fringes 15. The left opercular gill was absent, and nothing indicated its absence to be the result of an injury.

Mr. R. Lydekker, F.Z.S., exhibited a pale-coloured specimen of the Reed-buck (*Cervicapra arundinum*), and read the following notes on it, extracted from a letter addressed to him by Mr. Ewart S. Grogan:—

"I have much pleasure in forwarding to you the horns, head-skin, and hide of what appears to be a white Reed-buck. I shot the latter on the Longwe, at the north end of Lake Nyasa. Capt. Verhellen, of Mohun's expedition, first called my attention to it, by asking me (he knows nothing of the game in this part) what those little grey antelope were; he was *very* positive as to having seen four: one, a female, he wounded and lost; but though I hunted the small plain where he states he saw them, I never found any but the ram I killed, and it is the Reed-buck's habit to generally run in the same party; *i. e.* four running together would, I think, never go far apart, at any rate at the same season of the year. The natives whom I questioned closely say they have seen one only; but this counts for little. The buck showed no signs of albinism—lips, nostrils, *eyes*, and hoofs being of the normal colour. On comparing the skull with two others I thought I detected considerable variations, especially in the base of the skull. Will you kindly describe the animal for me, and bring it before the notice of those who are interested in this branch of zoology? Personally I am inclined, owing to the persistent rumours of similar animals in this country, the striking and *very* definite assertion of Capt. Verhellen, and the complete absence of the usual signs of albinism, to think that it is a distinct form. I have taken what measures I could to preserve the skin and trust that it will arrive in good order."

The following papers were read:—

1. On the Primitive Type of the Plexodont Molars of Mammals. By Florentio Ameghino, C.M.Z.S.

[Received February 13, 1899.]

The majority of placental Mammals, and especially the Ungulates, are distinguished by the plexodont character of their molars—that is, by molars having a complicated crown, and each tooth being provided with more than one root.

The origin of this dentition has been explained by two completely different theories—the theory of a gradual complication, and that of fusion. According to the former, the plexodont molars are the result of a progressive complication of the simple and conical primitive tooth of Reptilia. According to the latter, these same teeth are the result of fusion of the dental germs or embryos of several simple teeth. It is this latter theory which I have been upholding for the last 15 years.

In a memoir published about three years ago[1], I showed that the tritubercular theory, contrary to what has been asserted, does not agree with the facts furnished by either the embryology, palæontology, or general morphology of the mammalian dentition. I observed, moreover, that triconodonty and trituberculy, far from being stages leading to the more complicated forms of teeth, are, on the contrary, the result of the reduction of the latter. It was not until after the publication of my paper that I learned that Dr. Forsyth Major had expressed views similar to mine in the Proceedings of this Society.

As a complement to my preceding work, I shall now endeavour to determine the most primitive type at present recognizable in the crown of the lower plexodont molars of Mammalia. In a subsequent paper I shall deal with the upper molars.

Firstly a few words on the terms used by me. I recognize in the dentition :—

(1) The deciduous molars (milk-teeth) and the persistent molars (true molars), representing together the *first series*, which is the oldest from an embryological as well as from a palæontological point of view.

(2) The replacing molars (premolars), representing the *second series*, which is of more recent date and always remains incomplete.

I assign to the teeth behind the canines the progressive numbers 1 to 7, since they are perfectly homologous in the Placentals and Marsupials, the only difference being that some teeth may belong to the first series in certain genera (*e. g.* the fourth of Marsupials) and to the second series in others (*e. g.* the fourth of Placentals).

Each of the lower complicated molars exhibits two lobes, an anterior and a posterior, and six cusps or denticles, three for each lobe. According to the authors of the tritubercular theory, these cusps have made their appearance gradually in successive geological periods, and they assign to each cusp a different name. These names have different suffixes in the molars of the two jaws; furthermore, there are different names for the same cusps in the premolars, for the lobes according to their form, for the colonnettes (styles) and crests (lophs), &c.; constituting altogether such a complicated terminology, that it remains absolutely unintelligible for all who have not specially studied the argument, and discourages many persons who wish to become initiated in the study of palæontology. Besides, these names correspond with conceptions which are often uncertain and sometimes preconceived.

I shall only make use of the old and vulgar names designating the different parts according to their position. Every complete plexodont molar has an anterior and a posterior lobe, each of them carrying three cusps. The three cusps of the anterior lobe are the median-anterior, the antero-external, and the antero-internal; the

[1] F. Ameghino, "Sur l'Évolution des Dents des Mammifères," in Bol. Acad. Nac. de Cienc., t. xiv. pp. 381–517 (1896).

