rufous-fawn with very faint traces of spotting nearly down to the fetlocks; while from the latter to the hoofs they are dirty greyish white.

The foregoing evidence clearly establishes the right of the North Rhodesian Giraffe to rank as a distinct local race; and if it be true that the one herd is completely isolated, there is probably no intergradation with the Kilimanjaro race.

EXPLANATION OF PLATE LXXXVI.

Adult bull of *Giraffa camelopardalis thornicrofti*.

46. On Antler-Growth in the Cervidæ, with special reference to *Elaphurus* and *Odocoileus* (*Dorcelaphus*). By R. I. Pocock, F.R.S., F.L.S., F.Z.S., Superintendent of the Gardens and Curator of Mammals.

[Received and Read June 4, 1912.]

(Text-figures 108–112.)

Index.

Introduction.

Most, if not all, the attempts that have hitherto been made to understand the antlers of Deer and arrive at correct conclusions regarding the homology of the tines have been based upon comparisons between the fully formed antlers of different species. This, in my opinion, is the reason why there has been failure in some cases to detect homologies which study of the growth of individual antlers reveals.

The importance of this question depends upon the circumstance that twenty years ago Mr. Gordon Cameron * proposed a classification of the Cervidæ, based upon the antlers, as a substitute for the classification, founded upon the skeletal structure of the fore feet, which Sir Victor Brooke had suggested †.

To make clear the purpose of the present paper, it is necessary to summarise briefly the rival classifications put forward by these two authors. Sir Victor Brooke divided the Cervidæ into two

* 'The Field,' 1892, pp. 265, 703, 741, 860.
† P. Z. S. 1878, pp. 883–928.

sections. The first, which he called Telemetacarpi (Telemetacarpalia) because the distal ends of the lateral metacarpals persist, comprises the Roe (*Capreolus*), the Chinese Water-Deer (*Hydropotes*), the Reindeer (*Rangifer*), the Elk (*Alce*), and all the exclusively American deer with the single exception of the typical Wapiti (*Cervus canadensis*); the second, called Plesiometacarpi (Plesiometacarpalia) because the proximal ends of the lateral metacarpals are usually present, whereas their distal ends are suppressed, comprises all the deer of the Old World, except the four genera mentioned above, but none of those of the New World apart from the Wapiti. Amongst the Old World forms the most important species for the moment figuring amongst the Plesiometacarpalia is Père David's Chinese Deer (*Elaphurus davidianus*).

Mr. Cameron's classification was widely different. Dismissing as unimportant the character relied upon by Brooke, he divided the Cervidæ into three sections: one for the Reindeer with antlers in both sexes, the second for the Elk with laterally extended antlers, the third for the remaining species with antlers restricted to the male and erect or suberect. This third section, which alone concerns us now, was subdivided into two categories of species, one comprising those in which the antlers consist, as in the typical Old World deer and the Wapiti, of a "brow-tine" and a "beam," to use Gordon Cameron's terminology, and the other those in which the antler has, as he thinks, no brow-tine but consists of a "forked beam," as in all typical American deer (except the Wapiti) and in the Roe and Père David's Deer amongst the Old-World species.

Now with regard to the affinities of the species composing Cameron's third division, there is only one point in which there is complete divergence between him and Brooke. This concerns Père David's Deer, a species classified by Brooke with the Red Deer, Sambar, and other Elaphine stags, and by Cameron with the American forms allied to the Virginian and Mule Deer, the correct name of which seems to be *Odocoileus* *.

So far as I can see, the only *à priori* objection to be raised against Mr. Cameron's system, if we accept his premises, is that it is based upon a secondary sexual character. But although it cannot be justifiably consigned to oblivion on that account, it may be doubted if it would ever have come into sufficient prominence for serious discussion had it not been for the unqualified acceptance accorded it by Mr. Lydekker. However that may be, it is clear that if Mr. Cameron's assumption that there is a fundamental difference in structure between the antlers of the groups of deer mentioned above is wrong, his classification, based on that claim, goes by the board.

