I*. *On the Osteology of the* Hyopotamidæ. *By Dr.* W. Kowalevsky. *Communicated by Professor* Huxley, *Sec. R.S.*

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Introduction.

The paper which I lay before the Society is an attempt to treat with sufficient osteological detail an extinct family of Ungulates which had an immense range of distribution and a great variety of forms in the two periods of the earth's history which preceded our own. The fate this family has met with at the hands of palæontologists is a somewhat sad one, presenting a warning example of the unscientific method that was paramount in the palæontology of the Mammalia after the time of Cuvier. With the exception of England, where the study of fossil Mammalia was founded on a sound basis, and some glorious exceptions on the continent, we have very few good palæontological memoirs in which the osteology of extinct mammals has been treated with sufficient detail and discrimination; and things have come to such a pass, that we know far better the osteology of South American, Australian, and Asiatic genera of fossil mammals than of those found in Europe. Nearly all fossil Mammalia which have been described in detail belong to genera that still exist on our globe, or whose differences from fossil forms are trifling. After the splendid osteological investigations of Cuvier had revealed to science a glimpse of a new mammalian world of wonderful richness, his successors have been bent rather on multiplying the diversity of this extinct creation, than on diligently studying the organization of the fossil forms that successively turned up under the zeal of amateurs and collectors.

From the year 1828, and even before, when Laizer, Pomel, Croiset, and others began to give short notices on the Mammalia of Auvergne, mammalian genera and species from this locality have been multiplied at a prodigious rate, every private collector giving his own generic and specific names, with no better description than stating the real or supposed number of teeth, and some phrases as to the general resemblances of the fossil in question. Others substituted in their short notices other names, while the scientific work of description did not proceed further than the mere counting of the number of teeth. This process has given rise to such an utter confusion in the palæontology of the extinct Paridigitata, that even now (forty years after the date of the earliest notices) we are utterly ignorant of the true extent and organization of the Miocene mammalian fauna of Auvergne, for instance—though materials for a detailed study of the subject abound in all great public, and many private, collections, the fossils being very common. No palæontologist, even of the highest standing, could boast of knowing,

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in our own time, what *Dremotherium*, *Dorcatherium*, *Elaphotherium*, *Gelocus*, and so on really are, what are the bones belonging to each set of teeth (as the names were mostly given to these last), whether they had horns or were hornless like the *Tragulidæ*, and so on. If we add that German authors described the genera of Paridigitates which were found and named in France under different names (as *Palæomeryx*, *Microtherium*, *Hyotherium*, and so on), when they came from German localities, the confusion may be guessed. Having no good descriptions and no figures of the genera noticed in France, the German authors almost necessarily fell into the mistake of renaming what was already named. Once named, the genus was allowed to go forth with the short and wholly insufficient characteristics given to it by the first describer, the impossibility of adding one's name after the generic or specific designation seeming to take all interest from it. And this, moreover, is the best case; for frequently the same form was described by another palæontologist under a different generic name, or, if this was utterly impossible, a new species was made of it, founded on some difference in size or other trifling character. Happily, however, a reaction began to set in, one of the first to head it on the Continent being Rütimeyer, who did not confine his study merely to the teeth of fossil Mammalia, but aimed with brilliant success at a complete investigation of the osteology of the extinct genera and of their affinities with the living ones. Gaudry's work on the fossils of Pikermi (the best palæontological work that has appeared in France since Cuvier's 'Ossemens Fossiles'), Fraas's 'Fauna von Steinheim,' Alphonse Milne-Edwards's 'Oiseaux Fossiles,' and many others may be cited as examples to prove that the new tendency has fairly set in and will bear good fruit. The wide acceptance by thinking naturalists of Darwin's theory has given a new life to palæontological research; the investigation of fossil forms has been elevated from a merely inquisitive study of what were deemed to be arbitrary acts of creation to a deep scientific investigation of forms allied naturally and in direct connexion with those now peopling the globe, and the knowledge of which will remain imperfect and incomplete without a thorough knowledge of all the forms that have preceded them in the past history of our globe.

The foregoing observations are intended only as a sort of apology for the somewhat minute osteological details into which it seemed to me necessary to enter in my description of the two genera which form the subject of the present memoir; before, however, we proceed to the concrete description of their skeleton, it is necessary to offer a few remarks on the position they hold among other fossil Paridigitata, as it seems to me that it has not been duly recognized by any previous author.

In all our speculations about the history and origin of the Paridigitata, a paramount importance has always been ascribed to *Anoplotherium*, as the most ancient form of the Paridigitate series. Now, seeing the reduced state of the skeleton of *Anoplotherium*, there cannot be the slightest doubt that this position is an entirely usurped one. How this state of things originated is easily accounted for. *Anoplotherium* had the good fortune to be found and described by Cuvier, who gave a thoroughly good description

of its osteology, and, comparing it with some of the living Paridigitates, found that it and they possess many features in common. The naturalists who have ventured to theorize during the period of purely descriptive science which lies between the time of CUVIER and the complete revolution caused by DARWIN'S great work, looked always at the accurate and talented description of CUVIER, finding no good materials in the works of modern palæontologists from which to draw their means of generalization. As this absence of detailed descriptions of fossil European Mammalia was prolonged till our own time, we can understand how, even after the great revolution caused by the publication of DARWIN'S views, all writers that were leading the new movement of evolution, and trying to apply the theory of descent to our modern Paridigitata, had still to consult the works of CUVIER to find full and accurate information. There they could find only *Anoplotherium* fully described (as the *Xiphodon* and, especially, *Dichobune* were very much neglected in the 'Ossemens Fossiles'); and as it was, moreover, the most ancient form known, they placed it at the commencement of their pedigrees of Paridigitata. But if we consider the structure of the feet in *Anoplotherium*, we cannot avoid the conclusion that this genus is only an exceedingly reduced form, descended from some earlier Ungulate of the early Tertiary or, more probably, Cretaceous period. *Anoplotherium* is clearly the last remnant of a dying-out branch, in no case the progenitor of the wonderfully rich and diversified Paridigitata which succeeded it in the Miocene period, and which became so enormously developed in the Upper Miocene and Pliocene epochs, forming in our own time perhaps one of the most richly developed of animal groups. The feet of *Anoplotherium* are so much reduced, presenting only two developed metacarpals and metatarsals, with merely rudiments of the lateral toes, which certainly existed in its ancestors, that we cannot imagine such a reduced form giving rise to Miocene or even modern Paridigitata, many of which have four completely developed metacarpals and metatarsals. Besides, it is a very general truth that only those families which were exuberantly developed in bygone times, presenting many subgenera and a great variety of specific forms of different size, have had any chance of leaving a progeny behind them. We see examples of this in some of our recent genera the pedigree of which is now very completely known. There can be, in my opinion, no reasonable doubt that the Horse descended from the *Palæotherium* (very probably the Rhinoceros had the same origin from a Palæotheroid form, though this is not so certain); and see what immense diversity we find in the *Palæotheridæ* of the Eocene and Miocene epochs. The quantity of described species of *Palæotherium* is only a small fraction of the quantity that really existed, as every one who looks through a large collection of Eocene teeth becomes aware. Besides, the *Palæotheridæ* range in size from *P. minimum* (known only by its metapodium), not larger than a rabbit, through all intermediate sizes to *P. magnum*, fully as large as our Rhinoceros. We may mention that the *Paloplotherium* and *Anchilophus* belonged also to this group, and are extensively developed in the Eocene epoch. Only such prolific types, sending branches in all directions, have any chance of not wholly dying out in the course of time. If, in the struggle

for existence, through geological changes of climate, slow submergence of continents, and elevation of the former sea-bottom to the height of the Himalayas, many genera must have been destroyed, still some one branch may have remained, and by gradual modification through natural selection, and perhaps by the agency of some other unknown cause, has given rise to new genera and species better fitted for the changed circumstances of life.

We see the same truth illustrated in the case of the Tapir, which is the last representative of a group extensively developed in the Eocene epoch, as all those genera known under the names of *Pachynolophus*, *Lophiodon*, *Hyracotherium*, *Pliolophus* belonged clearly to the family of *Tapirinæ*.

On the contrary, *Anoplotherium* is exceedingly poor in specific forms, only two being known with certainty, without any great difference of size; and though future discoveries may possibly increase the number of species, it is doubtful if ever they were as numerous as those of other genera which peopled the earth at the same period. In my opinion, as I shall try to prove further on, the *Anoplotherium* is an aberrant and very reduced branch of the early Eocene Paridigitata, which has no direct connexion with the living ones, and the true line of descent of our Ruminantia must be traced through other genera of the early Eocene epoch.

If, on the other hand, we turn our attention to the *Hyopotamidæ*, it must be confessed that the richness of this family in subgeneric and specific forms ranging through all sizes is really astonishing; and we shall be hardly guilty of exaggeration in saying that the diversity of *Hyopotamidæ* in the Eocene and Miocene times was as great as the wonderful diversity of the Ruminantia is at the present day. That this is not fully acknowledged by palæontologists is due to the neglect with which this family has been treated, and which I shall endeavour to repair.

Under the name of *Hyopotamidæ* I understand all the Eocene and Miocene Paridigitata which had crescentic teeth, with five well-developed lobes on their upper molars. The family might be termed *Anthracotheridæ*, as the *Anthracotheria* are among the most prominent representatives of this group; but the *Hyopotamidæ* being richer in subgeneric forms, the family may perhaps better bear their name.

The chief character on which the genus *Hyopotamus* (under the different names of *Ancodus*, *Cyclognathus*, *Bothriodon*) was founded is the shape of the upper molars, of greater breadth than length, and having five well-developed crescents or lobes. No author has mentioned any bones belonging to different sets of teeth, on the real or supposed differences of which many species were founded. The priority of mentioning these teeth under the name of *Ancodus* is claimed by Pomel in his 'Catalogue;' but as he neither gave a good description of them, nor illustrated his short notices by figures, no palæontologist has accepted this name, and it may be considered extinct. In fact, long before Pomel, Cuvier, having received a jaw of this genus from Puy, compared it with *Chœropotamus* and *Anthracotherium*; and as he had only the back molars, he deemed it unnecessary to separate the new animal from *Anthracotherium*, and designated

it under the name of *Anthracotherium velaunum*. In the year 1847, however, Professor OWEN, having received from the Marchioness of HASTINGS very good materials, as far as the dentition was concerned, studied with great accuracy the structure of these teeth, and found in them sufficient characteristic differences to justify their separation from *Anthracotherium* under the name of *Hyopotamus*. Notwithstanding that one of the characters on which the distinction was based (the complexity of the upper premolars) was found to be a mistake, these complex teeth being milk-molars and not premolars of the permanent dentition (see Quart. Journ. Geol. Soc. vol. iv. 1848, pl. vii. fig. 6; p^4 and p^3 are in reality d^4 and d^3), still there were other characters which entirely justified the distinction, as I shall show when we arrive at the description of the teeth. Professor OWEN gave such a thoroughly good and accurate description of these teeth, accompanied with plates, that he may be considered the founder of the genus. One year later, M. AYMARD, of Puy, in a footnote to his paper on *Entelodon*, mentioned the *Hyopotamidæ* from Ronzon (Puy) under the name of *Bothriodon*, as he believed them different from those described by Professor OWEN from Hempstead. But having compared an extensive series of jaws and parts of skulls from both localities, I have been unable to detect any difference in them, and therefore the fossils from Puy must be included under the same generic name as those from Hempstead. The only author who has accepted the genus *Bothriodon* of AYMARD is Professor GERVAIS, who, in his 'Paléontologie Française,' p. 192, says that the *Hyopotamus* is to be distinguished from *Bothriodon*; but I have not been able to find any reasons adduced in the descriptions of the two genera why Professor GERVAIS considers them distinct, or on what characters he has founded his distinction. Notwithstanding the care with which I instituted my comparison, I could not detect any differences between the *Hyopotamidæ* from Puy and those from Hempstead; and, so far as I can see, their separation into two distinct genera is entirely unfounded. Professor GERVAIS has described many portions of jaws from different localities in France, and has given them different specific names, the distinction being founded on size and on the fact of their having been found in different localities. As I reserve the discussion of specific differences for the end of my paper, I will not enter into the criticism of these doubtful species just now.

In the year 1861, Professor RÜTIMEYER figured and described, with great accuracy, some few upper molars of a small Hyopotamoid animal from Egerkingen. These teeth had, however, been previously referred by H. v. MEYER to a new genus, *Tapinodon*. Professor RÜTIMEYER had only true molar teeth from Egerkingen, and as they really did not present any fundamental difference from the *Hyopotami* of Professor OWEN, he considered them to belong to the same genus. The Egerkingen specimens being very small, RÜTIMEYER separated them specifically under the name of *Hyopotamus Gresslyi*. This discovery was very important, as it carried the genus into undoubted and even early Eocene strata*. Then came the discovery of the wonderfully rich Eocene fauna of

* I have no doubt that the small Eocene *Hyopotamidæ* will one day be generically separated from the true *Hyopotami*, as known from Puy and Hempstead, as their premolars are somewhat different. I shall not do

Mauremont, described in two memoirs by PICTET, DE LA HARPE, and HUMBERT. Here the *Hyopotamidæ* were much more numerous than at Egerkingen, and presented a great variety of size. Among these remains were some specimens identical with those found at Egerkingen, and they were correctly referred to the *Hyopotamus Gresslyi*. The largest species was said to be identical with *Hyopotamus crispus*, Gerv.; but as Professor GERVAIS, in the second edition of his 'Paléontologie Française,' referred the *Hyopotamus crispus* to *Xiphodon* (without any suitable ground, as it seems to me), the whole matter must be revised once more. I cannot refrain from stating here that, in their second memoir, Messrs. PICTET and HUMBERT have mixed jaws belonging to different animals in a very strange manner. For instance, the upper jaw figured (*l. c.* plate xxiv. fig. 3, *c*) as *Rhagatherium* is in reality a *Hyopotamus*, and the lower jaw (fig. 2) bears not the least resemblance to the true *Rhagatherium* mandible figured in the first memoir, and, in my opinion, belongs to *Hyracotherium* or *Anchilophus*. In the same paper, moreover, the two authors have figured and described a very interesting small Paridigitate mammal, which they called *Cainotherium Renevieri*; but there is not the slightest doubt that this small Ungulate cannot be referred to the genus *Cainotherium*. I have stated before that the chief characteristic distinction of the molars of *Hyopotamus*, as described by Professor OWEN, consists in having five distinctly developed lobes or crescents to their upper molars. These five lobes or crescents are disposed transversely, three on the anterior half and two on the posterior half of each upper molar, as may be distinctly seen in Plate XXXIX. fig. 1. With the exception of *Dichodon* and *Merycopotamus*, all Eocene and Miocene Paridigitata with crescentic teeth had always five lobes on their upper molars, disposed in the same way as in *Hyopotamus*; and, so far as we know at present, the position of the five cusps of the upper molars is reversed only in two very characteristic genera, two being placed in front and three behind. These two genera are *Dichobune* and *Cainotherium*, which also by their osteological characters seem to stand in a very near and direct relation. Every mammalogist is aware how constant are the dental characters in large groups of Mammalia; and if I state that such different genera as *Camelopardalis*, *Camelus*, *Cervus*, and *Bos* show less amount of difference in the structure of their upper molars from one another* than exists between the molars of *Cainotherium Renevieri* and the *Cainotheria* from Auvergne, every one will readily admit that the so-called *Cainotherium Renevieri*, in which the five cusps of the upper molars are disposed in the same way as in all Hyopotamoids (three in front and two behind), cannot be put into the same genus with the true *Cainotheria*, in which the disposition of the cusps is reversed—two in front and three behind. (Messrs. PICTET and HUMBERT noticed this difference in their description, but they did not consider it important enough for a generic distinction.) The upper premolars show also some

this in the present paper, as I hope to collect more ample materials, not only for the dentition, but also the skeleton of the Eocene *Hyopotamidæ*.

* Professor OWEN in Quart. Journ. Geol. Soc. vol. iv. p. 111.

differences from the true *Cainotheria*, and the lower molars even more. If we consider each lower molar as composed of four parts, two crescents on the outer side and two pillars closing the crescents on the inner side (Plate XXXIX. figs. 8–12, *ac*, *pc*, *ap*, *pp*), then we may state that, in the true *Cainotheria* from Auvergne, the back part of each posterior inner pillar is a little prolonged backwards into a small additional cusp; this prolongation is especially marked on the inner side of the last inferior molar, making the posterior additional talon of this tooth quite double. This difference may be clearly seen in comparing a lower jaw of a *Cainotherium* from Auvergne with the enlarged figures of PICTET ('Faune sidérolitique,' plate xxvi. fig. 9, *c*). By all these characters the *Cainotherium Renevieri*, Pict., differs from the true *Cainotheria*, and agrees entirely with the Eocene *Hyopotamidæ* figured by RÜTIMEYER and by PICTET himself. Therefore the *Cainotherium Renevieri* cannot remain in the genus in which it was put by PICTET, but must be arranged with the rest of the Eocene *Hyopotamidæ*, as *Hyopotamus Renevieri**.

I cannot refrain from stating that, in my opinion, the five-lobed character of the upper molars is of a too general value to be used for generic distinction. In fact all the Eocene and Miocene Paridigitate genera (with crescentic teeth) have five-lobed upper molars†, and therefore this character is as unfit for generic distinction, in this large assemblage of animals, as the fact of having four-lobed molars would be found unfit if we tried to apply it to the living Ruminantia; it is of too general a nature, all living Ruminantia having four-lobed upper molars.

In such cases where the true molars present too great a uniformity for furnishing good distinctive characters, the shape of the premolars may be of great use, as was well shown by Professors RÜTIMEYER and HENSEL, in reference to Suina and Ruminantia. And, in fact, if we compare the premolars of the Eocene *Hyopotamidæ* figured by PICTET and HUMBERT, *Hyopotamus Gresslyi*, *H. Renevieri*, and even his *H. crispus* (*l. c.* plate xxiv. fig. 11), we shall see that all these Eocene *Hyopotamidæ*, though of such different size, agree together in the shape of their premolars, while they differ by the same character from the true Miocene *Hyopotamidæ* from Hempstead and Puy. As I hope soon to collect materials for a description not only of the dentition but even of the skeleton of these Eocene species, I will not enter further into this matter here, and I will only state that, by comparing the figures of PICTET with my plates, the reader will perceive that the premolars of all the Eocene *Hyopotamidæ* are, so to say, more ruminant-like: this is especially the case with premolars p^2 and p^3; they are considerably more elongated and not so high as in the *Hyopotamus* and *Anthracotherium*. Besides, I suspect from some bones seen in the collection in Lausanne, and especially from a metatarsal of *Hyopotamus* (*Cainotherium*) *Renevieri* figured by PICTET (*l. c.* plate xxvii. fig. 2), that some, if not all, of the Eocene *Hyopotamidæ* were didactyle, at least the metatarsal

* The Eocene *Cainotherium Courtoisi* from Vaucluse is identical with *C. Renevieri*, and therefore must share its fate, and be united to the *Hyopotamidæ*.

† Except *Dichodon* and *Merycopotamus*.

figured by PICTET belonged undoubtedly to an Ungulate with only two metatarsals. At all events, these Eocene *Hyopotamidæ* seem to form a separate group; and as soon as their organization is better known, they will certainly be generically separated from the true *Hyopotami*. As the matter now stands, however, this *Hyopotamus* (*Cainotherium*) *Renevieri* is the smallest representative of the family, being hardly larger than a good-sized rat; the *Hyopotamus Gresslyi* had perhaps the size of our recent *Tragulidæ*. Between these small *Hyopotami* and the largest *Hyopotamus bovinus*, Ow., we have all the intermediate sizes distinguished as separate species under the names of *Hyopotamus porcinus*, Gerv., *crispus*, *borbonicus*, *velaunus*, Aym., *leptorhynchus*, *platyrhynchus*, *vectianus*, Ow., and finally *bovinus*. All these numerous species were, for the most part, founded merely on real or supposed differences in the size of the true molars, no author having figured or described any other part of the skeleton. Now, as every naturalist is aware, there can be no worse method of specific distinction than size, especially in richly developed families. Take our living Ruminantia, imagine them to be extinct, and some future palæontologist trying to give them generic and specific names by the characters of their upper and lower molars. I do not think he could arrive at any thing approaching truth. We may certainly form a large series of ruminant molars, entirely similar in shape, and ranging in size from the small *Antilope pygmæa* to the largest Antelopes and Bovidæ*, and then distribute all this assemblage of teeth into different species according to size; but the scientific value of such species would be indeed very doubtful. Still this is what we see constantly done in palæontology. In my opinion, we have, in most cases, not the least chance of hitting right in establishing specific distinctions on fossil remains; and most of the published species of extinct animals are certainly only productions of our palæontological methods of inquiry, which had no real distinction whilst living. On the other hand, it is just possible that the real number of so-called distinct species was greater than we can distinguish by fossil remains; at all events we have very little security that most of our specific distinctions correspond to the real state of things which existed in past geological time. Seeing the impossibility of arriving at any thing like an accurate knowledge of the specific distinction of extinct forms, it would be much more profitable to science if we were to give a pretty large range, as far as size is concerned, and concentrate all our discriminating powers on such characters as are really organic and fundamental, and may be taken as a basis for generic or subgeneric distinction. To found a new genus, a palæontologist is required to adduce some good reason for doing so; he is obliged to point out some organic difference, and this leads to a more complete study of the fossil forms; while the laxity with which we regard species requires, in a great majority of cases, no other reason than the phrase "this tooth *seems* to me to be specifically distinct from one already described," and a new name is formed which goes to the large number of others uselessly obstructing the science. Every one who has tried to ascer-

* The upper molars of some Ruminantia sometimes present distinctive characters in the form of additional pillars, but these are often present or absent in widely different forms.

tain the true organization of extinct types, and who is aware of our ignorance in this respect, will concur with my statement, that if, from the beginning of mammalian palæontology, all specific distinctions had been disregarded, and only the generic forms had been studied in detail, we should know much more about the extinct creation than we do now. The family of *Hyopotamidæ* may also serve as an instance of the unscientific methods which are paramount in palæontology. During the twenty-five years that the genus has been introduced to science, we have contrived to make more than ten species out of it; while nobody has ever cared to ascertain what its organization really was, and not a single bone has been figured up to this day.

This was the state in which I found our knowledge respecting *Hyopotamus*, when I determined to study it more completely than had been done heretofore. I knew that the principal collections, containing large materials for the study of this genus, were at Puy in Central France and in the British Museum. My kind friend Professor GAUDRY, of Paris, gave me letters of introduction to M. AYMARD, who is the possessor of the largest collection in Puy, and to M. ROBERT, Director of the public museum of the same town. I met with the most cordial reception from both these gentlemen; M. AYMARD especially, with the utmost liberality, placed the riches accumulated by him, during thirty years of diligent collecting, entirely at my disposal, and allowed me to make casts from every specimen I liked. This permission, which is so seldom accorded by private collectors, was of immense value to me, as my Plates could not be drawn at Puy, but had to be made in London. The same facility was afforded me by M. ROBERT; and I take the opportunity of expressing my warmest thanks to both these gentlemen. My thanks are also due to the artist, M. PELLEGRINI, in Puy, who made my casts, sparing no time and taking much trouble, the specimens from which the casts were taken being generally exceedingly brittle.

I found in the collection of M. AYMARD a large quantity of bones, which enabled me to get a complete conception of the skeleton of the interesting genus described in this paper. The bones proved that the *Hyopotamus* was one of the extinct Paridigitata with crescentic teeth, and had four completely developed digits on the fore and hind legs. The size of the teeth and bones enabled me to distinguish two or three species, as had been previously supposed by M. AYMARD. From Puy I came to London, where, by the kind permission of Professor OWEN and Mr. WATERHOUSE, the bones of the *Hyopotamus* contained in the collections of the British Museum were placed at my disposal. The jaws and bones from Hempstead, part of which were described by Professor OWEN in 1848 (Quart. Journ. Geol. Soc.), proved to be entirely identical with those found at Puy; so that the name of *Bothriodon*, which was applied to teeth and bones found at Puy, under the impression that they were distinct from those found at Hempstead, could not be retained, and the priority remains with the name *Hyopotamus* given by Professor OWEN to specimens from Hempstead. But, besides the bones from Hempstead, I found in the British Museum a number of well-preserved long bones, some metacarpals and metatarsals, as well as a well-preserved tarsus, which came from Hordwell from a true

Eocene bed, and were supposed to belong to *Hyopotamus bovinus*, under which determination they were placed in the Museum. At first I thought that these bones might really have belonged to the *Hyopotamus bovinus*, though the British Museum possessed no teeth of this genus from Hordwell. The long bones from Hordwell were strikingly similar to the *Hyopotamus* bones from Hempstead and from Puy; the calcaneus, astragalus, and phalanges were so entirely similar to *Hyopotamus* bones from these two localities, that it seemed impossible to doubt their generic identity. What looked very convincing also was the shape of the last, or ungual, phalanges. These ungual phalanges are very peculiar in the *Hyopotami* from Hempstead and from Puy; they resemble somewhat a large and thick human nail, and we know not a single living or fossil Ungulate having such peculiar ungual phalanges; however, even in this the animal from Hordwell entirely resembled the *Hyopotamus*. But the metacarpals and metatarsals of the Hordwell animal proved very different from any thing found at Hempstead or in Puy; they were considerably larger, and their shape was altogether different; the section was much more round, and the inferior or distal ends proportionately thicker. At first I could not find any plausible reason why the animal from Hordwell, being so similar to the *Hyopotamus* in all the long bones of the skeleton, should present this very striking difference in the shape of the metacarpals and metatarsals. But gradually, as I grew more familiar with all the peculiarities of these bones, and after having compared them with a large series of metacarpals and metatarsals of extinct and living Paridigitata, it became quite clear that the animal from Hordwell, although so similar in all its long bones with the *Hyopotamus* from Puy and Hempstead, differed widely from this genus in having only two metacarpals and metatarsals, and not four—being in fact didactyle, like the *Anoplotherium*. As we have never yet found at Hordwell a complete fore or hind foot in its natural connexion, I was very cautious in drawing my inferences from scattered and mostly broken bones; but the study of the relat ions of the carpal and metacarpal, and especially tarsal and metatarsal bones, gave altogether the same result; indeed there was no possible doubt that the animal from Hordwell could not have more than two complete digits to its fore and hind foot. Unfortunately I could not find any teeth belonging to the new animal whose almost entire skeleton was before me. The only authority who has noticed *Hyopotamus* teeth from a deposit in Hampshire is Professor P. Gervais. In his 'Paléontologie Française,' while speaking of *Hyopotamus* (p. 191), he tells us of having met *Hyopotamus* teeth, similar to those described by Professor Owen, in the collection of Bowerbank; "they came from a fresh-water stratum in Hampshire." As the bed in which the bones of the new didactyle animal were found at Hordwell has really an outcrop in the New Forest, I suspect that the teeth seen by M. Gervais really came from this bed. However, the absence of these teeth, though much to be regretted, is not an obstacle to a complete knowledge of the new genus. The classification of Paridigitata is based entirely on osteological characters; and as nearly all the bones of the new animal from Hordwell are known, it is perfectly characterized, and, in my opinion, much better than many genera of which

only the dentition is known. Besides, we must not forget that the *Hyopotamidæ*, as proved by the fauna of Mauremont and Egerkingen, are a true Eocene family; and the presence of a large representative of this family in the Upper Eocene of England is a very natural occurrence. I stated before that, even in the Mauremont and Egerkingen fauna, some of the *Hyopotamidæ* seem to have been didactyle; and we may take this as pretty certain as regards the small *Hyopotamus Renevieri*. The new didactyle animal from Hordwell is only a larger representative of these Eocene didactyle *Hyopotamidæ*; and we may expect that when its dentition is completely known it will very probably resemble that of the Eocene *Hyopotami* as found at Mauremont and at Egerkingen, and differ by its more ruminant-like premolars from the true *Hyopotami* which occur at Hempstead and in Puy. The presence of didactyle genera in Eocene deposits, while we find tetradactyle genera belonging to the same family in the Miocene, is no objection to the theory of descent as it is often argued by the adherents of the special creation hypothesis. The primary stock was undoubtedly tetra- or even pentadactyle; and under the incessant tendency to greater reduction and simplification of the limbs, which we witness in all Ungulata without exception, there were given off side branches which reached this utmost reduction of the limbs in the Eocene and became extinct, while the original unreduced stock continued to live till the Miocene period. A similar case may be imagined in relation to the recent Suinæ. There is no doubt that the *Dicotylidæ* represent one of the most advanced and reduced branches of the family of Suina; they practically reach nearly the same state of reduction of their limbs as the didactyle genera, their lateral digits being only useless appendages, having no importance for locomotion. Imagine that, by some geological change, the *Dicotyles* should become extinct in South America, while other continents should continue to be peopled by unreduced typical Suina: in this supposed case we should have an extinction of the filial branch, while the parent stock would continue to live and flourish. In the same manner I have little doubt that the didactyle *Hyopotamidæ* found at Hordwell and Mauremont descended from a tetradactyle stock, which very probably presented the same structure of the skeleton as we find it in the Miocene *Hyopotamidæ* from Puy and Hempstead*. And though the didactyle genus is found in strata older than those which gave us such complete materials for the restoration of the tetradactyle *Hyopotamidæ*, still, seeing the similarity of their skeleton, we may consider the didactyle genus from Hordwell as a reduced descendant of a form very similar in its skeleton to the *Hyopotami* of Puy and Hempstead.

Having ascertained the existence of this reduced representative of the family of the *Hyopotamidæ*, I could not, in view of the difference in the number of digits, permit the new form to remain in the genus *Hyopotamus*; and though I strongly object to the creation of new names, there is no help for it in this case, and a new generic division must be made to receive the didactyle Hyopotamoid from Hordwell, as well as similar forms which may turn up in the future. As the chief distinction of this genus is its

* The probability is converted nearly into complete certainty if we consider that the reduced didactyle genus presents rudiments of two additional digits, the second and fifth.

didactylity, I propose to name it *Diplopus*, and to add to the special form found at Hordwell the name of M. AYMARD, who has contributed so much towards the advance of our knowledge of this extinct group. I will therefore describe the animal from Hordwell under the name of *Diplopus Aymardi*.

