Anatomy. — *"On the Development of the Form of the Vertebral Spines in Mammals, especially in Man."* By W. A. MIJSBERG. (Communicated by Prof. L. BOLK.)

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The form of the vertebral spines differs largely in the different regions of the spinal column of man. It is especially the processus spinosi of the 2d, up to and including the 6th cervical vertebra that differ from the others in possessing a bifid spine. In the so called lower races this terminal bifurcation is less pronounced and also less frequent than in the European. In other mammals it is entirely absent; only in apes, especially in anthropoids, do the spinous processes of some cervical vertebrae sometimes bifurcate. The records in the literature vary largely on this point; from them and from his own investigation LE DOUBLE [1]) concluded that only the epistropheus in the Chimpanzee possesses as a rule a bifid spine.

So with regard to the form of the processus spinosi of the cervical vertebrae man differs considerably from the other mammals. It is intelligible, therefore, that the question has often been considered what may be the cause of this deviating structure in man. According to the hypothesis, which has well-nigh become a dogma, that man has descended from more ape-like ancestors, this question has ever been formulated as follows: How did, in the phylogeny of Man, the bifurcated spinous processes in recent man originate from the unsplit cervical spines of his ancestors.

In his Memoir on the influence of the assumption of the erect attitude on the human frame RUGE [2]) has expressed the opinion that also the characteristic form of the cervical spines in man is due to his erect stature. RUGE writes: (l.c. p. 10): "Auch die am Schädel festgeheftete Muskulatur beeinflusst am Rumpfe ihre Ausgangpunkte. Als augenfällige Zeichen hierfür sind die gespaltenen Dornen des 2. bis 6. Halswirbels zu nennen. Sie dienen unter anderem den selbständigen Muskeln des Nackens beiderseitig zum Ursprung und haben sich zugleich mit ihnen ausgebildet." VON EGGELING [3]) has endeavoured to furnish further evidence for RUGE's hypothesis. He examined the cervical muscles of many monkeys and prosimiae, studied the form of the spinous processes of the cervical vertebrae of the animals he dissected, and subsequently tried, by comparison with

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1) DOUBLE, A. F. LE, Traité des variations de la colonne vertébrale de l'homme. Paris. 1912.

2) RUGE, G., Die Körperformen des Menschen in ihrer gegenseitigen Abhängigkeit und ihrem Bedingtsein durch den aufrechten Gang. Leipzig. 1918.

3) EGGELING, H. VON, Die Gabelung der Halswirbeldornen und ihre Ursachen. Anat. Anz. Bd. 55. 1922. Idem, Die Halswirbeldornen und deren Muskeln bei Halbaffen. Ibidem.

the conditions in man, to ascertain whether there is any relation between the form of the spinous processes and the development of the muscles that take origin from them or are inserted in them. Three muscles are attached to the spinous processes: the musculi spinales, interspinales and semispinalis cervicis. The first-named muscle is so variable even in man that we need not take account of it. The musculi interspinales and the m. semispinalis, however, are muscles that are well-developed in man only in the cervical portion of the vertebral column, and consequently are characteristic of this region. They are much less pronounced in monkeys, where they are even vaguely differentiated from the musculature composing the deep muscles of the back. It will be seen then that the strong development in man of the muscles just mentioned, concurs with the terminal bifurcation of his cervical spines. VON EGGELING considers the strong development of the muscles in man to be owing to his having assumed the erect attitude, the muscles now having to sustain the head and to perform the movements of the head and the neck which had become more mobile in consequence of the erect attitude. These muscles having become stronger during the phylogeny of man should by their traction have caused the formation of the paired processes at the end of the cervical spines.

In this paper I shall abstain from criticizing VON EGGELING's work, referring for my critique and for details of my own investigation to my extensive treatise that will appear in the "Zeitschr. für Anatomie und Entwickelungsgeschichte". Nevertheless I wish to raise an objection to two essential points in the exposition given by RUGE and VON EGGELING.