In the following pages I shall endeavour to show that his classification is untenable, because a study of the seasonal growth

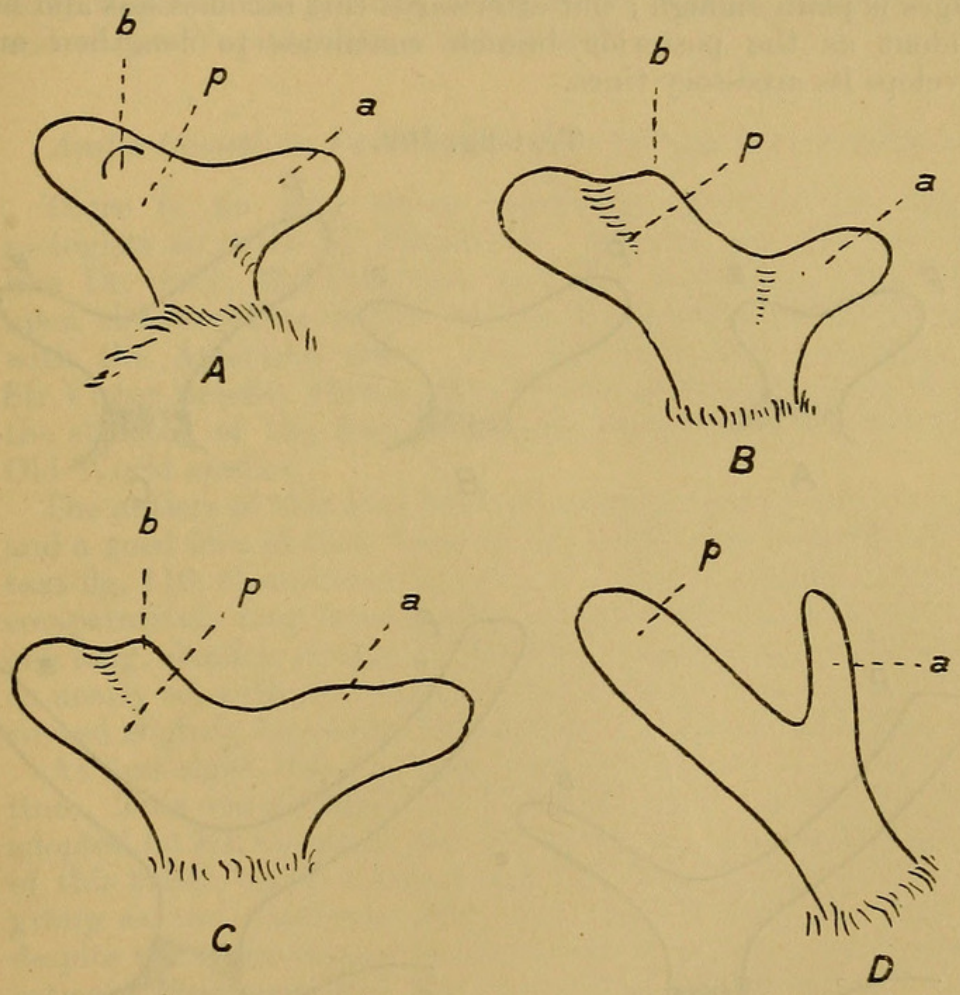
* *Dorcelaphus* and *Cariacus* are better known but superseded terms.

of an antler of Père David's deer and of an American deer, allied to the Virginian, proves that the homologue of the brow-tine of the Elaphine stage is present in both—a conclusion which is by no means evident from an examination of the fully-formed antlers.

Antler-Growth in typical Old-World Deer.

In the Zoological Gardens I have repeatedly watched, year after year, the growth of the antlers of deer belonging to the Elaphine, Sikine, and Rusine types without finding any variation

Text-fig. 108.



Early growth-stages of Antlers of some Old-World Deer.

