE, and Mr. R. LYDEKKER. These criticisms were embodied in a '*Second Trial Sheet*' which was issued about April 15, 1898. This sheet was used as a basis for further personal discussion with the above palæontologists, also with Professor LEPSIUS of Darmstadt, Doctor FORSYTH MAJOR of the British Museum and others. In course of a tour in foreign museums, I was greatly aided by many other critics, and made also numerous observations of my own which bear upon the Holarctic parallels. A '*Third Trial Sheet*' is issued in connection with this address; it is probably more accurate than its predecessors but it is still lacking both in the desired exactness and fullness. The closer comparison of the post-Eocene divisions of the Tertiary fauna of Europe and North America must be deferred for a full report which is in preparation.

### I. AVAILABLE EVIDENCES OF PARALLELISM

Among the tests of approximate synchronism of deposition in the Nearctic and Palæarctic regions are the following:

1. COMMON GENERA AND SPECIES: the presence of identical or closely allied genera and species. This time honored and obvious basis of comparison is now rendered most difficult by the diversity of usage in generic and specific definitions.

2. SIMILAR STAGES OF EVOLUTION: the similarity in the stage of development of allied phyla, as expressed in the pattern of the molar teeth, in the transformation of the premolar teeth, complication of the molar teeth, in the reduction of digits, etc. This test of synchronism is comparatively novel. For example, the remarkably definite transformation of the fourth

premolar of the *Plagiaulacida* or of the premolars of the *Perissodactyla* afford certain very exact data for correlation purposes.

3. **SIMULTANEOUS INTRODUCTION OF NEW FORMS:** the sudden appearances in both Nearctic and Palæarctic regions of types which have no known ancestors in lower horizons and have apparently originated elsewhere, either in Africa or in South America. The value in chronology of these immigrations has not been fully recognized.

4. **PREDOMINANCE OF CERTAIN TYPES:** the predominance or spread of certain types as of the *Perissodactyla* in the Middle Eocene, or of the *Artiodactyla* in the Upper Eocene and Oligocene are in the nature of supplementary evidence.

5. **CONVERGENCE AND DIVERGENCE OF PALÆARCTIC AND NEARCTIC FAUNÆ:** far closer than in any known Tertiary or Quaternary stage, were the relations existing in the Holarctic region during the Upper Jurassic period. The resemblances among these minute mammals, as found in the Purbeck of England and the Como beds of Wyoming are most astonishing, for of thirteen genera, six have their English counterparts, and the family characters are very close as regards the remainder. (See OSBORN, '88, pp. 186-7.) It would be rash to say whether or not continuous close geographical connections existed from the Jurassic throughout the Cretaceous, but in the next Nearctic and Palæarctic parallels which we can draw, namely in the Basal Eocene between the *Torrejon* of New Mexico and the *Cernaysien* of France, the resemblances are again very close. During the Upper Eocene the faunal parallels became decidedly less close, in fact the correlation can only be established by relatively few forms. In the lower Oligocene the faunal relations suddenly became again much closer between the old and new worlds and they remained close throughout the later Tertiary until the middle of the Pleistocene period.

## II. CLASSIFICATION OF THE EUROPEAN TERTIARY

Invertebrate palæontologists have naturally taken the leadership in the classification of the old world Tertiary, their vertebrate confrères having followed, adapted and modified the system.

Without question the final classification will be by a synthesis of evidence derived from invertebrate and vertebrate remains, from the comparison of marine, fresh water and terrestrial forms of life with each other and with earth movements. In numerous instances the exclusive use of one class of evidence has led to serious errors.

The great faunal Periods or Systèmes, Eocene, Miocene, Pliocene, and Pleistocene we owe to LYELL. The Oligocene was proposed by BEYRICH ('84, pp. 640-666), chiefly on geological grounds, and although confirmed by the Berlin Geological Congress some doubts are entertained as to its ultimate utility and survival.

D'ORBIGNY, divided the Eocene into the lower (*I*) *Suessonien*, in which we find fossil mammals deposited chiefly north of Paris around the Suessonien gulf, and the upper (*II*) *Parisien* in which the deposits are chiefly around Paris and in the Helvetien canal of the south of France and Switzerland.

The stages and substages of the palæarctic Tertiary employed in the *Third Trial Sheet*, are chiefly the proposals of MAYER-EYMAR ('89), D'ORBIGNY, DUMÉRIL, SUESS, and LAPARENT ('85)—all invertebrate palæontologists. The history or authorship and synonymy of the *Étages, Montien, Thanétien, Suessonien*, etc., may be found in the two palæogeographical essays by MAYER-EYMAR ('89, p. 26), and CANU ('95, pp. 53-56), in which a reclassification of the entire Tertiary is advocated upon the hypothesis of the relation between the perihelions of the globe and the sedimentary substages, as shown in the Tableau 1, of CANU ('95, pp. 12-13). For the purposes of the mammalian palæontologist however, the Lyellian system is more convenient.

Valuable tables of European faunal parallels are given by v. ZITTEL ('93). The fullest lists of European mammals in different horizons are those collected by SCHLOSSER ('87-'90) and DÉPÉRET ('85-'95) in his memoirs on the Miocene and Pliocene. A mine of wealth for an investigation of this kind is SCHLOSSER's *Literaturbericht* ('83-'97); the writer has referred to it constantly and can hardly express his indebtedness.



TROUESSART's ('97) *Catalogus* would have been far more valuable if localities had been cited as well as the geological divisions.

The first step is to ascertain how far the Periods or *Systèmes* can be paralleled in America and Europe and similar permanent limits placed between them. The second is to establish, as convenient divisions of each, *Upper*, *Middle*, *Lower*, or *Lower and Basal*. It is not too much to hope that the synchronism of these periods in the entire Holarctic region during the Tertiary can be established with considerable exactness. The Stages and Substages present much greater difficulty and may prove impossible owing to the absolute independence of the earth movements which caused them in the old and new worlds. It is perfectly evident that the overlapping of these deposition stages would be the rule and that exact synchronism would be largely coincidence and therefore highly improbable. All that we can reasonably hope to establish in the near future is an *approximate parallelism of the Stages*; ultimately the lines of overlap may be determined.

### III. COMPARISON OF THE EOCENE IN EUROPE AND AMERICA

#### 1. The Puerco without a Faunal Parallel

The base of the American Eocene is the *Puerco*, which has been observed by COPE and WORTMAN to immediately overlie the upper Cretaceous in northern New Mexico.

Contrary to the prevailing opinion and usage there is in Europe no known fossil mammal deposit parallel to the basal Eocene or Puerco of America. The Puerco fauna proper is older than the oldest in Europe.

We may therefore provisionally conclude that the fresh water Puerco deposits were approximately of the same age as the earliest marine and brackish limestones of the Suessonian Sea, namely, the *Montien* (Calcaire grossier de Mons, Belgium), or marls, *Heersien*, (*Marnes de Heers*), *Maudunien* (*Marnes de Meudon*), all resting unconformably on the Cretaceous.

## 2. The Torrejon and Thanétien (Cernaysien) nearly Parallel

The oldest fossil mammal beds of Europe are the fluvio-marine *Glauconie de la Fère* (Aisne, 6 metres), containing *Arctocyon primævus*, equivalent to the marine *Sables-de-Bracheux*, also resting upon the Cretaceous which is immediately overlaid by the lacustrine *Calcaires et sables de Rilly* (38 metres). These together constitute the *Thanétien* (LAPPARENT, '85), with which the purely fresh-water *Cernaysien* (LEMOINE) beds in the vicinity of Rheims are closely parallel.

The *Cernaysien* has been almost universally paralleled with the *Puerco*, but many years ago, while studying the Cernaysien fauna of Rheims, with the kind aid of the late Doctor VICTOR LEMOINE, I reached the conclusion that it was more recent than *Puerco* (OSBORN, '90, pp. 51-62). This conclusion is now confirmed by the separation (WORTMAN and MATTHEW, '99, p. 28) of the true *Puerco* fauna underlying the Torrejon fauna. The Torrejon agrees closely with the Cernaysien, so far as we can judge from evidence which awaits a more exact study of the Cernaysien fauna than we have yet enjoyed.

a. MULTITUBERCULATES. It is especially interesting to compare the number of grooves and tubercles upon the *Neoplagiaulax* (Cernaysien) and *Philodus* (Torrejon) fourth premolars and first lower molars, as indicating a similar age.

b. Among the RODENTS or PRIMATES (for the systematic position of these animals is not definitely known, see SCHLOSSER and MATTHEW) compare *Protoadapis* (Cernaysien), dentition 2-1-3-3, and *Plesiadapis* with its reduced dentition, simple molar type and enlarged incisors, with *Indrodon* (Torrejon) (? 1. 3. 3).

c. CREODONTS. Of the *Mesonychidæ*, *Hyænodictis* (Cernaysien) is a little more modern than *Dissacus* (Torrejon) in its lower molars. Of the *Arctocyonidæ*, *Arctocyon gervaisii* (Cernaysien) and *Arctocyon* (Clænodon) *corrugatus* (Torrejon) are to be compared.

d. UNGULATES. As hypothetically ancestral to the Ancylopoda, *Pleuraspidothierium* (Cernaysien) is in an earlier stage

than *Meniscotherium* (Wasatch) which it somewhat resembles in teeth, skull and skeleton.

The fact that neither primitive UNGULATES (*Condylarthra* and *Amblypoda*) nor EDENTATA have been found in the *Thanétien* or Cernaysien beds, together with their absence in the Suessonien and later periods in the *Palaearctic* region, lends some *probability* to the hypothesis that *Condylarthra*, *Amblypoda* and *Edentata* were exclusively Nearctic during the lower Eocene. On the other hand the Cernaysien beds may present a very imperfect picture of life in France during this period.

### 3. Egerkingen Beds more recent than Puerco, Torrejon or Wasatch

Nor is the above probability lessened by the testimony of *Egerkingen* which has been widely accepted as proving the existence of the *Condylarthra* in Europe and as in part a very old fauna.

The suppositions of Rütimeyer ('88), already questioned by SCHLOSSER ('95), that the older portion of the famous fissure fauna of Egerkingen is of Puerco age and that it contains *Condylarthra* are rendered improbable by the following considerations.

FIRST: by my examination of the teeth referred to *Euprotogonia*, *Periptychus* and *Phenacodus* in the Egerkingen collection, which fails to sustain Professor RÜTIMEYER's identifications. Egerkingen is rich in small Eocene Primates; it is possible that the types of the supposed *Condylarthra* correspond with the larger Bridger or Middle Eocene American monkeys such as *Notharctus*, *Tomitherium* (COPE) *Telmatolestes*, *Limnotherium* (MARSH) which are astonishingly ungulate in appearance.

SECOND: I have certainly seen similar primate teeth in Professor DÉPÉRET's collection from *Lissieu*; this is also a fissure fauna and of similar age to Egerkingen.

THIRD: because of the absence in Egerkingen of many typical lower Eocene or Suessonien types and the abundant presence of typical middle and upper Eocene types. It is improbable that a Jurassic fissure would accumulate basal Eocene

types, omit lower Eocene types such as *Coryphodon*, and again collect middle and upper Eocene types.

FOURTH: the Tæniodonta, or ancestral Edentata, with enameled teeth, are apparently truly represented in Egerkingen by the *Calamodon europæus* of RÜTIMEYER, but this tooth is quite as probably in a *Stylinodon*, or Middle Eocene (Bridger), stage of development as in an older stage.

#### 4. Lower Eocene, Wasatch and Suessonien (Sparnacien, Yprésien) truly parallel

The *Sparnacien* of LAPPARENT is the middle substage of the more comprehensive stage *Soissonien* (MAYER-EYMAR); it marks a continuation of the north France depression or Suessonien Sea (Heersien, Thanétien or Suessonien) and is characterized by marine and fluvio-marine deposits bordered to the west and south by purely fresh water fluviatile or lacustrine deposits.

Of the latter the lacustrine *Lignites du Soissonais* (5 metres) contain *Coryphodon owenii*, *Palæonictis gigantea* (Muirancourt, Oise) and *Lophiodon larteti*. The *Argile plastique* (50 metres) is considered by some mainly aerial (fide CANU), by others lacustrine (GARDNER, LAPPARENT); it commences with the *Conglomerat de Meudon*, certainly fluviatile, which contains *Coryphodon anthracoides*.

In the London basin are the *Lower Bagshot Sands*, a marine formation, and below these the *London Clay* (166 metres), see CANU ('95, p. 54), an estuarine formation; these together constitute the *Londinien* of MAYER-EYMAR. The London Clay contains a primitive species of *Hyracotherium*, *H. leporinum*, a primitive *Coryphodon*, *C. cocæus*. These fossil mammals would cause us to consider the London Clay as parallel with the Sparnacien, but LAPPARENT and CANU, from the invertebrate standpoint, place the London Clay in the higher level of the Yprésien or Londinien.