From the point of view of pure descriptive osteology, it would be perhaps better to describe the *Hyopotamus* from Hempstead and Puy and the *Diplopus* from Hordwell separately. I have been prevented, however, by many reasons, from following this course, and I have preferred to give a comparative description of both genera: as the number of my Plates was limited, I could not figure all the bones belonging to both; and in the case of entirely similar bones, I gave preference to those which were better preserved. The present paper contains only the description of the long bones of the skeleton and of the limbs. I hope soon to be ready with the description of the vertebræ, skull, and dental characters. My best thanks are due to the officers connected with the Osteological and Geological Departments of the British Museum, as every thing which could in any way favour my studies was accorded in the most liberal way. My special gratitude is due to Mr. WILLIAM DAVIES, of the Geological Department, to whose kindness and the interest he has taken in my work I owe very much. I am indebted to him for many valuable suggestions, and for the unremitting kindness with which he assisted me in looking over and over again through the rich stores of fossil remains contained in the galleries of the National Collection, and for aiding me in my comparisons in every possible way.

The Bones of the Skeleton.

The Scapula (Plate XXXV. fig. 1, $\frac{2}{3}$ nat. size).—This is a bone that has generally the least chance of being preserved fossil, owing to its flat shape and consequent thinness. Happily, however, thanks to the excellent method by which the bones from Hordwell were collected by Mr. KEEPING, we have now in the British Museum, besides several detached fragments, a complete right scapula* from Hordwell, which belonged to the didactyle animal named by me *Diplopus Aymardi*. The chief characteristic of this fossil scapula is its enormous breadth compared with the antero-posterior length. No living Ungulate shows us such a broad scapula, the nearest approach to it being made perhaps by the scapula of *Hippopotamus*. Among the fossil Ungulata, the *Anoplotherium* (BLAINVILLE, Ost. *Anopl.* pl. iii.) comes even nearer to it, by the broad expanse of the horizontal part and by the large acromial process; there is, however, a marked difference between the two in the shape of the glenoid cavity, which is very oval in *Anoplotherium* and nearly circular in *Diplopus*. The coracoid process is not very prominent, but larger than in the recent Suinæ; it is separated from the glenoidal fossa by a slight notch, retreats a little backwards, and does not reach the level of the inner margin of the fossa. The fossa glenoidea is moderately deep, with a sharp margin raised all round.

The spine of the scapula is very high and sharp, set very obliquely on the horizontal

* As many bones were drawn without mirror (not reversed), it may happen that some of them described as right may be really left in the original. I shall, however, adapt my descriptions to the Plates, and describe the bones as they appear in the drawing.

part, and inclined to the outer side; its upper margin is rugose, but presents no flattening or expansion, as in many Ungulates of the Imparidigitate series. The pars acromialis is produced forwards in the same way as in *Anoplotherium*, the *Camelidæ*, and most Ruminants, but never in Pigs, where the spine rises very slowly from the neck backwards without any trace of an acromial process. The rising of the spine above the surface in *Hyopotamus* commences at a distance of 30 millims. from the glenoidal border; but the acromion is so produced forward that it reaches nearly to the level of the glenoidal cavity, overarching the neck of the bone. The supraspinous is a little smaller than the infraspinous fossa, but the difference is not important.

In considering the very great breadth of the scapula of *Hyopotamus*, we must not forget that all Ungulata have a very large upper cartilaginous border, which is wanting in our fossil: the scapula figured by me belonged to a young individual; and we may safely infer that by the gradual ossification of the cartilaginous upper margin, the breadth would not be so disproportionate to its length as it is now. On the outer side of the neck of this scapula we see a pretty deep and large elongated fossa, found also on two other broken specimens. In general shape this fossil scapula agrees most with the scapula of *Hippopotamus*, by its great breadth and by the production of the acromial extremity of the spine, in which respect it also closely approaches some ruminants. With the Suinæ, however, we find no relation at all; and I particularly insist on this point, as, owing to the poorness of the Paridigitate types in our recent fauna, we are very apt, whilst studying fossil Mammalia with unreduced skeleton, to find resemblances with Suinæ even where they are very slight, just because the pig has one of the most complete (unreduced) skeletons among the living Ungulata.

Unfortunately I could not find in the collection of M. Aymard, nor in that of the Puy Museum, a scapula of *Hyopotamus*.

Dimensions of the Scapula of *Diplopus Aymardi*.

	millims.
Height of the articular fossa	34½
Transverse breadth of the articular fossa	37
Height of the spine	31
Transverse breadth, including the coracoid process	57
Breadth of the neck	47
Largest transverse diameter	190
Whole length	218

This was written and my Plates were drawn in London in the summer; but having in November last paid another visit to Puy, in order to examine the collection of Mr. Vinay, which I was prevented from seeing on my first visit, I found there a very good specimen of the scapula of *Hyopotamus*. The upper margin of the bone was broken, and only about two thirds remained entire; the spine of the scapula was preserved, although its acromial part was broken; and I could not ascertain if it was prolonged forwards in

the same manner as in the scapula of *Diplopus*. My paper and Plates being already finished, I could not give a figure of this new specimen, and shall try to supply the want of it by a few explanatory remarks.

The scapula in the collection of Mr. VINAY belonged evidently to the largest species of *Hyopotamus* found at Puy, and in size equalled the scapula of *Diplopus* figured in Plate XXXV. The general aspect of this new specimen presented a great similarity to the one figured from Hordwell; beginning from the neck, the bone broadened rapidly to its upper and broken extremity, and acquired the same remarkable breadth which is so conspicuous a feature of the scapula of *Diplopus*. The spine of the scapula was also very oblique, inclining outwards as in the scapula figured in Plate XXXV. The fossa glenoidea had precisely the same exceedingly circular outline as is seen in the figured scapula; the coracoid process did not project much, and was recurved in the same characteristic manner. On the outer margin of the neck, however, where I found a deep fossa in *Diplopus*, the scapula from Puy presented only a flattening. In general the resemblance was as great as could be between two animals belonging to the same family but to different genera.

The Humerus.—I have been able to study many specimens of humeri belonging to *Hyopotamus* from the Isle of Wight, as well as from Puy, but unfortunately not a single complete one. As is generally the case with fossil humeri, their upper or proximal head, being very spongy, is destroyed during the process of fossilization, while the distal extremity is well preserved. Compared with a humerus from Hordwell, the humeri from Puy and Hempstead proved entirely similar to it; and as the Hordwell specimen, belonging to *Diplopus*, was the best preserved, I have figured it on Plate XXXVI. fig. 4, and my description of this humerus will apply equally well to both genera. As mentioned before, the proximal heads were broken in all specimens; but seeing the Anoplotheroid affinities presented by the distal extremity, we may presume that the proximal head also resembled rather the *Anoplotherium* than the Suidæ. In the first genus, as far as can be judged by a crushed *Anoplotherium* humerus in the British Museum, the great tuberosity did not overarch the bicipital groove so much as it does in Pigs and the Hippopotamus. We may, to a certain extent, infer the lesser overarching of the great tuberosity by marking the course followed by the crista anterior descending from this tuberosity, and which in *Hyopotamus* runs in the middle of the anterior surface of the humerus (fig. 4), and not so much on the inner side of it as in Suina. The deltoid ridge meets the crista anterior a little higher up than in *Anoplotherium*, nearly as in the Hog; and at the point of their meeting we see a conspicuous rugose flat surface for muscular attachment. The shaft of the humerus belonging to the *Diplopus* is very stout, thicker transversely than the humerus of a Reindeer, and much stouter in antero-posterior depth. The transverse section is not so regularly oval, but much more triangular than in Pigs or Ruminants, with the apex of the triangle turned forwards.

The inferior extremity of the humerus is very unlike that of any existing Ungulate, and presents a good intermediate form between the humerus of *Anoplotherium* and that

of the Suina. As this inferior extremity of the humerus seems to me a very important part, especially as showing the modifications which a bone may undergo in adaptation to different conditions of life and organization, I must describe it at length.

Looking at the distal extremity of the humerus in the two series of fossil Ungulata, we shall see that its shape is at first exceedingly and typically different in Paridigitata and Imparidigitata. In the oldest Imparidigitata, as *Palæotherium*, and even in the living Rhinoceros, the distal extremity of the humerus is quite hourglass-shaped—that is, it looks as if two truncated cones were joined together by their apices. At the point of meeting we have a middle groove, from which the two horizontal cones thicken gradually in both directions, inwards and outwards. As we have every reason to suppose that *Anoplotherium* is the descendant of a very old type of Paridigitata, we may look to its humerus as giving us the typical form of the distal extremity of this bone in old Paridigitata. Now the distal extremity of the humerus of *Anoplotherium* is totally different from what we have seen in *Palæotherium*; the difference may be best imagined if we say that in lieu of the middle groove, where the two cones meet, we find in *Anoplotherium* a round bulging, which goes all round the distal extremity of the humerus (see BLAINVILLE, Ost. *Anopl.* pl. iii.). This middle bulging is very characteristic of all mammals in which the humerus is very movable upon the two bones of the antibrachium—so in Man, in most Carnivora, and in those Rodents which use their fore paws as hands. With the reduced mobility of the humerus upon the antibrachium, we remark a concomitant change in its distal extremity; the middle bulging recedes gradually to the outer half of this extremity and becomes much sharper, till at last, in animals with greatly reduced limbs whose humeri are fitted only for a simple sliding movement in one vertical plane (as in our modern Ruminants, and in some Rodents, as Hares), this round bulging of the *Anoplotherium* is reduced to a sharp ridge, which enters deeply into a corresponding groove on the proximal extremity of the radius (which must necessarily be adapted to all the modifications of the humerus). It is exceedingly interesting to follow this gradual modification, step by step, through all the intermediate stages presented by the *Chœrotherium* of LARTET, the *Hyomoschus crassus*, to our modern Ruminants, whose humeri show, instead of the Anoplotheroid bulging, an exceedingly sharp ridge fitting closely into a corresponding groove of the radius, and preventing any other movements save those in one vertical plane. It is interesting to notice that we see the same change going on in the Imparidigitata, though their starting-point, from the simple hourglass-shaped form of the humerus of the *Palæotheridæ*, is so different. In this series a rising appears gradually on the outer half-cone: in *Palæotherium* medium; this rising goes on increasing with the gradual reduction of the free movements of the fore limb in *Anchitherium* and *Hipparion*, till it reaches the state in which we now find it in the Horse; and in this last the distal extremity of the humerus is nearly like that presented by Ruminants; but as I have discussed this case in my memoir on *Anchitherium**, I will not return to it in this place.

* Mém. Académie de St. Pétersbourg, 1873.

In the humerus of *Hyopotamus* and *Diplopus* the middle Anoplotheroid bulging (Plate XXXVI. fig. 4, *a*) is much lowered, showing a step toward the condition seen in Pigs, in which it is raised into a very slight eminence. The inner margin of the humeral extremity (fig. 4, *b*) is produced a little downwards, but much less so than in *Anoplotherium*. The supinator ridge is not prominent, though its rugose surface testifies to the attachment of strong muscles. There is a very large intercondyloid perforation (*c*), into which the olecranon entered deeply, as in modern wild hogs. The breadth of the articular surface is very great comparatively to the transverse diameter of the whole distal extremity of the humerus. The humerus figured in Plate XXXVI. fig. 4 belonged to the didactyle form, *Diplopus Aymardi*; it is from Hordwell: besides this humerus I had many specimens from Puy and Hempstead; and as the two genera are confined to their respective localities, the *Diplopus* to Hordwell and the *Hyopotamus* to Puy and Hempstead, there is no danger of intermixing their fossil remains. The humeri of different size, which belonged to the tetradactyle *Hyopotamus*, are entirely similar to the one figured; the only difference which may be noticed consists in the fact that the distal articular surface is relatively larger in the *Diplopus* than in *Hyopotamus*, as seen by the fact that in the three humeri of nearly equal size measured by me, the breadth of the articular surface is 42 millims. in *Diplopus*, and only 32 and 35 in two humeri of *Hyopotamus*.

Dimensions of the Humerus.

	Diplopus Aymardi. (Fig. 4.)	*Hyopotamus.*	
	Hordwell.	Hempstead.	Puy.
Largest transverse diameter of the distal extremity.....	54½	55	54
Transverse breadth of the articular surface	42	35	32
Vertical height, articular surface, internal border (*b*)	32	31	28
Vertical height, articular surface, external border	24	23	22½
Vertical height at the middle groove (*a*)	23	21	20
Transverse diameter of the shaft (inf. ⅓)	28	22	20
Antero-posterior diameter	39	27½	

The Ulna.—The antibrachium of *Hyopotamidæ* consisted of two completely separate bones, and there is no trace of their having been immovably connected together, as in nearly all living Ungulates. I had several specimens of this bone from Puy, and from the English localities of Hempstead and Hordwell; all, however, were more or less broken, save a splendid specimen from Hordwell in the British Museum. This right ulna (Plate XXXVI. fig. 1) fits the humerus figured in the same Plate (fig. 4) as exactly as if it came from the same individual. I will give the description of this complete specimen, and state the differences it presents from other ulnæ from Puy; the complete specimen figured in Plate XXXVI. belonged to the didactyle *Diplopus*. The shape of this bone in our didactyle genus is very striking from its extreme flatness and breadth; it is much arched forwards, and this curvature reminds one of the ulna of Suinæ. At the upper part we see a

very large and broad olecranon, which differs slightly from living Ruminants and Pigs by its greater transverse breadth, and by the more projecting hook of the fore part, which entered deeply into the intercondyloid perforation (fig. 4, *c*) of the humerus. The fossa sigmoidea is uninterruptedly united on the inner side to the radial facet, while its outer part presents a deep *échancrure*. The outer radial facet of the ulna is not united to the fossa sigmoidea in the *Diplopus*, though it is so in the smaller *Hyopotamus* from the Isle of Wight and from Puy (fig. 2, *or*). Both articular facets for the radius are nearly in one plane, whilst in Ruminants the outer facet projects much more forwards than the inner. The section of the ulna of *Diplopus* gives us a figure like a flat or low triangle, not quite regular on its external border. The posterior surface (Plate XXXVI. fig. 1″, *p*) of the ulna is the large basis of the triangle; the obtuse apex (*a*) presents a rugose ridge, seen in fig. 1′, running on the fore part of the ulna, and by which it is pressed against the radius; the sides of the ulna are inclined planes, uniting the extremities of the base to the apex. Just below the second third of its length the three planes of the triangular ulna begin to narrow whilst descending to the distal extremity, which retains the same triangular outline. The inferior extremity is cut nearly at right angles by the facet for the outer bone of the carpus.

If we compare smaller ulnæ from Puy and the Isle of Wight we shall see some differences not only in the shape of the sigmoid fossa, but likewise in the transverse section of the ulna. In some of the ulnæ, like the one figured from Puy (fig. 2), the lower and fore part of the fossa sigmoidea is much produced forwards, forming a sort of prominent bridge between the inner and outer radial facets of the ulna; the production of this connecting bridge creates a deep fossa in the middle of the anterior surface of the ulna. Having examined this part of the ulna in a large number of recent Suina, I found it very variable, and therefore cannot lay too great a stress upon it in the *Hyopotamidæ*. But besides this, the ulnæ from Hempstead and Puy, belonging undoubtedly to *Hyopotamus*, have a very different horizontal section, and they are by no means so much flattened as the ulna of the *Diplopus*; this difference is most clearly seen by comparing the horizontal sections of both ulnæ taken about the middle of the bone. The species from Puy have a much deeper and sharper posterior edge (fig. 2′, *p*), which is nearly absent in the *Diplopus*. Unfortunately I have not found a single entire ulna of the *Hyopotamus*, though I have seen a large number of broken specimens from Puy and the Isle of Wight. Comparing these broken ulnæ with the one figured, I found some notable differences in details, which will be clear to the reader by comparing the figure of a part of the ulna from Puy and its transverse section (figs. 2 & 2′) with that of the ulna from Hordwell (figs. 1 & 1′). The differences extended further than the shape of the sigmoid cavity, as the following Table of measurements will show.

Dimensions of the Ulna.

	Diplopus (fig. 1, Plate XXXVI.).	*Hyopotamus.*			
		Puy (Plate XXXVI. fig. 2).		Hempstead.	
Total length along the curvature	270				
Posterior chord	254				
Greatest breadth at the radial facets.....	32	30	26	25	30
Breadth at the middle	33	18	..	..	17
Antero-posterior diameter (at radial facets)..	22	24	23	25	30
Antero-posterior diameter (middle)	12	19	..	..	20
Transverse breadth, inferior extremity.....	16				
Antero-posterior diameter, inferior extremity	$11\frac{1}{2}$				
Antero-posterior diameter from the point of olecranon to the posterior surface....	48	..	..	..	46

The distal end of the ulna of *Diplopus* is triangular, with a slightly excavated triangular facet for the pyramidale of the carpus. I have not the pisiform bone; but as there is no facet on the posterior side of the distal end of the ulna, this bone probably did not articulate with the ulna, but exclusively with the pyramidale.

The great difference in the horizontal sections of the ulnæ of both genera (fig. 1″ and fig. 2′, Plate XXXVI.) is produced by the great flattening of the ulna of the didactyle *Diplopus*. The section of the ulna of a hog taken in the middle will give nearly the same figure as the section of the *Hyopotamus* ulna (fig. 2′). The same letters mark the corresponding parts in both sections. As an instance of a greatly compressed ulna, I may adduce the ulna of *Hyomoschus*; it is so compressed laterally that its antero-posterior depth is ten times as large as the transverse breadth; and the whole bone, from its radial articulation downwards, looks like a knife-blade with its sharp edge turned forwards towards the radius.

The Radius (Plate XXXVI. fig. 3).—I was not fortunate with this bone, as I have not a single complete specimen; even fragments are rare.. I found, however, in the collection of the British Museum an upper half and a distal extremity of a radius from Hempstead which belonged undoubtedly to *Hyopotamus*. I possess also the same parts from Puy, and they entirely agree with the English specimens.

The proximal extremity of the radius is always shaped so as to fit the distal end of the humerus, and their variations are always correlative. For this reason the radius of *Anoplotherium*, constructed to fit the very peculiar distal end of its humerus, is made on a pattern exceedingly different from that of all other Ungulata, and shows a striking likeness to the proximal extremity of the radius of a carnivore, especially the Dog; but in *Hyopotamus* we find a more Ungulate-like radius. Instead of the great oblique middle fossa of the *Anoplotherium*, we see in *Hyopotamus* a shallow and broad groove (fig. 3, *a*′), made to fit the middle bulging (fig. 4, *a*) of the distal extremity of the humerus. The inner part of the proximal surface is a plane (Plate XXXVI. fig. 3, *b*′) less inclined than in *Anoplotherium* (Blainv. Ost. *Anopl.* pl. iii.), but much more so than in Pigs, owing to the greater downward production of the inner condyle of the humerus (Plate XXXVI.

fig. 4, *b*). The two posterior small fossæ for the radial facets of the ulna are not very deep; they are separated by a posterior bony projection, which entered, or is thrust under, the connecting bridge of fig. 2, *cb*. We have no direct means of ascertaining the curvature of the radius, but it is given to us by the shape of the ulna (fig. 1), so that, at least in *Diplopus*, the radius must have been considerably arched forwards.

The distal extremity (fig. 3′) of the radius is very unlike that of any existing Paridigitate. In these we see generally on the distal end of the radius two longitudinal excavated facets, separated by an oblique prominent ridge running in the interspace between the scaphoid and the lunare (see BLAINV. Ost. *Anopl.* pl. iii.); we have no trace of this ridge in *Hyopotamus*. The inner half of the distal end (fig. 3′, *i*) is occupied by the oblique convex facet for the scaphoideum; the outer half presents a concave anteriorly broad facet for the lunare; this bone, having a very oblique position in the carpus, encroaches by its posterior narrow prolongation upon the scaphoidal half of the distal extremity of the radius. Both facets are separated anteriorly by a deep groove, seen opposite the number 3′ of the figure. The difference from the radii of all other Ungulata is considerable. To the external straight truncated surface (fig. 3′, *ex*) the distal extremity of the ulna was articulated; but I have had no specimen of *Hyopotamus* showing this distal end of the ulna.

The radius of *Hyopotamus* was articulated (as in all Ungulates having a completely developed ulna) only with the two inner bones of the carpus, the scaphoid and the lunare, while the outer bone, the pyramidale, is taken up entirely by the distal extremity of the ulna. All existing Suidæ show us the same relation; but in *Dicotyles*, whose skeleton is a little more reduced than that of the typical Pigs, we see that the distal extremity of the radius grows broader in consequence of the reduction of the ulna; and, besides its two typical carpal bones, makes an encroachment upon the outer one, the pyramidale. With the still greater reduction of the ulna in most Ruminantia, the radius goes on increasing, and not merely touches the pyramidale, as in *Dicotyles*, but takes the whole half of its upper surface for its own support, while the reduced ulna is pushed back to the posterior half of the pyramidale. In consequence of this changed relation between the carpal bones and the radius, the distal extremity of this bone in Ruminants acquires at its outer border an additional facet for the pyramidale, of which not a trace is to be seen in *Hyopotamus*. We may mention as another peculiarity of the distal end of the radius of *Hyopotamus*, the entire absence of any styloid process or prolongation of the inner border of the distal end of the radius, which is well seen in other Paridigitates, as *Anoplotherium* and *Hippopotamus*. Specimens of the distal and proximal extremity of the radius which I possess from Puy agree in every particular with the one described from Hempstead.

Dimensions of the Radius.

	Hyopotamus.	
	Hempstead.	Puy.
Transverse breadth of the proximal extremity.....	30	32
Antero-posterior depth of the upper surface.....	20	19
Transverse breadth of the distal extremity. These extremities seem to be epiphyses of radii of young individuals	32	30

The Femur.—Of this bone I had a complete specimen from Puy (fig. 5, Plate XXXVI.), an upper half of a smaller species from Hempstead (fig. 6), and a lower half (Plate XXXV. fig. 2) from the same locality, but belonging evidently to a larger individual or species than the upper half. I had no femur from Hordwell, and consequently this bone is unknown in *Diplopus*.

Confining our comparison only to the Paridigitate series of Ungulata, of which *Hyopotamus* is one of the old representatives, we find in our fossil femur characters that are very common to all the members of this division. In comparing the ruminant and non-ruminant Paridigitata, we find that the femur in the Suina has a more complete spherical head supported on a pretty distinct neck, the great trochanter rising very slightly or not at all above the level of the femoral head, and a small (or inner) trochanter not very prominently developed, and often consisting merely of a rugose thickening at the antero-posterior edge of the superior half of the femur. The general shape of the bone is very round in *Dicotyles*, more flattened in other pigs, and slightly arched from behind forwards. Both edges of the anterior part of the distal articular surface (rotular surface) are alike, while the internal condyle is thicker than the external; the transverse breadth of the trochlear surface for the patella is proportionately broader in comparison with the entire thickness of the distal end than in Ruminantia (*Dicotyles* forms an exception to this rule, and the rotular breadth of its femur presents the same relation to the whole thickness of the distal end as in Ruminantia). Now the femur of *Hyopotamus* shows characters that are common to both divisions of Paridigitata. The head of this femur is supported on a neck (fig. 6) even more distinct than in the Suina, and approaching that of *Hippopotamus*. The great straightness of the whole femur reminds us also of this last genus. The spherical head is provided with a deep pit for the round ligament, which is absent in *Hippopotamus*. This round articular head is connected with the prominent small (inner) trochanter by a very sharp ridge, as in some Suina, only the ridge is higher and sharper (fig. 6′). The bridge of bone (fig. 6, *a*) connecting the head of the femur with the great trochanter is much contracted in the middle, and lowered in such a way that both articular head and great trochanter rise considerably above the level of the connecting bridge—a character very general among the Paridigitata, with the exception of the *Camelidæ*, in which the superior end of the femur is shaped on a plan entirely different from other Ruminants, presenting a great resemblance to the Imparidigitata (*Rhinoceros*) in the breadth of the connecting bridge

and the shape and position of the great trochanter. The shape of the femur in *Hyopotamus* (fig. 5) is remarkably uniform in its thickness, is exceedingly straight, and presents on its posterior surface, above the internal condyle, no deep pit for the plantaris muscle, but a simple rugosity, as in hogs. Some comparative anatomists seem to attach a great importance to this fossa, though I cannot do so, seeing that this fossa is developed or absent in animals belonging to both series, Paridigitata and Imparidigitata. For instance, it is very large in the Horse, but absent in the Rhinoceros; developed in most Ruminants and *Hippopotamus*, but absent in *Camelidæ* and *Suidæ*, where we find, in place of the pit, a rugose surface for the attachment of the same muscle.

The fore part of the distal extremity (Plate XXXV. fig. 2), as in most living Ungulates of both series, with the exception of the Suinæ, *Hyomoschus*, and some Ruminants, has a more developed internal rotular edge, though the difference in thickness of the internal and the external edge is not carried to such a degree as in Bovidæ and Horses, but is comparatively slight. The internal condyle is also a little thicker than the external.

The lower extremity (Plate XXXV. fig. 2) of the femur from Hempstead may belong to *Hyopotamus bovinus* by size: this last specimen was kindly lent me by the Museum of Practical Geology in Jermyn Street; it is figured of the natural size.

Dimensions of the Femur of *Hyopotamus*.

	Puy.	Hempstead.	Hempstead (Plate XXXV. fig. 2).
Length	283	?	Transverse breadth of the upper broken end ..36
Transverse breadth of the proximal extremity between the articular head and the great trochanter..	62	47	Antero-posterior depth.....25 Transverse breadth of the distal end .....61 Breadth of the rotular surface 26

The Tibia (Plate XXXVI. fig. 7).—I had for the study of this bone two nearly entire specimens from Hordwell, belonging to the large didactyle form *Diplopus*, and some incomplete upper and lower ends from Puy; these last undoubtedly from the tetradactyle *Hyopotamus*, as no *Diplopus* is found at Puy. The tibia of the *Diplopus* from Hordwell approaches very nearly in length to that of a Reindeer, showing that the two-toed *Diplopus* must have been very high on the hind legs, and the long metatarsals confirm this view. The general shape of this tibia is triangular from the upper part down to the distal extremity, and not so much rounded in the lower half as the tibia of the Suinæ. The crista anterior is not very high, with only a slight patellar depression on its fore part, much shallower than in Pigs. The shaft of the whole bone is very straight; the outer edge, facing the fibula, is exceedingly sharp, while the inner is more rounded. The distal end (fig. 7′) shows a very rectangular outline, with two straight deep grooves for the upper pulley of the astragalus. The inner distal process of the tibia, or the so-called inner malleolus, which holds the astragalus from the inner side, is much longer than in Suina, approaching more to the size it exhibits in most Ruminants, with the exception of *Tragulina*, as these last have an exceedingly short

inner malleolus. The outer distal edge is truncated somewhat obliquely, and has a groove in the middle for a corresponding convex ridge on the inner surface of the fibula, which fits the tibia in the same way as in Pigs, and being produced distally together with the internal malleolus, firmly clasps the astragalus (figs. 7 & 7′, Plate XXXVI.). The posterior surface of the upper half of the tibia is very flat, showing some oblique, rough bony ridges for muscular attachment.

The upper or proximal articular surface for the femur presented more resemblances to Suinæ than with Ruminantia, especially in the deep outer groove for the muscular tendon, though the patellar fossa on the fore part of the crista anterior is shallower than in *Sus*.

In the broken upper and lower halves of the tibiæ of *Hyopotamus* I find no difference from *Diplopus*, save that of size.

Dimensions of the Tibia.

	Diplopus (fig. 7, Plate XXXVI.).	*Hyopotamus.*	
	Hordwell.	Puy.	Hempstead.
Length	280	240	
Transverse breadth, proximal extremity	68	55	
Transverse breadth, distal end	43½	31½	36

The Fibula.—Before describing this bone in the *Hyopotamidæ*, we must call to mind the principal differences it shows in the two series of Paridigitata and Imparidigitata. The proximal end is wanting in all our specimens; but this is not of any consequence, as all the chief characters are presented especially by the distal extremity. In all Imparidigitata which possess a complete fibula, this bone is applied to the outer side of the tibia, forming at the distal extremity the malleolus externus (Plate XXXVI. fig. 7); this distal extremity is truncated obliquely in such a way that the inner surface of it articulates only with the astragalus, forming its outer boundary; the fibula can never touch the calcaneum*, as this bone has no special surface developed on its upper lateral part to receive the distal end of the fibula. On the contrary, in all Paridigitata the fibula being applied in the same way to the tibia, presents at its distal end *two* articular facets for the articulation with *two* tarsal bones. The inner surface of the fibula (Plate XXXVI. figs. 7 & 7′, and Plate XXXV. fig. 3, nat. size) is pressed against the astragalus; but its inferior extremity does not thin out, as in Imparidigitata, but is truncated at right angles, and provided with a special articular facet for an articulation with the outer wall of the calcaneum. We shall see hereafter that this outer wall exists perhaps also in the Imparidigitata, but that it is thrust under the astragalus; and this seems to be the cause why the fibula of the animals belonging to this series cannot articulate with the calcaneum.

* *Macrauchenia* seems to present the single exception to this rule. The calcaneum of *Macrauchenia* is not known.

The fibula of *Diplopus* (Plate XXXVI. fig. 7, and Plate XXXV. fig. 3) is shaped entirely in conformability with the Paridigitate type; it is a considerably reduced bone, with a very thin shaft; the distal extremity, however, is widened considerably in the antero-posterior direction. The inner surface of this broad (it would be more correct to say deep, as the fibula is widened from before backwards) distal extremity (Plate XXXV. fig. 3) is shaped on the same pattern as in the Suidæ, presenting a more uniform arched and slightly raised platform pressed against the astragalus, and not a deep semicircular notch as in Ruminantia. (In these the shaft of the fibula is generally mostly reduced to a mere tendon, but its lower extremity remains under the name of the so-called "*osselet péronéen.*") The articular end for the calcaneum (fig. 7′) presents a very deep and narrow facet, which occupies the whole antero-posterior extent of the distal extremity of the fibula. The anterior part of this calcaneal surface is slightly convex, the posterior concave.

