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Article XXIX.— A NOTE ON THE LUMBAR VERTEBRÆ OF *SCUTISOREX* THOMAS.[1]

BY H. VON W. SCHULTE.

THE spine of *Scutisorex* is remarkable among insectivores for the extreme lengthening of its lumbar segment and perhaps unique among mammals for the peculiar modification of these vertebræ which are transformed at the sides into a series of tooth-like processes closely interlocking, but never synostosed, with those of adjacent vertebræ. The characters of these vertebræ have been described in detail by Dr. J. A. Allen,[2] and the reader is referred to his text and excellent illustrations for anatomical information which falls outside the scope of this note. It is a pleasure to express my obligations to Dr. Allen who has very kindly permitted me to make use of his paper while still in manuscript.

While these modifications are characteristic of the lumbar spine and attain their maximum at the midlumbar vertebra, the sixth, they are not limited to this region but encroach upon the thorax where their prodromata can be recognized as far rostrad as the sixth or fifth vertebra. This limit corresponds to the summit of the thoracic kyphosis which is conspicuous in this genus as in other insectivores, and depends, as is usual, on the shape of the intervertebral disks rather than upon that of the centra which are, if anything, rather thicker ventrad than dorsad in the thorax. The result is that the lower thoracic and lumbar vertebræ are coapted into a rigid arch which is qualified to supply a firm support to the more flexible upper thoracic and cervical regions. That this pronounced hump of the dorsal region is not due to distortion and is not confined to *Scutisorex* is shown in the accompanying skiagraphs (Plates LXXXIX and XC) where it is seen to be as pronounced in the *Crocidura* which was preserved intact and in normal position as in the wet specimen of *Scutisorex*. Such a mechanism might conceivably subserve the well-being of the beast in one of two ways: either in giving a fulcrum for rather free and forcible movements of the head, and that such occur may be surmised from the high spine of the second and the long one of the last cervical vertebra (Allen, fig. 7); or by affording protection against crushing of the trunk by a force acting from above,

[1] Scientific Results of the American Museum of Natural History Congo Expedition. Mammalogy, No. 4.

[2] Allen, J. A. The skeletal characters of *Scutisorex* Thomas. Bull. Amer. Mus. Nat. Hist. XXXVII, pp. 769–783, pls. LXXXIX–XCII, 1917. The citations of figures in my text refer to this paper.

which the animal is known to be able to sustain without injury to a highly remarkable degree. Mr. Herbert Lang states that natives exhibit this peculiarity of the animal by standing upon it, and has seen it run off apparently none the worse for thus sustaining the weight of a man. It is important to note, however, that the same observer was unable to find in the natural environment or habits of this shrew anything that throws light upon the extraordinary development of its spinal column.

From these preliminary considerations we may turn to the mechanism involved, and here the character of the articulations especially between the zygapophyses demands attention. These are modified in the lumbar region in a manner to preclude rotation and seemingly also lateral bending while permitting flexion and extension. The postzygapophyses are flatly convex from side to side and look ventrad and but slightly mesad. They are received in depressions bordered by well developed lips and it is these lips which interfere with the transverse gliding of the surfaces incident to rotation. In the lower thorax the lips subside but it is precisely here that another contrivance limiting rotation comes into play (Allen, figs. 4 and 5). The spines of the last three thoracic vertebræ are bifid, and each receives the spine of the next following vertebra between its points. The spine of the ninth is similarly modified but is too short to reach that of the tenth, and here rotation in the dried skeleton first becomes possible while it is excluded between the tenth and eleventh thoracic vertebræ and thence caudad. In connection with these bifid spines it is interesting to note a row of small spicular processes of the neural arch immediately mesial to the postzygapophyses in the caudal portion of the lumbar series, which rostrad converge and approach the spines. It is their union with those processes which in the lower thorax gives these elements their bifid character.[1]

A provision against extension, not otherwise limited, exists in the spines of the lumbar vertebræ. These are subrectangular, of moderate elevation attaining a maximum at the middle of the series, and so expanded sagitally that they are all but in contact, and actually so when the vertebræ are bent dorsad thus affording a bony obstacle to movement in this direction (Allen, fig. 7).

