VERTEBRATE ZOÖLOGY

BY

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THIS VOLUME IS DEDICATED
TO MY FATHER
ALBERT HENRY NEWMAN.

PREFACE

This volume is intended for use as a text-book in college courses in vertebrate zoölogy such as are required of premedical students and others who have had a course in general zoölogy. The aim of the book is to present those aspects of the subject which are not adequately brought out by laboratory work in comparative anatomy. It is taken for granted that the student who uses this as a text in connection with the lecture and recitational part of a course, shall also pursue a laboratory course in comparative anatomy, using a laboratory manual. It is also believed advisable to use as laboratory references the various text-books on comparative anatomy.

The book is avowedly dynamic in tone, emphasizing the physiological, developmental, phylogenetic, and ecological aspects of vertebrates. Structural features must of course be dealt with extensively, but purely anatomical details are as a rule subordinated to physiologic and evolutionary considerations.

The vertebrates are, moreover, viewed not merely as a group of animals belonging to the present, but, *historically*, as a very ancient assemblage of related forms, that arose from simple beginnings many millions of years ago and have passed through many vicissitudes involved in the mighty world changes of ancient times. Hence more than the usual attention is given to earlier chapters in the ancestral history of the vertebrate classes, chapters that are often of more dramatic interest than those of the present and that give to the student a new conception of the significance of modern end-products of evolution which, in themselves, are often relatively unattractive and devoid of interest.

The writer has for some years been much impressed with the far-reaching applicability to problems of animal morphology, of the *axial gradient* conception of his colleague, Professor Child, and one of the features of the present book is the attempt to interpret vertebrate structures in terms of this conception. In some cases it is probable that the theory has been stretched beyond the limits its author would consider justified; hence the present writer takes entire responsibility for the applications of Child's theory brought out in this volume.

The axial gradient conceptions have appeared to the writer to be strictly in accord with the principles of racial senescence as presented by H. F. Osborn and R. S. Lull in their recent volumes on evolution. The present volume has much to say about *adaptive radiation* and the various degenerative and senescent conditions so common among vertebrates. The writer has freely made use of the material found in Osborn's and in Lull's books. Many figures have been borrowed from both authors, for which the writer is deeply indebted.

Much of the data used has been taken from the several volumes on vertebrates of the Cambridge Natural History, and from the various comparative anatomies such as those of Wiedersheim, of Kingsley, and of Wilder. Kellicott's " Chordate Embryology " has been found excellent for much of the embryological data. A list of about a hundred references to which the writer has had access is presented in an appendix.

The illustrations have been borrowed to a considerable extent from Macmillan Company publications, but the great majority of the figures have been redrawn by Mr. Kenji Toda to whom I herewith express my hearty thanks. Many of the figures are made up of several related illustrations arranged in such fashion that they readily may be put into chart form. In our own laboratory we are already using a considerable proportion of these compound figures as charts. The sources of these redrawn figures are various and the author wishes to acknowledge with thanks the courtesy of those who have permitted their originals to be thus modified and used. The greatest care has been taken properly to acknowledge the source of each borrowed illustration. If in any case the figure has been incorrectly attributed to an author, information regarding the error will be gratefully received.

The author is not unaware of the shortcomings of the present book. Some critics will doubtless feel that much valuable, and to their minds necessary, data has been omitted. Others will probably believe that much that has been included, especially in connection with the notes on the natural history of certain types, might better have been omitted. But the selection of what to present and what to omit has been carefully canvassed and what appears to be a workable compromise has been decided upon. The teacher may readily omit what he feels to be superfluous, and will be glad to supply the data that he feels should be included.

Doubtless, errors of various kinds have crept into the text in spite of our scrupulous efforts to avoid them. Although the writer has been indebted to several competent readers of his manuscript, he holds himself entirely responsible for the book with all of its defects and whatever virtues it may have. He will be grateful for criticism and correction on the part of his readers.

H. H. NEWMAN.

Chicago, Ill.
May 1, 1919.