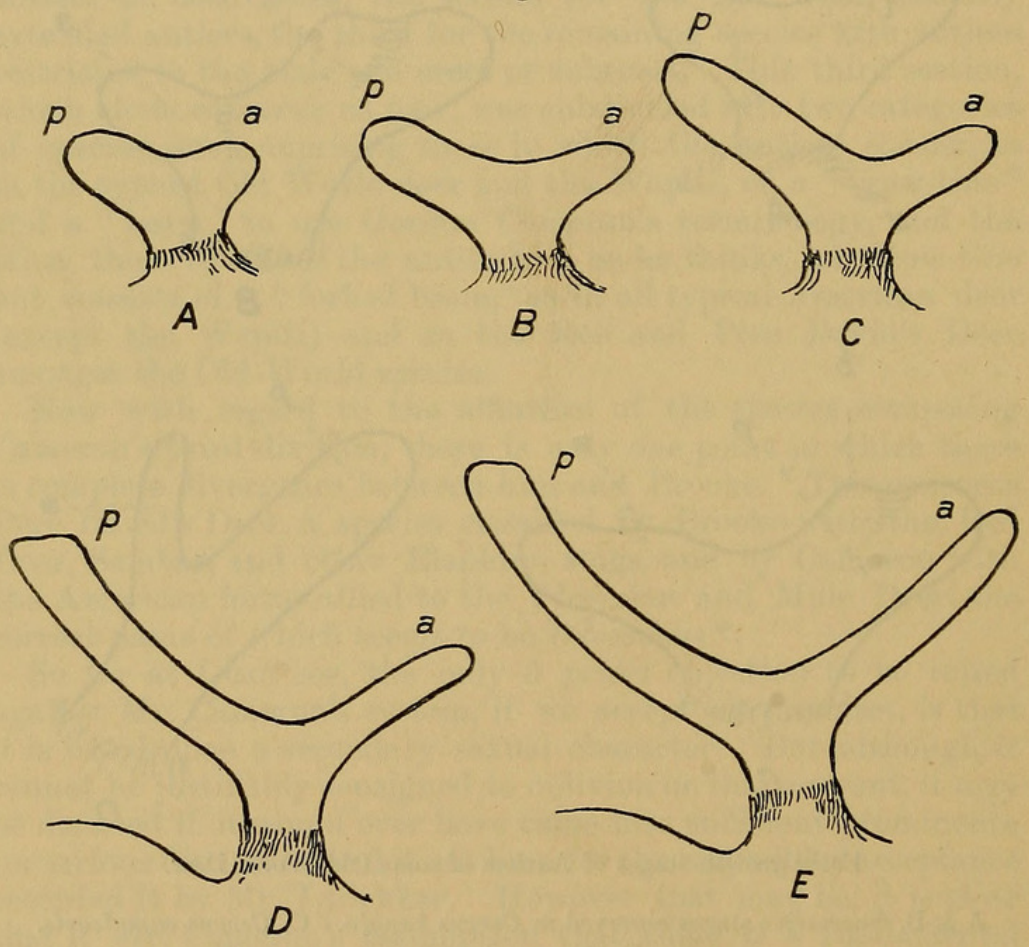
A & B. Successive stages observed in *Cervus hanglu*. C. *Cervus canadensis*. D. *Rusa aristotelis*.

a, the anterior branch or "brow-tine"; *p*, the posterior branch or "beam"; *b*, the rudiment of the bez-tine arising from the posterior branch.

of moment in the method of their development. The antler starts as an undivided bud. This bud then shows signs of division into two buds, an anterior and a posterior. These buds

gradually, and with nearly equal rapidity, increase in length, the anterior growing forwards and the posterior backwards. In the Sambar (*Rusa*, text-fig. 108, *D*) and some other species they show a marked inclination upwards; so that at one stage the antler may be likened somewhat to a short-stalked **Y**, and at this or even at a later stage in deer like the Sambar (*Rusa*) and others which have no "bez"-tine, the antler may be indifferently described as an "unbranched beam with a brow-tine" or as a "forked beam" or as a biramous antler. The anterior and posterior branches sometimes, as in *Cervus eldi*, grow at approximately the same speed until the anterior has almost attained its limit; but usually the growth of the posterior tine is from the first more rapid. However that may be, the equivalence of the two branches in the early stages is plain enough; but afterwards this becomes less and less evident as the posterior branch continues to lengthen and develops its accessory tines.

Text-fig. 109.



Five stages (*A* to *E*) in the growth of an antler of *Rucervus duvaucelli*.

a, anterior branch or "brow-tine"; *p*, posterior branch or "beam."

These facts are shown in the annexed figure (text-fig. 109), representing five stages in the growth of an antler of a specimen of the Swamp Deer or Barasingha (*Rucervus duvaucelli*). These were

sketched on May 13, 16, 22, June 6 and 12. Similar stages may be observed in other typical deer of the Old World*. In the Elaphine stags, however, which normally grow a "bez"-tine, the biramous stage is early complicated by the appearance of the bud of this tine. Now this tine has been regarded as a duplication of the brow-tine; and in Max Weber's† diagram showing suggested homologies of the tines in certain deer the brow- and bez-tines are tinted alike, suggesting his adoption of this view. Nevertheless I believe it to be quite incorrect, for in all cases where I have watched its origin, the bud of the "bez"-tine arises, not from the brow-tine at all, but from the "beam." It is, in fact, the basal or proximal tine of the posterior branch of the antler. This is illustrated in text-fig. 108, *A–C*, showing the early stages of the growing antler of the Hangul (*Cervus hanglu*) and of the Wapiti (*Cervus canadensis*).

Antler-Growth in Père David's Deer (Elaphurus davidianus).

