

## ON INTERCALATION OF VERTEBRÆ.<sup>1</sup>

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WHEN we have two nearly related animals, which have a different number of segments, the question arises, What is the origin of this difference? There are two possibilities in regard to the two forms; one may be derived from the other, either by increasing or decreasing the number of segments. In each of these two cases we have different possibilities. In the case of increase, the new segments may either be developed by intercalation, or by division of the original segments, or by addition at the caudal end of the animal. In the case of decrease, we can think of excalation, union, or loss of segments at the caudal end.

Most morphologists are inclined to the opinion of addition or subtraction of segments at the distal end. But there are others, like Jhering and Albrecht, for instance, who adopt intercalation.

Let us now consider some cases. In most of the higher vertebrates we have a sacrum which is united to the vertebral column by sacral ribs: this sacrum establishes a more or less fixed point in the vertebral axis. We distinguish presacral and postsacral, or caudal vertebræ. The increased number of presacral vertebræ may be produced, either by intercalation of new vertebræ, or by movement of the sacrum backwards. The decreased number may be the result of excalation, or of the movement of the sacrum forwards.

Cases of the movement of the sacrum have very often been described, and quite a number have come under my own observation. Positive cases of intercalation, however, have seldom been recorded.

Fürbringer<sup>2</sup> discusses the question in the chapter, "Über die Verschiebung (Wanderung) der Extremitäten," of his great

<sup>1</sup> Paper read before the American Morphological Society, Boston, Dec. 29, 1890.

<sup>2</sup> Fürbringer, Max: *Untersuchungen zur Morphologie und Systematik der Vögel*, Amsterdam, 1888, Vol. II, pp. 972-991.

work on the morphology of birds. He speaks also about the case of intercalation published by Albrecht (in the Bull. Mus. Roy. d'Hist. Nat. de Belgique, II, 1883). Page 975 he says:—

“Für die Verschiebung der Gliedmassen und die dadurch beeinflusste Umbildung der Wirbel sind manche Argumente bisher beigebracht worden, für die Inter- und Excalation habe ich sie dagegen bis jetzt vermisst.

“*Albrecht* statuirt Segmentvermehrungen durch Theilungen der Ursegmente, entscheidet sich somit für die Annahme einer Interpolation in embryonaler Zeit. Nach meinen bisherigen Anschauungen hatte ich gegen die Möglichkeit einer Interpolation nichts einzuwenden, aber bei dem völligen Mangel irgend welches sie stützenden Argumentes konnte ich ihr nur eine rein theoretische oder begriffliche Bedeutung, aber keine Wahrscheinlichkeit zuerkennen.”

Albrecht examined a skeleton of *Python sebae* in the Museum at Brussels. Between the 194th and 197th vertebræ, he found a complex of anchylosed vertebræ: this contained on the right side two vertebral elements, one foramen intervertebrale, and two ribs; on the left side three vertebral elements, two foramina intervertebralia, and three ribs. Albrecht considers the supernumerary vertebra on the left side as intercalated. Fürbringer, on the other hand, is inclined to regard it as the result of some pathological process, which reduced the right half of the vertebra. He says: “Welcher Art und Veranlassung dieser pathologische Process gewesen und wann er stattgefunden, kann ich natürlich nicht entscheiden, halte auch diese Frage für eine nebensächliche; aber die namentlich auf der Dorsalansicht sehr auffallende unregelmässige Schraegstellung des fraglichen Halbwirbels, der Umstand, dass er kein reiner Halbwirbel ist, sondern im Bereiche des Körpers und im Bereiche der Neurapophysen noch Rudimente der rechten Seite darbietet, endlich die anchylosirung der 2<sup>1</sup> Wirbel, während die Wirbelsäule sonst sehr ausgebildete Gelenke besitzt machen es mir unmöglich hier an einen normalen Fall von Wirbelinterpolation zu denken.”

