

PHYLOGENY OF THE DEER.

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The modern representatives of this phylum, and the fossil representatives to a considerable extent also, have been largely classified on the peculiarities of the antlers. At best the antler is a variable structure; and, with the exception of the reindeer, is present on the males only, beside which there is a considerable group of antlerless forms. In this last group it is not easy to distinguish deer from antelopes, bovids, and gazelles, though, as I have shown in a previous paper,¹ the manner of forming the fourth upper premolar is different in each of these groups. Using the principles developed in the above mentioned paper, I shall here undertake to show that, while the teeth of deer have been formed on the same general plan as those of oreodonts and all other selenodonts; still there are peculiar modifications of the fourth upper premolar distinctive of the deer, even among the antlerless forms; that the deer have been a polyphyletic group; that there is a close relationship with the giraffes and sivatheres; and will try to separate the early deer from the early representatives of the antelopes, bovids, etc.

The development of the four-cusped selenodont upper molar tooth of the deer follows the same methods as in oreodonts. *Amphitragulus* may illustrate this. Premolar 2 is as simple as any found in this family, a single cusped tooth with the primary cusp in the middle of the tooth. From this a crest runs forward which, as it develops, is seen as the anterior outer cusp (anterior crest of selenodonts) of molar 1. A second ridge runs to the rear, and corresponds to the posterior outer cusp (posterior crest) of the molar. On the inside there are two cingula developed, the anterior one making the anterior internal cusp (anterior crescent), while the posterior cingulum corresponds to the posterior internal cusp (posterior crescent). This much is characteristic of all selenodonts. In the deer group it is further characteristic that the posterior crescent is the longer, and the rear end of the anterior crescent overlaps it. In the forming of premolar 4 the shortening is attained by a fore-and-aft compression, both the anterior and posterior crescents being retained, but shortened, the prolonged anterior end of the posterior crescent projecting into the basin of the

¹ Bul. Geol. Soc. of Amer., 36, 591, 1925.

tooth. This is the distinguishing feature of the deer dentition and is seen on all the upper dentitions, unless too much worn down. In the later or more progressive forms the anterior premolars progressively acquire the character of the fourth premolar, as shown in Fig. 1.

In the case of the lower dentition, the primitive tooth, or first premolar, has a high median, or primary cusp. As in the upper dentition the anterior slope, or ridge, makes the anterior external cusp of the molar, but in this case the external cusps become curved, so as to appear similar to the inner cusps of the upper teeth. In like manner the posterior ridge makes the posterior external cusp or crest. In deer (and antelopes) there

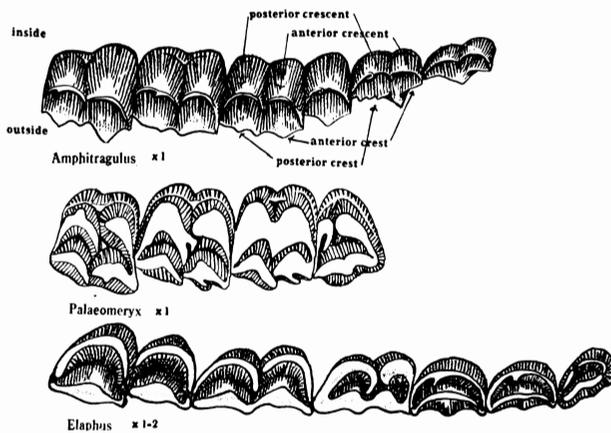


Fig. 1. Three upper dentitions to show the mode of formation of the molars from the premolar type, and the typical shortening of premolar 4.

are transverse ridges on the premolars, running toward the inner side. The most prominent of these is the median one which, as it increases in size and unites with the developing internal cingula, seems to spread front and rear to make the anterior inner and posterior inner cusps, or crescents. In some of the more primitive deer, like *Lophiomeryx*, these crescents are still incomplete on the molars; so that there is but little to distinguish the first molar from the fourth premolar. In general while the fourth premolar may become quite molari-form, the more anterior premolars do not take on its character.²

² In the case of all illustrations the upper dentitions are those of the left side, and the lower dentitions those of the right side; so that in case the relationship of uppers to lowers is desired a tracing of the lower can be put directly over the upper series and the occlusion be immediately apparent. Also in all figures the inside of the tooth is above and the outside is below.