There is no stag whose systematic position has troubled zoologists so much as *Elaphurus*. On the one side are those, like Dr. Gray, Mr. Cameron, and Mr. Lydekker, who, relying upon the structure of the antlers of the adult, placed the genus with the American deer. On the other side are those, like Sir Victor Brooke, Flower, Max Weber, and others, who, adopting the skeleton of the foot as a basis, classified it with the typical Old-World species.

The antlers of this stag have often been figured and described, and a good idea of their form in the adult may be gathered from text-fig. 110, *C*, and text-fig. 111, *I*. They typically consist of a comparatively long basal portion from which two branches arise: one long, slender, simple or divided, projects backwards parallel, or nearly so, with the animal's back; the other stout, erect, or curved slightly forwards, terminates in a pair of strong tines.

At first sight, these antlers appear to have no trace of a brow-tine. This was evidently Sir Victor Brooke's opinion, and it was adopted by Mr. Cameron and Mr. Lydekker, who, on the strength of this belief, boldly claimed that this stag belonged to the same group as the American deer, also held to have no brow-tine, despite the resemblances in other respects pointed out by Brooke between *Elaphurus* and the typical Cervidæ of the Old World. Prof. Garrod was more cautious, and frankly gave up the attempt to interpret the antlers of *Elaphurus* when he remarked that they "are at present quite beyond my comprehension."

This, then, was the state of the case when my researches on the specialised cutaneous glands of Ruminants‡ showed that the

* Mr. J. G. Millais ('Mammals of Great Britain and Ireland,' iii. plate facing p. 140, 1906) has published a series of figures of antler-growth in the Fallow Deer (*Dama*) illustrating precisely the same phenomenon.

† Die Säug. p. 667, 1904.

‡ P. Z. S. 1910, p. 840.

absence of interdigital glands on the feet and the smoothness of the integument between the hoofs in *Elaphurus* corroborated Sir Victor Brooke's views as to the relationship between this animal and such Old World deer as *Rusa*, *Rucervus*, and *Cervus*, and weakened to a corresponding degree the claim for affinity between it and the

Text-fig. 110.

