2. On certain Points in the Structure of the Cervical Vertebræ of the Okapi and the Giraffe. By Sir RAY LANKESTER, K.C.B., F.R.S., F.Z.S.

[Received March 14, 1908.]

(Text-figures 60–71.)

Among the material relating to the Okapi which has been acquired by the British Museum (Natural History), is a fine skeleton of a nearly but not quite adult male, obtained from Major Powell Cotton. It is the skeleton of the individual the skin of which was presented by that gentleman and is exhibited in the public gallery.

I have made some study of this skeleton, comparing the bones with those of the Giraffe. Since I commenced this study, Professor Fraipont of Liège has published his finely illustrated account of the specimens of Okapi preserved in the Museum of the Congo State at Tervueren near Brussels.

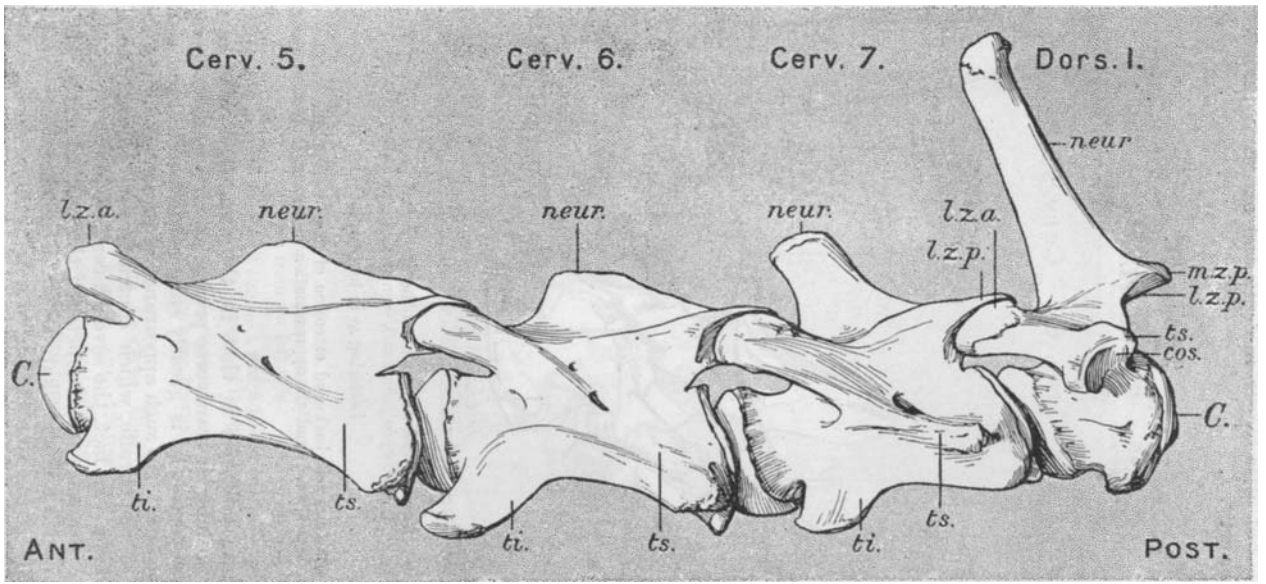
The most important difference between the general bony skeleton of Okapi and that of Giraffe—as distinct from the cranium—is one which is presented by the last three cervical and first dorsal vertebræ of the two animals. A certain difference in the form and proportions of the cervical vertebræ—as between Okapi and Giraffe—is what one expects as the necessary correlative of the much greater length of the neck in Giraffe. But the difference goes a good deal beyond this—as a glance at the drawings given in text-figs. 60 and 61, of the vertebræ, cervical 5, 6, 7, and dorsal 1, at once shows.

The neural spines (*neur.* in the figures) of the cervical vertebræ of the Giraffe are much shorter proportionately than are those of the Okapi—and this is especially the case in cervical 7. Further, the inferior transverse processes (*ti.* in the figures)—lateral outgrowths which in the mammalian vertebral series are peculiar to the cervical region—are very different in the Giraffe from those of the Okapi. In the Giraffe they are of small proportional size, entirely anterior in position on each vertebra (see text-fig. 60). In the Giraffe a right and a left inferior transverse process exist on the seventh cervical vertebra—as well as on the vertebræ in front of it.

Not so in the Okapi (see text-fig. 61). Whilst cervical 5 (as well as 4 and 3) has a large inferior transverse process (I speak of the side view as given in the drawing and therefore of one only of the pair of lateral processes) which grows downwards (abaxially) from the anterior part of the vertebra—and is larger than the corresponding process in Giraffe—cervical 6 has its inferior transverse process in the form of an enormous flange or plate extending the whole length of the vertebra. This does not exist in Giraffe: in that animal the inferior transverse process (*ti.* text-fig. 60) of

Text-fig. 60.

GIRAFFE.



The last three cervical vertebræ and the first dorsal vertebra of the Giraffe, seen from the left side.