In the Paris Basin a fresh return of the sea deposited the *Sables Nummulitiques du Soissonais* (50 metres, Aisne) embracing the overlying estuarine and littoral *Sables de Cuisse la Motte*; here FILHOL ('88, p. 155) records a small *Lophiodon de Cuis*,

this would correspond with *Heptodon*, the first of the American *Lophiodontidæ*. GAUDRY ('98, p. 302) parallels with these beds the freshwater *Sables Agéiens* (D'EPERNAY), *Étage Agéien*, LEMOINE, the mammalian fauna of which has been described by LEMOINE as containing *Lophiodon* and *Pachynolophus*; but this fauna belongs on a higher level, as in fact GAUDRY himself intimates.

The parallel between the Wasatch and the Suessonien of France was first recognized by MARSH in describing *Coryphodon*. In the meantime vast additions have been made to our knowledge of the Wasatch fauna and practically nothing to that of the Suessonien. Although we know only a fraction of the life of the period, there certainly existed at this time in Europe the successors to certain Cernaysien genera which are represented by descendants in the Upper Eocene.

The three known genera common to both countries, namely, *Coryphodon*, *Hyracotherium* and *Palæonictis* present close structural parallels.

Filhol records *Lophiodon larteti* of the *Lignites du Soissonais* as an ancestor of the true heavy bodied Lophiodontinæ, whereas in the Wasatch we find *Heptodon* belonging to the light bodied Lophiodonts of the "Helaletes-Colodon" line which subsequently appears in Europe. *Platycharops*, mistakenly compared with *Esthonyx* by LYDEKKER has no parallel in America unless among the *Arctocyoniidæ*. GERVAIS ('59) mentions a rodent-like type of incisor from the Suessonien, but this has not to my knowledge been subsequently described.

##### 5. Fissure Formations, Egerkingen and Lissieu, younger than the Wasatch

These formations both represent the remains of animals slowly accumulated in fissures of Jurassic age. The Lissieu fauna is of approximately the same Middle and Upper Eocene duration. As above stated the Egerkingen composite fauna almost certainly does not contain types as old as those of the Wasatch. There is one important exception: the *Proviverra typica* of Egerkingen is in the same stage of development as the *Sinopa* (Sty-

*polophus*) *viverrina* of the Wasatch, while RÜTIMEYER's supposed *Stypolophus* does agree with the *Sinopa brevicealcarata* of the Bridger. Notwithstanding these facts, in the absence of *Coryphodon*, *Palæonictis* and other typical Wasatch and Suessonien forms, the greatest age which can be positively assigned to the beginning of these fissure formations is the lower portion of the Middle Eocene.

#### 6. Middle Eocene, Lutétien, apparently parallel with the Wind River Fauna

Constituting the base of the greater *Parisien* stage, the *Lutétien* substage, first, marks the advance of the sea beyond its Suessonien limits southward around Paris, and to the west and north into Belgium; second, it marks the appearance of fossil mammal deposits in the south of France, in Switzerland (Helvetien Canal), and in Alsace.

The *Calcaire grossier* beds (45 metres) are entirely marine in their lower strata (*Calc. gros. moyen. et infér.*) but become fresh-water or fluviatile at the summit (*Calc. gros. supér.*) where they contain *Lophiodon* and many other ungulates.

Parallel with these beds are those of the *Gres d'Issel* (Aude, 24 metres) fully studied by FILHOL ('88); of *Argenton* (Indre); of the *Argiles à lignites*, or *Agiin* (Rheims) explored by Dr. Lemoine, of *Bracklesham* (England). Certain types of *Buchsweiler*, Alsace, seem to be somewhat more recent. Finally our knowledge of the mammals of this stage is greatly enriched by the older portions of the fissure deposits of Egerkingen (Vaud) and of Lissieu, near Lyons.

This fauna has been hitherto paralleled with that of our great Middle Eocene deposits of the Bridger; we shall see that it only corresponds with a section of the upper Wind River or the Lower Bridger Lake deposits of the Rocky Mountains.

Characteristics: FILHOL ('88, p. 1, 75), in his conclusion upon the Issel fauna, speaks doubtfully of the presence of a large Creodont, as *Palæonictis gigantea*.

This is the continuation of the reign of *Lophiodon*, a type predominant in number and variety.

Three perissodactyl phyla occur, namely the Hyracotheriinae, Lophiodontinae and Helaletinae, whereas at the same period in America we find the Hyracotheriinae, Tapiridae, and Helaletinae.

Without exception in the Lutétien representatives of the perissodactyl families Lophiodontinae and Hyracotheriinae the premolars are simpler than the molars and these animals are therefore in a stage of evolution corresponding with that which we find in the Wind River beds. The horses so far as I can judge from personal study, from FILHOL's descriptions and from figures, (GERVAIS, '59) *P. Suillus*, *P. parvulus*, *P. duvalii*, all belong to the primitive stage, namely, premolars simpler than molars, no mesostyle, and are therefore in a Wind River (*Protorohippus*) rather than Bridger (*Orohippus*) stage of development. FILHOL ('88, p. 182) lays great emphasis upon the fact that all the so-called 'Pachynolophus' of Issel, Pépieux and Lautrec have the premolars simpler than the molars. Furthermore in beds of undoubted Issel, Argenton or Buchsweiler age, no complete *Anchilophus* types of premolars (pm = m) occur. As for the oldest *Artiodactyla* in either country, COPE ('82, p. 71) has compared Lemoine's *Lophiodochærus peroni* of the Argiles-à-lignites with his *Trigonolestes brachystomus*, from the Wind River. Among the primates the little known *Heterohyus armatus* GERVAIS, distantly resembles *Microsyops* of the Bridger in its molar teeth only, the premolars being simpler than in the Bridger species.

These are significant facts. So far as they go they indicate that the known beds of Lutétien formation (having a thickness of 45-24 metres) are by no means equivalent to the Bridger Beds (having a thickness of 800 metres), as heretofore stated, but they merely correspond to a section of the Lower Bridger or more probably of the Upper Wind River formation.

It is true that in the Helaletinae, or cursorial Lophiodonts, in the fauna of Egerkingen and Lissieu, namely *H. cartieri*, *H. annectens* (and perhaps *Helaletes* (*Hyrachyus*) *internedius* of Selles-sur-Cher), the third and fourth premolars have double internal lobes like those of *H. (Desmatotherium) guyotii* of the Bridger. But it must be remembered as regards both Eger-

kingen and Lissieu that they are composite faunæ, containing *upper* Eocene forms mingled with the *middle* Eocene forms, therefore, they cannot be cited at all as proofs of synchronism. Similar *Helaletes*-like teeth are described by FILHOL from Buchsweiler, Alsace, namely the type 3d and 4th premolars of his *Palæotapirus buxovillanus* ('88, p. 179, pl. XIX, fig. 4), which certainly belong not to the *Tapiridæ* but to the *Helaletina*, a sub-family of *Lophiodontidæ*. On the other hand, the upper molar and the lower jaw assigned to *Hyrachyus intermedius* (FILHOL '88, p. 114, pl. XXX, figs. 8 and 6) from *Argenton* resemble the *Helaletina* in a Wasatch or *Heptodon* stage of development because they are small and simple.

#### 7. Middle Eocene, Bartonien, apparently Equivalent to the Lower Bridger

This substage receives its name from the *Barton Clays* of England (100 metres). The *Sables de Beauchamp*, marine (15 metres) is succeeded by the partly lacustrine *Calcaire de Saint Ouen* with which the fresh water *Grès de Cèsseras* (Hérault) are considered parallel.

From the *Grès de Cèsseras* a few mammals are recorded. The *Cesserasictis antiquus* (FILHOL '88, p. 182, pl. XIX, fig. 3) type is a small lophiodont jaw with molar teeth which resemble those of *Helaletes* of the Bridger except in the extreme simplicity of the supposed 4th premolar.

If FILHOL's identification and description is correct no comparison can be made with our Bridger *Helaletes* which has a partly compound fourth premolar. The *Lophiodon cesserasium* FILHOL (*L. occitanicum*, GÉRAIS) is judging by GÉRAIS' figures (pl. 18, fig. 7), one of the *Equidæ* in a Bridger stage of development.

The American parallel of the Bartonien is probably Lower Bridger but it cannot be determined until we secure a more exact knowledge of the state of molar and premolar evolution of the few ungulate fossils which it contains.

The writer is chiefly indebted to Professor ALBERT GAUDRY for the arrangement of the lower Eocene in the accompanying 'Third Trial Sheet.'



### 8. Upper Eocene, Ligurien

The summit of the French Eocene is characterized geographically by the recession of the northern gulf on its western borders and by numerous small freshwater lake and river deposits in the south and southwest of France, in Switzerland, and on the German border (CANU, '95, Plate 44).

In the Paris Basin, made famous by the classic researches of Cuvier and Brogniart, is the *Gypse de Montmartre* (55 metres) partly marine, partly lacustrine; at its summit are 20 metres of gypsum which contain most of the mammals described by CUVIER. Above are the lacustrine *Marnes de Pantin*.

Parallel with the *Gypse* are the rich *Lignites de la Dèbruge* (Vaucluse, 2 metres).

Parallel with the *Gypse* in the South are the beds of *St. Hippolyte de Caton* (Gard) recently described by DEPÉRET; of *Castelnaudry* (Aude); of *Lautrec* (Tarn) described by NOULET ('63) also by GERVAIS ('69).

There are also the lacustrine limestones of Carcassonne, near the Pyrenees, and the localities *Mas-Saintes-Puelles* and *Villeneuve-la-Comptal*, Castres. To the west in Germany are the fissure deposits or *Bohnerzen* of *Heidenheim* (Mittelfranken) *Ulm*, *Pappenheim*, *Fronstetten*<sup>1</sup> (Swabian Alps), *Sigmaringen*; to the south the older fissure deposits of the *Phosphorites du Quercy*, and the fissures of *Egerkingen* and *Lissieu*.

This period contrasts with all its predecessors by the superbly full fauna which it contains; we feel for the first time that the fossil record is approximately representative of the living fauna. It is greatly enriched by the composite parallel faunæ of the *Siderolithique de Mauremont* and the newer portions of the composite faunæ of *Egerkingen* and *Lissieu*.

Lautrec, undoubtedly Upper Eocene, contains a very large *Lophiodon*, *L. lautrecense* of especial interest, because it is apparently the last of its race. It is probable that the large *Lophiodon* of *Heidenheim*, with complex premolars, is related to the Lautrec type. In the Heidenheim specimen the second and

<sup>1</sup> Fronstetten fauna described by Jäger, Fraas, Quenstedt and v. Meyer.

third superior premolars have double internal cusps. *Lissieu* as studied by Depéret is mainly middle Eocene but it contains some important Upper Eocene forms, while *Egerkingen* has a rich representation of Upper Eocene types.

The large *L. rhinoceros* Rütimeyer, of *Egerkingen* is, however, not of the Heidenheim type because it has simple upper premolars associated with it; it is an older representative of the large race of *Lophiodontidæ*.

*Mauremont* is considered mainly, if not exclusively, of Upper Eocene age.

#### GENERAL CHARACTERS.

(1). This fauna is much more modern than that of the *Grès de Cèsseras*, or of the *Calcaire Grossier* and *Issel*; the great advance in the structure of the teeth especially seen in a comparison of *Propalæotherium* and *Palæotherium* is proof of modernization. *Palæotherium* is now the predominating type of Perissodactyl, although a large form of *Lophiodon* survives.

(2). Secondly, the composite beds of *Egerkingen* and *Lissieu* furnish the ancestry of certain types of *Gypse* Artiodactyla and in these beds we also find certain other forms transitional between the *Issel* stage and the *Gypse* stage.

(3). Thirdly, the *Gypse*, is a very highly specialized and differentiated fauna including many artiodactyls and other types the ancestry of which is known neither in Europe or America and has not thus far been found in *Egerkingen* or *Lissieu*.

(4). Fourth, the *Ligurien* is widely distinct faunally from the American Upper Eocene or Uinta with which it has been heretofore paralleled. At no period of the Tertiary were the Nearctic and Palæarctic faunæ so widely separated. In fact a much wider gap exists between Western America and Europe in the Upper Eocene than in the preceding Lower and Middle Eocene or in the succeeding lower Oligocene.

The resemblances or parallels with America are mostly limited to one genus of horses (*Pachynolophus*), which occur in both countries, to one Creodont *Hyænodon*, and to the ancestors of the *Canidæ* and *Viverridæ* which occur in both countries.

(5). Contrasts. The *Cheiroptera* and *Insectivora* of these two

regions cannot be compared until the American forms named by Marsh are adequately studied. The *Primates* have no direct parallels. Among the *Perissodactyla*, *Palæotherium*, *Palaplotherium*, and *Anchilophus* have no parallels in America. The *Selenodont Artiodactyla* of the two continents are widely distinct; the *Gypse* selenodont *Artiodactyla* have no parallels in America. The bunodont *Artiodactyla* have not yet been carefully compared.

(6). There are therefore comparatively few *direct* reasons for considering the *Gypse* and *Uinta* as nearly contemporaneous but there is a substantial indirect reason namely that they both closely underly Oligocene Beds in which there suddenly reappears a marked community of fauna in the Nearctic and Palæarctic regions. In other words the *Gypse* bears a relation to the Ronzon similar to that which the Upper Bridger bears to the Upper *Uinta* and White River.