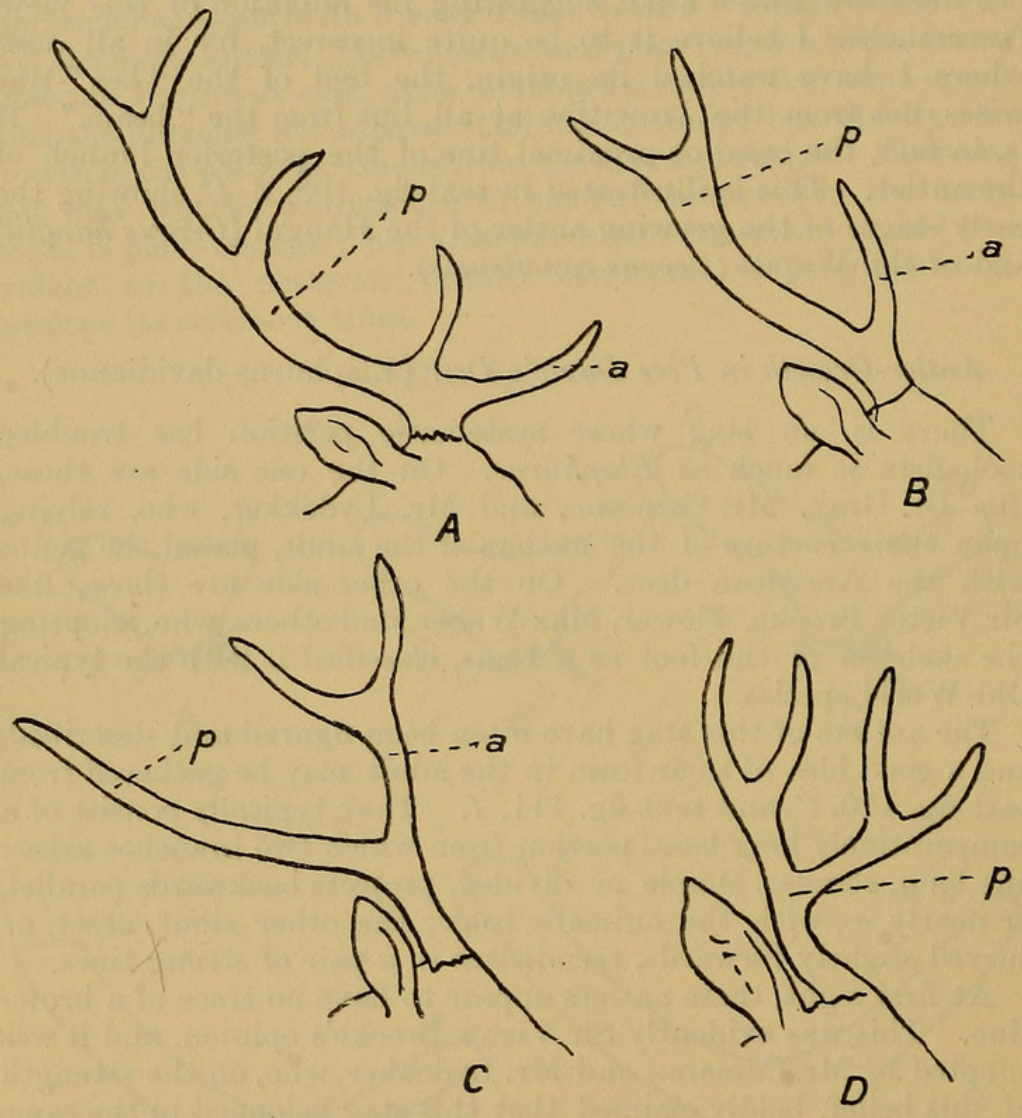


Diagram of the Antlers of four genera of Cervidæ, to illustrate the homologies established in this paper.

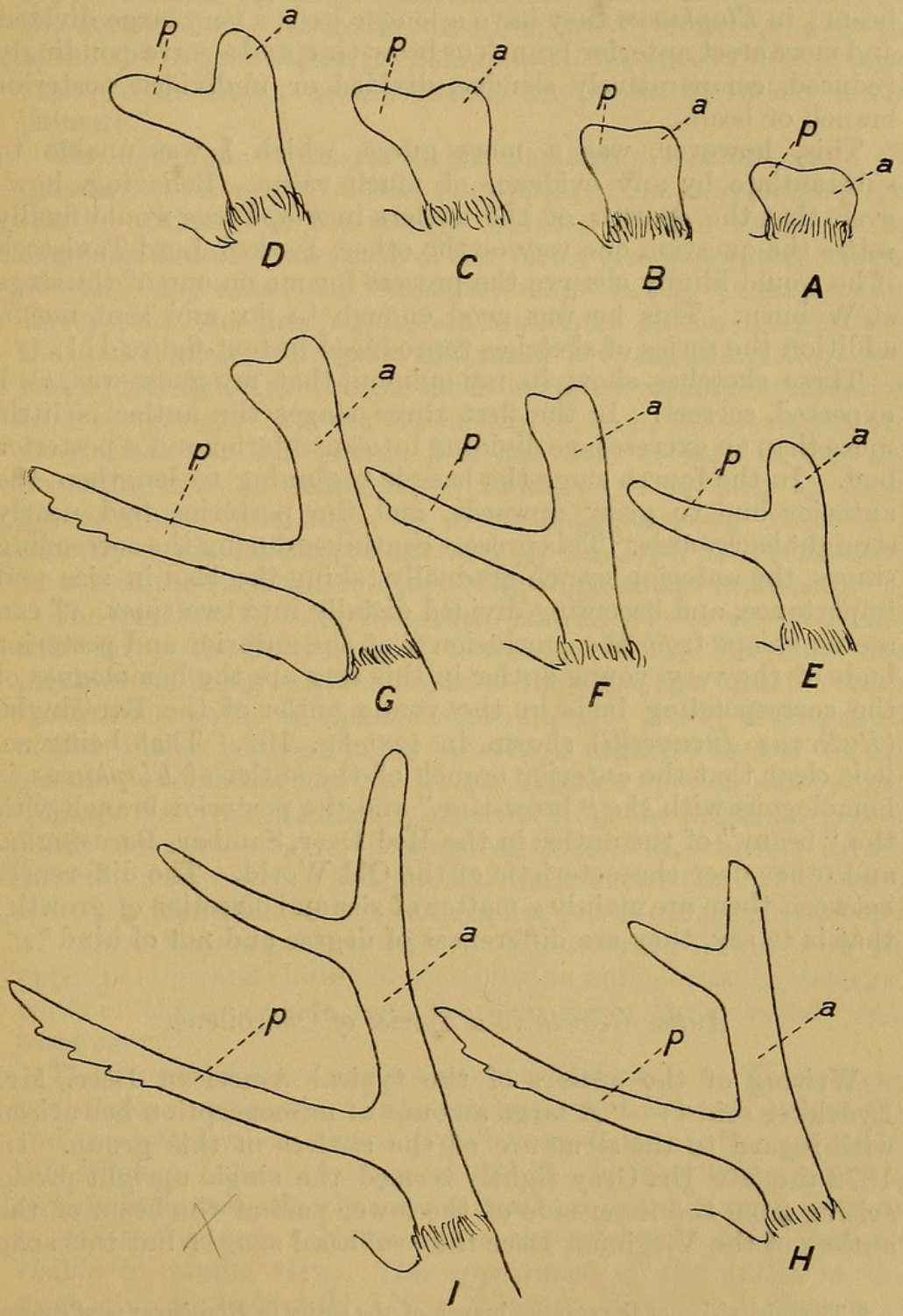
A. *Cervus*. B. *Rusa*. C. *Elaphurus*. D. *Odocoileus*.

