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ON THE OSTEOLOGY OF PÆBROTHERIUM: A
CONTRIBUTION TO THE PHYLOGENY OF THE
TYLOPODA.

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ALTHOUGH the theory of evolution is now accepted as an established fact by almost all naturalists, this general agreement does not extend beyond the point of believing that the present organic world has arisen by descent from simpler forms. The application of the theory to concrete cases is beset with grave difficulties, and gives rise to the most divergent views. The uninitiated reader who takes up a monograph upon some animal group may well be surprised to see the minuteness and accuracy with which the genealogy of the series is set forth, and the relationships of the various genera and species marshalled in orderly array. But another treatise upon the same animals will contain an equally complete family tree, which contradicts the first in almost every particular. To some extent this almost hopeless divergence is inherent in the very nature of the problem, it being largely a question of the value of evidence and of the balance of probabilities, as to which men must be expected to differ; but there is another potent cause of the discrepancy. When the contradictory phylogenetic schemes are analyzed, it is frequently found to be the case that the discussion rests upon certain postulates and assumptions, sometimes explicit, generally only implied, and even apparently uncon-

scious. Generally these postulates are, in the present state of knowledge, incapable of proof, and they appeal with very different force to different minds: what to one appears almost self-evident, another regards as not even probable. To remove this confusion, the first step is obviously to enumerate the assumptions upon which so much morphological reasoning is founded, and a few of them are therefore here stated, taking, however, only those which are applicable to the problems of mammalian phylogeny. No doubt every morphologist will find it easy to make a list of many such open questions which confront him in his own field, and perhaps they will need to be separately answered for each of the greater groups of living things, for we have as yet no right to assume that what may prove to be true of one group may safely be applied to another. These questions may be grouped together under the general inquiry as to the *laws of evolution*, or the *mode* of its operation.

As examples of the more obvious of these problems which especially affect the discussion of mammalian phylogeny, the following may be selected:—

(1) Is a genus which consists of several species, of single or multiple origin? Let us assume that genus A is descended from genus B, from which it differs by the presence or absence of some character. Now have all the species of A been derived from a single species of B, which first assumed the structure characteristic of A and then differentiated along diverging lines, thus forming several species of the new genus? Or, on the other hand, have several species of B independently assumed the new common character, so that species of one genus may be more closely related to those of the other genus than to each other? Or, again, does sometimes one method obtain and sometimes another?

(2) This question may be stated in more general terms by inquiring how far *parallelism* of development is possible; meaning by parallelism that forms having a common origin may independently run through a similar course of evolution, and finally arrive at similar results. The question here becomes of great importance, but of immense complexity and difficulty, because if we admit the possibility of such a mode of development, how is the extent to which it may go to be determined? The principle of analogical structures is thoroughly recognized,

and need not here detain us; the question is rather as to how far *homological* structures may arise independently, and how far they may undergo similar modifications. Clearly, until this problem can be definitely settled one way or the other, the difficulty of making out phylogenetic series must be very great, and especially so in those cases where our information as to extinct forms is incomplete, or even sometimes where the entire skeletal structure is before us. A notable example of such a difficulty is afforded by the extraordinary animal *Chalicotherium*, the skull and teeth of which were for many years referred to the ungulates, while the feet, under the names of *Macrotherium*, *Ancylotherium*, *Morotherium*, etc., were ascribed to the edentates, but of late the researches of Forsyth Major, and Filhol have shown that they all belong to the same type. The curious little artiodactyl, *Leptomeryx*, is known in almost every detail of its skeleton, and yet its relations to the other members of its suborder are very far from clear, as it has been variously referred to the traguline, the deer, and the camel series. This is simply because we cannot yet determine how far its resemblances to other groups are due to actual relationships, and how far to parallel development. In other families of extinct mammals we are continually encountering the same difficulty, and opinions on the subject of genetic connections are in a constant state of flux. One school of observers tacitly denies all such parallelism, and this assumption leads them to regard all similarities of structure as due to phylogenetic relation, and this again results in the most complicated cross-connections and reticulations instead of the ordinary view of diverging lines. In some treatises it is gravely argued that because a given specimen has been referred by one anatomist to one group, and by another to another group, the connection between the two series is thereby made at least probable.

(3) Even more difficult to decide is the question as to how far *convergence* of development is possible, meaning by this a similar result which is reached by two or more independent lines having a different starting-point. The view which is held with regard to this point is to a great extent conditioned by opinions as to the nature of heredity, and so some naturalists deny the possibility of any real convergence, while others accept it and push it to extreme limits. Mivart, for example (No. 22, p. 509),

seems inclined to believe that the South American monkeys have an entirely different origin from those of the Old World; or an even more striking example is the supposed dual origin of the horse in the Old World and the New.

Another aspect of this same question is the consideration of the relative value to be given to resemblances and differences in discussing the relationship between various groups. Huxley (No. 13, p. 657) believes that, in forming natural orders, "it is more important that similarities should not be neglected than that differences should be overlooked." This, again, requires the consideration of the nature of the resemblances and differences, whether they are due to advancing differentiation or to the retention of primitive characters, whether the characters be adaptive or inadaptive. Thus Flower says: "Too exclusive attention has been paid to the characters of the teeth in defining the family divisions of the order. The difficulty in the taxonomic use of these organs arises from the fact that the teeth of all the members of such a limited and well-defined group as the terrestrial or fissipedal Carnivora are formed on the same general type, but with infinite modifications of this type. And as these modifications are mainly adaptive, and not essentially indicative of affinity, they reappear in various degrees and combinations in many of the great natural divisions of the order" (No. 10, p. 5). Wallace, on the other hand, insists upon the instability of inadaptive characters (No. 34, p. 138). The classification of the Carnivora by the characters afforded by the base of the skull, as proposed by Turner and Flower, is rejected by Schlosser (No. 28, p. 236) on the ground of his studies of extinct forms. "Aus all dem gesagten geht so viel hervor, dass die als Aeluroidea zusammengefassten Formen in *einigen* Punkten einen gemeinsamen Entwicklungsprocess verfolgen. Das berechtigt aber noch lange nicht, auf eine nähere Verwandtschaft zu schliessen." In the same way the relations of the various forms of marsupials to the placental orders form the subject of endless diversities of opinion. The question as to the relative taxonomic value of the feet and the teeth has been very hotly disputed, and the list might be indefinitely extended, showing how the construction of phylogenies depends upon the answer to this problem of convergence in its protean forms.

(4) Can a structure which has once been lost ever be regained? Here again we find that assumptions, generally tacit, but sometimes very explicit, underlie the discussion of relationships. Schlosser, for example, holds very decided views upon this point. "Dass eine Regenerirung dieser Knochen stattgefunden hätte, ist ganz undenkbar; es gibt kein einziges Beispiel, wo ein rudimentär gewordenen Organ sich wieder vervollständigt hätte. Es wird sich vielmehr höchst wahrscheinlich herausstellen, dass in Fällen, die allenfalls in dieser Weise gedeutet werden könnten, das betreffende Organ nur durch andere vorübergehend verdeckt war und dann wieder deutlich hervorgetreten ist" (No. 29, p. 420). Boas, on the other hand, does not share this opinion. "Während die Metacarpalia, resp. Metatarsalia, 2 und 5 bei den ausgebildeten typischen Wiederkäuern stets nur fragmentarisch vorhanden oder gänzlich rückgebildet sind, werden dieselben bekanntlich bei den Embryonen in ihrer ganzen Länge knorpelig angelegt und es erscheint deshalb die Deutung nicht ohne Weiteres unberechtigt die vollständige Elemente bei den erwachsenen Traguliden als einen retardirten embryonalen resp. atavistischen Charakter aufzufassen" (No. 2, p. 514).

(5) Analogous to this is the problem as to whether the differentiation of any group is a steadily advancing one (or retrograding, as the case may be), interrupted only by stationary periods of rest, or whether it should rather be regarded as progressing in a spiral, advancing on the whole and in the long run, but with many set-backs and retrogressions; such a process, in short, as Wallace has supposed to occur in the history of the flowering plants, in order to account for the endless variety and complexity in the arrangements for cross and self-fertilization (No. 32, p. 331).

(6) Another question arises with regard to the higher animals, whether advancing differentiation is always by means of the reduction of parts, or whether these may not sometimes be increased in number. More depends upon this than would at first sight appear to be the case. The question is usually answered in the negative, and nearly all phyletic series are constructed on this presupposition. If this assumption be invariably correct, it will of itself solve some of the problems which have already engaged our attention. With regard to the

teeth, Wortman says: "There are no cases known to me in which teeth have been added. On the contrary, I am firmly of the opinion that not so much as a single tooth has ever been added to the diphyodont mammalian dentition in the course of development, but that specialization has invariably gone in the other direction, as almost all evidence of palæontology goes to show" (No. 34, p. 454).

The bearing of this question upon phylogenetic discussions will be made clear by a single example. Among the *Canidæ*, as in other placental mammals, the normal number of true molars is not more than three, and, except as a rare and occasional variation, this number is not exceeded by any known fossil member of the family, or even by any creodont, even as far back as the earliest Eocene; yet the existing genus *Otocyon* has four molars, though in other points of structure this genus shows no important differences from other dogs. Nearly all palæontologists have agreed in regarding this as proof that the ancestors of the *Canidæ* had four molars, which have been retained only in *Otocyon*, and that the occasional appearance of a fourth molar in other genera of the family is clearly due to reversion (Huxley, No. 14, p. 262), and it is further argued that the dogs must be connected with the carnivorous marsupials. This view may be entirely correct, and yet it involves consequences which have an important bearing upon phylogenetic reasoning. We may suppose: (a) that all the fossil forms with three molars, which are ordinarily regarded as ancestral to the recent dogs, such as *Miacis*, *Daphænus*, *Cynodictis*, etc., etc., are in reality not connected with them at all, but that when the cynoid series is made out, it will be found to consist of forms with four molars down to comparatively recent geological times; or, (b) that there are two lines, one of which is through *Miacis*, *Daphænus*, etc., to *Canis*, and the other through unknown ancestors to *Otocyon*, both starting from a type with four molars. This alternative, however, involves the assumption of a remarkable degree of convergence, for the early forms of the *Canidæ* differ much from the recent members in the structure of the brain, skull, vertebral column, and limbs, while in all these points *Otocyon* presents no differences of importance from the other recent genera, and must therefore have reached its present identity with them by an entirely different path. (c) This fourth molar, of *Otocyon*

might be regarded as being re-acquired, and therefore atavistic. If none of these alternatives can be accepted, it only remains to assume that the accessory molar has been added *de novo*. A somewhat similar case is that of the llama with four lower molars recorded by Rüttimeyer (No. 25, p. 55).

(7) In cases of the reduction of parts, is such reduction always accomplished in the same manner? For example, Fürbringer maintains that the reduction of vertebræ must always proceed from the hinder end of the column, and that interpolation or reduction of vertebræ in the median or anterior region does not take place (No. 11, p. 328). Ihering, on the contrary, expressly states that such interpolation and suppression does take place (No. 15), a view which is adopted by Parker on the basis of his studies of the development of *Chelone viridis*: "In the adult I can find only 41 developed vertebræ; viz. 8 cervical, 10 dorsals, 2 sacral, 21 caudal. But in the third and fourth stages there are at least 15 somatomes in the cervical region; in the dorso-lumbar-sacral, 12 (as in the adult); and 24 in the caudal — 51 in all. Thus we miss in the adult 7 in the cervical and 3 in the caudal — 10 in all" (No. 23, p. 47).

(8) Besides the questions of a more general nature already mentioned, there are many obvious ones of a special character, of which we may select as an example the following: What are the effects which follow as a mechanical necessity from great increase or diminution of the size of the body?

This list of "open questions" with regard to the mode in which evolution operates in any given case might, of course, be greatly extended; but for the purposes of the present investigation it will suffice. At first sight it might seem that the questions here propounded were unanswerable, because the solution of them must be drawn from the careful study of phyletic series, while the proper construction of the latter depends upon a correct understanding of the method of development. Fortunately, however, certain series of extinct mammals offer us a way of escape from this "vicious circle," because they present us a series of forms which we have every reason to believe stand to each other in the relation of ancestor and descendant, a relationship which may be verified by tracing the changes of form and function through the minutest gradations back to starting-points very different from the final results. Furthermore, in

these cases we are not restricted to a study of fragments and conjectural restorations, but of many genera we have nearly complete skeletons and satisfactory information as to geographical and geological distribution. Of course, our knowledge of these phyla is very far from complete, but it is sufficiently so to promise very important aids to the solution of the evolutionary problems which have been enumerated.

Aside from the questions as to the mode in which development operates, there are others of more fundamental importance; viz. those as to the efficient causes or factors of development and the laws of heredity. The essays of Weismann have of late aroused widespread discussion as to these factors, and have thrown grave doubts upon the transmission of acquired characters, which we have hitherto accepted as a fundamental axiom. Weismann's objections to assuming such transmission are two-fold: (1) the impossibility of imagining how changes in the adult organism can so affect the germ-plasm as to cause corresponding changes in the offspring; and (2) the entire absence of proof that characters so acquired ever are transmitted. Of course neither of these reasons can be conclusive, as Weismann unhesitatingly admits. "It is perfectly right to defer all explanation and to hesitate before we declare a supposed phenomenon to be impossible, because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces, and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable" (No. 33, pp. 80, 81). "It appeared to me to be necessary to state this weighty and fundamental question, and to formulate it concisely and definitely, for only in this way will it be possible to arrive at a true and lasting solution of the problem. We must, however, be clear on this point—that the understanding of the phenomena of heredity is only possible on the fundamental supposition of the continuity of the germ-plasm. The value of experiment in relation to this question is somewhat doubtful. A careful collection and arrangement of facts is far more likely to decide whether, and to what extent, the continuity of germ-plasm is reconcilable with the assumption of the transmission of acquired characters from the parent body to the germ,

and from the germ to the body of the offspring. At present such transmission is neither proved as a fact, nor has its assumption been shown to be unquestionably necessary" (pp. 104, 105). "If, as I believe, these phenomena can be explained without the Lamarckian principle, we have no right to assume a form of transmission of which we cannot prove the existence. Only if it could be shown that we cannot now or ever dispense with the principle, should we be justified in accepting it. . . . Only if the phenomena presented by the progress of organic evolution are proved to be inexplicable without the hypothesis of the transmission of acquired characters, shall we be justified in retaining such an hypothesis" (p. 448).

Closely akin to this most important problem is the question whether development is always by minute gradations or whether it may not be *per saltum*.

The study, detailed and minute as it must be, of mammalian phyla, which can be regarded as at least approximately determined, promises to throw much very welcome light upon these vexed questions; for we have here, as it were, a great series of physiological experiments carried out, not through a few generations or even centuries, but through long ages. It would certainly seem that an examination of the steps of gradual and progressive change must afford weighty evidence upon one side or the other, and make clear which hypothesis best accords with the observed facts.

One of the series which will prove the most serviceable for our purpose is undoubtedly that of the Tylopoda, which has been so satisfactorily worked out by Cope (No. 6, p. 341; No. 9) both on account of their great numbers, their excellent preservation, and their persistence with steadily advancing differentiation through long periods of time. Leaving aside for the present the discussion of the mutual relationships of the various genera of this series, we have here merely to enumerate these forms in the order of their appearance in geological time. The earliest member of the series would appear to be the genus *Pantolestes*, Cope, of the Wasatch, which is followed by *Homacodon*, Marsh, of the Bridger, a genus which is very closely allied to, if not identical with, the European *Dichobune*, from which Schlosser derives the true ruminants and the tragulines. In the Bridger also occurs *Ithygrammodon*, O. S. and S., but

this form is very imperfectly known and is of no importance for our purpose. The Uinta representative of the series is *Leptotragulus*, Scott and Osborn; *Parameryx*, Marsh, of the same formation, is a mere *nomen nudum*, as to which we have no information. In the White River beds is found *Pæbrotherium*, which also occurs in the John Day, and is followed by *Protolabis*, Cope, of the Deep River and Loup Fork, *Procamelus*, Leidy, *Homocamelus*, Leidy, *Protomeryx*, Leidy, and *Megalomeryx*, Leidy, and *Pliauchenia*, Cope, of the Loup Fork. The Pliocene yields the genera *Holomeniscus* and *Eschatius* of Cope and *Protauchenia*, Branco, the line terminating in *Auchenia* and *Camelus* of the existing fauna.

The Princeton expedition of 1890 had the good fortune to obtain an almost complete skeleton of *Pæbrotherium* of the lower or White River Miocene, the middle member of the Tylopodan series. This beautiful specimen, which was discovered by Professor W. F. Magie, with other specimens in the Princeton museum, and some which have been very kindly put at my disposal by Professors Cope and Agassiz, forms the main subject of this paper. The plan proposed is to give a detailed description of *Pæbrotherium*, followed by a discussion of the evolution of the skeletal and dental structures of the *Camelidæ*, the phylogeny of the family and its relation to other artiodactyls. In the second paper a similar plan will be followed for other mammalian series, and then an attempt will be made to apply the results of these studies to the solution of the evolutionary problems already enumerated.

PÆBROTHERIUM, Leidy.

This genus is quite abundant in the lower and middle Miocene formations of the West (White River and John Day). Hitherto it has not been adequately described. Leidy's type specimen is the much-fractured skull of an immature animal, which does not allow a complete account to be given. Cope has published some very valuable notes (Nos. 6, 8, 9, etc.) upon the vertebræ, limbs, and teeth; but these are all too brief to serve our purpose, which requires a careful consideration of all the minute points of structure.