First of all, in studying any problem in human phylogeny it is not right to start from the hypothesis that man descends from more ape-like ancestors. Facts carefully studied and discussed by BOLK, who based on them his fetalisation-theory, induce me to believe, as I have set forth in several papers, that in many respects the ancestors of man cannot be imagined more ape-like than recent man. In my opinion, therefore, for every problem concerning the descent of man we should try to find a solution by studying the available facts without vitiating our results by any preconceived idea.

My second objection to the exposition of RUGE and VON EGGELING is that they have endeavoured to establish the cause of the special form of the cervical spines in man, without ascertaining beforehand how the bifurcated spinous processes have sprung from the nonbifurcated processes. We gather from their reasoning that they consider it self-evident that the paired terminal processes are new osseous formations, new projections which they suppose to have been developed under the influence of muscular traction. They omitted to afford any evidence for this assertion. In order to obtain a better insight into the cause of the terminal bifurcation in man it was necessary to make a preliminary inquiry into the ontogenetic mode of development of the bifid spines of the cervical vertebrae in man, as well as of the unsplit processus spinosi in the other regions of the spinal column in man and in other mammals.

In the following pages I shall give a brief account of the results of this investigation beginning with a diagram of the modes of development of the cartilaginous processus spinosi.

Each vertebra develops from four cartilaginous centres. Two of them arise in the vertebral body and one in the basal part of each of the neural processes. The two cartilaginous centres in the vertebral body are soon fused. The cartilaginous processus neurales develop dorsad, and gradually enclose the spinal cord as semi-arches. Ultimately they unite dorsally to the spinal cord. The development of the processus spinosus may take place in various ways : we distinguish six types of development, as represented schematically in fig. 1.

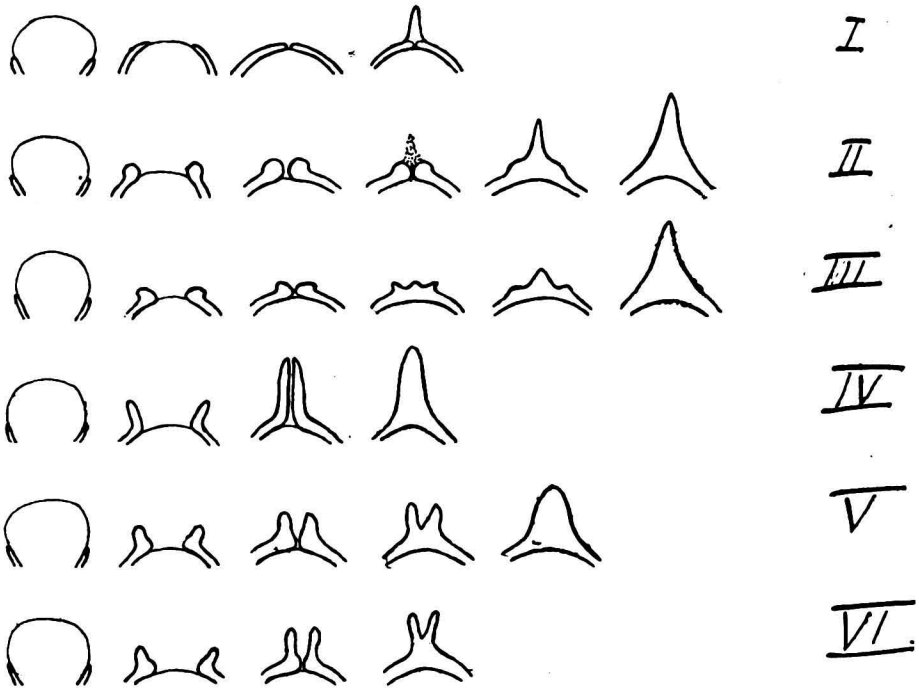

Fig. 1

Diagram of the different modes of development of the cartilaginous spinous processes in mammals.