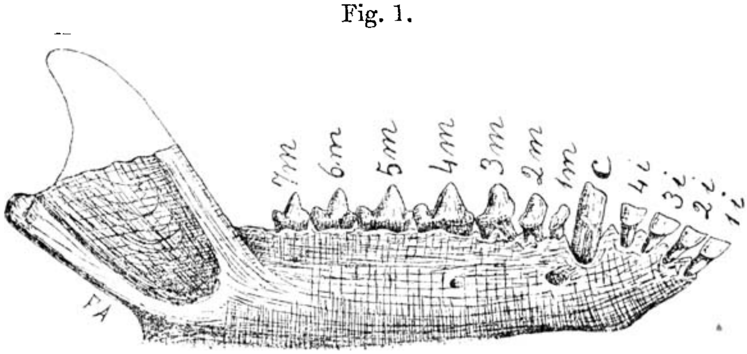
three cusps of the posterior lobe are the median-posterior, the postero-external, and the postero-internal.

According to the theory of gradual complication, the molars provided with these six cusps ought to belong to the most recent of Mammals. I shall show, however, that in all Mammalia, with the exception of the Monotremes, the Edentates, and the Cetaceans, the plexodont type is the most ancient and the starting-point of the different forms of complicated molars.

For the demonstration of the antiquity of this type, I shall avail myself of the numerous palæontological materials which the Cretaceous and Lower Tertiary deposits of Argentina have yielded.

The oldest fossil Mammalia of Argentina come from the variegated sandstones which in Patagonia underlie the Guaranian formation with gigantic Dinosaurians. The best-known genus, recently discovered, is the *Proteodidelphys præcursor*, the mandible of which, four times enlarged, is represented in fig. 1. *Eodidelphys*

Fig. 1.



Proteodidelphys præcursor: right mandibular ramus, outer aspect, four times nat. size.—Lower Cretaceous; Patagonia.

and *Microbiotherium*, of the Upper Cretaceous and Eocene, connect the former genus with the recent Didelphyidæ, so that *Proteodidelphys* represents the most ancient stem of this group; it has at the same time many affinities with *Paurodon* of Marsh, and other allied genera from the Upper Jurassic of North America.

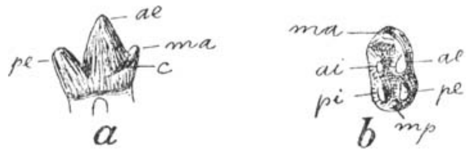
Fig. 2 represents the sixth lower molar, right side, of *Proteodidelphys*—*a*, outer view, *b*, upper view (magnif. 8 times). It may easily be seen that this tooth is composed of the two lobes and the six cusps before mentioned, which I designate by the following letters, the names in parentheses being those of Osborn's nomenclature.

ma, median-anterior (paraconid).
ae, antero-external (protoconid).
ai, antero-internal (metaconid).
pe, postero-external (hypoconid).
pi, postero-internal (entoconid).
mp, median-posterior[1] (hypoconulid).

[1] This cusp is generally diminutive and in the small forms to be seen only with the help of a strong lens. It loses its independence at an early date, by becoming fused either with cusp *pi* or with cusp *pe*, the latter occurrence being the more frequent.

On the outer side of the anterior lobe of the same tooth there can also be seen a small enamel ridge or *cingulum* (fig. 2 *a*, *c*), the presence of which must not be overlooked.

Fig. 2.



Proteodidelphys præcursor: sixth right lower molar, external (*a*) and superior (*b*) aspect, eight times nat. size.—Lower Cretaceous; Patagonia.

Finding thus in the teeth of such an old animal a complication which is said to be the result of a successive addition of cusps through geological ages, we have a right to doubt this latter assertion, and to assume as more probable that we are in presence of a primitive conformation, the vestiges of which are to be traced in nearly all the orders of Mammalia.

Let us begin with recent Didelphyidæ, the unworn molars of which are not only sextuberculate, but also exhibit these tubercles (cusps) disposed in the same manner as in *Proteodidelphys*, the anterior lobe showing also the same cingulum (*c*). In these animals, therefore, the complication in question is not of recent origin, but an inheritance of their oldest known predecessor.

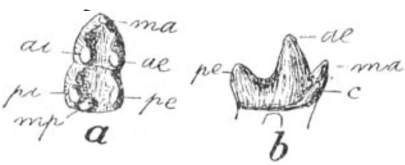
Proteodidelphys is a representative of the family Microbiotheridæ. In several of my publications I have had the opportunity of showing that this family constitutes the stem not only of the Didelphyidæ but equally of the Sparassodonta, Dasyuridæ, Creodonta, Insectivora, and Carnivora. The lower molars of these different groups are merely modifications, generally not very considerable, of the molars of *Proteodidelphys*. In the Eocene Microbiotheridæ the modifications are insignificant. The molars of Cretaceous Sparassodonta still preserve the vestiges of all the cusps, which in their Eocene descendants are reduced by the disappearance of cusp *ai*, or its fusion with *ae*, followed by the atrophy of the posterior lobe and its corresponding cusps. The same is to be seen in the Australian Dasyuridæ, cusp *ai* being still present in *Dasyurus*, whilst it has disappeared in *Thylacinus*. The six cusps characteristic of Didelphyidæ are known to exist in most of the genera of Creodonta (*Palæonictis*, *Proviverra*, *Myacis*, &c.), the predecessors of the Carnivora; they equally persist in many of the latter, especially in Procyonidæ, recent (*Procyon*, *Nasua*) and fossil (*Cyonasua*), in primitive Canidæ (*Cynodon*) and Ursidæ, in the Viverridæ, &c. In some genera of Carnivora this form has scarcely undergone any appreciable modification: on examining the first inferior molar of *Cyonasua* (fig. 3), one is struck by its perfect resemblance to the corresponding tooth of *Proteodidelphys* and *Didelphys*. The same tooth-pattern is met with again in many Insectivora (*Talpa*, Tupaidæ, Soricidæ, &c.), and likewise in the Chiroptera, especially in Vespertilionidæ, the most numerous and ancient family. In all these groups the molars differ from those of *Proteodidelphys* only by the greater or lesser development of cusp *ma*, by the suppression of cusp *ai* or its fusion with *ae*, and by the varying degree of simplification of the posterior lobe.