The method of forming the fourth upper premolar, as described above, was first recognized by Rüttimeyer,³ and he also recognized that the premolar teeth offered the best clues for the study of this group; but he emphasized especially the deciduous dentition. These milk teeth do confirm the manner in which the molars have been derived from the simplest premolars; but, while they have the fundamental characters of the adult dentition, they have peculiarities of their own, which are neither recapitulatory nor prophetic, but represent specializations to the needs of the young.

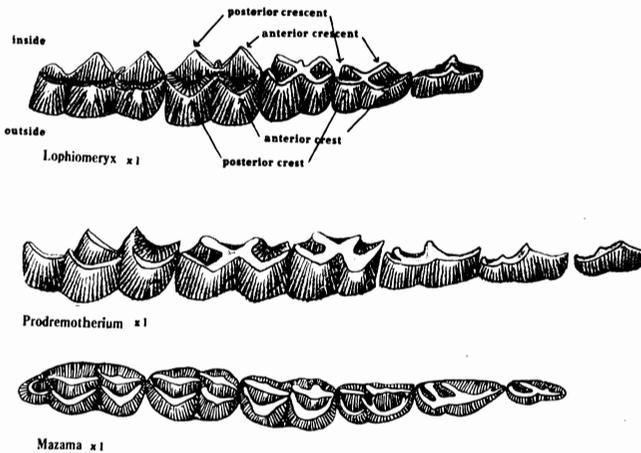


Fig. 2. Three lower dentitions to show the mode of formation of the molars from the premolar type.

Typical deer have antlers, structures so peculiar that it is most improbable that they originated more than once. Thus we must feel that all the antlered genera were derived from a common stock, and that the differences among them have been acquired since the acquisition of the antlers.

Among the antlered deer there are two distinct types of dentition, the two groups being most easily recognized by peculiarities in the lower dentition, though there are also characteristic peculiarities in the upper teeth. One group, the more primitive one as far as the dentition is concerned, has the posterior crest of the lower molars more or less completely isolated, and the same is true for the anterior crescent. This is due to the

³ Beiträge zu einer Naturischen Geschichte der Hirsche, Abh. der Schweiz, Paläont. Geschellsch., 10, 6, 1883.

more or less complete fusion of the anterior crest with the posterior crescent. The reindeer (*Rangifer*) shows this in a most striking manner both on the molars and premolars, but *Alces* has it almost equally highly developed. This cross-over character is seen clearly as early as *Dicrocerus* in the middle Miocene. It is also seen in such genera as *Axis*, *Rusa*, *Odocoileus*, and *Mazama*, though in the last two mentioned genera it is not so completely developed (see *Mazama* in Fig. 2). In its less marked development it is still characteristic of many of the antlerless genera such as *Amphitragulus* and *Prodermothorium* (Fig. 2) and also in *Palaeomeryx*, *Micromeryx*, *Hyamoscus* and *Lophiomeryx*. It is present too in *Dremo-*

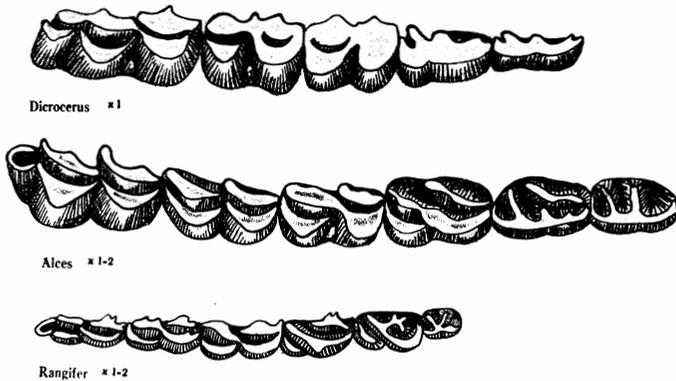


Fig. 3. Lower dentitions showing the cross-over, characteristic of the more primitive deer.

therium, *Dorcatherium* and *Hydropotes* but with slight modifications, so that I consider these three genera to represent a side line of early and antlerless deer.