I. *The Dentition* (Pl. I, Figs. 8 and 9).

A. *Upper Jaw*. — I have not seen any specimens of the superior incisors, but there can be no doubt that they were present in the typical number. The canine is short, compressed, and trepchant, and is relatively much smaller than in the recent genera. There is, however, not a sufficient number of specimens available to determine accurately whether or not this small size of the canine is a sexual characteristic. The first premolar is isolated by a diastema, both in front of and behind it; it is implanted by two fangs, and has a very simple, compressed, and trenchant crown, which is remarkable for its antero-posterior elongation. Pm. 2 and 3 are similar in general character, but are even more elongated; on the outer side they exhibit a prominent median ridge with anterior and posterior depressions. Some specimens show a well-marked antero-external buttress on pm. 3; in others this is but feebly developed. A very small internal festoon is shown on the posterior half of the crown in some individuals; others have no trace of it. Pm. 4 is much less elongate (antero-posteriorly) than the anterior premolars, and resembles the corresponding tooth in the ruminants generally in being made up of two crescents, an external and an internal one.

The true molars are all brachyodont, and are not strongly extended antero-posteriorly, the true molar series but slightly exceeding the premolar in length. M. 1 is the smallest of the three in both dimensions. M. 2 is slightly longer and narrower than m. 3. In each of them the crown is composed of four crescents, no trace of the unpaired fifth lobe ever appearing; the valleys are very narrow and rather shallow, so that they are obliterated at a comparatively early stage of wear. The outer wall of the crown has a distinct, though very much compressed, median buttress, and a much less prominent anterior buttress: each crescent has a well-defined median ridge. In the recent genera, and especially in *Camelus*, the posterior half of m. 3 is decidedly narrower than the anterior half; in *Pæbrotherium* this difference is indicated but slightly. The presence of internal basal pillars is subject to much variation. In one specimen I find a minute trace of such a structure on m. 1 and 2, and a fairly well developed pillar on m. 3; a second specimen shows

a trace on m. 3, and none on the others, while a third specimen is entirely devoid of them.

B. Lower Jaw.—The incisors are small, and have simple, compressed crowns, very different from the curious, shovel-like teeth of existing species. They differ also from the latter in relative size, the median incisor being the smallest and the external the largest of the series. In position they are quite strongly procumbent. The canine, in all the specimens which I have seen, is very small, though larger than the incisors; it is more erect than the latter, and has a very much compressed crown, the anterior and posterior edges of which meet at nearly a right angle. The first premolar, as in the upper jaw, stands isolated, both from the canine and from pm. 2; it is implanted by a single stout fang, and has a very small simple crown. The other premolars increase in size from pm. 2 to 4, and are all much alike, have elongate and very much compressed crowns, with an acute apex and trenchant edges; each has a distinct anterior basal cusp, and on pm. 3 and 4 there is an internal ridge which runs backwards from the median apex. This is barely indicated on pm. 3, but is well shown in 4, and in some specimens encloses a distinct "lake" with the external wall; in others it is open internally. The molars are elongate but very narrow, and show a distinct tendency toward hypsodonty; the valleys are very narrow, but perfectly simple, and not complicated by any projections from the walls; the internal faces are much flattened, and there are no pillars or anterior "compression-folds," which are so conspicuous in *Auchenia*. The fifth crescent of m. 3 varies very much in size, being nearly twice as large in some specimens as in others. Basal pillars are much less frequent than in the upper molars. I have seen them in but one specimen, and then as a mere rudiment on m. 1.

The chief peculiarity of the dentition of *Pæbrotherium* consists in the very elongate, simple, and trenchant premolars which recall those of *Xiphodon* rather than those of any existing ruminant.

The Milk Dentition.—I have not been able to determine whether the first premolar has a predecessor or not; at all events, the tooth which represents it in the temporary series is of similar size and constitution. The second upper milk-molar (D. 2) is like its successor pm. 2 in the permanent set, but the

third one is very different ; it consists of a posterior pair of crescents, internal and external, while the anterior portion of the tooth is a long cutting blade with hardly a rudiment of the antero-internal lobe. In the structure of D. 3 *Pæbrotherium* thus agrees with the tragulines and the more ancient selenodonts generally ; seen from the outer side there are three cusps, but only one internal one, the posterior. In *Pæbrotherium*, however, the anterior blade is very much elongated. Rüttimeyer has laid great stress upon the construction of this tooth in his classification of the selenodonts, but, as will be seen later, it is of very doubtful value. D. 4 is composed of four crescents like a true molar, but is proportionately broader. In the lower jaw the three anterior milk-molars are very similar to their successors in the permanent series ; as to the first one, it is not certain whether it is changed, though it probably is, at least in some cases. Thus in all the adults which I have seen pm. 1 is implanted by a single fang, while in some young animals the first milk-molar is inserted by two fangs, in others by only one. D. 4 is like that of the selenodonts generally, consisting of three pairs of crescents, of which the posterior pair is markedly broader than the others.

The milk dentition remains long in place, until the true molars have all appeared and are in full use.

II. *The Skull* (Pl. I, Figs. 1-3, 7).

In general appearance the skull of *Pæbrotherium* is decidedly like that of the llama, though with many important differences. The cranium is short and rounded, the face very long and tapering ; the upper contour of the skull is nearly straight, the orbits very large and prominent and situated further back than in either of the living genera ; the occiput is rather high and narrow, the face very shallow, especially anteriorly, and the narial opening is low, narrow, and nearly vertical. The zygomatic arches are rather short and very slender. The cranio-facial axis is straight, and the sagittal crest is long, but low and thin.

Examined more in detail, the skull of *Pæbrotherium* exhibits its tylopodan affinities very clearly, though, as would naturally be expected, in a less extreme degree than in the existing forms. The basi-occipital differs in shape in the two species ;

in *P. Wilsoni* it is long, narrow, and rounded, being reduced to a mere rod by the enormously inflated tympanic bullæ, while in *P. labiatum* the more moderate size of the bullæ allows it to expand into quite a broad plate, with well-defined keel and lateral rugosities. The condyles are sessile, not projecting at all behind the plane of the occiput; inferiorly they meet in the median line, and are not separated by a groove, as is the case in the recent species. Though the articular surface is continued well forward on the basi-occipital, there is not formed that accessory surface for the inferior arch of the atlas, which is to be found in the camel. The ex-occipitals are broad and low; the supra-occipital high and narrow, forming a prominent lambdoidal crest, and is continued well forward upon the roof of the cranium. The shape of the occiput and especially of the crest is rather more like the condition found in *Camelus* than in the llama; the median line is strongly prominent, caused partly by the shape and position of the vermis of the cerebellum, partly by a thickening of the bone in this region and development of a diploëtic structure. The foramen magnum is nearly circular in outline, and differs from that of the recent species chiefly in the character of the upper margin, which is more horizontally directed, and in the median line is notched, with a slight projection on each side of it. The paroccipital processes are quite long, broad, and very thin plates, ending in an obtuse point; they are flattened antero-posteriorly, and when seen from the side present hardly more than their edges to view; for most of their length they are closely applied to the auditory bullæ. These paroccipital processes are placed more in advance of the condyles than in the recent species, and are separated from them by deep fossæ.

The basi-sphenoid is longer and narrower than the basi-occipital, and, like it, is different in the two species, being decidedly broader and more flattened in *P. labiatum*; its anterior termination is just within the pterygoids. The presphenoid is so much obscured by the long, sloping vomer that very little of it is visible. The alisphenoids have narrow descending pterygoid plates, which, compared with those of the llama and more especially the camel, are extremely short, and terminate in distinct hamular processes, which, however, are by no means so prominent as in the modern species. The ascending portion of

the ali-sphenoids is rather small, and on each side of the basi-sphenoid they flatten out into broad surfaces which slope gradually to the glenoid cavities, the latter being but little above the level of the cranial axis. This shape of the ali-sphenoids does not occur in the recent species, as in correlation with the heightening of the molar crowns the glenoid cavity is placed at a higher level, so that this portion of the ali-sphenoids has become almost vertical. The orbito-sphenoids seem to have about the shape and proportions seen in the llama.

The tympanics are inflated into enormous bullæ, which in both species of *Pæbrotherium* are relatively much larger than in the recent genera, and are more rounded. In the small species, *P. Wilsoni*, they are larger and less compressed than in *P. labiatum*, and in both the long diameter is directed nearly parallel to the cranial axis, while in the modern forms it is placed at a wide angle with it. The postero-external angle of the bulla shows a deep styloid groove, "a vertical gutter ending below in a pit with a process for the conjunction of the styloid bone" (Leidy, No. 19, p. 143). The pit is decidedly smaller and shallower than in *Auchenia*, and is less distinctly separated from the groove. The stylo-hyal does not appear to have been ankylosed with the tympanic; at all events, I find no trace of it in any of the specimens which I have examined. As in the Tylopoda generally the bulla is filled with cancellous bony tissue. The external auditory meatus is a closed ring, opening slightly upwards and backwards; its rim does not project at all beyond the surrounding parts of the squamosal. The mastoid portion of the periotic is exposed on the occipital surface, filling a very narrow space between the squamosal and the ex-occipital.

The parietals are very long, and form almost the whole of the roof of the cranium, but for most of their length they are narrowed by the great extension of the squamosals, in front of which they send down very long descending processes to meet the orbito-sphenoids. Throughout their entire length they unite to form the low and very thin sagittal crest which rises posteriorly to join the crest of the inion. Anteriorly the parietals diverge to receive the pointed ends of the frontals, and are thus much shorter in the median line than on the sides. This region of the cranium is very like the corresponding part in the camel, but the sagittal crest is not so prominent and the parietal

zone hardly so long; in the llama this zone is very much shorter and the sagittal crest is reduced to very small limits. The shape of the cranium in *Auchenia* is very different from that of *Pæbrotherium*, being dome-shaped with its highest point at the fronto-parietal suture, and the upper contour sloping downwards and backwards to the occiput and anteriorly to the forehead, while in *Pæbrotherium* and the camel the highest point is at the crest of the inion, and from here the upper contour inclines downward to the forehead.

The squamosals are very large and form most of the side walls of the cranium. The root of the zygomatic process is less extended antero-posteriorly than in the llama, and the process itself is rather shorter and straighter; it is received anteriorly into a deep notch of the jugal. The glenoid cavity is much extended from before backwards, and is nearly flat; the postglenoid is high and broad but very thin, and in close contact with the bulla; its articular surface is continuous with that of the glenoid cavity, but in some specimens they are slightly separated, while in the recent genera a wide and deep depression intervenes between the two. There is no elevation of the outer margin of the glenoid cavity into a process, such as occurs in the camel. The post-tympanic process of the squamosal is short and closely united with the posterior lip of the meatus auditorius. This process is placed much farther in advance of the occipital condyles than in the existing species, and in consequence the lambdoidal crest, when viewed from the side, has a much more oblique course downward and forward. This elongation of the posterior region of the cranium is common to the primitive forms of many mammalian groups, and is brought about, so far as we can judge, by the greater proportionate size of the medulla oblongata and cerebellum.

The jugal has a nearly straight course, running forward nearly parallel with the axis of the skull and forming the lower rim of the orbit in such a manner that it opens nearly straight outwards and but little forward, though this eversion of the posterior part is more strongly marked in the larger specimens of *P. labiatum*. The postorbital process of the jugal is long, slender, and curved, but does not quite reach the corresponding process of the frontal, so that the orbit is not completely enclosed by bone. The jugal extends further forward upon the

face than in either of the living genera, and there is a marked rugosity for the attachment of the masseter muscle. The lachrymal is rather small, but extends more on the face than in the camel, and articulates with the frontal, maxillary, and jugal, but not with the nasal, from which it is separated by a process of the maxillary. There is, however, no such vacuity at this point, as occurs in the llama and to a less extent in the camel. The lachrymal foramen is double, and is situated within the rim of the orbit.

The frontals are broad but short; they are widest just above the orbits, and from this point they taper in posteriorly and are received into a deep notch formed by the diverging parietals. From the anterior end of the sagittal crest distinctly marked supra-orbital ridges diverge, and curving forward and outward, terminate in the long and rugose postorbital processes. Near the front of the upper rim of the orbits there is a deep and widely open notch. Anteriorly the frontals terminate little if any in advance of the front of the orbits. There are considerable frontal sinuses, but they do not produce any bulging of the skull. The frontal zone of the cranium is less developed than even in the camel, and has hardly any share in roofing over the cerebral hemispheres. The orbits are very large and situated low down in the face; they are much farther back than in the camel, the anterior rim being over the second molar, and in some specimens over the third. This is a decided advance over the condition found in the primitive selenodonts generally. The alveolus of the third molar makes a hardly noticeable projection into the antero-inferior portion of the orbit. The orbits are also remarkable for their depth, which is so great that a veritable interorbital septum is formed as in the tragulines. In existing tylopodans there is no such appearance.

The nasals are very different from those of either of the recent genera, especially in their greater length. At their junction with the frontals they are quite broad, but rapidly taper, and for most of their length they are extremely narrow: anteriorly they extend nearly to the tips of the premaxillaries.

The maxillaries are long and low; the alveolar portion is especially low, in correspondence with the brachyodont condition of the molars, and thus the inferior rim of the orbit is separated from the teeth by a much narrower space than in the

modern types. But even the facial portion of the maxillaries is very low, especially in front, and the nasal chamber is not nearly so high as in the camel and llama. Just below the line of suture with the nasals there is a long depression in the maxillaries, which is constant in all the specimens, and cannot therefore be entirely due to pressure. Seen in section the nasal passage thus has a curious shape, very narrow above, but broad and very low beneath. Posteriorly the maxillary sends up a short process between the lachrymal and nasal, which reaches the frontal, as in *Camelus*, while in *Auchenia* the vacuity developed at this point prevents more than the minutest contact with the frontal. The alveolar border is prolonged much farther back of the last molar than in the existing forms. The face of *Pæbrotherium* does not exhibit the sudden constriction in advance of pm. 3, which is so characteristic of recent Tylopoda, but tapers gradually to the muzzle, and as the premolars are still present in unreduced number, there is a much shorter edentulous region of the maxillary than in the camel and llama.

The premaxillaries are only partially preserved in any specimen which I have examined, but it can be seen that the ascending rami are short and nearly vertical, and that they are in contact with the nasals. The anterior nares have thus the low, narrow shape and nearly vertical position which occurs in *Anoplotherium*, *Cainotherium*, *Oreodon*, and in fact most of the primitive selenodonts, and very different from the long, obliquely placed opening of the recent tylopodans. Apparently the palatine plates of the premaxillaries are large in proportion and but little reduced by the incisive foramina. The palatine processes of the maxillaries are long, narrow, and tapering anteriorly, giving to the palate the triangular shape, very narrow in front, which is characteristic of the *Camelidæ*, but there is hardly any indication of the constriction of the palatal surface at the diastema behind the first premolar and re-expansion at the canine alveoli, which is so marked in the recent genera. The palatine fissure between the alveolus and the posterior nares is very shallow, though subject to considerable variation: in some specimens it hardly reaches the third molar.

The palatines are narrow and are intermediate in character between those of *Camelus* and those of *Auchenia*; they extend well forward, as far as the first molar, and have their anterior

edges truncate as in the camel, but do not form so much of the hard palate as in that animal, on account of the more anterior position of the nares: on the other hand, they have a greater extension on the roof of the mouth than in *Auchenia*. The posterior nares resemble those of *Auchenia* in shape and position; they are very long and narrow and with a lancet-shaped anterior margin which extends as far forward as the interval between the second and third molars. The canal is, however, very much lower than in the existing forms. The pterygoids are short and end in very small hamular processes, and the pterygoid fossa is a mere shallow slit. The vomer is conspicuous as a septum through nearly the whole length of the posterior nares.

The mandible has a very long and slender horizontal ramus with sinuous lower border; the symphysis is long and spout-like, but is shorter than in the modern genera; and as all of the premolars are present, the edentulous portion is very much shorter. The angle is prolonged into a great hook-like process which is far more conspicuous, though of much less vertical extent, than in the recent genera. The ascending ramus is low and more sloping than in the recent forms; the coronoid process is more recurved and pointed, and the masseteric fossa is deep but of small extent and situated very high up. The condyle is more transversely extended and less rounded than in the camel and llama, and the articular surface for the postglenoid process is very small. Aside from the great production of the angle, the ascending ramus of the jaw is more like that of a true ruminant than of the llama.

The *Foramina* of the skull of *Pæbrotherium* are for the most part like those of the modern Tylopoda. The external opening of the supra-orbital canal is placed near the median line, as in the camel; the infra-orbital foramen is over the fourth premolar, the position which it occupies in the existing species, but the less height of the alveolus brings it nearer to the teeth. The posterior palatine foramina are very far forward, opposite the third premolars, and I can detect but a single pair of them. The two optic foramina are placed low down and very close together, though not quite in contact: the outer lip is not produced into a spine. The foramen lacerum anterius and the foramen rotundum have coalesced, but the opening is not so

large as in the recent species. The foramen ovale and foramen lacerum medium occupy the same position as in *Auchenia*. There is a large postglenoid foramen which does not occur in the llama. The carotid canal is distinct from the foramen lacerum posterius. In *Auchenia* there are at the root of the zygomatic process of the squamosal three venous foramina, the anterior one of which is small, the two posterior very large: only the former is present in *Pæbrotherium*, and in both of the modern genera there is a large foramen between the mastoid and exoccipital, which is very minute in *Pæbrotherium*.