Fig. 3.

Cyonasua argentina: fifth right lower molar, superior (*a*) and external (*b*) aspect, nat. size.—Eocene; Patagonia.

Another branch, likewise originating from the most primitive Microbiotheridæ, are the diprotodont Marsupials, which comprise the extinct Multituberculata of the Northern Hemisphere and Argentina, the numerous Paucituberculata of South America, and the Diprotodonts of Australia (Hypsiprymnoïdea). Their most primitive type is that of the Garzonidæ. The lower molars of *Garzonia* or *Halmariphus* (fig. 4) are not distinguished by any

Fig. 4.



Halmariphus didelphoides: fifth right lower molar, superior (*a*) and external (*b*) aspect, eight times nat. size.—Eocene; Patagonia.

essential character from those of the Didelphyidæ; their teeth exhibit the six cusps of those of *Proteodidelphys*, with an almost similar disposition and with the same external cingulum, *c*. Some species depart slightly from this form by the internal displacement of the two median cusps, the anterior and the posterior, so that each molar presents on the internal margin a range of four cusps, as can be seen in the molars of a Cretaceous species of *Halmariphus*, or a nearly related genus (fig. 5). In the Epanorthidæ the paired cusps *ae*, *ai*, and *pe*, *pi*, are connected, forming two semicircular crests. In the Abderitidæ the same cusps constitute two feebly accentuated, transverse crests. The slightly more recent Diprotodonts of the Paraná deposits (*Zygolestes*) exhibit the same crests more accentuated; they are still more developed in the existing South-American genus *Cœnolestes* of O. Thomas, the molars of which have assumed the same form as those of the Australian

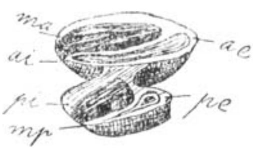
Diprotodonts. The latter are the descendants of the Diprotodonts which in former times inhabited Argentina. The multituberculate condition of the fossil Diprotodonts of the Northern Hemisphere is the outcome of the duplication of the molar cusps of the Paucituberculata. The Cretaceous and Eocene fossil forms of Argentina exhibit all the intermediate stages between the Multituberculata and the Paucituberculata; amongst these there is one, the *Mannodon*, in which the molars show a complication of exactly the same type as that presented by the classical molar of *Microlestes antiquus*, figured in all the manuals of palæontology.

Fig. 5.

Halmariphus guaraniticus: fifth right lower molar, superior (*a*), internal (*b*), and external (*c*) aspect, eight times nat. size.—Upper Cretaceous; Patagonia.

In the molars of the Cretaceous Rodents of Argentina the derivation from the sexcuspidate type is equally recognizable. The Caviidæ, with their molars formed of two triangular or cordiform prisms, and with an open cavity at the base, are those which depart most from the primitive form: it seems absolutely impossible to make out in these molars anything approaching those of the Didelphyidæ. However, the numerous fossil forms of this series graduate without interruption between the recent Caviidæ and the Eocene Eocardidæ, and between the latter and the Cretaceous Cephalomyidæ. Fig. 6 shows the seventh (ultimate)

Fig. 6.



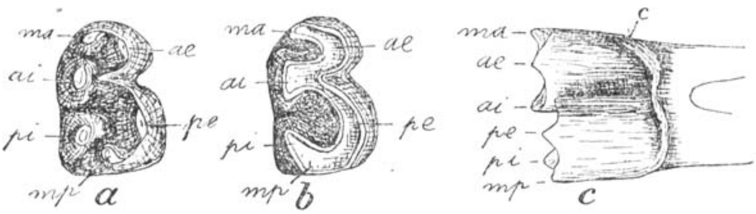
Cephalomys prorsus: last right lower molar, superior aspect, eight times nat. size.—Upper Cretaceous; Patagonia.

right lower molar of *Cephalomys prorsus*, 8 times nat. size. In the two lobes of this tooth it is easy to recognize the two prisms of the Caviidæ; but the six elements corresponding to the six primitive cusps are likewise discernible, though disposed slightly differently from the ordinary. The three cusps of each lobe are disposed in a triangle, the two external, *ae*, *pe*, maintaining their position; but the two median, the anterior *ma* and posterior *mp*, are limited to the internal margin. A somewhat similar disposition is seen in the molars of some Cretaceous Diprotodonts of the family Garzonidæ, *e. g.* the molar of *Halmariphus guaraniticus*, represented in fig. 5. This agreement in the disposition of the primitive molar elements seems to imply that the Rodents, the origin of which is still a mystery, may represent a side branch of the Diprotodonts, which originated towards the middle of the Cretaceous period.