a, anterior and *p*, posterior branch. In *A* and *B* the anterior branch is called the "brow-tine" and the posterior branch the "beam." *B* is somewhat intermediate between *A* and *C*. They differ collectively from *D* in having the anterior branch well developed. In *D* it is small and concealed behind the highly developed posterior branch.

Telemetacarpal species, in all the members of which examined by me, belonging to the genera *Mazama*, *Odocoileus* (*Dorcelaphus*), *Capreolus*, *Rangifer*, and *Alce*, the skin between the hoofs is

thickly hairy and, in all but *Alce*, a large pouch-like interdigital gland is present at least in the hind foot.

Text-fig. 111.



Nine stages (*A* to *I*) in the growth of an Antler of *Elaphurus davidianus*, showing that the branches marked *a* and *p* correspond precisely in origin with the brow-tine and the beam of other genera of Old World Deer. Compare *D* and *E* with fig. 108, *D*.

(From sketches made at Woburn and kindly supplied by Lord Tavistock.)

Thinking, for these reasons, that there must be some flaw in the claim that the antlers of *Elaphurus* differ fundamentally from those of, say, *Rusa*, I suggested the following homologies:—In *Rusa* the antlers have a short base, a short undivided anterior branch or brow-tine, and a large divided posterior branch or beam; in *Elaphurus* they have a longer base, a very large divided and more erect anterior branch or brow-tine, and a correspondingly reduced, comparatively slender, divided or undivided posterior branch or beam.

This, however, was a mere guess, which I was unable to substantiate by any evidence of much value. Believing, however, that the growth of the antlers in *Elaphurus* would finally settle the question one way or the other, I asked Lord Tavistock if he would kindly observe the process for me on one of the stags at Woburn. This he was good enough to do, and sent me in addition the series of sketches reproduced in text-figure 111.

These sketches show, in my opinion, that my guess was, as I expected, correct. In the first three stages the antler is little more than an excrescence dividing into an anterior and a posterior bud. In the fourth stage the base is beginning to lengthen, the anterior bud to grow upwards, and the posterior bud nearly straight backwards. This process continues during the succeeding stages, the anterior branch gradually taking the lead in size and importance, and becoming divided distally into two tines. I can see no escape from the conclusion that the anterior and posterior buds of the very young antler in this stag are the homologues of the corresponding buds in the young antler of the Barasingha (*Rucervus duvaucelli*) shown in text-fig. 109. That being so, it is clear that the anterior branch of the antler of *Elaphurus* is homologous with the "brow-tine" and the posterior branch with the "beam" of the antler in the Red Deer, Sambar, Barasingha, and other deer characteristic of the Old World. The differences between them are mainly a matter of size and direction of growth; that is to say, they are differences of degree and not of kind *.

Antler-Growth in a Species of Odocoileus.

Writing of the antlers of the typical American Deer, Mr. Lydekker said †:—"A large amount of misconception has arisen with regard to the structure of the antlers of this group. In 1872 the late Dr. Gray rightly termed the single upright prong arising from the inner side of the lower part of the beam of the antlers of the Virginian Deer the 'subbasal snag'; but this snag

* The subdivision of the anterior branch of the antler in *Elaphurus* is, of course, no argument against it being the homologue of the "brow-tine," for the latter not infrequently, though abnormally, produces an additional snag in Elaphine and allied groups of deer. In some species indeed, as in the Irish Elk and *Cervus eldi*, it is commonly and normally provided with supplementary processes.

† 'Deer of All Lands,' p. 246.