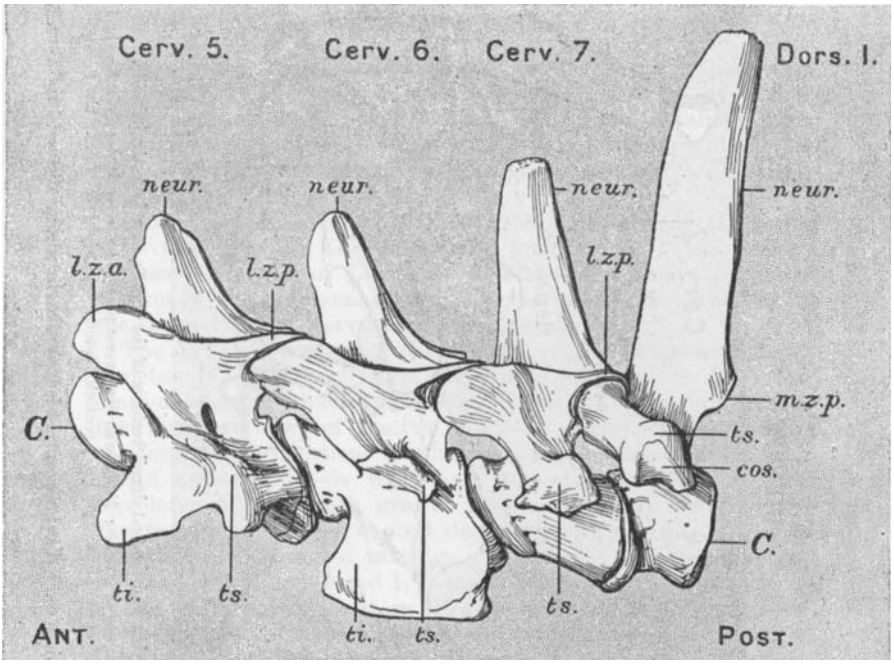
C., centrum; *neur.*, neural spine; *ts.*, superior transverse process; *ti.*, inferior transverse process; *cos.*, articular facet for the tubercular process of the first rib; *l.z.a.*, anterior lateral zygapophysial facet; *l.z.p.*, posterior lateral zygapophysial facet; *m.z.p.*, median zygapophysial (so-called) facet.

Note the small size of *ti.* on the sixth cervical and the contrast between the size of *neur.* of Dors. 1 and Cerv. 7.

cerv. 6 is but little bigger in depth and extension than is that of cerv. 5 or cerv. 7.

Text-fig. 61.

OKAPI.



The last three cervical vertebræ and the first dorsal vertebra of the Okapi (*Okapia johnstoni*), seen from the left side.

Lettering as in text-fig. 60.

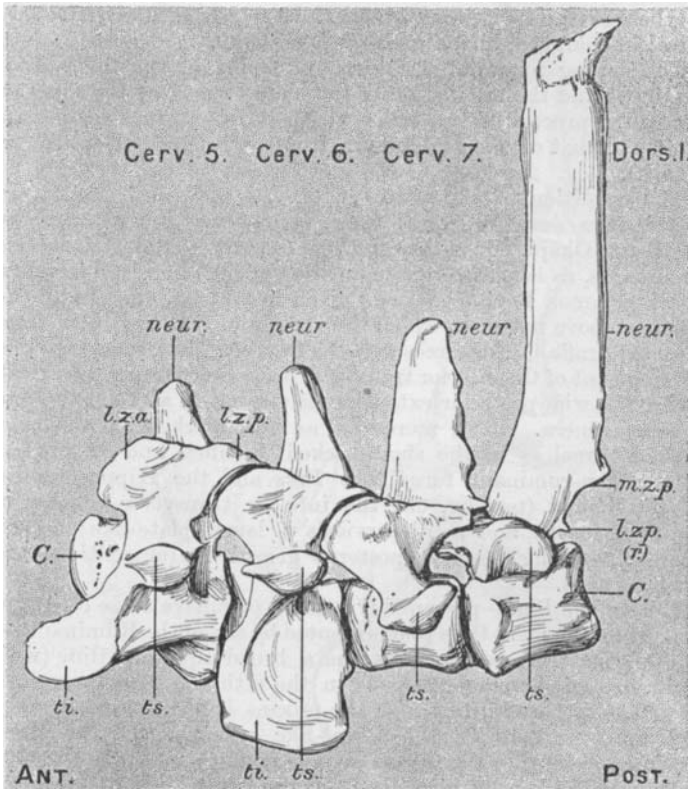
Note the great size and backward extension of *ti.* of Cerv. 6, the complete absence of *ti.* from Cerv. 7, and the approximation in general proportion of Cerv. 7 to Dors. 1.

The next difference is that in the seventh cervical of Okapi there is no inferior transverse process at all; whilst the superior transverse process *ts.* is greatly enlarged, expanded and flattened at its free end. No such appearance is presented by the seventh cervical of the Giraffe, which contrasts very strongly with that of the Okapi. In fact, the seventh cervical of the Giraffe has the general appearance and character of the cervical series, whilst the seventh cervical of the Okapi is, in all its characters except that of actually giving articulation to a bony rib, a dorsal. We may describe this by saying that the last cervical is "dorsalized."

The contrast in this respect between Giraffe and Okapi is very great, as text-figs. 60 and 61 clearly show.

Text-fig. 62.

BOS TAURUS.



The last three cervical vertebræ and the first dorsal of a domestic Ox (*Bos taurus*), seen from the left side.

Letters as in text-fig. 60, except *l.z.p.(r.)*, which points to the *rudimentary* posterior lateral zygapophysial process of the first dorsal vertebra.

Note the close agreement of these five vertebræ with those of Okapi and their difference from the same group in Giraffe.