I have found at Puy many distal extremities of the fibula, which belonged undoubtedly to *Hyopotamus*; and even this bone bore a great resemblance to the same part of *Diplopus*. This is another fact testifying to the very close relationship of both genera, notwithstanding the difference in the number of toes. A resemblance which holds good even in such slight details is a conclusive proof that both genera—the *Diplopus* from Hordwell and the *Hyopotamus* from Puy (and Hempstead)—belonged to the same family, and that one may be considered the reduced form of the other, notwithstanding the seemingly adverse fact that the reduced form is met with in the Upper Eocene, and the more complete in the Lower Miocene. This last certainly had Eocene ancestors, which may be considered to have given rise to the reduced form, while they continued to live themselves until the Miocene period.

Dimensions of Fibula, distal end.

	Diplopus (Plate XXXV. fig. 3, nat. size).
Antero-posterior diameter of the upper broken end..	8
Thickness of the same	4
Antero-posterior diameter of the distal end	29, 26½
Thickness of the same	9

General considerations on the carpal and tarsal, metacarpal and metatarsal bones in Hyopotamus, Diplopus, *and other Paridigitata.*

If, generally speaking, the long bones of the limbs in Ungulata often present but few characters decisive enough to tell us at once the natural series to which an Ungulate mammal belongs, the converse is the case with the smaller bones of the extremities, which have therefore a great systematic importance. We may very often know most of the long bones of the skeleton, the scapula, the humerus, the antibrachium, the tibia and fibula of a fossil Ungulate, without being able to determine quite certainly the natural series to which it belonged; nay, even more, we may discover the skull and the complete

dentition without being made much wiser by it. The history of palæontology swarms with such examples; but the discovery of a single carpal or tarsal bone very often clears the whole question, by showing in the most unmistakable manner the true affinities of a fossil form. Seeing this great importance of the carpal and tarsal, metacarpal and metatarsal bones, I feel obliged to enter into more minute details than I have done in the case of the long bones of the limbs; and I shall try to show how constant and important are the characters which we may derive from the study of these small bones, and what excellent data they may furnish towards a complete understanding of the development in time of the large and extensive group of modern Ungulata. As in one of my former memoirs* I tried to follow this course in reference to the Imparidigitata, I will confine myself in this paper only to the Paridigitate series. As the chief differences for subgeneric or specific division of the *Hyopotamidæ* are furnished by the bones of the feet, I shall describe these first, leaving the skull and the dental characters to be treated afterwards.

Although I found at the British Museum and in the private collection of M. Aymard at Puy very extensive materials for the restoration of the fore and hind feet, still it is to be regretted that as yet we have never found a complete fore or hind foot, in its natural connexion, belonging to the same individual; still less was there a chance of finding the bones associated in an undoubted manner with a certain set of teeth: all bones of the *Hyopotamus* occur very much scattered, and no complete skeleton belonging to one individual has ever been found, at least to my knowledge. The happy circumstances which enabled Cuvier to refer, without any doubt, certain sets of bones to certain skulls (as whole skeletons were sometimes found in the gypsum of Montmartre) did not favour my research. But if the actual connexion of specific bones and teeth should still remain not entirely cleared up, the general osteology of the genus will not in the least suffer by it; and with the materials I had at my disposal, I am conscious of being able to reconstruct both generic forms in a very satisfactory manner, though even for the carpus I had no complete set of bones belonging to one individual. But in certain series of animals the peculiar form and general relations of these bones are so constant, that we may expect variations only in the smallest particulars; so that the general structure of the feet and the mutual relation of the carpal and tarsal bones between themselves, and to the bones of the metacarpus and metatarsus, may be considered undoubtedly settled for the *Hyopotamidæ*. To make my description more clear to the reader, I will take care to make comparisons with animals accessible to every naturalist; and I think that for the full comprehension of the relations of these irregular bones drawings are wholly inadequate, and a direct comparison with the feet of a pig and a ruminant should be resorted to.

Notwithstanding the great external diversity of the recent Ungulata, taking both series of Paridigitata and Imparadigitata, where we meet with animals so different in their aspect, habits, and size, running through all the intermediate stages from a rabbit

* "Sur l'Anchitherium," Mém. Acad. St. Pétersbourg, 1873.

(*Hyrax*) to the largest Rhinoceros, Hippopotamus, or Giraffe, their osseous structure is exceedingly uniform and simple, presenting only two chief types, which are completely defined by the terms Paridigitata and Imparidigitata. Beginning with the oldest Eocene deposits, these two types are entirely separated by the structure of their skeleton, and we have not a single living or fossil form that could truly be considered a link between these two typically different series. I have little doubt that all Ungulates must have sprung from some common form; but if so, their division was effected in very ancient times, perhaps in the early Cretaceous period. I say *early*, because just at the close of the Cretaceous period, in the lignites of Soissons and the calcaire grossier, or in beds that are contemporaneous with them, we find large Mammalia of both series with a very reduced skeleton. Considering the rate at which the reduction of the limbs in Ungulates proceeded in the Eocene, Miocene, and Pliocene periods, we are obliged to grant a long time for the branching off of the two series of Ungulates from a common pentadactyle form, and the subsequent reduction of each branch to the three- and two-toed forms, met with in ancient Eocene beds.

In the recent period, notwithstanding the great diversity and very wide distribution of Ungulates, they present an extreme poverty of type. The Imparidigitate series is strikingly poor, not only in generic but also in specific forms; they go on evidently declining from the Eocene; and in the recent period we have only three different types of these animals—the *Equina*, *Rhinocerotina*, and *Tapirina*; and even these three present such a fundamental resemblance in the structure of their limbs and skeleton, that no reasonable doubt can be entertained as to their descent from a common progenitor. On the other hand, the Paridigitata, though presenting in the recent period an exceedingly great diversity of size and habits and a great variety of specific forms, outnumbering tenfold those of the Imparidigitata, present also only two distinct types, Ruminantia and Suina; and, even in these, the fundamental structure of the limbs and skeleton is so uniform that we may safely infer their descent from one common form. In the present memoir I have taken up only the second series, the Paridigitata; and I shall try to show, as clearly as possible, the common bond that holds them all together. I shall point out that the uniformity of this fundamental type adapted to different conditions of life is so great that, notwithstanding extreme diversity of size, difference of habits, aquatic or terrestrial life, we may trace through the whole complexity of these diversified forms not only the number and shape of their carpal and tarsal bones, but even each separate facet of these bones, and point it out as clearly in the reduced limb of a land Antelope as it is displayed in the complete unreduced limb of the aquatic Hippopotamus. Further, I shall try to show that this uniformity of type holds good, not only of the living, but also of the extinct forms of Paridigitata.

If we cast a glance on the first section of the fore foot, or the carpus, of any Paridigitate whose skeleton has not suffered too considerable a reduction (as for instance a Pig or Hippopotamus, Plate XXXVII. fig. 1), we shall find that it consists of two rows, containing seven small irregular bones, with an additional one (the

pisiform) on the outer end of the upper row. We find in the upper row, beginning from the inner side, the scaphoid, lunar, pyramidal, and pisiform; in the lower, trapezium, trapezoid, magnum, unciform. In all extinct Paridigitata, even those with a very reduced skeleton, we find the full number of these carpal bones (so in *Anoplotherium*, *Xiphodon*, *Hyopotamus*, Plate XXXVII. figs. 2, 3, 20); and, only in consequence of the still greater reduction of the limbs, in some recent Ungulata one of the carpal bones (the trapezium) seems to be entirely lost, while another (the trapezoid) becomes confluent with the magnum; that the trapezoid is not lost but is confluent with the os magnum, is shown by the two different points of ossification in the cartilage of the os magnum in young sheep. As we shall hereafter see, the number and shape of the carpal and tarsal bones of all animals belonging to the Paridigitate series present an extreme uniformity, individually as well as in their relation to one another and to the metacarpal and metatarsal bones; and this similarity is indeed so great that we cannot explain it in any other way than by community of descent. The extreme constancy in the relations of these bones in all Paridigitata being ascertained, the problem which is unavoidably presented to the mind of the observer may be stated thus:—Very irregular small bones, intended to constitute a movable articulation between the long bones of the extremity and the metatarsals and metacarpals, arranged themselves in a certain way in reference to one another and to these metacarpals and metatarsals; this arrangement remains the same in all Paridigitata, recent as well as fossil, notwithstanding the greatest diversity of form, size, and habits of life; and if some slight change is to be seen, it is due clearly to the overdevelopment of certain digits and consequent reduction of others; but in all cases the reason of change is at once apparent: how can such similarity in animals so entirely different be explained? To all naturalists who accept the gradual descent and differentiation of all Paridigitata from one common form, the fact must appear as a perfectly reasonable and intelligible one. If the immediate progenitor of the Paridigitates presented the given arrangement of the carpal and tarsal bones, then, at the gradual differentiation of this type, every small change in one bone called forth a corresponding change in all its neighbours. And as the link which connects all the forms together was never destroyed, and the changes were slowly going on, we meet now, in the extremely differentiated descendants, a unity of organization which was inevitable if all these forms descended from one common progenitor. But if, leaving the point of view of evolutionists, we look at the matter on the special-creation principle, this similarity of structure in animals so widely different is really an awkward fact. To the supporters of special creation the question presents itself in its simplest form thus:—We have now on the earth a large assemblage of Paridigitate mammals, presenting widely diversified generic and specific forms, fitted for the most different conditions of life, some leading an amphibious existence, sharing the large streams with Crocodiles, while others inhabit inaccessible rocks or burning sand plains, some heavy and sluggish, others light and swift, &c.; and yet the creative force, in calling separately into existence these diversified forms, made them all on one plan,

and this to such an extent that even the seven bones of the carpus and tarsus, notwithstanding their irregular shape, were always arranged in the same way, so that a certain facet of one bone always touched a certain particular facet of another, and never otherwise. That this could really occur in every separate case of creation, is almost as probable as that seven dice thrown out of a dice-box should give us the same number of points, similarly arranged in a hundred successive throws. Notwithstanding the thousands of different relations which might exist between such seven multangular bones, we get always only one; and in the whole range of living and extinct animals we see no exception to the common rule of typical arrangement of the carpal and tarsal bones. The point at issue is, can this uniformity be accounted for by the principle of special creation, or by the theory of descent and modification? No naturalist can in our time hesitate between the two; and while all the adduced facts are wholly inexplicable by the first theory, they seem most natural in the light of the second. We may still not be fully informed as to all the true causes which induced the variation and consequent differentiation of animal types; but the principle of descent must be conceded as the only one by which all future researches into the structure of the extinct world must be guided.

I have mentioned chiefly the carpal bones; but the study of the tarsus leads to precisely the same result, and the likeness of the tarsal bones in all Paridigitata is perhaps even more striking than that of the carpals. All Paridigitata have a calcaneum with a special facet for the fibula, an astragalus with a double pulley, a cuboid supporting the fourth and fifth digits, and a navicular, with three cuneiforms, for the support of the third and second digits; the first digit being always lost, its tarsal bone is gone to give support to the second toe, or, if this be lost, to the rudiment of it. We shall see these relations by-and-by, when we come to the special description of the tarsal and metatarsal bones.

The Carpus of Hyopotamus, *or the Four-toed Form.*

In describing the bones of the carpus of the *Hyopotamus*, I will try to confine my comparisons exclusively to the nearest living relatives of the extinct genus, as only such likeness and difference between nearly related forms belonging to one natural series can be of any immediate use for our purpose. Resemblances to the bones of animals belonging to other series are mostly only analogies, not homologies; and if some similarities which we may find to the carpal bones of animals belonging to the other natural series of Imparidigitates are of importance as testifying their common descent from some ancient form, still we lack so completely any links between these two series (which are entirely distinct from the oldest Eocene deposits) that it would be idle to speculate about their relation on such trifling characters as these. I will therefore as much as possible confine myself to the series of Paridigitata. The carpus of *Hyopotamus*, like that of all Paridigitata, consisted of eight typical bones, four in each row; of these eight bones I have only five, the trapezium, pisiform and magnum being absent from

all the collections I had an opportunity of studying; but their absence will not interfere much with the complete restoration of the fore foot.

The *scaphoid* (Plate XXXVIII. fig. 5, *s*) is not very different from the corresponding bone of the pig in its upper part; but the general form tends more towards the *Hippopotamus*. The proximal surface reminds us of the same surface of the *Anoplotherium* (Cuv. Oss. Foss. v. p. 217), and shows a very shallow platform, sloping radially; in correspondence with this, the inner part of the distal extremity of the radius (articulating with the scaphoid) is also very flat. In our recent Suidæ, this proximal facet of the scaphoid has a great rising on the fore part and a deep excavation behind; and, correspondingly, the extremity of the radius is more deeply excavated, and the interlocking of the two is firmer.

The distal surface of the scaphoid in the *Hyopotamus* is very distinct from the same surface in the pig, and reminds us more of what we see in *Hippopotamus*; namely, it is divided by an oblique ridge into two slightly concave facets, of which the radial or posterior facet articulates with the trapezoid (Plate XXXVIII. fig. 5, *t*), and the ulnar or anterior reposes on the os magnum (Plate XXXVIII. fig. 5 and Plate XXXVII. fig. 20), which being absent, its place is left blank in our figures.

The posterior extremity of the scaphoid is elongated into a thick recurved portion, which bends inside the carpus. The inner or ulnar surface exhibits nothing particular; its upper margin is occupied by a long narrow facet for articulation with the lunare. The outer free surface is uniformly rounded.

Dimensions.

Length antero-posteriorly . . .	30 millims.
Height	16 „

The scaphoid (from Hempstead) described above belongs to the tetradactyle form of the *Hyopotamidæ*, or to the genus *Hyopotamus*; but I have found in the collection of the British Museum another scaphoid bone (from Hordwell), which I may with great probability refer to the didactyle form called *Diplopus*. This scaphoid is very different from that just described; and all the differences point to a reduction of the foot. Its proximal surface does not slope outwards, but is perfectly horizontal, with a transverse rising in the fore part, a hollow in the middle, and an elevated posterior border; such a surface of the scaphoid ensured a firmer interlocking with the radius. It reminds one strikingly of the same surface in the *Anchitherium*; and it is possible that the distal end of the radius in the *Diplopus* was shaped on the Cameline type, which is very similar to that of a Horse or *Anchitherium*.

The distal surface is not divided into two facets, but is uniform, like the distal surface of the same bone of a pig; and this is very intelligible, seeing that the trapezoid, having no complete second toe to support (as in *Hyopotamus*), did not press on the distal surface of the scaphoid, leaving there such an impression as it did in *Hyopotamus*.

The *semilunar* (Plate XXXVIII. fig. 5, *e*, and Plate XXXVII. *l*).—I had several

lunar bones of different sizes from English deposits as well as from Puy. Those from the latter place agree entirely with smaller lunars from Hempstead; and we may safely infer that they belonged to the *Hyopotamus*.

In general shape the lunar has the same character as the same bone in other Paridigitata, especially the Suina—with this difference, that it is relatively much thinner and higher in *Hyopotamus*, as might be expected from the form of all the bones of the skeleton, showing that the Hyopotamidæ had a much more elegant and higher skeleton than our recent Suina. The proximal or upper surface of the lunar, which articulates with the outer half of the distal extremity of the radius, has a considerable rising in the fore part and an excavation behind; this upper surface, looking on it from above, has a very oblique direction inwards; this is effected in such a way that the radial upper margin of the lunar is pressed closely to the scaphoid, while there is a great interval between its upper ulnar margin and the pyramidale: a glance at the proximal surface of a pig's carpus will explain this disposition much better than long descriptions.

The distal surface of the lunar is prolonged into a prominent beak inserted between the os magnum and unciforme. This insertion of the lunar between the two principal bones of the lower row is a feature common to all Paridigitata; only in *Hippopotamus* (Plate XXXVII. fig. 1, *l*) the beak, owing to the squareness of all the bones, is much blunted; but it is very well seen in *Anoplotherium*, *Xiphodon* (Plate XXXVII. figs. 2 & 3, *l*), the Suina and Ruminantia. The beak is limited on both sides by two oblique facets, one radial for the os magnum, the other ulnar for the unciforme; a ridge running from the anterior point of the beak through the whole antero-posterior depth of the bone separates the two facets from one another. On the anterior half of the distal surface of the lunar, the ulnar facet for the unciforme is larger than the radial or os-magnum facet; but on the posterior half this relation of the two facets is inverse: this disposition is obviously an adaptation for the better interlocking of the carpals.

The posterior termination of the lunar is very like that of the lunar of the Suidæ: the lateral facets for the two adjoining bones show nothing particular; only the upper radial facet covers the whole upper and inner margin of the lunar, while the ulnar is only developed on the fore part, the ulnar side not touching the pyramidal in its middle and posterior part. I have, from Hempstead, a lunar bone much larger than the one described and figured by me in the restoration of the carpus (Plate XXXVIII. fig. 5); it may have belonged to the largest species, called *Hyopotamus bovinus*, although it looks too large for it; there is no difference in shape whatever.

Dimensions.

	Hyopotamus.	
	Hempstead.	Hempstead.
Height, anterior	19, 22	$27\frac{1}{2}$
Breadth, anterior	14, 17	20
Depth, antero-posterior	22, 22	$28\frac{1}{2}$

The unique specimen of the lunar I possess from Puy, although agreeing entirely with that from Hempstead, is somewhat too much crushed to admit of accurate measurements.

The *pyramidal* (Plate XXXVIII. fig. 5, *p*) has the shape which is so characteristic of it in all Paridigitata. We may remark, in reference to this bone, that it is the least changeable of all the carpal bones, its shape being very similar, even in animals of widely different families and even orders. For instance, it is very like in both Paridigitata and Imparidigitata; and a pyramidal of Rhinoceros is hardly to be distinguished from that of a Hippopotamus. We may suppose that, as this bone has a very similar function to perform in all Ungulata, it did not change its shape, while the other bones, more directly acted upon by the different condition of life, did.

The pyramidal of *Hyopotamus* presents therefore a certain likeness to that of an *Anoplotherium*, and also to that of a common hog; the chief distinction lies in the fact that all its edges are much sharper, and not so much blunted as in Suidæ; this applies particularly to the ridge separating the facet of the ulna from the facet for the pisiforme (Plate XXXVIII. fig. 5, *p*).

The distal surface, adapted to the outer proximal facet of the unciform, is shaped very much as in all other Paridigitata.

I have this bone only from Puy.

Dimensions.

Height	$18\frac{1}{8}$
Greatest antero-posterior depth	18
Breadth	12

The *pisiform* is wanting; it is, however, not a very important bone, partaking more of the character of a sesamoid than of a true carpal.

The *second row of the carpus*.—I could not find the trapezium in any collection, although a facet on the radial side of the trapezoid and the second metacarpal clearly show that it was present. As the first digit is always abortive in all living and fossil Ungulata, the trapezium, which is the true carpal bone of this digit, has lost all its importance. However, it is to be seen in *Hippopotamus* and *Anoplotherium* (Blainv. Ost. *Anopl.* pl. iii.), where it articulates with the posterior face of the trapezoid, and assists in holding the second metacarpal in *Hippopotamus*, or the rudiment of the second in *Anoplotherium*. It is present in the Suidæ (Plate XXXVII. fig. 4, *tz*); and I found it

also in *Phacochœrus* and *Babirussa*; it seems to hang only on the back part of the trapezoid (*t*), without touching the second metacarpal. The trapezium is very small in *Dicotyles* (Plate XXXVII. fig. 5, *tz*), and is entirely lost in ruminants, not being even present as a distinct point of ossification in the trapezoido-magnum cartilage. It is worthy of notice that, though the metatarsus in all Ungulata is always more reduced than the metacarpus, still the homologue of the trapezium (the first cuneiform) is often found in the pes when no trace of its homologue exists in the manus. So, for instance, in the Horse (coalesced with the second cuneiform) and most, if not all, Ruminants, in which the first cuneiform is present, while the trapezium is lost.

It is difficult to say if it existed in the *Diplopus*, seeing the reduction of its metacarpals to two; but as it exists in *Anoplotherium* there is no reason why it should be lost in the two-toed *Diplopus*.

The *trapezoid* (Plate XXXVIII. fig. 5, *t*).—I have this bone from Puy, belonging to *Hyopotamus* or the four-toed form. In considering only the shape of this trapezoid, without heeding the size, it is almost identical with the trapezoid of *Hippopotamus*; only its upper or proximal surface is more convex. The distal surface is deeper than it is broad, slightly concave, and fits exactly the proximal surface of the second metacarpal (Plate XXXVIII. fig. 5, *t*). On its radial side is seen a well-developed articular facet for the trapezium. If we compare this trapezoid with that of a pig (Plate XXXVII. fig. 4, *t*), we shall find a great difference, especially in the distal surface. In *Hyopotamus*, as well as in *Hippopotamus*, the trapezoid is destined to support only its typical metacarpal (the second), while in the Suidæ, owing to the larger development of the middle, and consequent reduction of the lateral metacarpals, one half of the distal surface of the trapezoid is taken by the third metacarpal, and only the remaining half supports the second (Plate XXXVII. fig. 4, *t*). In consequence of this, the distal surface of this bone in the true Suidæ, instead of being flat, is spear-shaped, with a sharp edge running through its whole antero-posterior depth. In *Dicotyles* (Plate XXXVII. fig. 5, *t*), where the reduction of the lateral metacarpals has gone still further, the distal surface of the trapezoid, being wholly taken by the third metacarpal, has resumed its flat form, thus resembling more the trapezoid the *Hyopotamus* than that of the pig. But notwithstanding this similarity, the part played by this bone in *Dicotyles* and *Hyopotamus* is wholly different; and while in the first it has no connexion with the second metacarpal, in the last it is entirely connected with it, and gives no facet to the third metacarpal.

Dimensions.

Height	$10\frac{1}{2}$
Breadth, inf.	8
Antero-posterior depth . . .	15

Unfortunately the *os maynum* is wanting in all the collections I have visited; but the interval included between the surrounding bones gives an idea of its shape, which

certainly must have approached that of *Anoplotherium*. I pass on to the most important of the bones of the second row—the *unciform*.

Happily we are very well off as to this bone, there being some excellently preserved specimens from Puy. The shape of this bone and its connexion with the adjoining parts present considerable interest.

The *unciform* of *Hyopotamus* (Plate XXXVIII. fig. 5 *u*, fig. 7) presents some likeness to the same bone of *Anoplotherium* and also of *Sus*; but nevertheless its differences from both, especially the last, are numerous. Comparing the front view of fig. 5 and the view of the distal surface (fig. 7) with the corresponding aspects of the unciform of *Anoplotherium* in CUVIER (plate 102, fig. ii. A 2 & 3), we shall see that they present many features in common in both genera; I shall add that in CUVIER'S figure (A 3), the letter *k* corresponds with our III., the letter *h* with our IV., and the letter *i* with our V.*

Looking at the bone from above or in front (Plate XXXVIII. fig. 5, *u*), we see that its radial facet articulates with the outer face of the lunar bone, while its ulnar facet is occupied by the pyramidal. The facet for the pyramidal is larger than that for the lunar, both in *Hyopotamus* and *Anoplotherium* (Plate XXXVIII. fig. 5, *u*, and Plate XXXVII. fig. 2, *u*), while it is just the reverse in *Sus*, where the lunar facet of the unciform is much larger than the pyramidal facet. Both facets are divided by a pretty prominent ridge. The whole bone is relatively higher than in *Anoplotherium*, in correspondence with the lighter and more elegant stature of the *Hyopotamus*.

The distal articular surface is shown in Plate XXXVIII. fig. 7, and may be compared with the same aspect of the unciform of *Anoplotherium* (CUV. pl. 102. fig. ii. A 3). We find on our bone the same facets; only their relative development is different. III. is the radial inferior facet, giving articulation to the prolonged beak of the third metacarpal (*k* in CUVIER); IV. is the middle, principal, or central facet, articulating with the fourth metacarpal (*h* in CUVIER); outside from it is seen another smaller, facet (V.) for the lateral or fifth digit (CUV. *i*)†; and we see just the same in the Suidæ, which have a complete fifth digit, and in *Anoplotherium*, where there is only a rudiment of it. In *Hyopotamus* and *Hippopotamus* (Plate XXXVII. fig. 1), however, owing to the greater development of the fifth metacarpal, this facet is not pressed so much backwards and upwards as in the pigs; in the living *Hippopotamus* it is entirely on the same level with the facet for the fourth metacarpal (Plate XXXVII. fig. 1, *u*).

* In CUVIER the bone is turned in an opposite direction, though it is from the same side, the left.

† CUVIER (Oss. Foss. 4th ed. vol. v. p. 425), describing this facet *i* as supporting the rudiment of the fifth toe, adds, "On n'en trouve l'analogue ni dans le bœuf, ni dans le cochon, ni dans le Tapir, &c." It is certainly not found in *Bos*, as the Ox has no rudiment of the fifth toe; but it is always to be found in the Suidæ as well as in the Tapir, both these having a completely developed fifth toe, which is articulated to the homologue of this facet. In all Mammalia, without exception, the unciform supports the fourth and fifth metacarpals; therefore in all mammals both these facets are homologous, whether they support completely developed toes or only rudiments of such, as in *Anoplotherium*.

In examining the radial side of the unciform of *Hyopotamus* we shall see that the upper lunar facet of this bone nearly meets the lower facet (Plate XXXVIII. fig. 7), the two being separated merely by a ridge*, while in *Anoplotherium* (Plate XXXVII. fig. 2, *u*, and Cuv. plate 102. fig. ii. A 5 *m*) these two facets are separated by a vertical facet, which articulates with the neighbouring os magnum. In the *Suidæ* this facet is exceedingly developed, and the homologue of the lower facet III. (Plate XXXVII. fig. 7) is confluent with it in such a way that both together (*k*+*m*, Cuvier, Oss. Foss. pl. 102. fig. ii. A 5) form the radial high and perpendicular border of the pig's unciform; at the upper part of this perpendicular border abuts the os magnum, at the lower the beak-like projection of the third metacarpal; this last projection, therefore, is more horizontal in Suidæ, and not so oblique as in *Anoplotherium* and *Hyopotamus*. The posterior projection of the unciforme is tolerably broad and well developed, as is seen in Plate XXXVIII. fig. 7.

Dimensions.

	Unciform from Puy.	Unciform from Hempstead (fig. 9).
Transverse breadth	22	17
Depth, antero-posterior . . .	22½	17
Height	17	12

I had already completed this description when I received unexpectedly, through the kindness of Mr. Davies, sen., of the British Museum, two carpal bones from the Museum in Cambridge. On examination both proved to be unciforms. One of them (Plate XXXVIII. fig. 9 & 9′) corresponded very closely to our unciform from Puy, being, however, much smaller; it may have belonged to some of the smaller *Hyopotami*, whose metacarpals, corresponding entirely in shape with those from Puy, are often found at Hempstead. This small unciform is figured in Plate XXXVIII. fig. 9, front view, 9′ the distal surface; it is from the left side, like the corresponding one (figs. 5 & 7) from Puy. Its distal articular surface (Plate XXXVIII. fig. 9′) has three facets—one for the beak-like projection of the third metacarpal, a central one for the fourth metacarpal, and an outer (v.) for the metacarpal of the small or fifth digit. The posterior part of this small unciform is drawn out into a tolerably broad backward projection.

The second of the two unciforms received from Cambridge was found at Hordwell; it proved a most valuable addition to my materials, as, after a careful study, I arrived at the conclusion that it undoubtedly belonged to the large didactyle form referred by me to the genus *Diplopus* with the specific name *Aymardi*. Figs. 8 & 8′, Plate XXXVIII. give a front and a distal view of this interesting bone. Comparing it with the same bone from Puy, or the small one from Hempstead, we are at once struck by their difference. The front view, in consequence of the large development of the inferior radial angle, presents a much squarer outline; the inner vertical wall of the bone has become much

* This makes the *Hyopotamus* unciform look exceedingly like that of a *Palæotherium crassum*; but this similarity is only superficial, as the distal surface and the posterior beak are very different from what we see in Palæotheridæ.

higher, reminding one precisely of what is seen in *Sus*, and even more so in *Hyomoschus*. The distal surface (Plate XXXVIII. fig. 8′) is also very different. The facet for the third metacarpal, instead of being oblique as in the bone figs. 5 & 7, *u*, Plate XXXVIII. (where it forms an oblique truncature of the inferior radial angle on the unciform), has gone over to the inner or radial vertical wall of the bone, forming a facet homologous to that of the Hog, composed of the facets *k*+*m* of the *Anoplotherium* (CUVIER, pl. 102. fig. ii. A 5). In consequence of this the beak-like projection of the third metacarpal in the two-toed form is more horizontal (Plate XXXVIII. fig. 6, III.) than in the four-toed form (fig. 5, III.), approaching what is presented by the *Suidæ*. The distal surface (fig. 8′) shows no trace of the outer facet for the fifth metacarpal, and is entirely taken up by the greatly enlarged facet of the fourth; and the margin of this facet is so sharp that it is evident that the rudiment of the fifth metacarpal (whose existence is proved by a facet on the outer side of the fourth metacarpal) did not touch the unciform, confining itself to the lateral upper facet of the fourth metacarpal.

The *posterior* projection of the unciform (fig. 8′) is very much broadened, so that the whole distal surface acquires a somewhat square outline; but what is more interesting, the inner or radial inferior margin of this projection has a large round facet* by which it articulated posteriorly with the os magnum. We never meet with such an enlargement of the posterior par tof the unciform in the true *Suidæ*, as in these the posterior and inferior parts of the unciform and magnum do not articulate together. Such an enlargement, however, is seen in *Dicotyles*, where the unciform sometimes touches the magnum, while in *Hyomoschus* we see, on the inner side of the same posterior enlargement of the unciform, a round facet for the magnum; this facet is also very characteristic of the unciform of all true ruminants. The reason of this closer articulation between the magnum and unciform seems to lie in the reduction of the lateral metacarpals, which caused the carpal bones to concentrate more towards the central part of the carpus.