Sir Victor Brooke incorrectly identified with the brow-tine of the typical Old World deer. This error has been pointed out by Mr. A. Gordon Cameron, [who stated that] these characteristic tines have nothing in common with the true brows of Old World types, and rise vertically from the inner side of the beam between the coronet and the main furcation, usually converging at the apex. They are subject, in common with the antlers that produce them, to all kinds of eccentricities; are frequently forked or subpalmate."

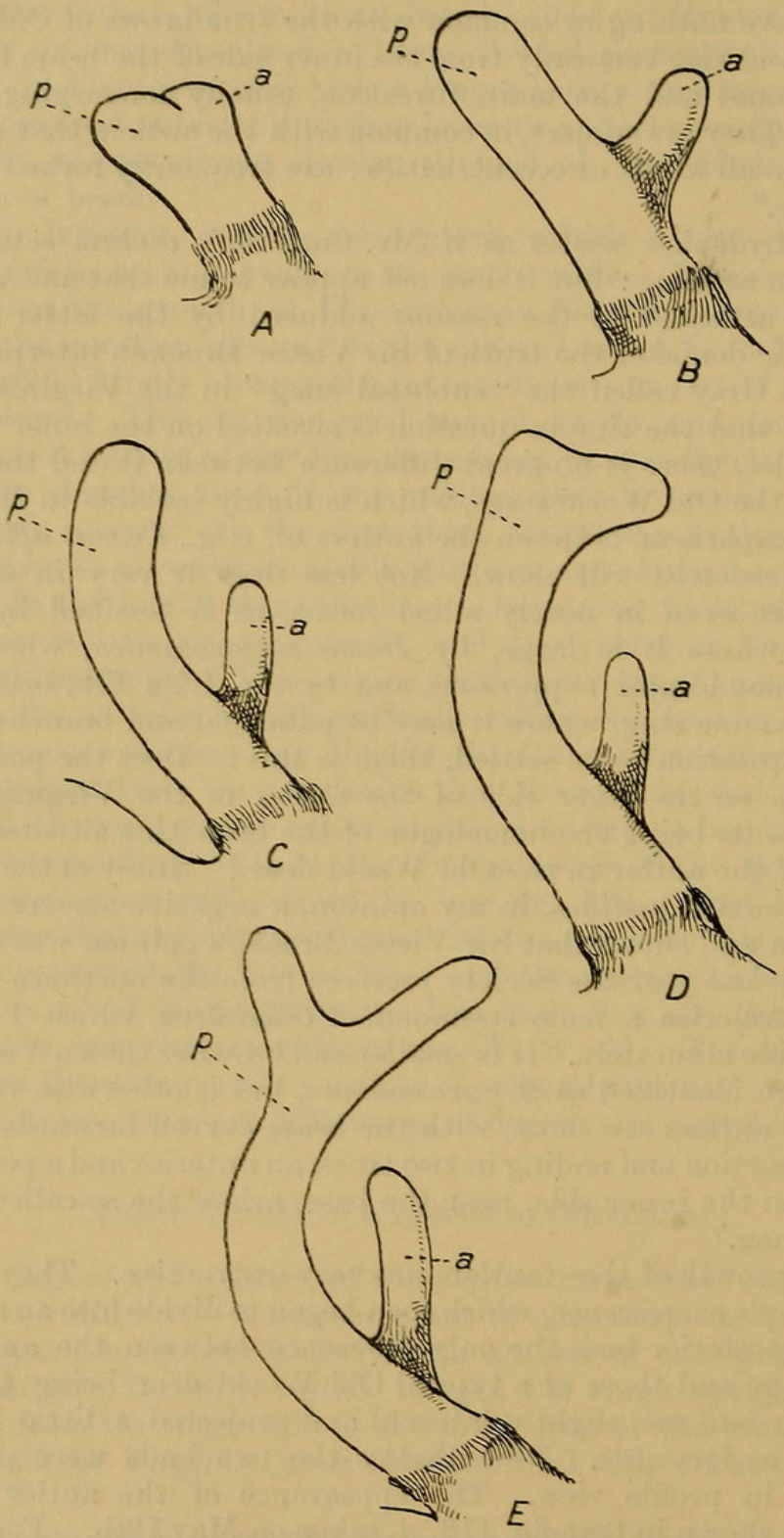
Mr. Lydekker writes as if Mr. Cameron's *dictum* settled the question at issue: but it does not appear to me that much weight can be attached to the reasons adduced by the latter for his dogmatic denial of the truth of Sir Victor Brooke's interpretation of what Gray called the "subbasal snag" in the Virginian deer. Except that the tine in question is situated on the inner side of the antler, there is no great difference between it and the brow-tine of the Old World stags, which is highly variable in direction, as a comparison between the antlers of, e. g., *Cervus affinis* and *Rusa aristotelis* will show. Not less does it vary in size and structure even in nearly allied forms, as is testified by *Dama dama*, where it is large, by *Dama mesopotamica*, where it is sometimes almost suppressed, and by the Irish Elk, believed to be a Damine stag, where it may be palmated and branched.