It may perhaps be possible to show that these differences of proportion in the neural spines and transverse processes are connected with the special mechanism of the very long neck of Giraffe. The greater size and breadth of these bony processes is merely an expression of the greater size of the muscle-tendons and of the ligaments, of which they may be regarded as but denser

ossified parts. The fact, however, as we have seen, is that the long-necked Giraffe presents a smaller development of these processes of the vertebræ of the cervico-dorsal region than does the shorter-necked Okapi; the Giraffe's cervicals (from cerv. 3 backwards) are practically all alike, and even the first dorsal is not so marked in the contrast it presents to the cervicals as is the first dorsal of Okapi to the cervicals in front of cerv. 7, which is, itself, strongly dorsal in character in the contrast it presents.

The sloping forwards of the neural spine of the first dorsal of Giraffe and the inclination of the plate formed by the superior transverse process and anterior zygapophysis in that vertebra is similar to that of the vertebræ in front of it (see text-fig. 60, *ts.* & *l.z.a.*).

The condition of the vertebræ cerv. 5, 6, 7, and dors. 1, in Okapi, thus seen in lateral view, is however not in any way peculiar to Okapi. It is the condition common to the Artiodactyle Ruminants, as is shown by the drawing of the same four vertebræ of the common Bovine (*Bos* sp.) given in text-fig. 62. In all the features above noted, in which the vertebræ of Okapi differ from those of Giraffe, Okapi agrees with the Bovine. The large flange-like development of the inferior transverse process of the sixth cervical, giving it a wide posterior extension, is present in all Cavicorn and Cervine genera. It is, moreover, as well marked in the long-necked Camel as in the short-necked Bovines, and is present in the non-ruminant forms, the Pigs and the Hippopotamus. In the Camel (text-fig. 63) the inferior transverse process of the fifth, fourth, and third cervicals is large, plate-like and triangular, wanting the large posterior growth characteristic of the sixth cervical.

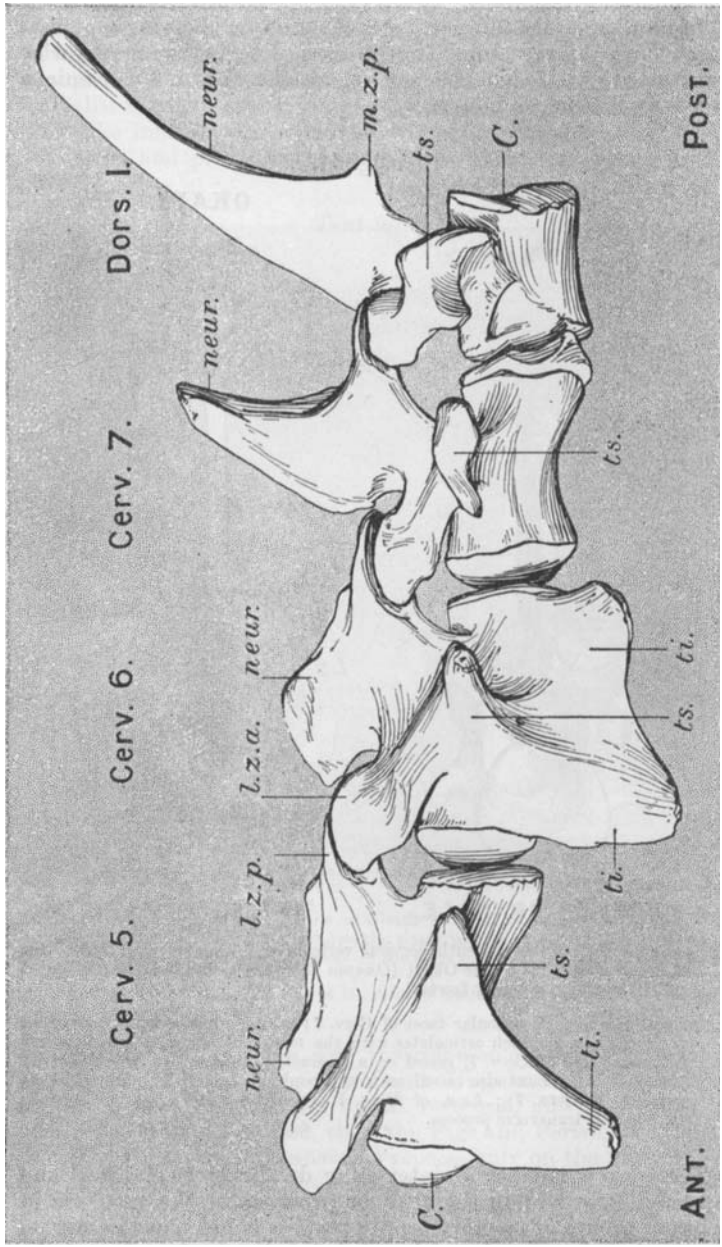
But in the Pigs—presumably a more primitive stage of Artiodactyle development than that presented by any of the Ruminants—the inferior transverse process has a broad square outline (with posterior region well developed), in the fifth and fourth cervicals as well as in the sixth, though the process is biggest in the sixth and totally absent in the dorsal-like seventh. In the third cervical the inferior transverse process is much less in lateral outgrowth, but still has a strongly developed posterior region projecting backwards below and behind the superior transverse process.

The inferior transverse process of the cervical vertebræ is well developed in the Carnivora as in the Pig, the special enlargement and plate-like character of that of the sixth cervical being as in the Ungulata.