III. *The Brain* (Pl. II, Fig. 10).

The brain of *Pæbrotherium* has been described by Bruce (No. 5, p. 39), but we shall need to examine it from a somewhat different point of view. To render the significance of the description clear, the following account of the camel's brain is quoted from Krueg (No. 18, p. 322): "Beide Gehirne [*i.e.* of camel and dromedary] fallen hauptsächlich auf durch die Charakteristica der Gehirne grosser Thiere, und zwar jenes des Kamels noch mehr als das, von einem jungen Thiere stammende, des Dromedars: gedrungene Gestalt, übergrosser, fast verwirrender Furchenreichthum und ausserordentlich starke Pronation. Zwischen Fissura Sylvii und Fissura suprasylvia sind mancherlei accessorische Furchen eingeschoben, welche die Fissura suprasylvia so hoch nach aufwärts drängen, dass sie bei seitlicher Ansicht eben nur noch sichtbar bleibt. Auf der obern Seite rückt in gleicher Weise die Fissura lateralis so stark an den (abgerundeten) medialen Rand, dass sie schon mehr der medialen als der obern Fläche anzugehören scheint. Gleicherweise rückt das hintere Ende der Fissura coronalis sammt dem Bügel auch dem medialen Rand zu, und noch über diesen hinaus. . . .

"Die Fissura rostralis ist vorhanden, bezugs der Fissura postica bestehen, eben wegen des Reichthums an Furchen, einige Zweifel über die richtige Deutung. Aehnliche Zweifel bleiben auch bezugs der Fissura diagonalis. Endlich sei noch erwähnt, dass sich die Fissura rhinalis wie gewöhnlich bei reich gefurchten Gehirnen nach vorne oben in eine Furche fortsetzt und dass der Lobus pyriformis eine Längsfurche trägt.

“Alle bisher angegebene Merkmale sind vielmehr durch die Grösse als durch die Art des Thieres bedingt. Das einzige auffallende Merkmal, wodurch sich die Tylopoden dann allerdings von den meisten Hufthieren unterscheiden würden, besteht in der schiefen Stellung der Fissura coronalis, die von hinten median, nach vorn lateral gerichtet ist.”

In *Pæbrotherium* the hemispheres are rather short and narrow, ending posteriorly a little in advance of the auditory meatus and tapering anteriorly, as in the brains of the smaller ungulates, such as the tragulines, *Moschus*, etc. In the anterior part of the hemispheres the vertical depth is conspicuously small. The cerebellum is large and completely uncovered, the cerebrum not extending over it at all. The frontal lobes of the hemispheres are extremely small, while the parietal, occipital, and temporo-sphenoidal lobes are fairly well developed. The cortex is much less richly and complexly convoluted than in the camel and llama, and the convolutions are but very slightly sinuous. The sulci which are present are, with few exceptions, those which Krueg has mentioned as being characteristic of all ungulates. In general shape and appearance the brain of *Moschus* is very like that of *Pæbrotherium*; but there are important differences, especially in the degree of “pronation” and “supination” (to use Krueg’s terms). In *Moschus*, as in *Tragulus*, the hemispheres are strongly supinated; *i.e.* the sulci, which are typically confined to the medial surface, make their appearance on the dorsal side. In *Pæbrotherium* the opposite tendency is apparent; *viz.* for the sulci of the dorsal surface to move toward the middle line. The fissura lateralis is thus brought close to the medial edge, from which it is separated only by a very narrow median gyrus; it is long and nearly straight, and is closed in front by the union of the median and medi-lateral gyri. An accessory sulcus runs parallel with the lateral for about three-fourths of its length. The suprasylvian sulcus is placed very high up, nearly, though not quite so high as in the camel: it is very long and but slightly sinuous, and anteriorly passes into the coronal sulcus. The latter, if correctly identified, is placed higher than in the recent species; and its posterior limb runs inward and forward, almost reaching the median line. The diagonal fissure, if present at all, is represented by a very short sulcus which connects the sylvian fissure at its anterior end with the suprasylvian. The

fissura postica is longer than in the camel, and has a somewhat less oblique position, running nearly parallel with the suprasylvian. Between these two sulci there is a short accessory sulcus which runs from the hinder edge of the hemisphere, and then curves downward to join the suprasylvian. The sylvian fissure is quite long and nearly straight, and passes somewhat obliquely upward and forward; it appears to be both straighter and longer than in the camel, especially the *pars posterior*, which in the camel is very short. The cast shows no indication of a *processus acuminis*. The rhinal sulcus is but very faintly marked.

The cerebellum is too much damaged in the two available specimens for accurate description. It is relatively large, both transversely and antero-posteriorly, and has a very broad, prominent vermis, which rises from the medulla at nearly a right angle, and when the skull is placed in a horizontal position, is seen to project somewhat above the plane of the hemispheres. The lateral lobes of the cerebellum are broader than the vermis, and have high, nearly vertical, posterior faces.

IV. *The Vertebral Column* (Pl. II, Figs. 11-23).

I. *Cervical Vertebrae*. — The atlas, as compared with that of the recent Tylopoda, differs in some important respects, especially in its greater elongation in proportion to its transverse breadth, and has a shape not altogether unlike that of *Anoplotherium*. The anterior cotyli for the occipital condyles are deeply concave and quite depressed; inferiorly, they are almost in contact in the median line; superiorly, they are separated by a deep emargination which is wider than in the existing tylopodans. In the latter the external margin of each cotylus is marked by a deep notch, which is but slightly indicated in *Pæbrotherium*. The neural arch is higher, narrower, and more convex than in the camel and llama, in which it is flattened, and the neural spine is more distinctly indicated. The inferior arch in the larger species, *P. labiatum*, resembles that of *Auchenia* in having a strong median keel with a deep depression on each side of it; in the smaller *P. Wilsoni*, this appearance is less distinct, and in the camel the arch is regularly convex from side to side. In the latter genus the anterior edge of the inferior

arch shows on each side of the median line an articular surface for the accessory facets on the basi-occipital: *Pæbrotherium* agrees with *Auchenia* in showing no trace of this. The posterior facets for the axis are high and narrow, and are reflected upon the inner surface of the arch; the facets of the two sides have a somewhat more oblique position than in the recent genera, where they lie in nearly the same transverse plane. The transverse processes differ from those of the recent genera in their much greater antero-posterior extension, as they are produced considerably behind the condyles for the axis, and terminate posteriorly in blunt points, as in the ordinary ruminants; from these points the thickened margins of the transverse processes sweep forward in gentle curves, dying away upon the anterior cotyli. Seen from the side, the edge of the process is not sinuous, but nearly straight. In *Auchenia* the transverse processes project hardly at all behind the facets for the axis, and in the camel they terminate in advance of these surfaces. In both of the living forms the edge of the transverse process is bent in a sigmoid curve, running anteriorly and dorsally. The foramina of the atlas are much as in the recent genera. The neural arch is perforated by a foramen for the superior branch of the first spinal nerve, and the forward extension of the transverse process converts the anterior notch at its root into a foramen. The posterior opening of the vertebrarterial canal enters the base of the transverse process from behind, while in the camel and llama it is placed upon the dorsal side.

The axis has already assumed a strikingly tylopodan character. The centrum is very long, narrow, and depressed, and is faintly keeled throughout its length, the keel terminating behind in a high and quite rugose hypapophysial tubercle. The anterior end of the centrum is quite suddenly expanded to form the articular surfaces for the atlas, which rise high upon the sides of the neural canal, and inferiorly are continuous with each other and with the facet upon the ventral face of the odontoid process. The lower edge of this compound facet is, however, emarginated in the middle line, indicating that formerly the surfaces of the two sides were separated, while in the existing forms of both Pecora and Tylopoda this margin is uninterruptedly curved from side to side. The odontoid process is peculiar in being exceedingly short and semi-cylindrical in shape,

the inferior surface being convex and the superior flattened, and the free anterior margin is gently rounded, not abruptly truncated. In the existing genera of the *Camelidæ*, as well as in the true ruminants, the odontoid process is spout-like, with deeply concave dorsal surface, while that of *Pæbrotherium* resembles rather the odontoid of *Anoplotherium*, the *Oreodontidæ*, and other primitive selenodonts, except that it is decidedly smaller. The anterior end of the axis in *Pæbrotherium* differs from that in *Camelus* in being much less oblique, and in the fact that the odontoid is not directed dorsally as well as forwards: in these respects it is more like the axis of the llama. The posterior face of the centrum is slightly concave. The neural arch is high and narrow, and the neural spine is expanded into a high thin plate, which is very different in character from the spine of the recent genera, in that it is both higher and longer (antero-posteriorly), projecting behind the postzygapophyses, while in the llama, and especially in the camel, it terminates some distance in front of the zygapophyses, ending in a bifid rugosity, which is not indicated in *Pæbrotherium*. The postzygapophyses are small and slightly concave from side to side. The transverse processes are broken away in all the specimens which I have had the opportunity of examining, but it is evident that they were short and very thin, depressed plates. The anterior opening of the vertebrarterial canal is placed laterally, as in the camel (but not so far forward); in the llama the opening is inferior rather than lateral. This canal appears to enter the neural canal a little more than half-way toward the posterior end, though it is difficult to decide this question with accuracy from the available specimens. The pedicels of the neural arch are perforated by the second pair of spinal nerves.

The third cervical is slightly longer than the axis, and has a narrow, depressed centrum which broadens posteriorly, so that the hinder face is much broader than the front: the latter is slightly convex, the former concave. Throughout the entire length of the centrum there is an inferior keel, which, for the anterior two-thirds of its course, is a faintly marked ridge, but then becomes much more prominent and ends behind in a rugose tubercle. The transverse processes expand posteriorly and terminate in flat, depressed wing-like projections. There is already an indication of a division of the process into anterior

and posterior portions, but the former has not attained any such development as appears in the camel. The neural arch is low in front and rises behind, and the pedicels are deeply notched anteriorly for the passage of the spinal nerves. The neural spine is represented only by a very feebly marked ridge. The postzygapophyses are much larger and diverge much more strongly than the prezygapophyses, and from the base of the latter a sharp ridge runs posteriorly along the side of the pedicel of the neural arch. There is in this vertebra no visible opening for the vertebrarterial canal.

The fourth cervical is slightly shorter than the third, measuring about six-sevenths of its length, but is otherwise very much like it. The anterior portion of the transverse process is, however, more developed, and more clearly distinguished from the posterior portion, and projects downward, somewhat as in the recent forms, but to a much less marked degree. The inferior keel and tubercle are more prominent than on the third vertebra.

The fifth cervical is shorter than the fourth, about five-sevenths of its length, but differs from it in no other important respect, except that the separation of the transverse process into anterior and posterior portions is more distinct. On both of these vertebræ the down-projecting anterior portion of the transverse process is very different in shape from that which occurs in the recent genera, being much less massive and rugose, and having thickened and regularly curved margins, which extend somewhat in advance of the anterior face of the centrum. Neither this vertebra nor its predecessor has a neural spine or visible vertebrarterial canal.

The sixth cervical is strikingly different from the others, and is less like its representative in the modern genera than any other vertebra of the neck. The centrum is considerably shorter than that of the fifth vertebra, which, in the specimen we are describing, measures 56 mm. in length, while the sixth measures but 45 mm., and is higher in proportion to its breadth. The anterior face is quite strongly convex and nearly hemispherical in shape, the posterior as strongly concave. The inferior keel and tubercle are almost obsolete. The neural arch is high and is occupied throughout its length by a thick neural spine, which is unfortunately broken away in the only

specimen before me, so that its height cannot be determined, but it was obviously much better developed than in the llama, and was apparently quite as large in proportion as in the camel. The pedicels of the neural arch are higher than in the recent genera, and the zygapophyses project farther in front of and behind the centrum. The transverse process is a long, stout, depressed plate, which is much more prominent, and has a greater antero-posterior extent than in the living species, and the base of the process is perforated throughout its entire length by the vertebrarterial canal, which is not the case in the camel or llama. Beneath, and slightly in advance of the posterior opening of the vertebrarterial canal, there is another large foramen, which, however, merely enters the bone and does not perforate it (Pl. II, Fig. 16 *vc*). This second foramen is likewise absent in the modern Tylopoda. The inferior lamella is a very large and massive plate, which is longer than the centrum and very different in shape from that of the llama. In the latter the lamella is separated into two portions, an anterior one, which is compressed and projects downward, and a posterior one, which is depressed and projects outward. In *Pæbrotherium* this separation does not occur, the lower margin of the lamella being entire, and giving the whole vertebra an appearance quite like that of the horse. The vertebra is decidedly shorter in proportion than is the case in the llama. The sixth cervical of *Camelus dromedarius*, as figured by De Blainville, resembles that of the llama in the division of the lamella, while in a specimen of *C. bactrianus* I find this vertebra more like that of *Pæbrotherium*.

The seventh cervical is the shortest vertebra of the series, much shorter, proportionally, than in either of the living types. The centrum is broad and depressed for most of its length, but in advance of the transverse processes becomes suddenly constricted to form the small and nearly hemispherical anterior face. The posterior face is concave, broad, and low, and shows facets for the first pair of ribs. The pedicels of the neural arch are high, the neural spine thick and inclined forward, the prezygapophyses large, widely separated, and projecting more in advance of the centrum than is the case in the recent species. There is only the faintest trace of the hypapophysial keel and tubercle. In a specimen of this species kindly lent to me by

Professor Cope I find a minute canal through the base of the transverse process, but this is probably an individual peculiarity.

It will be plain from the foregoing description that the cervical vertebræ of *Pæbrotherium* have already assumed the features characteristic of the Tylopoda, but in a somewhat less marked degree than in the recent forms of that group. Indications of a more primitive condition are found in the structure of the transverse processes, the retention of the vertebrarterial canal in the sixth vertebra, the shape of the atlas, the character of the odontoid process, and the less elongated and less massive development of the neck as a whole. If we take the length of the humerus as a standard, and call that 100, the length of the neck in *Pæbrotherium* would be 197; in *Auchenia*, 280; and in *Camelus*, 286.

The Dorsal Vertebræ. — The number of dorsals characteristic of *Pæbrotherium* cannot yet be definitely determined, as no specimen has as yet been found with the series complete. In the individual upon which this description is for the most part founded, there are preserved twelve vertebræ of this region and, in addition, a fragment of a centrum which probably represents a thirteenth, though it may perhaps belong to a lumbar. The first dorsal has a centrum which is nearly as long as the last cervical, and is broad and flattened from above downward; the anterior rib-facets are nearly flat, but are on projecting processes, very much as in the llama. The inferior face of the centrum has on its anterior part a broad ridge with raised and rounded margins, and on each side of this a small pit, all of which occur also in *Auchenia*, the first dorsal of which this vertebra closely resembles, though its centrum is decidedly longer in proportion. The prezygapophyses are larger, higher, and project more in advance of the centrum than in the recent forms; the transverse processes, on the other hand, are rather shorter, and end in a large, deeply concave facet for the tubercle of the first rib.

The second, third, and fourth dorsals have centra which are shaped very much like that of the first, but they gradually become less distinctly opisthocœlous, shorter, narrower, and less depressed. In the middle region of the thorax the vertebræ are relatively large and heavy, with large spines which slope strongly backward; but these spines are very much more slen-

der than in the existing tylopodans, and so far as can be judged from the specimens at hand were also proportionately longer. Metapophyses first appear on the ninth vertebra, rising from the transverse process just above the facet for the tubercle of the rib; they increase in size on the tenth and eleventh, but retaining the same position, while on the twelfth and thirteenth they shift to the prezygapophyses. The centra of the posterior dorsals become elongated, broad, and depressed, and have nearly flat faces. The spines are strongly inclined backward until the twelfth vertebra is reached, which is the anticlinal, and has a curious plate-like spine, with deeply concave anterior and nearly straight and vertical posterior margin. The last dorsal has a broad, plate-like spine, like that of a lumbar vertebra. On the eleventh vertebra the postzygapophyses tend to become cylindrical, and are received into the concave prezygapophyses of the twelfth, on which vertebra and the thirteenth these processes are of the interlocking cylindrical type common to all artiodactyls. The spinal nerves pass out between the neural arches, and in no case are the pedicles perforated by them. The chief difference between the dorsal vertebræ of *Pæbrotherium* and those of the recent Tylopoda lies in the character of the spines, which in the latter, and more especially in the camel, are extremely massive, while in the Miocene genus they are very slender.

The *lumbar vertebræ* probably number six, or perhaps seven, and are relatively large. The centra are long, broad, and depressed, and become more so as we pass backward: they have nearly flat or slightly opisthocœlous faces, and are keeled inferiorly; while in the posterior part of the region there is a faintly marked ridge on each side of this keel. Both the neural spines and the transverse processes are, unfortunately, broken away in all the specimens which I have seen; but from the fractured surfaces, it is clear that the latter had a greater antero-posterior extent than in the recent genera, and that the neural spines were more compressed and decidedly less massive. The zygapophyses are of the typical interlocking shape, but they differ in detail from the structure seen in the modern genera. In the camel an additional complication has arisen, in the appearance of a concave surface above the postzygapophyses, the episphe-nial process, which also occurs in several of the true ruminants.

