LIVING EMBRYOS

Third Edition

by

JACK COHEN

and

BRENDAN MASSEY

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PREFACE

This, the 3rd edition of Living Embryos, has been prompted by the gratifying success of the first two. Obviously we are heartened by this success, but also conscious that in part at least it has been the format of the book that has contributed to its popularity. Accordingly, while trying to up-date this latest edition we have also attempted to retain the flavour of the previous two. In practice, this means that the superficial appearance of the text and illustrations will be reassuringly (we hope) familiar; it does not mean that the revision has been a superficial one. Every aspect of the book has received some attention, from the order of the sequence of the various sections, through re-writing most of the existing text to a greater or lesser degree, to completely new sections included for the first time; and many of the diagrams and photographs have been altered, too, in the hope of making them easier to understand.

Sections of the text have been reorganized in order to present more clearly the unfolding story of development; in particular, recent teaching experience has suggested that the tissue movements of gastrulation, often the stumbling block to an appreciation of development, can be more easily visualized if initially considered in a group such as the echinoderms —hence the reason for the apparently premature incursion into the mysteries of this phylum.

The "types" selected are *not* meant to be representative either of their phyla or of the wide range of development oddities found through the animal kingdom. The Nematoda have been chosen for the lesson of the eutelic creature, the ultimate in determinate development. A polychaete worm (*Pomatoceros*) has been chosen because it provides good practical material throughout the year and is cheap. It shows a complicated but readily understood cleavage pattern after post-fertilization interactions. Gastropod molluscs show the same kind of development and in addition the shell gland shows a post-cleavage induction. No excuse should be needed for inclusion of the arthropods, but their embryology is difficult to compare with other forms without considerably more space; the section has therefore been kept brief, but includes *Artemia* as an example since the embryology of this animal is easily demonstrated and eggs are available at all times from pet shops. The echinoderm serves as a good example of the indeterminate invertebrate, and is additionally both well-documented and good practical material at certain seasons. The tunicates have been included for two reasons: firstly, because they demonstrate radial cleavage in a determinate development and, secondly, to illustrate the dramatic resemblance between the determined areas of *Styela* and the frog fate map. This resemblance helps to introduce the vertebrates and underlines the importance of pre-cleavage events, for example the amphibian grey crescent.

The vertebrates have been emphasized, partly because man is a vertebrate and partly as a more detailed account was necessary from at least one phylum of the animal kingdom; the vertebrates were an obvious choice. The question of which organ systems to consider is also most important. Since the second edition our teaching in the areas of eye, ear, skin and urinogenital system embryology have prompted extensive re-writing of these sections (often to correct things that were plain *wrong* in the second edition!). New directions in embryological thinking, especially in the areas of reproductive theory and the maternal control of early embryology, have elicited completely new sections which we hope will stimulate readers to further investigation in texts which can afford a more generous cover than we can. Finally, diagrams have been added to this edition and most of the existing ones redrawn to some extent, mostly in response to student comment (or in response to their obvious, if unwitting, difficulty in understanding the old ones). However, the overall format is as of old and we hope it still pleases.

The aim of Living Embryos from its inception has been to treat embryology as a living subject, the very antithesis of the tedious plod through a set of slides, the pickled specimen, the list of someone else's photographs (which at best lead to boredom and at worst to a repetition of someone else's mistakes; and anyway it's much more fun to make your own mistakes from the start!). Wherever possible we have tried to encourage the student to refer to the living embryo, zygote, gamete or whatever, and the examples we have chosen to represent various diversions of the developmental theme are ones which are readily available to even the most impecunious devotees of embryology. It is worth emphasizing this last point (for those few of you who read the Preface!): all the examples chosen are *cheap*, reliable and easy to use as *living* developing material; all show something of the richness of the subject with particular clarity, be it the satisfaction of watching a *Pomatoceros* lay eggs or sperm, the precise cleavage of an echinoderm zygote, the magic of the first movements of a baby zebra fish, the beauty of the developing blood system of a 3-day chick, etc. Embryology seen like this is the most fascinating of sciences and deserves the widest audience.

