



**Lillie's**  
***Development of the Chick***  
***An Introduction to Embryology***

Revised by

**HOWARD L. HAMILTON**

*Associate Professor of Zoölogy,  
The Iowa State College,  
Ames, Iowa*

---

Advisory Editor

**B. H. WILLIER**

---

*Third Edition*

New York  
**HENRY HOLT AND COMPANY**

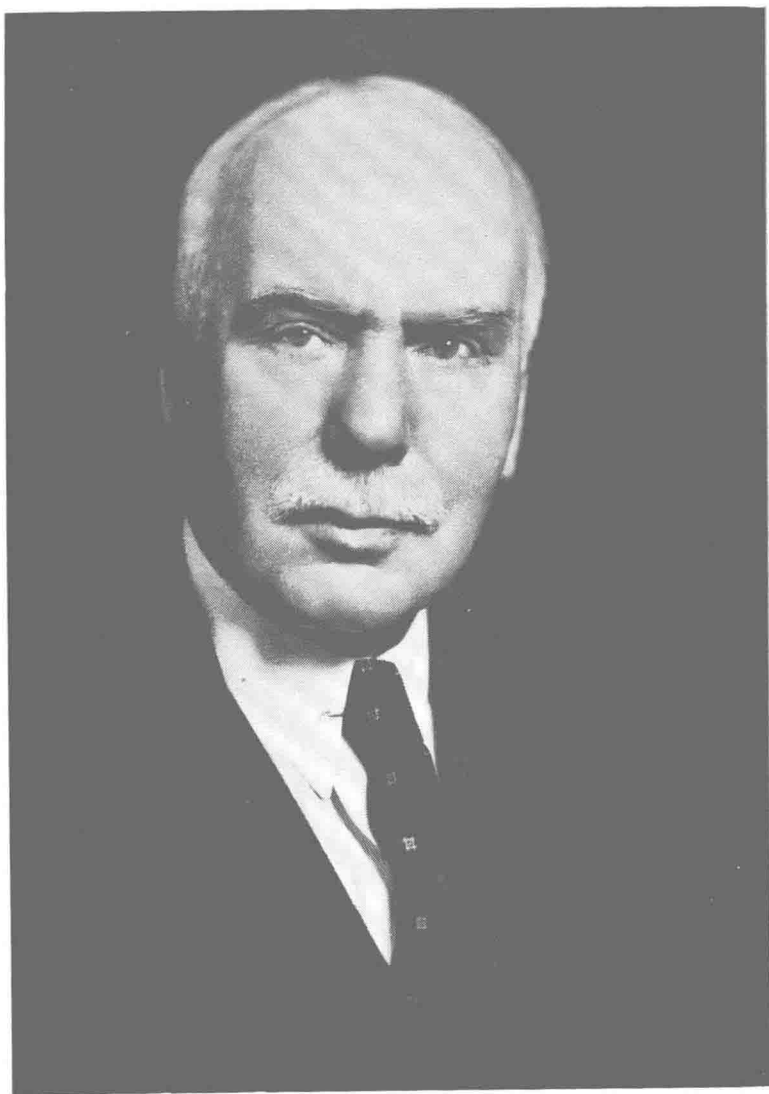
COPYRIGHT, 1908, 1919,  
BY  
HENRY HOLT AND COMPANY

COPYRIGHT, 1936,  
BY  
FRANK R. LILLIE

COPYRIGHT, 1952,  
BY  
HENRY HOLT AND COMPANY, INC.

Library of Congress Catalog Card Number 52-7484

PRINTED IN THE UNITED STATES OF AMERICA



FRANK RATTRAY LILLIE  
1870-1947

## Preface to Third Edition

The present edition of *The Development of the Chick* was begun in 1945 at the request of Dr. Frank R. Lillie, with Dr. B. H. Willier acting in the capacity of Advisory Editor. The work was thus placed in the hands of one of Dr. Lillie's own students and those of one of his "scientific grandchildren" (a term which he was fond of applying to those of us of the third "generation"). It was clear from the outset that to survey and incorporate thirty or more years of literature into the former editions of the book would entail more than a revision and would, in fact, require a rewriting of many portions of the text. Therefore, Dr. Lillie generously gave us free rein to do what seemed best with the text and illustrations, suggesting only that the general outline of the book be preserved.