The most significant fact is the apparent invasion of the Palæarctic region in the Upper Eocene by a great variety of *Artiodactyla* which mingled with the older phyla of France and Germany. Where did these animals come from? Not from Asia, certainly, because some of them would have found their way also into the Nearctic, probably therefore from Africa or the *Ethiopian Region*.

### 9. Composite, Imperfectly Stratified Fissure Deposits of Middle Eocene to Middle Oligocene Age

The most famous of these fissure deposits are those of Quercy, Egerkingen, Mauremont, Fronstetten.

In the Swiss Jura are the *Bohnerzen*, mainly non-calcareous reddish clay nodules with pisolithic iron grains. The siderolithic earths, *Sidérolithiques*, typically at *Mauremont*, found in Jurassic limestone fissures are so called because they contain grains of iron, imbedded in concretions probably of mineral spring origin, associated with travertines. A special type of fissure deposits, analogous to the above in certain respects are the *Phosphorites*, typically represented in *Quercy* but characteristic also of other periods.

The age of these various deposits is a very important matter. For reasons given above and below certain of these deposits appear to have overlapped or extended through one or more periods of regular stratigraphic deposition as follows:

Egerkingen (Canton Vaud) Middle to Upper Eocene inclusive.

Lissieu, Middle to Upper Eocene inclusive.

Fronstetten (Swabian Alps), Mainly Upper Eocene.

Heidenheim (Mittelfranken), " "

Mauremont (Canton Vaud) " "

Oerlinger Thal. u. Eselsberg, Ulm, Upper Eocene.

Quercy, Caylux, Mouillac, Phosphorites, Upper Eocene to Middle Oligocene.

The PHOSPHORITES DU QUERCY, the most extensive and famous fissure deposits of this kind, occur in Jurassic calcareous fissures of 3 to 6 metres in width and 35 metres in length. The matrix is a phosphate of lime probably of mineral spring origin (FILHOL, '77, p. 1-27). The fauna enjoyed a warm and moist climate. FILHOL believes that death was caused by asphyxiation, due to poisonous vapors arising from hot springs, many skeletons being found complete and showing no marks of teeth. In contrast with Quercy, which contains a fauna of extraordinary richness, beauty and completeness, EGERKINGEN and LISSIEU have yielded merely isolated teeth.

The Quercy fauna according to FILHOL predominates in Upper Eocene or *Gypsc* types. The Phosphorite rhinoceroses have by some authors and in many museums been referred to *A. lemanense* and *A. minutum*, both of which are Upper Oligocene or Aquitanian species—this is an error; the two rhinoceroses which this formation contains are probably the *Ronzotherium vclaunum* AYMARD, found also in Ronzon, and another species much simpler than the Aquitanian *Dicreratherium minutum* Cuv. (*R. pleuroceros* DUVERNOY), of Moissac. This small species has simple upper premolars; it either belongs to *A. gaudryi* RAMES, or represents a distinct species. These facts with the tables published by FILHOL ('77) show that the Quercy deposition probably terminated in the lower or Middle Oligocene.

Characteristic of the region of the Alps during elevation are the marine, brackish and freshwater *molasses*, that is, calcareous or argillaceous rocks easy to work, mingled with conglomerates called *nagelfluh* a littoral formation. These were produced in Switzerland on the shores of islands during oscillation periods.

#### IV. OLIGOCENE OF EUROPE

This Period is actually well defined in its geographical features, as well as in its fauna and flora; in France it begins typically with the *Ronson* fauna which contains a number of entirely new types, and it terminates with that of *St. Girand le Puy*. Some authors, however, LYDEKKER ('96, p. 191), LEPSIUS ('92, p. 550), include within the lower Oligocene the Ligurien or *Gypse*; this is a cause of great confusion in the literature.

The duration of the Oligocene may be estimated by deposits in Italy of 2900 metres in thickness.

**Earth Movements.**—According to LAPPARENT ('85, p. 1164) the Oligocene of Europe begins with the main elevation of the Pyrenees and is marked toward the close by the initial elevation of the Alps. Its first or early earth movements (*Étages Infra Tongrien* and *Stampien*) caused a recession of the sea at the south, and an invasion of the sea from the north—this invasion reached the centre of France; in the Rhine valley it extended as far south as Basle. The climate during this period was moderate. The second or *Étage Aquitanien* was one of elevation and strongly contrasted with the preceding by a general recession of the sea; it instituted a period of great freshwater lakes in France and Southern Europe, varied by lagoons with lignitic deposits. Under more temperate climatic conditions, with considerable moisture, the flora was of Indian and Australian type, the deciduous trees increased in number, but palms still flourished as far north as the Baltic; the bird life of central France (Allier, MILNE-EDWARDS) was similar to that of the lakes of Southern Africa. Along certain lake borders however, in Southern France (Aix and Gargas, SAPPORTA), the heat and drought during the latter part of the summer were extreme.

The Oligocene terminated by the deepening of valleys, drying of the lakes and substitution of the fluvial régime of the Lower Miocene.

Upper Oligocene 3.		Aquitanién.	Extensive freshwater lakes and lagoons. Recession of sea.
Middle Oligocene 2.	Tongrien.	Stampien.	Advance of sea in Paris Basin.
Lower Oligocene 1.		Infra Tongrien.	Marine and brackish deposits, lacustrine and marine Marls.

### 1. Infra Tongrien, Lower Oligocene

Ronzon was considered of Stampien age by LAPPARENT ('85, p. 1176); it is true the beds overlie the *Calcaire de la Brie*, which is undoubtedly lower Oligocene; GAUDRY accordingly places it in the Infra Tongrien, and its fauna certainly succeeds closely that of the *Gypsc*.

In 1881, M. FILHOL ('81, pp. 256-263) concluded that *Ronzon*, even after 30 years of exploration, could not be considered a locality typical of the French fauna of the period. Since 1881, however, considerable additions have been made to the *Ronzon*, fauna, so that now it must be considered fairly typical (see SCHLOSSER, '90).

The animals which make their first appearance here are the anthracotheres (*Anthracotherium* said to be absent in *Ronzon*), the elotheres, *Eutlodou* (Elotherium) and the rhinoceroses, *Ronzotherium* (Aceratherium), two new genera of dogs, *Amphicynodon* and *Cynodon*. Otherwise the fauna continues an evolution of that of the *Gypsc*, being especially distinguished as the last stage in which the *Palæotheriidae* and the creodont *Hyænodontidae* occur.

The marsupials are represented by *Peratherium*. Insectivores are represented by *Tetracus*. Among rodents we find representatives of the *Anomaluridae* and *Muridae*.

The European parallels with the *Marnes et Calcaires de Ronzon* (100 metres) fauna are mainly the newer portion of the PHOSPHORITES. If M. FILHOL'S identification is correct in establishing the three genera, *Leptomanis*, *Necromanis* and *Palæoryctecropus*, FILHOL ('93, p. 129), it is possible that during

this early Oligocene stage, the earliest edentates, pangolins and aard varks occur. Here also occurs the earliest of the European *Ancylopoda*, *Schizotherium priscum*.

The lignites of *Cadibona* (Piedmont) were considered Upper Oligocene (Aquitaniens) by LAPPARENT ('85) and WEITHOFER, but they contain a little rhinoceros with simple premolars of lower Oligocene type. A portion of the fauna of *Lobsann* (Alsace) is parallel (ANDRÉE, '84) containing *Anthracotherium*, *Hyopotamus velaunus* and a species of rhinoceros wrongly attributed to *Aceratherium incisivum*.

## 2. Stampien

The Mid Oligocene stage is according to all authorities chiefly represented by the marine phase *Sables de Fontainebleu et d'Étampes* (41 metres); freshwater parallels are as follows: the *Argiles de St. Henri* (Rhône) are placed in the Stampien by Gaudry because they contain *Anthracotherium* and (?) *Diccratherium minutum*. In the Paris basin are *Ferté-Alais* (Seine et Oise), lacustrine sands, also placed by Gaudry at this level; *Selles-sur-Cher* (lacustrine limestones), also in the Paris' Basin; *Villebramar* (Molasse, Lot et Garonne).

## 3. Aquitanien, Upper Oligocene

The typical mammal deposits of this stage are the famous lacustrine beds of *St. Gérard-le-Puy* (Allier), calcareous, with a rich fauna (FILHOL, '79). This directly underlies lower Miocene beds containing *Anchitherium* and *Mastodon*.

Distinctive types of this stage are:

- Palæoerinaceus,
- Palæogale (and other mustelines),
- Progenetta (and other viverrines),
- Amphicyon lemanensis,
- Protapirus douvillei (not certainly a tapir),
- Diceratherium minutum,
- Aceratherium lemanense,
- Anthracotherium magnum. (Lignites de Volx.)
- Anthracotherium hippoideum. (Lignites de Volx.)

The rhinoceroses show a very marked progression. The large *A. lemanense*, with complicated premolars represents one line; the small *Diceratherium* (? *croizeti*) *minutum* represents the Dicerathere line. Boule has reported a third line, *Cadurcotherium* (Moissac) representing the Amynodontidæ.

Parallel with St. Gérard-le-Puy are: *Moissac* (Molasse) containing the oft quoted *D. minutum* Cuvier; *Gannat* (lacustrine) containing the type of *A. gannatense* which is identical with *A. lemanense*; also *Randan* (lacustrine). Lignitic deposits of this stage are the *Lignites de Volx* (700 meters, Bas Alpes) and of *Manosque* (600 meters, Aix).

The former contains the large anthracotheres, *A. magnum*, *A. hippoidcum*, highly characteristic of the upper Oligocene stage.

Beds paralleled with these by v. ZITTEL ('93, p. 66), in Germany are those of Ulm (Eselsberg and Eckingen); the complete faunal list of Ulm (LEPSIUS, '92, p. 570) shows these beds to be transitional between upper Oligocene and lower Miocene age; v. ZITTEL however places St. Gérard-le-Puy in the lower Miocene.

## V. MIOCENE OF EUROPE

The lower Miocene of Europe is sharply separated from the Oligocene both geologically and faunally. Its duration may be judged from the thickness, 2700 metres, of marine deposits in Italy.

**Divisions.**—The Miocene is clearly divided in some regions into two stages, at others into three, as follows:

2d Mediterranean. (Suess.)	3. <i>Tortonien</i> (Oeningien, Grepp)	Recession of sea. Mainly fresh water, brackish and lacustrine deposits.
	2. <i>Helvétien</i> , M. E. 1857.	Maximum of sea, mainly marine and brackish deposits. Local fluviatile and lacustrine deposits in the south. (Falunien, d'Orb.)
1st Mediterranean. (Suess.)	1. <i>Langhien</i> . M. E. 1857.	Mainly fluviatile deposits. Invasion of sea on the south, partly marine and brackish deposits. (Burdigalien, Lapp. Depér.)



European geologists and invertebrate palæontologists are practically unanimous as to these divisions (DEPÉRET, '92). Certain vertebrate palæontologists, however, still include in the uppermost Miocene the Pikermi and Eppelsheim beds which clearly belong in the base of the Pliocene. Faunally (mammals) the Miocene is now divided into upper and lower but it is apparent that it is capable of division into three life-stages typified in France as follows :

3. UPPER, typified by *Grive-St-Alban*.
2. MIDDLE, typified by *Sansan* and *Sinorre*.
1. LOWER, typified by *Sables de l'Orléanais*.

The separation of these life stages we owe chiefly to Depéret.

**Physical Geography.**—The Miocene is in general distinguished by a relative *elevation* of Northern Europe and *depression* of Southern Europe ; accompanied by great volcanic eruptions in central France and Hungary ; and ending in the completion of the great chains of Alps and Himalayas.

1. *Langhien*. In France the Oligocene Lake Basins were drained off and replaced by great river valleys, as attested by the fluviatile deposits or *Sables de l'Orléanais*. 2. *Helvétien*. This stage has a thickness of 495 metres in the basin of Crest (Fontannes.) The sea invaded the west coast of France up the valley of the Loire, also upon the south, isolating Spain and extending up the Rhone Valley, surrounding the northern slope of the Alps and extending northward to the Mayence Basin, to the east and south into the Vienna Basin, submerging large parts of Austria and Italy and converting parts of Europe into an archipelago. 3. *Tortonien*. A general recession of the sea accompanied by a marked increase in the number of freshwater deposits characterize this stage. Among these deposits perhaps the most typical or complete at the present time is that of *Grive-St-Alban* (Isère), monographed by Depéret ('92). The lesser part of this fauna is equivalent to that of Sansan ; the greater part is somewhat newer. To the southeast, Austria was still partly submerged forming the *Leithakalk* or marine summit of the Tortonien in the Vienna Basin.

*Climate.*—If we can judge by the very gradual evolution of the fauna, the physical and biological conditions changed slowly.

The climate was extremely mild, subtropical but becoming more temperate, with a persistence of Sequoias and Palms (*Sabal*), even far north, a gradual increase in the number of deciduous trees which include a large proportion of North American types, and a marked increase in the grasses, stimulating the evolution of deer in the north and antelope in the south, especially towards the close of the period.