In the Insectivora—as shown more especially by *Centetes*—the superior transverse process of cervicals 7, 6, 5, 4, 3, 2, and even 1, is well developed, and it is only on cerv. 6 that the inferior transverse process is developed to any size; cervicals 5 and 4 have a small development of it. In the Hedgehog the inferior transverse process of cervical 6 is enormous and grows downward and backward on each side of the neck as a very obvious and striking pair of plates.

Text-fig. 63.

CAMEL.



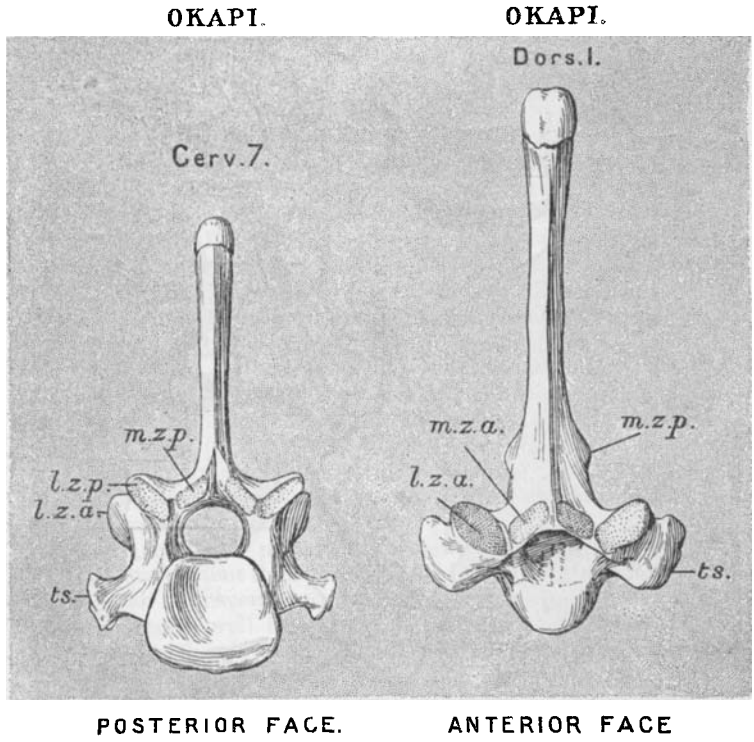
The last three cervical vertebræ and the first dorsal vertebra of the Camel seen from the left side.

Letters as in text-fig. 60.

[Note the general agreement with *Bos* and Okapi, together with the larger and more plate-like development of *ti.* on Cerv. 5.]

The inferior transverse process is to be regarded as a bifurcation of (or an accessory inferior plate of) the one transverse process which is usually recognised (in the cervical region) as the superior transverse process. On the present occasion it is not convenient to discuss further its morphology.

Text-fig. 64.



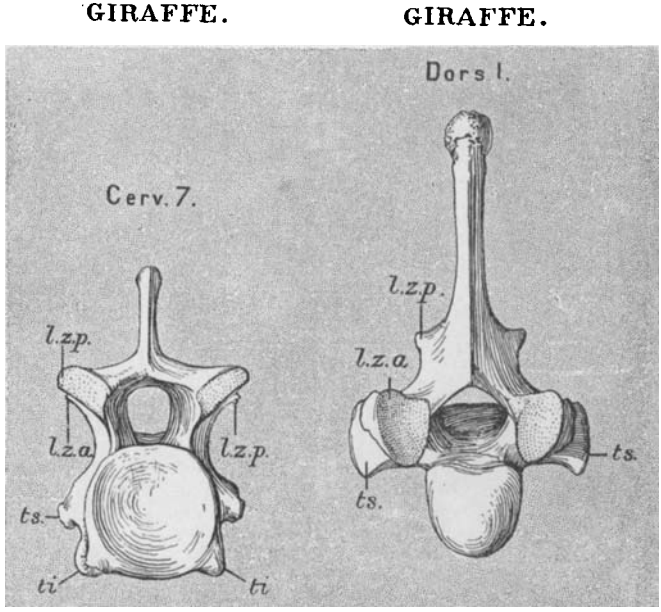
The posterior face of the seventh cervical vertebra and the anterior face of the first dorsal vertebra of the Okapi (*Okapia johnstoni*), to show the duplicated character of the articular facets.

m.z.p., posterior median articular facet of Cerv. 7; *m.z.a.*, anterior median articular facet of Dors. 1, which articulates with the foregoing; *l.z.p.*, posterior lateral articular facet of Cerv. 7, raised on a distinct zygapophysis; *l.z.a.*, anterior lateral articular facet also raised on a zygapophysis, seen fully in Dors. 1 (and partially in Cerv. 7); *l.z.a.* of Dors. 1 articulates with *l.z.p.* of Cerv. 7; *ts.*, superior transverse process.

There are a number of interesting details to be observed and discussed in regard to these minor processes of the vertebræ in different groups of mammals. My purpose is not now to enter on that subject, but merely to show briefly what is the value of the

difference between Okapi and Giraffe in regard to the inferior transverse process of the cervical region—when the chief facts as to this structure in other mammals are taken into view. Clearly enough it is Giraffe which is altogether exceptional, novel and specialised, not archaic or atavistic. Giraffe has not even the great plate-like inferior transverse process on its 6th cervicals, which is obvious and prominent in such widely separate forms as the

Text-fig. 65.