Thus the lumbar spine is deprived of mobility in the sense of extension and rotation by slight modifications of its normal processes. It remains to consider the highly peculiar changes that have affected the lateral regions of the vertebræ. These are initiated in the middle of the thorax by the

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[1] In these provisions for limiting rotation the spine of *Scutisorex* differs from that of *Crocidura* which has the usual simple zygapophyses and spinous processes.

appearance of conical tubercles on the margins of the transverse processes. The sixth vertebra has them only on its caudal margin, from the seventh caudad they beset both margins of the transverse process and increase rapidly in number and extent, reaching ventrad continuously as far as the facette for the capitulum of the rib and when this makes defect taking its place and encroaching though only to a slight degree upon the centra. These last in general bear but one short spicule on each side at the junction with the pedicle and even this is lacking upon the last three lumbar vertebræ which, however, are marked by a faint median ridge; on the other hand, the involvement is at its maximum in the 2d–5th lumbar, where the fronts of the centra are tuberculate and their margins crenulated. Further the mass of spicules projects ventrad in the lumbar series, most markedly at its middle so that this region of the vertebral column is transformed into an osseous gutter open ventrad (Allen, figs. 4–7).

A consequence of the modification of the side of the vertebræ is a displacement of the intervertebral foramina, which are displaced ventrad and dorsad and appear somewhat as do the sacral foramina. The ventral ones are formed largely at the expense of the rostral vertebra of each pair and are situated between the spicule arising from the body and the lateral mass of each vertebra. To these orifices a faint furrow may be followed from the vertebral canal on the caudal surface of each vertebra. These foramina may become reduced in size by coalescence of their bounding spicules; this is the case of those of the sixth, seventh and eighth pairs in the spine I have examined. In these the foramen is included wholly in the more rostral vertebra and is so minute that a reduction in size of the ventral division of the corresponding nerve must be inferred. The dorsal foramina are represented by small orifices lateral to the postzygapophyses, between them and the most mesial spicule of the lateral mass. They likewise are continued to the vertebral canal by shallow grooves on the caudal surfaces of the vertebræ.

The lateral mass of each vertebra consists of a plate of dorsoventral orientation, thickly and irregularly beset on both its rostral and caudal surfaces with slender conical processes or spicules of bone. These consist of a row at the periphery and in the vertebræ of largest size a second row smaller, often mere tubercles, between them and the vertebral canal (Allen, figs. 4–7). Those on the caudal surface are in general slightly larger. This disproportion permits of slight movement, flexion or lateral bending, between adjacent vertebræ notwithstanding the intimate interlocking of the spicules of successive vertebræ.

The question then arises, what elements of the vertebræ are involved in this spicular transformation? The condition of the lower thoracic vertebræ makes it clear that the transverse processes and pedicles are, but the great increase of the mass in the lumbar region requires additional explanation. It will be remembered that the capitular facette in the thorax forms the mesial limit of the change. Further caudad the spicules occupy this region also. It would seem therefore that the ankylosed costal element in the lumbar region becomes transformed into spicules. This deduction is strengthened by the position of the nervous foramina and by the contours of the rostral and caudal surfaces of the bones which are curiously like sacral vertebræ. Not only has the costo-transverse space been filled up as usual, but the costal process has expanded laterad and ventrad quite apart from its secondary equipment with spicules. The ventral tips of these modified ribs form the edges of the gutter which characterizes this portion of the spine.

These lumbar vertebræ have therefore undergone a change in general form such as is usual only in the sacral segment. To this as a mere formal statement of the approximation in shape of the lumbar costal element to that of the sacral series there can be no serious objection; but are we warranted in taking these vertebræ to be examples of actual sacralization? In other words, can the form of the costal element, abstraction made of its spicules, be accounted for together with the lengthening of the lumbar series numerically by a backward shift of the pelvis *en masse* along the spine? Some support may be gained for such an assumption in the variations within a species of the level of the first sacral vertebra. In man, for example, the first sacral may be the 24th or the 26th instead of as is usual the 25th of the series. Further, transitional vertebræ having the character of a sacral on one side, of a lumbar on the other, are among the not infrequent variations of the human spine. By way of historical explanation it has been shown that there is a numerical shortening of the spine among primates with the assumption of the upright position, a shortening which from a mechanical standpoint is obviously advantageous. For a time it was believed that this abbreviation of the spinal column was recapitulated in the development of the individual by a movement forward of the sacrum along the spine after the skeletal elements involved had been laid down in the membrane.[1] But this has been found erroneous by subsequent observers [2] and there are no grounds for holding that the number of presacral vertebræ are diminished during development. We can therefore accept

[1] Rosenberg, E. Ueber die Entwickelung der Wirbelsäule und das Centrale carpi des Menschen. Morph. Jahrb., Bd. I, 1876.