We may next consider the Ungulates, which by their molars, at least those of the present epoch, do not appear to bear any relation to the Didelphyidæ and their predecessors. This, however, is not the case. In a recent publication, I have declared that in the Cretaceous of Argentina all the groups of Ungulates exhibit in the form of their molars a great resemblance to each other: all show the sexcuspidate form; if not visible in the adult, it is seen in young stages.

The Argentine Proterotheridæ, resembling the Horses in their tridactyle and even monodactyle hoofs, and the Palæotheridæ in their molars, are amongst the most characteristic and most specialized of Ungulata. Their oldest known representative is the *Deuterotherium distichum* of the Upper Cretaceous; its fifth right lower molar, just in the beginning of wear, is represented from the upper aspect in fig 7*a*. This tooth shows the six conical and

Fig. 7.



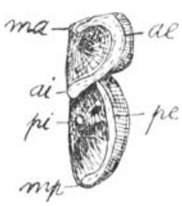
Deuterotherium distichum: fifth right lower molar, twice nat. size.—Upper Cretaceous; Patagonia. *a*, Superior aspect of tooth which has just pierced the gum; *b*, superior aspect of worn tooth of adult; *c*, external aspect of slightly worn tooth.

perfectly separated cusps, with a disposition closely similar to that of *Proteodidelphys*, and also with the *cingulum* (*c*) on the external side, visible in figure 7*c*, which represents a slightly worn specimen of the same tooth. However, in the present genus this conformation had become transitory, as shown by the figure, 7*b*, which exhibits the crown view of the same tooth in a worn condition; the positions formerly occupied by the primitive elements are marked by the corresponding letters, but the cusps are no longer recognizable, and without being acquainted with the unworn tooth it could not be guessed that its starting point is almost absolutely identical with the form presented by the same tooth of the Didelphyidæ and of *Proteodidelphys*. The last-named figure (7 *b*) demonstrates the origin of the similar characteristic molars in a considerable number of Ungulates—*e. g.*, the Protero-theridæ, Macrauchenidæ, Meniscotheridæ, Rhinoceridæ, Titanotheridæ, Palæotheridæ, &c.; as well as in the long series of ruminant and selenodont Ungulata. In the ancient Pleuraspidotheridæ of France the form of the inferior molars of *Proteodidelphys* is preserved almost without any change.

The characteristic molar pattern of omnivorous Ungulata is the result of the atrophy of the median-anterior cusp *ma* and the median-posterior *mp*, or of their being intercalated in the same transverse line between the internal and external cusps of each lobe, *ae*, *ai*, and *pe*, *pi*. The lophodont pattern of the Tapir's molar is the result of the atrophy of the median-anterior cusp *ma* and of the union of the external cusps *ae*, *pe* with the corresponding internal *ai*, *pi*, by means of transverse crests. The origin of the molars of Pyrotheridæ is the same, with the only difference that the median-posterior cusp *mp* is lengthened in a transverse direction, so as to form a sort of transverse heel (*talon*). The passage from the dentition of *Pyrotherium* to that of *Dinotherium*, and from this latter to that of *Mastodon* and of *Elephas*, is easily recognizable.

In other Ungulata the median-posterior cusp *mp* became fused with the postero-external *pe*, in order to form a large external curved or crescentoid lobe, whilst the postero-internal *pi* approached the antero-internal *ai*; so that the two median cusps *ma*, *mp* became separated by three notches on the internal margin. The Horses (Equidæ) are in this condition, as well as good number of Isotemnidæ, the Homalodontotheridæ, Leontinidæ, and Tillodonts. The oldest known predecessor of the Horse series is *Morphippus* of the Upper Cretaceous. Fig. 8 shows its fifth right lower

Fig. 8.

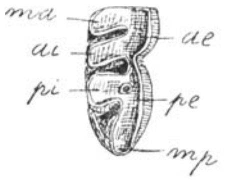


Morphippus imbricatus: fifth right lower molar, slightly worn, superior aspect, twice nat. size.—Upper Cretaceous; Patagonia.

molar of a young individual, the six cusps being distinctly visible and partly independent. The successive changes leading to the Equidæ are indicated by the same tooth of *Morphippus* in a worn condition (fig. 9), and by the corresponding tooth of the Upper Eocene *Notohippus*, represented in fig. 10 *b*, side by side with that of a recent Horse (fig. 10 *a*), so that the same elements with the identical fundamental disposition can be seen in them.