Naturally, the prezygapophyses are modified to fit them. In the llama these processes appear irregularly, sometimes present on one side and not on the other, and are often absent altogether. In *Pæbrotherium* a slight beginning of the same structure may be observed on some of the lumbar vertebræ (Pl. II, Fig. 23). In this genus, also, the postzygapophyses are more angulated than in the llama, the superior and inferior articular surfaces not passing into each other by such a gentle, regular curvature.

No sacral or caudal vertebræ are preserved in any of the specimens at my disposal; but if we may judge from the analogy of its contemporaries, *Pæbrotherium* probably had a longer tail than the modern representatives of the group.

V. *The Ribs.*

The ribs of *Pæbrotherium* differ decidedly from those of the camel and llama in their much greater slenderness. The anterior ribs are short and flattened, but by no means so broad as in the existing species; while those of the median and posterior regions are much more slender than is usual among recent artiodactyls, and are rather to be compared to the ribs of carnivores. This is, however, usually the case among the more ancient ungulates, and *Hyrax* still retains this type of rib-structure. In the existing Tylopoda, and especially the camel, the ribs are very irregularly curved, but in *Pæbrotherium* they have only the usual outward and forward curvature.

VI. *The Fore Limb.*

The scapula (Pl. II, Figs. 24, 25) is, on the whole, rather more like that of the llama than that of the camel, though individual variations of considerable extent occur, which approximate the condition found in *Camelus*. In the latter the scapula is much higher and narrower than in the llama; the spine rises nearer to the glenoid cavity, and runs in a nearly median position, dividing the blade into nearly equal pre- and post-scapular fossæ; the acromion is less developed, the neck is longer and broader, the coraco-scapular notch higher and more gently curved, and the coracoid much more massive and rugose. In *Pæbrotherium* the neck is very slender and contracted (in some speci-

mens it is considerably broader than in others), and the spine rises nearer to the coracoid than to the glenoid border, making the prescapular fossa much broader than the postscapular, but the difference is not so great as in *Auchenia*, and the outline formed by the coracoid border is rather more like what we find in the camel than in the llama. The spine rises abruptly to a considerable height and runs in a somewhat straighter and less sinuous line than in either of the recent genera; the acromion is very long, expanded at the free end, and somewhat retroverted. The glenoid cavity is shallow and nearly circular in outline, the antero-posterior diameter but slightly exceeding the transverse; this varies, however, in different specimens, as does also the degree of thickening and rugosity shown by the edge of the glenoid cavity. The coracoid process is less prominent than in the existing genera and very much less massive and rugose; as in them, however, it is curved inward at the free extremity.

The *humerus* (Pl. II, Figs. 26-28) is strikingly different from that of the modern representatives of the group, and in the same way as the humerus of *Mesohippus* differs from that of the existing horses. In *Pæbrotherium* the humerus is relatively long and slender, with feebly developed ridges for muscular attachments; the deltoid ridge and hook, so conspicuous in the recent forms, are here but a roughened line; and the supinator ridge, though running far up upon the shaft, is but faintly indicated. The shaft shows the same sigmoidal curve as in *Camelus* and *Auchenia*, but to a less degree, and is very much more slender, especially when seen from the front, for the antero-posterior extent of the proximal part of the shaft is considerable. The head is strongly convex, is more sharply constricted off from the shaft, and presents more decidedly backward than in the recent genera. The external tuberosity is a high and roughened ridge, which extends across nearly the entire anterior face of the bone, and ending in a prolonged and massive hook which overhangs the bicipital groove. The upper margin of this tuberosity is slanting on the external side, projecting but little above the head, but rising high above it on the internal side. The internal tuberosity is small and is separated from the outer one only by the narrow and deep bicipital groove, the bottom of which is occupied by the very small beginning of

what Kowalevsky has named the "bicipital tubercle" (No. 16, p. 6). The bicipital groove is thus confined to the antero-internal angle of the head, and is overhung by the external tuberosity so as to be hardly visible at all when viewed from the front. At first sight, therefore, the proximal end of the humerus of *Pæbrotherium* appears to be totally different from that of the modern Tylopoda, in which the external tuberosity is but little larger than the internal, from which it is separated by a very wide interval: the bicipital groove has immensely broadened, and is separated into two parts by the bicipital tubercle, which has become almost as large as the tuberosities proper, and is situated in the median line of the humerus. Great as this difference is, it is entirely bridged over, as we shall see later, by the intermediate genera.

The distal end of the humerus is proportionally narrow; the trochlea is set somewhat more obliquely to the long axis of the shaft than is the case in the modern forms, and has a considerably greater height on the internal than on the external side—a difference which is hardly indicated in the camel and llama. The intercondylar ridge is a faintly marked, low, narrow, and rounded swelling, and differs strikingly from the broad and prominent ridge of *Camelus* and *Auchenia*. The external epicondyle is but little developed, forming merely a stout ridge, but the internal one is quite large and forms a prominent rugose projection at the postero-internal angle, very much as in the camel: in the llama this is considerably reduced. The trochlea is higher than in the recent species, and especially is carried up on the posterior side of the bone very much higher than in the camel—a mode of development which reverses that which occurs in the true ruminants. The anconeal fossa is small but deep and perforates the shaft, thus forming a small supratrochlear foramen.

The ulna and radius (Pl. II, Figs. 29–32) are firmly co-ossified throughout their length, and are remarkably long and slender, though not quite so long as in the existing Tylopoda. Assuming the length of the humerus to be 100, that of the radius is 115, while in the camel it is 125. Just below the proximal end there is a small interosseous foramen which penetrates from side to side, and above the distal end there appears to be another; at all events there is a very deep anterior fossa between the two bones at this point.

In correspondence with the narrowness of the humeral trochlea, the head of the radius is but slightly broader than the shaft. The articular surface is divided into two concave facets by a very low ridge which forms an inconspicuous projection on the anterior margin. As the external facet is much larger than the internal, this projection is internal to the median line of the head, but placed nearly in that of the shaft, for the expansion of the head is principally towards the outer side. The shaft of the radius is very slender and of transversely oval section, with the inner border somewhat sharper than the outer: it gradually thickens below the middle of its length, as well as becoming broader. The bicipital tuberosity is very small and inconspicuous, and is placed some distance below the head, on the internal border. The distal end is much thicker and broader than the proximal, though less expanded than in the modern genera. The anterior face is slightly roughened and exhibits the grooves for the extensor tendons even more distinctly than in the camel. The distal face exhibits three well-separated facets for the proximal row of carpals, which are placed somewhat obliquely to the transverse axis of the radius. The surface for the scaphoid is concave in front, convex behind, and is reflected far up upon the posterior side of the radius, giving the bone greater depth (antero-posteriorly) here than elsewhere. The lunar facet is separated from the scaphoidal by a sharp ridge: it also is concave in front, convex behind, but is not reflected upon the posterior side of the radius, except for a small articular surface which is visible on the ulnar side of the projecting posterior portion of the scaphoidal facet. The cuneiform surface is large, and covers almost the whole of that bone, the ulnar contact with it being very much reduced. The cuneiform surface of the radius is saddle-shaped, concave from side to side, and convex from before backwards, and reflected upon the posterior side of the radius, passes into the surface for the pisiform, which is more on the radius than on the ulna. There is, however, no such projection at this point as is formed by the scaphoidal facet. Large as it is, the cuneiform facet of the radius is relatively smaller than in the modern forms, where it covers the entire proximal surface of the cuneiform when viewed from the front, the ulna being pushed to the postero-external angle.

The humeral facets of the ulna are peculiar in the Tylopoda, and quite different from those which occur in the ordinary ruminants: the peculiarity is already well established in *Pæbrotherium*. Externally the articular surface is confined to the superior border of the sigmoid notch, whereas on the inner border it is continued down the anterior face of the notch, and passes without interruption into the corresponding facet of the radius. The olecranon is high, but compressed and not massive; it is continued upward in almost the same straight line as the shaft, and is abruptly truncated at the end, its superior margin sloping downward and forward, and deeply grooved by a sulcus for the extensor tendons. Both the anterior and posterior margins of the olecranon are nearly vertical. In *Camelus* and *Auchenia* the olecranon is very different, in that it projects strongly behind the line of the shaft; and the superior margin is rounded, rugose, and not grooved by a tendinal sulcus.

The shaft of the ulna is much reduced, but decidedly less so than in the modern forms, in which it is almost entirely posterior in position, and even the distal end is concealed by the expansion of the radius. In *Pæbrotherium*, on the other hand, the shaft is visible from the front for its whole length, and when viewed from behind covers half the width of the radial shaft. The distal portion of the ulna is enlarged both in thickness and depth, fitting into a deep depression of the radius just above its distal expansion. From this point the ulna tapers rapidly to its distal end, terminating in a small tip which projects somewhat below the level of the radius, and showing facets for the cuneiform and pisiform, which in old animals pass into the corresponding facets of the radius without any visible line of separation.

The *carpus* (Pl. II, Figs. 33-35) has been figured, and briefly described by Cope, who has called attention to its more important characters, but a more detailed account is necessary for the purpose which we have in view. As a whole the carpus is broad and low—a change which has chiefly affected the distal row, as the height of the proximal series is still considerable. The scaphoid is narrow but deep antero-posteriorly; its radial surface forms a low broad ridge in front, and behind a deep concavity, terminating in an elevated hook, which extends well up upon the posterior surface of the radius, and necessitates the

peculiar facet on that bone which has been described. As the inner angle of the distal end of the radius is not so prominent as in the llama, the corresponding part of the scaphoid is but slightly depressed, and its internal surface is nearly plane, aside from minute rugosities. Distally, the scaphoid shows three facets, for articulation with the trapezium, trapezoid, and magnum respectively. The first is extremely small, and is placed at the postero-internal angle of the bone. The facet for the trapezoid is concave, and relatively decidedly smaller than in the llama, which fact is intelligible when we remember that in the existing forms the trapezoid plays a much more important part than it does in *Pæbrotherium*. The facet for the magnum is nearly flat, and is relatively very large, occupying nearly the entire width of the anterior part of the bone.

The lunar is rather higher and broader than the scaphoid, but of somewhat less antero-posterior diameter. Its proximal surface is convex, and irregularly quadrate in shape. The internal or radial side is nearly vertical, and abuts against the scaphoid without the distinct excavation which occurs in the llama. There is no superior facet for the scaphoid, but the inferior facet extends almost to the upper border. Posteriorly the lunar has a bifid projection, the longer and stouter arm of which curves toward the scaphoid, the other toward the cuneiform. The distal beak is long; the magnum facet is longer and more obliquely placed than that for the unciform, the two meeting at an acute angle. In the llama they are of about the same size, and meet at a right angle.

The cuneiform is a high, narrow, and deep bone, much less cubical and massive than in *Auchenia*; its proximal surface is shaped somewhat like that of the scaphoid, but is narrower, and the facet is carried farther down upon the external side to allow for the downward projection of the ulna. This is decidedly more marked than in the recent species. Posteriorly there is a narrow, oblique surface for the pisiform, and the distal surface is entirely taken up by the narrow and somewhat concave facet for the unciform.

The pisiform is short, and differs much in shape from that of the llama and camel. The neck is small and much contracted, but rapidly expands to form the thickened, rugose, and somewhat incurved free end. The facet for the cuneiform is long

but narrow, that for the radius and ulna very small. In the llama the pisiform has a much greater vertical depth and a much less constricted neck; the facet for the ulno-radius is even larger than that for the cuneiform, and the whole bone is longer, higher, and more compressed.

The presence of the trapezium in the carpus of *Pæbrotherium* is a very interesting fact, which was first demonstrated by Cope. It is a very small bone of nodular shape, attached to the scaphoid by a minute facet, and connected also with the trapezoid and the rudimentary second metacarpal. Baur has shown (No. 1, p. 117) that the trapezium probably still occurs sometimes in the *Camelidæ*.

The trapezoid is relatively smaller than in the recent genera, and as in them shows no tendency to coalesce with the magnum. There is a single, slightly convex surface for articulation with the scaphoid; the surface for the magnum is not separated into superior and inferior facets, as it is in the llama. Distally there are two facets which meet at a very open angle: the larger one is on the radial side, and is for the rudimentary second metacarpal; the smaller one is for a process of the third metacarpal. This is another example of Kowalevsky's "adaptive reduction."

The magnum is broad and low, hardly more than half the height of the unciform. The greater part of the proximal surface is occupied by the facet for the scaphoid, which is flat in front, but behind rises upon the convexity which articulates on one side with the scaphoid and on the other with the lunar. This convexity is decidedly more prominent than in the existing genera. The anterior portion of the lunar facet slopes downward at an open angle from the scaphoidal, and is decidedly smaller. The distal surface for metacarpal III is nearly flat and of triangular shape, with the apex behind. There is, of course, no facet for mc. II, which is excluded from contact with the magnum by the connection of No. III with the trapezium. The posterior hook of the magnum has become rudimentary.

The unciform is rather high and narrow, and so descends considerably below the level of the magnum. The proximal surface is unequally divided between the small oblique lunar facet and the large transverse but sinuously curved cuneiform facet, but the disproportion is not nearly so striking as in the modern genera. In the llama, for example, the cuneiform facet is many

times broader than that for the lunar, the proportion being 3 to 1; in *Pæbrotherium* it is as 9 to 5. Distally, the unciform is taken up, for the most part, by the large surface for the fourth metacarpal, but in addition there is a small but distinct facet at the inner angle for a projection of mc. III, and on the external side another and still smaller one for the rudimentary fifth digit. Both of these facets are, however, lateral rather than distal. The posterior process is well developed and forms a stout decurved hook, which is relatively longer than in the llama.

The *metacarpus* (Pl. II, Figs. 36, 37) consists of two functional digits, the third and fourth, with small scale-like rudiments of the second and fifth, all of them separate. Mc. II is very short, with a somewhat enlarged and thickened head, but tapering rapidly to a blunt point; it lies in an excavation in the radial side of mc. III, and is very closely applied to but not co-ossified with it. The proximal end is convex, and shows two very small facets, the larger of which is posterior and articulates with the trapezium, while the anterior one articulates with part of the trapezoid, but is altogether excluded from the magnum.

Mc. III is considerably elongated, but has not reached the relative length which occurs in the modern genera; its length is to that of the humerus as 85 to 100, while in the modern types the length is about 95, and in some individuals even exceeds the length of the humerus. The shaft is very slender throughout, especially in the distal third. The proximal portion of the shaft is of trihedral section, with flattened ulnar side which is closely applied to mc. IV, while the anterior surface is rounded. Near the distal end the flattening of the ulnar side disappears and the shaft becomes nearly cylindrical. The distal ends of the median metacarpals show a slight tendency to diverge, obviously the beginning of the peculiar structure which characterizes the cannon-bone of the *Camelidæ*. The proximal articular surface presents a large, slightly concave facet for the magnum, and a much smaller, though very distinct one, for the trapezoid. The head rises above that of mc. IV and sends out a process which abuts against the unciform, and thus mc. III articulates with three of the carpal elements; beneath this process there is a fossa which receives the fourth

metacarpal. The distal trochlea is very narrow, hardly expanding at all beyond the shaft, and is simply convex from before backwards. The carina is entirely confined to the palmar side, and is less prominent even than in the existing members of the family. In position, it is slightly to the medial side of the middle line. Besides the carina the elevation of the medial and external borders produce keels which are much sharper and more prominent than in the llama.

Mc. IV is the counterpart of mc. III, but is decidedly more slender and flattened in its proximal half. Its head is decidedly narrower, and its apparent breadth is reduced by the overlapping process from mc. III to the unciform. On the ulnar side of the proximal end there is a deep excavation in which lies the rudimentary fifth metacarpal.

Mc. V is a very much reduced and flattened scale, even smaller than the rudimentary second digit, and is attached to the side of the unciform by a minute facet.

The *phalanges* (Pl. III, Figs. 48, 49) of the manus are very different from those of the recent Tylopoda, and would seem to indicate that *Pæbrotherium* possessed a foot like that of the typical ruminants; not the broad pad or cushion which characterizes the existing forms. The phalanges of the first row are long and slender, but much shorter, relatively, than in the llama; nor are the proximal and distal ends so much expanded as in that animal: their shape is likewise more asymmetrical, owing to the less degree of divergence of the toes. In the true ruminants the strong degree of convergence produces decided asymmetry of the phalangeal articular surfaces. In *Pæbrotherium* the groove for the carina of the metacarpals is a mere emargination of the posterior edge. The phalanges of the second row are even more unlike those of the recent genera, in that they are short and much compressed, but of considerable antero-posterior diameter, while in the camel and llama they are broad and much depressed and flattened. The ungual phalanges resemble those of the antelope and deer much more than they do those of the recent Tylopoda; they are long, high, and pointed, somewhat rounded on the outer, but quite flattened on the medial surfaces. These phalanges are sufficient to show that *Pæbrotherium* could not have had anything more than a rudimentary pad.