### 1. Langhien or Burdigalien, Lower Miocene

The *Sables de l'Orléanais* (Paris Basin, max. 20 metres) at Neuville-aux-Bois, Chevilly, Avaray, Chitenay (Loire-et-Cher), with a rich typical fauna, constitute the base of the Langhien, overlying the Aquitanien (Calcaire de Beauce) and underlying the *Marnes de l'Orléanais*, and the *Calcaire-de-Montabuzard*, beds which are parallel with the *Sables-de-Salogne* (40 meters).

The *Calcaire-de-Montabuzard* has a mammal fauna which Douvillé compared with that of Simorre, while the *Sables de l'Orléanais* fauna was formerly compared with that of Sansan. But French palæontologists (GAUDRY, DEPÉRET, '92, p. 155) now consider the *Sables de l'Orléanais* fauna somewhat older than that of Sansan, especially because it contains successors of certain Upper Oligocene types such as *Brachyodus onoides*, the last of the anthracotheres in Europe, *Palæosclerus typus* also a survival, and *Procerulus* or *Dicroceras* (Depéret, '92, p. 155). On the other hand the *Sables de l'Orléanais* mark a faunal change from the Oligocene of the sharpest kind in the presence of the Proboscidea, *Dinotherium bavaricum* and *Mastodon angustidens*, both typically and exclusively Miocene species, which possibly had recently migrated into Europe from Africa by means of a favorable land connection. The *Sables de l'Orléanais* therefore constitute the typical lower Miocene of Europe. Freshwater equivalents (DEPÉRET, '95, p. 397) of these beds are the *Grauw Süsswasser Molasse* (Lausanne) containing a rhinoceros; *Engelhalde* (Bern); *Rappensfluh* (Aarburg). The *Brackische Schichten* (Ulm) are transitional; partly calcareous deposits near *Ulm* (Eckingen, Eselsberg, Hockheim), contain *Anchitherium* and a fauna which is partly Oligocene, partly

Miocene (LEPSIUS, '92, p. 570). Among the marine equivalents (Lepsius, '92, p. 546) are the *Oberer Meeres Molasse* (Switz.), *Muschelsandstein* (Baden). The marine molasse of *Eggenburg* is a noteworthy parallel as containing *Brachyodus onoidens* (DEPÉRET, '95, p. 397) and *Metaxytherium*, a Sirenian. *Brüttelen* (Studer, '95) also contains this true lower Miocene fauna including *Brachyodus onoidens* (SCHLOSSER, Lit'b., '95, p. 183) and *Hyopotamus helveticus*. The marine Cetacean of the period is *Squalodon barriense*.

Of exceptional importance is the presence of a similar fauna (*Amphicyon*, *Mastodon angustidens*, *Dinotherium*, *Anthracotheerium*, *Hyotherium* and *Listriodon*), in southwestern India, in the *Bugti Beds* of Sind. These beds (BLANFORD, '84, p. 37) are far below the horizon of the Siwalik (Pliocene) fauna and contain all the typical older Miocene forms mingled with many of newer type. We find here especially *Hyopotamus giganteus* which Depéret regards as merely distinguished by its greater size from *Brachyodus onoidens*. LYDEKKER ('96, p. 201) and Blanford both consider the Bugti beds as "not improbably of Upper Miocene Age," and as indicating a survival in this area of archaic types which at that time had completely disappeared in Europe; the same author refers also to *Tetraconodon*, a large eutherian, and to *Hyopotamus*; associated with the Miocene types therefore are true Oligocene types. The Bugti Beds are rich in Proboscidea and taken all together should be considered Lower and Middle Miocene rather than Upper Miocene.

Especially significant is this community of fauna between southern Asia and Europe at this time.

The lower, middle and upper Miocene faunas may therefore be contrasted as follows :

LOWER MIOCENE.	MIDDLE MIOCENE.	UPPER MIOCENE.
Typ.: <i>Sables de l'Orléanais</i> .	Typ.: <i>Sansan &amp; Simorre</i> .	Typ.: <i>Grive-St.-Alban</i> .
<i>Brachyodus</i> .....	○ .....	○
<i>Elotherium</i> .....	○ .....	○
<i>Rhinoceros aurelianensis</i> ...R. <i>Sansaniensis</i> .....	R. <i>brachypus</i> .....	×
<i>Anchitherium aurelianense</i> .....		×
<i>Dinotherium bavaricum</i> .....		×
<i>Mastodon angustidens</i> .....	×	×

Macrotherium.....	×	.....	×
Amphicyon.....		.....	Hyænarctos.
Lutra.....		.....	Ursavus (Ursus) primævus.
		.....	Pliopithecus (Sansan)..Pliopithecus.
		.....	Dryopithecus (St. Gaudens)..Oreopithecus (Mt. Bamboli)

o = extinct, or not recorded.

× = present, or recorded.

## 2. Helvétien, Middle Miocene

Fortunately for the mammalian palæontologist a large fresh water basin (termed '*Lac de l'Armagnac*' by Canu) was formed in southwestern France. Here were deposited the *Calcaires de l'Armagnac* (300 metres); in the lower levels are the famous *Calcaires de Sansan*, discovered in 1834; these were placed in the Langhien by LAPPARENT ('85, p. 1198) but are considered at the base of the Helvétien by Depéret; the rich Sansan fauna, containing both large and small animals and many skeletons, was first made known by LARTET ('51), and more recently has been monographed by FILHOL ('91).

Upon a higher level than Sansan, separated by conglomerates (LAPPARENT, '85, p. 1189), are the *Calcaires de Simorre* (originally compared with the *Calcaire de Montabuzard* by Douvillé) FILHOL ('91, p. 9) treated the Sansan and Simorre fossils as of the same age; he did not for example separate *Rhinoceros simorreusis* from *R. sansaniensis*; the writer finds that the former is specifically different from the latter and is of slightly more recent type. Simorre is thus geologically on a higher level and faunally somewhat younger than Sansan although still within the stage Helvétien, as arranged by Depéret. Parallel with Simorre is *Saint Gaudens* (Haute Garonne), according to Gaudry and Depéret. At the extreme base of the Helvétien and therefore parallel with Sansan or the 2d Mediterranean (Suess, DEPÉRET, '92, p. 156), are the *Lignites de Styrie* or the *Steiermark Braunkohle* (Eibiswald, Wies, Görtschach, Voitsberg); the fauna of these outlying lignites of the Mediterranean sea invasion has been fully described by Suess, Peters, Hoernes, Hoffman, Toulou. *Leiding*, in Southern Austria, is said to be of the same age.

The lignites of *Monte Bamboli* (Tuscany) are placed by LEPSIUS in the Langhien; their position is doubtful; they are here placed in the Tortonien.

### 3. Tortonien, Upper Miocene

This is the 'middle miocene' of Gaudry, Depéret, Gaillard and others who include Pikermi in the Upper Miocene; it is the 'upper miocene' of those who place Pikermi in the Pliocene.

*Grive-Saint-Alban* (Isère), explored by JOURDAN between 1845 and 1861, should now be regarded as typical upper miocene. That the mammalian fauna of this stage is distinctly more recent than that of Sansan and Simorre was maintained by DEPÉRET ('87, p. 22; '92, p. clvi) who showed that of 34 species 14 occur in Sansan; GAILLARD ('99, p. 75) has increased the faunal list of *La Grive* to 63 species and the new types he records all tend to emphasize the more recent age<sup>1</sup> of this remarkably rich and typical fauna; many of the forms, however, such as *Felis*, *Ursus*, *Sus*, recorded by Gaillard are Pliocene genera, which probably should receive different names.

The best known parallel of *La Grive* are the sands of *Steinheim*, Württemberg, in which upwards of 30 species have been recorded (fauna, see LEPSIUS, '92, p. 586); twenty of these species are common with those of *La Grive*. In Bavaria are the deposits of *Günzburg*, *Ries* (Nordlingen) and *Georgensgmünd*. In Switzerland are the *Enningen* beds (Obere süßwassermolasse, Molasse d'eau douce supérieure), famous not only for its fauna but for its remarkable flora. This flora, as monographed by Heer, indicates a climate similar to that of Madeira and Japan; other localities of the upper *molasse* are *Elgg* and *Käpfnach*. In the Paris basin is the *Molasse de l'Anjou* (DÉPÉRET, '92, p. 155); the *St. Jean de Bournay*; in the Rhone basin the *Cucuron* (Molasse) and *Cabrières* (Marnes).

<sup>1</sup> *Op. cit.*, "Les nouveaux mammifères rencontrés à la Grive tendent à donner à la faune de ce gisement une physionomie toute particulière et à la rapprocher davantage de la faune actuelle."

## VI. PLIOCENE OF EUROPE

The mammalian faunal base of the Pliocene is defined in its northern facies by the Eppelsheim beds, in its southern facies by the very rich Pikermi deposits—the differences being entirely explainable by climate and latitude. Lepsius, the chief authority upon the geology of the Mayence Basin, holds (in opposition to Schlosser) to the unmixed character of the Eppelsheim fauna and to their unquestionable Pliocene age. The early identifications of Eppelsheim rhinoceroses, etc., with those of Sansan by Kaup and others were erroneous; according to the writer's recent observations they are very distinct. In both the German and Greek beds as maintained also by Eymar, Blanford, Lapparent and Schlosser the Pliocene age is unquestionable.

A new type of horse *Hipparion*, with very complex teeth and apparently a new comer to Europe, is common to both horizons, so are certain rhinoceroses and Ancylopoda but among the ruminants the hardy deer of Eppelsheim are replaced by antelopes and giraffes in Pikermi. Thus fortunately the beginning of the Pliocene is as sharply determinable by its mammalian fauna as the beginning of the Miocene.

In time and geographical history the Pliocene period extends between the completion of the Alps and the establishment of the main coast lines of modern Europe, the last touches to these lines being given in the Pleistocene and establishing their modern aspect. Marked throughout by continuous volcanic disturbances the period included a prolonged land depression in southern Europe and extensive invasions of the sea as shown in the following table :

4. SICILIEN. (ARNUSIEN)	<div style="display: inline-block; vertical-align: middle;"> <div style="display: inline-block; vertical-align: middle;"> A marine phase in Sicily. Fresh water lacustrine deposits in the Val d'Arno. Marine, brackish and lacustrine deposits. </div> <div style="display: inline-block; vertical-align: middle; font-size: 3em; line-height: 1;"> }</div> </div>	Mammalian fauna of <i>Val d'Arno su- périeure</i> .
3. ASTIEN.	<div style="display: inline-block; vertical-align: middle;"> <div style="display: inline-block; vertical-align: middle;"> Recession of the sea from southern river valleys, followed by fluvial and lacustrine conditions (Sables jaunes astiens). </div> <div style="display: inline-block; vertical-align: middle; font-size: 3em; line-height: 1;"> }</div> </div>	Mammalian fauna of <i>Roussillon</i> .

2. PLAISANCYEN.	<div> <div>Maximum marine <i>subapennine</i> invasion, long arms of the sea up the Po and Rhone valleys. Mediterranean extends to the East. (Argiles bleues subapennines). Chiefly marine deposits.</div> </div>	<div> Mammalian fauna unknown, except that of <i>Casino</i> at the base of this stage. </div>
1. MESSINIEN.	<div> <div>Renewed advance of the sea, brackish and freshwater conditions. Mediterranean bounded by Sardinia on the east; great Caspian seas and lakes beyond.</div> </div>	<div> Fauna of <i>Pikermi</i> and <i>Eppelsheim</i>. </div>

*Climate.*—Owing to the warm Mediterranean invasion the climate was mild. DEPÉRET, our chief authority ('93, p. 529), shows that there was no decided change of flora; nevertheless the period was marked by the very gradual advance of northern forest types and by the recession of the more delicate southern types, the palms for example being driven 10 degrees further south. The decisive lowering of temperature came during the early Pleistocene period.

### 1. Messinien, Lower Pliocene

During the first or Messinien stage the fauna of the lake-bound Ægean region (Pikermi), altogether similar to that of Southern France (Mt. Léberon), indicates abundant if not highly watered vegetation and extensive grazing pasturages of central African type. This fauna was widely distributed and highly distinctive; the parallels are numerous and well known.

Orient.	<i>Pikermi</i> —typical southern fauna. <i>Samos</i> (Ægean Sea), <i>Maragha</i> (Persia).
France.	<i>Mt. Léberon</i> (Vaucluse). <i>Molasse d'eau douce supérieure du Rhône</i> (higher than beds of same name in Switzerland). <i>Cucuron</i> (Couches saumâtres). <i>Puy Courmy</i> (Cantal).
Austro-Hungary.	<i>Belvidère Schotter</i> , fluvialite gravels (Pontique, Depéret, '92. p. 156, Congeria Beds, Vienna Basin).
Spain.	<i>C. nucul</i> (Èbre Valley, near Madrid, a very extensive lacustrine formation), 'Alcoi.
Germany.	<i>Eppelsheim</i> gravels (4–7 metres), near Darmstadt. <i>Upper Dinotherium</i> sands, of Augsburg, Neuburg, Delsberg.

