

THE DEVELOPMENT OF THE VERTEBRATE SKULL

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VERTEBRATE SKULL

PREFACE

This book is the outcome of some fifteen years' work devoted to the study of the development of the skull in all the vertebrate groups. To pretend that I have personally controlled all the statements made herein would be a gratuitous and extravagant exaggeration. But I have had the privilege of studying and researching on embryonic material of all the groups of Vertebrates, and where I have had to make use of them I have interpreted the findings and descriptions of other workers in the light of my own experience, not hesitating to modify or even to reverse their conclusions if I considered it necessary.

My reasons for preparing this book have been numerous.

In the first place, I must claim (or confess) that I have always been attracted, aesthetically I suppose, by the actual shapes and transformations presented by the embryonic skulls of different forms at different stages, and the collection of information concerning them (which has formed the major part of my own practical work during the past fifteen years) has been a work of delight.

Next, from the didactic point of view, I have been dismayed at the lack of co-ordination displayed by the numerous workers in this field, leading as it has to a most confused and redundant nomenclature, and to neglect of a number of morphological principles and features of interest which escaped recognition largely because the objects of comparison bore different names. This difficulty is felt in acute form when comparing descriptions of the embryonic human skull with that of other Vertebrates.

To remedy this, I have devoted myself to a systematic description of all the vertebrate types using a uniform nomenclature, and stressing the points of comparison as far as possible. This programme has also entailed the redrawing of nearly all the figures so as to present them under a uniform

method of treatment.

I hope, therefore, that this work may be consulted with profit by vertebrate morphologists, palaeontologists, and human anatomists for purposes of both study and research: consulted, I say advisedly, for nobody will choose to read such a work from cover to cover. This fact has had an important bearing on the method of treatment of the subject, for it was obviously essential that each section should be reasonably complete and completely intelligible in itself, without the necessity for constant reference to some other place in the text. At the same time, mere repetition was to be avoided.

It may be objected that I have fallen a victim to the tendency to incorporate too much detail in my work. My answer is that in morphology general principles are founded on matters of quite intricate detail and require detail for their illustration, just as the geologist has found that in order to interpret the structure of a range of mountains, or of the whole earth, he has to look through a microscope. In morphology it is true that we have as yet but few general principles of wide application: it is precisely in the hope that readers and future workers may be able to formulate more that I have sifted and included such matters of detail as I considered to be least unlikely to further this end.

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The modern tendency is, quite rightly in my opinion, to appeal to the experimental method to advance knowledge in all departments. A glance at my chapter on 'Causal relationships in the development of the skull' will show how meagre is the information in this field. And this has been another incentive to the preparation of this work. Logical and fruitful experimentation must start from a factual basis of observation. It was the observation of the singleness of the lens in cyclopic eyes that suggested to Herbst that the correlation between eyecup and lens might be a causal one. As is well known, this hypothesis has formed the basis from which the magnificent experimental analyses of Spemann and Harrison have started.

The material presented by the development of the skull is so rich and varied that I venture to hope that it will be possible to suspect and subsequently to establish further correlations of this type. There are, for instance, the questions of the relations between the lateral line sense-organs and the bones which surround them, or the relations between a cartilage-bone and the cartilage whose place it takes. These hypotheses and doubtless others are susceptible of experimental verification or refutation, and to demonstrate our present ignorance and encourage such work is another reason why I have written

this book.

A close study of the development of such a structure as the skull in a group as compact as the Vertebrates might be expected to yield at any rate some conclusions concerning the phylogeny of Vertebrates, and, in general, the problem of the relation of embryology to evolution. Such as they are, my conclusions on this subject and on other general morphological considerations will, I hope, be found acceptable at least as a basis for further work; for the reader will find himself confronted with new problems of unexpectedly profound nature. He will see, for instance, that having followed the development of some bones in nearly all vertebrate groups, we are in the absurd position of still lacking a satisfactory definition of what is meant by the expression 'a bone'.

I may perhaps be permitted to stress the fact that I have found it necessary to make a distinction between the *developmental history* of structures and the *morphology* of embryonic structures. The latter is remarkably uniform throughout the Vertebrates, whereas the former is very inconstant, owing to variations in time at which the different parts of a structure may appear.

At the same time I must make it clear that this work in no way pretends to be a study of the complete morphology of the skull; if the comparative anatomy of living and fossil adult skulls had to be included the size of the work would have had to be five times what it is.

A few words may, perhaps, not be out of place as regards the construction of this book. The Introductory, Comparative, and General Sections are intended for 'general consumption' by biologists; the Systematic Section is a work of reference designed to illustrate in greater detail the principles and points raised in the other sections, and to provide information concerning the extent of knowledge (stages studied, times at which the various structures arise, progress of architectural craniogenesis, morphology) concerning the development of the skull in the various groups.

In each group, the first form is described fairly fully, so as to serve as a type for that group. Thus, the trout and the rabbit serve as general types

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for Teleostei and Placentalia respectively, and obviate the necessity for special sections on the 'Teleost skull' or the 'Placental skull'. The diagnostic features of the skulls of the various groups are considered together in the General Section.

Lastly, I wish to express the hope that this work, for all its size, will escape the lamentable fate of being regarded as exhaustive as regards the subject and exhausting to those who study it. In some cases, no doubt, the appearance of large works on particular subjects has had the effect of sterilizing them. Nothing could be more distant from my mind than to convey the impression that no further profitable work remains to be done on the development of one of the most important and interesting structures in the animal kingdom. For this reason, following the example of H.-B. de Saussure, I end my book with a list of a few of the more important problems requiring solution.

G. R. DE B.

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occupied me for some years.

I have indeed been fortunate in the friends and colleagues with whom I have discussed certain aspects of this work, either in conversation, or by correspondence, and from whom I have received material, information (in many cases unpublished), figures to reproduce in this book, reprints of their works or assistance in connexion with publications inaccessible to me. Among all these persons, I would especially like to record my indebtedness to Dr. M. Augier, Mr. F. H. Aumonier, Miss G. T. Brock, Dr. R. Broom, Dr. A. Chabanaud, Prof. W. E. Le Gros Clark, Prof. E. Fawcett, Miss H. B. Fell, Prof. R. A. Fisher, Mr. R. W. Haines, Prof. R. G. Harrison, Prof. J. P. Hill, Prof. N. Holmgren, Prof. C. J. van der Klaauw, Prof. E. Matthes, Prof. B. Matveiev, Mr. J. A. Moy-Thomas, Prof. A. Meek, Mr. J. R. Norman, Mr. H. W. Parker, Mr. H. K. Pusey, Prof. A. N. Sewertzoff, Mr. E. L. Seyd, Miss M. Tribe, Prof. D. M. S. Watson, Dr. T. S. Westoll, Prof. P. Wintrebert, and the late Prof. J. W. van Wijhe.

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