The question to be settled, then, is this:—Does the position of this tine on the inner side of the antler in the Virginian deer preclude its being the homologue of the brow-tine situated on the front of the antler in the Old World deer? Study of the growth of the antler justifies, in my opinion, a negative answer to this question and shows that Sir Victor Brooke's opinion was correct.

Early last year the Society received from the northern part of South America a male specimen of *Odocoileus*, which I cannot determine accurately. It is smaller and browner than a Venezuela specimen identified as *O. savannarum*, but is otherwise very like it. Its antlers are short, with the beam curved forwards in the upper portion and ending in two tines, an anterior and a posterior; while on the inner side, near the base, arises the so-called "subbasal snag."

The growth of these antlers was very instructive. They started as a simple excrescence, which soon began to divide into an anterior and a posterior bud, the only difference between the antlers at this stage and those of a typical Old World deer being that the anterior bud was slightly internal and projected a little inwards as well as forwards. Nevertheless the two buds were perfectly visible in profile view. The appearance of the antler at this stage is shown in text-fig. 112, *A*, taken on May 12th. Four more stages of the growth are represented in the following figures, *B–E*, taken respectively on May 22nd, May 30th, June 6th, and June 17th, which show very markedly the gradual assumption of an apparently more internal position by the anterior branch, its

Text-fig. 112.



Five stages (*A* to *E*) in the growth of an Antler of an American Deer (*Odocoileus* sp. incert.), showing that the "subbasal snag" (*a*) and the "forked beam" (*p*) were respectively the homologues of the "brow-tine" and the "beam" of the typical Old World Deer. Compare *B* with fig. 108, *D*.

point of attachment to the posterior branch being completely concealed from the external aspect in the last three stages *.

In view of these facts, I do not think it can be doubted that the anterior bud which develops into the "subbasal snag" in *Odocoileus* is the homologue of the anterior bud which forms the brow-tine in *Cervus*. In that case the "subbasal snag" and the "brow-tine" are homologous structures passing under different names, and to state that *Odocoileus* has no brow-tine is merely playing with terminology.

If this interpretation of the structure of the antlers in *Elaphurus* and in the species of *Odocoileus* above referred to be, as I believe, correct, it shows that these two genera are widely divergent in the very point upon which relationship between them has been claimed to exist, and that the likeness, such as it is, between the antlers of *Elaphurus* and of the Mule Deer (*O. hemionus*), for instance, which has the so-called forked antlers without a brow-tine or with the merest vestige of it, is purely a question of parallelism in development; that is to say, it has been brought about by growth and modification of fundamentally different parts of the antler. In the Mule Deer the anterior branch or brow-tine is to all intents and purposes suppressed, practically the whole antler being composed of the posterior branch or "beam," which is highly developed and heavily tined. In *Elaphurus*, on the contrary, the principal part of the antler is composed of the anterior branch or "brow-tine," which attains a large size and is divided into two prongs, while the posterior branch or beam remains comparatively small and slender and projects straight backwards as a long often undivided prong.

* In connection with the date of antler-change in this Stag, attention may be directed to its approximate coincidence with that of the typical elaphine deer of the Old World; that is to say, the antlers were in the velvet during the summer months and functional during the autumn and winter. They were shed in the early spring and at the time of writing (July 3) the new antlers are nearly full-sized though still in the velvet, exactly as in our Wapiti, Red Deer, Japanese Deer, and other Old World species. The same is true of a specimen of *Odocoileus americanus*. On the other hand an example of *Mazama bricenii* which shed in April 1908, and again in April 1909, did not repeat the process till May 1911. He then carried a pair of antlers for 25 months; and those that started to grow in May 1911 are still on his head. Thus Dr. Scharff ('Distribution and Origin of Life in America,' p. 111) is mistaken in saying that the antler-change in American deer takes place at a quite different time of year from that of Old World deer. It is well known too that the time of antler-change at all events in some tropical Old World deer is highly variable within specific limits. For instance, one example of *C. duvaucelli* in the Gardens regularly carries his antlers till about the end of May, while another of the same species has antlers at least half their full size at that time.