[2] Holl, M. Ueber die richtige Deutung der Querfortsätze der Lendenwirbel und die Entwickelung der Wirbelsäule des Menschen. Sitzungsb. d. K. Akad. d. Wiss. Math.-Naturwiss. Klass. Wien, Bd. 85, 1882. Paterson, A. M. The human sacrum. Sci. Trans. Royal Soc. Dublin, Vol. 5, 1893. Bardeen, C. R. Studies of the development of the human skeleton. Am. Jour. Anat., Vol. 4, 1905.

a shift of the pelvis only in a phyletic sense as revealed by discrepancies in the number of dorso-lumbar vertebræ among related species. Such differences are pronounced in the dorso-lumbar vertebræ of insectivores, their number ranging from 13 in *Myogale* and *Talpa* (Flower) to 21 in *Crocidura* (Allen), so that the first lumbar vertebra varies from the 21st of the total series in the former to the 29th in the latter. *Scutisorex* represents the upper limit of variation in this respect, having 14 thoracic and 11 lumbar vertebræ (Allen); the first sacral is accordingly the 33d of the vertebral series. This numerical lengthening of the presacral spine can hardly be accounted for otherwise than by a caudal shifting of the pelvis in the evolution of the long spined genera. But this granted, there is no evidence that such additional lumbar vertebræ ever retain any trace of their previous sacralization and even were the possibility admitted for purposes of argument, the assumption would explain too much in the case under consideration for the whole lumbar segment is similarly modified.

If then we cannot associate the unusual form of the costal element of the lumbar vertebræ with an ancestral more advanced position of the pelvis, we are in no better case if we attempt to explain this peculiarity as anticipatory of a forward shifting of the pelvis and for the same reasons. The relation of pelvis to spine is definitive from its first appearance in the embryo and the number of vertebræ involved is far in excess of any possible advance of the pelvis.

As there is no known developmental process, to excess or deficiency in which variation in the position of the pelvis may be attributed, we arrive at the conclusion that germinal factors are the presumptive cause of differences in the number of presacral vertebræ, whether in this case of *Scutisorex* a single mutation be operative or a series alike in direction, constituting an orthogenetic process and affecting at the same time the number of presacral vertebræ and the form of the costal elements in the lumbar segment.

In *Scutisorex* the widest lumbar vertebra is the 6th, that is, the 28th of the total series (Allen, figs. 4 and 5). If, on account of its breadth, it be taken as representing what was formerly the first sacral, it would follow that the shifting of the pelvis over five vertebræ to the 33d had taken place in a single mutation, for otherwise on the foregoing assumption its successive positions would each have obliterated the traces of its preceding one. What little plausibility there may be in such a line of reasoning is enhanced rather than diminished by the fact that the nearby related *Crocidura* has two species in which there are 27 presacral vertebræ, and the first sacral therefore corresponds numerically to the broad lumbar of *Scutisorex,* the 28th of the vertebral series. But great reserve is necessary in view of the plasticity of bone under the mechanical factors of stress and the broadening of this vertebra in *Scutisorex* may be due to its position in the dorso-lumbar arch.

The difficulty we feel in the presence of such extreme modifications as this lumbar lengthening and spicular formation, is the absence of intermediate forms to connect them with usual conditions obtaining within the order. In a species not otherwise aberrant one or two salient peculiarities are encountered, which in a single organ or system remove it widely from its nearest congeners. Analogous cases are afforded by the stomach of *Semnopithecus*, the tracheal bulla of *Taxidea*,[1] the peculiarly curved trachea of *Bradypus*[2] and the spermaceti-organ of the Physeterinæ. The lack of knowledge of intermediate related forms deprives us of a basis for classifying them as examples of orthogenesis or as the cumulative result of selection of fluctuating variations; and the absence of analogous modifications in members of other orders of similar habitus gives little ground for designating them as adaptations.