VII. *The Hind Limb.*

Of the *pelvis* but little is preserved in any of the specimens. The best is one consisting of the acetabulum, a considerable portion of the ilium, and the base of the ischium; this specimen is of *P. Wilsoni*, and belongs to the Museum of Comparative Zoölogy at Cambridge. The acetabulum is slightly more depressed and less circular than in the existing species and has a somewhat less prominent rim. The ilium is remarkable for its very long, shallow, and compressed peduncle. The fragment is preserved as far forward as the hinder edge of the surface for the attachment of the sacral vertebræ, and for this entire distance the ischial and acetabular borders are nearly parallel, giving to this region of the bone a very different appearance from that which occurs in the recent forms: in the llama the neck of the ilium is especially reduced in length. The expanded plate of the ilium is unfortunately broken away, but it obviously was not very large. The ischium, so far as it is preserved, is also shallow with nearly parallel borders; it does not show the high, thin, and arched crest, which is so prominent in the llama (but not to the same degree in the camel) above and behind the acetabulum. In the recent species there are above the acetabulum several prominent and rugose ridges for the attachment of the deep gluteus muscle, while in *Pæbrotherium* these are very faintly shown. The pubis, at its origin below the acetabulum, is slender and of trihedral section; it forms a somewhat more open angle with the axis of the ilium than in the camel and llama.

The *femur* (Pl. II, Figs. 38, 39) is characteristically tylopodan in appearance. Kowalevsky has called attention to the peculiarities of this bone in 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." (No. 17, p. 30). In *Pæbrotherium* the proximal end is less expanded laterally than in the living cameline genera; the head is small and projects less obliquely upward than in *Auchenia*, but is set upon a somewhat more distinct neck. The pit for the round ligament is an oval depression placed upon the posterior

aspect of the head, and is shorter, shallower, and nearer the border of the head than in the llama. The bridge connecting the head and the great trochanter is narrower, shorter, and less rugose, and the great trochanter rises higher above it, producing a decided notch. Though the great trochanter is higher than in the recent forms, it is much less massive and thickened antero-posteriorly, and in consequence the digital fossa is much shallower. The second trochanter is also less developed, especially in the vertical direction, than in the llama, though relatively larger than in *Camelus*, and forms a small conical protuberance. The shaft is long, slender, and arched forward, and except for its greater slenderness, very similar to the proportions found in the recent species. With the length of the humerus taken as 100, that of the femur in *Pæbrotherium* is 125, in *Camelus* 127, and in *Auchenia* 134. The rotular trochlea is broad and shallow, with sharp external and thickened internal lip, the latter being also somewhat the higher of the two—a more decided difference than occurs in either of the modern genera. The condyles are smaller, less strongly projecting, and less widely separated than in the latter. The trochlea rises higher upon the shaft, is less strongly arched, and less oblique to the transverse axis of the distal end of the bone, than in the recent genera. The external condyle is somewhat larger than the internal, and there is no such decided notch above the latter as occurs in *Auchenia*. *Pæbrotherium* agrees with most of the true ruminants, and differs from the *Camelidæ* in the presence of a distinct pit for the insertion of the plantaris muscle above the external condyle.

It is clear from the foregoing that the femur of *Pæbrotherium* departs but little from the cameline type, and that such divergences as are observable are in the direction of the more generalized artiodactyls.

The *tibia* (Pl. III, Figs. 40–42), like all the other limb bones, is long and slender; longer as compared with the humerus than in either of the existing genera, its length being 141, as compared with 130 in *Auchenia*, and 111 in *Camelus*. The facets for the femoral condyles are large and nearly flat, and separated by a prominent bifid spine; the external facet is considerably larger than the internal, but shows no tendency to assume the peculiar recurvature which occurs in the camel. The cnemial crest is

very prominent and runs far down the shaft; on the inner side of its proximal end there is the usual deep tendinal sulcus. The lower half of the shaft is flattened antero-posteriorly and is transversely oval in section. The distal end is somewhat expanded and thickened; the external astragalar facet is somewhat larger than the internal, from which it is separated by a tongue, much more prominent than in the existing types. In each of these astragalar facets there is a shallow depression, the beginning of the interruptions of the articular surfaces which are so noticeable in the camel. The internal malleolus is very prominent and is anterior in position. The fibular facet is continuous from before backward, and though emarginated by the groove for the rudimentary shaft of the fibula, this groove is not nearly so deep as in the camel, where it divides the facet into anterior and posterior portions.

The *fibula* (Pl. III, Fig. 41) is quite as much reduced as in the modern representatives of the *Camelidæ*. The proximal end is a small spine anchylosed with the tibia, and the distal portion is a nodule which is wedged in between the tibia and the calcaneum, forming a heavy external malleolus. It projects further beyond the line of the tibia than in the recent genera, and is deeply grooved on its outer side by the sulcus for the peroneal tendons. The nodule presents articular facets upon three of its sides, a proximal one for the tibia which is not interrupted in the middle, a distal one for the calcaneum, and an internal one for the astragalus.

The *tarsus* (Pl. III, Figs. 43-47) is essentially like that of the llama, but in correspondence with the lighter construction of the limbs, is higher and narrower. The astragalus has a narrower groove for the tongue of the tibia, and, indeed, is narrower throughout. The external condyle is separated quite widely from the distal trochlea, while the internal one is separated from the navicular facet only by a small prominence. The surface for the cuboid is quite narrow, that for the navicular much wider and hour-glass-shaped. The calcaneum is relatively longer and more slender than in the llama, and is especially of less antero-posterior depth towards its distal portion, nor is there any groove above the sustentaculum, to receive a process from the tibia. When the calcaneum of the llama is viewed from behind, there is seen a projection from the posterior part of the

distal end, which embraces the lower end of the astragalus, and between which and the sustentaculum there is a deep notch: nothing of the kind is observable in *Pæbrotherium*, and the sustentaculum itself is not so prominent. The fibular facet of the calcaneum is longer, lower, and less abruptly truncated in front than in the llama, and the cuboidal surface is likewise narrower. The tuber calcis is proportionately thicker, of less depth, and with the free end less thickened and rugose: its borders are also more nearly parallel.

The cuboid is decidedly higher and narrower than in the living genera, and its facets differently proportioned; that for the calcaneum being somewhat broader than that for the navicular, while in the recent forms the reverse is the case, though the difference is not very striking. The calcaneal facet in *Pæbrotherium* is a broad overhanging shelf, strongly convex from before backwards: a small fossa intervenes between it and the astragalar surface, where the two are on the same level. The astragalar facet is narrow and simply concave from before backward; in the middle of its course it is emarginated on both sides and greatly narrowed, though not entirely interrupted, by the fossa already mentioned, on the outer side and by another on the inner side; anteriorly it rises much higher above the calcaneal facet than in the llama. The posterior hook of the cuboid is very stout, but not quite so long as in the recent species, and fits closely against the projection from the fourth metatarsal. On the internal or tibial side of the cuboid are two facets for the navicular, — the hinder one a large projecting ledge, the front one a mere smooth surface. The distal end of the cuboid displays a large, somewhat triangular and concave surface for the fourth metatarsal, which is not emarginated and interrupted as in the camel. External to this is a minute facet for the rudimentary fifth digit, but this facet is entirely lateral in position, not at all distal.

The navicular is entirely free from the cuboid, never showing any tendency to coalesce with it; it is comparatively high and narrow, but of less antero-posterior depth than in the recent forms, and is devoid of a posterior hook. The astragalar surface is concave from before backwards, saddle-shaped from side to side, and is emarginated in the middle by a fossa on the fibular side. The posterior facet for the cuboid does not form a prom-

inence as in the llama. The distal surface displays two facets, — a large and nearly plane anterior one for the coalesced ecto- and meso-cuneiforms, and behind this a small and somewhat concave one for the ento-cuneiform.

Cope has incorrectly stated that the ento-cuneiform was missing, and that the ecto-cuneiform alone supported the third digit (No. 8, p. 487). As a matter of fact, the third digit is supported by a compound bone, composed of the coalesced ecto- and meso-cuneiforms, while the ento-cuneiform is also present. The latter is the smallest of the tarsal bones; it is wedged in between the navicular and the rudimentary second metatarsal, and behind is in contact with the stout posterior hook of metatarsal III, but does not touch the latter in front. The compound cuneiform is relatively higher and narrower than in the recent genera: it has no contact with mt. II. Except for differences of proportion and a few variations in details, the tarsus of the Tylopoda had already attained in *Pæbrotherium* to substantially the same condition which it still retains.

The *metatarsus* (Pl. III, Figs. 50, 51), like the metacarpus, consists of two functional digits, the third and fourth, and of two reduced, scale-like rudiments, the second and fifth. Mt. II has an enlarged head with an oblique facet, directed downward and backward, which articulates with the ento-cuneiform; it is entirely excluded from any contact with the meso-cuneiform by the extension of mt. III over that bone. In some specimens mt. II is free, while in others it is firmly co-ossified with mt. III, though its limits are always plainly visible; it is considerably longer than the corresponding metacarpal, but is nevertheless short, and rapidly tapers to a point.

Mt. III and IV are much longer than the metacarpals, while in the recent genera the fore and hind cannon-bones are of almost the same length. In *Pæbrotherium* the length of the metacarpus is 85, that of the metatarsus 95 (that of the humerus being 100); in *Camelus* these proportions become 93 and 97, in *Auchenia* 101 and 99; so that the Miocene genus has nearly attained the modern standard so far as the length of the metatarsus is concerned. Mt. III is considerably stouter than its fellow, to which it is very closely applied, and the two were held together by the manner in which the long hook-like processes from the plantar side of the proximal ends are wedged in

between the ento-cuneiform on the one side and the posterior hook of the cuboid on the other. On the tibial side of mt. III and the fibular side of mt. IV there are near the proximal end small deep fossæ for the rudimentary metatarsals. Mt. V is never, in any specimen which I have seen, ankylosed with mt. IV, and its contact with the cuboid is very small and almost entirely lateral—a fact which we shall see to be not without importance. The distal ends of the functional metatarsals are broader than those of the metacarpals, but the carinæ are not more prominent, and are likewise entirely confined to the plantar side.

The *phalanges* of the pes are in general like those of the manus, but those of the proximal row appear to be decidedly shorter (which is not sufficiently indicated in the restoration) in the hind foot than in the fore foot. Kowalevsky has pointed out the same difference in *Anchitherium* and the horse (No. 16, p. 65).

The metapodials of *Pæbrotherium*, even the rudimentary ones, are very similar in form and proportions to those of *Xiphodon*, but with the important difference that in the latter genus the reduction is an inadapative one, while in the former it is adaptive. Schlosser, following Cope's description of the pes, has regarded *Pæbrotherium* as inadapatively reduced (No. 27, p. 114); but this is incorrect. In the manus, mc. III is in contact with the trapezoid and has entirely excluded mc. II from the magnum, though the contact of mc. III with the unciform is still considerable. In the pes, mt. III is supported solely by the entocuneiform, the extension of mt. III taking up the whole of the mesocuneiform, and excluding mt. II from it altogether: the heads of Nos. III and IV are also on the same level, and mt. III is no longer in connection with the cuboid. This is "adaptive" reduction in its most typical form, and so far as the Tylopoda are concerned, Kowalevsky's law holds good.

VIII. *Restoration* (Fig. A).

The abundant material now at command, and especially the larger part of a skeleton belonging to a single individual, enables us to give a restoration of this curious animal, in which there would seem to be but little opportunity for error. *Pæbrotherium* was a long-limbed, slender, and graceful animal with a long neck and delicate, pointed head. In general appearance it

FIG. A. — *Pebrotherium labiatum*, Cope. — Restoration $\times \frac{1}{6}$. The drawing is for the most part from the skeleton of a single individual, supplemented by specimens belonging to Professor Cope and the Museum of Comparative Zoology.

was not unlike the llama, but with manifold differences. In size, the Miocene genus is very inferior to the recent one. A llama skeleton is about 112 cm. high at the shoulder, while the tallest individuals of the large species, *P. labiatum*, which I have seen, do not exceed 69 cm. in height. The head of *Pæbrotherium*, and especially the face, is longer, lower, and more pointed, and the neck, though much elongated, is still distinctly shorter than in the living genus. The thorax is longer, and, owing to the lightness of the ribs, more open in appearance; the lumbar region, on the other hand, is rather shorter. The limbs are quite as long, if not longer, and in particular more slender, giving the animal quite the look of some of the antelopes, which is increased by the fact that the metatarsals are decidedly longer than the metacarpals, and the ungual phalanges are long and pointed, very different from the nodules of the modern Tylopoda.

No other known genus from the White River beds had even a remote resemblance to *Pæbrotherium*; among European animals *Xiphodon* at once suggests itself as the one most like it in appearance, though, of course, no question of near relationship between these genera can be entertained.

STRUCTURAL CHANGES IN THE CAMELINE SERIES.

We have next to consider the steps by which the *Camelidæ* have reached their present differentiation, assuming for the present that the series of genera usually referred to this group represent the stages in its evolution, and reserving the discussion of relationships until the facts of structure have been presented.

I. *The Dentition.*

The oldest member of the Cameline series is, according to Cope (No. 9), the genus *Pantolestes* of the Wasatch Eocene. In this form the superior molars are of the primitive tritubercular type, which originally caused the reference of the genus to the pseudo-lemuroids, but are complicated by the addition of the para- and metaconules, making five in all, but the protocone is still median in position. The inferior molars correspond in structure, being of the type which Cope has named

"tuberculo-sectorial," and consisting of an anterior triangle composed of the proto-, para-, and metaconids, and a low posterior heel or talon. The paraconid is much reduced, and in some species cannot be distinguished. The talon is more or less distinctly basin-shaped, and two cusps (the hypo- and entoconids) can be observed in it; on the last molar there is an additional median lobe, which represents the fifth cusp so universal among the artiodactyls. No other known artiodactyl (except the problematical genus *Leptochaerus*, Leidy) has such a primitive molar dentition as this. There is nothing to distinguish it from some of the Condylarthra, the pseudo-lemuroids, or even certain creodonts, which is to say that it has still preserved the plan common to all these groups—a fact of the highest morphological interest.

In view of the fact first pointed out by Schlosser (No. 30, p. 267), that the premolars even when entirely like the molars in structure, have passed through an entirely distinct course of development, and that the similar parts in the two series are not homologous, the premolars of *Pantolestes* deserve careful examination. Of the superior series only the fourth is known, and this is entirely like the corresponding tooth of most creodonts, consisting of a single compressed and trenchant external cusp, the protocone, and a conical internal cusp, which may be called the deuterococone. It is important to remember that the protocone is external in position, while in the superior molars it is internal. The inferior premolars are all simple, compressed, and trenchant cusps, implanted, except the first, by two fangs. More or less distinct anterior and posterior basal cusps are present, and in one specimen of *P. brachystomus* I find in the fourth premolar of one side (but not of the other side) a distinct *deuteroconid* occupying the same position as in the supposed creodont genus *Chriacus*.

The second member of the series is the genus *Homacodon*, Marsh, from the Bridger, which presents us with a great advance in the dentition, in that the molars have become quadrate in outline and quadrituberculate in structure. In the upper series this change is brought about by the addition of the hypocone; strictly speaking, these molars are sextituberculate; for though the metaconule has become larger, the protoconule is frequently, if not generally, present as well, though evidently about to dis-

appear. The principal cusps are now pyramidal in shape, so that when worn they exhibit the first step toward the acquisition of the selenodont pattern. The lower molars still retain a trace of the paraconid, the talon has been raised to the height of the anterior triangle, and the hypo- and entoconids have completely separated. *Homacodon* is evidently very closely allied to *Dichobune*, and may well be identical with it, but in the absence of more complete information it will be best to separate them provisionally.

The superior dentition of the Uinta genus, *Leptotragulus*, is unfortunately not known. The lower molars are distinctly selenodont, but show their connection with the buno-selenodont type of *Homacodon* by the fact that the inner cusps are thick and conical, not flattened out into thin plates, and the outer crescents are somewhat trihedral in section, and rather angular than curved. The valleys are widely open above, but narrow rapidly below, becoming mere slits after a moderate degree of attrition. External basal pillars appear on some of the molars. The premolars are simple and trenchant, much as in the tragulines: the fourth is, however, somewhat more complicated than its predecessors, and consists of a high, acute, and compressed cone, with a small and sharp antero-internal cusp. From the inner side of the apex of the principal cusp there runs downwards and backwards a thin ridge enclosing a very narrow valley; this ridge appears to represent the deuteroconid. All the teeth of *Leptotragulus* are very brachyodont, and the molars are rather broad in proportion to their antero-posterior extension; the premolars have but a moderate extension in the same direction.

In the White River genus *Pæbrotherium* the dentition is still unreduced; the canines are small; the first premolar in each jaw has become isolated by diastemata both in front and behind it, and the inferior one is implanted by a single fang. The other lower premolars are still very simple, but have become greatly elongated antero-posteriorly, and the enlargement of the antero-internal tubercle gives rise to an anterior valley. The inferior molars show a decided advance toward the modern type of structure as compared with those of *Leptotragulus*. The inner crescents are much flattened, the outer more curved; the crown has become narrower and higher, and shows a distinct tendency to assume the hyposodont condition. The upper

molars are still very brachyodont and of the typical tetra-selenodont character; the median ribs of the external crescents are still prominent, and the antero-external buttresses small. Premolars 1 to 3 are simple, compressed, and trenchant cones, much elongated antero-posteriorly; pm. 4, on the other hand, has assumed the structure which it has in all ruminants, consisting of an internal and an external crescent. Apparently this tooth corresponds to half a molar, but from what we have seen in *Pantolestes* it is plain that the protocone is here the outer crescent, while in a true molar it forms the antero-internal crescent, and the deutocone, which forms the inner crescent, has no strict homologue in the molar crown at all. It is rarely the case among Artiodactyla that the premolars become molariform, but this does occasionally occur (e.g. *Agriochærus*, *Dicotyles*); and though the molar pattern may be fully attained, the elements which compose the crown are differently arranged and are not homologous with those which occupy similar positions in the crowns of the true molars. The first step towards the assumption of the molar pattern in the last upper premolar, is the addition of a second external cusp behind the protocone, which may be called the *tritocone*. This occupies the same place as the metacone of the true molars; but as its position with reference to the protocone is entirely different, it cannot be given the same name. The addition of the tritocone produces a tritubercular crown similar to that of the primitive molars, but with the elements which compose it not homologous with those of the molar crown. A second internal cusp, which may be called the *tetartocone*, is next added, and this corresponds to the hypocone of the true molars, and completes the molar pattern. In *Agriochærus* (Fig. B) this tetartocone is still very small, in some specimens hardly noticeable.