Although Cohen started, Massey has been involved in the teaching for 15 years and has added his flavour throughout—we hope it is to your taste. In the preparation of this book in all its various manifestations, however, a large number of other people have cooperated as well and to thank them all personally would extend this preface beyond its already burgeoning length (and increase the price of the end product!). However, a special word of thanks is due to Chris Taplin, then a second year Zoology student in Birmingham, for his work on the existing diagrams and the very competent job he made of the many new ones—also for the patience he showed when we consistently mangled his efforts in an attempt to clarify our thoughts on what we wanted. And, of course, above all, thanks to those who made this edition necessary, the generation of students of all ages whose comments, criticism and advice are enshrined in it and whose successors, we hope, will be no less forthcoming.

Jack Cohen

Birmingham 1981 *Brendan Massey*

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INTRODUCTION

The study of embryology is concerned primarily with the process by which the adult arises from the fertilized egg. It encompasses on the one hand those processes by which the genetic material expresses its message in material terms and on the other hand the maintenance of the adult organism, its progress into senility and its liability to suffer defects, such as tumours, which may result from developmental accident or design.

Until the beginning of this century embryology was essentially descriptive, but the development of experimental techniques has led to many unifying concepts. Not only the topology of embryological processes but also the causal relations between these processes should now be considered.

Let us first consider very briefly the history of the subject. The naive **preformationist** view that the egg or even the sperm was a miniature adult, requiring only to grow, was popular among natural philosophers (e.g. the animalculists). Some early drawings of human sperms purported to show a "homunculus" in the sperm head (Fig. 1). This view was current among scholastics until the end of the eighteenth century, when it became obvious that the facts could not be accounted for by such a simple story. Preformationist theories became very much more sophisticated and to account for the observed facts the process of **entelechy** was imported: the egg contained a "demon" which, during the process of development, organized the egg material in space to form the right kind of animal or plant. It is important to appreciate that neither the preformationist nor the entelechist considered the environment to be a necessary part of the process of development. During the nineteenth century workers began to be impressed by the apparent succession of stages in the life history of many creatures and those who were philosophers considered development in terms of a philosophical **evolution** (Aristotle had considered embryology in these terms): having exhausted the possibilities of each stage, the embryo *of necessity* progresses to the next stage. This viewpoint is held by many contemporary embryologists in a more or less sophisticated form, and human embryology still suffers considerably from the difficul-

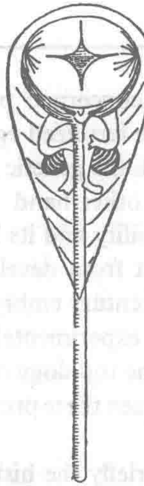

FIG. 1. *Early drawing of a human sperm by Hartsoeker (redrawn from Needham 1959).*

ties inherent in a consideration of stages (called "**horizons**") instead of processes.

It may well be noted here that the view of DNA as "all of life; the rest is commentary" is a preformationist view with undertones of entelechy. The nucleic acids are an integral part of the structure of the egg and must not be considered as separate from it. They may play the part of the conductor, or indeed the composer, of the symphony of development; but the orchestra is absolutely necessary for its realization. Another analogy is that of a tape recording: the linear pattern of magnetic variation on the tape must interact with the complex and specific mechanism of the tape recorder for it to appear as a pattern of sound; similarly, the linear code of the DNA on the chromosomes must interact with the rest of the egg. The naive view that the DNA code is comparable to the sequence of frames making up a cine-film, requiring only to be expanded into space as the characters of the organism, shows its absurdity at first inspection. It has had an insidious effect, however, and still appears in many learned treatises as well as in newspaper popularizations. In such publications, the DNA is called the "blueprint"; if it *were* a blueprint, of course, the thalidomide tragedy would never have happened, for the embryos could have referred to their blueprints and corrected the developmental abnormalities.

Most contemporary biologists consider development in terms of **epigenesis;** this is the belief that the observed increase of complexity as an animal develops is due to *interaction* between its parts and often between these parts and the physical or chemical environment. The environment may contain **teratogens,** substances which divert the normal course of development into abnormal paths, like thalidomide. Abnormalities can also be produced by genetic differences, or by mechanical or chemical accidents to the egg or early embryo. It will be seen that the questions asked by entelechists or evolutionists can usually be answered in purely descriptive terms, whereas those of the epigeneticist require the experimental approach.