Here it may be well to point out that these interlocking spicules are in no way comparable to the accessory articulations of *Xenarthra*, primarily because they are not articular: they are not covered with cartilage but are embedded in the ligamentous tissue which surrounds the spine, as could be ascertained from the wet specimen available for study. That the spicules are the result of ossification in this tissue or in attached tendons is an assumption hard to avoid. They are present largely but not exclusively in the domain of the ilio-costalis. Very unfortunately this muscle was damaged in skinning the animal and thereafter desiccated almost beyond recovery. I do not think, however, that I am mistaken in believing that I traced several of its tendons to the tips of spicules. The ventral gutter of the lumbar region was largely and towards the pelvis completely filled with muscle, the psoas minor, psoas major and quadratus lumborum being all of them well developed and arising by numerous slips from the ventral tip and mesal surface of the costal elements. The plane of the psoas parvus was prolonged rostrad to the diaphragm by a series of muscular slips which arose from the centra at and about their single spicule on each side and coursed obliquely ventrad and caudad to the tip of the costal process of a more caudal vertebra. The groove on each side dorsally between the transverse process and spine was occupied by a feebly developed sacrospinalis, its feebleness bearing out the inference of loss of extension in this segment.

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[1] Huntington, G. S. The eparterial bronchial system of the Mammalia. Annals New York Acad. Sci., Vol. 11, 1898.

[2] Specimen in the Department of Anatomy, Columbia University.

There is then some evidence for the associations of spicule formation with ossification at points of tendon insertion and perhaps of tendons themselves, but there is no marked peculiarity of the musculature [1] ascertainable to explain why it occurs in precisely this genus and no other. Whether the underlying process is biologically allied to changes which in man are referable to disease is perhaps worthy of discussion in view of Larger's [2] recently published theories on this subject. In general the spicules are clean cut and have little but their irregularity to suggest disease. Here and there, however, they are thickened or even fused together — this applies only to adjacent spicules of the same vertebra, there is no synostosis between vertebræ — and in a very few places small bony nodules are present. Elsewhere the skeleton is hardly open to the suspicion of degeneration save perhaps in the rugose surface of the parietals and a small and doubtful calcification of the ligamentum nuchæ which did not show in the skiagraph. The spicules do not closely resemble either in situation or appearance the ossified muscles of dinosaurs described by Dollo [3] and interpreted as evidences of racial degeneration by Larger. Further the spicules of an immature skeleton are not materially different from those of the larger adults and an abnormal process of this sort might perhaps be expected to become more pronounced with age.

Morphologically therefore we must conclude that the peculiarities of the lumbar vertebræ of *Scutisorex* consist in the unusual size of the costal elements and the production from their surfaces and from the amalgamated transverse processes of osseous spicules at the sites of muscular insertions and origins, a process possibly predisposed to by the relative immobility of the spine occasioned by the character of its zygapophyses and spinous processes, and resulting in an arch of great strength able to resist pressure from above and to afford support to vigorous movements of the head and forelimbs. It is not evident that these modifications are useful, but is it not necessary to assume that mutations are always favorable, nor that a useless or even slightly detrimental structure must at once disappear or entail the extinction of the species, for another factor comes into play, the severity of the struggle for existence. While the general process of evolution secures a harmony between organism and environment, luck or cunning may afford a respite to impending fate for a time or in a minority of instances.

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[1] Leche, W. Zur Anatomie der Beckenregion bei Insectivora, mit besonderer Berücksichtigung ihrer morphologischen Beziehungen zu diejenigen anderer Säugethiere. Kongl. Svenska Vetenskaps-Akad. Handl., B. 20, No. 4, Stockholm, 1883.

[2] Larger, R. Théorie de la contre-évolution ou dégénérescence par l'hérédité pathologique. Paris. 1917.

[3] Dollo, L. Note sur les ligaments ossifiés des dinosauriens de Bernissart. Arch. de Biol., T. 7, 1887.

While it seems necessary to ascribe the lengthening of the lumbar spine of *Scutisorex* to mutation, it is not certain that the spicular processes of the vertebræ are so immediately dependent upon changes in the germ-plasm. The extreme plasticity of bone and its sensitiveness to changes in the internal medium as well as to mechanical forces dispose one to see in the osseous system the summation of many factors. Like the blood vessels, determined by mechanical laws, and presenting in their changing patterns an integration of the relative rates of growth of all the parts of the developing organism, so the skeleton in the detailed conformation of its many parts is the resultant of many chemical and physical factors and through their determinants rather than independently may be represented in the chromosomes. In this connection much interest attaches to Larger's insistence upon the resemblances of certain skeletal types among existing and extinct animals to conditions of the human skeleton associated with abnormalities of the ductless glands. It seems not too much to hope that these and other chemical alterations of the internal medium may throw light upon modifications of the bony structures at present inexplicable or referred solely to mechanical causes.

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New names of genera, subgenera, species, and subspecies are printed in **heavy-faced** type, also the main reference in a series of references.