The upper dentition of the group which has the typical cross-over in the lower teeth is peculiar in that the rear end of each of the crescents on the molars is bifurcated. This may appear as a simple split as in *Dicrocerus* (Fig. 4) or as a more marked notch as in *Alces*. In some stages of wear this notch may appear as a pit in the rear of the crescent, as in the case of the anterior crescent of molar 1 of *Alces* (Fig. 4) In the case of *Rangifer* the bifurcation is obscured by the one end of the split being elongated and the other end appearing as a small spur well forward from the rear of the crescent. These bifurcations may and do appear in the modified fourth pre-

molar or in others of the premolars. The genera *Axis*, *Rusa*, *Mazama* and *Odocoileus* also show this character well, while the early and antlerless genera, *Amphitragulus*, *Prodremotherium*, and *Palaeomeryx* show it in a little less marked condition. The three genera which were mentioned as a side line are peculiar in not having the bifurcation, which is the main reason for considering them as aberrant.

In contrast to the above group of deer stands another section of the antlered deer, in which the lower molars, though having originated in the same way, have lost the cross-over character, the two outer crests uniting with each other and the two crescents doing the same (see Fig. 5). This I take to

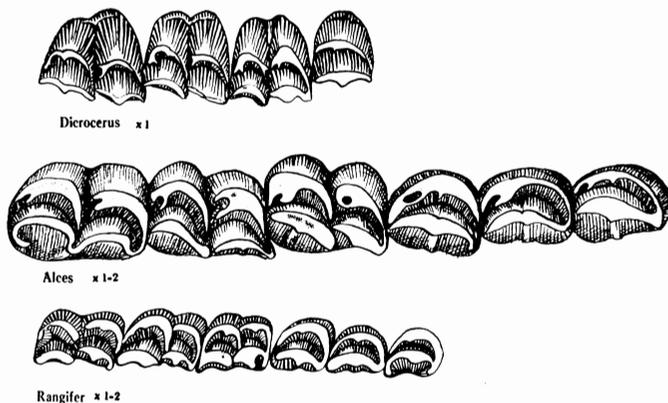


Fig. 4. Upper dentitions to show the bifurcation of the posterior ends of the crescents.

be less primitive as I do not find it in the antlerless genera, and it is not the simplest development to be expected from the mode of origin of the lower molars. It however is established in the middle Miocene genus *Blastomeryx*.⁴ Closely related to this genus is the upper Miocene and Pliocene genus *Merycodus* of America, with which is also allied the European deer, *Elaphus*. The rather aberrant genus *Cervulus* also has the same type of dentition.

These same genera are distinguished as a group by having the rear ends of the crescents on the upper teeth, simple; i. e.

⁴ *Blastomeryx*, as here used, is the genus defined by Matthew and includes such species as *B. primus*, *B. adventa*, and *B. orcolti*. Matthew, W. D., Bul. Amer. Museum Nat. Hist., 24, 535, 1908.

they lack the bifurcations so characteristic of the previous group.

The typically antlered deer are disposed of as belonging to one or the other of the foregoing groups. There remains

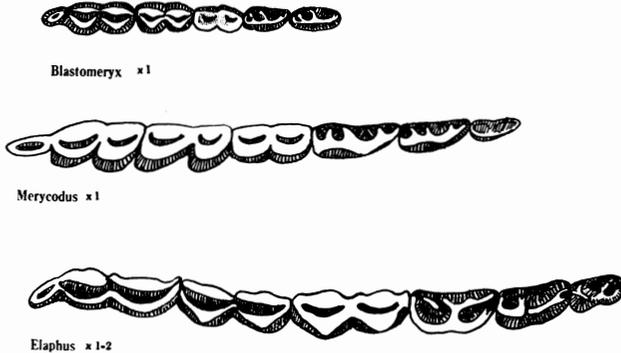


Fig. 5. Lower dentitions showing the tendency for crest to unite with crest, and crescent with crescent.

however that strange form known as *Sivatherium*, along with its less well known relatives, which has antlers very suggestive