I think I shall be able to show that Albrecht was correct in his interpretation. Already Koken, in writing a review of Albrecht's paper (in one of the numbers of the “*Neues Jahrbuch für Mineralogie*,” which I have not at hand), states that he has

observed similar cases as Albrecht's in *Tropidonotus*. R. Owen<sup>1</sup> has also described a case of the same nature in the skeleton of a *Python tigris*, of which he says: "Anchylosis has occurred between the 148th and 149th vertebræ. The 166th and the 167th vertebræ have been more completely and abnormally blended together, so as to seem but one vertebra on the left side, where that half of the neural arch and spine have completely coalesced, whilst on the right side each vertebra supports its own rib. A similar abnormality occurs between the 184th and 185th vertebræ."

If intercalation takes place at all, we ought to expect traces of it in such forms as show a great increase in the number of vertebræ, for instance, snakes, different groups of lizards, and Plesiosaurs. In looking over such material I have found some additional cases.

In a specimen of *Pelamis bicolor* (No. 763, Yale University Museum) I find the 212th vertebra simple on the left side, double on the right side; it bears one rib on the left, two ribs on the right side. Exactly the same condition I have observed in a cervical of a Plesiosaur, *Cimoliasaurus plicatus*, No. 48,001 of the British Museum, London. One side has one, the other two ribs. Mr. R. Lydekker<sup>2</sup> makes the following remark about this vertebra:—

"The centrum of a small and malformed cervical vertebra, from the Oxford Clay near Oxford. This specimen is immature, and on one side is divided into two portions, each with its distinct costal facet."

I do not doubt at all that in all these cases we have examples of incomplete intercalation; and I am convinced that this intercalation is the result of the division of myotomes, as expressed by Albrecht. The possibility of such intercalation I have expressed already in No. 306 of the "Zoologischer Anzeiger," 1889, where I said: "Ich glaube, dass eine Verschmelzung oder Spaltung von Myomeren auch schon während der Anlage des Embryo möglich ist. Mein Freund A. Böhm in München theilte mir mit, dass er verschiedene Anzeichen von Spaltung von Myomeren beobachtet habe."

<sup>1</sup> Descriptive Catalogue of the Osteological Series contained in the Museum of the Royal College of Surgeons of England, Vol. I, p. 123, London, 1853.

<sup>2</sup> Lydekker, Richard: Catalogue of the Fossil Reptilia and Amphibia in the British Museum, Part II, London, 1889, p. 238.

Of course the direct proof of splitting of myotomes could only be given by the study of the living embryo, which, if possible at all, is exceedingly difficult. If we have the complete segments in the embryo or in the adult animal, we cannot decide whether they consisted originally of a single myotome, or whether they are the result of division. For instance, in the peculiar consolidation of vertebræ in snakes, mentioned by Owen, and also observed by me at different times, we do not know whether this consolidation is the result of real union of two segments, or of partial division of one segment. At least we may adopt one explanation just as well as the other. I am inclined, however, to accept partial division in these cases. A great number of observations is necessary to see in what relations the frequency of such consolidation stands to the increased number of segments; in other words, whether such complexes are more frequent in animals with the number of segments considerably increased, as it appears to-day, than in such which have a relatively small number.

By very careful study and comparison of the structure of the single vertebræ, however, it is sometimes possible to determine whether we have a case of intercalation or not. It is well known that the typical number of the presacral vertebræ in the living Crocodilia is twenty-four; there are two sacrals: the first caudal is peculiar, by being biconvex. In a specimen of *Gavialis gangeticus* I found twenty-five presacral vertebræ.<sup>1</sup> As in all living Crocodiles the first caudal vertebra is biconvex; but in this case it is the twenty-eighth, in the other the twenty-seventh. Is it not evident, therefore, that at some place between the occipital condyle and the first caudal a new vertebra has been inserted? By careful comparison I find that this new vertebra has been intercalated between the ninth and tenth.