It was Dr. Lillie's hope that he might live to see the new edition in print, but this was not to be. We wish, therefore, to dedicate it in memory of him and his influence on the development of embryology, in general, and of the inquiring mind among his students, in particular. For the pleasure of the latter, and all others who had the good fortune to be associated with him, the frontispiece opposite has been selected by Mrs. Lillie at our request.

This book is intended, as was the original edition, to introduce the student to the field of embryology. For reasons of space, the content has necessarily had to remain essentially descriptive, but an attempt has been made wherever possible to include the experimental basis for our account, in line with the modern emphasis on experimental embryology. Historical and comparative embryological notes are introduced wherever practicable to clarify or add interest to certain points, but the amount of such inclusions has had to be very restricted. Considerable reference has been made, particularly in Part II, to the literature and to still unsettled problems, with

the hope that the interested student will read further for himself to ascertain the current status of certain problems in the development of the chick. Wherever a subject has become so specialized as to preclude a summary here (as, for example, the development of the finer vascularity, or neurology), the student has also been referred to the original literature. It is hoped, therefore, that, in addition to its primary function as an introductory book, the new edition may be of use as a guide to further research by the advanced student. To aid in the latter objective, an illustrated and condensed description of development by stages has been prepared by Dr. Viktor Hamburger and the author and included in Chapter 3 as a replacement for the older and unsatisfactory chronologies.

Certain chapters (e.g., 7 and 11) have remained relatively unchanged. Chapters 4, 8, and 13 are more or less completely rewritten, and Chapter 15 is new. The others are extensively revised, with rewritten or new sections interspersed with the original text. The new accounts are necessarily based mainly on the recent literature. Whenever possible, however, within the feasible limits of time and materials, we have tried to follow Dr. Lillie's example of going to the chick itself to check questionable points. To this end, some original work has been done which is noted at appropriate places.

First and foremost among those who have contributed time, effort, and materials to the new edition is Dr. B. H. Willier, who generously placed his file of references at my disposal, spent many hours in critically reading the manuscript and advising the author, and contributed many original illustrations. To Dr. Viktor Hamburger I am indebted for suggesting the series of normal stages and collaborating on it, and for reading and advising me on Chapter 8. Others who have read portions of the manuscript and offered suggestions are: Dr. Mary E. Rawles; Dr. Nelson T. Spratt (Chapters 2 and 4); Dr. Rita Levi-Montalcini (Chapter 8); Dr. Chester L. Yntema (part of Chapter 8); Dr. Alexis L. Romanoff (part of Chapter 1); and Dr. Frank R. Lillie (Introduction).

Those who helped with the collecting of illustrations are all of those mentioned above, as well as Drs. Honor B. Fell, D. E. Holm-

dahl, Nils Holmgren, Mary Juhn, Olof Larsell, R. S. McEwen, William Montagna, Carl R. Moore, J. T. Patterson, D. P. Quiring, Dorothea Rudnick, C. H. Swift, Hsi Wang, and Ray L. Watterson, and Mrs. F. R. Lillie. The drawings in Plates 5 and 8 of Chapter 3, and Figs. 96 and 142 are by Mrs. Elsie H. Froeschner; Figs. 27, 28, 44, 262, 267, 268, 271, and 274 were made by Mr. John S. Spurbeck.

Acknowledgment is also due the many publishers whose courtesy has permitted the use of new illustrations in this edition. Among those who have thus cooperated are: Akademische Verlagsgesellschaft, Leipzig; Albert Bonnier, Stockholm; The Long Island Biological Association; The McGraw-Hill Book Company, Inc., New York; The Royal Society of London; H. Stieve, Berlin; John Wiley & Sons, Inc., New York; The Williams & Wilkins Company, Baltimore; The University of Chicago Press; and The Wistar Institute of Anatomy and Biology, Philadelphia.

Finally, I am grateful to the many friends who have written of their interest in the new edition, and to the Iowa State College for their trust and tolerance during this five-year period of seeming non-productivity.

The digestion of more than thirty years of literature in a rapidly moving general field is no small undertaking. Human nature being what it is, I can scarcely expect to have covered all points adequately, clearly, or correctly, and will be sincerely grateful to my colleagues for their tolerance and suggestions for improvements.