1. In the first type the non-thickened ends of the semi-arches come in contact with each other. At the junction an unpaired outgrowth develops representing the anlage of the spinous process. This mode of growth occurs among Marsupials (Dasyurus, Didelphys).

2. While the vertebral canal is still wide open there appear at the semi-arches latero-dorsally directed terminal buds. When the spinal cord has been completely enclosed by the semi-arches, the thickened ends of the semi-arches meet in the dorsal median line. Then an unpaired median cartilaginous mass develops dorsally on the point of junction. In the typical

cases the growth of this median cartilaginous process is preceded by the formation of an unpaired, median precartilaginous outgrowth. A small part of the base of the cartilaginous processus spinosus is thus formed by the paired terminal protuberances of the semi-arches. In the beginning these buds can be recognized by a slight bulging, later on they are completely assimilated with the median process. This mode of development of the cartilaginous spines is very common among mammals. Typical cases, in which initially a precartilaginous median spine develops between and on the thickened ends of the semi-arches, I encountered in the thoracic vertebrae of man and the superior thoracic vertebrae of Tarsius. I detected a fine intermediate form at the 8th thoracic vertebra in a fetus of Sciurus vulgaris, 30 mm. in length. In this intermediate form there occur two cartilaginous terminal protuberances on the semi-arches, between and on which protuberances an unpaired mesenchymatous spinal anlage is found.

3. This developmental type differs from the preceding in that the terminal protuberances of the semi-arches are directed more laterad, and in that the median rudiment of the process is not very strong at first, so that a transient dorsal eminence is originated that is provided with three apices. Afterwards the median point gets more developed, in fact it constitutes nearly the whole process; the end-knobs of the semi-arches are merged into the base. This mode of development I could observe at the inferior dorsal vertebrae of Tarsius.

4. In this type the end knobs of the semi-arches are markedly prolonged. When the semi-arches come together dorsally to the spinal cord, their projections also adjoin, thus forming the paired rudiment of the whole spinous process; afterwards the halves coalesce over the whole length. This mode of development I observed very beautifully in the superior thoracic vertebrae of the sheep; probably it also occurs at some vertebrae of some other mammals (Talpa, Sciurus).

5. Just as in the preceding type long processes appear at the ends of the semi-arches, representing the paired rudiment of the spinous processes. The coalescence of the two halves takes place only in the basal part at first, so that for a time there exists a projection that is split at the end. Only after some time does the fusion become complete. The processus spinosus of the epistropheus of the rabbit, the rat, and the squirrel develops in this way; it would seem to me that probably the split process I found at the epistropheus of a Didelphys auritus (20 mm. crown—rump length) also belongs to this group.

6. Here the growth occurs initially in the same way as in the preceding type. The difference, however, is that the two processes, each of which represents the anlage of half a spine, only coalesce in their basal parts not transiently, as in the former type, but permanently.

The order in which the 6 developmental types have been described is not arbitrary: on the contrary they have been arranged so as to present progression in the intensity of two developmental changes. Generally

speaking we can say that a spinous processus is built up of an unpaired median rudiment growing out from the cartilaginous mass formed by the coalescence of the semi-arches, and a paired lateral rudiment : the protuberances or projections at the extremities of the semi-arches. In the first developmental type the spine develops from a median rudiment only, in the second a small paired rudiment shows itself which, as soon as the semi-arches come into contact, is overlapped by the median rudiment. With the third mode of growth the lateral rudiment persists a little longer, so that during a certain interval of time there exists a stage with three knobs. In the fourth type the lateral rudiment predominates : the median cartilaginous mass serves only to unite the semi-spines formed from the paired rudiment, but does not develop into an independent median rudiment of a process. In the fifth and the sixth type the median cartilaginous mass does not extend transiently, resp. permanently as far as the end of the semi-spines that have sprung from the lateral rudiment.

The extension of the median cartilaginous mass and its significance as median rudiment of the spinous processes decreases from the first to the sixth developmental type, whereas the significance of the paired, lateral rudiment rises.