Distinctive types of this stage are *Pliolylobates* (Eppelsheim), *Hystrix* (Pikermi), *Pliohyrax* (Samos) *Hipparion gracile*. *Acera-*

*therium incisivum* of Eppelsheim succeeds the *A. tetradactylum* of Sansan; the above are dolichocephalic rhinoceroses, possibly ancestral to *Elasmotherium*; *R. schleiermacheri* possibly is a very large successor of *R. sansaniensis*; *R. goldfussi* (Eppelsheim), a successor of *R. brachypus* of la Grive-Saint-Alban; *R. blanfordi* (Maragha) also represents the short skulled or brachycephalic race; *R. pachygnathus* is probably an African immigrant. *Dinotherium giganteum* replaces *D. bavaricum*. So throughout the Mammalia, besides numerous newly introduced forms, such as *Pliohyrax* and *Oryetropus*, there is a marked evolution beyond the upper Miocene types.

## 2. Plaisancien, Lower Pliocene

As this is chiefly a marine phase the terrestrial mammalian fauna is unknown except in the lignites of *Casino* (Tuscany) at its base; these are equivalent to the *Couches saumâtres à congeries*, according to Depéret, and Lapparent. Here are found *Hipparion gracile*, *Sus crymaulhius*, *Antilope massoni*, *Tapirus priscus*, *Scnuopithecus monspessulanus* and other lower Pliocene types. This is the 'pliocène inférieure' of Gaudry, Depéret and others who have maintained the upper Miocene age of Pikermi. Upon a somewhat higher level than *Casino* are the following marine formations of England in which many cetacean and a few terrestrial types occur; the parallels are:

Coralline Crag (Suffolk), marine, containing *Mastodon*, *Rhinoceros*. Red Crag, inferior or Nodule Beds, Marine, containing a fauna equivalent to that of the Astien stage in part.

## 3. Astien, Middle Pliocene

This stage contains the 'faune pliocène ancienne' of Depéret, or the 'older pleiocene fauna' of certain English authors who have not recognized Pikermi as the typical older Pliocene. Typical localities are the following:

- |                           |  |
|---------------------------|--|
| <i>Roussillon.</i>        | Sables sillicieux gris (25 metres), fluviolacustrine, fauna very similar to that of Montpellier.             |
| <i>Montpellier infér.</i> | Sables jaunes marins (50 metres), described by Gaudry and representing the Plaisancien faunal stage in part. |



*Perpignan.* Fluvatile.

*Maximienx* (Ain) tufas, famous for its characteristic Pleistocene flora: Bamboo, Sassafras, Magnolia, Laurel.

*Sables de Trévoux* (Saône)

DEPÉRET'S fine memoir upon *Ronsillon* ('90, p. 538, 539) tends to make this locality typical. Characteristic species not found in Pikermi are *R. leptorhinus*, *Mastodon arvernensis*, *Tapirus arvernensis*, *Ursus arvernensis*.

Types with Messinien or Pikermi affinities are *Hipparion*, *Palæoryx*, *Hyænarctos*, *Dolichopithecus*. The Asiatic apes are *Dolichopithecus* and *Semnopithecus*. The African antelopes are *Palæoryx cordieri* and *P. boodon*.

#### 4. Sicilien, Upper Pliocene

This embraces the 'newer pleiocene fauna' of English authors, the '*faune pliocène récente*' of Depéret. *Hipparion* disappears, being replaced by *Equus stenonis*; *Rhinoceros etruscus* succeeds *R. leptorhinus*. *Macacus florentinus* appears, related to the living Gibraltar form. The Proboscidea are represented by the last of the European mastodons, *Mastodon arvernensis* and *M. borsoni*; *Elephas meridionalis*, the great southern elephant and precursor of the mammoth, is found in Italy and the Saône Valley. This species is absent locally (Depéret) in the *Sables à Mastodontes* of Puy, Coupet, Vialette. The typical locality is in the classic valley of the Arno in Italy, the so-called *Val d'Arno supérieure*; its richness contrasts with the general poverty of Italy in middle and lower Pliocene types.

- |          |  |
|----------|--|
| Italy.   | <i>Olivola</i> , a little higher than Val. d'Arno. Summit of Pliocene.                           |
|          | <i>Val d'Arno supér.</i> Thick fluviolacustrine beds (60 metres). Fauna fully listed by Stefani. |
|          | <i>Astesan</i> , <i>Villafranca</i> (San Paola), Tossano.  |
| France.  | <i>Sainselles</i> (Puy) a little higher than Perrier.  |
|          | <i>Perrier</i> (Issoire) fluvatile gravels.  |
|          | <i>Montpellier supér.</i> (Rhône), fluviolacustrine.   |
|          | <i>Coupet supér.</i> , volcanic deposits.  |
|          | <i>Vialette</i> (Haute Loire, near Puy).   |
|          | <i>Chagny</i> (Saône) fluvatile clays and sands.   |
|          | <i>Sables à Mastodontes du Puy.</i>  |
| England. | Red Crag (Suffolk) Marine.   |
|          | Norwich Crag (Norfolk) Fluvio-marine.  |

This arrangement is mainly upon the authority of Depéret.

It is important to note that Boule, another eminent French authority, differs in the arrangement of the Pliocene in particulars which will be discussed later.

To the north, in the Red and Norwich Crag of England, are said to appear the earliest arctic types of shells, the prophets of the glacial period. Also here (Norwich Crag) occurs the earliest giant beaver *Trogouthcrium minus*. The roe and stag deer become varied in southern France.

## VII. PLEISTOCENE

In the Pleistocene period the fullness of European investigation is in strongest contrast with the indecisive results of American work and in no other period can we anticipate more weighty inductions from Holarctic correlation. The period is distinguished as the Ice Age and by the first recorded traces of man in beds which have been claimed as Tertiary but are properly Quaternary.

The Pleistocene history of Europe is still in a formative stage but it is absolutely evident that a final and positive time scale and subdivision of the early Age of Man is not far distant and that the vast labors of European geologists, botanists, zoologists, palæontologists and anthropologists will be rewarded with a harmonious theory of all the phenomena of the Pleistocene.

Combined attack by geological and biological methods has nowhere produced more brilliant results. The unaided testimony of the rocks and soils fails to tell us of the successive advances and retreats of the ice but where, owing to the obliteration of surface deposits, geology is in confusion, plant and animal life serves both biology and meteorology like a vast thermometer actually recording within a few degrees the repeated rise and fall of temperature. This record consists of the invading and retreating life waves of river, forest, field, barren ground, steppe, tundra and arctic types with increasing cold, or the reversed order with diminishing cold, in the same localities or geographical areas. There seems to be sufficient evidence for a subdivision of the Pleistocene as shown in the Table below.

UPPER PLEISTOCENE : Post Glacial.

MIDDLE PLEISTOCENE : Glacial.

LOWER PLEISTOCENE : Preglacial.

Briefly, the glacial story presented in the second column of our Table is as follows: (1) The preglacial stage presents a mingling of south temperate, temperate and northern forms. (2) The long first glacial advance was followed (POHLIG) by the Rixdorf stage, intermorainal, colder than the succeeding Mosbach and Thuringian stages which have a more temperate facies in the recurrence of some of the Forest Bed fauna. (3) The faunal evidence for a colder mid-glacial period is conclusive; the evidence for a second or mid-glacial advance, between the first and last great glacial stages, is mainly biological, that is subarctic are followed by more temperate life forms, as we gather largely from studies of the rodent fauna by NEHRING, STUDER and others. The hypothesis of three distinct glacial advances and of two interglacial retreats rests therefore upon a combination of geological and biological evidence which is not as yet conclusive. We shall consider it more fully after discussing the fauna. It is supported geologically by observations of Penck and Böhm in the Bavarian Alps. Upon this theory the Pleistocene history with its fluctuations of temperature is epitomized in the following Table. This Table is an attempt to combine the chief results of the masterly work of DAWKINS, POHLIG, BOULE, NEHRING, STUDER, WOLDRICH, SCHLOSSER, and others. None of these authors has treated the whole period; yet there is an evident harmony and synthetic trend in their work.

**Deposits.**—Geologically we have to do with the characteristic glacial deposits, boulders, boulder clay or drift, gravels and till. The origin of the fine calcareous loam termed "Loess" distinguishing the upper middle Pleistocene is still under debate; it is partly glacial mud; partly subærial, it is also subsequent to the second glacial stage, and in part postglacial. We find also the river deposits of the lower and mid-Pleistocene (Forest Bed, and Mosbach) as well as of all higher divisions. The mid-Pleistocene was distinguished by volcanic disturbance, as attested in Thuringia by the volcanic travertines and tufas. There are also

PARTLY THEORETICAL DIVISIONS OF EUROPEAN PLEISTOCENE, AFTER  
POHLIG, DEPÉRET, NEHRING AND OTHERS

I.	II.	III.	IV.	V.
Main Stages.	Partly Theoretical Relations of Glacial Oscillations.	Characteristic Geological Deposits.	Faunal Div. (Pohlige) Localities. Gen. Fauna.	Human Remains and Characteristic Mammals.
Neolithic implements.	Recession of Glaciers.	Humus, Lake Terraces. Post-Glac. Löss.	<b>Prehistoric Stage.</b> N. temperate. Forest, Upland, River and Field Fauna.	<b>Forest and Lake Dwellers.</b> Recently exterminated types. Felis, Hyæna, Ursus spelæus, Cyon alpinus, Capra ibex, Ovis, Rangifer, Bison priscus, Equus, R. tichorhinus, Elasmotherium, Elephas primigenius.
UPPER PLEISTOCENE. Post-Glacial or Alluvial.	3d Glacial.		<b>Elephas primigenius stage.</b> N. temperate and Boreal. Steppe and Forest Fauna.	
(Moustièren Human type.)	2d Interglacial.	Löss, Valley Gravels, Cave Clays, Diluvium, Sands.	{ Up. Rodent. Steppe Fauna, Yellow Culture Layer: Lower Rodent Tundra Fauna. Subarctic Tundra Fauna.	<b>Neanderthal and Spy human types.</b> Steppe and Cave Dwellers.
Paleolithic implements.	2d Glacial.		<b>RHINOCEROS MERCKII.</b> <b>Elephas antiquus stage.</b> N. Temperate Thuringian tufa, Taubach (Weimar).	<b>Oldest human remains known. Molar teeth (Nehring).</b> Saiga prisca, Alces machilis, Capreolus, Lemmus, Alactaga saliens, Lepus, Elephas antiquus, E. primigenius, Rhinoceros merckii.
MIDDLE PLEISTOCENE. Glacial or Diluvial. (Cheléen Human type.)	1st Interglacial.		<b>Elephas trogontherii stage.</b> { Temperate. B. Mosbach Sands (Lower Terraces). { A. Rixdorf Beds, Subarctic. (Higher Terraces.)	Felis spelæa, F. lynx, Hsion, Sus scrofa, Cervus elaphus, Equus caballus, Rangifer, Hippopotamus, Arctomys. Megaceros, Ovis, R. tichorhinus, R. merckii, Elephas trogontherii.
	1st Glacial.	Fluviatile, River Sands, and Gravels, Gravels, Conglomerates, Sands.	Arctic.	Fauna unknown.
		Boulders, Erratics, Clays, Drifts, Sea-terraces, Moraines.	<b>Elephas meridionalis stage.</b> { Forest Beds (Norfolk). St. Prest. Dufort. Maubattu (Auvergne Puy-de-Dôme). Chalon - St. - Cosme (Bresse).	<b>Earliest palæoliths.</b> Machærodus, Hyæna spelæa, Ursus spelæus, Lutra, Ovis, Hippopotamus, Bos primigenius, Equus stenonis, Rhinoceros cruscus, Elephas meridionalis, E. antiqua, Trogontherium.
LOWER PLEISTOCENE. Preglacial or Transitional to Pliocene.	Advance of Glaciers.	Estuarine and Fluviatile, Marls, and Sands.		

lake and sea-beach deposits constituting the lacustrine and marine terraces. The very characteristic cave deposits, breccias and earths belong to the upper mid-Pleistocene. Then there are

the younger river alluvia, lake bottoms, æolian sands, peats and mosses.

**Geographic Changes.**—The beginning of the Pleistocene is remarkable for its broad land connections and it represents the last stage of that community of fauna which during the Pliocene distinguished the entire region of Europe, Asia and Africa. The mid-Pleistocene period in Europe is mainly one of continental depression; (1) at the climax of the first glacial advance extensive portions of northern Europe were submerged beneath the sea; (2) at the close of the first interglacial or temperate period (*Elephas antiquus* stage) occurred the volcanic disturbances in Central Europe and the hot spring formations of Thuringia (Taubach, Weimar); at this time *all the old continental connections characteristic of the Tertiary and serving as land bridges for free Holarctic, Oriental and Ethiopian migration began to break up in the following manner*: during the early mid-Pleistocene or *Elephas antiquus* stage (POHLIG) the English Channel broke through the long preëxisting land-bridge between England and France; Great Britain was faunally isolated; similarly the Irish Channel was depressed and Ireland lost its land connection with Wales in the early Pleistocene and with Scotland in the newer Pleistocene.<sup>1</sup> In the Mediterranean region, also, at the close of the first interglacial period (Pohlig) the land bridge across Gibraltar, also that between Italy, Sicily and Africa was broken; Malta<sup>2</sup> was isolated as an Island and the great *Elephas antiquus* dwindled into the small insular type *E. melitensis*. To the eastward the Mediterranean extended into the Ægean plateau, which had previously been terra firma, and the Ægean sea cut off the land connection between Greece and Asia Minor. It is important to note as observed by Wallace and Lydekker, that the arid and desert land connection still existing between Europe and Africa at the Isthmus of Suez constitutes practically a faunal barrier as impassable for most mam-

<sup>1</sup> According to Scharff, Ireland has yielded only ten Pleistocene species, including the Northern *Lepus variabilis* and Reindeer and the great *Megaceros hibernia*, which is found in the post-glacial peat moors.