The proximal, or upper, surface of this unciform is also much broader and flatter than in the four-toed form, both facets for the lunar and pyramidal being more on one plane. These two facets are very nearly equal in size, not as in the Pig, where the lunar facet is much longer and broader than the facet for the pyramidal.

Dimensions.

	Unciform of *Diplopus*, from Hordwell.
Transverse breadth	21½
Antero-posterior depth	21
Height	19

Tarsus of Diplopus *and* Hyopotamus.

The general structure of the tarsus in the Hyopotamidæ is quite conformable to the typical structure shown by all Paridigitata; and, in considering the shape of each of its constituent bones, I shall point out the features in which it resembles, or differs from,

* This facet is seen in fig. 8′ from below, as a projection of the posterior and inner margin of the bone.

the other representatives of the same order. Fortunately the bones of the tarsus are much more numerous than the carpal bones both at Puy and in England; and I have been enabled to restore it completely, with the exception of the first cuneiform, which is wanting.

Calcaneum (Plate XXXV. fig. 4, Plate XXXVII. fig. 21, *c*).—This bone presents a remarkably uniform shape through the whole range of Paridigitata; in *Hyopotamus* (Plate XXXVII. fig. 21, *c*) and *Diplopus* (Plate XXXV. fig. 4) it is very similar to the calcaneum of a pig. Owing to this uniformity of the calcaneum in the Paridigitata, we must extend our comparison to the other series, or Imparidigitata, if we intend to find out what are really the characteristic and essential features of a Paridigitate calcaneum.

The general shape of the calcaneum in the entire order of Ungulata is, on a cursory glance, very similar; indeed, to find the typical differences we must enter into a deeper analysis of the bone in question. If we put before us some calcanea belonging to animals of the Imparidigitate series, for instance that of a *Palæotherium*, Tapir, Rhinoceros, or Horse, and try to compare them with those figured in our plates, or, still better, with the calcaneum of a Pig *in naturâ*, we shall immediately see that in the first* the upper and outer edge of the calcaneum, where it bends down to enlarge into the *sustentaculum*, forms a large articular projection (fig. 4′, *e*), which enters below and behind the external pulley of the astralagus; to the inner side of this articular facet we have the *sulcus sustentaculi* (fig. 4′, *s*), and, on the other side of this sulcus, another large articular oblong internal facet for the astragalus (fig. 4′, *i*). In correspondence with this, the posterior part of the astragalus of all Imparidigitata presents two large principal facets for the calcaneum—an outer facet, under the outer pulley, and an inner oblong facet.

Looking now, with a view to a strict comparison, at the same upper edge of the calcaneum of a Paridigitate (Plate XXXV. fig. 4; Plate XXXVII. fig. 21), we see that, at the point where the anterior edge bends down into the *sustentaculum*, it is divided into two parts by the *sulcus sustentaculi*; the external part, being the direct prolongation of the anterior edge, forms a prominent articular facet for the fibula (Plate XXXV. fig. 4, *ff*); the inner part, being situated on the sustentaculum proper, gives a large single facet for the posterior part of the astragalus (*as*). Considering these two facets in reference to the sulcus sustentaculi, I thought that the outer astragalean facet of the calcaneum of the Imparidigitata (*e*, fig. 4′) ought to be homologized with the fibular facet of the calcaneum of the Paridigitata (fig. 4, *ff*), and the inner oblong astragalean facet of the calcaneum of Imparidigitata (*i*, fig. 4′) with the single astragalean facet on the sustentaculum of Paridigitata. Comparing *in naturâ* the calcaneum of a pig and a horse, this is the view which seems most natural: it looks quite as if the outer astragalean facet of the Horse's calcaneum, instead of being buried under the outer pulley

* To make my comparisons better understood I figure the front view of an Imparidigitate calcaneum (Plate XXXV. fig. 4′); it belongs to *Anchitherium*. The calcaneum (Plate XXXV. fig. 4′) is a left one, while the two calcanea (Plate XXXV. fig. 4 and Plate XXXVII. fig. 21) are right.

of the astragalus, had got to the outside of it, and were articulated with the fibula. Such a view of this homology is still more strengthened if we consider the relation between the two bones in *Anoplotherium* (Plate XXXVII. fig. 11, and De Blainville, *Anopl.* iv.); in this animal the fibular facet of the calcaneum is still covered by a process of the astragalus; it seems as if it were just one of the stages of the progressive march of the fibular process from under the outer pulley to the outer side of the astragalus.

As all *Imparidigitata* have *two* chief astragalean facets on their calcaneum (Plate XXXV. fig. 4′, *e* and *i*), and no facet for the fibula, and as all *Paridigitata* having a fibular facet on their calcaneum (fig. 4, *ff*) have only *one* chief astragalean facet, it seems natural to say that the second (external) astragalean facet of the Imparidigitate calcaneum is not lost in the Paridigitata, but has been made use of for the formation of the fibular facet. But there seems to exist an objection to this view; and it is furnished by the *Macrauchenia*, the strange South-American form, which seems really to be a sort of Imparidigitate Camel. The calcaneum of *Macrauchenia*, however, is *not known*; but the astragalus figured by Professor Owen in the 'Zoology of the Voyage of the Beagle' (plate xiv. fig. 4) clearly shows that there were two principal facets for the calcaneum, as in all typical Imparidigitata. Now the fibula has also on its distal extremity an articular facet for the calcaneum*; and this facet presupposes unerringly a similar fibular process on the calcaneum, as it exists in the Paridigitata. If this should be really the case, then the existence of two astragalean facets and a third fibular one will perhaps invalidate the view as to the homology explained above, and it would in this case stand thus:—that the single large astragalean facet in the calcaneum of the Paridigitata is homologous to *both* facets of the Imparidigitata (*e*+*i*, fig. 4′), the fibular facet of the former being a new superadded character, not found in any of our living or fossil Imparidigitata, but exhibited by the South-American *Macrauchenia*. So that, even with the large material in our hands we cannot quite certainly determine the homology of different parts of such an important bone as the calcaneum in both the chief series of Ungulata; and as we have no forms linking these two typically different calcanea together, this is one proof more of the very ancient separation of this order into its two principal groups.

The calcaneum of *Hyopotamus* (figured in ½ nat. size, Plate XXXVIII. fig. 21) and of *Diplopus Aymardi* (Plate XXXV. fig. 4, nat. size) resembles very much that of a pig, with some slight differences. The sulcus which divides the fibular facet (*ff*) from the astragalean is very deep; this last facet has a slight angular rising or ridge nearer to its inner border, which fits into a corresponding slight depression in the posterior (calcaneal) surface of the astragalus; besides, as in all Ungulata, there is, at the inferior and inner border of the processus anterior, a smooth and large surface (Plate XXXV. fig. 4, *a s*) by means of which the inner wall of the calcaneum fits to the outer border of the inferior pulley of the astragalus. The fibular process (*ff*) is not so high, but much deeper antero-posteriorly than in the Suina; and we have seen that the distal extremity of the fibula is also extended in the same direction. The inner surface of the fibular

* Voyage of the Beagle, p. 51.

process is very smooth, without the large prominence we see in pigs, where it enters deeply into the external wall of the astragalus. The inferior surface of the processus anterior is occupied by one tolerably broad facet for the cuboid (Plate XXXV. fig. 4, *cb*).

On the posterior surface of the thickened back end is seen a groove for the tendon of the musculus plantaris, which, as in all Ungulata, was certainly developed as a flexor digitorum; this groove is shallower than in the Suina.

Dimensions of Calcaneum.

	Hyopotamus, from Puy.	*Diplopus*, from Hordwell (Plate XXXV. fig. 4).
Length	95	96
Height at the fibular facet	37	47
Length of the processus anterior	34	40
Greatest breadth	22	23½

The *astragalus* (Plate XXXVII. fig. 21).—This is an extremely characteristic bone for determining the natural affinitiesof Ungulata; in *Diplopus* it is very nearly like as in *Hyopotamus*, and conforms to the general shape of this bone through the whole range of Paridigitata. It has a double pulley—a proximal one, fitting the distal ends of the tibia and fibula, and a distal pulley fitting the navicular and cuboid. In all Imparidigitata the astragalus has only one pulley, on its upper or proximal end, while the lower or distal is flattened, though articulating with the same two bones. (In *Macrauchenia* and in the Horse, the distal surface of the astragalus articulates only with the navicular bone.) This character of the astragalus is one of the best by which to distinguish at a glance the two series of Ungulata; and we know of no living or fossil animal which presents an astragalus linking these two divisions together. True, in the astragalus of *Hippopotamus* (Plate XXXVII. fig. 9, *a*), owing to the broadness and thickness of all the tarsal bones, the inferior pulley is so exceedingly low that it reminds one of the same distal surface of the astragalus in *Rhinoceros* (see De Blainville's plates); but this likeness seems to be only an analogical one, both animals having heavy tarsal bones adapted very nearly to the same function.

Although extremely like in general shape to the astragalus of a pig, that of the *Hyopotamus* is proportionately much higher, the distal and proximal pulleys being divided by a larger interval than in the Suidæ. That part of the distal pulley which fits the cuboid is perhaps produced a little more downwards than in the Suina, though the difference is very slight. In comparing the large astragali of the didactyle *Diplopus* with the smaller ones of *Hyopotamus*, we find very few differences indeed; but it may be mentioned that the proximal pulley of the two-toed form is relatively a little higher and enters more deeply into the distal end of the tibia (Plate XXXVI. fig. 7), which may be due to the greater narrowness of the reduced foot, requiring a more close articulation with the tibia.

Dimensions.

	Hyopotamus.		*Diplopus Aymardi.*
	Puy.	Hempstead.	Hordwell.
Length, tibial side	40 , 47	44, 43, 40	52
Length, fibular side	44½, 52	50, 50, 45	55½
Anterior breadth in the middle	21 , 29	25, 24, 23	28½
Transverse breadth, proximal pulley	23½, 27	26, 26, 23½	26½
Transverse breadth, distal pulley	24½, 30	28, 28	29

The *cuboid* (Plate XXXVIII. figs. 1, 3, 10, 11).—I have examined numerous and well-preserved specimens of this bone from Puy, Hempstead, and Hordwell; the cuboids from Puy and Hempstead (figs. 1, 10) clearly indicate the four-toed form called *Hyopotamus*, while the bones from Hordwell (figs. 3, 11) belonging to the genus called by me *Diplopus*, indicate, in the most unmistakable manner, that in this last animal the foot was didactyle, as the inferior surface of the cuboid shows no trace of a facet for a fifth digit as in *Hyopotamus*.

As the cuboid is one of the most important bones of the tarsus, I will give a detailed description of it, with as many figures as I can afford; but should the reader take a cuboid of a hog *in naturâ*, then many points that are difficult to explain by words will at once be plain to him.

I will begin, as I have nearly always done, with the description of the cuboid of *Hyopotamus* (Plate XXXVIII. figs. 1, 10), and afterwards compare it with that of the *Diplopus* (figs. 3, 11). As in all Paridigitata, which have the navicular and cuboid distinct, the front face of the cuboid of *Hyopotamus* is cut out *en équerre* (Cuv.); this is brought about by the circumstance that the cuboid articulates with two bones of the first row of the tarsus, the calcaneum and astragalus; and the facets for these two bones lie in different levels, the rounded crescentic facet for the outer half of the distal pulley of the astragalus rising in front, while the facet for the processus anterior calcanei presents a flat surface sloping forwards, as is plainly to be seen in the figures (fig. 1 *cl* and *as*). *The upper* or *proximal* surface of the cuboid is occupied entirely by these two facets, one internal, shaped like a concave crescent for the astragalus, the other external, like a convex sloping surface for the calcaneum. The proximal surface of a hog's cuboid shows the same facets; only the external one is often cut transversely in two by a rough deep notch for the passage of vessels and ligaments: this division of the astragalean facet of the cuboid is nearly constant in the Hog and *Dicotyles*, though I did not find it in *Phacochœrus* and *Babirussa*. The relations between the transverse breadth of the two proximal facets vary in different genera. In *Anoplotherium*, the calcaneal facet is much broader than the astragalean (Plate XXXVII. fig. 11); but in *Hippopotamus* and *Hyopotamus* the relation is reversed, while in most Suidæ both facets are very nearly of equal breadth.

The *internal wall* of the cuboid shows on its upper margin a small facet for the neighbouring navicular, and a little lower a very small rising which corresponds to the

nterval between the distal surface of the navicular and proximal of the great or third cuneiform; the rising was very slight on our specimen, and is only imperfectly seen in the drawing. On the posterior part of the inner wall we see two facets divided by a groove for the external and posterior part of the navicular (in the Hog these *two* facets have coalesced into an elongated *single* facet on the posterior border of the inner wall of the cuboid). This posterior margin of the internal wall shows in *Hyopotamus* a considerable bulging inwards, into the middle of the tarsus (seen in Plate XXXVIII. fig. 10), which makes this cuboid much broader than the corresponding bone of the *Diplopus* (fig. 11), where this bulging is much less, nearly identical with that of a hog's cuboid.

The *outer surface* of the cuboid is rounded. If we look at the external surface of the cuboid of a hog we shall see a deep sulcus for the peronæus tendon situated between the posterior prolongation of the cuboid and the distal articular facet; this sulcus is absent in *Hyopotamus*, owing to the fact that the posterior part of the cuboid is not produced downwards, as we shall immediately see. The *posterior* surface of the cuboid is considerably broader than the anterior, as is to be seen in fig. 10, while in *Diplopus* (fig. 11), and especially in the Hog, the converse is the case. Besides, looking at the cuboid from the posterior aspect, we perceive a very broad and rough transverse ridge for muscular and ligamentous attachment, running through the whole breadth of the bone as it is seen in fig. 10 from below. The *Anoplotherium* and the *Hippopotamus* have nearly the same transverse ridge on the back part of the cuboid; only it descends lower down, while in *Hyopotamus* this ridge does not reach the level of the distal articular surface of the cuboid, which is the lowest point of the bone; we shall by-and-by indicate the difference presented in this respect by the cuboid of *Diplopus*.

The *distal* surface (Plate XXXVIII. fig. 10) is the most important, as it presents the articular facets for the two outer metatarsals. Not only in Ungulates but in *all* recent and fossil Mammalia the cuboid of the tarsus, as well as its homologue (the unciform) in the carpus, gives an attachment to the two outer metatarsals and metacarpals of the foot (the fourth and fifth) if they are not entirely reduced. In looking at the distal surface of the cuboid in *Hippopotamus*, we shall perceive a large central facet for the fourth metatarsal, and outwards from this another good-sized facet for the well-developed fifth metatarsal. In the common Hog, nearly the whole distal surface of the cuboid is taken up by the much developed fourth metatarsal; but still there exists at the outer part of this large facet a smaller and oblique facet for the still functionally developed fifth digit. In *Dicotyles*, where the fifth digit is lost, or only a short rudimental metatarsal of it remains, the whole distal surface of the cuboid is taken up by the fourth metatarsal, the rudiment of the fifth being only attached to the outer side of the fourth metatarsal, without touching the cuboid (De Blainville, *Sus*, plate vii. *Dicot. labiatus*, lowest left figure). In the *Anoplotherium commune*, as well as in *A. tridactylum*, there is not the slightest trace of a facet for a rudimentary fifth digit; but in *Xiphodon*, which also has only two developed metatarsals, we have on the distal surface of the cuboid a large facet for the fourth metatarsal, and an outer small facet for the rudiment of the fifth, which certainly existed, as the outer border of the fourth metatarsal

has also a small facet, to which this rudiment was attached (CUVIER does not mention this, as he treats both *Dichobune* and *Xiphodon* very briefly). This additional facet for the rudiment of the fifth metatarsal is to be seen in DE BLAINVILLE (*Anopl.* plate v.); it certainly existed in *Dichobune* and *Cainotherium*, as both have a completely developed fifth digit in the *pes* and *manus*.

Now, looking at the distal surface of the cuboid of *Hyopotamus* (Plate XXXVIII. fig. 10), we clearly perceive two large articular facets (IV. & V.) nearly in the same mutual relation as in *Hippopotamus*; the two facets are numbered IV. and V. in correspondence with the metatarsals they support; and their outline corresponds very nearly with the proximal surfaces of these two metatarsals (Plate XXXVIII. fig. 1, IV., V.). The inner border of the facet IV. is convex, the outer (near the ridge that separates the two facets) concave; and corresponding to this the inner border of the fourth metatarsal is concave, and the outer convex, to fit the cuboid. The facet V. is a little convex and triangular; and the metatarsal V. is shaped in a corresponding manner.

Besides the cuboid figured from Puy, I had a smaller cuboid from Hempstead, with two facets on its distal surface for the fourth and fifth metatarsals, and another from the same locality much larger than the Puy specimen, but corresponding closely with it; unhappily this last large specimen is much rolled, and the articular facets are not quite distinct.

If we compare with the cuboid just described the same bone from a nearly complete foot found at Hordwell (Plate XXXVIII. figs. 3, 4, and, distal view, 11) belonging to the *Diplopus*, or the two-toed form of this family, we shall see important differences which must clear away any possible doubt as to the number of digits in the genus *Diplopus*. The front view of the cuboid, fig. 3, shows it to be a little narrower than the same bone in its smaller but four-toed congener; and this is especially the case if we compare the posterior parts of both bones, as seen in figs. 10 and 11. On the inner wall, the middle anterior rising which enters into the interval between the navicular and third cuneiform is more distinctly developed, as seen in fig. 3; the rising, with a facet for the distal surface of the navicular, on the posterior border of the cuboid, is not so thick and not produced so much inwards as in *Hyopotamus*, but repeats entirely the arrangement seen in the Hog.

The external surface is more hog-like in appearance, and differs from the same surface of *Hyopotamus* by the presence of a deep sulcus (fig. 11) between the distal articular facet and the posterior prolongation (fig. 11, *f.my*), which, in this genus, is produced much lower down than in *Hyopotamus*. Instead of the broad transverse ridge seen on the posterior surface of the cuboid in the *Hyopotamus* (fig. 10, *tr*), the cuboid of the two-toed *Diplopus* has this ridge prolonged downwards in a beak-like process quite of the same shape as in the common Hog (fig. 4, *b.cb*). This posterior beak descends lower down than the distal articular surface of the cuboid, and exhibits on its inner side an elongated facet (fig. 11, *f.my*) by which this beak articulates with a corresponding cuboid facet on the outer side of the posterior prolongation of the fourth metatarsal (fig. 4″, IV. *cb.f*). This articulation is observable, though imperfectly, in fig. 4, where the beak of the cuboid (*b.cb*) is seen descending on the other side of the fourth metatarsal. In my

specimens of *Hyopotamus* from Puy the posterior prolongation of the fourth metatarsal is not well preserved (Plate XXXVIII. fig. 2′, IV.); but as there is no downward prolongation in the cuboid and no facet, the cuboid seems not to have articulated with this posterior prolongation of the fourth metatarsal, and it does not so articulate in *Anoplotherium* and *Hippopotamus*. In the Hog the relations are just the same as in the didactyle *Diplopus*; only this beak has on its outer side another small facet, for the posterior prolongation of the outer or *fifth* metatarsal—which is wanting in *Diplopus*, and, though present in *Hyopotamus*, has no such posterior prolongation as in the Hog. A glance at a hog's tarsus will make all this much clearer.

The *distal* surface of the cuboid in *Diplopus* (Plate XXXVIII. fig. 11) is entirely taken up by a single large facet for the fourth metatarsal, leaving no place at all for an additional digit as in fig. 10, though a rudiment of such fifth digit certainly existed, as is proved by a small facet on the outer border of the fourth metatarsal, to which this rudiment was undoubtedly attached, without ascending, however, so far as to touch the cuboid.

All these differences clearly indicate that the Hyopotamoid form to which this cuboid (fig. 11) belonged had no fifth metatarsal, but only a rudiment of it; we have seen the same thing in the manus, where the unciform, instead of supporting two toes, is shown by the distal articular facets to have supported only one (the fourth) while a rudiment of the fifth, indicated by an external facet of the upper border of the fourth metacarpal, did not reach the unciform and left no trace upon it.

Dimensions of the Cuboid.

	Hyopotamus, from Puy (Plate XXXVIII. figs. 1, 10).	*Hyopotamus*, from Hempstead.	*Diplopus*, from Hordwell (Plate XXXVIII. figs. 3, 11).
Height, anterior	26	19, 31	23
Breadth, upper part	21	17, 24	19
Breadth, inferior, on the distal surface	18	15, 21	16½
Antero-posterior depth	25	25, 28½	25

The *navicular* (Plate XXXVIII. figs. 1–4, *n*).—This bone is nearly identical in both genera, and has the same general shape as in all Paridigitata, in which the navicular is separate from the cuboid. The upper or proximal surface is entirely the same as in the Hog, except that the middle rising which fits into the groove of the distal pulley of the astragalus is more rounded. The inner (fibular) surface has, on the anterior and posterior part, facets corresponding with those already described on the tibial side of the cuboid. The posterior termination is rounded and only moderately produced downwards (as seen in figs. 2 and 4), without such large beak-like prolongation as is seen on the posterior side of the navicular of a hog (Plate XXXVII. fig. 12, *n*) or *Dicotyles* (fig. 13, *n*).

The *distal* surface is the most important one, as it supports the three cuneiform bones, which carry the digits. All the anterior part of the distal surface of the navicular is

occupied by a broad facet for the great or third cuneiform, which supports the third metatarsal. I have not figured the distal extemity of the navicular; but, by looking at the distal surface of the *Anoplotherium* navicular (Plate XXXVII. fig. 17) or that of a hog, the reader may form a correct idea of it. This facet is much narrowed in its posterior part, and then expands slightly again, forming a small facet for the *second cuneiform*; behind this there is a slight sharp ridge, which is seen tolerably well in the side view, fig. 4, Plate XXXVIII., as well as on a navicular of the Hog (Plate XXXVII. figs. 12, 13, *n*); behind this ridge is the facet for the first cuneiform. This last facet is concave on some of the naviculars of *Hyopotamus*, and convex on the two others belonging undoubtedly to the two-toed *Diplopus*; whether the difference was constant I cannot tell without ampler materials. I find no essential differences in the shape of the navicular bone in the two genera; and my description, made from good specimens of the *Diplopus*, may apply to the *Hyopotamus* also; of this last I had only one, not quite perfect, specimen of navicular from Puy.

Navicular of the Tarsus.

	Hyopotamus. from Puy.	*Diplopus*, from Hordwell.
Anterior height	11	$12\frac{1}{2}$, 14
Breadth, proximal face	$15\frac{1}{2}$	15, 17
Depth, antero-posterior	24	26, 30
Breadth, distal surface	14	$14\frac{1}{2}$, 20

The *cuneiforms* (Plate XXXVIII. figs. 1–4, c^3).—These are small but very important bones, on account of their relation to the digits which they have to support. The second row of the tarsus, containing the three cuneiforms and the cuboid, exhibits very clearly the complete homology of the fore and hind limbs. As in the complete manus we have in the second row of the carpus three distinct bones (the trapezium, trapezoideum, and magnum), each supporting a separate toe, and one external bone, the unciforme, giving support to the two outer digits (the fourth and fifth), so in the pes we perceive also an entirely homologous set of three cuneiforms (first, second, and third), each supporting a separate toe, and one external bone, the cuboid, giving support to the two outer digits of the pes (the fourth and fifth). Where all the five digits are completely developed this rule admits of no exception whatever in the whole range of Mammalia; but where, as in Ungulata, the number of the digits becomes sometimes greatly reduced, the relation of the carpal and tarsal bones to the remaining digits is slightly changed, though all the three cuneiforms are still retained, and I know of no instance where one of them is wanting. This persistence of cuneiforms is a strange fact; for in the carpus, which is generally less reduced than the tarsus, the trapezium (homologue of the first cuneiform) is certainly lost in Horses and Ruminants, while its homologue in the tarsus is still retained in a recognizable state. These relations, slight as they may seem, are important; we must know all the details and the true homology of the

smallest bones to establish clear lines of descent. I shall be obliged to discuss the question of the cuneiforms again when I come to describe the metatarsals, and will confine myself in this place to a general review of them in the Paridigitata, and a special description of these bones in *Hyopotamus* and *Diplopus*. As the *Hippopotamus* is the most complete of the living Paridigitata, we see in the side view of its tarsus (Plate XXXVII. fig. 10) all the three bones (c^1, c^2, c^3) fully developed; but as the first digit is aborted, its typical tarsal bone, the first cuneiform (c_1), gives additional support to the second digit. Each of the two inner digits (the third and second) are supported by a separate cuneiform. We see besides, in this side view of the tarsus, that the second digit (fig. 10, II.), besides its own tarsal bone (the second cuneiform), seeks additional support from the large third cuneiform: we shall discuss this relation when we come to the metatarsals; and I will merely observe here that it seems to be a very ancient one, which existed perhaps in the progenitor of the whole class of Mammalia. In the Hog (Plate XXXVII. fig. 12) we find the three cuneiforms quite distinct; but there is a great change in their relative position: instead of the third cuneiform giving additional support to the second digit, it is now not only entirely occupied by the enlarged third digit, but even the greater part of the *second cuneiform* leaves the reduced second digit to give additional support to the enlarged third.

The *first cuneiform* is also peculiar in the Hog; it is thrust like a wedge between the posterior beak-like prolongation of the navicular, the head of the second metatarsal, and a posterior process of the third metatarsal, to which it gives an articular facet. Remembering what we have said in reference to an analogous beak-like prolongation of the cuboid in hogs, and looking at a hog's tarsus *in naturâ*, we shall see that the wedge-shaped first cuneiform, together with the cuboid, press from within and without on the posterior processes of the third and fourth metatarsals, and make the two middle metatarsals act like a single undivided bone: this is moreover aided by a special provision in the articulation of the distal extremities of these metatarsals with the first phalanges; namely, the outer borders of the *combined* distal extremities of the two metatarsals are produced down less than the inner, so that the digits, being expanded in treading on the ground, tend to meet by their proximal ends and compress both metatarsals firmly together, thus materially aiding the compression of their upper extremities by the beak-like prolongation of the cuboid and the wedge-like first cuneiform. There is nothing of the sort in *Hippopotamus*; but the same provision existed in the two-toed *Diplopus*.

Dicotyles (Plate XXXVII. fig. 13) presents nearly the same relations; only the second cuneiform (c^2) has gone entirely over to the third digit; and after this there was no assignable reason why these *two* bones, giving support to a *single* metatarsal, should not coalesce: and this they have done in *Hyomoschus* and *Tragulus* (figs. 14 and 15, c^3, c^2), where the navicular has also coalesced with the two cuneiforms, the first cuneiform (c^1) remaining entirely distinct in both. In a Miocene ruminant from Auvergne, fig. 16 (*Amphitragulus*?), with a rudimentary second metatarsal, we may also clearly

perceive that the large cuneiform is formed by the coalescence of the second and third, while the first cuneiform remains distinct, giving support to the rudimentary metatarsal II. The same relation may be seen in our recent Ruminantia, whose large cuneiform bone is therefore to be taken as the homologue of the third and second, the first remaining distinct.

Having traced our three cuneiforms, even in the most reduced Paridigitata, it is natural to ask how the matter stands in *Anoplotherium*, the reputed prototype of every Paridigitate. In this respect the confusion is very great; and it originated with CUVIER. In his description of the Anoplotherian pes he says ('Oss. Foss.' 4th ed. p. 147, plate 128), that he found "le grand cunéiforme *C*" (which is our third cuneiform) and, besides, another bone (plate cxxviii. fig. 2, *h*), which he calls "osselet surnuméraire," and assumes to be a rudiment of the second digit, saying (p. 147) that it articulates to the facet *i* of the scaphoid, and the facet *k* of the third metatarsal. (This bone is, no doubt, our first cuneiform, Plate XXXVII. fig. 11, c_1.) If we look at the restoration of the pes of *Anoplotherium* in DE BLAINVILLE, and read his text, we shall see that he speaks of three cuneiforms, and even figures them (DE BLAINVILLE, 'Ostéogr.' *Anopl.* plate iv., side view of pes); *B* is the third cuneiform, *C* the second; and the bone lying backwards from it is certainly the first cuneiform. I take this restoration to be in the main right; only the second cuneiform, which is represented in the side view as articulated to the scaphoid, has, in his figure of the distal extremity of the scaphoid (a little below), no such facet on this bone, the facets figured being for the first and third cuneiform only. But if we read his text we shall find the confusion which is so characteristic of his palæontological writings. He says:—"Les os cunéiformes sont au nombre de trois: le *premier*, assez allongé . . . . collé contre le métatarse; le *second* presque de même forme, un peu moins reculé, articulé avec le scaphoïde d'une part et le métatarsien du medius de l'autre, et enfin le troisième . . . . articulé carrément avec le scaphoïde en haut et la métatarsien du medius en bas."—*Anopl.* p. 35.

