THE EARLY DEVELOPMENT OF THE VERTEBRAL COLUMN OF THE ALLIGATOR.

GEORGE M. HIGGINS, KNOX COLLEGE

This study upon the early development of the vertebral column in the alligator was made upon the collection of vertebrate embryos in the zoological laboratories of the University of Illinois. Successive stages of young alligators, ranging in length from 6 mm. to 30 mm., were sectioned transversely; and the attempt was made to determine the origin of those mesodermal elements which contribute toward the formation of the vertebra, as well as their subsequent relation to each other in this formation. Reconstructions in wax have been made of the developing vertebra in the caudal, sacral, lumbar and thoracic regions of the various stages; so that careful comparisons could be made within these areas. This preliminary report will concern itself with the earlier differentiation only, and the more complete discussion will follow in a later paper.

In an embryo 6 mm. long, the entire skeletal support rests in the notochord, a fibrous rod-like structure which lies ventral and parallel to the central nervous system. At this stage those cells which comprise the chorda are already migrating toward the periphery, so that a more or less indefinite epitheliomorph layer may now be identified (Fig. 1.) As a result of this migration, large vacuoles have appeared within the chorda, some of which measure fully one-third the diameter of the notochord itself. Immediately external to the epitheliomorph layer is a rather prominent deeply stained notochordal sheath, which, in the alligator, is not differentiated into two layers as is true for the Elasmobranchs and Ichthyopsida in general. In these embryos this sheath is a relatively thin layer, and under a magnification of 700 diameters it presents a fibrous appearance. It would further appear that this notochordal sheath is probably not a product of the tissue external to the chorda; but that it may arise from those cells within the notochord itself, and possibly as a secretion from the epitheliomorph layer.

Those cells, which are potentially scleroblastic and later contribute toward the development of the membranous vertebrae, are derivatives of the median wall of the lateral myotomes, which lie between the spinal cord and the external body wall. Unfortunately, I have been unable to secure any sufficiently early stages which show the migration of these scleroblastic cells; but, following Schauinsland (1906) in his study of the very early stages in the development of the vertebral column of Sphenodon, the Australian lizard, it would appear that all of the cells of the lower half of the medial plate of each myotome are potentially scleroblastic. During the process of the migration these cells come to be arranged into very definite groups which occupy characteristic positions along the notochord and the spinal cord (Fig. 2.)

In the earliest embryo of my series, these groups or masses of scleroblastic cells are definitely located in positions along the dorso-lateral and ventro-lateral margins of the notochord. These groups may be readily recognized by the large size of their constituent cells and likewise of their nuclei, as well as by the deeply staining quality of the cytoplasm. It is quite possible, in this stage, to recognize eight such cell groups within each body segment, all of which are concerned in the development of the definitive membranous vertebra. Of these vertebral elements, four lie upon each side of the notochord, two in the angle between the notochord and the spinal cord and two along the latero-ventral margin of the chorda. (Fig. 3.)

Since the segmental blood vessels, which course upward from the dorsal aorta within the dissepiments between successive somites, afford an excellent means for the identification of the limits of each body segment, it is possible to designate these eight vertebral elements by such terms as characterize their position in the segment. Accordingly, upon that basis, those elements which lie more anterior in each segment may be designated as cranial and those most posterior as caudal. Furthermore that element which is cranial and lies along the upper margin of the notochord may be called a cranineural; while the more ventral one, because of its association with the blood vessels, would be known as a cranihaemal element. On the same basis, then, the more posterior of these elements in each segment would be designated as the caudineural or the caudihaemal depending upon its dorsal or its ventral position. These terms were suggested by Professor J. S. Kingsley, with whom the writer frequently conferred during the investigation. Thus it is evident that each body segment would be characterized by a pair of cranineurals, a pair of cranihaemals, a pair of caudineurals and a pair of caudihaemals. This method of identification is entirely satisfactory, because it not only affords an accurate determination of the position of each element, but it also does away with the use of such terms as pleurocentrum, hypocentrum and arcualia, the homologies of which are so uncertain.