Throughout the study of embryology the time element must constantly be borne in mind. Even if certain stages in development may be described and recognized, the transition into and from these stages is a gradual process and indeed many events are occurring during what is apparently one stage. Models of stages of embryological development, which were very popular in the thirties, cannot show subtle physiological interactions, but are still useful for the modern biologist to get his anatomy straight. Films of the development of a great variety of forms are available on loan from several sources. Appropriate use of film material is often better than the living organisms in inexperienced hands; for one thing it always works! Viewing of a good film is also a useful preliminary to laboratory work. The student should gain some idea of the scale of the events he is to examine and, more important, should be able to select those organisms which are behaving normally and may be expected to continue to do so. Animated cartoon films have obvious dangers; the instructor should view them very critically himself before screening them for the students.

Reproduction involves the reproducing of parents from parents. When a cat has had kittens, reproduction has not yet occurred; only when the kittens in their turn have had kittens has the cycle been completed. **Embryology** is the central series of events whose scope extends from the gametes of one generation at least to the juveniles of the next. In fact,

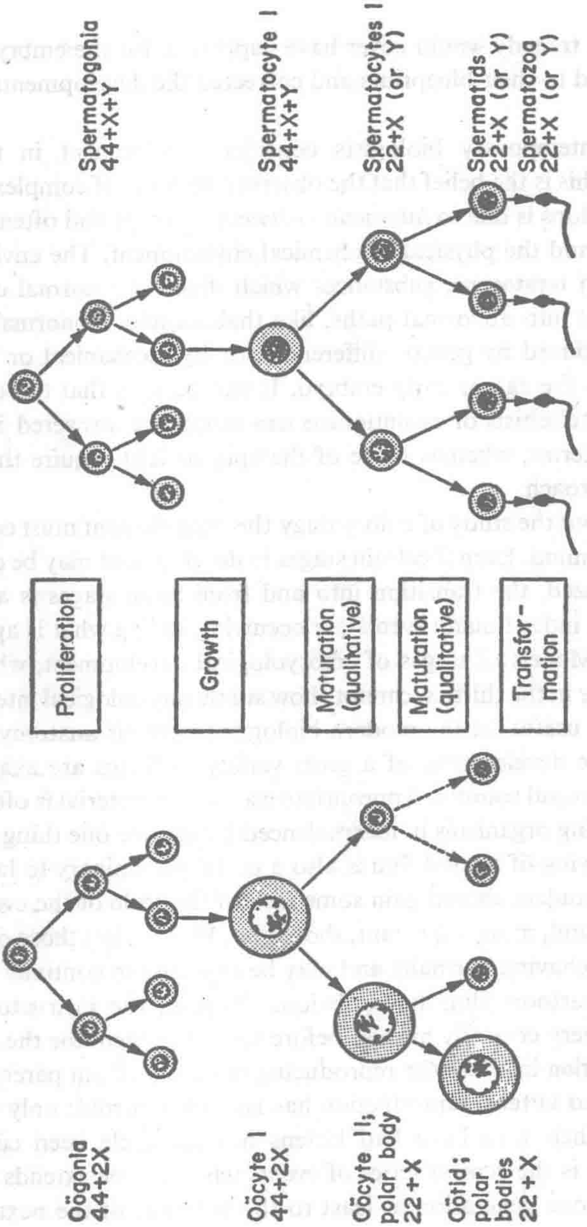

FIG. 2. *The production of eggs and sperms compared. This diagram shows the number of chromosomes for the human. Sex is determined by X or Y containing sperms; Y is male determining.*

many embryologists include the whole developmental process within embryology, i.e. not just the production of juveniles but also all the processes which enable them to produce their own gametes in the next generation. In this wide definition, embryology covers all the events necessary for reproduction.

Nearly all the organisms that we shall consider in this book reproduce sexually. The two sexes are *usually* housed in separate bodies and there is usually some specific behaviour associated with the transfer or fertilization of gametes. Such **sexual congress** often involves the animals in behaviour which is quite different from their normal **vegetative** activities, e.g. feeding, escaping from predators, remaining camouflaged. The reader should consult books on general reproductive topics for further information.