The steps of differentiation by which the inferior premolars become molariform are not quite so clear, but they may be made out in *Agriochærus* and *Dicotyles*. Comparing pm. 4 of *Oreodon* with that of *Agriochærus*, we see that the first addition to the protoconid is a cusp on the inner side, which may be called the deutoconid, and then the only further step which is necessary to the assumption of the molar pattern, is the elevation of the talon and its division into hypo- and entoconids. The almost perfectly molariform pm. 4 of this genus retains an inter-

esting reminiscence of its previous condition, in that the deutoconid is a conical tubercle, and that the anterior valley opens inwards in front of it, as in the true molars of *Lophiomeryx*, while in the molars of *Agriochærus* the functionally equivalent metaconid expands into a plate which closes the anterior valley. Likewise, if we compare the fourth lower premolar of *Thrinohyus* from the John Day beds with that of *Dicotyles*, the same process of development may be made out: first, the addition of the deu-

FIG. B, p. 4 of *Agriochærus latifrons*. *pr*, protocone. *me*, deutoconcone. *op*, tritocone. *ep*, tetartocone.

FIG. C, p. 4 of *Oreodon Culbertsoni*. *pr*, protoconid. *me*, deutoconid. *ec*, hypoconid. *en*, entoconid.

FIG. D, p. 4 of *Agriochærus latifrons*. (Letters as in Fig. C.)

teroconid, and then the elevation and division of the talon into hypo- and entoconids. It is plain, therefore, that the parts of an inferior molariform premolar are much more nearly homologous with the corresponding elements of the molars than is the case in the superior series; the protoconid having the same position; viz., forming the antero-external crescent or cusp, as have also the hypo- and entoconids. In the upper series only one element, the protocone, is common to both premolars and molars; and while, in the former it is the antero-external cusp, in the latter it is the antero-internal. It is not asserted that the transformation of the premolars always takes place in this manner, but it may be regarded as the usual method.

The camels of the John Day formation do not present any important modifications of the dentition; in some of them the first upper premolar has but a single fang, and others are decidedly reduced in size: the former Cope has erected into a separate genus, *Gomphotherium*. It seems probable that these forms are not in the direct line of cameline descent.

In the succeeding formation, the Deep River (*Ticholeptus* beds of Cope), occurs the genus *Protolabis*, Cope, which is also

continued up into the overlying Loup Fork. This animal retains the full number of teeth, but the superior premolars (the inferior are not known, unless, as is very improbable, *Protomeryx*, Leidy, should belong to the same form), are much reduced in size and especially in antero-posterior length, as compared with those of *Pæbrotherium*. The canine is longer and more pointed, and the external incisor has become caniniform and larger than the true canine. The true molars are still very brachyodont. In the Loup Fork species of *Protolabis*, *P. heterodontus*, the external incisor and canine have become very large, quite as large in proportion as in the camel and much larger than in *Procamelus*. I suspect, however, that this species will prove to belong to the genus *Homocamelus*, Leidy. Leidy describes the teeth of this genus as follows: "The caniniform incisor, the canine, and the first premolar were all separated from each other, and from the succeeding continuous row of premolars and true molars by wide-arching intervals.

"The second and third premolars (Figs. 16, 17), forming the advanced pair of teeth of the closed molar series, differ from those occupying the jaw fragments ascribed to *Procamelus occidentalis*, both in shape and relative position to each other. In *P. occidentalis* the antero-posterior diameter of the two teeth mentioned extends along the same line, and this is parallel with the alveolar border. In the present fossil the two teeth have their antero-posterior diameter directed obliquely, so that the back part of the first premolar is external to the fore part of the second. Both teeth are inserted by distinct pairs of fangs.

"The crown of the second premolar, slightly worn, is moderately compressed, conical, with its posterior portion curving outward and backward in a wing-like expansion. Internally it is bounded by a crescentoid basal ridge.

"The crown of the third premolar is a more developed form of that of the preceding tooth. The internal basal ridge is produced into a thick fold or process before and behind, extending towards the triturating border. It has nearly the constitution of the corresponding tooth, or first premolar, of the camel, but is relatively shorter and wider, and has the antero-internal fold relatively better developed. The worn triturating border exhibits a uniform surface of dentine, with the notch outward" (No. 19, p. 158).

The most abundant of the Loup Fork camels is *Procamelus*, which is represented by several species. In this genus the upper incisor series is as reduced as in the existing forms, but the first and second persist for a somewhat longer time, as Cope has pointed out. The premolars are not reduced in number: the first is implanted by two fangs, though they show a strong tendency to coalesce. The second is likewise small, with a compressed trenchant crown and small anterior basal cusp. Except for its relatively small size this tooth has changed very little from the condition found in *Pæbrotherium*. The third premolar differs considerably in the specimen of *P. occidentalis* figured by Cope from that given by Leidy. In the former it "consists of a small anterior cusp and a long posterior blade. A strong basal cingulum represents the interior crescent" (No. 6, p. 332, Pl. LXXVI, Fig. 2). This tooth is decidedly the most extended antero-posteriorly of the premolar series. In Leidy's specimen (No. 19, Pl. XX, Fig. 1) the third premolar is decidedly shorter and shows a strong tendency to form an internal crescent, by the elevation and extension of the anterior and posterior basal cusps, but which is incomplete in the middle. We have here, therefore, the formation of a tooth very similar to pm. 4, but in quite a different manner. The fourth premolar is of the typical pattern, and need not detain us. The upper true molars differ from those of the earlier genera only in their tendency to form prismatic crowns, and in the greater prominence of the anterior and median external buttresses. The median ribs on the outer walls of the external crescents are still distinct.

In the lower jaw the premolars are undiminished in number, but considerably reduced in size. The first is a small, simple cone, implanted by a single fang. The second is larger and compressed, with indications of internal basal cusps. The third and fourth are much more elongate and compressed; when viewed from the outer side, they show two concavities separated by a median convexity: internally there are parallel ridges which enclose one or two valleys. The true molars are more hypsodont than in the earlier forms, more flattened on their inner walls, and the fifth lobe of the last one is larger and contains a more distinct valley.

Contemporary with *Procamelus* is the genus *Pliauchenia*, Cope,

which resembles the former in the character of its dentition, but has lost one premolar, the second, in the lower jaw. "The canine and first premolar are especially short, and separated by a very short diastema; that separating the first and third premolars is also short, being less than that which separates the first and second in *Procamelus occidentalis*" (Cope, No. 6, p. 344).

In the Pliocene beds occur the highly specialized genera *Holomeniscus* and *Eschatius*, Cope. In these the reduction of the premolars has reached its maximum, there being but one left in each series. In the former genus the fourth superior premolar is of the ordinary pattern, composed of an external and an internal crescent, while in *Eschatius* this tooth is reduced to a simple cone.

In the existing genera the changes in the dentition are chiefly confined to the increased size and trenchant shape of the external upper incisors and canines, and the reduction in number and size of the premolars; in *Camelus* the number is $\frac{3}{2}$, and the first superior premolar is a large caniniform tooth. In *Auchenia* this tooth is lost, and the premolars reduced to $\frac{2}{3}$; the molars are prismatic, though by no means to the same degree as in the Cavicornia, and the anterior and median buttresses of the upper ones much more strongly developed. In *Auchenia* there are strong transverse "compression folds" on the anterior walls of the lower molars.

The *milk dentition* is not known in any of the older genera of the series. In *Pæbrotherium* it agrees essentially with that of the tragulines and the more ancient selenodonts generally. The last upper milk molar resembles a true molar in form and construction. D. 3 is composed of a posterior pair of crescents and a long anterior blade consisting of two imperfectly separated external cusps and but the rudiment of an internal cusp. D. 1 and 2 resemble the corresponding teeth in the permanent series, if, indeed, the first one changes at all. In the lower jaw D. 1 appears to change, at least sometimes, for in some specimens it is implanted by two fangs, whereas pm. 1 has but a single root; in other specimens the first tooth in the temporary series is like that in the permanent set. D. 2 and 3 are not different in any important respect from pm. 2 and 3. D. 4 has the constitution usual among the selenodonts, consisting of three pairs of cres-

cents arranged in transverse pairs, of which the anterior pair is by far the largest. In *Procamelus*, to which genus I attribute the "milk dentition of a camel" figured by Cope (No. 6, Pl. LXXVII, Fig. 4), the character of the temporary molars has undergone an important change. D. 2 is like pm. 2, consisting of an elongated and trenchant external cusp, and an imperfect internal crescent formed by the elevation and extension of the anterior and posterior basal cusps in the manner already described. D. 3 is the longest tooth, antero-posteriorly, in the temporary series. It consists of two pairs of crescents, of which the anterior pair is the smaller and especially narrower: the rudimentary antero-internal cusp of *Pæbrotherium* has now become a complete crescent. The accessory anterior basal cusps of the White River genus now forms a transverse "compression fold" across the whole of the front face of the tooth. D. 4 is like a true molar in constitution, and has a fairly well developed basal pillar at the junction of the two inner crescents. The upper milk incisors and canines, as well as the entire lower temporary dentition, are unknown to me.

In the recent genera of the *Camelidæ* the milk molars are very much reduced. In the upper jaw D. 3 has a compressed anterior half, and is of irregular molar form. D. 2 is rudimentary. In the lower jaw D. 4 is of the usual selenodont pattern; D. 3 is very much reduced with the anterior portion trenchant, and D. 2 is wanting. There is thus in the cameline phylum a similar change in the character of the milk dentition to that which occurs in the true ruminants, *Gelocus* and *Prodremotherium* agreeing in this respect with *Pæbrotherium* and the tragulines. As I have pointed out elsewhere (No. 31, p. 370), the same transition occurs in the *Oreodontidæ*, *Oreodon* having the older type of milk dentition, in which D. 3 consists of a posterior pair of crescents and an elongated antero-external blade, but no antero-internal cusp, while in *Merychys* this tooth is molariform and consists of two pairs of crescents. The transformation has occurred, therefore, at least three times independently among the selenodonts, in the true ruminants, the camels, and the oreodonts.

II. The Skull.

The skull of the more ancient genera of the tylopodan series, *Pantolestes*, *Homacodon*, and *Leptrotragulus*, is quite unknown;

and we can therefore follow the evolution of this region only from the lower Miocene upward. The recent *Camelidæ* have a peculiar type of skull, markedly different from that of the true ruminants. Rütimeyer has summed up these peculiarities as follows: Characteristic of the Camelina is the presence of upper and lower canines and the approximation of the molar series, the properly masticating surface of which is very short, to the premaxillary dentition and the corresponding part of the inferior dentition. The premaxillæ are very complete, and reduced only by small incisive foramina. Nevertheless, the skull is distinguished by the very rapid tapering of the face anteriorly, which is expressed particularly in the triangular form of the palate and in the very oblique position of the molar series (somewhat as in the *Toxodontia*). The maxillary region of the skull is peculiarly limited, and mainly taken up in the formation of the nasal passage, having but a low alveolus and very limited muscular surfaces. Even the jugal, as well as in the lachrymal (which at least in the camel hardly appears on the face), takes almost no share in the formation of the face. The infra-orbital foramen lies far back, above the last premolar. There is no masseter crest, and the masseter surface is almost obsolete. The nasal canal is high, and roofed over by short nasals, which in the llama are very broad posteriorly. The posterior nares are also very high, especially in the pterygoid portion. The pterygoid wings are placed vertically; and in the llama, as in young animals, are perforated by unusually large sphen-orbital foramina. Characteristic in the cranium is the small extent of the frontal zone as compared with the parietal zone, in the formation of which the very high squamosals take a large share. The orbits are very prominent, in spite of which the external openings of the supra-orbital canal are in the camel almost median in position, less so in the llama. A further consequence of these relations is the displacement of the orbits into the facial region above the molar alveoli, and the extraordinary length of the temporal fossa, at least in the camel. Of the occipital bones, only the supra-occipital extends upon the roof of the cranium, and in the camel is raised into a great crest. The paroccipital processes are in both forms reduced to a minimum; the auditory bullæ are much inflated in the llama, in the camel they are strongly compressed, and with a very deep styloid groove.

The glenoid cavity is very small, but has a high post-glenoid process, as in the horse. The sphenoid region has the relations general among artiodactyls; the foramen ovale lies in the *ala posteriora*, and there is no ali-sphenoid canal. The condyle of the lower jaw is spherical, instead of being transversely extended as in the true ruminants; the coronoid process is straight and pointed, not curved, and a process for muscular attachment arises from the *angulus mandibulæ*.

Of the two genera, *Camelus* presents the family characteristics in excess, as compared with the llama, which is in so far a less extreme form. In the latter the frontal zone is more extended, and encroaches upon the parietal zone behind the orbits. The orbits are not placed so far forward, and the jugal and lachrymal are more extended upon the face. In front of the jugal there is a considerable vacuity. The premaxillæ reach the nasals. The posterior nares are not so high, but extend farther forward than in the camel; and the spheno-maxillary fossa is, even in old animals, not entirely obliterated. The external supra-orbital openings are opposite the internal ones.

"All this probably places the group of the camels outside of any other relations to existing ruminants than those of physiological similarity, and even the selenodont type of dentition appears to be rather analogical to than identical with that of the ruminants proper. Among living ungulates no group stands nearer to the camels, with regard to the plan of skull-structure, than that of the perissodactyl horse" (No. 26, p. 19).

These peculiarities occur in a less marked degree in the skull of *Pæbrotherium*. The cranium is shorter, narrower, less capacious and less rounded. The orbits are placed further back even than in the llama, and approach very near together, so that an inter-orbital septum is formed, almost as in the tragulines. They are not so prominent, nor directed so much anteriorly as in the recent forms, and are not quite enclosed by bone; the supra-orbital fissure is widely open, though not so deep as in the recent genera. The face is very low, especially in front; and its upper contour descends regularly from above the orbits to the anterior nares. Owing to the completely brachyodont condition of the upper molars, the alveolus is extremely low, and the orbit is separated from the molars by a very small space. The nasals are extremely long and narrow, and do not show the

posterior expansion in width which is so characteristic of the llama. Below the suture of the nasals and maxillaries the latter show a long, deep depression. The anterior nares have an altogether different shape from that seen in the existing genera; they are very low, and their lateral edges are not nearly so oblique, but more vertical in position. The lachrymal and jugal are about as much extended upon the face as in *Auchenia*; but the notch in the latter, which receives the anterior end of the zygomatic process of the squamosal, is not deep as in the modern species. There is no fontanelle between the nasal, frontal, and maxillary, as is so markedly the case in the llama; and sometimes even in the camel there is a small vacuity present. The face is not abruptly constricted in front of pm. 4, but tapers gradually forward. The nasal chamber is very low, especially in front; and in consequence the maxillary has no such vertical extension as in the recent species. The palate is also very different in shape, especially in the absence of the deep constriction in front of the molar series and the very much shorter diastema behind pm. 1. The alveolus is continued further back of the last molar, and forms a very small projection into the orbit; the palatal notches between the alveoli and the palatines are very short, and the posterior nares have a much less vertical extent. The latter are in shape and position very like those of *Auchenia*, being long, narrow, and pointed anteriorly, extending to the space between m. 2 and 3. The vomer extends lower, and is more conspicuous than in the modern genera. The descending plates of the ali-sphenoids are shorter, somewhat broader, and do not terminate in such distinct hamular processes; the same statement applies to the pterygoids, of which the free ends are short and inconspicuous. The tympanic bullæ are relatively larger and more rounded, and the styloid groove and pit are shallower and more widely open behind. The zygomatic process of the squamosal is shorter, and the glenoid cavity is not separated into two parts. The occiput is rather high and narrow, and there is a strong lambdoid crest, as in the camel. The construction of the roof of the cranium agrees best with the latter genus, as is seen in the shortness of the frontal zone, the long sagittal crest, and prominent lambdoid crest; but owing to the more posterior position of the orbits, the zygomatic arch and temporal fossa are much shorter. A primitive feature is the

length of the posterior region of the cranium and the anterior position of the paroccipital processes.

In the lower jaw the horizontal ramus is relatively longer and more slender than in the recent genera, the symphysis is much shorter, and the ascending ramus much lower, in correspondence with the more brachyodont dentition; the angular process is very much longer, extending far back of the line of the condyle, but much lower from above downwards. The condyle is more extended transversely, and the articular surface for the postglenoid process much less developed, and in general the condyle departs less decidedly from the ordinary ruminant pattern than does that of the living Tylopoda. The coronoid process is shorter, more regularly recurved, and more like that of the Pecora: it is compressed and thin, and shows no tendency to assume the massive condition found in *Camelus*. There is a rather small but deep masseteric fossa.