So, in the interpretation of DE BLAINVILLE, the first cuneiform does not touch the scaphoid at all (in the description of the scaphoid, p. 35, he says:—"le scaphoïde a à son bord interne un tubercule ovale un peu saillant pour l'articulation du *second* cunéiforme, outre un beaucoup plus grand pour le troisième"), but is applied to the third metatarsal, the second cuneiform being, in his description, also articulated with the same metatarsal; and the third cuneiform is the chief support of the third digit. All the three cuneiforms, then, are said by DE BLAINVILLE to articulate with the third metatarsal; but I regret to say that this is entirely incorrect. I enter into such detailed descriptions only because such matters should be at once set right; the real state of things is this:—The *Anoplotherium* possessed all the three typical cuneiforms * in their

* Their relations to the metatarsals were entirely identical with what we see in *Hippopotamus*: the third cuneiform supported the third digit; the second cuneiform supported (the rudiment of) the second digit; and the first cuneiform was articulated to the navicular above the second cuneiform in front, and the rudiment of the second digit below.

typical relation; and, besides, a rudiment of the second digit pressed against the upper margin of the third digit. To prove this, I have figured the pes of the *Anoplotherium* from Vaucluse, where this rudimentary digit is completely developed (Plate XXXVII. fig. 11), we see in this foot the three typical cuneiforms nearly in the same relation as in *Hippopotamus*; the third cuneiform articulated to the third metatarsal, the second cuneiform to the metatarsal of the short second digit; the first cuneiform, seen behind, aids to support this short second digit. I have represented in Plate XXXVII. fig. 19 the distal surface of the navicular of this *Anoplotherium tridactylum*; and we distinctly see the three facets for the three cuneiforms, which all articulated with the navicular bone. Together with these navicular bones from the tridactyle form, we have from Vaucluse some naviculars of the didactyle species (fig. 18): the complete second digit is reduced in this species to a mere rudiment; and we see a corresponding diminution of the facet for the second cuneiform which supported this rudiment, the facet for the third remaining nearly of the same size. Now in the *Anoplotherium* from the Paris gypsum, as I see by a navicular in the British Museum (fig. 17), this facet for the second cuneiform is even smaller, but it exists still. As far as I can judge by a cast of another Anoplotherian pes in the Museum, the facet for the second cuneiform is absent from it; but still we see a trace where this very reduced second cuneiform leaned against the third, perhaps not touching the navicular; the posterior navicular facet for the first cuneiform remains very large. The reduction of metacarpal and metatarsal bones always precedes that of the carpals and tarsals; and when a rudiment of the former still lingers, we may be sure to find the corresponding tarsal or carpal; and so it is in *Anoplotherium*, which possessed besides its three typical cuneiforms a rudiment of the second metatarsal.

Proceeding now to the *Hyopotamus*, we find that it, as well as the *Diplopus*, had three cuneiforms to its tarsus; but unfortunately the first is absent from all collections examined by me; the second is preserved, thanks to its tendency to coalesce with the third or great cuneiform. The shape of the third cuneiform is very like that of the same bone in the Hog or *Anoplotherium*; it is articulated to the third metatarsal below (Plate XXXVIII. figs. 1–4); and its tibial or inner border gives additional support to the second metatarsal *, as its homologue, the magnum, does in the carpus. The *second cuneiform* is a small nearly cubic bone. I have never seen it separately, as it is always lost owing to its small size; but it is represented in fig. 2, having coalesced with the third cuneiform, and giving support to the second metatarsal. The third cuneiform of *Diplopus*, figured in the nearly complete tarsus (Plate XXXVIII. figs. 3 and 4), is in all respects similar to that of *Hyopotamus*; only, as seen in fig. 4, it did not give any attachment to the rudiment of the second metatarsal, as it does to the complete second metatarsal in *Hyopotamus*; nay, more, the tibial upper margin of the third

* In fig. 2, Plate XXXVIII., the second metatarsal rises a little higher than the third, and touches the internal side of the third cuneiform. The same is to be seen in *Hippopotamus* (Plate XXXVII. fig. 10) and *Anthracotherium*. This relation is essential in an unreduced tarsus.

metatarsal in this specimen has a very slight truncature or oblique facet, by means of which this third metatarsal touched the second cuneiform, a deviation from typical relations which is enormously developed in the Hog (Plate XXXVII. fig. 12, III. c_2); the proximal surface of the rudimental second metatarsal (Plate XXXVIII. fig. 4, II. r) is therefore a little lowered in this specimen, to allow the second cuneiform to touch the third metatarsal. On the contrary, in two other specimens not figured, the relations remain true to type, and it is the third cuneiform which gives a small facet to the rudiment of the second metatarsal.

I have found, moreover, in the British Museum a specimen of the *Diplopus* from Hordwell in which the two cuneiforms (2+3) had coalesced in the same manner as the two cuneiforms of the *Hyopotamus* of fig. 2. The distal surface of these two coalesced cuneiforms is given in outline below fig. 4, Plate XXXVIII., to show its correspondence with the proximal surface of the third metatarsal; and it answers so exactly to the third metatarsal with the coalesced rudiment of the second, figured in fig. 4″, that one may think they belonged to the same individual [my coalesced cuneiforms, however, are from the other (right) side]; and the correspondence to the figured foot is so exact that even the *second* cuneiform presents a small facet (the shaded bit of the outline below fig. 4) to the third metatarsal. So that in this specimen the overdeveloped third metatarsal seeks additional support from an adjoining tarsal bone. In the Suina it accomplished the passage long before the loss of the second lateral digit, as seen in figs. 12 and 13, Plate XXXVII.

A similar case is described in my Memoir on *Anchitherium* *: here also the third cuneiform became, in the same way, confluent with the second, to pave the way for the overdeveloped third (and single) metatarsal to enlarge and usurp the second cuneiform, which bone typically belongs to the second digit.

The first cuneiform is absent; and, judging from the absence of a facet for this bone on the posterior prolongation of the third metatarsal in *Hyopotamus* (Plate XXXVIII. fig. 2), we may infer that it did not articulate with it; but in *Diplopus* such facet on the posterior prolongation of the third metatarsal is clearly seen (fig. 4″, fc_1), and furnishes a conclusive proof that the first cuneiform was articulated to it in the same manner as in the Hog. Above, it was articulated to the somewhat convex posterior facet of the navicular (seen in figs. 4 and 2, Plate XXXVIII.), then touched the back part of the small second cuneiform, and, being prolonged lower down, leaned against the posterior part of the second metatarsal (as proved by a facet on this bone) in *Hyopotamus* (fig. 2), or against the rudiment of this second metatarsal in *Diplopus*, as seen in fig. 4, Plate XXXVIII. In this latter the first cuneiform was probably thrust like a wedge between this rudiment and the posterior prolongation of the third metatarsal, in the same way as it is to be seen on a hog's tarsus (Plate XXXVII. fig. 12).

Metacarpus and metatarsus.—When I began to study the structure of the anterior and posterior extremities of the Anthracotheridæ and Hyopotamidæ in the collections of

* Mémoires de l'Académie de St. Pétersbourg, 1873.

the Museums of Lausanne and Puy I had no doubt whatever that the genus imperfectly known under the names of *Hyopotamus* and *Bothriodon* had four completely developed digits on both extremities; and all I had seen in the collections of Puy confirmed this inference; besides, as I could not find any difference in the dental or osteological characters between these two supposed genera, I was obliged to unite them, giving priority to Professor OWEN'S denomination. But, whilst studying the fossil remains from Hordwell and Hempstead in the collection of the British Museum, I gradually acquired the conviction that we have, in the English deposits, two very different forms of the same natural family, which, though entirely similar in most of their osteological characters presented a wide difference in the composition of their manus and pes, a difference somewhat similar to the difference we see in our own times between *Hyomoschus* and the true Ruminants. One form had clearly four completely developed digits, while the other had only two. At first I struggled against this conclusion, as the fact seemed too singular, considering the similarity of all the other bones of the skeleton; but by-and-by, as I got more materials, all doubt cleared away; and having once ascertained this point, I felt obliged to subdivide the family of Hyopotamidæ into two groups or genera, *Diplopus* and *Hyopotamus*, whose chief distinction lay in the number of digits. It is more than probable that each group or genus was represented by several species, though this specific distinction is very difficult to establish. But I shall return to this question at the end of my memoir; at present I proceed with the description of the bones forming the metacarpus and metatarsus in both genera. As I have generally done, I commence with the tetradactyle form, or the *Hyopotamus*, and shall proceed afterwards to the didactyle, or *Diplopus*.

Before, however, proceeding with the Hyopotamidæ, it seems necessary to cast a glance at the composition of the manus and pes in all Paridigitata, living and fossil, as such a general review will throw more light on the importance and value of the distinctions found in our fossil Hyopotamidæ than a tedious and minute description of their bones could do. Studying in detail the structure of the extremities of the living and extinct Ungulata Paridigitata, and especially their metacarpals and metatarsals, we meet everywhere, through all the great diversity of their forms, such striking similarity in all the smallest details, such adaptation of one typical structure to widely different conditions, that there seems to be no possibility of explaining it otherwise than by a common descent (with modification and adaptation) from some single ancient form which presented the arrangement we call typical for the whole of the Paridigitata. Looking upon the whole community of Paridigitata as modified descendants of one ancestral form, the theory of evolution says that each form must have inherited the typical structure of the common ancestor, modifying it in each particular case to the condition of its own life; and though, after the lapse of a great period of time, the diversity acquired by different forms would be prodigious, still every member of the cycle, even at the furthest points of descending lines radiating from the common ancestor, would by every single bone testify its relation to this common ancestor. And such is really the

case with our recent Paridigitata. If the *Hippopotamus* and *Phacochœrus*, *Tragulus* and *Antilope*, seem wonderfully different, as being on the furthest points of the radiating lines, still they have every one of them strikingly similar typical characters inherited from the ancestral form which was the common progenitor of them all.

The chief and most obvious characters of a Paridigitate foot are to be seen in the shape and connexions of its two middle fingers; therefore I will commence with these, and state some general features common to all Paridigitata, living or fossil, without exception.

While, in the Imparidigitata, the axis in relation to which the whole foot is shaped is given by the middle or third digit, the axial line passing through its centre, we have in a Paridigitate foot always two middle digits (the third and fourth), which form the centre in relation to which the foot is arranged, the axial line passing in the interval between these two digits. These, then, may be taken as the principal digits of the manus and pes; they exhibit nearly always a certain mutual symmetry, and are interlocked at their upper extremities by a peculiar arrangement which is common to all fossil and living Paridigitata, as far as we know them now.

The mutual interlocking of the middle metacarpals is effected in this way. The fourth metacarpal has always, at its upper radial end, a process, or a smooth salient margin, uninterruptedly connected with its proximal articular surface: this process enters deeply into a corresponding excavation of the third metacarpal; and this excavation is overarched by a special ulnar process of the third metacarpal, which is inclined outwards, and abuts against the unciform. This is to be seen on all the figures of the carpus (Plates XXXVII. and XXXVIII.), and better still in De Blainville's Plates. In consequence of this projection of the third metacarpal the fourth stands always a little lower than its neighbour, and is supported entirely by the unciform, while the third is supported by the os magnum and partly by the unciform (Plate XXXVII. figs. 1, 2, 3, 20; Plate XXXVIII. figs. 5, 6), upon which it glides by means of its oblique outer and upper process.

The two middle metatarsals (the third and fourth) (Plate XXXVIII. figs. 1 & 3) show us something quite analogous; the fourth gives off from its upper tibial side a prominent process (not uninterruptedly connected with the proximal surface as on the fourth metacarpal), which enters into a deep corresponding cavity in the outer side of the third metatarsal. The fourth metatarsal is supported by the cuboid, the third by the third cuneiform.

Such is the general rule of the interlocking of the two middle metacarpals and metatarsals in all living and extinct Paridigitata: there is not a single exception to it; and the old Eocene *Dichobune*, as well as the recent *Hippopotamus*, present us with the same relation. But it may be urged against me that such a relation is certainly not to be seen in the recent Ruminantia, whose middle digits have coalesced into one single cannon bone. However, I think that the rule is even applicable to them. Although in the recent geological period the Ungulata Paridigitata, generally, acquired an exceedingly

reduced skeleton, we still possess nearly all the intermediate stages between four completely developed and distinct metacarpals and metatarsals, and their reduction to two coalesced middle ones. Besides, the links which are wanting in the fossil state are often furnished by the living forms in the course of their individual development before they reach the adult age. Such links are presented by the Tragulidæ and the posterior extremities of *Dicotyles* and *Hyomoschus*. If we examine the bones of their feet at an early age, when the fourth and third digits are yet distinct, we shall see exactly the same relation as is laid down in our general rule. But even after the complete coalescence of these two metacarpals and metatarsals, some traces of the original disposition are to be detected. Examining the fore "cannon" of the typical Ruminantia (especially Deer) we shall see that one half of the proximal surface, answering to the third metacarpal, is a little higher than the other half, and always presents a produced ulnar margin, by means of which it abuts against the unciform; the same is to a certain extent seen in the back cannon, where the proximal surface for the cuboid is often a little lower than the surface for the third cuneiform.

These two middle digits (third and fourth) form the chief basis of the foot of a Paridigitate Ungulate; to these are added, on the inner and outer sides, one digit more, the second and the fifth. But so much is the skeleton reduced in the existing Paridigitata, that there exists at present only a single form (the *Hippopotamus*), represented by a single species (or two, as *Chœropotamus liberiensis* appears to be distinct), in which these two lateral digits have a true functional importance; and although the lateral digits still exist in all the Suidæ, Tragulidæ, and *Hyomoschus*, they have no real functional importance. Even in the Suidæ the two middle digits are so largely developed in comparison with the lateral ones, and all the bones of the carpus and tarsus have been so completely taken for the use of these two middle digits, that we shall be guilty of no exaggeration in stating that the Suidæ might lose the lateral digits without their locomotion being at all impaired. We even witness this process going on in *Dicotyles*—in which the lateral digits are still more reduced than in the true Suina, and they begin to disappear altogether, beginning at the external metatarsal. If the lateral digits are still retained in the Suidæ, it is chiefly owing to the fact that the Hogs live generally in marshy places and on muddy river-banks, where a broad foot is of great importance for not allowing them to sink deeply into the mud. But if, by some geological change, their habitat should be transformed into dry grassy plains, there can be no reasonable doubt that they would as readily lose their lateral digits as the Palæotheroids have lost theirs (perhaps by an analogous change of habitat) in becoming transformed into the monodactyle Horse. Should this occur only in a limited locality, and under circumstances admitting of no migration (for instance, on a large island), it is very possible that the Suidæ of this particular island might lose their lateral toes, while others, which continued to live under the old conditions, would retain theirs. If this should really occur, we should have two groups of the same family, quite similar as to the large bones of the skeleton, but dissimilar as to the structure of their feet, which is just what we witness

in the two groups of the didactyle and tetradactyle Hyopotamidæ of the oldest Miocene and Upper Eocene.

What, then, are the relations of these lateral digits to the whole manus and pes, considered in their primitive unreduced condition. The inner, or the second lateral digit of the manus is supported by the trapezoid; it is not, however, limited only to this bone, but leans a little over the inner edge of the third metacarpal, and goes to touch the os magnum, which presents a special facet to this second metacarpal. We may see this typical relation in the second digit of the *Anoplotherium tridactylum* (Plate XXXVII. fig. 2), in the rudiment of the second metacarpal in the Paris *Anoplotherium* from the gypsum (see De Blainville, *Anopl.*), and in the very complete fore foot of *Hippopotamus* and *Hyopotamus* (Plate XXXVII. figs. 1 & 20, II. *t*, *m*). In the posterior limb, the inner or second metatarsal is supported entirely by the second cuneiform (the homologue of the trapezoid), and by the tibial edge of the great or third cuneiform (the homologue of the os magnum), as may be seen in *Hippopotamus*, figs. 9 & 10, *Anoplotherium*, fig. 11, *Hyopotamus* (Plate XXXVIII. fig. 2), and *Anthracotherium**.

The outer or fifth digit of the manus and pes in all Ungulata Paridigitata (and, in fact, in all existing Mammalia) is supported by the same carpal bone as the fourth. There is not a single exception to this rule; and in all Mammalia, wherever the fourth and fifth digits of the manus and pes are present, they are always supported by one bone —the unciform in the manus, and its homologue (the cuboid) in the pes.

Seeing that the full number of digits in Mammalia is five, while the number of carpal and tarsal bones which give support to them never exceeds four—three inner digits being supported each by a separate bone, while the two outer are always supported by a single carpal and tarsal bone—the question may arise, is this relation primitive for all Mammalia? or is it a result of coalescence of two outer carpal and tarsal bones into one? As we have not the slightest notion of the skeleton of the first mammals, nor even of the geological time when they made their appearance, the solution of this question is not to be expected now. Turning to some of the Amphibia and Reptilia with completely developed digits, we generally, or at least very often, find, as has been proved by the beautiful researches of Gegenbaur, that each of their digits in the manus and pes is supported by a special carpal and tarsal bone, there being five distinct bones in the second row in the manus and pes. Now it is very possible that the first progenitor of the class Mammalia had also five carpal and tarsal bones in the second row, or, what is more probable, seeing that there is not a single instance of these two outer bones being found separate in any mammal, living or fossil, that their coalescence was effected before the evolution of the first truly mammalian type, and that they passed into this class already coalesced.

I have already mentioned that, beginning with the mammals of the oldest known Eocene deposits, the oldest mammals of whose skeleton we are able to form a tolerably clear idea (the oldest Mammalian remains, though proving the existence of the class as

* This relation is very characteristic, not only as regards Ungulata, but nearly all Mammalia.

far back as the Jurassic and even the Triassic period, have not yet furnished the slightest clue as to their skeleton), we meet always with Ungulates which belong unmistakably to the one or the other series; a fossil Ungulate may be at once said to belong either to the Paridigitate or Imparidigitate division; we have not a single form in which the characters of the two groups can be said to be mingled together, or which could be reputed to be the progenitor of both these great divisions of the Ungulata. Some of the early Eocene Paridigitata and Imparidigitata seem undoubtedly to be more nearly related, and have more common characters, than the greatly reduced forms we meet with in the recent epoch; but this shows only, if we imagine these two series to be diverging lines meeting in some old Cretaceous Ungulate, that they occupy certain positions on these two different lines nearer to the point of divergence, but still so far from it that all the intermediate links had time to be completely destroyed before the Eocene period. We may imagine that in the Cretaceous epoch there existed an Ungulate form with a very complete skeleton and five digits to the manus and pes; from this common form the divergence of Paridigitata and Imparidigitata may have been effected in such a way that, with the commencement of the reduction of the skeleton of this typical primary Ungulate, the chief development fell in one case on the middle (3rd) digit of the manus and pes, the laterals becoming more or less reduced and arranged symmetrically on both sides of this central digit of the manus and pes, so as to originate the series of Imparidigitata; while in the other case the chief development fell on the two contiguous middle digits of the manus and pes (the 3rd and 4th), giving rise to the series of Paridigitata. But as the overdevelopment of a single middle digit, to such an extent as to support the body effectually, is a task much more difficult to the organism than the development of the two middle digits to a comparatively less extent, the reduction of the Paridigitate skeleton proceeded at a much quicker rate than that of the Imparidigitate; and while we meet with many animals of the Paridigitate series having only two digits in the Eocene, the Imparidigitata have always three. In the Miocene epoch, the two middle reduced digits of Paridigitata have already coalesced to form a single digit, the cannonbone of Ruminants; but the most reduced member of the Imparidigitata, the *Anchitherium*, still walked on three toes, though the laterals began to be greatly reduced; and it is only in the later Miocene and the Pliocene periods that, with the appearance of the *Hipparion* and Horse, the skeleton of the Imparidigitata attained as great a reduction as the skeleton of Paridigitata did in the earliest Miocene, *Gelocus* (Aymard) being the first Paridigitate with a complete cannonbone in the adult. In the skeleton of this Ungulate progenitor, before the divergence of the two series was effected, we may imagine a pentadactyle manus and pes constructed in the way given in the following scheme.

Scheme of the Ungulate Manus and Pes.

Manus.					Pes.				
Unciform.		Magnum.	Trapezoid.	Trapezium.	Cuboid.		Cuneif. 3rd.	Cuneif. 2nd.	Cuneif. 1st.
Metacarpal 5th.	Metacarpal 4th.	Metacarpal 3rd.	Metacarpal 2nd.	Metacarpal 1st.	Metatarsal 5th.	Metatarsal 4th.	Metatarsal 3rd.	Metatarsal 2nd.	Metatarsal 1st.

The two outer digits of the manus and pes are supported by one bone—the unciform in the manus, the cuboid in the pes; the three following digits in the manus were supported, the *third* by the os magnum, the *second* by the trapezoid, the *first* by the trapezium; and in the pes each of the inner digits was supported by its corresponding cuneiform. The reduction of the manus and pes commenced at the first or inner toe; and we have not a single living or extinct Ungulate presenting this first digit developed; nay, more, I know of no positive case where even a rudiment of the first toe is present. All the bones described as such rudiments have turned out, on close inspection, to be the trapezium or the first cuneiform* mistaken for the rudiment of the first digit. This is constantly the case in regard to the rudiments described in the 'Ossemens Fossiles.'

Fortunately, even in the recent period, there still exists an Ungulate upon which we may well study the structure of the typical Paridigitate manus and pes. This is the *Hippopotamus*: no trace of the first digit is left in the fore or hind limb; but, owing to the very complete development of the remaining four digits, they must have retained their typical relations to the bones of the carpus and tarsus. Looking at the fore foot of the *Hippopotamus* (Plate XXXVII. fig. 1) we perceive that the two middle digits are mutually interlocked in the manner described above as common to all Paridigitata. The two outer digits, the fourth and fifth, are supported by the unciform; the third is supported by the os magnum, and gives besides, at its ulnar margin, a projecting beak, by means of which it hangs on to the unciform; the second digit goes a little higher than its neighbours, is supported by the trapezoid, and touches a small facet on the radial side of the os magnum; the first digit is entirely reduced, and its proper carpal bone, the trapezium, assists to support the second digit.

What do we see in the hind foot? The cuboid (Plate XXXVII. fig. 9, *cb*), which is the homologue of the unciform, supports the fourth and fifth digits; the interlocking of the two middle metatarsals is effected in the usual way, the fourth giving a projection which enters into a concavity of the third; the third cuneiform (c_3) (the homologue of the os magnum) supports the third metatarsal; the second metatarsal is

* If this absence of even a rudiment of the first digit is really constant among fossil and living Ungulata, it may possibly be supposed that at the branching off of the Ungulate division this first digit was already reduced and even entirely lost.

supported by the second cuneiform (c_2), and its tibial margin touches the third cuneiform (just as the homologous parts on the fore foot do); the first digit is entirely lost, and its typical tarsal bone, the first cuneiform, aids in supporting the second digit (Plate XXXVII. fig. 10, c_1).

This should be the place to consider the structure of the feet in the Suina; but, as in the recent members of this family, owing to the overdevelopment of the middle digits, the typical relation between the bones is a little changed, I will describe it after having treated those Paridigitata which preserve this typical relation unchanged.

Of the fossil Paridigitata whose skeleton is known to us with any thing amounting to completeness, we have only the *Anoplotherium* and *Xiphodon*; and we shall see by-and-by with what wonderful persistence the typical relations are adhered to in the skeletons of these animals, notwithstanding the great reduction of the number of their metacarpals and metatarsals.

As the *Anoplotherium tridactylum* is certainly a less-reduced form than the species from the gypsum, and as, except a sketch in GERVAIS'S 'Paléontologie Française,' there are no good drawings of its extremities, I represent them on Plate XXXVII. figs. 2, 11, from the original specimens of BRAVARD now in the British Museum. Though the number of digits on the fore and hind limbs is odd, it is nevertheless a very typical Paridigitate, and differs from the Paris *Anoplotherium* only in this respect, that the second digit, which is represented only by a small rudiment in the animal from Montmartre, is developed to a complete (though short) digit in the *Anoplotherium* from the lignites of Vaucluse. The manus of the *Anoplotherium* is so well described by CUVIER that I will not enter into any details, and only point out its chief peculiarities. As seen in Plate XXXVII. fig. 2, this manus is entirely true to the general type: the interlocking of the two middle metacarpals is effected in the same way as described above; the fourth metacarpal is supported by the unciform; the third hangs to the os magnum, and sends a prolongation of its ulnar margin to meet the unciform; the second, though too short to touch the ground, is complete and supported by the trapezoid, and it sends a projection to articulate with the os magnum; the trapezium aids in supporting the short second digit. At the outer margin of the foot there exists a rudiment of the fifth digit, leaning against the unciform and the ulnar margin of the fourth metacarpal.

The pes of *Anoplotherium tridactylum* (Plate XXXVII. fig. 11) shows us the same typical persistence in the relation of the bones. The interlocking of the two middle metatarsals takes place, as usual, by a process from the fourth fitting into an excavation of the third metatarsal; this last is supported by the third cuneiform (c_3). As the second digit is developed, the corresponding bone, the second cuneiform (c_2), very small or nearly obsolete in the Paris *Anoplotherium*, is largely developed in the *A. tridactylum*, and supports the second digit; the first digit is absent, and its tarsal bone, the first cuneiform (c_1), aids in supporting the second digit.

As the chief difference between the *Anoplotherium* from the gypsum of Paris and the *A. tridactylum* lies in the development of the second digit and its corresponding

carpal and tarsal bones, I have represented the distal surface of the navicular (to which the cuneiforms are attached) of the tridactyle form (fig. 19) and of the Paris *Anoplotherium* (fig. 17); the navicular (fig. 18) is from the same locality as the tridactyle one; and though undoubtedly belonging to a didactyle *Anoplotherium*, the intermediate facet for the second cuneiform still presents some development, while in the Paris specimen it is exceedingly small and is even absent in some specimens; indeed it seems that the second cuneiform, being very small, did not always touch the navicular; and this led CUVIER into the erroneous belief that this bone was altogether wanting*.

The manus and pes of *Xiphodon* (Plate XXXVII. fig. 3) present exactly the same peculiarities: though reduced to only two metacarpals and metatarsals, these two are in no way adapted more completely to the distal surface of the carpus, and are supported only by their typical carpal and tarsal bones. The persistence of typical relations is so great that even the rudiment of the second metacarpal, though a mere bony nodule, persists not only in its articulation with the trapezoid, but even with the radial facet of the os magnum (as seen in Plate XXXVII. fig. 3, II., *m*, *t*), as truly as in the case of the complete second metacarpal in the four-toed foot of a Hippopotamus.

In the pes, as far as I am able to see by the figures of CUVIER and DE BLAINVILLE, the relation between the metatarsal and tarsal bones is quite such as we laid it down in our general scheme. There are three distinct cuneiforms; the third metatarsal is supported entirely by the third cuneiform; and though there is only a small rudiment of the second metatarsal, nevertheless this rudiment has not surrendered its typical articulation, and retains the whole of the second cuneiform for itself; the first cuneiform is articulated upwards with the scaphoid, touches the posterior part of the second cuneiform, and is articulated lower down with the rudiment of the second metatarsal, presenting in this way entire agreement with the typical structure of a Paridigitate tarsus†.

Now, if we turn to CUVIER (Oss. Foss. v. 4to ed. p. 181), we shall see that he noticed the three cuneiforms in *Xiphodon*, calling only the first (marked *e*) "osselet surnuméraire;" he did not notice the true rudiment of the second metatarsal (DE BLAINVILLE is entirely wrong in saying that there were only two cuneiforms, *Anopl.* p. 50); he did not describe or mention the rudimentary second and fifth metatarsal, though he very correctly noticed the corresponding bones in the metacarpus.

After this brief notice of the structure of the metapodium in the fossil Paridigitata, we may proceed with the description of the same parts in *Diplopus* and *Hyopotamus*; but I wish, before doing so, to take a short survey of the same part of the skeleton in the remaining living representatives of the Paridigitate series, the Suidæ and Ruminantia.

* Passing through Paris, I tried to settle this question; and in fact there exists in the 'Galerie de Paléontologie' a nearly complete foot with the three cuneiforms. It is in a block of gypsum, and placed high on the top of the wall-cases in the gallery.

† I find on the posterior part of the distal articular surface of the cuboid of *Xiphodon* a small facet clearly destined for the rudimental fifth metatarsal.

The general conclusion to be drawn from our survey of the fossil forms, is that they exhibit an extreme uniformity in the structure of their metapodium, and that these uniform and typical relations between the metapodium and the bones of the carpus and tarsus are remarkably constant, and, as regards the fossil forms, unpliant and rigid. Even with the utmost reduction of the metapodium in *Anoplotherium* and *Xiphodon*, the typical relation between the two remaining metacarpals and metatarsals remains just the same as it probably was in their tetra- or pentadactyle ancestors; so long as even a rudiment of a metacarpal or metatarsal remains, it holds just the same relation to the supporting bones as if it were complete. We meet with no distinct adaptation by means of which the median metacarpals and metatarsals which are left after the dropping off of the laterals, enter into a more complete articulation with the remaining bones of the carpus and tarsus. Considering, for instance, the two slender separate metacarpals and metatarsals of *Xiphodon*, we must confess that a foot so badly adapted for the use of a swift animal is rarely to be met with The middle digits, being unankylosed, are liable to be broken separately by a much less exertion of force than it would require to break the two coalesced middle digits of a Ruminant; besides, seeing in what manner the whole weight of the body is transmitted to the two middle digits, we shall find that it is not effected in such a way as to ensure the most complete and stable equilibrium. To effect this we might expect that the proximal ends of the two remaining metacarpals (Plate XXXVII. fig. 3) would be enlarged to such a degree as to underlie the whole distal breadth of the carpus; in this case the weight of the body would be transmitted much more equably and effectually to the two middle digits of the metacarpus. However, we see nothing of the kind: the transmission of the weight of the body is effected only by the two bones of the second row of the carpus; and the two useless rudiments remaining on both sides, and occupying the whole trapezoid and a large facet of the unciform, diminish by so much the stability of the foot, in comparison with an arrangement in which the facets occupied uselessly by them should be taken by the functional middle digits. We meet with exactly the same relation in the pes; so that it will be needless to recapitulate in reference to it all we have said in reference to the manus. The same may be, to a great extent, said of the *Anoplotherium*, though the digits which remain are so stout and short that the want of stability of the foot is not so clearly shown by this form as by its slender congener.

On the whole we may, with sufficient probability, say that, while in these two genera the reduction of the manus and pes was going on and the lateral digits aborted, the remaining middle digits did not adapt themselves as fully as could be imagined* to altered circumstances of life and to a different distribution of weight of the body; they remained too true to ancestral traditions; there was no pliancy in their organization which, by adapting them more fully to altered conditions of life, would have enabled them to carry on successfully the struggle for existence with other competing genera.

* And as we actually see in other genera which outlived *Anoplotherium* and *Xiphodon*.