H. L. H.

*Iowa State College*  
July 22, 1952

# ***Preface to First Edition***

This book is a plain account of the development of the never-failing resource of the embryologist, the chick. It has been necessary to fill certain gaps in our knowledge of the development of the chick by descriptions of other birds. But the account does not go beyond the class Aves, and it applies exclusively to the chick except where there is specific statement to the contrary. Projected chapters on the integument, muscular system, physiology of development, teratology, and history of the subject have been omitted, as the book seemed to be already sufficiently long. The account has been written directly from the material in almost every part, and it has involved some special investigations, particularly on the early development undertaken by Doctor Mary Blount and Doctor J. T. Patterson, to whom acknowledgments are due for permission to incorporate their results before full publication by the authors. As the book is meant for the use of beginners in embryology, references to authors are usually omitted except where the account is based directly on the description of a single investigator. A fairly full list of original sources is published as an appendix.

Figures borrowed from other publications are credited in the legends to the figures. The majority of the illustrations are from original preparations of the author:<sup>1</sup> Figures 46, 48, 50, 51, 52, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 71, 72, 73, 74, 75, 99, 105, and 106 were drawn by Mr. K. Hayashi; the remainder of the original drawings were executed by Mr. Kenji Toda. The photographs in Figures 118, 119, 120, 168, 181, 182, 189, 194, 197, and 231 are the work of Mr. Willard C. Green. Some of the figures may be studied with advantage for points not described in the text.

Acknowledgments are also due my colleague, Professor W. L.

<sup>1</sup> Figure numbers given here are those of the first edition.



Tower, for much assistance, and to Doctor Roy L. Moodie for special work on the skeleton, and photographs of potash preparations reproduced in Figures 242, 246, 249, and 250.

The best introduction to the problems opened up by the study of embryology is a careful first-hand study of some one species. It is in this sense that the book may serve as an introduction to embryology, if its study is accompanied by careful laboratory work. In some respects it is fuller, and in others less complete, than other books with which it might be compared. On its comparative and experimental sides, embryology is the only key to the solution of some of the most fundamental problems of biology. The fact that comparative and experimental embryology receive bare mention is not due to any lack of appreciation of their interest and importance, but to the conviction that the beginner is not prepared to appreciate these problems at the start; to the belief that our teachers of embryology are competent to remedy omissions; and finally to the circumstance that no one book can, as a matter of fact, cover the entire field, except in the most superficial way.

The development before laying and the first three days of incubation are treated by stages as far as possible, and this matter constitutes Part I of the book. It involves the study of the origin of the primordia of most of the organs. The matter concerning the later development is classified by the organs concerned, which seems to be the only possible way, and this constitutes Part II. The first part is complete in itself, so far as it goes, and no doubt it will be the only part consulted by some students.

The attempt to present a consecutive account of the development of the form on which so many classics in the history of embryology have been based is no slight undertaking. The author can hardly hope that he has avoided omissions and errors, and he will be sincerely grateful to those who call such to his attention.

# Contents

## *Introduction*

I. The Cell Theory . . . . .	1
II. The Recapitulation Theory . . . . .	4
III. The Physiology of Development . . . . .	8
IV. Embryonic Primordia and the Law of Genetic Restriction . . . . .	10
V. General Character of Germ Cells . . . . .	11
The Spermatozoön . . . . .	12
The Ovum . . . . .	13
Comparison of the Germ Cells . . . . .	15
VI. Polarity and Organization of the Ovum . . . . .	17

## **PART I**

### *The Early Development to the End of the Third Day*

CHAPTER 1 — THE EGG . . . . .	23
Chemical Composition of the Hen's Egg . . . . .	27
Formation of the Egg . . . . .	29
Abnormal Eggs . . . . .	35
Oögenesis . . . . .	36
CHAPTER 2 — THE DEVELOPMENT PRIOR TO LAYING . . . . .	42
I. Maturation . . . . .	42
II. Fertilization . . . . .	46
III. Cleavage of the Ovum . . . . .	50
The Hen's Egg . . . . .	51
The Pigeon's Egg . . . . .	55
IV. Origin of the Periblastic Nuclei, Formation of the Germ Wall . . . . .	59
V. Origin of the Entoderm . . . . .	64
CHAPTER 3 — OUTLINE OF DEVELOPMENT, ORIENTATION, CHRONOLOGY . . . . .	70
Orientation . . . . .	71
Chronology (Classification of Stages) . . . . .	74