Though the skull of the more ancient genera referred to the cameline series is unknown, yet from the analogy of other ungulate lines we may infer with considerable confidence that several features of the skull structure of *Pæbrotherium* indicate advance and differentiation, as, for example, the posterior position of the orbit, the shortened cranium, and very long face; the great size of the auditory bullæ, etc., etc. Indeed, in some respects *Pæbrotherium* is more modernized than the camel.

The skull of *Protolabis* exhibits no very important changes; the nasals are somewhat shortened, and the anterior nares higher and more obliquely placed than in *Pæbrotherium*; the face is deeper and the orbit rather smaller; the face is constricted in front of pm. 2, and the distance from the tip of the premaxillaries to the infra-orbital foramen, which is still placed above pm. 4, is considerably lessened; the posterior nares are situated further back, apparently altogether behind the molars. The superior alveolus is continued some distance back of the third molar.

The skull of *Procamelus* (Pl. I, Figs. 4-6) has two well-distinguished types of structure, one of which, *P. occidentalis*, Leidy, resembles the llama; the other, *P. angustidens*, Cope, is more like the camel (cf. Cope, No. 6, Pl. LXXVII, Fig. 1, and our Pl. I, Fig. 6). In both the orbit is decidedly smaller than in *Pæbrotherium* and separated by a wider interval from the molars

The whole face has become shorter and deeper, and the anterior nares are much higher and more oblique, while the posterior nares have increased in height and are placed behind the molar series. In *P. occidentalis* there is a small prelachrymal vacuity, and the shape of the cranium is much like that of the llama, with extended frontal zone, much shortened sagittal crest, and very low occiput and inconspicuous lambdoid crest. There is a small prelachrymal vacuity. On the other hand, the orbit, though situated far back, is in relative size more like that of the camel, and the posterior nares are almost precisely like those of that genus. In *P. angustidens*, for an opportunity to study which I am indebted to the kindness of Professor Cope, there is no prelachrymal vacuity, the sagittal crest is much higher and longer, and the lambdoid crest is much more prominent. In this cranium the highest point is at the junction of the two crests: in *P. occidentalis* it is in the middle of the parietal zone. The cranium of *P. angustidens* thus strongly recalls that of the camel, as that of the other species does the llama. In both the orbits are enclosed by bone, and the palatal notches are deeper than in the White River genus, while the nasals remain much longer and narrower than in either of the recent genera.

The mandible is known only in the case of *P. occidentalis*, and this is most like that of the llama; but the ascending ramus is relatively lower and wider, and the masseteric fossa is much better developed. As compared with the mandible of *Pæbrotherium*, the most important changes, aside from the general increase in size, are the greater depth and robustness of the horizontal ramus, the reduction of the angular process in length, and its increase in height, and the less clear definition of the masseteric fossa.

The differences between the skull structure of *Procamelus* and that of the modern genera are sufficiently indicated in Rüttimeyer's description already quoted. Unfortunately we know too little about the skulls of the Pliocene and Quaternary forms to enable us to trace these changes step by step. It should be emphasized, however, that the skull of *Procamelus* unites peculiarities both of *Camelus* and *Auchenia*, and that these characters are not merely primitive features which have been retained by one or other of the modern genera, but actual specializations; e.g. the position of the orbit and construction of the cranium on the

one hand, the shape and position of the posterior nares, on the other, in *P. occidentalis*; in *P. angustidens* the extension of the frontal zone and posterior position of the orbits, combined with the very camel-like cranium.

III. *The Brain.*

The salient features of the brain of *Pæbrotherium* are the large relative size of the cerebellum and medulla, the short, narrow, and tapering hemispheres, which in the anterior region have very slight vertical depth. The convolutions are few, simple, and straight; and the sulci present are, with the exception of a few accessory ones, those which are common to the whole series of ungulates, and closely resemble those of a foetal sheep. The frontal lobes are strikingly small.

The brain of *Procamelus*, as described and figured by Cope, shows a decided advance upon that of *Pæbrotherium*. The cerebellum is relatively smaller and the hemispheres larger, and they have assumed a more rounded and less tapering shape: the frontal lobes are decidedly enlarged, the accessory sulci have become more numerous, and the convolutions somewhat more sinuous, though they are still much simpler and straighter than in the recent genera. This brain is "not materially smaller than that of the llama, an animal which *Procamelus* equalled in general proportions. The hemispheres are, however, not produced so far posteriorly as in the *Auchenia*, reaching only to the line of the meatus auditorius externus.

"The orbital portion of the hemispheres is extensive and nearly smooth from the olfactory lobes to the supra-orbital border. This is not prominent, but is represented by a short longitudinal ridge. Above each of these, on the superior or front aspect of the hemispheres, is a massive convolution, but crescent-shaped, with the convexity inwards. The posterior part of the convolution is a sub-round tuberosity, which stands opposite to, and in front of, the furrow separating the Sylvian and median convolutions" (No. 6, p. 339).

The change from *Procamelus* to the recent species in brain structure consists less in increase of size, though there is some such increase, than in the rounder and deeper shape of the hemispheres, and in the very much more numerous and more

sinuous convolutions. The main sulci are already present in *Pæbrotherium*, so that the brain of this genus stands to that of the recent genera in the relation of embryo to adult, and affords an interesting confirmation of Krueg's results obtained by embryological investigation.

IV. *The Vertebral Column.*

Cope states (No. 7, p. 718) that the lumbar vertebræ of *Pantolestes* have flat articular faces.

The vertebræ of *Pæbrotherium* have reached a stage of development which, except in a few points, is almost like that of the existing forms. The neck is elongated, though decidedly shorter than in the recent genera; the transverse processes are not so distinctly separated into anterior and posterior portions, and on the sixth cervical the vertebrarterial canal is clearly visible. The atlas has longer and more recurved transverse processes; the anterior cotyli are not notched; there is no accessory articular surface on the anterior face of the inferior arch, and the vertebrarterial canal has its posterior opening at the base of the transverse process, not on the dorsal side of it. The axis has a high, thin, plate-like neural arch, more expanded antero-posteriorly, but much less massive and rugose than in the modern genera; the odontoid process is short and flattened on the dorsal side, with a rounded tip.

The dorsal vertebræ appear to number 13; they have long, slender, backwardly directed spines and elongated compressed centra.

The lumbar vertebræ have depressed centra with inferior median keels and lateral ridges; the spines are thinner and more compressed, and the zygapophyses show the faint beginnings of the episphenial processes which are so well developed in the camel.

The cervicals of *Procamelus* described and figured by Cope (No. 6, p. 335, Pl. LXXVIII) are intermediate between those of the recent genera and those of *Pæbrotherium*. The atlas agrees with the latter in the continuation of the transverse processes behind the surfaces for the axis, and with the former in the position of the vertebrarterial canal, the deep emargination of the outer rims of the occipital cotyli, and, apparently, in the

presence of an articular surface on the anterior edge of the inferior arch. The odontoid process of the axis is somewhat more concave on its superior surface than in *Pæbrotherium*, much less so than in the recent forms. The other cervicals are relatively smaller than in the llama, the transverse processes more expanded and less completely separated into anterior and posterior portions, and there are no neural spines. As in the recent genera, the third and fourth vertebræ are of nearly equal length, while in *Pæbrotherium* the third is considerably the longer.

The dorsal vertebræ of *Procamelus* are imperfectly known, but the character of the spines agrees best with that of the recent genera, except that they are rather longer.

The lumbar vertebræ have in the anterior region an inferior angulate keel, while in the posterior ones there is an angle on each side of the median one. The episphenial processes of the zygapophyses are quite distinct and much better developed than in *Pæbrotherium*.

The ribs of *Procamelus*, so far as they are known, agree best with those of the recent species, being much broader and more flattened than in *Pæbrotherium*. They appear, however, to be more simply and regularly curved than in the camel.

V. *The Fore Limb.*

The fore limb is entirely unknown in *Pantolestes*; and with regard to *Homacodon*, we know only that the manus contains four digits. Of *Leptotragulus*, fragments of the fore limb are preserved which throw some welcome light upon the questions at issue.

The glenoid cavity of the scapula is oval in shape, the antero-posterior diameter exceeding the transverse, and is placed somewhat obliquely to the vertical axis of the bone; the coracoid is much less prominent than in the later genera, and is not at all rugose, and but little recurved at the tip. The spine is placed nearly in the median line, but not quite, so that the postscapular fossa is slightly larger than the prescapular.

The distal end of the humerus is narrow; the internal epicondyle is pushed to the posterior angle; the outer condyle of the trochlea is narrow, the inner somewhat broader, and the

intercondylar ridge is narrow and sharp. The articular surface is high both in front and behind; the anconeal fossa is deep and appears to penetrate the shaft.

The ulna and radius are closely applied together, but do not coalesce, except partially at one point in the proximal portion, whatever may be true of the distal. The former has a heavy and prominent olecranon, which, so far as it is preserved, is continued upward in the line of the shaft, and does not project backward at all; the sigmoid notch is deeply incised with a decurved proximal margin; both internal and external humeral facets are continued down the anterior face of the notch. At the level of the head of the radius the shaft is quite broad and thick, but rapidly tapers below this point. The head of the radius is narrow, and the groove for the intercondylar ridge is very shallow and does not notch the front margin. The shaft, so far as preserved, is much more slender and rounded than in *Pæbrotherium*.

In *Pæbrotherium*, the shape of the scapula agrees best with that of the llama, as do also the position of the spine, shape of the acromion, and relative size of the pre- and post-scapular fossæ, but the coracoid, though much larger than in *Leptotragulus*, is much smaller and less rugose than in the llama. The neck and coraco-scapular notch are more like those of the camel.

The humerus is very different from those of the later genera; the distal end is like that of *Leptotragulus*, but the intercondylar ridge is broader and more rounded, though less so than in the existing genera. The shaft is much more slender than in the latter, the proximal end remarkably different; the external tuberosity is very high and broad, extending across the whole anterior face of the bone and overhanging the bicipital groove. This groove is narrow, deep, and placed at the antero-internal angle of the head, and the very small rudiment of a bicipital tubercle may be seen at the bottom of it. The internal tuberosity is very small.

The ulna and radius are firmly co-ossified throughout, but are separated at two points by the proximal and distal interosseous foramina. The shaft of the radius is much broader and flatter than in *Leptotragulus*, though much more slender than in the recent species. The head is also narrower than in the latter;

the groove for the intercondylar ridge of the humerus is very shallow, and to the inner side of the median line there is an elevation of the anterior margin, which is more prominent than in *Leptotragulus*. The distal end is but moderately expanded, and the three carpal facets are of nearly the same transverse breadth. The olecranon is very high and in the line of the shaft, projecting backwards but slightly, and has a deep tendinal sulcus on its extremity. The shaft of the ulna is decidedly less reduced than in the modern species.

The proximal row of carpals is of considerably greater height than the distal: in width the three bones of this row are nearly equal. The radial facet of the scaphoid is considerably broader in front than behind and is not emarginated on the internal side. The proximal articular surface of the lunar is nearly quadrate in outline; distally there is a long median beak formed by the junction of the facets for the magnum and unciform, which meet at an acute angle; the former is the longer and so obliquely placed as to be rather lateral than distal. The cuneiform has considerable antero-posterior depth, but is relatively narrow. The pisiform is short and very much compressed, with a very contracted neck, and expanded, rugose, and incurved free end; its articulation with the ulno-radius is much less extensive than in the recent genera. The trapezium is present and forms a small nodule, which is applied to the scaphoid and the rudimentary second metacarpal. The trapezoid is free; it is a very small bone, little larger than the trapezium; distally it is divided into two facets of unequal size — a small one for mc. II, and a somewhat larger for mc. III. The magnum is broad and very low; it is broadest in front, and narrows almost to a point behind; its proximal surface is chiefly occupied by the scaphoid, the lunar facet being much narrower and more obliquely placed; distally it is in contact only with mc. III, the extension of which upon the trapezoid excludes mc. II from the magnum. The unciform is a large bone, chiefly remarkable for its vertical height, which is nearly double that of the magnum, thus extending much below the level of that bone; the lunar facet is relatively larger than in the recent species. The unciform is connected with three metacarpals; the whole distal surface proper is occupied by mc. IV, but on the radial border there is a small facet for the projection of mc. II, and on the ulnar border a still smaller one for mc. V.

The metacarpus consists of two functional and two rudimentary digits. Mc. II is a short scale which is closely applied to and apparently sometimes even slightly co-ossified with mc. III: it articulates with the trapezium and trapezoid, but not with the magnum. Mc. III is very long, though relatively shorter than in the recent forms, and very slender, especially in the distal portion. Owing to the different levels at which the distal surfaces of the magnum and the unciform stand, mc. III rises higher than mc. IV, and so abuts against the unciform; on the radial side its head has extended over so as to occupy much of the trapezoid. Mc. IV is a trifle shorter and somewhat more slender than No. III, but is otherwise shaped like it. The distal ends are very slightly expanded; the carinæ are low and entirely confined to the palmar side. Mc. V is even smaller than No. II.

The phalanges are very unlike those of the existing species; those of the first row are not so long, less expanded at the extremities, and more regularly rounded. Those of the second row are short, slender, and rounded: their greatest diameter is from the dorsal to the palmar side. The unguals are long, pointed, and slender, with the medial surfaces flattened; the external rounded, and altogether much more like the unguals of antelopes or deer than like the nodules of the Tylopoda.

The skeleton of the John Day genus, *Gomphotherium*, so far as it is known, does not differ sufficiently from that of *Pæbrotherium* to require description, and the skeleton of *Protolabis* is quite unknown.

The fore limb of *Procamelus occidentalis* (that of *P. angustidens* is not known) has been described and figured by Cope. It is very like that of the llama, which it about equals in size, but is decidedly more slender.

In the scapula the spine rises close to the coracoid border; the coracoid process has very greatly increased in size and massiveness, and its free end forms a long recurved hook.

The humerus has become markedly stouter than that of *Pæbrotherium*, but less so than that of the llama, and the deltoid ridge and hook much more prominent; the distal end is broader, the supracondylar foramen no longer present, and the intercondylar ridge broader and more rounded. The external tuberosity is very much reduced in width, but it still rises high above

the head, higher, indeed, than in *Pæbrotherium*, terminating in a long, massive, and incurved hook. The internal tuberosity is increased in size, and the bicipital groove becomes very much wider, occupying nearly half the width of the proximal end, and the rudimentary bicipital tubercle of *Pæbrotherium* has become a prominent ridge dividing the groove into two parts.

The radius, though still slender, is much broader and more flattened than in the White River genus, and has received the inward curvature of the recent forms; the head is expanded, especially towards the outer side; the distal end has also expanded, and the carpal facets are no longer of equal width, that for the cuneiform being now the broadest. The shaft of the ulna is still further reduced, and is no longer visible from the front, except just above the distal end. The interosseous foramina penetrate, as in *Pæbrotherium*. The olecranon is not so high, and projects more strongly backward than in the latter, but it descends more steeply from the coracoid process.

In the carpus (Pl. III, Fig. 52) the scaphoid has become more massive and broader in front, producing a notch on the internal side. The lunar is relatively narrower; its distal beak is less prominent, the magnum and unciform facets being more nearly equal and inclining to each other at a more open angle. The cuneiform is heavier and wider and is less excavated upon the outer side for the descending distal end of the ulna. The pisiform is more thickened and increased in depth. No facets on the scaphoid or trapezoid indicate the presence of the trapezium, though it may have been preserved. The trapezoid is larger than in *Pæbrotherium*; the magnum is higher in proportion to its breadth; the lunar surface is broader and less oblique. The unciform, on the other hand, has become

FIG. E.

Humerus of *Procamelus occidentalis*; anterior view of proximal end (after Cope).

reduced in height, and its distal surface projects but little below that of the magnum.

The metacarpus is now represented by a cannon-bone, which is as long as, but more slender than in the llama. The lateral metacarpal rudiments have disappeared, unless, as I believe to be the case, the proximal end of mc. II be anchylosed with mc. III, forming the projection at the inner side of the cannon-bone. Even in *Pæbrotherium* there is a tendency for this co-ossification to occur. The fifth metacarpal, on the other hand, appears to have vanished completely. The cleft at the distal end of the cannon-bone is wider and deeper than in the llama, and the articular facets wider.

The phalanges of the first row only differ from those of the llama "in the greater prominence of the proximal ligamentous insertions and the rather more slender shafts." The unguals are very different from those of *Pæbrotherium*, being broad, depressed, and flattened with obtuse points; but they are relatively larger than in the recent genera.

The changes from *Procamelus* to the existing forms in regard to the structure of the fore limb are not very striking. They consist in an increased robustness of all the shafts, articulations, and ridges for muscular attachment, and naturally to a greater degree in the camel. The most important change is in the proximal end of the humerus, where the external tuberosity is much reduced and the internal tuberosity and the bicipital tubercle increased, so that all three are nearly of the same size, and the bicipital groove is much widened. The shaft of the ulna is further reduced, and the olecranon receives a different shape. In the carpus the lunar is reduced in width, and the proximal row of carpals is higher in comparison with the distal row; the pisiform becomes wider and more compressed. The ungual phalanges are reduced to mere nodules.

VI. *The Hind Limb.*

The pelvis of *Pantolestes* is peculiar in many ways. The ilium has a long and very deep peduncle, and a very wide iliac surface. Both the pubic and acetabular borders are raised into arched prominences just in advance of the acetabulum. There is little to suggest that this belongs to an artiodactyl at all.