<sup>2</sup> Malta shows evidences of two periods of elevation and depression. See POHLIG, also Leith Adams, "The Nile Valley and Malta," London, 1870.

mals as water. The Sahara desert although elevated during the Tertiary was another faunal barrier and northern Africa was zoologically a part of Europe. In the far northeast the Behring Straits were formed and after a complete community of arctic, boreal and north temperate faunas had been established, the Nearctic region or North America was completely isolated from the Palæarctic or Europe and Asia. (See Fig. III.)

*Stratigraphy.*—Faunally the strata record is far less exact than in the preceding Tertiary periods owing to the wide spread removal of easily eroded materials. Yet definite stratigraphic succession occurs in many places and upon the whole the faunal succession as shown in column V of the Table; p. 36, is as fully and definitely known as in any previous division of the Tertiary. In the sands of St. Acheul, near Paris, *Elephas antiquus* occurs at 7 metres, *Hippopotamus amphibius* at or below 5 metres, *Elephas primigenius* never below 3 metres. The most exact stratigraphic records are those of the caves near Schaffhausen for example; here a general succession of types is positively ascertained.

### 1. Preglacial, *Elephas meridionalis* Period

The typical preglacial deposits are the *Forest Beds* of Norfolk. The weight of opinion and of fact is all upon the side of considering these beds as Pleistocene. DEPÉRET ('93, p. 538), is strongly of opinion that they are transitional between Pliocene and Pleistocene with prevailing affinities on the latter side. He places with them as of the same age *St. Prest* (Eure et Loire), *Durfort* (Gard) where a magnificent skeleton of *Elephas meridionalis* was obtained for the Paris Museum; *Malbattu*, *Peyrolles* (Auvergne, Puy-de-Dôme).

From the list given by DAWKINS ('80, '94), SCHLOSSER and other writers the Preglacial period is found to contain :

- 12 Pliocene species ;
- 32 Pleistocene species and races, now extinct ;
- 17 Living species, of which 7 are Insectivora and 1 Cheiroptera.

Some of the determinations are questionable. Pohlig states that the true *Cervus megaceros hibernæ* is post-glacial, the pre-glacial type being more primitive; also that the straight tusked *Elephas antiquus* first appears in the north in the Mosbach interglacial bed; elsewhere he refers to it as occurring in the south of France (St. Prest) preglacial beds.

The remarkable feature of this fauna is the mixture of African and North Asiatic forms. The great *Elephas meridionalis*, a precursor of the Mammoth, is the most characteristic type.

The first traces of man in the palæolithic flints of the Cheléen type occur upon this level.

The climate, judging by the flora and Conchylien fauna, was somewhat cooler than that of the Upper Pliocene. The first arctic flora in England is in a layer which separates the *Forest Bed* from the glacial Boulder Clays.

## 2. Glacial and Interglacial, or Mid-Pleistocene

### a. Lower Mid-Pleistocene. First Interglacial Period (*Elephas trogontherii*) Lower Stage, Pohlig.

In climate the early part of this period, immediately during and succeeding the first ice advance, was very extreme. None of the first ice advance fauna is known unless we except *Elephas (primigenius) trogontherii* or *intermedius* and *Cervus elaphus*, the latter being doubtfully recorded from the Boulder Clay of England. Here we find the first arctic and sub-arctic types in central Europe. Geologically, these post-glacial deposits consist (Rixdorf Beds) of gravels, conglomerates and sands, constituting (Pohlig) the highest post-glacial terraces, or *Higher Terraces*. It is marked by the first appearance of *Elephas trogontherii*, *Rhinoceros merckii*, *R. tichorhinus*, and the following species of northern type: *Ovibos moschatus*, *Cervus* (Megaceros) *germanicæ*. Among the new forms we note the megarhine rhinoceros, *R. merckii*, as most distinctive. The mammoth *Elephas (primigenius) trogontherii* succeeded the *Elephas meridionalis* of the preglacial beds.

*b. Lower Mid-Pleistocene. First Interglacial Period (Elephas trogontherii) Middle Stage, Pohlig.*

This stage marks the recurrence of a *more temperate climate*, first observed by Lyell and Evans in England and abundantly known in Germany and France. Two only of the characteristic Pliocene species recur, *Hippopotamus amphibius*, and *Elephas antiquus*. These alone have been universally cited as evidence of a south temperate climate but the more numerous northern types still living which are found in this stage constitute still stronger proofs of a *north temperate climate*.

*Geologically* the deposits are of fluviatile origin, consisting of river sands and gravels containing *Hippopotamus*, *Rhinoceros merckii* and *Elephas trogontherii*. *Trogontherium cuvieri* makes its last appearance here.

*Geographically* the southern continental depression has not begun and the Lower Pleistocene land bridges persisted. Parallel faunæ are those of Essex (Ilford, Grays Thurrock, Clacton) and Kent (Erith and Crayford) fully listed by Dawkins ('80, p. 397; '94, p. 243) and Woodward ('83). In Germany the typical fauna is that of Mosbach (Lepsius, '92, p. 652).

The Mosbach and Essex faunæ give the following results :

- 4 Pliocene species, (including two living types) ;
- 7 Pleistocene species, now extinct ;
- 16 Living species (including 2 Pliocene species).

The characteristic Pleistocene species which are first recorded in Mosbach are *Cervus megaceros*, *Cervus (Alces) latifrons*, *C. elaphus typus*, *C. Capreolus typus*, *Felis spelæa*, *Ursus spelæus*, *Bos taurus*, *Bison priscus* ; in Essex, *Cervus (Megaceros) belgrandi*, *Hyæna spelæa*. Among the living species recorded for the first time or making their first appearance at this stage are *Rangifer tarandus*, *Sus scrofa*, *Equus caballus*, *Felis lynx*, *Meles taxus*, *Arctomys marmotta*. The Essex Fauna is fuller but although of more southern latitude is not of more southern type, including the northern and north temperate forms *Felis catus*, *Canis (Vulpes) alopes*, *Canis lupus*, *Ursus ferox*, *Ursus arctos*, *Lutra lutra*.



*c. Mid-Pleistocene. Elephas antiquus stage, First Interglacial Period Upper Stage, Pohlig.*

According to Pohlig the Mid-Pleistocene proper, or succeeding stage, was characterized by volcanic disturbances in central Europe and by the deposition of gypsum and tufas. Probably these earth movements were connected with the marked geographical changes brought about by wide-spread depression of the continental borders and isolation, which the same author assigns to this period. The fauna, typically represented in the Thuringian tufas, indicates a cooler or north temperate climate. *Elephas antiquus* is very abundant, making its last appearance north of Italy. The typical locality is the Thuringian Tufa in which Pohlig records 61 species. Parallel with this is the Taubach Weimar fauna.

In 1895, NEHRING ('95, p. 369) reported from this level what he regarded as the oldest human remains thus far found in Europe, consisting of two very large molar teeth resembling in some respects those of the chimpanzee; this he considered of Cheléen type. In the same year Newton described a human skeleton of Esquimaux type in the still older 'higher terraces' or Hippopotamus level; the antiquity of this skeleton is, however, rendered somewhat doubtful by the fact that the skull is of much newer type than those of Néanderthal and Spy, and the evidence for its extreme palæolithic age is not considered absolutely conclusive.

In this fauna Hippopotamus no longer appears—an indication perhaps of a decidedly colder climate. *Elephas antiquus* however persists and is most abundant. Among the other characteristic Pleistocene forms are *Rhinoceros merckii* which disappears soon after this stage; *E. primigenius typus*; *Cervus gastaldi*. The faunal list is provisionally analysed as follows:

- 3 Pliocene species still living (Castor, Hyæna, Arvicola);
- 7 Pleistocene species, now extinct;
- 23 Living species (including living pleistocene Northern types).

The number of recorded living species increases, there being

a marked increase especially in the number of reindeer. The most important new living types are: the steppe antelope *Saiga prisca* (*tartarica*), the moose *Alces machlis*, the lemming, *Myodes lemmus*, the Siberian jerboa *Alactaga saliens*, *Hystrix*, *Lepus timidus*. These constitute a distinct invasion of north Asiatic forms into the southern steppes.

#### THEORY OF A MID OR SECOND GLACIAL ADVANCE

In all the preceding summary a certain faunal succession is noted consisting chiefly of elimination of southern types and introduction of northern.

WOLDRICH ('96) maintains that all the loess and cave types are of postglacial age—the tundra and steppe types alone representing the last great glacial advance—after which came the meadow or field (Weide-fauna) and the forest fauna (Wald-fauna); he considers the alleged ice periods as mere local oscillations.

The possibility must also be freely admitted, as discussed by BULMAN ('93, p. 261), of the existence of south temperate types remote from the Ice Sheet; we find, for example, in southern Alaska, a very mild climate in proximity to great glaciers; similar conditions may have existed in southwestern Ireland and southern Europe.

Other authors such as Boule, have maintained the glacial age of the Tundra and Steppe fauna and the post-glacial age of the Forest fauna. If they are correct the theory of an interglacial or second glacial advance would lose its strongest support. It is evident, however, that such a succession of faunas might recur more than once. Nehring has observed in different localities (Westeregeln, Thiede), the *unquestionable interglacial age of the steppe fauna* and he considers Schweizerbild as interglacial.

#### d. Upper Mid-Pleistocene. *Elephas primigenius* Stage, Pohlig

As we enter the next succeeding life stage, namely, the Loess and Cave Fauna of Central Europe, the stage of *Elephas primigenius*, *Rhinoceros antiquitatis* or *tichorhinus* and *Rangifer tarandus* we note the decline of *Rhinoceros merckii* and the ab-

sence of *Elephas antiquus* in geological deposits which are chiefly diluvial valley gravels and sand clays. These facts alone indicate a prolonged colder period, a northern or boreal climate. The fauna presents a great variety adapted to different degrees of temperature but decidedly of northern type. Other facts indicate that this colder period was initiated by a distinct second advance of the ice followed by a gradual recession, namely the occurrence of arctic and subarctic types succeeded by north temperate types, in a number of localities, typically near Schaffhausen (Schweizerbild, STEINMANN, '93, p. 117) (Franken, SCHLOSSER, '95, p. 211).

These successive northern faunas in single localities are typically as follows:

1. TUNDRE FAUNA.	2. STEPPE FAUNA.
(Frozen subsoil, arctic and subarctic.)	
<i>Myodes torquatus</i> ,	<i>Alactaga</i> ,
" <i>obensis</i> ,	<i>Spermophilus</i> ,
<i>Lepus glacialis</i> ,	<i>Lagomys pusillus</i> ,
<i>Rangifer tarandus</i> ,	<i>Arvicola</i> ,
<i>Ovibos moschatus</i> ,	<i>Cricetus phæus</i> ,
<i>Lagopus mutus</i> ,	<i>Equus</i> ,
" <i>albus</i> ,	<i>Antilope saiga</i> .

The prevailing types of this stage are the typical *Elephas primigenius* which succeeded *Elephas trogontherii*, *Rhinoceros tichorhinus* and *Rangifer tarandus*. The reindeer, first the barren ground then the woodland variety, increased rapidly in number during this period and constitute its most distinctive form; hence this is known as the Reindeer period.

It includes the most remarkable diversity of life of Asiatic both Siberian and Oriental, and of African origin. The persistence of the following southern forms: *Felis (leo) spelæa*: *Felis pardus*, *Hyæna (crocuta) spelæa*, *Equus caballus*, *Equus (asinus) hemionus*, *Rhinoceros tichorhinus* (with affinities to *R. sinus*), *Elephas primigenius*. All these types, excepting possibly the Mammoth, now inhabit warm, dry, semi-arid regions. There is therefore an Ethiopian and Oriental fauna, in certain localities succeeding a steppe and tundra fauna. At no period either before or since was Europe so thoroughly cosmopolitan, a fact

which has not been sufficiently emphasized previously. The climate was cold and relatively dry.

The close of this period is also the close of the Palæolithic human period which after a long interval was succeeded by the Neolithic period.