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CHAPTER I

PRINCIPLES OF VERTEBRATE MORPHOLOGY

Definition.—The vertebrates may be defined as animals having:—pronounced antero-posterior, dorso-ventral, and bilateral axes; internal metameric segmentation, especially of the mesoblast; a central nervous system dorsal in position and tubular in structure, with a well-defined central canal or neurocoel; a well-defined head, characterized by highly specialized sense organs and by a concentration of nervous tissue into a complex brain; the alimentary tract opening by anterior mouth and posterior anus, and provided with paired pharyngeal clefts; a notochord derived from the primitive endoderm and situated between the central nervous system and the alimentary tract; an open cœlom, at first segmented, but later the segmental cœlomic cavities unite to form the large pericardial, peritoneal, and, in the mammals, thoracic cavities; a closed circulatory system quite distinct from the cœlom; a post-anal prolongation of the body into a metamerically segmented tail, without cœlomic cavity; usually paired appendages, pectoral and pelvic. These characters and a few others serve to mark off the vertebrates quite sharply from all other groups. Several of the most fundamental of these characteristics must now be discussed. The diagrams on the following page (Fig. 1) illustrate most of these characters.

THE FUNDAMENTAL ARCHITECTURAL PLAN OF VERTEBRATES

The Three Morphological Axes

The Axis of Polarity (Primary Axis).—A typical vertebrate has an elongated form, with head and tail ends clearly defined. An imaginary line drawn from the extreme anterior to the extreme posterior end indicates the primary structural and functional axis of the body, which is designated the *antero-posterior* or *apico-basal* axis. *The or-*