In addition to the segmental blood vessels which mark the limits of body segments, each cranineural and caudineural bears a very definite relation to the nerve roots of the spinal nerve. Passing backward through a segment, the order of sequence in the position of these parts is as follows. Just posterior to the segmental blood vessel is the ventral nerve root; this is followed by the cranineural, the ganglion of the dorsal root, the caudineural, and the next succeeding segmental blood vessel, each in the order indicated. The cranihaemal and the caudihaemal of each segment lie along the ventro-lateral margin of the notochord, but in approximately the same plane as do the corresponding neural elements. (Fig. 3.)

Schauinsland (1906) in his description of the development of the vertebral column of Sphenodon, describes the single sclerotome or mass of scleroblastic cells upon each side of a body segment. Subsequently, by means of sagittal and frontal sections, he was able to demonstrate a transverse cleft in each sclerotome; so that the terms cranial half-sclerotome and caudal half-sclerotome were employed to designate the resulting parts. Unfortunately, in this study, frontal and sagittal sections were not available, and such transverse clefts as Schauinsland describes were not identified in my material.

Immediately following the formation of the eight vertebral elements there occurred a fusion of the two cranial elements upon each side, as well as of the two caudal elements. In each case cells of the cranineurals and caudineurals grow ventrally to meet the cells of the cranihaemals and caudihaemals; so that as a result four vertebral components may now be identified within each segment. Partially following the terminology of Schauinsland, the term cranial part-sclerotome is employed to designate the fused cranineural and cranihaemal component; while the term caudal part-sclerotome likewise identifies the fused caudineural and caudihaemal component. Since the caudal vertebral component in each case is considerably larger than the cranial, the term part-sclerotome seems more adequate in its designation than the term half-sclerotome of authors.

Following the fusion of the original vertebral elements to form part-sclerotomes, as above described, there occurs a subsequent fusion of these part-sclerotomes to form entire sclerotomes within which the definitive membranous vertebra will later arise. The fusion of these part-sclerotomes is affected as follows. The caudal part-sclerotome, considerably larger than the cranial, extends somewhat dorsalwards, and reaching more posteriorly comes to unite with the smaller cranial part-sclerotome of the next posterior segment. Thus it is evident that entire sclerotomes are formed, not by the fusion of part-sclerotomes within a segment but rather by a fusion of part-sclerotomes of adjacent segments. So that sclerotomes come to alternate in their position with the myotomes from which the trunk musculature is to arise; affecting thereby the alternate relations of vertebrae and muscles in the adult condition. Dorsally these sclerotomes extend to the level of the spinal ganglia, while ventrally each reaches downward a very short distance from the notochord. (Fig. 4.)

In an embryo 7 mm. long, three parts of the above described sclerotome may be identified. The upper more narrow portion, which lies adjacent to the spinal cord, is clearly the first stage in the development of the membranous neural arch. Likewise, the lower or haemal portion is as clearly the beginning of the membranous haemal arch; while the larger intermediate area, a probable derivative of the original cranial element, will contribute largely toward the primary centrum of the vertebra. At this stage, also, a rapid cell proliferation has occurred between the bases of the haemal processes along the ventral surface of the notochord and form a series of hypochordal bars which are to form the lower portions of the primary centra. (Fig. 5.)

It is very evident that the scleroblastic cells comprising the sclerotome are clearly of two kinds. Those cells which compose the areas of the developing neural and haemal arches are spherical and contain very large and deeply stained nuclei; while those of the primary centrum as well as those cells which comprise the hypochordal bar are strikingly oval or spindle-shaped and are more closely applied to each other. As yet the scleroblastic cells do not appear in the area between the notochord and the spinal cord, so that the primary centrum is incomplete in that region. Since the primary centrum in the alligator is formed entirely external to the notochordal sheath, a considerable contrast exists between that condition which maintains within the Elasmobranch fishes and certain other Chordates. In these latter groups, openings occur in the notochordal sheath, through which the scleroblastic cells may enter the chorda and form the primary centrum within it. But in the alligator, at this stage, these centra appear as a series of membranous rings, incomplete dorsally, which lie just external to the notochordal sheath and in the same transverse plane as do the neural and haemal membranous processes. These centra are separated from each other by wide spaces, into which scleroblastic cells will later migrate and which will subsequently be known as the intercentra; so that the notochord presents at this time a very characteristic moniliform appearance.