### 3. Upper Pleistocene, Postglacial

As above observed there is a difference of opinion as to the interglacial or postglacial age of the loess. All the North Siberian, Oriental and African types gradually disappear, the modern European forest and field fauna alone survives. There is some evidence that both the mammoth and reindeer lived for a time in this period, the latter being now confined to more northern Europe. The Irish deer, *Megaceros hiberniæ*, the reindeer, the bovidæ *Bos taurus*, *Bos longifrons*, *Bos brachyceros*, are the characteristic ruminants. *Alces palmatus* is a postglacial Russian moose. The horse, *E. caballus*, of larger and smaller varieties is now domesticated and used for food. The carnivora, rodentia and insectivora are all of modern type.

The detailed comparison of the Pleistocene of Europe, America, and Asia is still under way, and very important results may be expected from it. It will be equally serviceable to American anthropologists and palæontologists, for our own Pleistocene is far from being understood. The stages represented by our horse or *Equus Beds*, which are usually considered Lower Pleistocene, as well as of the *Megalonyx* and Cave Fauna of the East remain to be exactly fixed. Interest in this problem is greatly enhanced by the fact that we may at any moment discover the remains of man or of his ancestors associated with *Equus* and positively demonstrate the existence of man upon this continent at a period contemporaneous with the first proofs of his appearance in Europe in the existence of preglacial palæolithic flints.

PART II. FAUNAL RELATIONS OF EUROPE AND  
AMERICA DURING THE TERTIARY PERIOD  
AND THEORY OF THE SUCCESSIVE  
INVASIONS OF AN AFRICAN  
FAUNA INTO EUROPE

In an address before the Academy last year the various steps which have been taken to secure correlation were described. The work proves to be a very difficult one and is by no means complete. The kind co-operation of the leading palæontologists of Europe was enlisted and as a result an approximate correlation sheet was prepared. This was virtually a report of progress in this investigation, main emphasis being laid upon geological succession. In continuing the subject this year, main emphasis will be laid upon *faunal succession* or the distribution of the different orders and families of mammals, concluding with the latest views as to the succession of life during the Pleistocene period in Europe.<sup>1</sup>

I. STRATIGRAPHICAL CORRELATION: PRELIMINARY

LYELL'S SYSTEM.		Approximate American Parallels.
PLEISTOCENE.	UPPER. Post Glacial	
	MIDDLE. Glacial & Interglacial	
	LOWER. PREGLACIAL	? EQUUS BEDS
PLIOCENE.	UPPER. SICILIEN	? BLANCO
	MIDDLE. { ASTIEN PLAISANCIEN	
	LOWER. MESSINIEN	Upper Loup Fork
	UPPER. TORTONIEN	LOUP FORK
MIOCENE.	MIDDLE. HELVETIEN	Lower Loup Fork and
	LOWER. LANGHIEN	Upper John Day

<sup>1</sup> This portion of the second address is placed in its proper order above after Pliocene.

OLIGOCENE.	UPPER.	AQUITANEN	Lower John Day (Diceratherium Layer)
	LOWER.	{ STAMPIEN INFRA TONGRIEN	WHITE RIVER
EOCENE.	UPPER.	LIGURIEN	BRIDGER & UINTA
	MIDDLE.	BARTONIEN	LOWER BRIDGER
		LUTETIEN	WIND RIVER
	LOWER.	SUBESSONIEN	WASATCH
	BASAL.	THANETIEN	TORREJON
		MONTIEN	PUEBLO

Preliminary Correlation Table of European and American Tertiary Horizons.  
On all the levels above the Stampien the parallels are imperfectly established.

The preliminary correlation sheet abbreviated in this table sets forth the results of the geological succession and correlation so far as it has been carried at present and illustrates the rapid progress of the knowledge of our own horizons. It includes the latest results of the American Museum explorations in the Miocene of Colorado and Kansas, as roughly studied by MATTHEW, but these correlations are not to be understood as final. SCOTT has already transferred our John Day of Oregon, from the Miocene, where it was formerly placed, to the Upper Oligocene. The lower part at least of these beds belongs in the Oligocene, while the Upper John Day may prove to correspond with the Lower Miocene of Europe. Our Pliocene record as compared with the magnificent Pliocene of Europe is extremely meagre, and our Miocene succession rich as it is, is not as fully understood as the Miocene of France; we look for more exact results from the American Museum explorations which are now being collated. It is only when we pass into the great time period from the Oligocene downwards that the American record becomes a superbly complete time standard for the whole Northern Hemisphere or Holarctic Region.

## II. TERTIARY GEOGRAPHICAL DISTRIBUTION

The importance of Geographical distribution was first recognized by HUMBOLDT, and set forth by DARWIN in the 'Origin of Species,' in 1858. In the same year SCLATER divided the world

into six great regions and into eastern and western divisions or Palæogæa and Neogæa, to embrace the Old and New Worlds respectively, a division which has proved to be illogical. This led DARWIN's distinguished colleague, ALFRED WALLACE, to his great work upon the 'Geographical Distribution of Animals' and the division of the world into life regions; in which Sclater's scheme was adopted and developed.<sup>1</sup> In 1868 Huxley divided the world into a northern division, Arctogæa, and a southern division Notogæa to include the Northern and Southern Hemispheres respectively; this division was a little nearer the truth than Sclater's. Between 1868 and 1890, SCLATER, ALLEN, NEWTON and BLANFORD, working upon living birds and mammals, continued this investigation, but it remained for BLANFORD, in 1890, to prove that the world zoologically should be divided into three great divisions; an Australian, a South American and a third region, Arctogæa, comprising North America, Europe, Asia and Africa.<sup>2</sup>

Now it is clear that exactly as our understanding of the relations of living animals and plants to each other depends upon their fossil ancestors or upon their palæontology, so the final test of a scheme of zoological distribution must be a palæontological test. The animals of various families and orders have either originated in or migrated into their present habitat in past time, so that the geological record as to their order of appearance becomes of first importance. Here again the necessity of an *absolutely reliable correlation time scale* such as we are now establishing becomes evident, for the very first step toward an exact solution of the problem of past migration is to establish, as far as possible, the faunal parallels upon different continents; we can then determine where certain types of animals first appeared, and distinguish between the autochthonous endemic or native types and the migrant or new types.

<sup>1</sup> The history of opinion upon this subject is fully set forth by LYDEKKER's valuable work the "Geographical Distribution of Mammals," published in 1896.

<sup>2</sup> Dr. Theodore Gill has kindly called attention (*Science*, June 8, 1900) to my oversight of an important paper of his ("On the Geographical Distribution of Fishes," *Ann. Mag. Nat. Hist.*, 1875, pp. 251-255). He unites South America, Australia and Africa into a single division EOGÆA, in contrast with CÆNOGÆA, which includes North America, Eurasia and India.

*This then is our problem, to connect living distribution with distribution in past time and to propose a system which will be in harmony with both sets of facts.*

The tests of synchronism between European and American depositions are four-fold: *First*, the presence of a number of identical or closely allied genera and species. *Second*, similarity in the steps of evolution in related animals. *Third*, the predominance and spread of certain animals, as of the odd-toed Ungulates in the middle Eocene and of the even-toed Ungulates in the Upper Eocene. *Fourth*, the sudden appearance of new types which have apparently originated elsewhere and have enjoyed an extensive migration, so that they appear simultaneously in different regions of the earth. An instance of this kind is afforded by the unheralded appearance of new types in the base of the Oligocene (Rhinoceroses) and of the Miocene (Proboscidea) in Europe and America. (See Part I, pp. 22 and 26.)

Unfortunately there is still no agreement among zoölogists as to the faunal geographical divisions. LYDEKKER well versed in both palæontology and zoölogy, has for the first time brought together both classes of evidence in his recent valuable work upon the "Geographical Distribution of Mammals," he shows conclusively that zoö-palæontology favors the division of the world into three great realms as proposed by BLANFORD; to these may be applied the terms ARCTOGÆA, NOTOGÆA and NEOGÆA, as proposed anonymously (SCLATER) in 1893.<sup>1</sup> (Fig. 1.)

Geographically, these realms are connected by low lying portions of the earth, which, during long periods of submergence beneath the sea, have completely isolated them. At the same time we are forced to conclude that there were shorter intervals of elevation or land continuity at various times during the Tertiary period.

Now it is a well-known principle of zoölogical evolution that an isolated region, if large and sufficiently varied in its topography, soil, climate and vegetation, will give rise to a diversified

<sup>1</sup> In a review of papers by Merriam and Allen (The Nearctic Region and its Mammals, *Natural Science*, 1893, p. 289), P. L. Sclater observes "Thus we have a very obvious threefold division of the earth's surface, taking mammals as our text, into what may be called *Notogaea*, *Neogaea*, and *Arctogaea*."



fauna according to the *law of adaptive radiation*<sup>1</sup> from primitive and central types. Branches will spring off in all directions to take advantage of every possible opportunity of securing food. The modifications which animals undergo in this adaptive radi-

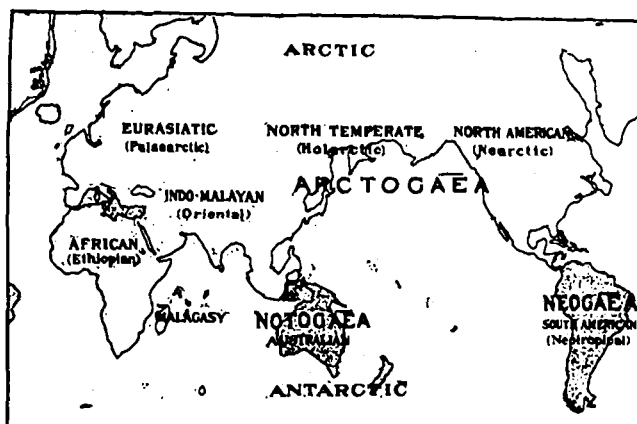


FIG. 1.—Division of the World into three Realms and nine main Geographical Regions. The continental platform is raised to the 200 metre line showing the main Tertiary land connections.

ation are largely of mechanical nature, they are limited in number and kind by hereditary, stirp or germinal influences, and thus result in the independent evolution of similar types in widely separated regions under the *law of parallelism or homoplasy*.

### Adaptive Radiation of Orders and Families

This law causes the independent origin not only of similar genera but of similar families and even of similar orders. Nature thus repeats herself upon a vast scale, but the similarity is never complete and exact. When migrations are favored by over-population or geographical changes, a new and severe test of fitness arises by the mingling and competition of the parallel types.

<sup>1</sup> So termed by the writer (OSBORN, '93 and '99).

Under the operation of these laws a most interesting generalization or hypothesis can be made as to the three realms: geographical isolation has been so continuous and prolonged that great orders of mammals have been evolved (Fig. III) in each. Thus *Arctogæa*, containing the broadest and most highly diversified land area, appears hypothetically as the center in which fourteen primitive and specialized orders radiated from each other. In the southern portion of *Neogæa* at least four orders sprang from primitive members of the above orders, and the Hystri-comorph rodents enjoyed their chief radiation. In *Notogæa* two orders were cut off by the sea; one of them a rapidly declining type, the Monotremes, the other, the Marsupials, enjoying a very highly diversified radiation. This hypothesis is expressed in Fig. III. Two other orders of mammals, the Sirenia (probably a branch of the hoofed tribe) took the rivers and coasts of America, Europe and probably Africa as their radiating center, while the Cetacea occupied the fourth or oceanic realm.

We mean to express by this hypothesis that REALMS *were the main centers of adaptive radiation of orders of mammals*, but by no means the exclusive areas of distribution, for during the periods of land contact certain members of these orders found their way into adjacent realms. Each realm, therefore, contains its pure autochthonous types and its migrant or derived types. REGIONS, on the other hand, may be distinguished from realms as geographical and zoölogical areas, which have been isolated from each other for shorter periods, either by climatic barriers, as in the case of the Arctic or circumpolar region or by great physical barriers, such as masses of water and of desert sands. In certain cases these regions, such as Africa, appear to have been so large, distinct and isolated as to have become important centers of the radiation of certain *orders* of mammals and almost attain the rank of realms, but regions in general are chiefly and permanently distinguished by the *adaptive radiation of families of mammals*.

Arctogæa may thus be still divided on the old lines into five or six regions, the *Arctic* or Circumpolar; the *Ethiopian* or African, south of the Sahara; the *Indo-Malayan* or Oriental, in-

cluding southern Asia and the Malayan islands; the *Malagasy*, including Madagascar; the *Nearctic* and the *Palæarctic*. There is no question, as suggested by Professor Newton in his term "Holarctic," and by Professor Allen in 1892, in his term "North temperate," that the North American (Nearctic) and Eurasiatic (Palæarctic) regions are now so closely similar that they might be united into one. When, however, the zoölogical or existing characteristics of these regions are put to a palæontological test it is found necessary to separate them, because throughout the Tertiary period North America and Eurasia were so remote that, to a certain extent, they constituted centers, not only of independent family, but to a limited degree of ordinal radiation. At the same time they were unified, both by frequent intermigrations and by a simultaneous evolution of allied animals.