Now the question arises, which of these developmental types is phylogenetically the most primitive. In order to find a plausible answer to this question I examined the way in which the spinous processes in lower vertebrates develop. Some Amphibians examined appeared to possess only a median unpaired rudiment ; the paired lateral rudiment is lacking. Among the Reptiles I detected only in a few cases a slight, paired, lateral rudiment, arising only very late in the ontogeny and contributing little to the formation of the spinous process. It is presumable, therefore, that the developmental type sub 1 is to be considered also for the mammals as the most primitive mode of development of the spinous processes. During the phylogeny of different mammals changes have occurred, consisting in the progression of the paired lateral rudiment and a regression of the median rudiment. In this respect the various mammalia have deviated to a greater or lesser extent from the primitive mode of development : differences are even noticeable at the different regions of the spinal column of one and the same animal. The developmental type sub 6 may be considered as the most progressive (= non-primitive) type.

It appears then that in the phylogeny of mammals, in which spinous processes develop in one of the modes described sub 4, 5 or 6, a regression of the median rudiment has taken place. In contradiction to the principle laid down in the biogenetic law this regression is not repeated in the ontogenetic development ; the new condition is brought about because the median rudiment no longer develops as completely as is the case with the primitive mode of development. We see, then, that phylogenetic regression takes place because an ontogenetic developmental process is arrested before it has reached completion. In this connection it is remarkable that with

a less intense departure from the primitive mode of development we do not yet find an arrest but only a retardation of the ontogenetic process of growth; thus with the 3rd developmental type the median rudiment no more prevails directly over the paired lateral rudiment; thus in the 5th type only transitorily a spine is formed, which is split at the end. It is clear especially in the transition from the 5th to the 6th type that the changes in the ontogenetic development which bring about the phylogenetic regression correspond to the principle expressed in BOLK's Fetalization.

On the whole a certain relation is to be noted between the part played by the lateral, paired rudiment and the median non-paired rudiment in the formation of the spinous processes: when the median rudiment gets strongly developed the paired rudiment is of little importance and conversely. Therefore, if we wish to solve the problem: what etiological factor is answerable for the appearance among mammals of modes of development that depart from the primitive one, we shall first have to answer the question whether the regression of the median rudiment or the formation and strong development of the lateral rudiment is the primary change. The latter supposition can hardly be called in question, since the paired rudiment reveals itself already as processes at the extremities of the semi-arches long before the spinal cord is enclosed completely by the semi-arches, that is long before the median rudiment can manifest itself in the ontogeny. Undoubtedly the primary deviation of the phylogenetically primitive mode of development consists in the appearance during the ontogeny of protuberances at the end of the semi-arches. The more intense the outgrowth of these protuberances into processes constituting the paired rudiment of the processus spinosi, the less will be the part played by the median rudiment in the formation of the spinous processes. When half a spine totally arises from the paired rudiment the median rudiment no longer develops into a separate apex; the median cartilaginous mass does not extend farther than the extremities of the semi-spines (type 4). So far the regression of the unpaired rudiment is to be considered as the immediate consequence of the strong development of the lateral paired rudiment. Apparently the regression of the median rudiment, once begun, can go farther independently; from which ensue the 5th and the 6th types, where, transiently or persistently, the median cartilaginous mass no more extends as far as the extremity of the semi-spines.