CHAPTER 4 — FROM LAYING TO THE FORMATION OF THE FIRST SOMITE . . . . .	92
I. Structure of the Blastoderm in Freshly Laid Eggs . . . . .	92
II. Changes Prior to the Formation of the Primitive Streak . . . . .	93
III. The Primitive Streak . . . . .	95
Formation of the Primitive Streak . . . . .	95
Formation of Entoderm During Streak Stages . . . . .	100
IV. Regression of the Primitive Streak . . . . .	105
Formation of the Head-process . . . . .	105
The Fate of the Primitive Streak . . . . .	108
V. Maps of the Blastoderm during Stages of the Primitive Streak . . . . .	111
Organ-presumptive Areas . . . . .	111
Histogenetic Potency . . . . .	112
VI. Significance of the Primitive Streak . . . . .	117
VII. The Mesoderm of the Opaque Area . . . . .	118
VIII. The Germ Wall . . . . .	123
CHAPTER 5 — HEAD FOLD TO TWELVE SOMITES . . . . .	125
I. Origin of the Head Fold . . . . .	125
II. Formation of the Fore-gut . . . . .	127
III. Origin of the Neural Tube . . . . .	130
The Medullary Plate . . . . .	130
The Neural Groove and Folds . . . . .	134
The Anterior Neuropore . . . . .	139
The Sinus Rhomboidalis . . . . .	143
Primary Divisions of the Neural Tube . . . . .	143
Origin of the Primary Divisions of the Embryonic Brain . . . . .	144
IV. The Mesoderm . . . . .	145
Primary Structure of the Somites . . . . .	149
The Nephrotome, or Intermediate Cell Mass . . . . .	150
The Lateral Plate . . . . .	151
Development of the Body Cavity or Coelom . . . . .	151
Mesoderm of the Head . . . . .	151
Vascular System . . . . .	153
Origin of the Heart . . . . .	156
The Embryonic Blood Vessels . . . . .	159
V. Description of an Embryo with Ten Somites . . . . .	162
The Nervous System . . . . .	166
Alimentary Canal . . . . .	166
Vascular System . . . . .	166
General . . . . .	167
Zones of the Blastoderm . . . . .	167

CHAPTER 6—FROM TWELVE TO THIRTY-SIX SOMITES	170
I. Development of the External Form, and Turning of the Embryo	170
Separation of the Embryo from the Blastoderm	170
The Turning of the Embryo and the Embryonic Flexures	173
The Tail Bud	175
II. Origin of the Embryonic Membranes	176
Origin of the Amnion and Chorion	176
Yolk Sac	184
Origin of the Allantois	184
The Umbilicus	186
Summary of Later History of the Embryonic Membranes	187
III. The Nervous System	188
The Brain	188
The Neural Crest and the Cranial and Spinal Ganglia	197
IV. The Organs of Special Sense (Eye, Ear, Nose)	207
The Eye	208
The Auditory Sac	212
The Nose (Olfactory Pits)	214
V. The Alimentary Tract and Its Appendages	216
The Stomodeum	217
The Pharynx and Visceral Arches	218
Esophagus and Stomach	224
The Liver	224
The Pancreas	227
Mid-gut	227
Anal Plate, Hind-gut, Post-anal Gut, and Allantois	227
VI. History of the Mesoderm	229
Somites	229
The Intermediate Cell Mass or Nephrotome	237
The Vascular System	245
VII. The Body Cavity and Mesenteries	260

## PART II

### *The Fourth Day to Hatching.—Organogeny, Development of the Organs*

CHAPTER 7—THE EXTERNAL FORM OF THE EMBRYO AND THE EMBRYONIC MEMBRANES	267
I. The External Form	267
General	267
Head	269