And these last, as we shall presently see, being better adapted to altered conditions of life, got the upper hand, multiplied largely in specific and generic forms, and peopled the earth with their successors, while *Anoplotherium* and *Xiphodon* died away without leaving any*. In this inflexibility and rigidity of organization, in this inability to alter it as completely as the competing genera were able to do, lay perhaps one of the causes of the extinction of some genera and their replacement by others. All that I attempt here is to show in what peculiarities of structure this rigidity of some genera and pliancy of others consisted. I do not wish to put this as the *only* cause, but as one of the *many* still unknown causes which led to the extinction of so many animals that preceded the present population of the earth.

I have adduced here only such cases as are known and described; but having carefully examined large collections of bones from the Eocene and Miocene deposits, I have been struck with the recurrence of similar facts. Trying to reconstruct the extremities of some Paridigitata of the Lower Eocene from Mauremont and Egerkingen, and of Miocene forms from Rochette, I could distinctly perceive that all genera which have left no direct successors, and which are entirely extinct, present the same rigidity and persistence of the typical relations; on the contrary, those which have representatives in the living creation, their direct successors, exhibit much more pliancy and much better adaptation to altered circumstances of locomotion, along with the reduction in the number of digits.

Before proceeding to consider the two remaining groups of Paridigitata, the Ruminantia and the Suina, we may draw the attention of the reader to the fact that these two groups of Paridigitata are the only ones† which now people the earth; there is no greater diversity than this; and every living Paridigitate (if we except the Hippopotamus) is always clearly a ruminant (including the Tragulidæ and Camelidæ) or a *Sus*. How striking is this poorness of different types if we compare it with the rich and diversified forms presented by the recent Carnivora or Rodentia. The extreme diversity of generic forms and specific modifications, coupled with the enormous range of distribution of living Paridigitata, produces a false impression of the diversity presented by this order; but in reality there is no such diversity, and all the extremely rich assemblage of Paridigitate Ungulates that people the earth in our time are only the result of the modification of two typical forms, the Suina and the Ruminantia. The latter term is a very objectionable one, as the faculty of rumination has nothing to do with the skeleton, and in reality it would be no wonder if some of the Imparidigitates possessed the same faculty. As the teeth have so great a value in systematic zoology, it would be perhaps more advantageous to distinguish all Paridigitata into those which have tubercular and those which have crescentic teeth. To the first division will

* The reduction of the limbs in *Anoplotherium* and *Xiphodon* is so great that I regard them only as the last representatives of dying-out branches that did not leave any direct descendants.

† If we except *Hippopotamus*—this last remnant of a Paridigitate series once rich in generic forms, but which is now reduced to only two distinct groups.

belong all the existing Suina and the Hippopotamus; to the second, the remaining Paridigitata, which all possess, more or less completely, the faculty of rumination coupled with the absence of incisors (Camel?) in the premaxillaries. Such a division of Paridigitata would allow a place in the zoological scale to the extinct forms which were distinguished by the non-confluent metapodium, and the presence of incisors in the premaxillaries, and very probably did not ruminate.

We shall now proceed to cast a comparative glance at the structure of the feet in both these divisions as they exist in our own time, and endeavour to discover if their structure does not present some characters which show that they are better adapted for new circumstances of life than were their Eocene and Miocene predecessors; and that to this better adaptation may be, in part, ascribed the victory they obtained in the battle of life, and their spreading over all the surface of the globe.

As the Paridigitata with tuberculated teeth are represented, in the recent period, only by the Suina, and those with crescentic teeth only by the Ruminantia, we shall have to confine ourselves to these two orders; in the latter we shall particularly call the attention of the reader to the Tragulina, as the less reduced members of this family, and therefore more likely to furnish us with typical characters.

The true Suina have four complete digits in their manus and pes, but only the two middle ones are subservient to the purpose of locomotion; the laterals are always so reduced that they do not regularly touch the ground, or only do so on muddy soil, when the foot sinks deeply into the earth. According to the general rule laid down for all the Paridigitata, the interlocking of the two middle (third and fourth) metacarpals in the manus is effected as usual; the fourth digit is supported by the unciform, while its radial upper margin is fitted into an excavation on the ulnar side of the third metacarpal, which, by means of an ulnar process of its upper margin, articulates with the unciform, while its proximal surface is supported by the os magnum (see figs. in Cuvier, 'Oss. Foss. Atlas,' and De Blainville, 'Ostéographie, *Sus*,' also our fig. 4, Plate XXXVII.). However, in examining more attentively this proximal surface of the third metacarpal of the Hog, we remark something quite new, and not met with in most of the fossil Paridigitata. Owing to the over-development of the middle digits, the radial side of the third metacarpal (Plate XXXVII. fig. 4) has spread inwards and pushed the second metacarpal away from its typical articulation with the os magnum; nay even more, this second metacarpal has yielded one half of the surface of its carpal bone to the encroachment of the third digit; this last, besides the magnum, occupies now one half of the trapezoid—a new fact in the history of the Paridigitate foot that had important consequences. To show the reader more clearly that this modification is a recent one, we turn to the fossil Suidæ. Unhappily, our knowledge of their skeleton is very imperfect; and while genus after genus (not to speak of species) of the fossil Suidæ have been created merely on dental, often very slight and unimportant, characters, the study of their skeleton has been much neglected. As far as I am aware,

not a single bone of their skeleton was figured or discussed comparatively until the appearance of Professor GAUDRY'S work on the Fossils of Pikermi*.

However, I was so fortunate as to see many bones of the skeleton of the Miocene Suina, distributed into divers genera, in the collections of Paris and London; and on comparing the third metacarpal of the *Palæochœrus*† (Plate XXXVII. fig. 6) from Auvergne, and the *Chœromorus*, Lrt., from Sansans, with that of the recent Suidæ, I found that this broadening of the third metacarpal did not exist in *Palæochœrus* nor in the *Chœromorus*, the second digit taking for its support the entire surface of the trapezoid. Plate XXXVII. fig. 6 represents a third metacarpal of *Palæochœrus*; and by comparing it with fig. 4 we immediately perceive the difference. This broadening of the metacarpals, with the purpose of taking the whole of the distal surface of the second row of bones of the carpus, took place in the Suina only after the middle Miocene epoch. But, among the recent Hogs, we have one more advanced form which, in this character, stands to the other Suidæ nearly in the same relation as the Suidæ stand to the Palæochœridæ; this is *Dicotyles*. The structure of its fore limb agrees entirely with that of *Sus*, only the lateral metacarpals are reduced a step further; and looking at fig. 5, Plate XXXVII., we shall see that the enlarged third metacarpal has taken, not the half, as in *Sus*, but the whole of the distal surface of the trapezoid, the second metacarpal being pushed entirely away from its typical carpal bone. Moreover, this facet for the trapezoid (as in fig. 4) is transformed from an oblique into a horizontal one, thus giving better support to the third digit; while the corresponding distal surface of the trapezoid instead of having a spear-shaped form, as in the Hog (fig. 4, *t*), is quite flat in *Dicotyles* (fig. 5, *t*). The trapezium (fig. 5, *tz*) is greatly reduced, has no distinct articular facet on the trapezoid, and is disappearing altogether, without coalescence with the trapezoid. Thus, then, we find that, in the Miocene Pigs, the whole trapezoid is, according to the typical relations, taken by the second digit; in the recent Hog only half of its distal surface is left for the second digit, and none at all in *Dicotyles*.

On the outer side of the manus, the relations are much simpler, as the fourth and fifth metacarpal are supported, in all Ungulata, by a single bone, the unciform; therefore, by the gradual broadening of the fourth metacarpal, the outer or fifth digit is pushed to the outer side of the distal surface of the unciform, until, in the Hog and in *Dicotyles*, it occupies only a small lateral and outer facet on this bone, in such a way that the fifth digit has practically no upper carpal facet, but is suspended laterally to

* GERVAIS, 'Paléontol. Française,' has figured a third metacarpal, which is very interesting, as it shows none of the broadening of the radial margin so characteristic of *Sus*. It is from the right side, while all figured by me are left.

† In its dental characters, as well as in its skeleton, *Palæochœrus* stands so near to the Hog that even their generic distinction might be questioned. The *Chœromorus*, being also a true Hog, stands further from the recent Suidæ; one of the very curious characters of this remarkable genus is the central ridge of the distal extremities of the metacarpals and metatarsals, which, instead of encircling the whole extremity, is limited to its back part only; the first phalanges are modified accordingly.

the outer side of the unciform; and this lateral position is more pronounced in *Dicotyles* than in the Hog, in consequence of the greater reduction of the former.

Moreover, if we examine attentively the proximal surfaces of the two middle metacarpals in *Dicotyles*, we shall see that they are much more joined together than in the common Hog or any other *Sus*; their inner flat sides are so closely united that it will require only a little step further to make them coalesce; and as the os magnum and trapezoid are now both resting on one metacarpal they cannot remain long distinct, but must coalesce: if this should occur, we should have a structure nearly analogous to, and hardly to be distinguished from, that of a typical ruminant.

If we turn now to the structure of the *pes* in the Paridigitata with tuberculated teeth, or Suina, we shall meet with precisely the same phenomena; and the homologous bones of the manus and pes undergo a strikingly similar course of variation.

The two middle digits of the *pes* interlock, in the usual way, by a process from the fourth metatarsal, which fits into an excavation of the third. The cuboid supports the two outer digits, the fifth and fourth; the third digit is supported by the third cuneiform. If we compare the third metatarsal of the recent Hog (Plate XXXVII. fig. 12, III.) with the same metatarsal of *Palæochœrus*, fig. 12′, and of *Chœromorus*, we perceive just the same difference as in the homologous bones of the manus. While in *Palæochœrus* the third metatarsal is confined entirely to the third cuneiform*, leaving the second cuneiform for the support of the second metatarsal, in the Hog (fig. 12, III. c_3, c_2) this third metatarsal is greatly enlarged; it has pushed the second digit away, and encroached on nearly the whole of the distal surface of the second cuneiform, leaving only a very narrow facet of this bone for the second metatarsal (fig. 12, II. c_2), which is now chiefly supported from behind by the wedge-shaped first cuneiform.

On the outer side of the pes, the enlargement of the fourth metatarsal has taken the greater part of the distal surface of the cuboid, the fifth metatarsal being pushed very much backwards, and being supported partly by a small facet on the distal surface of the cuboid, and partly by a posterior prolongation to the beak-like downward process of the same bone. The pes of the *Dicotyles* shows us the same disposition in an exaggerated form; the inner side of the third metatarsal (Plate XXXVII. fig. 13, III.) has completely occupied the second cuneiform, so that the second digit is supported only from behind by the first cuneiform. On the outer side, the fifth digit is completely lost; or, if a rudiment of the fifth metatarsal remains, it is generally a flat elongated bone attached to the outer side of the fourth metatarsal, and having no articular surface on the cuboid, which is taken up by the over-developed fourth metatarsal. Besides, the two middle digits have coalesced in the whole upper half of their length, simulating the cannonbone of a Ruminant. The navicular and cuboid are still separated, but are very firmly pressed together; and now, both these bones, having the coalesced metatarsal below them, cannot have much separate movement, and their coalescence, as well as that of the

* As the hind limbs are always more reduced than the fore, it seems that, even in *Palæochœrus*, the third digit encroached in a perceptible way on the second cuneiform.

second and third cuneiform, is only a question of time, the modification going on uninterruptedly in the direction of the greater reduction of the limb-bones.

Can the general tendency of this steady reduction be doubtful? Is not the fact eloquent enough, that, proceeding from the middle Miocene times until the recent period, we meet with a whole series of Suina in which the skeleton is gradually more and more reduced, until it culminates in the Post-tertiary time in *Dicotyles*, a form very analogous, in the structure of its limbs, to the Ruminants, whose middle digits are quite ready to coalesce into a cannonbone, and the laterals to drop off? Indeed, this has begun in the posterior limb, in which reduction is always in advance, and on its outer side, which is generally more reduced than the inner. If any inference from one series of phenomena is allowed to be applied to another, then, inasmuch as the Paridigitata with CRESCENTIC TEETH, or the recent Ruminantia, proceeding from tetra- or even pentadactyle forms, arrived in the Miocene period at didactyle forms, in which the coalescence of the two middle digits simulates monodactylity, we have a full right to infer, seeing the parallelism of these two groups, that the Paridigitata with TUBERCULAR TEETH have followed just the same line of reduction. And if nature should be allowed to follow its course, or if man had made his appearance only in the Post-quaternary instead of the Post-tertiary period, he would no doubt have found only two groups of Paridigitates remaining, one with crescentic, the other with tubercular teeth, but both having a cannonbone in their fore and hind limbs, and no lateral digits. These two groups of Paridigitates undergo exactly parallel modifications in the course of time, as far as their limbs are concerned—only in the group with crescentic molars these modifications have gone on much more rapidly than in the parallel group with tubercular teeth. The cause of this greater rapidity lay very probably in the more specialized, instead of an omnivorous, diet, and was perhaps influenced by the commencing faculty of rumination, which gave them an enormous advantage over the other group, by allowing them to store food in their paunch in the most favourable, or least dangerous, part of the day, and chew it afterwards when retiring to rest.

If we turn now to the Paridigitates with crescentic teeth, represented in our times only by the living Ruminantia, we meet in the typical (which in this case means the most reduced) genera both middle metacarpals and metatarsals coalesced so as to simulate a monodactyle foot, forming the so-called cannonbone. The rudiments of the lateral digits are mostly lost (in *Bovidæ* and *Antilopidæ*) or retained only as small filaments of bone, having no articulation with the carpal or tarsal bones, but merely pressed to the outer and inner sides of the two middle digits. The trapezium is entirely lost; the trapezoid is confluent with the magnum *. In the tarsus, the navicular is confluent with the cuboid, and the second cuneiform with the third; the first remains nearly always separate, and in case of confluence with the coalesced second and third cuneiforms, as in the Giraffe, the division is clearly seen. This is the general structure of the foot in the typical Ruminantia, or the most reduced Paridigitata with crescentic

* Except in *Camelidæ*.

teeth; but fortunately we have still a living form which stands to the typical Ruminantia nearly in the same relation as our *Dicotyles* would stand to the Post-quaternary Suinæ with a cannonbone. The parallel is really complete, with the exception of some small points*. This living form is the *Hyomoschus aquaticus*, hardly distinguishable from its fossil congener of the Middle Miocene. If we examine the manus of this animal (Plate XXXVII. fig. 8), from the inner side, we shall meet with characters common to all Paridigitata. The interlocking of the two middle metacarpals is effected in the usual way; the inner, or radial, margin of the third is enlarged in the same way as we saw it in *Dicotyles*—only the two carpal bones which support this enlarged third metacarpal, the magnum and trapezoid, are already confluent (fig. 8, *m* & *td*); the reduced, but still complete, second digit has a small facet on the back part of the coalesced trapezoideo-magnum. On the outer side of the manus, the large fourth metacarpal is supported by the unciform, and the distal surface of this bone gives also a small facet to the reduced and thin, but still complete, metacarpal of the fifth digit.

The pes of *Hyomoschus* will show us something similar to what we have seen in the manus. As seen in fig. 14, Plate XXXVII., the inner side of the third metatarsal is enlarged, and has taken the whole of the second cuneiform, the second metatarsal being supported entirely by the first cuneiform, which is distinct, while both the others have coalesced mutually and with the navicular (c_3+c_2+n, fig. 14).

On the outer side of the pes we find that the large fourth metatarsal has taken nearly the whole distal surface of the cuboid; however, it leaves a very small facet for the articulation of the complete fifth digit. The length of the lateral metacarpals and metatarsals nearly equals that of the middle ones, though, owing to their thinness and the want of direct firm support from the carpals and tarsals, they are, as it seems, not subservient to locomotion. The middle metatarsals are confluent in the adult.

In the Tragulidæ (Plate XXXVII. figs. 7 & 15) the middle metacarpals and metatarsals are distinct in the young, even after their complete ossification; in this state we may ascertain that their mutual interlocking is effected as in all other Paridigitata. The inner margins of the third metacarpal and metatarsal are enlarged even more than in *Hyomoschus*, and their relation to the trapezoid and second cuneiform is altogether the same. The lateral digits persist during the whole of life as filiform bones on both sides of the middle cannonbone. Although of the same length as the cannonbone, they are useless for locomotive purposes, owing to their extreme thinness. At last, in the typical Ruminantia, the two middle metacarpals and metatarsals coalesce into the cannonbone during the process of ossification. All particulars we have remarked in the Tragulinæ

* The chief are these:—the trapezoid is confluent with the magnum, while it is only preparing to become so in the anomalous *Dicotyles*; the navicular of the pes is confluent with the coalesced second and third cuneiforms (as in all the Tragulidæ); the fifth digit of the pes is completely developed, not lost, as in *Dicotyles*. The articular ridge of the distal end of the metacarpals and metatarsals is confined only to the palmar side, and the first phalanges are modified accordingly. If we remember that some of the ancient Pigs, as *Chœromorus*, show just the same smoothness of the distal ends of the metapodium, the parallelism of both groups of Paridigitata appears to hold good, even in the slighter details.

are exaggerated in the true Ruminants. The trapezoid and the second cuneiform are always, even in the cartilaginous state, confluent with the magnum and third cuneiform, and can be detected only as distinct points of ossification. The rudiments of the lateral digits are generally preserved as slender elongated bones in the metacarpus, especially in Deer, much more seldom in the metatarsus. In the fossil Ruminantia from Auvergne these lateral rudiments are present, as a rule, on both the fore and hind limb (Plate XXXVII. fig. 16, II.). The rudiment of the fifth metatarsal is usually free, and has even a small facet on the cuboid; while the second metatarsal, being jammed in between the inner enlargement of the third metatarsal and the posterior beak-like prolongation of this digit, has generally coalesced; but its proximal extremity is mostly free, and articulated with the first cuneiform (and this is sometimes to be seen even in living Ruminantia).

The upper and posterior beak-like prolongations of the middle metatarsals of Paridigitata constitute a very characteristic feature of these bones; they grow larger and larger with the reduction of the pes, and are firmly pressed together by a special process of the cuboid and the first cuneiform in those genera in which locomotion is almost entirely performed by the two middle digits. Finally they coalesce, and the confluence of the metatarsals seems to proceed from these processes downwards, as is to be seen at a certain age in the metatarsus of *Dicotyles*.

Metacarpus and Metatarsus of Hyopotamus *and* Diplopus.

Having thus discussed at some length the shape and mutual connexions of the bones which compose the fore and hind limbs in the chief fossil and living Paridigitata, our task is made much easier in reference to *Diplopus* and *Hyopotamus*; and without dwelling too long on the description of very minute particulars of these bones, which to a certain extent are visible in the Plates, I shall merely state the chief features they present to the observer, and the points of agreement or difference with the corresponding bones of allied genera.

I begin with the metacarpals of *Hyopotamus*, or the tetradactyle form, and will afterwards pass to the didactyle *Diplopus*. The restoration of the manus of *Hyopotamus* from Puy is given in Plate XXXVII. fig. 20, $\frac{1}{2}$ nat. size, and the upper part of the same manus, fig. 5, Plate XXXVIII. The separate bones belonged to different individuals, and were not found in connexion. The fourth metacarpal especially is defective; but it is the only specimen of this digit I could find in the collections from Puy; it comes from a very young individual, and is therefore too small for the adult unciform by which it is supported. I have seen the same bones from Hempstead, but somewhat rolled.

The interlocking of the two *middle metacarpals* is effected in the usual way, the radial margin of the fourth being thrust under the ulnar prolongation of the upper margin of the third (Plate XXXVIII. fig. 5). This ulnar prolongation of the third metacarpal going to meet the unciform is very oblique in the *Hyopotamus*; its axis forming, approximately, an angle of 45° with a horizontal line. In the Suidæ, as well

as in the corresponding bone of *Diplopus* (Plate XXXVIII. fig. 6, III.), this projection is much more inclined (perhaps 30° with the horizon). The reason of this difference is given by the unciform, as the radial inferior truncature of this bone (Plate XXXVIII. fig. 5, *u*), to which the projection of the third metacarpal is articulated in *Hyopotamus*, becomes nearly vertical, and helps to constitute the inner radial wall of the same bone in *Diplopus* (Plate XXXVIII. fig. 8).

The *proximal surface* of the third metacarpal (fig. 5, III.) has an elongated, somewhat triangular, flat facet for the os magnum; this upper surface is sloping inwards, so as to allow the second metacarpal to lean laterally on this margin, and reach its facet on the os magnum, as seen in fig. 5. In *Diplopus*, on the contrary (fig. 6, III.), this upper radial margin of the proximal surface is produced upwards (as in *Palæochœrus*, Plate XXXVII. fig. 6); and therefore I think that, in the didactyle form, the rudiment of the second digit could not reach as high as the os magnum.

The *ulnar side* of the third metacarpal has an anterior reniform and a posterior oval facet; both articulate with corresponding facets on the radial side of the fourth digit. In the didactyle *Diplopus*, this anterior reniform facet is excavated into a deep hole for a corresponding large projection of the fourth metacarpal, as seen in Plate XXXVIII. fig. 6 : thus the interlocking of the two middle digits is much closer in the didactyle genus; and this is quite natural, as the foot, having no lateral digits, required a firmer structure.

The *radial side* of the third metacarpal in *Hyopotamus* has on its anterior part a tolerably long (7 millims.) facet, which is uninterruptedly united with the somewhat sloping radial margin of the proximal surface.. This facet is destined for the second metacarpal, which has a corresponding surface on its inner (ulnar) side; the bone on this side is flattened by the pressure of the complete lateral digit, as may be seen in the sections of the four metacarpals given below the fig. 5. If we compare this part of the third metacarpal with the corresponding region in *Diplopus* (fig. 6, III.), we shall see a great difference. In this last genus, as there is no lateral second metacarpal, but only a rudiment of it, we find a deep depression, with small longitudinal facets, where the rudiment (seemingly a nodular bone, as in *Anoplotherium*) adhered to the third metacarpal. We meet with an exactly similar hollow on the inner (radial) side of the third metacarpal in *Xiphodon*. On the upper and front part of this third metacarpal is a rough tuberosity for the tendon of the extensor carpi radialis muscle; this is not so prominent in the same bone of *Diplopus Aymardi* (fig. 6), perhaps owing to the younger age of the individual to which the third metacarpal of fig. 6 belonged.

The *fourth metacarpal* (Plate XXXVIII. fig. 5, IV.) of *Hyopotamus*, though represented very badly by a proximal half of the bone belonging to a young individual from Puy, shows, nevertheless, nearly all we require to know about it.

The *proximal surface* is flat, and has the shape of an isosceles triangle. On the radial upper margin we have a thickening at the point where the fourth digit is thrust under the ulnar prolongation of the third. The ulnar, or outer, side of the fourth metacarpal has two distinct facets, an anterior and a posterior one, for the articulation of the outer or fifth metacarpal.

The general shape of both middle digits in *Hyopotamus* is very flat in front, with two tolerably sharp edges, which form the outer and inner border of each metacarpal; the two inner, or contiguous, edges are formed by the metacarpals being pressed against each other in the axial line, while the outer edges result from the pressure of the lateral digits on the two middle ones from without and within (see fig. 5, and section). In the *Diplopus*, as we shall see hereafter, we have only the contiguous edges, while the outer sides of both metacarpals are rounded and smooth, there being no lateral digits. The section of the four metacarpals given below fig. 5 may give an idea of the flatness of these bones in the middle: it may be possible that they are somewhat flattened by pressure; but in the living Hippopotamus the metacarpals are perhaps relatively as flat. The length of the third metacarpal (drawn in outline) from Puy is given by a complete specimen in the collection of M. AYMARD. I have also several rolled specimens of both middle and internal lateral digits from Hempstead.

The distal ends of the two middle metacarpals (Plate XXXVII. fig. 20) are quite smooth in front; but on the posterior or palmar surface of each a median prominent *ridge* is seen corresponding with a *sulcus* on the proximal extremity of the first phalanx. In the Hog, this ridge goes round the whole distal end of the middle metacarpals. The outer half of this distal end is a little shorter than the inner, though the difference is not, by far, so great as in Suina; and the first phalanges being modified accordingly to fit the distal extremity of the metacarpals, the outer half of the proximal surface of each is slightly higher than the inner. This corresponding inequality of the distal ends of the metapodial bones and the proximal surface of the first phalanges is seen in many fossil genera, but is most manifest in the recent Suina. The purpose of this arrangement seems to be the compression of the metacarpals of the middle digits and the approximation of their distal ends. The two middle digits diverge in treading on the ground; but, by the same action, their proximal extremities tend to converge; and, owing to the special disposition of the metacarpo-phalangeal articulation, they compress the two metacarpals or metatarsals together. In such animals as the Hog, in which this disposition is strongly developed, and aided by a special adaptation of the tarsal, and to some extent carpal, bones to bring together the proximal extremities of the two middle digits, these two practically work like the cannon of a Ruminant. In *Hyopotamus*, however, this disposition is only indicated, while it is developed much better in *Diplopus*.

The lateral digits of the *Hyopotamus* are very well developed, and, in fact, besides the *Hippopotamus*, we know of no animal in which they are so complete and relatively large as in *Hyopotamus*. It is possible that in *Anthracotherium* they took even a more important part in locomotion; but the complete limbs of *Anthracotherium* are not fully known at the present time.

The *inner or second* metacarpal (Plate XXXVII. fig. 20, & Plate XXXVIII. fig. 5, II.) is represented in all collections I have visited only by its proximal half. The upper or proximal extremity of the second digit presents an elongated and concave articular surface for the distal face of the trapezoid; its ulnar margin, as seen in fig. 5, is blunted by an oblique facet, which must have abutted against the os magnum.

On the posterior edge of this second metacarpal is a small facet, probably for the trapezium; although I did not find this last bone, its existence must be inferred from a facet on the trapezium and this posterior metacarpal facet.

The general shape of the bone is somewhat triangular; on its flat side it is pressed against the third metacarpal.

The fifth *metacarpal*.—Of this bone I have seen only somewhat less than the upper third. As shown by this small fragment, the fifth digit was relatively well developed; our fragment probably comes from a larger individual than the other metacarpals. The proximal surface has a facet which occupies its entire antero-posterior depth and articulated with the unciform (fig. 5, v.); the inner side shows two separate facets, one anterior and one posterior, which entirely correspond with similar facets on the outer side of the fourth metacarpal (the Hog and Hippopotamus has only one such facet). The outer edge of this fragment is thickened and rugose for the attachment of ligaments.

The Metacarpus of Diplopus.

The chief differences exhibited by the two middle metacarpals of the didactyle *Diplopus* (Plate XXXVIII. fig. 6) have been to a certain extent already stated in the course of the discussion of the metacarpals of *Hyopotamus*; something may, however, be added. The general shape is exceedingly different, as may be seen by the sections. The two metacarpals of the didactyle *Diplopus* are much more mutually symmetrical than those of *Hyopotamus*; the contiguous sides are flattened in such a way that the two bones are pressed together on their flat surfaces, while their outer rounded outlines sweep in and out in a nearly regular quadrant, so that the two united metacarpals represent in section the half of a solid cylinder. These inner flattened faces are very rough, showing the attachment of numerous ligaments that held them firmly together. The distal extremity is turned a little outwards and broadened transversely; its inner half is much thicker or deeper than the outer, more so than in the recent Suina. The distal articular ridge of the metacarpals is limited only to the posterior or palmar side, although a faint trace of it is visible even on the anterior face of the distal extremity of the metacarpals. The semicircular line, where the anterior surface of the metacarpal passes into the distal articulation for the first phalanx, is only slightly excavated, while in the metatarsals this line presents a deep crescentic concavity; this furnishes a very good practical character for distinguishing broken distal ends of the metacarpals from the metatarsals.

We have already mentioned the difference in the proximal surface of the third metacarpal, by the radial edge (fig. 6, III.) being more raised, by the more horizontal direction of the ulnar process, and by the depth of the excavation, into which is fitted the radial projection of the fourth digit. The posterior surface of the metacarpal is flat, as seen in the section. The fourth metacarpal (Plate XXXVIII. fig. 6, IV.) shows similar differences; the proximal surface is of a rounded triangular outline to fit the similar facet of the unciform (fig. 8′, IV.); the projection on the radial flat

surface is very prominent, in order to enter into the deep pit on the ulnar side of the third and bring about a firm interlocking of the two digits. On the outer and posterior side, we see an excavation for the nodular rudiment of the fifth metacarpal, which, as it seems, did not touch the unciform, at least had no facet on it. The posterior surface is very nearly flat, and the section of the bone is a rounded triangle instead of being a flat trapezium as in the *Hyopotamus*. I have seen a complete specimen of only this single metacarpal; fortunately this gives us the length of the metacarpus in the didactyle genus; it is considerably longer than the metacarpus of *Hyopotamus*, as may be seen by comparing figs. 5 and 6 of Plate XXXVIII.

As we have no means of distinguishing with complete certainty the phalanges of the fore from those of the hind foot, they will be noticed after the description of the metatarsals.

The Metatarsals of Hyopotamus *and* Diplopus.

My materials for the hind foot are fortunately more complete than those for the fore limb, and the striking dissimilarity we noticed between *Diplopus* and *Hyopotamus* in considering the manus, is still more confirmed by the study of the pes. According to the order adopted by me, I shall describe at first the middle metatarsals, as they always exhibit the fundamental features of the pes, and consider the lateral digits afterwards. I begin with the tetradactyle *Hyopotamus*.