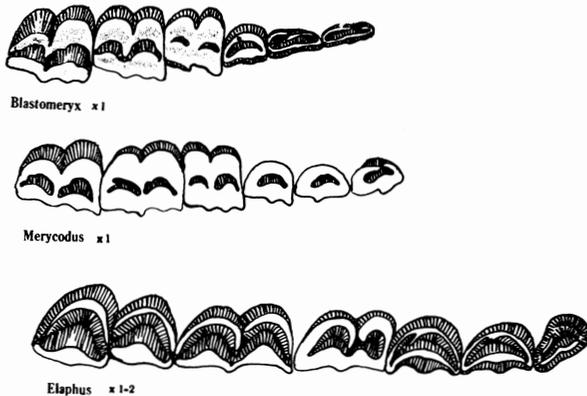


Fig. 6. Upper dentitions showing the rear ends of the crescents simple instead of bifurcated.

of those of *Alces*. *Sivatherium* has usually been treated as though close to the giraffes. This I can not see. First, the antler is a structure so peculiar, that it is hard to conceive of it as being developed more than once. And second, when we

compare the build and general outline of *Sivatherium* with that of other animals, it has the character of that of the moose (*Alces*) rather than that of a giraffe. The lower dentition of *Sivatherium* (Fig. 7) is distinctly of the cross-over type as in the moose and reindeer. The upper teeth also correlate with those of *Alces*, differing however in that the posterior portion of the crescents is thickened, so that their bifurcation is obscured. The bifurcation is however indicated by the outer

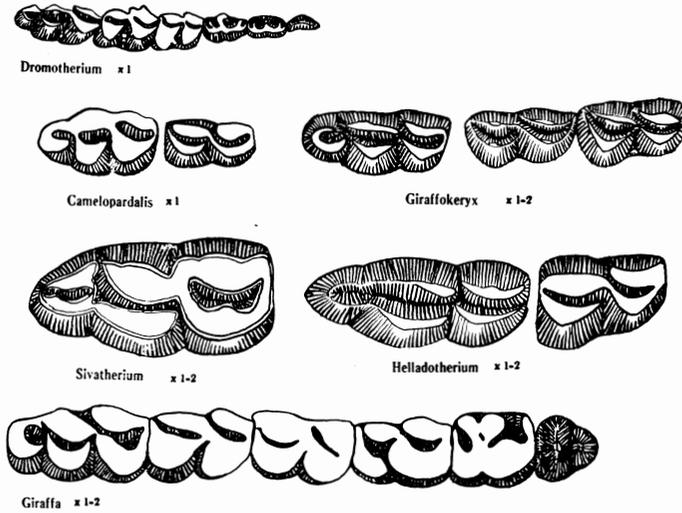


Fig. 7. Lower dentitions of giraffes and *Sivatherium* for comparison with the *Alces-Rangifer* group.

spur of the anterior crescent connecting with the posterior crescent; while the inner spur projects into the basin of the tooth. The general association of this form with giraffes has its basis in dental resemblances, but I shall show that giraffes are also derivatives of the same group of deer as the one from which *sivatheres* came; so that the relationship is to a common ancestor rather than to each other.

The giraffe group does not have antlers, but does have a longer or shorter bony process (which may be lacking as in *Helladotherium*) projecting above the orbit, and in the same position as that occupied by the antler. This differs from an antler in not being shed annually, and in being covered with skin. All of the giraffe group have the molars and premolars of the lower dentition strikingly similar to those of the *Dicro-*

cerus-Alces-Rangifer group of deer, with the distinctive cross-over of the anterior crest to the posterior crescent (Fig. 7). The posterior crest is typically isolated, and the anterior crescent tends toward isolation, but does not go as far as in the case of *Alces* or *Rangifer*.

On the upper teeth of giraffes the posterior portions of the crescents are swollen; but in the less worn, or unworn teeth,