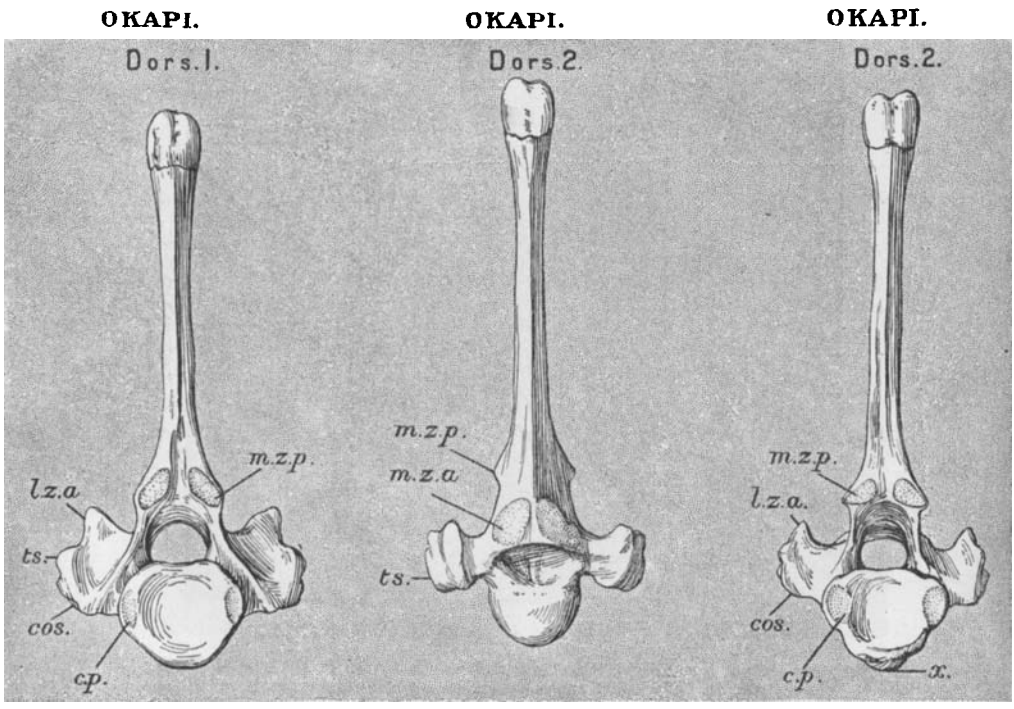
The same view of the same vertebræ in Giraffe as that given in the case of Okapi in text-fig. 64. The figure shows the single pair of articular facets raised on zygapophyses. No median facets on the sides of the neural arch are developed.

Letters as in text-fig. 64, except *ti.*, inferior transverse process of Cerv. 7.

Hedgehog, the Carnivora, and the commoner Ungulata. Okapi merely agrees with other Ruminant Ungulates in the matter of its adjacent cervical and dorsal vertebræ, and they seem to be a little more specialised, than the Pigs and Perissodactyles, in having a large inferior transverse process only on the 6th cervical and quite small ones on the vertebræ in front; whereas Pigs and Perissodactyles have that process more equally developed on all the cervical series 3, 4, 5, 6. The emphasis of the inferior transverse process on cerv. 6 appears to be the rule in Mammalia and

is carried very far in *Erinaceus*. Whether the existence of an inferior portion or inferior transverse process should be regarded as a primitive feature of all these vertebræ in Mammalia is not clear. It certainly seems to belong as an original element of structure to cervicals 3, 4, 5 and 6—to be increased greatly in size on cerv. 6 in most groups, and sometimes to practically disappear from the other cervicals whilst remaining there.

Text-fig. 66.



View of the articular surfaces which connect dorsal 1 and dorsal 2 of the Okapi, and of the anterior half of the articulation between dorsal 2 and dorsal 3. The articular facets are seen to be single pairs and to consist of an oval surface (*m.z.p.*, *m.z.a.*) placed entirely on the neural arch. The left anterior articular facet of dorsal 2 (middle figure) shows a tendency to divide into two.

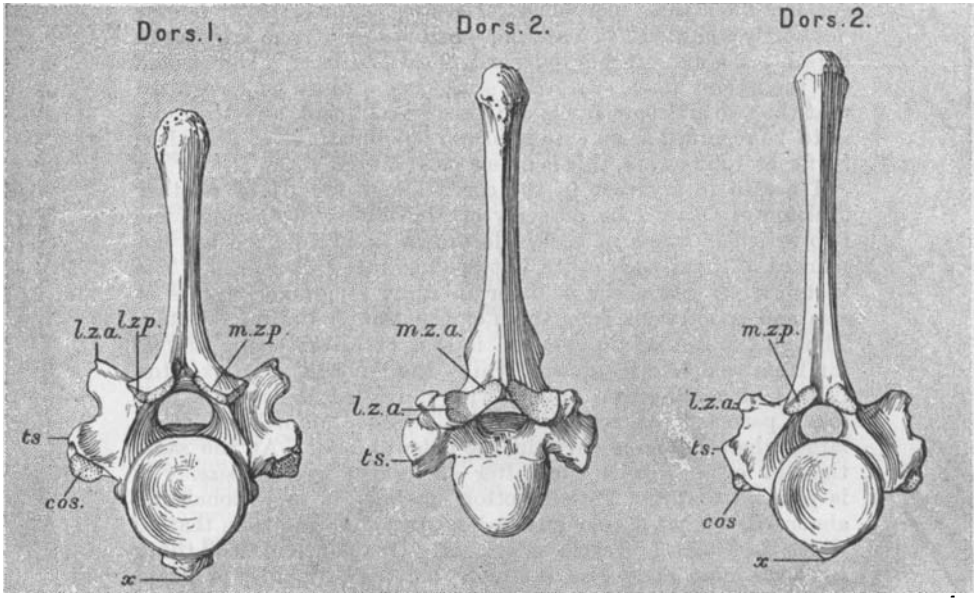
Letters as in text-fig. 64, with the addition of *cos.*, process for the articulation of the tubercle of the first rib; *c.p.*, concave facet for the head of the second rib; *x.*, hypapophysial tubercle.