The *third metatarsal* (Plate XXXVIII. fig. 1, III.).—As in all Paridigitata, this meta tarsal is distinguished at once by the presence, on its fibular side, of a deep pit, into which fits the corresponding projection of the tibial side of the fourth (fig. 1, IV.), giving rise to the characteristic interlocking of the middle digits. The proximal surface of the third metatarsal (fig. 2′, III.) is of a rounded triangular outline, and slightly concave to meet the slight convexity of the distal surface of the third cuneiform (fig. 1, c_3). The third metatarsal is supported entirely by the third cuneiform; and as the lateral internal (tibial) side of this third cuneiform descends a little lower than the second cuneiform, the second metatarsal going to meet its typical second cuneiform, may lean also against the third cuneiform (fig. 2, II.), a constant feature in all unreduced Ungulata. The posterior projection of the metatarsals is very long, and pressed against a similar projection of the fourth metatarsal (fig. 2′, III., IV.); on the inner (tibial) side of this projection we see no trace of a facet for the first cuneiform, such as is presented by *Diplopus* (fig. 4″, fc_1) and the recent Suina. The inner or tibial edge of the proximal surface is slightly elevated, though not enough to exclude the second metatarsal from its facet on the third cuneiform, as it may be seen also in *Hippopotamus* and *Anthracotherium*. The outer, or fibular, side of the third metatarsal is flattened (section, fig. 1) in correspondence with the adjoining side of the fourth; besides the deep pit mentioned before, we see, on this side, a long narrow facet on the posterior projection (fig. 2′), articulated to a similar facet of the posterior projection of the fourth. (As the fourth metatarsal was slightly defective in my specimen, the posterior

projections of the two middle digits that must in reality articulate together are separated in the drawing.) The inner or tibial side of the third metatarsal shows an oval facet for the articulation of the second digit; a like facet is seen in the Suina and Hippopotamus, only much shorter.

The *fourth metatarsal* (Plate XXXVIII. fig. 1, IV.).—What at once strikes the observer on looking at this metatarsal, is the large projection of its tibial side, which enters into the corresponding pit of the third metatarsal; a little below it the inner surface of the bone is very rugose and bulging a little inwards. The proximal surface (fig. 2′, IV.) is slightly concave at its fore and inner part, and somewhat raised in the postero-external angle (the elevation is indicated in fig. 2′ by a deeper tint); this raised joint fits exactly into the postero-external concavity of the distal surface of the cuboid (fig. 10, IV.), while the remaining, and slightly convex, cuboidal surface is fitted to the slight concavity of the inner and fore part of the proximal surface of the fourth metatarsal.

The *outer side* of the fourth metatarsal has a lengthened oval facet for the articulation of the fifth digit; such a facet is to be seen in the Hog, only a little shorter. Whether the fifth digit articulated with the fourth by a second facet I am unable to say, as my specimen is a little defective; but very probably it did.

As the two middle digits, in their general shape, bear a great likeness to each other, all I shall say of one will be referable to the other. Their symmetry is somewhat disturbed by the slight bulging of the inner side of the fourth metatarsal; although, if we look at the anterior surface of the whole pes, this slight disturbance does not interfere with the general symmetry of the two middle digits.

The section of the middle digits (Plate XXXVIII. below, fig. 1) has a flattened trapezoid outline, especially if we take it in the upper part, where the posterior projection is prolonged downwards as a flattened platform in the upper half of the posterior surface of the metatarsals; towards the middle this platform subsides, and we have a more rectangular section. This flatness of the metatarsals is very striking in comparison with the rounded outline of the metatarsals in the didactyle genus; but one of the living Paridigitata, the Hippopotamus, has even much flatter metatarsals *, their thickness being only half of their transverse breadth. The outer margins of both middle metatarsals are made conspicuous and angular by the pressure of the completely developed lateral digits; their anterior surface is therefore very flat, even more so than in the living Hippopotamus. The middle metatarsals preserve a uniform breadth along their entire length, and we see no such conspicuous broadenings of the distal ends as in the didactyle form. The restored pes (Plate XXXVII. fig. 21) does not show this very clearly, as the complete digits from Puy were much disfigured by pressure; but it could be readily seen on some well-preserved fragments of the distal extremities. The distal end is quite

* I find in a Hippopotamus with epiphysed bones that the fourth and third metatarsal have 32 mm. transverse breadth each, and 16 and 17 mm. thickness or depth, while in *Hyopotamus* the breadth is 16 each and the depth 11 mm.

smooth anteriorly, the articular ridge for the first phalanx being limited to the posterior or palmar half of the distal surface.

The lateral digits were completely developed in *Hyopotamus* and, no doubt, played an active part in the process of locomotion. The second metatarsal, seen from the inner side in Plate XXXVIII. fig. 2, II., is articulated to the second cuneiform by a nearly circular, flat proximal facet; this facet occupies the whole upper, somewhat attenuated, head of the second metatarsal; the anterior part of this proximal head is pressed against the third cuneiform, as seen in fig. 2, II. c_3. On its postero-tibial side, a little lower down, is seen another elongated facet, to which was articulated the first cuneiform, although this last bone was not to be found in any of the collections I visited. The shaft of the second metatarsal was closely pressed against the third, and reached very low down the metacarpus, considerably lower than in the Hog; and in my restoration of the pes (Plate XXXVII. fig. 21) the lateral digits, as I am aware now, are too much shortened. The section of the second digit is perhaps more elongated than in my figure. The distal extremity is unsymmetrical, but very well developed, the ridge for the first lateral phalanx being very high and confined to the back part of the distal end. The truncated posterior border of the proximal end of the second metatarsal is very characteristic of all Paridigitata which have retained the lateral digits: it is to be met with in the Suina, in *Cainotherium*, and even in *Hippopotamus*; this truncature is intended for the first cuneiform, which articulates with the navicular, with the posterior part of the small second cuneiform, and, by a large facet, with the truncated posterior edge of the second metatarsal *.

The *fifth* (Plate XXXVIII. fig. 1, v., Plate XXXVII. fig. 21, v.) or outer metatarsal presents, at its proximal end, a triangular facet, corresponding to the facet v. on the distal side of the cuboid (Plate XXXVIII. fig. 10); the posterior end of this fifth digit is prolonged backwards into a projection which has very nearly the same antero-posterior length as the fore or articular part. The inner or tibial side has a half reniform facet for the articulation with the fourth metatarsal. The section of this digit in the middle gives a somewhat roundish outline; its general shape is oval, the proximal third is a little curved forwards to fit more exactly the outline of the neighbouring fourth metatarsal.

The Metatarsals of Diplopus.

Of these I found several specimens in a perfect state of preservation in the collection of the British Museum †. They are all said to come from Hordwell;

* In *Hyopotamus*, although the third cuneiform has no regular truncated edge, as in *Hippopotamus* (Plate XXXVII. fig. 10, c_3) and *Anthracotherium*, for the articulation of the second metatarsal, still this metacarpal, owing to the fact that the second cuneiform is situated a little higher than the third, is allowed to touch this last, remaining thus true to typical relations.

† On my second visit to Puy, after this paper was written, I saw, in the collection of Mr. VINAY, a detached second metatarsal of unusually large size. It belonged to the large species, and, judging by this bone, all the four metatarsals of the larger species of *Hyopotami* were nearly subequal, as in the recent *Hippopotamus*.

and I must state that I have not seen a single specimen belonging to the didactyle *Diplopus* from Hempstead, and, *vice versâ*, not a single specimen of the tetradactyle *Hyopotamus* from Hordwell. The state of preservation of the fossils in both deposits is very different, and, as far as I can judge from information received in the British Museum, the tetradactyle genus *Hyopotamus*, identical with the genus from Puy, seems to be confined to Hempstead, while the didactyle form is found only at Hordwell *. I hope, however, to discuss the stratigraphical questions more fully at the end of my paper.

The two middle metatarsals of *Diplopus*, seemingly from the same individual, with three tarsal bones, are figured of the natural size in Plate XXXVIII. figs. 3 & 4, and two others, from a larger individual, Plate XXXV. fig. 5. The three phalanges of the fourth digit are a restoration, as I had only the corresponding phalanges from the other side; the two metatarsals are also from different individuals, and the third is a little smaller than the fourth.

The difference of these two middle digits of the pes from the corresponding bones of *Hyopotamus* is very great in general shape, section, and in some of the minor relations to the tarsal bones, the principal relations being the same in both genera.

The dissimilarity in shape is of the same order as that noticed in reference to the metacarpals. Instead of the flattened and angular metatarsals of *Hyopotamus* as seen in section Plate XXXVIII. fig. 1, we have, in *Diplopus*, very rounded, mutually symmetrical digits, which adapt themselves mutually by a large, flat inner side, and are symmetrically rounded both in and outside, so as to present in section nearly a perfect half cylinder (Plate XXXVIII. v., figs. 3, 4, 5). By this shape they differ much from the middle digits of the equally didactyle *Anoplotherium* and *Anthracotherium magnum* (the digits of which I have from Rochette, Lausanne), but present a resemblance to the same bones of the *Xiphodon* and *Entelodon* (didactyle), and also to that of the common Hog, as this last may be said to be practically didactyle. As seen in Plate XXXV. fig. 5 the distal ends are considerably broadened, and the articular ridge, though confined to the palmar side of the distal extremity, is prolonged in the form of a very low, but visible, elevation along the lower end to the anterior surface of the distal articulation (see Plate XXXVIII. fig. 6, and Plate XXXV. fig. 5). These slight peculiarities, which are too numerous to be all noticed, clearly indicate a somewhat better adaptation to didactyle locomotion, or at least some nearer approach to our recent didactyle forms than is exhibited by older forms, such as *Anoplotherium*—every new experiment of nature to produce a didactyle genus seeming to be more successful than the preceding one. However, I have no doubt the experiment ended there; and no direct connexion exists between the didactyle

* I have seen a *very large* lunare from Hempstead, which appears to indicate the presence of a larger *Hyopotamus* in this deposit; a very large cuboid from the same locality, though much rolled, seems to indicate, so far as can be judged by its imperfect state, the presence of another very large tetradactyle species at Hempstead. The cuboid in question presented on its distal surface two facets for the fourth and fifth digits, and no beak-like posterior projection.

Hyopotamidæ and the living genera of Paridigitates, which, as it seems to me, have descended from a branch given off by the tetradactyle Hyopotamidæ of the Eocene epoch.

The proximal articular surfaces of the two middle metatarsals of *Diplopus* (Plate XXXVIII. fig. 4″) may be compared with the corresponding proximal surfaces of the tetradactyle *Hyopotamus* (Plate XXXVIII. fig. 2′), when the differences are seen at a glance. The facet (*cb.f*) is intended to meet a like facet on the inner side of the beak-like posterior projection of the cuboid (fig. 11, *f.my*); it is wanting in *Hyopotamus*, as well as the cuneiform facet (fig. 4″, fc_1) for the first cuneiform, which was wedged in between this posterior projection of the third metatarsal and the rudiment of the *second digit* (fig. 4″, II*r*). This rudiment was confluent with the third metatarsal in one of the figured specimens (fig. 4 and 4″, II*r*), but it was absent (because not so coalesced) from all the other specimens of the third metatarsals in the British-Museum collection—for instance, from the third metatarsal represented in Plate XXXVIII. fig. 12. On the free (outer and inner) sides of both metatarsals are longitudinal facets to which the rudiments were articulated; these last, however, I could not find, save the one of the second metatarsal ankylosed to the third represented in fig. 4, Plate XXXVIII.

The interlocking of the two middle metatarsals was effected by a very prominent tubercle of the fourth entering a deep pit on the fibular side of the third, as seen in the figures; besides there is an oval facet on the inner faces of the posterior projection of each metatarsal. The beak-like downward process of the cuboid and the wedge of the first cuneiform pressing laterally from the inner and outer sides upon these posterior projections of the two middle digits held them firmly together. This close fitting of the two metatarsals (and metacarpals) together was further assisted by the mode of metatarso-phalangeal articulations universal among Paridigitata—namely, by the outer halves of the distal surface being a little shorter than the inner (as is clearly seen in Plate XXXVIII. fig. 6): in the phalanges the relation is inverse, and therefore in treading on the ground their upper ends are made to converge and to press the two metatarsals and metacarpals together; the two separate metatarsals, compressed in this way, approach as near as possible to the cannonbone of modern Ruminantia.

Phalanges.

The *first phalanges.*—In a set of mixed phalanges belonging to both *Diplopus* and *Hyopotamus* it would be utterly impossible to distinguish the bones belonging to each genus: as difficult is it to separate those of the manus from the phalanges of the pes; their relative height and thickness present no good constant characters. One of the best authorities, Professor HENSEL, in his memoir on *Hipparion*, printed in the Transactions of the Berlin Academy for 1861, tells us that it is even impossible to distinguish the fore and aft phalanges of living Ungulata in the case of several individuals being mixed together. This may serve as an excuse for my not trying to do it among the fossils; and I therefore intend to give only a general description, which will apply to both the fore and hind limb.

The phalanges of *Hyopotamus* found at Puy, where the didactyle *Diplopus* is not present, are, by this fact, already separated by nature. As seen in Plate XXXVII. figs. 20 & 21, they strike us as being much longer than in most of the living genera, and considerably longer than in *Anoplotherium*. In *Xiphodon* and *Entelodon*, however, the first phalanges are also very long.

The upper, or proximal, articular surface is not symmetrical, as the inner side of the first phalanx is considerably thicker than the outer, in correspondence with the same inequality of the distal extremities of the metacarpal and metatarsal bones. The same difference in the thickness of the inner side is also to be seen on the distal extremity. The proximal surface is concave, and the groove for the articular ridge of the metacarpal is limited to its posterior third only. This thickening of the inner side makes also the inferior end not completely symmetrical; and this want of symmetry is much greater in the first phalanges of the didactyle *Diplopus*.

The *second phalanges*.—The second phalanges of all Paridigitata (with the exception of *Hippopotamus* and *Camelidæ*) are very characteristic, as their distal extremity is shaped unsymmetrically in a peculiar manner, so as to cause the ungual phalanges to converge in treading on the ground. For this purpose, the outer half of the distal articular surface is not only much larger than the inner, but bends obliquely inwards, and the ungual phalanges following this inner curve tend to converge. This arrangement is very strongly developed in the second phalanges of *Anoplotherium* (see De Blainville, Ostéogr. *Anoploth.* pl. iii.); it may be seen in every Ruminant as well as in the Suidæ. *Hyopotamus* and *Diplopus* also have second phalanges shaped on this pattern; only this want of symmetry is not so clearly developed as in the Suina or Ruminantia.

The *third phalanges*.—These have a very peculiar shape and are quite identical in both genera. This strange shape I can compare to nothing better than to a very thickened and rounded human nail. Their proximal surfaces are unsymmetrical, to fit the unsymmetrical distal end of the second phalanges; but the remaining part is much more symmetrical than in the Suina or Ruminantia, the inner side not being flattened at all, or very slightly. The palmar surface is quite flat. The lower and anterior margin shows the usual vascular foramina and a certain crispness to allow a firmer fitting of the horny hoof.

With this I conclude my description of the long bones of the skeleton and the bones of the limbs; the latter are all figured of the natural size, and the sections give a correct idea of their breadth and antero-posterior depth. Some exact dimensions which could be taken are given in the general Table (p. 90) I have taken the liberty of disposing right and left as best suited my purpose; and while some bones from the collection of the British Museum were drawn directly from nature, and therefore in the Plates appear to belong to the opposite side, others have been reversed.

Table of Measurements of the Extremities *.

	Hyopotamus.				*Diplopus.*	
	Puy.		Hempstead.		Hordwell.	
METACARPALS.	III.	IV.	III.	IV.	III.	IV.
Length	105	....	....	....	....	138
Transverse breadth, proximal face	17	16½	17	16	19	20
„ „ middle	16	15½	....	15	....	18
„ „ distal extremity	20	....	....	....	....	22
Antero-posterior depth in the middle	10½	....	10	10	14	16
METATARSALS.						
Length	113	....	....	....	140	156
Transverse breadth, proximal face	18	18	....	14, 13	18, 15	22, 18
„ „ middle	16	16½	....	9, 10	15, 14	16, 17
„ „ distal extremity	....	....	....	....	20	24½
Antero-posterior depth in the middle	11	10	....	....	16, 15	17, 16
FIRST PHALANGES.						
Length	48, 49, 50		37, 38, 40		51	
Transverse breadth, proximal face	21, 21, 22		16, 16, 17		25	
„ „ distal extremity	15, 16, 16½		13		17½	
SECOND PHALANGES.						
Length	25, 24		....		25, 30	
Transverse breadth, proximal face	16, 15½		....		18, 19	
„ „ distal extremity	14, 13½		....		16, 17	
THIRD PHALANGES.						
Length	27, 28		....		29	
Transverse breadth, proximal face	14, 14½		....		15	

EXPLANATION OF THE PLATES.

PLATE XXXV.

Fig. 1. Scapula of *Diplopus*, Hordwell, ⅔ nat. size. Brit. Mus.
a, acromion; *cp*, coracoid process.

Fig. 2. Distal extremity of the femur of *Hyopotamus*, Hempstead. Mus. Pract. Geology.
it, internal trochlea.

Fig. 3. Extremity of the fibula of *Diplopus*, nat. size, Hordwell. B.M.

Fig. 4. Calcaneum of *Diplopus*, Hordwell. B.M.
ff, fibular facet; *as*, astragalean facet; *cb*, cuboid facet.

* The absence of a number indicates that the bone was broken at that particular place and did not allow of exact measurement. My materials for the lateral digits were much more scarce than for the middle ones, as the former, through their slenderness, are often broken and lost. Nearly all the bones of *Hyopotamus* figured, from Puy and Hempstead, belong to the small species *Hyopotamus velaunus*, Aym. Such measurements as I could take of the lateral digits show that they have half the breadth of the middle ones. So the breadth of the second metacarpal from Puy is 8 millims., the depth 10 millims.; the second metatarsal is 8½ millims. broad, and 6 deep at the attenuated proximal end; the fifth metacarpal is 9½ millims. broad and 8 millims. deep at the proximal end; the fifth metatarsal is 9½ millims. broad and 9 millims. deep.

Fig. 4′. Calcaneum of a Perissodactyle (*Anchitherium*).
i, internal astr. facet; *e*, external astrag. facet; *s*, sulcus sustentaculi.
Fig. 5. Two metatarsals of *Diplopus*, left foot, from the New Forest (Brockenhurst). B.M. The phalanges of the third digit are restored.
Fig. 5′. Section of these two metatarsals in the middle.

All the figures except the scapula are of the natural size.

PLATE XXXVI.

Figs. 2 & 3 are of the natural size, all others two thirds of the natural size.

Fig. 1, side, and fig. 1′, front view of the ulna of *Diplopus* from Hordwell. B.M.
or, outer radial facet; *ir*, internal radial facet.
Fig. 2. Front view of the upper part of the ulna of *Hyopotamus*, Puy: *or*, external radial facet; *ir*, internal radial facet; *cb*, connecting bridge.
Figs. 1″ & 2′. Sections of both ulnæ: *e*, external; *i*, internal edge; *a*, anterior; *p*, posterior surface.
Fig. 3. Proximal part of radius of *Hyopotamus*, Hempstead. B.M.
Fig. 3′. Distal extremity of the radius of *Hyopotamus* from Hempstead.
ex, external; *i*, internal side, B.M.
Fig. 4. Humerus of *Diplopus*, from Hordwell. B.M.
c, intercondylar perforation; *a*, middle bulging; *b*, internal projection.
Fig. 4′. Section of the same.
Fig. 5. Femur of *Hyopotamus* from Puy.
t.mj, trochanter major; *t.mn*, trochanter minor.
Fig. 6. Smaller femur from Hempstead. B.M.
Fig. 7. Tibia and fibula of *Diplopus*, Hordwell. B.M.
Fig. 7′. Distal view with the fibula. Fig. 7″. Section about the middle of the bone.

PLATE XXXVII.

Letters common to all the figures:—*s*, scaphoid; *l*, lunar; *p*, pyramidal; *tz*, trapezium; *t*, trapezoid; *m*, os magnum; *u*, unciform; *c*, calcaneum; *a*, astragalus; *n*, navicular; *cb*, cuboid; c_3, third, c_2, second, and c_1, first cuneiform.
Fig. 1. Right fore foot of *Hippopotamus*; fig. 2 of *Anoplotherium tridactylum* from Vaucluse; fig. 3 of *Xiphodon*.
Fig. 4. Side view of the right fore foot of the Hog; fig. 5 of *Dicotyles*; fig. 7 of *Tragulus Kantchil*; fig. 8 of *Hyomoschus aquaticus*.
Fig. 6. Third right metacarpal of *Palæochœrus* (Allier), to show the absence of the radial enlargement.

Fig. 9. Right hind foot of *Hippopotamus*. Fig. 10. Side view of the same, to show the articulation of the third and second metatarsals with the first, second, and third cuneiforms.

Fig. 11. Left hind foot of *Anoplotherium tridactylum*.

Fig. 12. Side view of the right hind foot of the Hog; articulation of the third and second metatarsals with the three cuneiforms. Fig. 12′. Third metatarsal of *Palæochœrus*. Fig. 13. *Dicotyles*. Fig. 14. *Hyomoschus aquaticus*. Fig. 15. *Tragulus Kantchil*. Fig. 16. *Amphitragulus* (?) from Allier.

Fig. 17. Distal surface of the navicular of *Anoplotherium commune*, Paris gypsum, to show the facets for the three cuneiforms.

Fig. 18. The same bone from Vaucluse. Fig. 19. The same bone, *Anoplotherium tridactylum*, to show the great development of the facet for the second cuneiform (c^2), which carries the second digit.

Fig. 20. Fore foot of *Hyopotamus* from Puy (partly restored).

Fig. 21. Hind foot of the same.

Figs. 1, 9, and 10, $\frac{1}{5}$ nat. size; figs. 2, 11, 20, and 21, $\frac{1}{2}$ nat. size; all others of the natural size.

PLATE XXXVIII.

Same letters as in Plate XXXVII.

Fig. 1. Hind foot of *Hyopotamus*, Puy.
as, astragalean; *cl*, calcaneal facet of the cuboid.

Fig. 2. Same, side view. The third and second cuneiforms are coalesced; the first cuneiform is absent.
Below fig. 2, proximal faces of the four metatarsals and section of the same.

Fig. 3. Hind foot of *Diplopus*, Hordwell. B.M.

Fig. 4. Side view of the same.
b.cb, beak of the cuboid; fc_1, facet for the first cuneiform; II*r*, rudiment of the second metatarsal coalesced with the third.
Fig. 4′. Section of the two middle metatarsals at half their length.

Fig. 4″. Proximal view of the metatarsus of *Diplopus*.
cb.f, facet for the descending beak of the cuboid; fc_1, facet for the first cuneiform; II*r*, rudiment of the second metatarsal coalesced with the third.
Outline of the distal face of the two coalesced cuneiforms (third and second) of *Diplopus*, fitting the proximal face of the third metatarsal with the coalesced rudiment of the second metatarsal (II*r*). B.M.

Fig. 5. Fore foot of *Hyopotamus*, Puy.

Fig. 6. Two metacarpals of the fore foot of *Diplopus*, Hordwell. B.M.

Fig. 7. Distal view of the unciform of *Hyopotamus* from Puy.
III, IV, V, facets for the corresponding metacarpals.

Figs. 8 & 8′. Front and distal view of the unciform of *Diplopus*, Hordwell. Mus. Cambridge.
ln, lunar facet; *py*, pyramidal facet; III, V, facets for the two metacarpals.

Fig. 9. An unciform of *Hyopotamus* from Hempstead. Fig. 9′. Distal view of the same. Smaller than the unciform from Puy. B.M.

Fig. 10. Distal view of the cuboid of *Hyopotamus*, Puy.
tr, transverse ridge; IV, V, facets for the two corresponding metatarsals.

Fig. 11. Distal view of the cuboid of *Diplopus*. B.M.
f.my, facet for the fourth metatarsal on the posterior beak; IV, facet for the single fourth metatarsal.

Fig. 12. Another third metatarsal of *Diplopus*, without the rudiment of the second.

All the hind feet are right; the fore foot is left.

PLATE XXXIX.

Fig. 1. Cranium of the largest species of *Hyopotamus*, from Puy. Two thirds nat. size.

Fig. 2. Side view of the head of a smaller *Hyopotamus*, from Puy. Nat. size.

Fig. 3. Lower jaw of the same; said to come from the same block.

Fig. 3′. Upper view of the anterior extremity of the lower jaw.

Fig. 4. One molar (m^1) and three milk-molars of *Hyopotamus*, Puy.

Fig. 5. Part of the head, from the postglenoid process to the occipital condyle.

Fig. 6. Dorsal vertebra of *Hyopotamus*.

Fig. 7. Second cervical vertebra of *Hyopotamus*, from Puy. Collection Pichot.

Fig. 8. Left lower molar of *Chalicotherium*. Fig. 9. *Anoplotherium*. Fig. 10. *Dichobune bavarica*, Fraas. Fig. 11. *Hyopotamus*. Fig. 12. Ruminant from Allier.
ac, anterior crescent; *pc*, posterior crescent; *ap*, anterior pillar; *pp*, posterior pillar.

Fig. 13. Left upper molar of *Rhagatherium*; fig. 14 of *Hyopotamus Gresslyi*. Fig. 15. Intermediate form between the *Hyopotamus* and *Dichodon*; the anterior middle (fifth) lobe is coalesced with the internal. Fig. 16. *Dichodon*, from Mauremont.
el, external anterior lobe; *ml*, middle anterior lobe; *il*, internal anterior lobe.
The teeth (figs. 13, 14, 15) have the three lobes on the fore part of the tooth.

Fig. 17. Left upper molar of *Dichobune leporina*, Cuv.; and fig. 18 of *Cainotherium*: the three lobes are on the posterior part of the tooth.

Fig. 18. The so-called *Cainotherium* (*Hyopotamus*) *Renevieri*, Pict., having, like all the other *Hyopotamidæ*, the three lobes on the anterior part of the tooth.

PLATE XL.

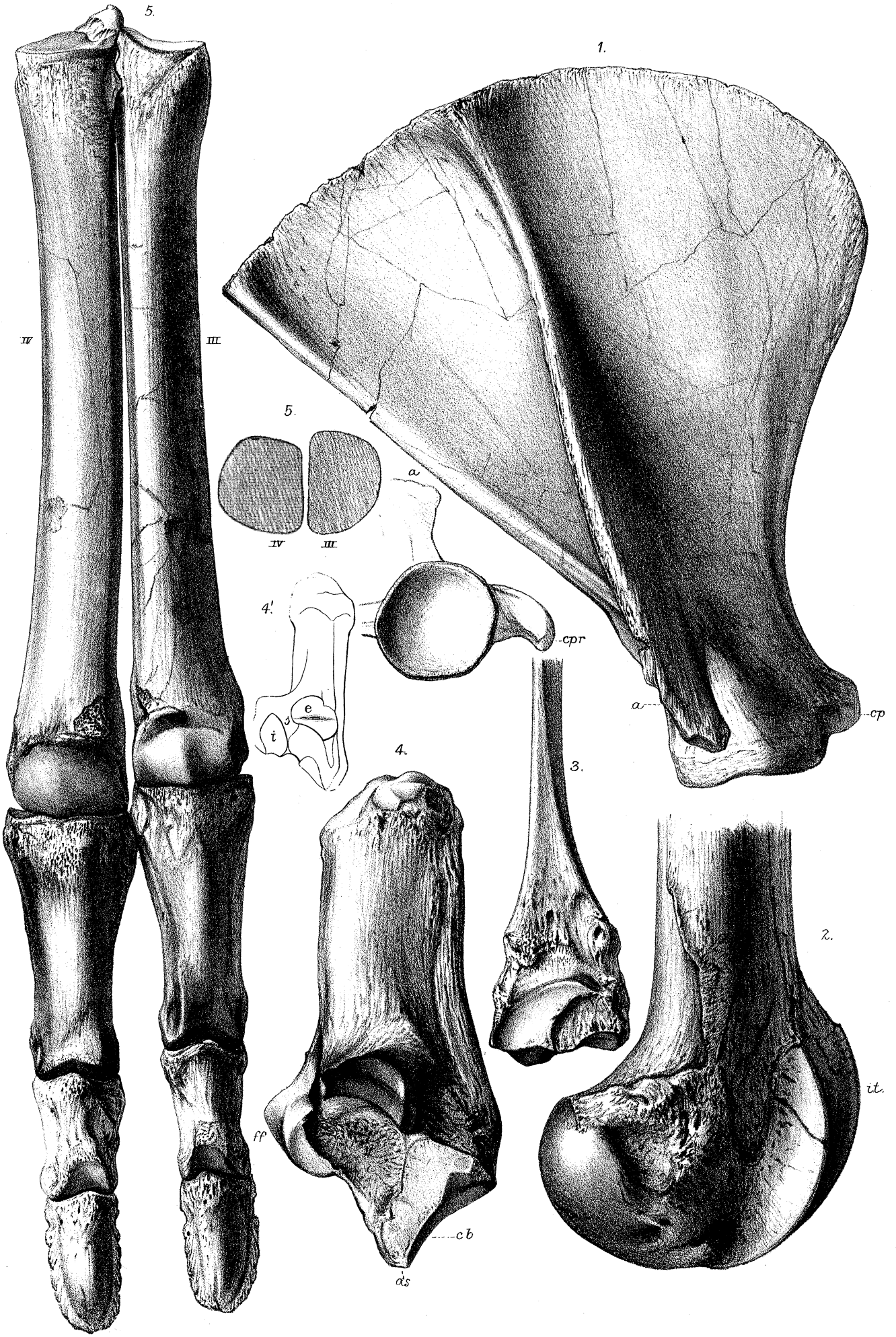
Fig. 1. Head of *Hyopotamus velaunus*, Aym., from Puy; restored, but belonging to one individual: all the pieces were found together in the same block. Side view.

Fig. 2. View from above, to show the great sagittal crista.

Fig. 3. Lower jaw of a very young *Hyopotamus* from Puy; the first molar is concealed in the jaw.

d^1, d^2, d^3, the three milk-molars; p^4, the first premolar which has no milk-tooth to precede it.