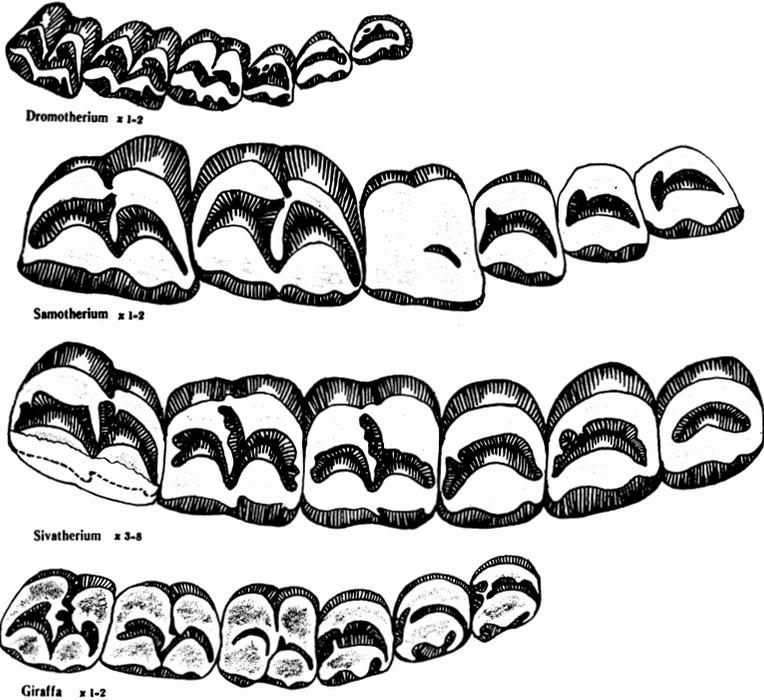


Fig. 8. Upper dentitions of giraffes and *Sivatherium* for comparison with those of the *Alces-Rangifer* group.

the bifurcation of the rear ends of the crescents is apparent (see *Giraffa*, Fig. 8). *Samotherium* seems to be peculiar in that the process extending into the basin of each molar appears to be the rear of the anterior crescent. This I think, however, is an illusion, the process being really the anterior part of the posterior crescent, as would be normal. The apparent separation of this process is due to the extreme development of the notch into the posterior crescent, which while developed to a

lesser degree, is present in all the other giraffes. This fundamental relationship of giraffes to the deer was recognized by Rüttimeyer⁵; but since his time it has been customary to place them in a more or less isolated group. They must have separated from the deer phylum in the early Miocene, just about the time the antler was being acquired. The giraffes acquired bony processes but never went the length of having them deciduous. The processes are long to short in samotheres, short in giraffes, and lacking (lost) in helladotheres. Besides these better known genera there are several others from India and Greece which so far are known mostly from the dentitions only. The group is represented by forms from the Pliocene, Pleistocene, and Recent times, in Europe, Asia and Africa.

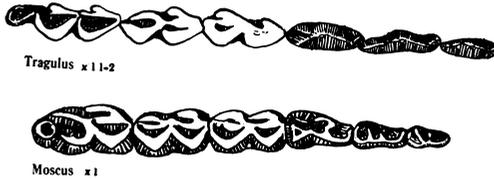


Fig. 9. Lower dentitions showing the peculiar inner lobe.

In the middle and upper Miocene of America occur two closely related, and peculiar genera, *Dromomeryx*⁶ and *Aletomeryx*.⁷ They are very close to each other in relationship. Both genera are peculiar in having bony processes over the orbits, which were covered with skin and were not shed annually. The tips of these processes are not known in *Dromomeryx*, but they were swollen in *Aletomeryx*. The dentition of both genera is strikingly like that of the giraffes on the one side, and like that of *Palaeomeryx* (as Douglas pointed out) on the other side. I can not but take these genera to represent the intermediate representatives between the early deer and the giraffes. They are just the sort of forms one would have postulated as required for such intermediate position, and occur at the time when there is a gap in the series.

Tragulus and *Moscus* are two peculiar antlerless forms, which have on the inner side of the lower molars a most

⁵ Loc. cit., p. 35.

⁶ Douglas, Ann. Carnegie Museum, Vol. 5, 457.

⁷ Lull, This Journal, 50, 83, 1920.

peculiar extra lobe on each crescent, which in worn teeth seems to be grown to the crescent; so that each crescent acquires a considerable thickness (Fig. 9). This is a deep-seated feature, which sets these two genera off by themselves; but at the same time, this extra lobe being left out of consideration, the background plan is that of the deer. The upper molars are typically those of deer; so that I take these two genera (and any which may later become associated with them) to represent a side line, which has been independent since early Miocene times, or even earlier.