In Giraffe, as a marked exception, it is small in all the cervicals and smaller in cerv. 6 than in the cervicals in front of that one, indeed so much reduced that it has no posterior extension at all but is represented by a small triangular anterior growth only.

Double Zygapophysial Articular Surfaces in Okapi.

The posterior face of cerv. 7 and the anterior face of dors. 1 of the Powell Cotton skeleton of Okapi are drawn in text-fig. 64 in order to show a remarkable condition of the articular surfaces which bring these two vertebræ into relation. Whilst cerv. 6 of Okapi has only the usual single pair of anterior and posterior articular facets, common in cervical vertebræ, and situated on the zygapophyses themselves, the seventh cervical of this specimen of Okapi shows on the posterior face an additional mediad pair of

Text-fig. 67.



A similar view to that given in text-fig. 66 of the corresponding vertebræ of the Giraffe. The posterior face of dorsal 1 and the anterior face of dorsal 2 show duplicated facets (*l.z.p.* and *m.z.p.*, *l.z.a.* and *m.z.a.*) *unlike* dorsal 1 and dorsal 2 of Okapi, but *like* cervical 7 and dorsal 1 (see text-fig. 64) in that animal. The lateral element, however, entirely disappears from the articular surfaces connecting dorsal 2 and dorsal 3, as shown by the view of the posterior face of dorsal 2.

Letters as in the preceding text-figures.

articular facets quite distinct from the lateral pair (text-fig. 64, *m.z.p.*, *cerv.* 7), whilst the anterior face of dors. 1 drawn in the same figure shows two articular surfaces on the anterior face (*l.z.a.*, *m.z.a.*).

If we pursue the enquiry as to the articular surfaces, we find on examining the posterior face of dors. 1 and both faces of dors. 2

as shown in text-fig. 66, that it is obvious that the mediad articular surfaces which co-exist in cerv. 7 (posterior face) and dors. 1 (anterior face) with the lateral articular surfaces, are new and independent morphological entities and are identical with the articular surfaces of the dorsal vertebræ, whilst the laterally placed articular surfaces of the cervicals raised upon distinct "zygapophyses" have no existence in the dorsal series except on the anterior face of the first dorsal.

It seems to me that we are entitled to conclude from the specimen here figured (text-figs. 64 and 66) that the zygapophyses of the cervical vertebræ of the Mammalian series are not merely in a different position from that occupied by the articular facets of the dorsal vertebræ, but that the cervical and the dorsal articular surfaces are *distinct* morphological entities. The articular facet is not bodily "shifted" in position, when we pass from cervical to dorsal, but a distinct and independent mediad facet is substituted for the lateral facet. At the same time it must be recognised that the two articular facets can become confluent, and that one is to be regarded as an extension and "pullulation" of the other. So far as I am aware, this is a new observation.

I hasten to say that in the cerv. 7 and dors. 1 of another skeleton of Okapi (the property of Mr. Walter Rothschild) the two articular facets of each side drawn in text-fig. 64 are not marked off from each other, but confluent and ill-defined. The vertebræ of that skeleton differ in many remarkable points of size and proportions from those of the Powell Cotton skeleton. Though the Rothschild skeleton is that of a very young animal far from complete in growth, whilst the Powell Cotton skeleton is that of a full-grown animal with nearly adult dentition, yet many parts of the vertebræ of the younger animal are much larger than the same parts in the older animal. At the same time in other details the latter shows the greater size. It is possible that the Powell Cotton specimen is exceptional and abnormal, or that it belongs to a local race differing from that to which the Rothschild skeleton belongs. Or again, and this I think to be the most likely case, it seems from the variability of Okapi in regard to the striping of the skin and various proportions of the skull, also as to the symmetry of the horns of either side and as to the molar teeth, that there is great range of variation in the species—and that this variability extends even to such points as the exact form of the vertebræ and the development of articular facets connecting successive vertebræ. It is also possible that the absence of a distinct second pair of facets at the articulation between cerv. 7 and dors. 1 in this particular specimen of Okapi is due to its immature stage of growth.

A comparison of these vertebræ of Okapi with those of Giraffe—in regard to the zygapophyses and articular surfaces or facets—becomes now especially interesting.

In text-fig. 65 the same views of the two vertebræ (cerv. 7 and

dors. 1) of Giraffe are shown as are shown in the case of Okapi in text-fig. 64. It is at once seen that there is no question of the presence of a second pair of articular surfaces, of mediad position, in Giraffe, so far as this articulation is concerned.