Fig. 4. Upper view of the three milk-molars.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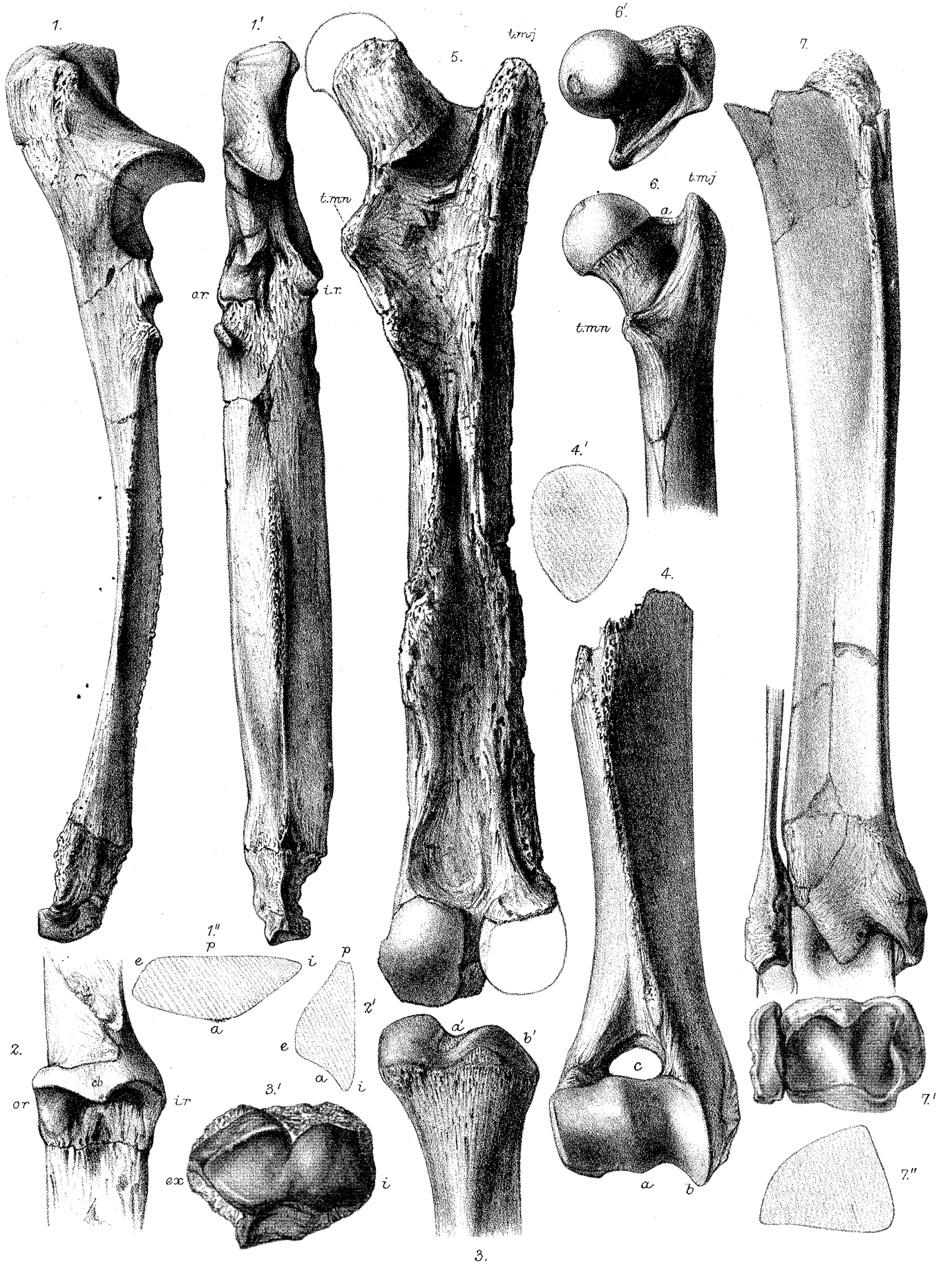
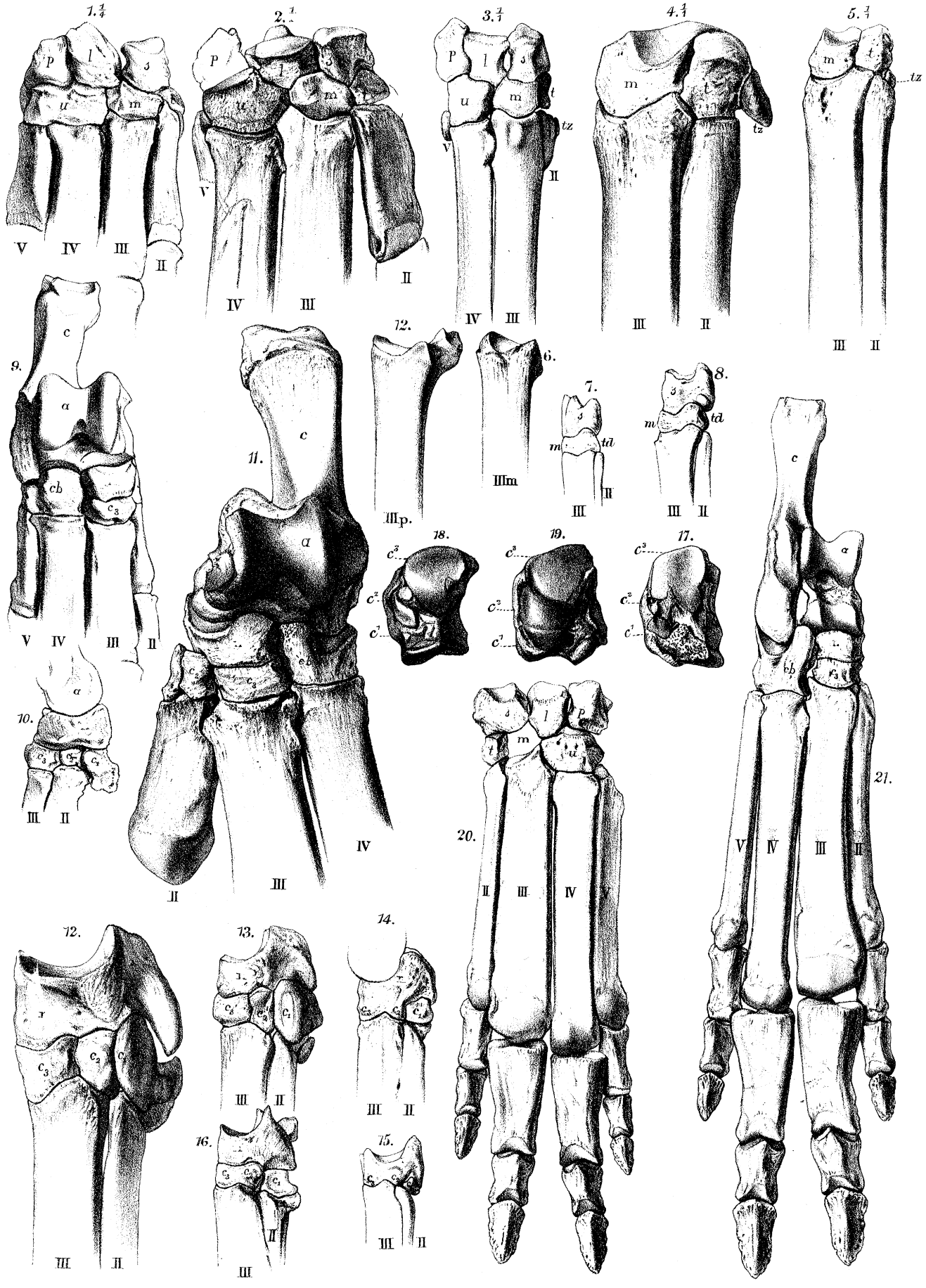
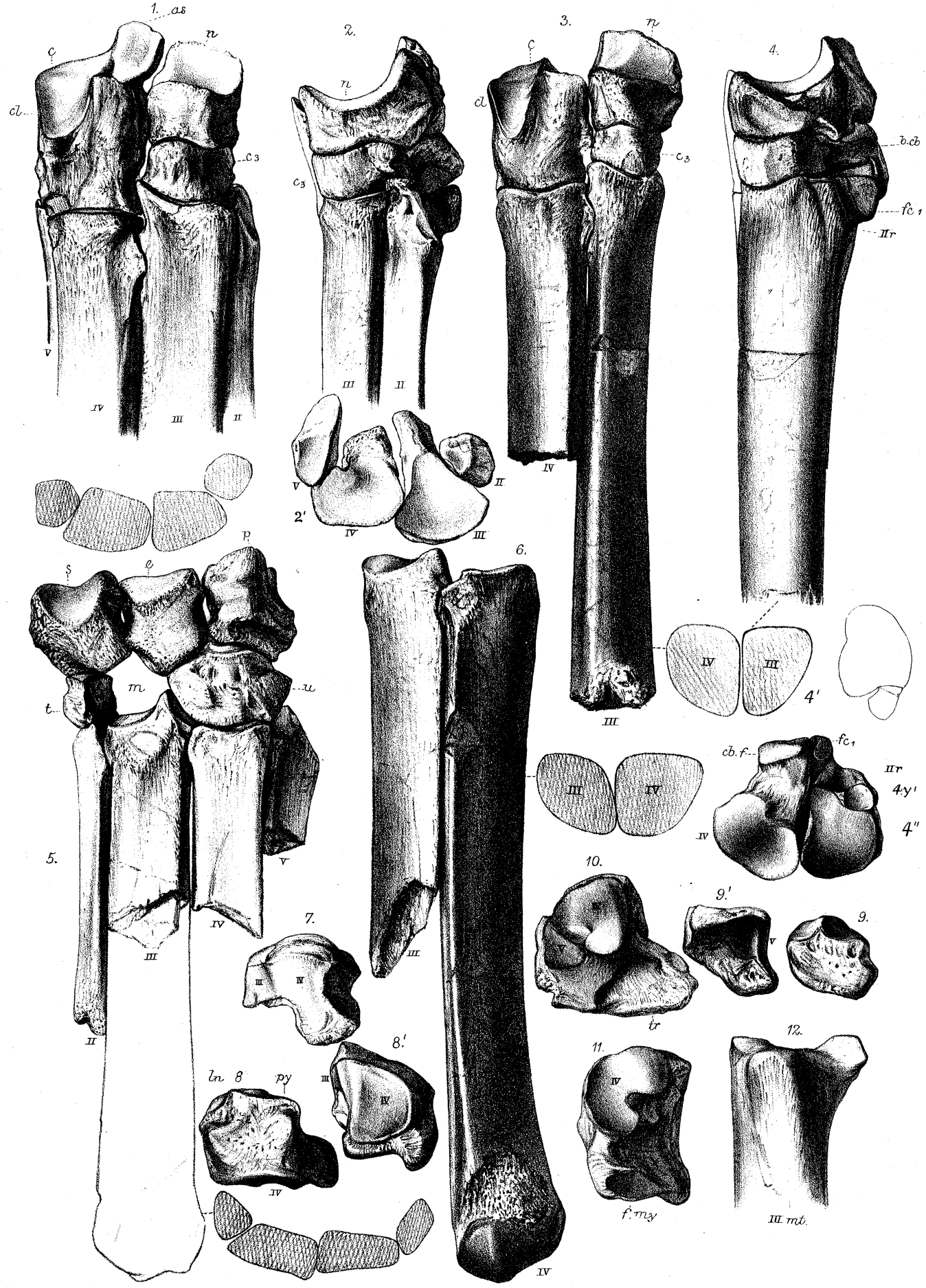


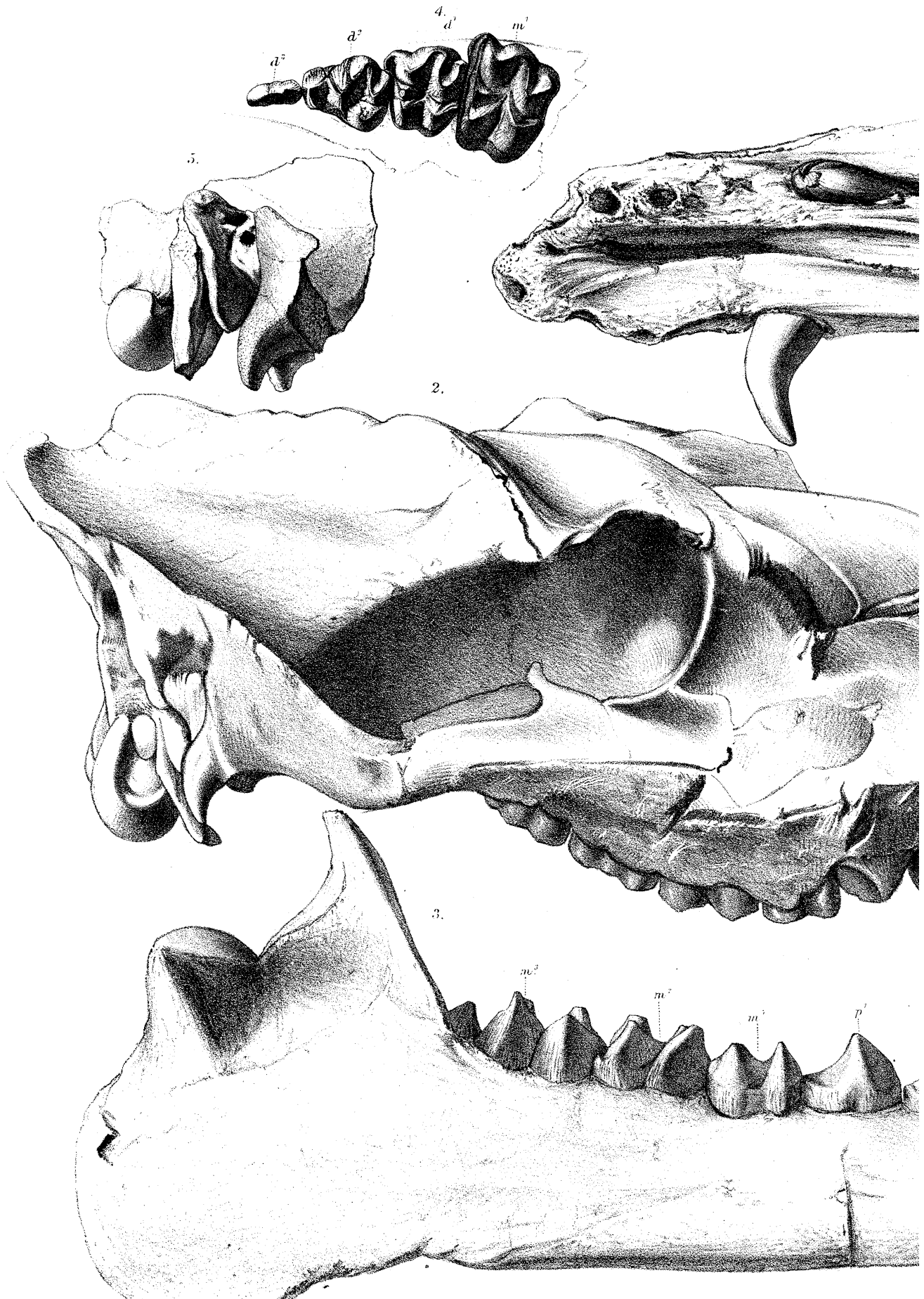
C.L. Griesbach lith.

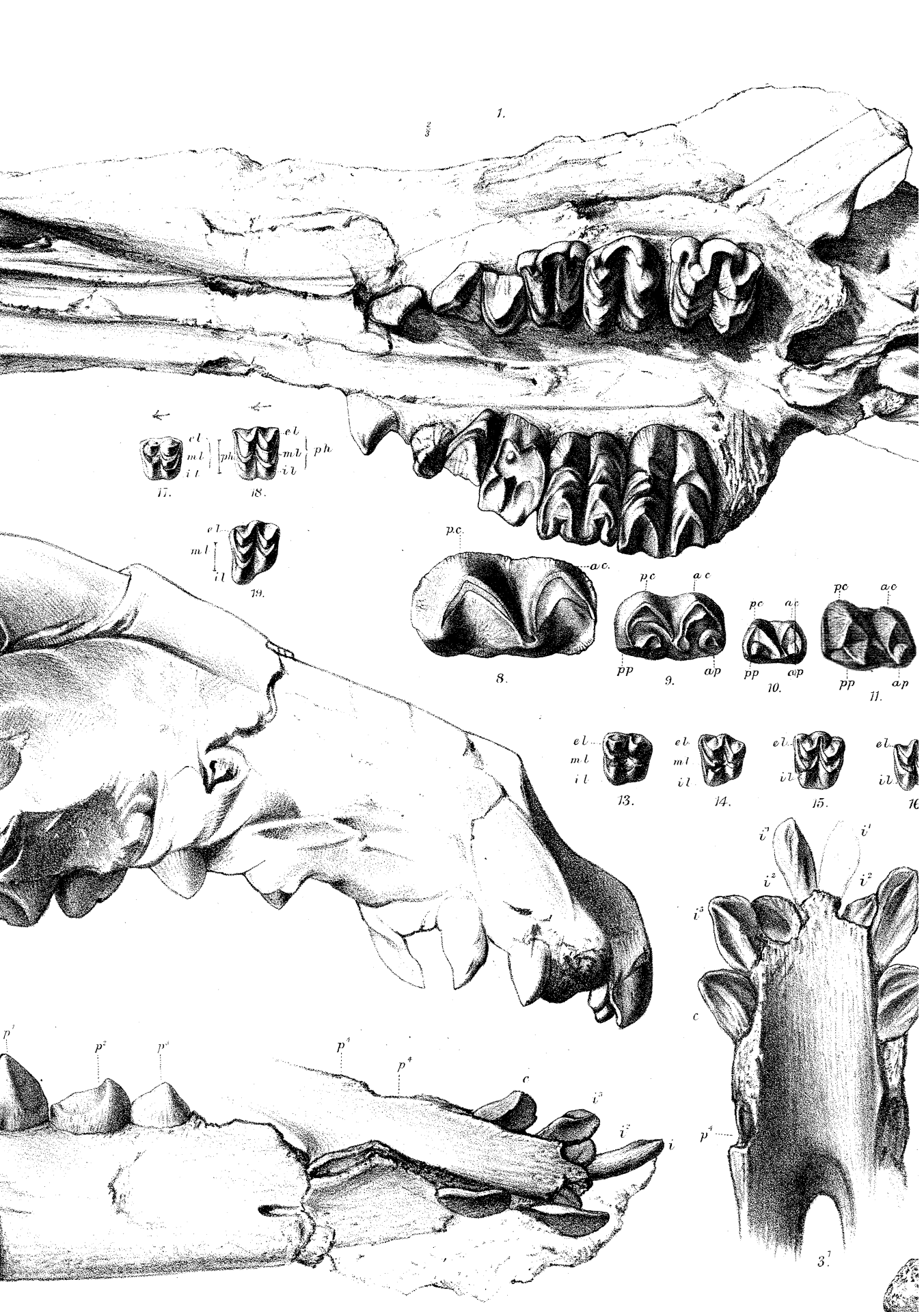
Mintern Bros. imp.

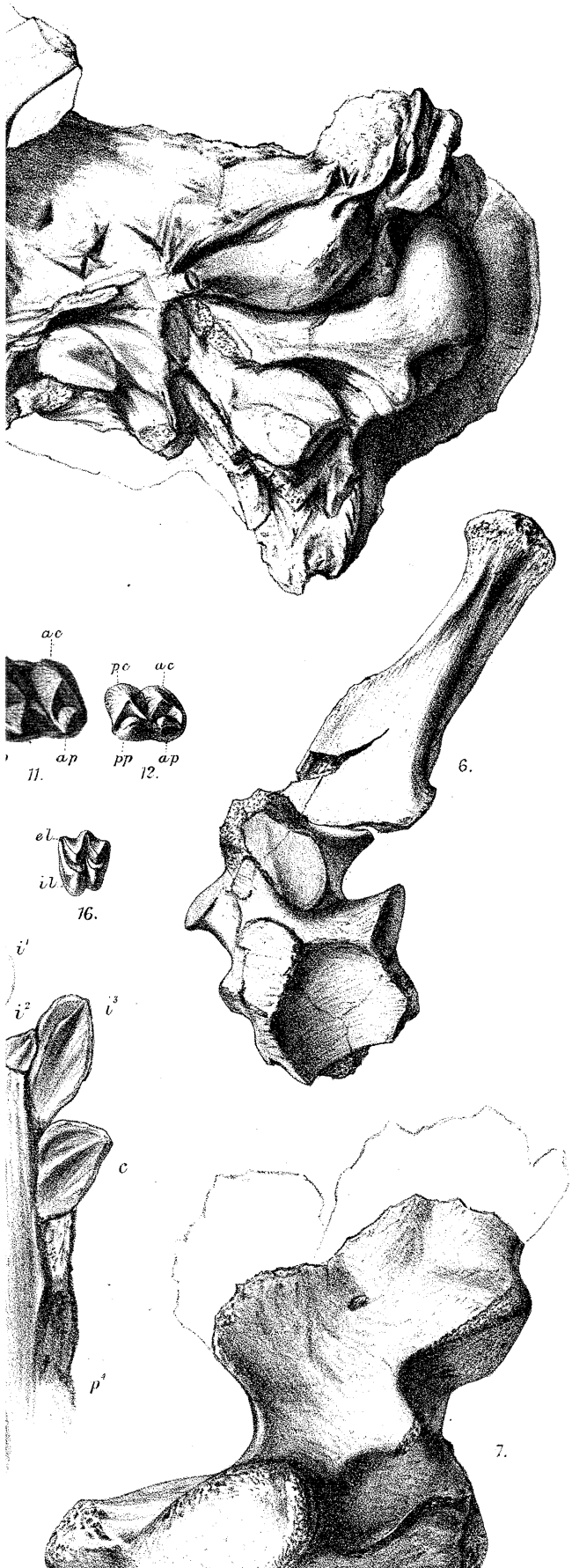

1. 1/4
2. 1
3. 1/1
4. 1/1
5. 1/1
P
l
s
u
m
t
tz
V
IV
III
II
9.
c
a
cb
c3
10.
11.
12.
IIIp.
6.
IIIm
7.
td
8.
18.
19.
17.
c3
c2
c1
20.
21.
16.
15.



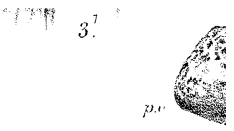
C.L. Griesbach lith. Mintern Bros. imp.

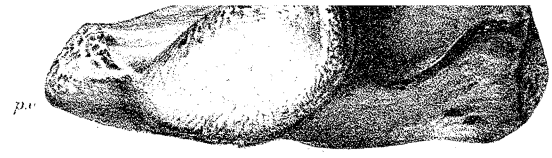

4.
d²
d¹
m¹
d³
5.
2.
3.
m³
m²
m¹
p¹


1.
2/3
el
ml
il
ph
17.
18.
19.
pc
ac
8.
pp
ap
9.
10.
11.
13.
14.
15.
16
i'
i²
i³
c
p⁴
3.

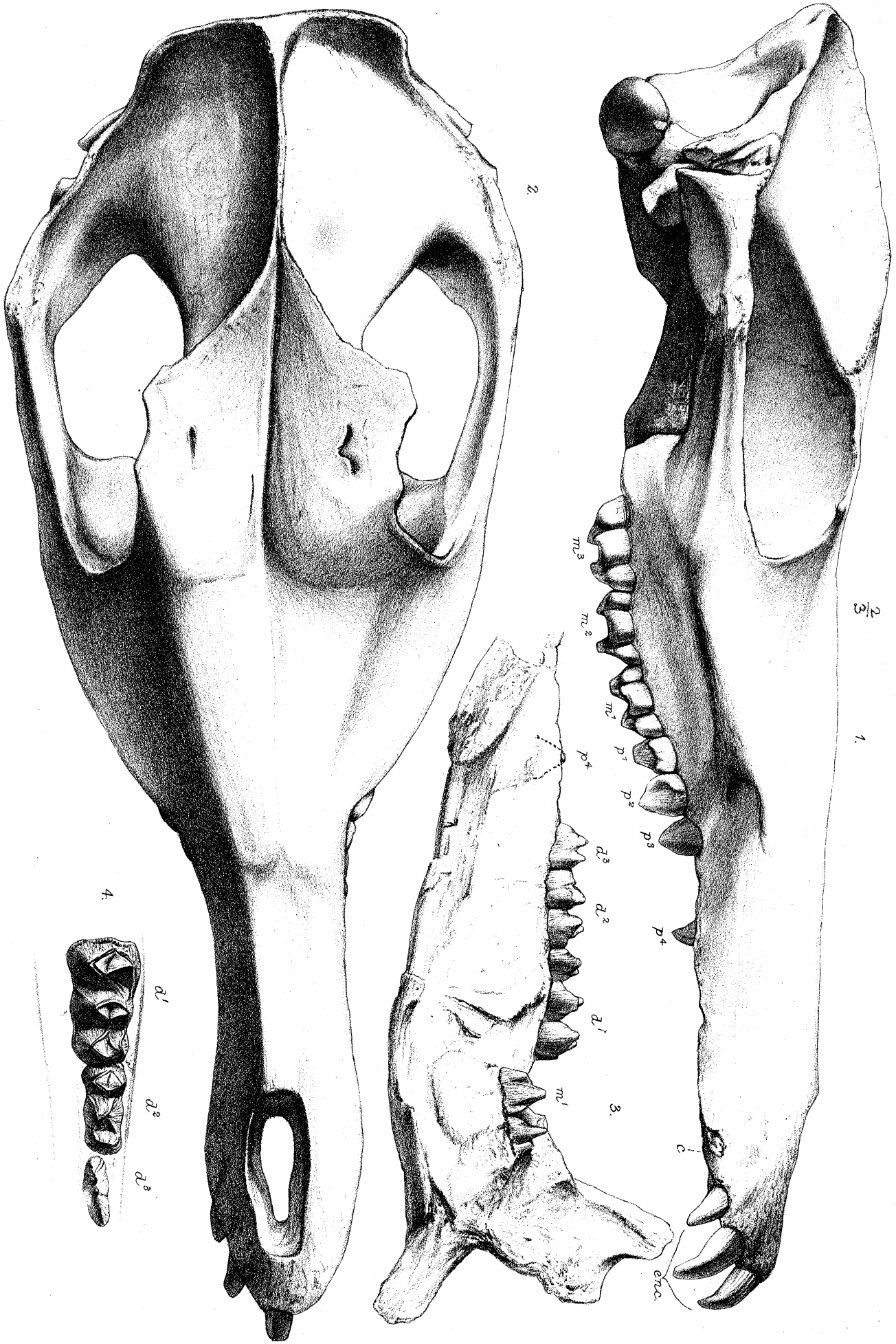
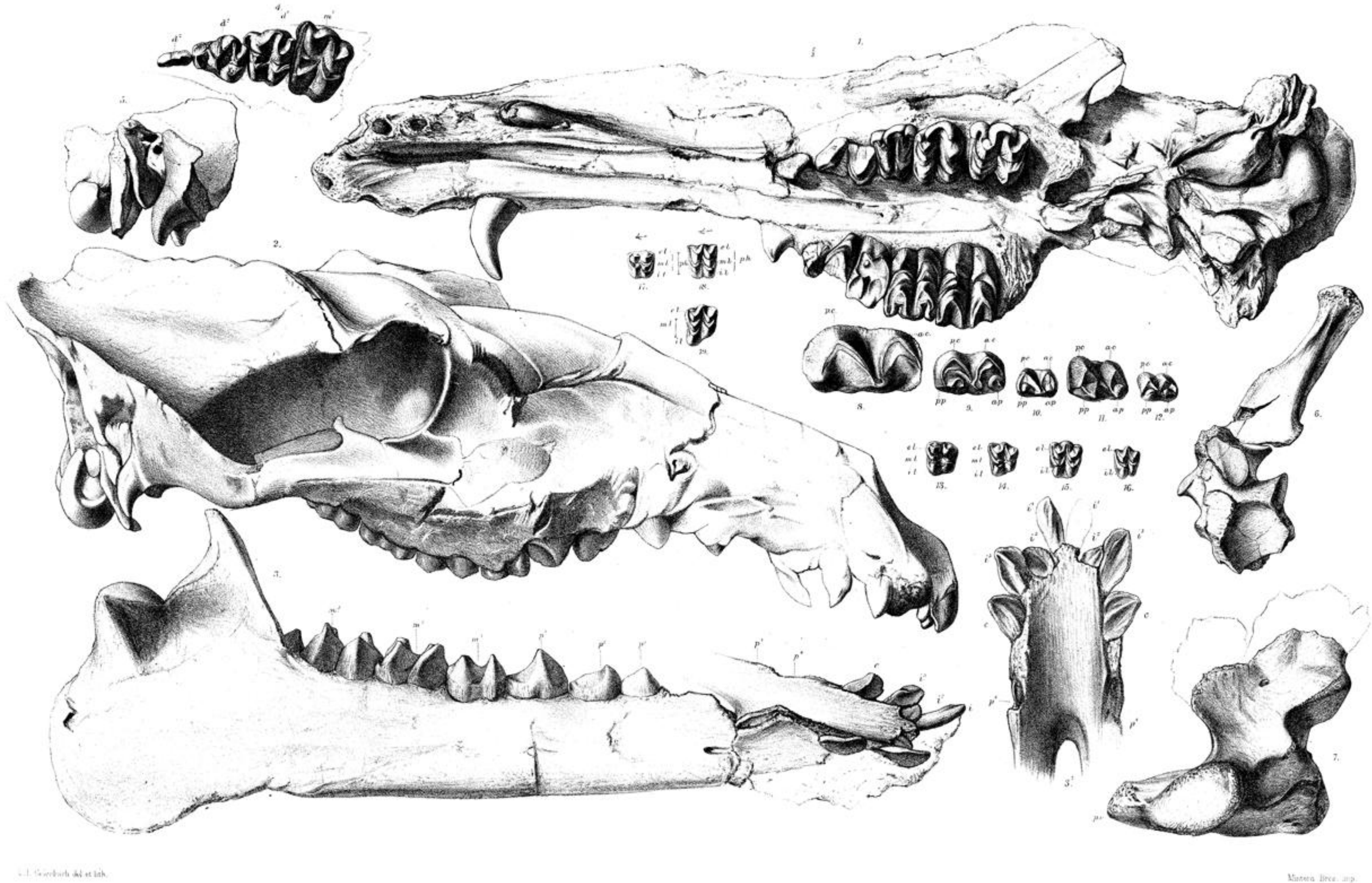

ac
ap
11.
pc
ac
pp
ap
12.
6.
el
il
16.
i'
i²
i³
c
p⁴
7.

C. L. Griesbach del et lith.





Mintern Bros. imp.



G.L. Griesbach lith. Mintern Bros. imp.