II. Embryonic Membranes . . . . .	272
General . . . . .	272
The Allantois . . . . .	275
The Yolk Sac . . . . .	282
The Amnion . . . . .	288
Hatching . . . . .	289
CHAPTER 8 — THE NERVOUS SYSTEM . . . . .	292
I. The Neuroblasts . . . . .	292
The Medullary Neuroblasts . . . . .	292
The Ganglionic Neuroblasts . . . . .	296
II. The Development of the Spinal Cord . . . . .	299
Central Canal and Fissures of the Cord . . . . .	303
Neuroblasts, Commissures, and Fiber Tracts of the Cord . . . . .	305
III. The Development of the Brain . . . . .	305
Telencephalon . . . . .	306
The Diencephalon . . . . .	310
The Mesencephalon . . . . .	312
The Metencephalon . . . . .	312
The Myelencephalon . . . . .	312
Commissures . . . . .	314
IV. The Peripheral Nervous System . . . . .	314
The Spinal Nerves . . . . .	314
The Cranial Nerves . . . . .	326
Ganglia and Nerves of the Heart . . . . .	337
CHAPTER 9 — ORGANS OF SPECIAL SENSE . . . . .	338
I. The Eye . . . . .	338
The Optic Cup . . . . .	338
The Vitreous Humor (Corpus Vitreum) . . . . .	342
The Lens . . . . .	343
Anterior Chamber and Cornea . . . . .	345
The Choroid and Sclerotic Coats . . . . .	347
The Eyelids and Conjunctival Sac . . . . .	348
Choroid Fissure, Pecten, and Optic Nerve . . . . .	349
II. The Development of the Olfactory Organ . . . . .	354
III. The Development of the Ear . . . . .	358
Development of the Otocyst and Associated Parts . . . . .	358
The Development of the Tubo-tympanic Cavity, External Auditory Meatus, and Tympanum . . . . .	367
CHAPTER 10 — THE ALIMENTARY TRACT AND ITS AP- PENDAGES . . . . .	372
I. Mouth and Oral Cavity . . . . .	372

Beak and Egg-tooth . . . . .	374
Teeth . . . . .	375
The Tongue . . . . .	376
Oral Glands . . . . .	377
II. Derivatives of the Embryonic Pharynx . . . . .	378
Fate of the Visceral Clefts . . . . .	378
Thyroid . . . . .	379
Visceral Pouches . . . . .	379
The Thymus . . . . .	380
The Parathyroid Glands . . . . .	381
The Postbranchial Bodies . . . . .	381
III. The Esophagus, Stomach, and Intestine . . . . .	382
Esophagus . . . . .	384
Stomach . . . . .	386
Large Intestine, Cloaca, and Anus . . . . .	388
IV. The Development of the Liver and Pancreas . . . . .	393
The Liver . . . . .	393
The Pancreas . . . . .	398
V. The Respiratory Tract . . . . .	400
Bronchi, Lungs, and Air Sacs . . . . .	400
The Laryngotracheal Groove . . . . .	407
CHAPTER 11 — THE BODY CAVITIES, MESENTERIES, AND SEPTUM TRANSVERSUM . . . . .	409
I. The Separation of the Pericardial and Pleuroperitoneal Cavi- ties . . . . .	409
Septum Transversum . . . . .	410
Closure of the Dorsal Opening of the Pericardium . . . . .	414
Establishment of Independent Pericardial Walls . . . . .	414
Derivatives of the Septum Transversum . . . . .	416
II. Separation of Pleural and Peritoneal Cavities; Origin of the Septum Pleuroperitoneale . . . . .	416
III. The Mesenteries . . . . .	419
The Dorsal Mesentery . . . . .	419
The Origin of the Omentum . . . . .	420
Origin of the Spleen . . . . .	422
CHAPTER 12 — THE LATER DEVELOPMENT OF THE VASCULAR SYSTEM . . . . .	425
I. The Heart . . . . .	425
The Development of the External Form of the Heart . . . . .	425
Division of the Cavities of the Heart . . . . .	428
Fate of the Bulbus . . . . .	435
The Sinus Venosus . . . . .	435