Let us now go on to examine the posterior face of dors. 1, and both faces of dors. 2 in Giraffe. These are drawn in text-fig. 67 for comparison with similar views of the same vertebræ of Okapi drawn in text-fig. 66.

The remarkable fact is at once obvious that the articulation between dorsal 1 and dorsal 2 in Giraffe shows some of the characters of the articulation between cervical 7 and dorsal 1 of the Powell Cotton Okapi. There is on the posterior face of the Giraffe's dors. 1, a lateral and a median articular surface which are not separate from one another but confluent. And the same is true as to the corresponding articular surface on the anterior face of the Giraffe's dorsal 2.

The lateral articular facet belonging to the true zygapophysis of the cervical vertebræ is in Giraffe continued into the dorsal series—and does not disappear until we come to the articulation between dorsal 2 and dorsal 3 (see below as to Rhinoceros). In fact the first dorsal of the Giraffe is in this respect drawn (as it were) into the cervical series. The break in the vertebral series which occurs in Okapi (and normal Ungulata) between the anterior and posterior faces of dorsal 1 is in Giraffe pushed down the series and shows itself in the contrast between the anterior and posterior faces of dorsal 2. There is, what has been called in regard to such serial metameric elements of structure, "homœosis" of the first dorsal of the Giraffe—assimilating the articular facets of that vertebra to those of the seventh cervical.

The complete investigation of this question of the characters of the last cervicals and first dorsals—and the transition from the one group to the other and the greater or less abruptness of the break between them in the whole Mammalian series, would form an interesting enquiry.

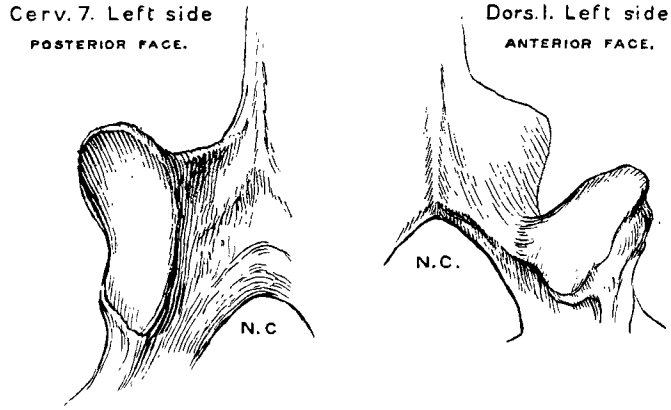
At present I must content myself with formulating the facts, *firstly*, that in both Okapi and in Giraffe there is (as an exception in Ungulata) a co-existence of lateral and mediad articular facets of independent morphological value—at one of the vertebral articulations at the base of the neck: and *secondly*, that the articulation at which this occurs is in Okapi that between cervical 7 and dorsal 1—whereas in Giraffe it is shifted one place backwards in the series and occurs between dorsal 1 and dorsal 2.

The relation of these peculiarities to the elongation of the cervical region or to any other peculiarities of the animals in question, is a matter for further enquiry.

I am able to add to this the following additional observations which I have made in the Museum of the Royal College of

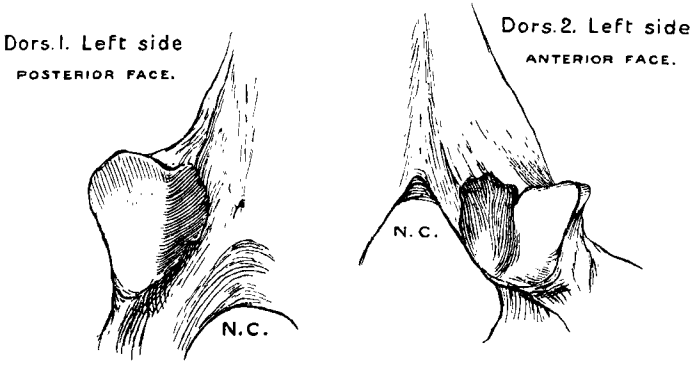
Surgeons*. In the Ruminants generally the substitution of

Text-fig. 68.



The articular facets of the left side on the posterior face of Cervical 7 and anterior face of Dorsal 1 of *Rhinoceros sumatranus*. $\frac{2}{3}$ nat. size.
N.C., neural canal. To show single lateral facet.

Text-fig. 69.



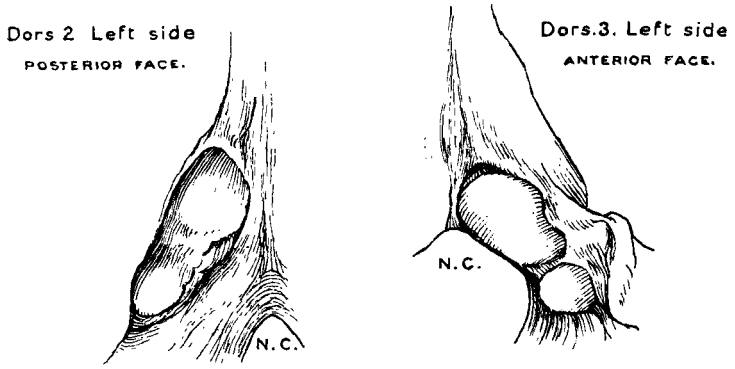
The articular facets of the left side on the posterior face of Dorsal 1 and anterior face of Dorsal 2 of *Rh. sumatranus*. $\frac{2}{3}$ nat. size.
To show elongated facet, including lateral and mediad factors.

the mediad pair of facets for the more laterally placed pair

* I desire to take this opportunity of pointing out that though the osteological series of the Hunterian Museum is a most valuable and useful one, it is yet not very large and does not contain second and third specimens for comparison. Such a collection as the zoologist really requires ought to be formed at the Natural History Museum. The osteological collection of that museum is at present very small and not such as is necessary for reference and comparison. A large room in the basement was arranged by me to receive such a collection, which I had intended to keep mounted on flat boards and movable: the boards to be fixed as sliding-shelves in dust-tight cabinets. An assistant was appointed in 1907 for the purpose of making and looking after this proposed collection.