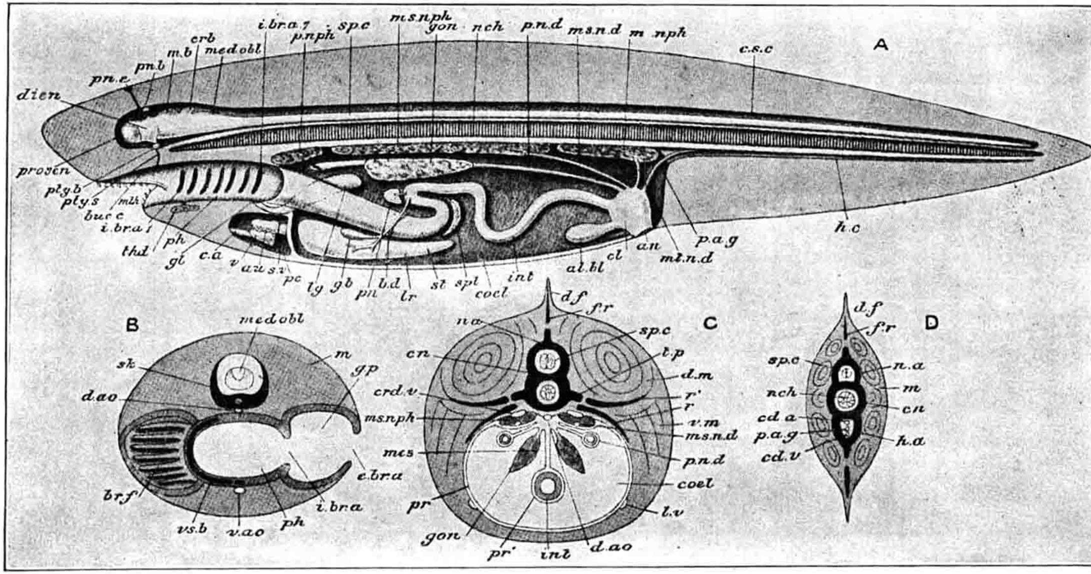

Fig. 1.—A, sagittal section of an ideal craniate, to show among other things the axial organization; B, transverse section of the head; C, of the trunk; D, of the tail; *al. bl*, allantoic bladder; *an*, anus; *au*, auricle; *b. d*, bile-duct; *br. f*, branchial filaments; *buc. c*, buccal cavity; *c. a*, conus arterio; *cd. a*, caudal artery; *cd. v*, caudal vein; *coel*, cœlom; *crd. v*, cardinal vein; *cn*, centrum; *crb*, cerebellum; *c. s. c*, cerebro-spinal cavity; *d. ao*, dorsal aorta; *dien*, diencephalon; *d. f*, dorsal fin; *d. m*, dorsal muscles; *e. br. a*, external branchial aperture; *f. r*, fin-ray; *g. b*, gall bladder; *gl*, glottis; *gon*, gonad; *g. p*, gill-pouch; *h. a*, hæmal arch; *h. c*, hæmal canal; *i. br. a*, internal branchial aperture; *int*, intestine; *lg*, lung; *lr*, liver; *l. v*, lateral vein; *m*, muscles; *m. b*, mid-brain; *med. obl*, medulla oblongata; *mes*, mesentery; *ms. n. d*, mesonephric duct; *ms. nph*, mesonephros; *mth*, mouth; *mt. n. d*, metanephric duct; *mt. nph*, metanephros; *n. a*, neural arch; *nch*, notochord; *p. a. g*, post-anal gut; *pc*, pericardium; *ph*, pharynx; *pn*, pancreas; *pn. b*, pineal body; *pn. d*, pronephric duct; *pn. e*, pineal eye; *p. nph*, pronephros; *pr*, peritoneum, parietal layer, and *pr'*, visceral layer; *prosen*, prosencephalon; *pty. s*, pituitary sac; *r*, sub-peritoneal rib; *r'*, intermuscular rib; *sk*, skull; *sp. c*, spinal cord; *spl*, spleen; *st*, stomach; *s. v*, sinus venosus; *thd*, thyroid; *t. p*, transverse process; *v*, ventricle; *v. ao*, ventral aorta; *v. m*, ventral muscles; *vs. b*, visceral bar. (From Parker and Haswell.)

gans of highest dynamic activity and most pronounced sensitivity are at the apical or anterior end and the organs of lowest dynamic activity and least sensitivity are at the basal or posterior end of this axis. Between these extremes, or opposite poles, of the axis the remaining organs or functions are arranged, at least primitively, in a graded series of diminishing dynamic activity and sensitivity. These geometrical relations serve as an index of an inherent spatial orderliness in the arrangement of the functions with reference to one another, and demonstrate that the organism is based on a single plan—is a coherent entity.

From a purely physiological point of view this gradient represents a linear series of functions, ranging from dominant or controlling functions to subordinate or controlled functions, a series which, broadly speaking, runs somewhat as follows:—olfactory and visual, the most anterior and dominant functions, entirely sensory in character; motor functions associated with movement of the eyes, and motor centers for most voluntary functions; sensory and motor activities associated with feeding, including the sense of taste, and the motor activities of jaws and tongue; sensory and motor activities associated with hearing and equilibrium; the active functions of respiration and circulation, which are closely correlated; the most anterior locomotor functions, associated with the pectoral appendages; the most active phases of the alimentary or digestive functions, associated with the stomach and the larger glands; the excretory and lower alimentary functions, associated with the kidneys, the lower intestine and rectum; the reproductive functions, associated with ovaries and testes, their accessory ducts and copulatory organs; the functions of the tail or post-anal body, which may be considered as a developmental afterthought and as more or less beyond the limits of the original primary axis. The tail has a gradient of its own and does not belong to the primary gradient. This is only a rough outline of the real physiological gradient, but is clear enough for our purposes. The true gradient no longer exists in modern vertebrates because there has been a great deal of secondary concentration at various levels, especially at the anterior end, where the original metameric arrangement of the functional series has been profoundly disturbed and distorted. The primary gradient is further obscured by the fact that various systems of organs, such as the heart and blood vessels, the brain, the alimentary tract, etc., have developed secondary axes of functional activity and structural differentiation that are largely independent of the primary axis and have little reference to the polarity of the body as a whole. In the embryo, however, the axis is less distorted than in the adult.

The Dorso-Ventral Axis (Secondary Axis).—If we take a cross section at any level of the primary axis, we at once perceive that a line drawn from the mid-dorsal to the mid-ventral line represents another main architectural axis. In the diagram (Fig. 2) it will be noted that the central nervous system occupies the high point or apical end of the axis and that, at this level, one loop of the intestine occupies the ventral or basal point of the axis. The gradient of functions in between the two poles has been so decidedly disturbed by lateral foldings and secondary displacements, that any attempt to construct a list of graded functions would be futile. We know in general, however, that the dorsal side is the dominant part of the axis and that, during embryonic development, the various functions differentiate almost exactly in the order of their relative dynamic activity.