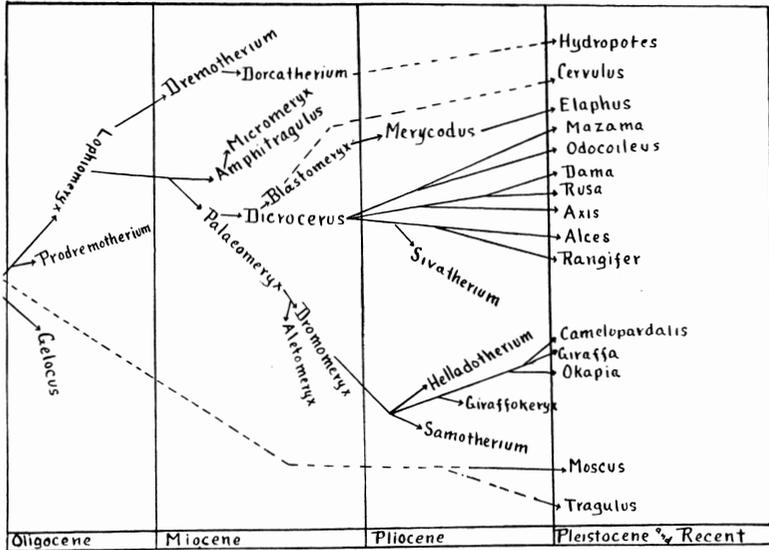


Fig. 10. Phylogeny of the deer.

In Fig. 10 I have attempted to represent the phylogenetic relationships of all these forms of deer. We do not know the Eocene ancestor of the group, but the phylum must run back into that period. During the Oligocene all the representatives were small, antlerless, and lived in Europe. *Gelocus* closely resembles the deer, but is highly specialized for a deer of that time, so it is here regarded as a side line. The less modified members of this Oligocene group continued on into the Miocene as *Dremotherium* and *Dorcatherium* and it is still represented by the chevrotains and *Hydropotes*. These give us a picture of the earliest deer, but have, in the long time since

early Miocene, acquired some peculiarities of their own. The long canines seem to be relics of similar structures in the early deer, where they are quite general. In the early Miocene a group of deer, generally larger, and represented most typically by *Palaeomeryx*, began the acquisition of bony processes over the orbits. In part of them these processes remained simple and were covered with skin, and this group leads to the giraffes. Curiously the first giraffes are represented by American genera, but by the end of the Miocene they disappear from the American continent, and continue their record in Asia, Europe and Africa. This line reaches its maximum in the Pliocene in samotheres, helladotheres and true giraffes. The living representatives of the group are but a remnant of an over-specialized group. Again in the early Miocene other forms developed the bony process over the orbit to a greater extent, and acquired that strange habit of having the major part of the bone die and become an exposed dead bone. This then began to be shed and a new one grown to replace it, and we have to deal with the antler proper. In *Dicrocerus* the antler is relatively simple, but rapidly acquires all sorts of modifications, like multiple branches, flattening, etc., until in its extreme it makes those over-developed structures like the antlers of a moose *Alces* or reindeer. This group has spread, especially during Pliocene times, from Europe to Africa, Asia and the two Americas. Early in the Miocene some of the deer, with many-branched antlers, separated off to one side and gave rise to the typical genera *Blastomeryx*, *Merycodus*, and *Elaphus*.

All the above forms I believe are true deer. In addition to them there are a considerable number of antlerless genera which have been associated with the deer at one time or another. While going over the camels, antelopes, bovids, and sheep, as well as the deer, it has become necessary to arrive at some conclusions as to such genera, before I could decide not to include them in the deer. These may be mentioned, but with the understanding that they are tentative, and given simply to show why these genera are not included in the deer phylum.

Xiphodons and caenotheres are bunoselonodonts in their affinities and this group is as far away from deer as any artiodactyl can be. *Hypotragulus* and *Nanotragulus* are clearly early representatives of the bovid line, to which group *Leptomeryx* may also belong, but it is not so clearly marked.

Hypisodus is a gazelle. *Protoceras* belongs with the camels. *Capromeryx* and *Antilocapra* are close to each other, but I have not yet been able to place them definitely, except that they are not deer.

The above study has been primarily based on dentitions, but the other structural characters have been taken into consideration. It associates some forms which have been considered as in different groups, and separates several forms which have been thought close to each other; but I am confident that the teeth offer fundamentally safe characters, while the antlers do not.

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