These sclerotomes, together with the hypochordal bar, constitute the beginning of a membranous vertebra. (Fig. 6.) At first, in all the regions of the body, the lower or haemal processes lie in approximately the same transverse plane as do the neural processes; but in the sacral and the caudal regions, it would appear, however, as though the haemal process had shifted toward the anterior margin of the segment. As a result, in these posterior regions, this ventral part of the sclerotome lies just posterior to the segmental blood vessel and adjacent to the ventral root of the spinal nerve. In this stage these haemal processes are more elongate in the tail where they extend ventrally to a position lateral to the caudal artery and vein. In the region of the trunk and thorax, however, they are greatly reduced and appear only as mere rudiments; while in the neck, there is no evidence whatsoever of any haemal process.

In an embryo 10 mm. long, a further migration of the constituent cells of the notochord has taken place, so that a clearly defined epitheliomorph layer is produced. As a result the vacuoles are relatively larger than before. The notochordal sheath is relatively thicker than before, and under higher magnification its fibrous composition is more evident.

A marked increase in the relative thickness of the primary centrum is apparent at this stage. Differentiation of the cells has resulted in the formation of two distinct layers, the inner one of which lies just external to the notochordal sheath. This inner layer is composed of the long spindle-shaped cells which characterized the earlier primary centrum, and it extends entirely around the chorda connecting the bases of the neural arch processes beneath the spinal cord. The outer relatively thinner layer is composed of larger spherical scleroblastic cells similar to those of the earlier part-sclerotome; and they are evidently a product of these part-sclerotomes together with additional cells from the original myotomes.

In addition to these primary centra, primary intercentra may now be identified. Cells, which comprise the latter, have apparently arisen from the original sclerotomes, and have migrated anteriorly and posteriorly along the notochord, forming a series of intercentra which alternate with the successive primary centra. These intercentra, which lie opposite the original somatic myotomes, differ from the centra in the absence of the inner layer; but are composed entirely of the larger spherical cells.

By a further proliferation of the cells of the membranous neural arches, the origin of which occurred in the earlier stage, and by a further addition of cells from the myotome, the entire spinal cord is at this 10 mm. stage covered dorsally and laterally by a continuous membranous structure. Openings, of course, occur for the exit of the spinal nerve roots and for the inclusion of the dorsal ganglion within each segment. This structure, although continuous, is much thinner in the intervertebral regions, since the cartilaginous vertebrae are to arise in the position of the original sclerotomes.

The first appearance of a cartilage vertebra may be identified in this same 10 mm. embryo. In the approximate position of the original caudal part-sclerotomes of the trunk region, the cells of the membranous sclerotome have transformed into a procartilage neural arch which rests upon the inner layer of the primary centrum. This procartilage neural arch extends dorsally and slightly posteriorly, and terminates just back of the upper margin of the dorsal ganglion. The lower or haemal arches appear as mere stumps in the trunk region, but in the tail these structures are much longer than before and nearly encircle the caudal blood vessels. However in neither region is there any evidence of a procartilage formation within these lower processes. Nor has such a transformation yet occurred within the primary centrum. So that the vertebral column of a 10 mm. alligator may be said to be composed of a series of independent procartilage neural arch processes which rest upon the membranous primary centrum and lie along the lateral aspect of the spinal cord.

A further consideration of the later development of the column will appear in a subsequent paper.

BIBLIOGRAPHY.

Gotte, A., 1897. Ueber den Wirbelbau bie den Reptilien und einige anderen Wirbelthieren. Zeits. wiss. Zool., 62, 1897.

Hay, O. P., 1897. Structure and mode of development of the vertebral column. Science, IV. 1897.

Howes, G. B., & Swinnerton, H. H., 1901. On the development of the skeleton of the tuatara, Spenodon punctatus. Trans. Zool. Soc. London. 1901.

Schauinsland, H., 1906. Die Entwickelung der Wirbelsaule der Wirbeltiere nebst Rippen und Brustbein. Handb. d. Entwicklungslehre, 3 pt. 2, 1906.