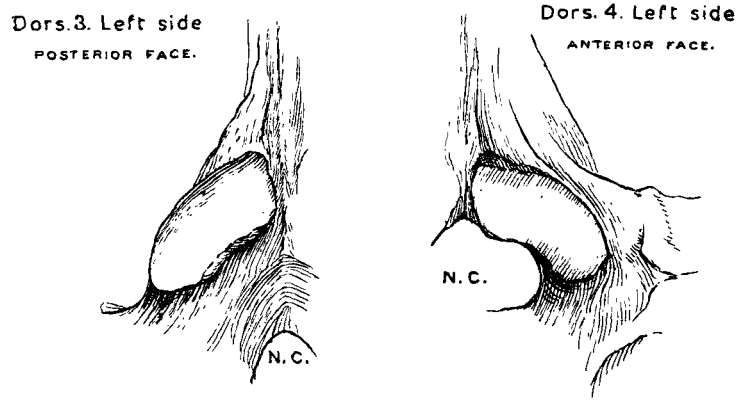
takes place abruptly and sharply at the articulation between dors. 1 and dors. 2. Occasionally a trace of the lateral process is retained on the posterior surface of dors. 1, as shown in text-fig. 62, *l.z.p.* on dors. 1. In the Pigs and the Hippopotamus the same is the case.

Text-fig. 70.



Similar drawing, to show the duplicate facets connecting Dorsal 2 and Dorsal 3 in the same animal. $\frac{2}{3}$ nat. size.

Text-fig. 71.



Similar view, to show the single facets (now the median not the lateral factor) connecting Dorsal 3 and Dorsal 4 in the same animal. $\frac{2}{3}$ nat. size.

In Tapir and Horse the articulation between dorsal 1 and dorsal 2 does *not* exhibit an abrupt change, but the facets are intermediate in position to those shown in the joints in front and behind.

In the Carnivora (Cats, Dog, and Fox) the break occurs at the joint between dorsal 2 and dorsal 3: the anterior joint (that between dorsal 1 and dorsal 2) resembling that of the cervicals.

The Rhinoceros is the only case in which I found actually two pairs of facets marked out, almost but not quite as separate from one another as in Okapi. In several specimens of this genus I find that the facets between cervical 7 and dorsal 1 are purely lateral: between dorsal 1 and dorsal 2 the facets are very large and each is incompletely separated into a lateral facet and a mediad facet. Between dorsal 2 and 3 this is even more marked: there are two facets on each side of each of the articulating vertebræ. On the posterior face of dorsal 3—and the anterior face of dorsal 4—we find only the mediad pair of facets. These articulations are shown in the four drawings, text-figs. 68, 69, 70, & 71. In Rhinoceros then the transition is quite gradual—from the "cervical" condition of the joint to the "dorsal" condition—the articulations dors. 1 : dors. 2, and dors. 2 : dors. 3 showing clearly the lateral or cervical facet as well as the mediad or dorsal facets on each side. This observation requires of course further confirmation and may prove not to indicate a rule without exception when a larger series of Rhinoceros is examined.

Thus we may tabulate the conditions in regard to this matter in Ungulata as follows:—

NORMAL IN RUMINANTS:—

Cerv. 7 $\overset{\text{lat.}}{\longleftrightarrow}$ *dors.* 1. *dors.* 1 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 2. *dors.* 2 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 3. *dors.* 3.

OKAPI:—

Cerv. 7 $\overset{\text{lat. \& med.}}{\longleftrightarrow}$ *dors.* 1. *dors.* 1 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 2. *dors.* 2 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 3. *dors.* 3.

GIRAFFE:—

Cerv. 7 $\overset{\text{lat.}}{\longleftrightarrow}$ *dors.* 1. *dors.* 1 $\overset{\text{lat. \& med.}}{\longleftrightarrow}$ *dors.* 2. *dors.* 2 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 3. *dors.* 3 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 4.

RHINOCEROS:—

Cerv. 7 $\overset{\text{lat.}}{\longleftrightarrow}$ *dors.* 1. *dors.* 1 $\overset{\text{lat. \& med.}}{\longleftrightarrow}$ *dors.* 2. *dors.* 2 $\overset{\text{lat. \& med.}}{\longleftrightarrow}$ *dors.* 3. *dors.* 3 $\overset{\text{med.}}{\longleftrightarrow}$ *dors.* 4.

The multiplication of articular facets between successive vertebræ is of course well-known in another region of the Mammalian vertebral column. At the lumbar end of the dorsal series in the Great Anteater (*Myrmecophaga jubata*) we find that dorsal 12 exhibits no less than three pairs of zygapophysial facets—the most dorsal and median of which, though horizontal in dorsal 12, becomes tilted to a vertical position in dorsal 13 and the following vertebræ.