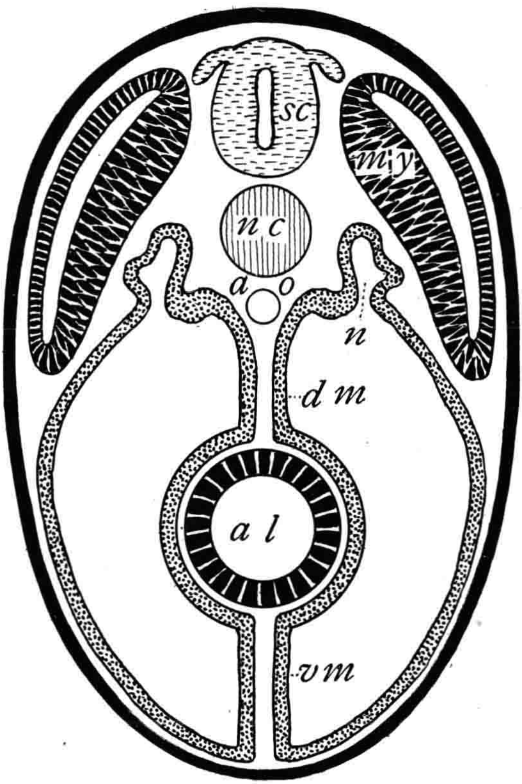

Fig. 2.—Diagrammatic transverse section of a vertebrate to illustrate the dorso-ventral (secondary) and bilateral (tertiary) axes of organization. *al*, alimentary tract; *ao*, aorta; *d. m*, dorsal mesentery; *my*, myotome; *nc*, notochord; *n*, nephrotome; *o*, omentum; *sc*, spinal chord; *v. m*, ventral mesentery. (Modified after Kingsley.)

The Bilateral Axis (Tertiary Axis).—The dorso-ventral axis divides any level of the antero-posterior axis into two mirror-image halves (Fig. 2), so that each side is the reversed counterpart of the other. It would appear then that the bilateral axis is a necessary consequence of the dorso-ventral axis. The axis has a single median or apical point and two lateral or basal points. Any vertical level in the dorso-ventral axis may constitute the apical point of a double bilateral axis. A good example of this type of axial organization is seen in connection with the differentiation of the segmented mesoblast of the chick (Fig. 3). The median dorsal part of the somite forms the myotome (segmental voluntary muscles), the most highly dynamic of all mesodermal structures; next comes the dermatome which forms the deeper skin and many complex sensory and glandular structures, etc.; next comes the nephrotome or primordium of the excretory system; next,

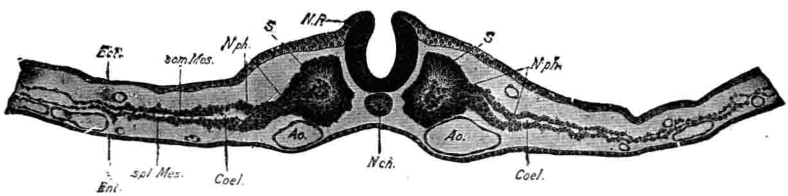

Fig. 3.—Transverse section across the primary axis of a 10 somite chick embryo, to illustrate the bilateral (tertiary) axis of vertebrate organization. *Ao*, aorta; *Coel*, cœlom; *ect*, ectoderm; *ent*, entoderm; *nch*, notochord; *N. F.*, neural furrow; *N. ph*, nephrotome; *s*, somite; *som. Mes*, somato-pleure; *spl. Mes*, splanchopleure. (From Lillie's "Development of the Chick" [Henry Holt and Co].)

but only at posterior levels, the gonatome or primordium of the reproductive system; next, the embryonic cœlom, from which are derived mainly such passive structures as the peritoneal lining of the body cavities and the mesenteries; and finally, the extra-embryonic body cavity, which has to do primarily with the formation of embryonic membranes that serve as protective and respiratory organs during the life of the embryo, but play no rôle in the organization of the adult.

It should be understood that the appendages are, as the name indicates, truly added structures and are not to be considered as part of the original bilateral gradient. Each appendage has its own three gradients, with the free end representing the apical end and the fixed end, the basal. It need hardly be said that the main specializations of the appendages take place at the apical or free end, while the basal parts remain comparatively conservative and undifferentiated.