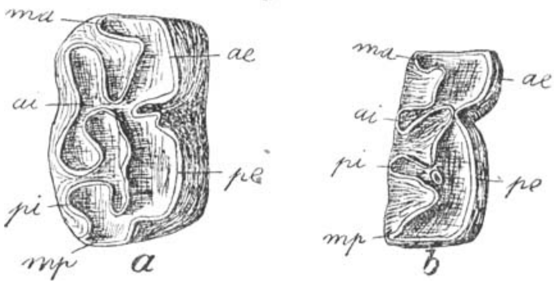
The hypselodont molars with open cavity at the base, of several Ungulates, *e.g.* the Toxodontia and Typotheria, show the greatest departure from the primitive type by the complete fusion of their elements; however, by means of their oldest predecessors, they can be traced to the same origin. The slightly worn molars of

Fig. 9.



Morphippus imbricatus: fifth right lower molar of adult, superior aspect, nat. size.—Upper Cretaceous; Patagonia.

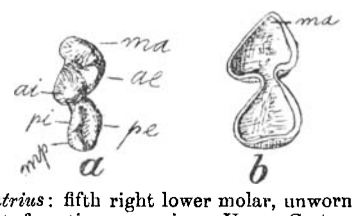
Fig. 10.



Notohippus toxodontoides: fifth right lower molar, superior aspect, twice nat. size.—Upper Eocene; Patagonia. *a.* Crown of homologous tooth of existing *Equus caballus.*

the Cretaceous Toxodonts (*Proadinotherium*, *Pronesodon*) are completely similar to those of *Morphippus*; so that it becomes almost impossible to distinguish isolated molars of animals of the series terminating with the Equidæ from those belonging to animals of the Toxodont line.

Fig. 11.



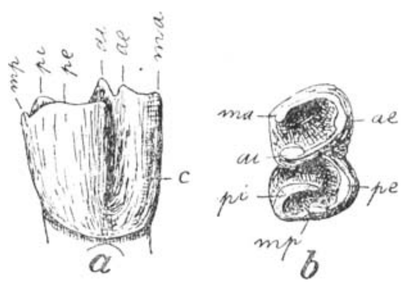
Archæophilus patrius: fifth right lower molar, unworn (*a*) and worn (*b*), superior aspect, four times nat. size.—Upper Cretaceous; Patagonia.

The teeth of Typotheria are a little different. Fig. 11 *a* represents the unworn fifth right lower molar of *Archæophilus patrius*, from the Upper Cretaceous; the six cusps are perfectly distinguishable, although very low and disposed a little differently. The cusp *mp*, which is very large and completely separated from cusp *pe*, has moved to the internal side, and these cusps disappear without leaving any trace as soon as the teeth begin to be functional; so that the molar acquires an entirely different contour and appearance, as shown by fig. 11 *b*, representing the same tooth of an adult specimen.

In the unworn lower molars of *Prosotherium*, another Cretaceous genus of the same order, the cusps *ma* and *mp* are placed towards the outer side, so that the six cusps are disposed in two longitudinal series separated by a deep longitudinal furrow. The cusps *ae* and *ai* being also higher and thicker than the others, the crown assumes a certain resemblance to that of the molar of *Microlestes antiquus*, a very remarkable and suggestive fact.

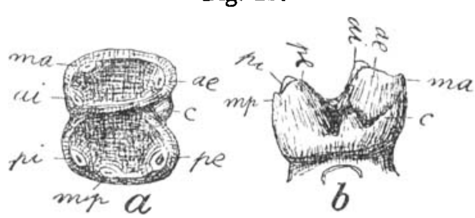
The origin of the molars of Primates is the same. Here, too, as in the bunodont Ungulata, the mound-shaped, bulky, and thick cusps, characteristic of the omnivorous condition, are a recent and gradual acquisition.

Fig. 12.



Notopithecus fossulatus: fifth right lower molar, slightly worn, external (*a*) and superior (*b*) aspect, four times nat. size.—Upper Cretaceous; Patagonia.

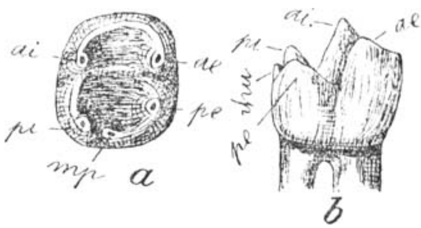
Fig. 13.



Pitheculus australis: fifth right lower molar, superior (*a*) and external (*b*) aspect, four times nat. size.—Upper Eocene; Patagonia.

Fig. 12, *a*, *b*, exhibits the fifth lower molar, not much worn, of *Notopithecus fossulatus*, from the Upper Cretaceous, external view and upper view. This tooth shows distinctly, although not much accentuated, the six primitive cusps, as also a trace of the cingulum, *c*; the chief difference from *Proteodidelphys* being seen in cusp *ma*, which has moved to the inner side. Fig. 13 represents the same molar of the Eocene genus *Pitheculus*, a Monkey of the family Homunculidæ. This tooth is more square and has lost the indentation on the internal side of each lobe; the cusps are more in the shape of mounds, while the median anterior cusp is very small, forming part of an anterior crest, from which it is scarcely distinct. In *Homunculus*, of the Upper Eocene, the same tooth (fig. 14) shows the median-anterior cusp *ma* to have become effaced

Fig. 14.