The femur is long, with a slender rounded shaft. The head is nearly hemispherical, set upon a very distinct neck, and has a minute circular depression for the round ligament. The great trochanter is relatively very large and massive, but does not rise above the level of the head, and encloses a deep digital fossa. The lesser trochanter is also prominent, but not much extended vertically. Cope states (No. 7, p. 718) that there is no third trochanter; but I find what I conceive to be a remnant of it on the outer side of the shaft, a considerable distance below the great trochanter. The distal end is much thickened, and the rotular trochlea very prominent, but narrow. The distal end of the tibia shows a very large internal malleolus, and deeply excavated condyles for the astragalus. The fibula seems to have been complete; its distal end is much enlarged, and shows a tendinal sulcus upon the outer side.

The tarsus is typically artiodactyl, and shows considerable differentiation. The calcaneum is long and compressed, with a high fibular facet, a prominent sustentaculum, and a broad surface for the cuboid. The astragalus is high and narrow, and has the usual double pulley. The cuboid is also high and narrow. The navicular is low, especially behind, where there is a relatively large facet for the ento-cuneiform. The meso- and ecto-cuneiforms have coalesced in such a fashion that there seems to be a step cut in the compound bone, caused by the fact that the meso-cuneiform is much lower than the ecto-cuneiform; and while the proximal surfaces of the two are on the same level, distally the latter projects much below the former.

Only the third metatarsal is preserved; but the facets of the tarsus show that the pes was tetradactyl, with the median digits enlarged, and the lateral much reduced. The reduction is so far inadapative that mt. II occupies the whole of the meso-cuneiform, and is in contact with the side of the ecto-cuneiform.

The hind limb of *Homacodon* has not been described further than the statement that the pes has four digits, and that the astragalus is "suilline" (Marsh, No. 20, p. 120; and No. 21, p. 364). In *Leptotragulus* the proximal end of the femur is broad, with a hemispherical head set upon a long and very distinct neck; the second trochanter is relatively large.

The distal end of the tibia has a narrow facet for the fibula, showing that the latter had begun to shift beneath the tibia;

but the narrowness of this facet, the absence of any groove on the outer side of the tibia, and the presence of a large rugose surface in place of it, make it probable that though the reduction of the fibula had begun, it was by no means complete.

The tarsus of *Leptotragulus* is very like that of *Pæbrotherium*. The calcaneum is long and compressed and of less vertical extent (*i.e.* from the dorsal to the plantar side) than in the Miocene genus. The astragalus is high and narrow, with the proximal trochlea deeply and widely grooved. The cuboidal surface is very narrow. The cuboid is remarkably high, narrow, and deep. Both the surfaces for the astragalus and calcaneum are narrow, the latter a little the broader of the two; the posterior hook is longer and less massive than in *Pæbrotherium*; the distal surfaces for mts. IV and V are very much as in that genus.

The mts. III and IV are enlarged, but, though broken, obviously elongate and slender; their distal ends are almost exactly like those of *Pæbrotherium*. Judging by the fossæ upon the median metatarsals, it appears probable that the lateral ones are not quite so much reduced as in the White River type.

The phalanges of the first row are very slender and rounded and the unguals are long, compressed, and pointed like those of the antelopes.

In *Pæbrotherium* the ilium has a very long and narrow peduncle and a plate, which apparently was not much expanded; the ischium is also slender and compressed and without the arched prominence above and behind the acetabulum, so prominent in the recent forms. The femur is very tylopodan in appearance; but the bridge connecting the great trochanter and the head is shorter and narrower, and the great trochanter less massive there than in the living forms. The condyles are smaller and less prominent and the rotular trochlea wider and shallower; a pit for the insertion of the plantaris muscle is present.

The tibia is long and slender, with very prominent and extended cnemial crest. The distal facets for the astragalus are partly interrupted on each side of the tongue. The fibula is very much reduced, the shaft having disappeared, and the distal end moved beneath the tibia; but the groove for it on the latter

is not so deep, nor does it divide the fibular facets into two parts, as in the recent genera.

The tarsus is high and narrow. The calcaneum is long and slender, the astragalus high; the cuboid is likewise high and narrow, and the calcaneal facet deeply incised and broader than the astragalar; the latter and the astragalar facet of the navicular are emarginated by a median but shallow and small fossa. The ecto- and meso-cuneiforms are co-ossified.

The median metatarsals are longer and stouter than the metacarpals, the increased diameter being the antero-posterior rather than the transverse, and the posterior hooks are very long and stout. Mts. II and V are small scale-like rudiments; the former sometimes, but not always anchylosed with No. III, the latter always free.

Of the hind limb of *Procamelus* (Pl. III, Fig. 53) I have the distal end of the tibia, proximal end of the cannon-bone, the calcaneum, astragalus, and navicular of a large species from the Loup Fork of Oregon, and Cope has figured the cuboid. Judging from these remains, it would appear that the hind limb of this genus has very nearly reached the modern condition. The distal end of the tibia is broad and heavy; the malleolus is shorter and more massive than in *Pæbrotherium*; the intercondylar ridge, lower and broader, and its articular surface is interrupted by a deep fossa. The groove for the fibula is very deep, and separates the fibular facet into a smaller anterior and larger posterior portion.

The astragalus has become much broader in proportion to its height, and the rim of the external condyle much thicker. The calcaneum is compressed and deep, with prominent sustentaculum and long narrow cuboidal facet. On the inner side of the distal end can be seen the beginning of the projection which in the llama extends far inwards behind the astragalus; the distal end extends little if any below that of the astragalus. The navicular is very low; the fossa, which in *Pæbrotherium* emarginates the fibular edge of the astragalar surface, is here larger and deeper. The cuboid is also very low vertically; the calcaneal facet is but little incised.

The upper end of the cannon-bone is heavy and deep antero-posteriorly. The posterior hook-like projections are relatively shorter but more massive than in *Pæbrotherium*. The prox-

imal end of mt. II is clearly a part of the cannon-bone, forming a large facet for the ento-cuneiform; its line of suture with mt. III is still visible. A comparison with the modern forms shows that in them also this bone is preserved, as Boas (No. 3, p. 52) and Gaudry (No. 12, p. 117) have found to be the case in the true ruminants. I find, however, no trace of mt. V, and from its altogether lateral attachment to the cuboid in *Pæbrotherium* it appears probable that it has entirely disappeared.

The changes in the structure of the hind limb from *Procamelus* to the recent genera are not sufficiently important to call for description.

THE PHYLOGENY OF THE TYLOPODA.

The immediate ancestors of the modern *Camelidæ* are, unfortunately, not known to us, though the *Protauchenia* of Branco (No. 4, p. 110) not improbably stands in this relation to the llama series, the forms which occur in the Pliocene of the United States being highly specialized side branches, which have died out without leaving successors. Toward the end of the Miocene the ancestors of the modern forms probably migrated from North America to South America and the Old World, as is indicated by the Siwalik fossils and others. In the upper Miocene, or Loup Fork beds, we meet a large number of species of this group. *Homocamelus*, so far as known, is very camel-like, and it might seem at first sight that we have here a direct ancestor of the camels; but the peculiar and reduced character of the premolars, though still present in full numbers, renders it probable that this genus is not in the direct line, but is perhaps the forerunner of *Holomeniscus* or *Eschatius*. *Pliauchenia* has frequently been regarded as the forerunner of the llamas, but the known remains of it are altogether too imperfect to enable us to form a decision on this question, and the great shortening of the disastema would seem to oppose this view.

Procamelus, on the other hand, if not itself the common ancestor of the two recent lines, obviously stands very near to their point of divergence. It may be objected that this genus has already become too highly specialized in both directions to be the ancestor of either series; e.g. agreeing with the llama in

the position of the orbits and the extension of the frontal zone, with the camel in the shape and position of the posterior nares. But this objection is of no great weight, for this differentiation is as difficult to explain on the assumption that *Procamelus* is a side branch. The two species *P. occidentalis* and *P. angustidens* very strongly suggest themselves as the starting-points of the llama and camel series respectively.

Protolabis is obviously the connecting link between *Procamelus* and *Pæbrotherium*; and so far as known, is exactly what it should be to assume this position.

Pæbrotherium has frequently been regarded as ancestral to the camels only, but its relation to the llamas is quite as unmistakable. Branco's suggestion (No. 4), which was adopted by Schlosser (No. 27, p. 49), that *Leptauchenia* is the earliest known member of the *Auchenia* line, I have elsewhere shown to be entirely untenable (No. 31, p. 356).

Leptotragulus is so very like *Pæbrotherium* that no one can hesitate to regard it as the forerunner of the White River genus. Every known detail of its structure thoroughly confirms this view.

The position of the Bridger genus *Homacodon* is much less clear, for as yet only the most meagre accounts of that form have been published; but so far as it is known, it gives us every reason to believe that it is connected on the one hand with *Pantolestes* and on the other with *Leptotragulus*.

If these conclusions are correct, it follows that the Tylopoda are but remotely connected with the true ruminants, and that they have no common ancestors nearer than the *Dichobunidae*, to which Schlosser also traces the Pecora. However this may be, no one will dispute the view that *Pæbrotherium* cannot be ancestral to any of the ordinary ruminants; and, therefore, that all the structural points in which the modern *Camelidae* agree with the Pecora, but which do not occur in *Pæbrotherium*, must have been independently acquired. As we have already seen, Rüttimeyer reached this same conclusion from the study of the existing forms alone.

I have elsewhere given my reasons (No. 31, p. 389) for believing that the oft-repeated view of the connection between the *Oreodontidae* and the *Camelidae* is altogether untenable, and I need not repeat them here. The present investigation further

confirms the position reached in the article cited; viz. that all the great groups of selenodont artiodactyls when traced back are seen to arise independently from the abundant and widespread Eocene type, which may be called the Buno-Selenodonta; and which forms, as it were, a lake from which several streams, flowing partly in parallel, partly in diverging directions, are derived. It seems very clear that the term "selenodont," though most useful as a descriptive word, has no value as a term of classification.

In the discussion of the structure and succession of the Tylopoda, I have merely endeavored to establish the facts, reserving for the second paper all attempts at explaining those facts; for such explanation will be rendered easier by the study of some other lines of mammalian descent, and by the comparison of the facts thus obtained with those which the history of the camels offers for our consideration.

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EXPLANATION OF PLATE I.

FIG. 1. *Pebrotherium Wilsoni*. Skull of a young animal, side view $\times \frac{4}{3}$. Museum of Comparative Zoölogy.

FIG. 2. *Pebrotherium Wilsoni*. The same, top view $\times \frac{4}{3}$.

FIG. 3. *Pebrotherium Wilsoni*. The same, base view $\times \frac{4}{3}$.

f. ov. foramen ovale; *f. opt.* optic foramen; *f. l. a.* foramen lacerum anterius and foramen rotundum.

par. oc. paroccipital process; *p. sp.* presphenoid; *b. sp.* basisphenoid; *f. l. p.* foramen lacerum posterius; *pal.* palatines.

FIG. 4. *Procamelus occidentalis*. Skull, top view $\times \frac{1}{2}$, after Cope.

FIG. 5. *Procamelus occidentalis*. Skull, base view $\times \frac{1}{2}$, after Cope.

FIG. 6. *Procamelus angustidens*. Skull, side view $\times \frac{1}{2}$. Cope collection. *p. gl. for.* postglenoid foramen; *po. ty.* post-tympanic process of squamosal; *p. oc.* paroccipital process.

FIG. 7. *Pebrotherium labiatum*. Tympanic region, natural size. *con.* occipital condyle; *par.* paroccipital process; *ty.* tympanic bulla; *m. a. e.* external auditory meatus.

FIG. 8. *Pebrotherium Wilsoni*. Superior molar series, crown view, natural size.

FIG. 9. *Pebrotherium Wilsoni*, inferior molar series, crown view, natural size.

EXPLANATION OF PLATE II.

FIG. 10. *Pæbrotherium Wilsoni*. Intracranial cast. *cb.* cerebellum; **1.** median convolution; **2.** medi-lateral; **3.** lateral; **4.** suprasylvian.

FIG. 11. *Pæbrotherium labiatum*. Atlas, base $\times \frac{2}{3}$. Cope collection. *v. c.* vertebrarterial canal.

FIG. 12. *Pæbrotherium labiatum*. Atlas, side $\times \frac{2}{3}$. Cope collection.

FIG. 13. *Pæbrotherium labiatum*. Atlas, rear $\times \frac{2}{3}$. Cope collection.

FIG. 14. *Pæbrotherium labiatum*. Axis, side $\times \frac{2}{3}$. *o.* odontoid process; *pt. z.* postzygapophysis.

FIG. 15. *Pæbrotherium labiatum*. Fourth cervical, side $\times \frac{2}{3}$.

FIG. 16. *Pæbrotherium labiatum*. Sixth cervical, side $\times \frac{2}{3}$. *v. c.* vertebrarterial canal; *v. c.* accessory foramen.

FIG. 17. *Pæbrotherium labiatum*. Sixth cervical, rear $\times \frac{2}{3}$.

FIG. 18. *Pæbrotherium labiatum*. Seventh cervical, side $\times \frac{2}{3}$.

FIG. 19. *Pæbrotherium labiatum*. Seventh cervical, base $\times \frac{2}{3}$.

FIG. 20. *Pæbrotherium labiatum*. First dorsal, base $\times \frac{2}{3}$.

FIG. 21. *Pæbrotherium labiatum*. Ninth dorsal, side $\times \frac{2}{3}$.

FIG. 22. *Pæbrotherium labiatum*. Lumbar vertebra, side $\times \frac{2}{3}$. *pt. z.* postzygapophysis. Cope collection.

FIG. 23. *Pæbrotherium labiatum*. Lumbar vertebra, rear $\times \frac{2}{3}$. Cope collection.

FIG. 24. *Pæbrotherium labiatum*. Scapula, side $\times \frac{1}{2}$. *c.* coracoid; *a.* acromion.

FIG. 25. *Pæbrotherium labiatum*. Scapula, distal end, natural size.

FIG. 26. *Pæbrotherium labiatum*. Humerus, front $\times \frac{1}{2}$. *e. t.* external tuberosity.

FIG. 27. *Pæbrotherium labiatum*. Humerus, proximal end, natural size. *e. t.* external tuberosity; *i. t.* internal tuberosity; *bc. t.* bicipital tubercle.

FIG. 28. *Pæbrotherium labiatum*. Humerus, distal end, natural size.

FIG. 29. *Pæbrotherium labiatum*. Ulna-radius, front $\times \frac{1}{2}$. *R.* radius; *U.* ulna.

FIG. 30. *Pæbrotherium labiatum*. Ulna-radius, rear $\times \frac{1}{2}$.

FIG. 31. *Pæbrotherium labiatum*. Ulna-radius, distal end, natural size. *s. l. c.* facets for the scaphoid, lunar, and cuneiform.

FIG. 32. *Pæbrotherium labiatum*. Ulna-radius, proximal end, natural size.

FIG. 33. *Pæbrotherium labiatum*. Carpus, front. Cope collection. *s.* scaphoid; *l.* lunar; *c.* cuneiform; *td.* trapezoid; *m.* magnum; *u.* unciform; natural size.

FIG. 34. *Pæbrotherium labiatum*. The same, proximal face.

FIG. 35. *Pæbrotherium labiatum*. The same, distal face.

FIG. 36. *Pæbrotherium labiatum*. Metacarpals, front $\times \frac{1}{2}$.

FIG. 37. *Pæbrotherium labiatum*. The same, proximal end, natural size.

FIG. 38. *Pæbrotherium labiatum*. Femur, proximal end, front view, natural size. Cope collection.

FIG. 39. *Pæbrotherium labiatum*. The same, proximal end, top view.

EXPLANATION OF PLATE III.

- FIG. 40. *Pæbrotherium labiatum*. Tibia, front $\times \frac{1}{2}$.
- FIG. 41. *Pæbrotherium labiatum*. The same, distal end, natural size. *T.* tibia; *F.* fibula.
- FIG. 42. *Pæbrotherium labiatum*. The same, proximal end, natural size.
- FIG. 43. *Pæbrotherium Wilsoni*. Tarsus, front, natural size. *cb.* cuboid; *n.* navicular; *c.* 2 + 3, coalesced meso- and ento-cuneiforms.
- FIG. 44. *Pæbrotherium Wilsoni*. The same from the inner side. *II.* rudiment of second metatarsal; *III.* third metatarsal.
- FIG. 45. *Pæbrotherium Wilsoni*. Astragalus, plantar surface, natural size.
- FIG. 46. *Pæbrotherium Wilsoni*. Calcaneum, tibial side, natural size. *fb.* fibular facet; *a.' a.11* astragalar facets.
- FIG. 47. *Pæbrotherium Wilsoni*. Cuboid and navicular, proximal surface, natural size.
- FIG. 48. *Pæbrotherium labiatum*. Phalanges of manus, natural size.
- FIG. 49. *Pæbrotherium labiatum*. First phalanx, proximal end.
- FIG. 50. *Pæbrotherium labiatum*. Metatarsals, front $\times \frac{1}{2}$.
- FIG. 51. *Pæbrotherium labiatum*. The same, proximal end, natural size.
- FIG. 52. *Procamelus occidentalis*. Manus, front $\times \frac{1}{2}$. After Cope.
- FIG. 53. *Procamelus sp.?* Tarsus, front $\times \frac{1}{2}$. This specimen is of an undetermined species from the Loup Fork of Eastern Oregon, which was presented to the Princeton Expedition of 1890 by Mr. William Day.