II. The Arterial System . . . . .	437
The Aortic Arches . . . . .	437
The Carotid Arch . . . . .	442
The Vertebral and Subclavian Arteries . . . . .	443
The Aortic System . . . . .	445
III. The Venous System . . . . .	446
The Anterior Venae Cavae . . . . .	446
The Primitive Omphalomesenteric Veins . . . . .	448
The Umbilical Veins . . . . .	451
The System of the Inferior Vena Cava . . . . .	452
IV. The Embryonic Circulation . . . . .	457
V. The Lymphatic System . . . . .	462
CHAPTER 13 — THE UROGENITAL SYSTEM . . . . .	465
I. The Later History of the Mesonephros . . . . .	465
II. The Development of the Metanephros or Permanent Kidney . . . . .	471
The Metanephric Diverticulum . . . . .	473
The Nephrogenous Tissue of the Metanephros . . . . .	475
The Formation of the Secreting Tubules . . . . .	477
III. The Organs of Reproduction . . . . .	479
Development of Ovary and Testis . . . . .	482
Development of the Genital Ducts . . . . .	497
IV. The Adrenal Glands . . . . .	501
Origin of the Cortical Cords . . . . .	501
Origin of the Medullary Cords . . . . .	502
CHAPTER 14 — THE SKELETON . . . . .	505
I. General . . . . .	505
II. The Vertebral Column . . . . .	510
The Sclerotomes and Vertebral Segmentation . . . . .	510
Membranous Stage of the Vertebrae . . . . .	513
Chondrification . . . . .	516
Atlas and Axis (Epistropheus) . . . . .	519
Formation of Vertebral Articulations . . . . .	520
Ossification . . . . .	522
III. Development of the Ribs and Sternal Apparatus . . . . .	523
IV. Development of the Skull . . . . .	527
Development of the Cartilaginous or Primordial Cranium . . . . .	528
Ossification of the Skull . . . . .	533
V. Appendicular Skeleton . . . . .	534
The Fore-limb . . . . .	535
The Hind-limb . . . . .	540

CHAPTER 15 — THE INTEGUMENT . . . . .	546
I. General . . . . .	546
II. Formation of the Down Feather . . . . .	550
III. Formation of the Contour Feather . . . . .	554
IV. Pigmentation of the Integument . . . . .	562
Lipochromes . . . . .	562
Melanophores . . . . .	562
Patterns in Feathers . . . . .	565
V. Influence of Hormones on the Integument . . . . .	569
Secondary Sexual Characters . . . . .	569
Sexual Dimorphism of Feather Structure . . . . .	569
Sexual Dimorphism of Pigmentation . . . . .	570

### **Appendix**

General Literature . . . . .	575
Introduction and Chapter 1 . . . . .	575
Chapter 2 . . . . .	577
Chapter 3 . . . . .	579
Chapter 4 . . . . .	580
Chapter 5 . . . . .	581
Chapter 6 . . . . .	582
Chapter 7 . . . . .	586
Chapter 8 . . . . .	588
Chapter 9 . . . . .	591
Chapter 10 . . . . .	593
Chapter 11 . . . . .	596
Chapter 12 . . . . .	597
Chapter 13 . . . . .	599
Chapter 14 . . . . .	602
Chapter 15 . . . . .	604
INDEX . . . . .	607



# Introduction

## I. The Cell Theory

The fundamental basis of the general conceptions of embryology, as of other biological disciplines, is the cell theory. The organism is composed of innumerable vital units, the cells, each of which has its independent life. The life of the organism as a whole is a product of the combined activity of all the cells. New cells arise always by subdivision of pre-existing cells, and new generations of the organism from liberated cells of the parental body. The protozoa, however, have the grade of organization of single cells, and the daughter-cells arising by fission constitute at the same time new generations. In some metazoa new generations may arise asexually by a process of budding, as in *Hydra*, or of fission, as in some *Turbellaria*; such cases constitute exceptions to the rule that new generations arise from liberated cells of the parental body, but the rule holds without exception for all cases of sexual reproduction.

The body consists of various functional parts or organs; each of these again consists of various tissues, and the tissues are composed of specific kinds of cells. The reproductive organs, or gonads, are characterized by the production of germ cells, ova in the female gonad or ovary, and spermatozoa in the male gonad or testis. However large the ovum may be—in the hen it is the part of the egg known as the yolk—it is, nevertheless, a single cell at the time that it leaves the ovary in all animals. Similarly, the spermatozoon is a single cell. An ovum and spermatozoon unite, in the manner to be described later, and constitute a single cell by fusion, the fertilized ovum or zygote. This cell divides and forms two cells; each of the daughter-cells divides, making four, and the number of cells steadily increases by successive divisions of all daughter-