Homunculus patagonicus: fifth right lower molar, superior (*a*) and external (*b*) aspect, four times nat. size.—Upper Eocene; Patagonia.

by fusion with the anterior crest, whilst the tubercular or bunodont form is more pronounced. In recent Monkeys and in Man the transverse anterior crest, the last vestige of cusp *ma*, has also disappeared, there remaining only the four cusps *ae*, *ai*, *pe*, *pi*, which are in the form of mounds or tubercles almost equal in size and imparting to the crown the perfect omnivorous aspect. The cusp *mp* often remains visible, generally placed between the two posterior cusps *pe* and *pi*, but always of minute size.

At different times I have supported the contention that the complicated molars of Mammalia have retained the same form from one end of the series to the other, with no other change than that of the relative size of their different parts. On this hypothesis, the simplification of the deciduous molars and of the premolars must be considered as a secondarily acquired character, due to the want of space for the complete development of these teeth—a simplification which must have been acquired progressively from before backwards.

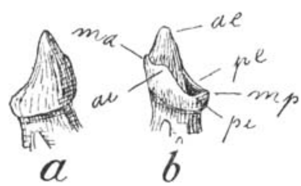
I have insisted on the fact that the deciduous molars, although remaining in function for a short time, are almost always more complicated than those which replace them. This is in agreement with the theory of fusion and primitive complication, since the deciduous teeth are the older dentition of the two; but it is in contradiction to the theory of gradual complication. I have also drawn attention to the fact, almost universal in Placentals that the last deciduous molar more closely resembles the first true molar than the last premolar. Recently I wished to make sure if this fact could also be observed in Marsupials; and I am able to state that in several small species of *Didelphys* the unique deciduous molar—which corresponds with the third deciduous molar of Placentals—does not at all resemble the premolar by which it is replaced, but exhibits the form of the fourth persistent tooth (true molar), which in Marsupials is homologous with the fourth deciduous molar of Placentals, *i. e.*, belongs to the first series. These facts prove conclusively that the deciduous molars had originally the same form as the persistent (true) molars.

We next come to the question of the degree of complication of the deciduous and of the replacing molars (premolars). On looking over the whole of the Tertiary and Recent Mammals, we observe that those of the first half of Tertiary times, especially those of the Northern Hemisphere, have, generally speaking, more simple premolars than the more recent. This fact has been considered as a proof of the theory of complication; but I hold that the explanation is a very different one.

Firstly, the rule is not general, there being many exceptions. Secondly, this recent complication, which is very evident in several phylogenetic lines, is but a reversion to the primitive complicated type. Of this I proceed to give proofs.

The mandible of *Proteodidelphys*, seen from the external side (fig. 1), shows the three anterior molars of the simple form as in the Recent and Tertiary *Didelphys*. However, in examining these same teeth of *Proteodidelphys* from the inner side, the vestiges of a complication comparable to that of the posterior molars may be seen, a complication which in this genus seems to be on its way to disappear. Fig. 15 shows the third right lower molar, seen from

Fig. 15.



Proteodidelphys præcursor: third right lower molar, external (*a*) and internal (*b*) aspect, eight times nat. size.—Lower Cretaceous; Patagonia.

the outer side (*a*), which is simple, and from the inner side (*b*), which shows the rudimentary traces of the cusps of the posterior molars; these same rudiments are visible, although successively less accentuated, on the anterior molars, the second and the first. The molars of Didelphyidæ exhibit no traces of this complication, neither are they to be seen in the Microbiotheridæ of the Eocene and the Upper Cretaceous. Now, since it is evident that the Didelphyidæ are the descendants of the Microbiotheridæ and that the oldest known representative of the latter is *Proteodidelphys*, we conclude that originally the anterior molars were composed of

Fig. 16.

Homunculus patagonicus; second to sixth lower molars, superior aspect, four times nat. size.—Upper Eocene; Patagonia.

the same elements as the posterior. These elements were already almost suppressed in the *Proteodidelphys* of the beginning of the Cretaceous, and had completely disappeared in the molars of the Eocene Microbiotheridæ, which in this respect resemble the recent Didelphyidæ.

The traces of the vanished elements are only visible on the inner side, because the teeth in question are inserted obliquely, as shown by the figures 1 and 15, which represent them, together with the anterior root, from the outer side, the posterior one being scarcely visible. On the inner side the inverse takes place, viz., the posterior root occupies almost the whole of the internal face, while the anterior root is almost invisible. As these anterior molars, which are more simple but bear the traces of a vanished complication, are in an uninterrupted, closely arranged series with the posterior molars, the idea arises, quite naturally, that the oblique insertion is the outcome of the want of space for their development, so that the cause of the simplification of the elements on the postero-internal side would be the oblique insertion as a consequence of the want of space. The oblique insertion, but not the complication, is still discernible in the Eocene

Microbiotheridæ, but no traces of it are to be seen in recent Didelphyidæ, although the molars have again assumed their original longitudinal disposition.