The occurrence of the paired lateral spinous process which initiates the new modes of development, depends on a change in the relation of the deep dorsal muscles to the spinous processes. In Amphibians the deep dorsal musculature is still arranged segmentally; the muscle-masses stretch from myoseptum to myoseptum, the processus spinosi are so to say supporting elements of the myosepta. In Reptiles and mammals the conditions are different; the deep dorsal muscles are no longer inserted in the myosepta but in the skeleton of the vertebral column itself, consequently also in the spinous processes. This change shows itself

already in the ontogeny in a typical way. While in Amphibians the dorsal musculature develops quite independently from the skeleton and has already reached the dorsal median line in a stage, in which the cartilage has only been formed in the basal part of the semi-arches, we see that in Reptiles and in mammals the dorso-median extension of the musculature goes on pari passu with the growth of the semi-arches round the spinal cord. As soon as the first rudiment of the cartilaginous neural laminae appears, the musculature attaches itself to the semi-arches, above all to their extremities, and thus follows the dorsal extension of the spines. This relation between musculature and extremities of the spines, which appears already early in the ontogeny, gives rise to the development of the terminal protuberances in which the muscles are inserted. The intense development of these protuberances, which represent the paired rudiment of the spinous process, induces regression of the median rudiment. As stated before, this regression must be considered in the beginning as a direct result from the intense development of the lateral rudiment; eventually it can proceed independently; it culminates in the persistence of a bifid neural spine.

My material for the study of the development of the osseus processus spinosi was not quite sufficient. Still, from my observations I may deduce that developmental types can be distinguished that are, in principle, similar to those of the cartilaginous processes. Special mention should be made of the fact that I could establish at some cervical vertebrae, especially at the epistropheus, of some young anthropoids, that the spinous process consists originally of a paired osseous mass. The unpaired condition of the spines in the adult sometimes results from complete coalescence of the halves, sometimes from the development of an unpaired rudiment between and on the previously formed paired, osseous mass. Also the origin of the *osseus* cervical spines in man which are permanently split at the end, must therefore be ascribed to fetalization.

It should be pointed out at the conclusion of this exposition that on the ground of the described mode of development variations at the cervical spines in man may be expected in two directions.

It may very well be possible that as an atavistic phenomenon the regression of the median mass of cartilage (resp. bone) is not so strong as usual, so that the semi-spines coalesce up to their extremities. Then the unsplit spinous processes appear, which occur very frequently from the 3rd up to and including the 6th cervical process in the lower races, and are not rare also with Europeans.

In the European, however, an unsplit spinous process at the epistropheus is of rare occurrence; among 782 epistrophei of Dutchmen I detected this variation only in 3 cases.

Neither does it appear improbable that the regression of the median mass of bone is stronger than usual, so that the semi-spines do not unite at all and the split reaches as far as the vertebral canal. Among the 782 cases just-mentioned I found this variation in 5 cases. I doubt, however, whether

these are really cases of pure regression of the median rudiment, since with all of them the spinous processes were only little developed, so that perhaps a pathological inhibition of growth and coalescence of the halves may come into play here. I did find, however, this variation 5 times at the first vertebra of the sacrum in man where well developed semi-spines were separated as far as the sacral canal by a narrow slit.

Finally I wish to consider the question, whether RUGE and VON EGGELING are right in assuming a correlation between the terminal bifurcation of the cervical spines in man and the erect attitude of man. As has been set forth in the foregoing the bifurcation results from regression of the median rudiment of a spine which regression has taken place in a different degree among the mammals, and which culminated at the cervical vertebrae of man. Consequently the assumption of the erect attitude cannot possibly be regarded as the real cause of the bifurcation. The question may be propounded, however, whether the erect attitude might have promoted the considerable regression of the median rudiment which at the cervical vertebrae of man has taken place in so high a degree. It seems to me superfluous indeed to seek for a cause why this regression is stronger in man than in all other mammals, since in many other respects man deviates farther than all other mammals from the assumed primitive condition or mode of development. On the other hand there is no repudiating the possibility that the erect attitude has promoted the said regression. The bifid spine is no doubt a less strong attachment for muscles and ligaments than a spine whose halves have grown together up till the end ; now it is just with the erect attitude of man that the traction exercised upon the cervical spines by the muscles and especially by the ligaments is less intense than in the quadrupeds. For in man the head balances more or less on the vertebral column, whereas in the quadrupeds the head must be carried by muscles and ligaments, above all by the ligamentum nuchae.