### The Continent Antarctica

We now come to one of the greatest triumphs of recent biological investigation, namely, the concurrence of botanical, zoölogical and palæontological testimony in the reconstruction of a great southern continent to which the name Antarctica has been given. Following BLANFORD ('90), FORBES ('93) made the first strong plea for this continent. The flood of evidence for the Antarctica theory has now become so strong that only a few details can be mentioned: FORBES ('93) and MILNE-EDWARDS from the consideration of the birds; BEDDARD from the study of worms and other invertebrates; MOORE from the study of the flora of South Africa; SPENCER from the study of the fauna of Australia; AMEGHINO, HATCHER and ORTMANN from studies and collections of vertebrate and invertebrate fossils in Patagonia not yet fully published; MORENO, from the discovery of *Miolania*, an Australian fossil reptile recently found in South America; from these and many other sources has been brought fourth the body of testimony which draws us almost irresistibly<sup>1</sup> to the conclusion that there was an antarctic continent at various times connecting South America, South Africa, Aus-

<sup>1</sup>After discussing the evidence with great fairness LYDEKKER ('96), takes a more conservative position.

tralia and New Zealand. Such a connection strengthens the conception announced by HUXLEY in 1868, that the zoölogical regions were mainly upon lines of latitude, rather than as suggested by the present configuration of the earth, upon lines of longitude. With the theoretical elevation of this submerged continent (Fig. II), which may be called the "Ant-



FIG. II.—Restoration of Antarctica by elevation to the 3040 sounding line, showing old continental lines and greater depth between Africa and Antarctica.

arctic Region," so as to connect the southern land masses at various times, all present and past geographical distribution of mammals may be theoretically accounted for. Elevation to the 10,000 foot (3040 meter) line still leaves a broad channel south of Africa. Without such elevation we are still met by many insuperable difficulties.

Among other problems, a land connection between Africa and South America across the South Atlantic enables us to explain the remarkable distribution of the *Sirenia*, sea-cows, dugongs and manatees, now found exclusively in the tropical belt of Africa and the Americas. (See *Sirenia*, Fig. III.) These animals first appear in the Oligocene of Germany. It is also, of course, possible that they may have taken a northern route, as indicated by the remains of *Rhytina* in the North Pacific.

Before confining our attention to ARCTOGÆA, let us further consider the mesozoic relations of the three realms. (Fig. I and Fig. III.)

In the Jurassic period stem forms of insectivores, marsupials and possibly of monotremes<sup>1</sup> are found in Arctogæa and seem to establish the theory of the northward origin of the mammalia as a class.

DOLLO ('99), has recently endeavored to demonstrate that all *Marsupials* have been evolved from arboreal forms like the Opossum. If we can draw a parallel with the adaptive radiation of the placentals during the 3,000,000 years, more or less, of the Tertiary, we may safely conclude that such a primitive family, entering the Australian region during the Cretaceous period either by way of Antarctica (SPENCER) or by way of the Oriental region (WALLACE and LYDEKKER), might have peopled Australia with all its wonderfully diversified forms of Marsupial life. The Didelphyidæ are to the Marsupials what the Creodonta are to the Placentals in point of potential evolution. The *Monotremes* also may have entered NOTOGÆA by either of these routes.

North America is the only part of the globe where Cretaceous mammals are known at present. In the late Cretaceous we appear to discover evidence of the existence of the following orders: Insectivora, Creodonta or ancestral carnivores, hoofed animals or Amblypoda and perhaps the earliest monkeys or Mesodonta. In the basal Eocene we certainly find primitive

<sup>1</sup> The writer's view (OSBORN, '88) that the Jurassic mammals of England and Wyoming embrace primitive placentals or insectivores as well as marsupials and multituberculates (? monotremes) is now generally accepted.

monkeys or Mesodonta, Rodentia and Tæniodonta or ancestral Edentata. A land connection with South America in the early Eocene would therefore have supplied *Neogaea* with the edentates as well as the stem forms from which might have been derived its wonderful radiation of hoofed animals, the Litopterna, Typotheria and Toxodontia; together with the remarkable radiation of the hystricomorph or porcupine-like rodents and of two families of monkeys.

The exact zoological affinities of the oldest mammalian or *Pyrotherium* fauna of South America remain to be determined.

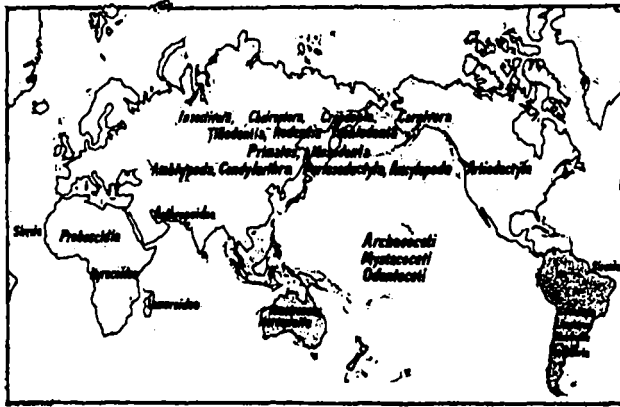


Fig. III.—Orders of Mammals placed in their hypothetical chief centers of adaptive radiation during the Tertiary Period.

*Pyrotherium* itself is considered by AMEGHINO as the source of the order PROBOSCIDIA while other ungulates are believed to be related to the HYRACOIDEA; upon the affinities of these forms turns the problem whether South America derived the sources of its great radiation from Africa or from North America. (See Fig. III).

Four streams of migration to and from NEOGÆA appear to have occurred; the first established its autochthonous fauna or distinctive radiation of peculiar ungulates and edentates. The second related this region with Africa, via Antarctica; this contact, in addition to the problematical Proboscidea and Hyracoidea

above alluded to, apparently introduced stem forms of Edentates into the Ethiopian region from which were derived the pangolins and aard varks; these peculiar edentates together with armadillos all occur in southern France in the lower Oligocene (FILHOL, '94); this land bridge also distributed the Cape golden moles, *Chrysochloridæ*; these facts and others too numerous to mention serve to show the vast importance of the explorations in Patagonia and make us impatient for the exact conclusions which are forthcoming from the materials brought together by Ameghino and Hatcher.

The third migration into Neogæa established its links with Australia, bringing in Marsupials, both polyprotodont and diprotodont. The fourth was from the north, Arctogæa, and is positively known; it occurred at the end of the Miocene, and brought in the northern Carnivora, bears, wolves, cats, and sabre-tooth tigers, raccoons and mustelines, the Artiodactyla, deer and camels, the Perissodactyla, horses and tapirs, three types of rodents, the squirrels, mice and hares or rabbits and the mastodon. The Notogæic types, as well as the animals of the first invasion, in the meantime had largely died out, and the introduction of more vigorous Arctogæic types, especially the carnivores, together with a change of climate, exterminated a further portion of the autochthonous Neogæic fauna. At the same time, that is of this second invasion, many of the South American forms entered North America; they seemed to have reached this continent in the upper Pliocene.

We now turn to ARCTOGÆA. In the Eocene period we find in Europe and North America what may be considered the pure or autochthonous fauna of the Holarctic region, in the absence of all knowledge of Asia. Southern Asia is an absolute *terra incognita* the earliest known deposits in this region being in the Upper Oligocene in which the fauna is remarkably similar to that of Europe. Northern Asia is unknown palæontologically until the Pleistocene—here is a region for explorers. However, we may consider it as part of a broad Eurasiatic land area—extending from the Rocky Mountain region to Great Britain. The faunal relations are astonishingly close, between the new and

old worlds at this time. Every year's discovery increases the resemblance and diminishes the differences between Europe and the Rocky Mountain region. Distinguishing North America, however, are the Tylopoda; this sub-order includes the peculiar Artiodactyla of the camel-llama tribe; these Professor Scott in a recent paper considers as including all the early types of American ruminants which we have been vainly endeavoring to compare with European types. The radiation of the tylopod phylum into a great variety of types is quite conceivable and it is thoroughly consistent with the fundamental law of adaptive radiation which we find operating over and over again.

### III. THEORY OF SUCCESSIVE INVASIONS OF AN AFRICAN FAUNA INTO EUROPE

In Europe there are in the upper Eocene two classes of animals, first, those which have their ancestors in the older rocks; second, the class including certain highly specialized animals which have no ancestors in the older rocks—among these, perhaps, are the peculiar flying rodents or *Anomaluridae*, now confined to Africa, and secondly the highly specialized even-toed ruminant types—the anoplotheres, xiphodonts and others, the discovery of which in the *Gypse* near Paris Cuvier has made famous. It is tempting to imagine that these animals did not evolve in Europe but that they represent what may be called the first invasion of Europe by African types from the Ethiopian region.

It is a curious fact that the African continent as a great theater of adaptive radiation of Mammalia has not been sufficiently considered. It is true that it is the dark continent of palæontology for it has practically no fossil mammal history; but it by no means follows that the Mammalia did not enjoy there an extensive evolution.

Although it is quite probable that this idea has been advanced before, most writers speak mainly or exclusively of *the invasion of Africa by European types*. Blanford and Allen it is true have especially dwelt upon the likeness of the Oriental and Ethiopian



fauna but not in connection with its antecedent cause. This cause I believe to have been mainly an invasion from south to north correlated with the northern extension of Ethiopian climate and flora during the Middle Tertiary. It is in a less measure due to a migration from north to south. Let us therefore clearly set forth the hypothesis of the *Ethiopian region or South Africa as a great center of independent evolution* and as the source of successive northward migrations of animals, some of which ultimately reached even the extremity of South America—I refer to the Mastodons. This hypothesis is clearly implied if not stated by BLANFORD in 1876 in his paper upon the African element in the fauna of India.

The first of these migrations we may suppose brought in certain highly specialized ruminants of the upper Eocene, the anomalures or peculiar flying rodents of Africa; with this invasion may have come the pangolins and aardvarks, and possibly certain armadillos, *Dasypodidæ*, if M. FILHOL's identification of *Necrodasypus* is correct. A second invasion of great distinctness may be that which marks the beginning of the Miocene when the mastodons and dinotheres first appear in Europe, also the earliest of the antelopes. A third invasion may be represented in the base of the Pliocene by the increasing number of antelopes, the great giraffes of the Ægean plateau, and in the upper Pliocene by the hippopotami. With these forms came the rhinoceroses with no incisor or cutting teeth, similar to the smaller African rhinoceros, *R. bicornis*. Another recently discovered African immigrant upon the Island of Samos in the Ægean plateau is *Pliohyrax* or *Leptodon*, a very large member of the Hyracoidea, probably aquatic in its habits, indicating that this order enjoyed an extensive adaptive radiation in Tertiary times.

It thus appears that the Proboscidea, Hyracoidea, certain edentata, the antelopes, the giraffes, the hippopotami, the most specialized ruminants, and among the rodents, the anomalures, dormice, and jerboas, among monkeys the baboons, may all have enjoyed their original adaptative radiation in Africa; that they survived after the glacial period, only in the Oriental

or Indo-Malayan region, and that this accounts for the marked community of fauna between this region and the Ethiopian as observed by BLANFORD and ALLEN.

Against the prevalent theory of Oriental origin of these animals are: first, the fact observed by BLANFORD and LYDEKKER in the Bugti Beds (Sind) that the Oligocene or lower Miocene fauna of the Orient is markedly European in type; second, that if these animals had originated in Asia some of them would have found their way to North America; third, the fact that all these animals appear suddenly and without any known ancestors in older geological formations. These are the main facts in favor of the Ethiopian migration hypothesis.

In the meantime the unification of the North American and Eurasiatic regions was proceeding by intermigration. In the lower Oligocene the giant pigs or elotheres, the tapirs and peculiar amphibious rhinoceroses known as amynodons, found their way from America to Europe, while Europe supplied us with a few anthracotheres, both *Anthracotherium* and *Hyopotamus*. In the Miocene Europe sent us the true cats and we supplied Europe with the destructive sabre tooth tigers; in the upper Miocene Europe sent us our first deer and cattle or *Cervidæ* and *Bovidæ*, also probably the mastodons *en route* from Africa. In the Pliocene we supplied Europe with the rabbits and hares, and possibly with the raccoons, if the Panda belongs to this family. In the Pleistocene the camels wandered into Asia from America, while the bears passed them *en route* to America. These are a few instances out of many which are already well known.

On the other hand certain families had an exclusively Eurasiatic history, so far as we know. These are, among animals related to the horse and tapir, the palæotheres and *Lophiodon*; among ruminants the traguline deer and muntjacs; among insectivores the hedgehogs; among primates, the anthropoid apes and the lemurs. The latter are peculiar to the Malagasy and Ethiopian regions. At the same time America exclusively raised the titanotheres, the *Hyracodontidæ* or cursorial rhinoceroses, the pouched rodents or *Geomyidæ*, all the early families

of Tylopoda, the peccaries. It is paradoxical that so many animals which we are wont to consider typically American came from the Eurasiatic region, while so many others which we always associate with Asia and Africa came from this country. Herein lies the necessity of a palæontological basis for zoö-geography.

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New York Academy of Sciences, Vice-President 1894-1898, President, 1898-1900.  
 DeCosta Professor of Zoölogy Columbia University, Curator of Vertebrate Palæontology  
 American Museum of Natural History, Chairman Executive Committee New  
 York Zoölogical Society.

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