These observations can be confirmed by the examination of all the old groups of Mammalia. Not wishing to pass all of them in review, I limit myself to the Primates, the great antiquity of which had not been guessed before their discovery.

The genus *Homunculus* of the Patagonian Eocene—a true Monkey with rather specialized characters—is particularly interesting. Its lower premolars, seen from the outer side, exhibit a single convex lobe as in the Cebidæ, and totally different from the persistent (true) molars, which bear two well-developed lobes. Nevertheless, on examining these same premolars from the inner side or from above, they present a completely different appearance. These teeth are seen to be inserted obliquely or almost transversely, so that they show on the outer side only the enlarged anterior lobe with the three well-developed primitive cusps; whereas the posterior lobe has moved inside and is partly atrophied, showing only the postero-internal cusp *pi*, and the postero-external *pe*, which has moved inside and with which the median posterior cusp has become fused.

In the line of the Primates the anterior molars have therefore also possessed the same form as the posterior ones, their secondary and recent simplification being due to the want of the space necessary for their development. The premolars, in consequence of being pressed together, have assumed an oblique position, partly overlapping one another, and producing the atrophy of the posterior lobe, which is no longer visible in the same teeth of more recent Monkeys and of Man. In the Primates this atrophy began during the Cretaceous, since it is already to be seen in the Notopithecidæ, all the members of which exhibit the same oblique insertion of the anterior molars. I have also found it in several lines of Ungulates, especially in the Protypotheridæ, the Isotemnidæ, the Astrapotheridæ, &c. I draw the conclusion that the plexodont molars of Mammals, the anterior as well as the posterior, had originally the same degree of complication, and that the simplification of the anterior molars, observable in numerous Mammals of the latest Cretaceous and of the beginning of the Tertiary, is a secondarily acquired character. This simplification was the outcome of a concentration of the dental series, by want of the necessary space for their development[1].

The diminution of the space assigned to the development of the

[1] To those desirous of becoming acquainted with a similar instance in a mammal of the Northern Hemisphere, I will point out one which at this moment comes under my notice. I have just received Prof. Osborn's memoir on the "Evolution of Amblypoda, Part I.," in Bull. Amer. Mus. of Nat. Hist. xi. 1898; and on page 172 I find the figure of the mandible of *Pantolambda cavirictus*. A glance at this figure shows that in this ancient genus the premolars are inserted obliquely, the posterior lobe being turned inwards and atrophied in the same manner as in *Proteodidelphys*, *Protypotherium*, *Homunculus*, &c.

premolars seems to bear a relation to the greater or lesser retardation in the development of some teeth belonging to the same series. In a considerable number of cases the immediate cause of the simplification of certain molars is simply to be found in the accelerated or retarded development of neighbouring teeth. When the molars find the place unoccupied, they preserve their form or even may become more complicated. Those teeth which at the moment of piercing the gum find the place anterior to them occupied, extend posteriorly, and *vice versa*, or they become reduced if the place is occupied on their anterior as well as on their posterior side.

It is well known that in the majority of modern Placentals, as also in those belonging to the most recent geological periods, the adult dentition is composed of teeth belonging to two different series. The posterior, persistent teeth belong to the first series, of which the deciduous teeth also form part; while that anterior portion of the dentition which is represented by the premolars belongs to the second series, the posterior part of which, that corresponding to the persistent (true) molars, is not developed. The molars of the first series are accordingly not all in function at the same time, being developed in a very unequal manner; when the last persistent teeth come out, the anterior teeth of the same series have already been replaced by those of the second series.

The same was not the case formerly. Ancient Mammals, *e. g.* the Nesodontidæ, Adiantidæ, Homalodontotheridæ, Notohippidæ, &c., had, during part of their life, all the deciduous teeth (the anterior part of the first series) in function at the same time as all the persistent teeth; in other words, the complete first series was in function at the same time. In these families the deciduous molars, as well as the premolars, were well developed and always exhibited the same form from one end of the series to the other, so that the molars of the second series, replacing the deciduous teeth, occupied the same space and reached the same size. Later on, however, as a consequence of the accelerated development, by which the deciduous molars came to be shed before the animal was adult, whilst the persistent molars remained in function, these latter acquired a greater development and encroached on part of the space left free by the deciduous teeth. As to the premolars, finding the space between the canine and the first persistent molar greatly reduced, they were pressed together and had to assume an oblique position, the posterior lobe being turned towards the inner side. This oblique position of the teeth, together with the want of space necessary for their complete development, caused the reduction of their interior side and especially of the posterior lobe, which in many genera disappeared completely[1].