EXPLANATION OF PLATE.

Fig. 1. Cross section of a notochord of an alligator embryo, 6 mm. long.

Fig. 2. Diagrammatic sketch of the myotomes in the trunk region of a 6 mm. embryo, showing the origin of the scleroblastic cells.

Fig. 3. Side view of the notochord and the spinal cord of a young alligator, showing the position and arrangement of the vertebral components.

Fig. 4. A single pair of sclerotomes, which show their position and their relation to the notochord and the spinal cord.

Fig. 5. A ventral view of the notochord, showing the series of hypochordal bars in the trunk region.

Fig. 6. Neural arch and haemal arch formation, and their connection with the hypochordal bar.

cah	caudihaemal	na	neural arch
can	caudineural	ns	notochordal sheath
crh	cranihaemal	s	sclerotome
crn	cranineural	sb	scleroblastic cells
dt	dermatome	sbv	segmental blood vessel
el	epitheliomorph layer	sc	spinal cord
ha	haemal arch	sg	spinal ganglion
hb	hypochordal bar	v	vacuole
mp	muscle plate	vn	ventral nerve root
n	notochord		

PLATE

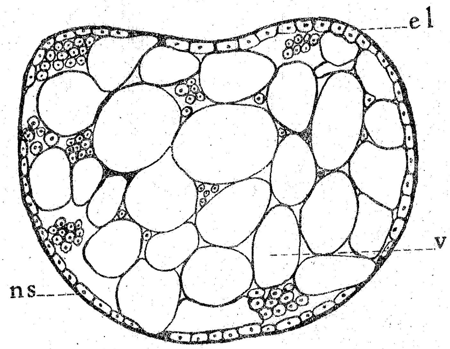

fig 1

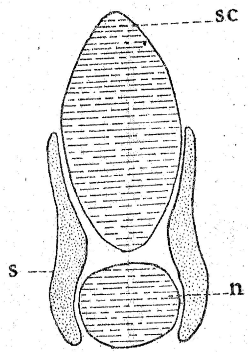

fig 4

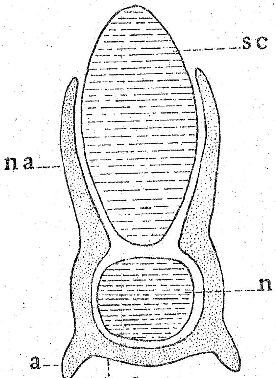

fig 6

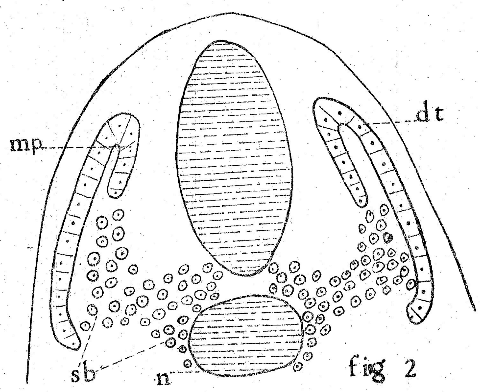

fig 2

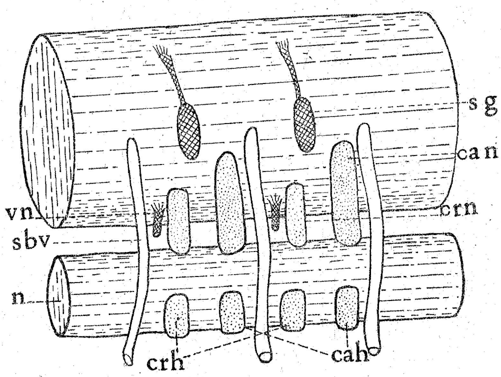

fig 3

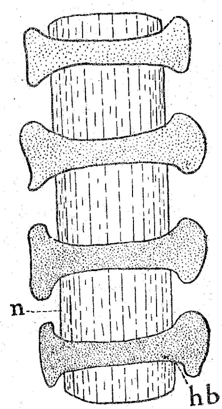

fig 5