A similar case I have observed in *Heloderma*. In this lizard the first caudal vertebra has also a peculiar character. The small rib connected with it is perforated; this perforation is absent in the other vertebræ. By this peculiarity the first caudal vertebra is distinguished from the rest. Four specimens of *Heloderma* show the following condition. In the first speci-

<sup>1</sup> G. Baur: *Anzahl der praesacralen Wirbel der Crocodilia*. Zool. Anz. No. 238, 1886.

men the first caudal is the thirty-sixth (*Heloderma horridum*);<sup>1</sup> in the second, the thirty-seventh (*Heloderma horridum*, observed by me); in the third, the thirty-eighth<sup>2</sup> (*Heloderma suspectum*); in the fourth it is the thirty-ninth (*Heloderma suspectum*, Clark University). We have, therefore, four variations in four specimens. There seems to me very little doubt that this difference in the number of vertebræ is produced by true intercalation.<sup>3</sup>

By these few but characteristic examples I believe to have given positive evidence that intercalation of segments takes place in vertebrates. I do not doubt that further examination of more material will bring out more cases. What is necessary to do, is to examine a great number of specimens of the same and allied species of such forms as show an unusual increase of segments, like the Varanidæ, Scincidæ, Anguidæ, Amphisbænidæ, Snakes, and so on. The embryology of such forms would probably give important evidence, because we may expect to find indication of myomeric division.

*My opinion is that in the increase of the number of segments not only in vertebrates, but also in invertebrates, intercalation has played a much greater rôle than is generally admitted.* At the same time I admit addition of segments at the distal end, as well as occasional *slight* migration of the shoulder girdle and pelvis in both directions. The question is an important one, and I hope that some embryologist may take up the subject for further study.

This question of increase of the number of segments is a very interesting one from the standpoint of the evolutionist. It is evident that intercalation can only take place in the very early life of the embryo, when the myotomes are forming, and that it is absolutely impossible that new segments can be intercalated through any effort and exercise of the animal

<sup>1</sup> Troschel, F. H.: *Über Heloderma horridum*. Wiegmann's Archiv für Naturgeschichte, Jahrgang 19, Vol. I, Berlin, 1853, pp. 294-315. I am indebted to Mr. S. Garman, Cambridge, for looking up this reference for me, the Journal not being at hand.

<sup>2</sup> Shufeldt, R. W.: *Contributions to the Study of Heloderma suspectum*. Proc. Zool. Soc., London, 1890, p. 214 (the peculiar character of the first caudal is not mentioned by Dr. Shufeldt).

<sup>3</sup> Whether this intercalation is produced by division of myotomes, or by addition of myotomes from the beginning, I do not know; both ways are possible. I am convinced that in a great number of cases intercalation takes place by adding new segments in the embryo without division.

during the later period. *The disposition to increase the number must be, therefore, in the germ itself.* The question is then, Is the increase of the number of segments "accidental," and are forms which show this "accidental" increase of segments preserved through natural selection; or is this tendency to increase the number of segments common to all individuals, not appearing accidentally, but rather as the result of a definite stimulus? I can only adopt the latter possibility.

But how is it in this case? Many animals increase the length, that of the neck for instance, not by addition of new segments, but simply by elongating the single segments present. For instance, the Giraffe among mammals, Chelys, Chelodina, Diroschelys, Hydromedusa among the tortoises. How is it that the Plesiosaur elongates its neck by adding new segments, and the Tortoise by stretching the single segments? Here we are before a difficult question. It is clear the long neck of the Giraffe and of some of the Tortoises develops during the evolution of the animal, but this tendency must be potentially in the germ. It is again the tendency to elongate the neck which is impressed on the germ, but in a different way. An interesting case of addition of segments is offered by the Sirenians. The Sirenians are the only mammals, the Cetaceans excepted, which show an increase of phalanges (four instead of three); a fourth phalange is added in some digits at the distal end, but this takes place during the postembryonic life of the animal, the embryo having only three phalanges.

I am not able at present to give any explanation for these phenomena, but I thought it worth while to mention them in this connection.