[1] All that has been stated with regard to the lower premolars applies equally also to the upper premolars, in which the atrophied lobe is the posterior, especially its inner portion.

These changes were brought about during the Cretaceous and the early portion of the Tertiary period. In the later Tertiary a change in the opposite direction took place, viz., a progressive retardation in the evolution and the development of the persistent molars; so that the moment arrived when all the deciduous teeth were in function, without any of the persistent teeth having made their appearance. Finding the place free, the deciduous molars were able to assume a greater development, the last of them advancing gradually backwards, thus increasing the space for the replacing molars, and diminishing in the same proportion the space destined for the persistent (true) molars. As a consequence of this reduction of space, these latter have become proportionally smaller, and in the end cut the gums successively one after the other, sometimes at rather long intervals. For the opposite reason, viz. as a consequence of an increase of space, the replacing molars increased in size; this enlargement was accompanied by a gradual complication, giving to the molars a uniform appearance from one end of the series to the other, just as during the Cretaceous. The complication of the anterior molars is therefore a reversion to a primitive form.

To sum up. As a result of the comparison of the palæontological materials with those furnished by recent Mammals, it can be stated that, in the same proportion as the duration in function of the deciduous molars decreases, the space assigned to the replacing molars also decreases; and in the same proportion as the development of the persistent molars is retarded, the space occupied by the deciduous molars and the premolars is increased.

This discovery explains a number of facts which have hitherto remained almost incomprehensible. I shall confine myself to a few examples which are easily understood.

The third lobe of the last lower molar of Ungulates represents the median posterior cusp *mp*, which was enabled to assume this greater development because there are no other teeth behind to prevent it. In the other molars this cusp is, on the contrary, obliged to maintain its median position between the posterior cusps *pe* and *pi*, which are fused together. For the same reason the posterior lobe is to be seen also in the last deciduous lower molar of recent Ungulates, since in the latter this tooth remains for a long time in function, before the first persistent tooth makes its appearance. As a consequence, in these Mammals the last deciduous molar differs both from the one by which it is replaced (the fourth premolar), and from the first persistent molar, resembling the last persistent molar. In the primitive Ungulates, on the contrary, which had all the teeth of the first series in function at the same time, the last deciduous molar could not extend posteriorly, its cusp *mp* being prevented by the next following molar; and therefore the tooth in question (the last deciduous molar) is different from the last persistent and resembles the first persistent and the fourth replacing molar.

On examining the mandible of a young sheep having the three deciduous molars in function, and before the first persistent molar has appeared, it can be seen that the last deciduous tooth, having more than the necessary space for its development, is strongly inclined posteriorly, so that it diminishes the space which will have to be occupied by the persistent molars, and increases in the same proportion the space assigned to the replacing molars.

This inequality in the development of the molars also explains why the last upper replacing molar of Ruminants and Artiodactyla generally is notably smaller and simpler, not only than the one on its posterior end, but also than the one anterior to it. This fourth replacing molar is the last to cut the gum, and must adapt itself to the space left free by the penultimate replacing and the first persistent tooth.

Lastly, I have to observe that the sexcuspidate form of tooth, which is represented as the last term of evolution of molars, is very frequent in the oldest Tertiary Mammalia of Europe, and especially in those of the Cernaysian Fauna. To judge from the figures of the recent publication by Mr. Matthew on the Mammalian Fauna of the Puerco, a great number of Mammals of this epoch also have sexcuspidate inferior molars. Going a step backwards, we can perceive, with the help of Osborn's and Marsh's publications, that almost all the Mammals of the Upper Cretaceous of North America are provided with sexcuspidate or even more complicated (multituberculate) molars. Going another step backwards, the figures published by Marsh enable us to recognize the same type amongst several Jurassic genera, *Peralestes*, *Peraspalax*, *Paurodon*, *Laodon*, *Dryolestes*, &c., which show their posterior molars resembling those of Didelphyidæ and of *Proteodidelphys*. Going still farther backwards, we find the oldest known fragments belonging undoubtedly to a mammal, *Microlestes antiquus*, with plexodont molars not far removed from those of *Proteodidelphys*, and with a crown more closely resembling the crown of unworn deciduous molars of certain primitive Ungulates (*Prosotherium*, *Prohegetotherium*, &c.) than the molars of the Plagiaulacidæ (*Plagiaulax*, *Neoplagiaulax*, &c.).

I do not maintain that the first complicated molars were sexcuspidate, rather than quadri- or quinque-cuspidate. On this point I have sufficiently explained my opinion in my memoir "Sur l'Évolution des Dents des Mammifères." The clear result of all these facts is, that the famous theory of the gradual complication, of triconodonty and tritubercuły, is an untenable hypothesis. Nowhere do we meet with the stages leading from haplodonty to plexodonty; all those which have been mentioned are, on the contrary, as I believe I have demonstrated, but the result of simplification of molars which were formerly more complicated. Plexodonty therefore presents itself as a primitive character, having made its appearance suddenly; and it is only the theory of fusion which can explain it in a satisfactory manner.