Such sexual organisms are commonly diploid and the production of gametes involves reduction division **(meiosis)** to produce haploid products. Again this is outside the scope of this book and the reader is referred to a textbook of genetics. In most animal species, the sexes are recognized primarily by the production of small, motile sperm or of large non-motile eggs; see FIG. 2 for a simple diagram of the development of both sperms and eggs. Many animals, especially many Protozoa, do not have any sexual process and in such forms there are no such **gametes;** here the embryology may be considered to commence with the division of the parent body. Many rotifers, insects and a few other forms normally reproduce parthenogenetically; that is to say, the eggs develop without fertilization by sperms. **Parthenogenesis** has been induced experimentally in many other groups and these parthenogenetic eggs and the embryology of the animals will not be considered separately, for in other respects they resemble their sexual relatives.

SPERMS

Spermatozoa (or **sperms**) of most animals (Fig. 3) move by means of a posterior flagellum, the tail, which is attached to the **head** by a **middle piece** (or **mid-piece**) containing mitochondria. The head of the sperm contains little other than the chromosomes and the **acrosome** which is used

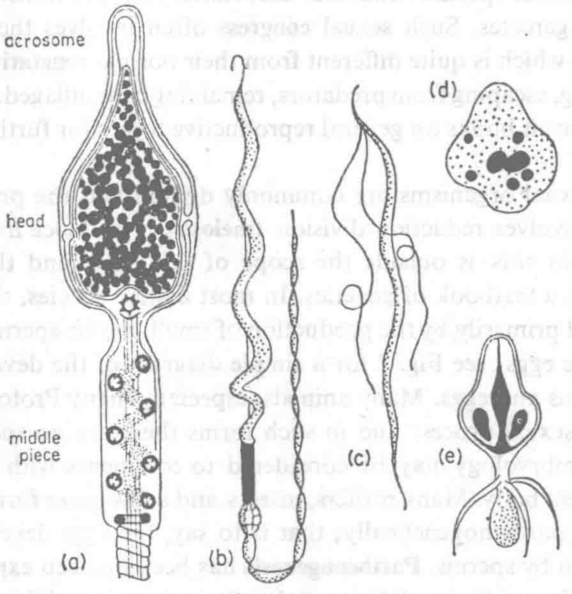

FIG. 3. *Sperms of various animals. (a) Detail of head and middle piece of bull sperm. (b) Sperm of a dogfish* (Squalas). *(c) Sperm of a planarian* (Dendrocoelum). *(d) Sperm of a nematode* (Ascaris). *(e) Sperm of a lobster* (Homarus). *Note that (d) and (e) are not flagellate.*

to penetrate the egg membrane. The acrosome of mammalian spermatozoa has been shown to contain enzymes, including hyaluronidase and proteases, which penetrate the membranes round the egg.

The sperms of many arthropods do not possess a true locomotory tail and some of them are very peculiar indeed; many are transferred in packets called **spermatophores.** Figure 3(e) shows the sperm of a lobster; crayfish sperm resemble tiny catherine wheels, with fibres extending tangentially from the edge of the disc; the sperms of some mites are rod-shaped, with a posterior bulge containing the nuclear material and minute grooves along their length which are thought to aid in locomotion. Some insects and spiders, on the other hand, have almost "normal" sperms.

Nematodes and some other Aschelminthes have sperms which are amoeboid in shape but do not seem to move very actively. Those of *Ascaris* may easily be seen in smears from the proximal oviduct of large females and a tiny rhythmic movement may be distinguished as they stick to the surface of eggs prior to entering them.

In order to produce the tiny heads characteristic of most sperms the chromosomes have to condense very greatly; their normal basic proteins, histones, are lost and replaced by protamines or other arginine-rich, very basic proteins, which bind the nucleic acids very tightly. They may be aligned very precisely; the use of polarizing microscopy of great delicacy has identified all of the chromosomes of a grasshopper arranged end-to-end in the long thin head of its sperm. However, most mammalian sperms have the chromosomes in no particular orientation; here, in addition to arginine-rich proteins, sulphur bridges between proteins give the head extra rigidity which enables it to penetrate the thick zona pellucida (p. 19) around the egg.

EGGS

The **egg** (Fig. 4) is usually more or less spherical and may be enclosed in a series of **membranes** which are often protective or contain nutrient materials. Eggs contain a nuclear apparatus in a very complex and highly organized **cytoplasm** whose components come from many sources; they also usually have some yolk. Most of the egg's substance has been accumulated during the process of **oogenesis;** ribosomes have been produced