Cambridge University Press
978-1-107-65448-8 - Form and Causality in Early Development
Albert M. Dalcq
Excerpt
More information

CHAPTER I

The recent embryological movement and the scope of this book

Embryology may seem, at first sight, a kind of Penelope's web. From the end of the eighteenth century, and especially from the middle of the last one, the same eggs of various species have been again and again minutely examined by research workers who have devoted themselves to the enigma of development.

In spite of the enormous amount of data which have in this way been heaped up in an abundant literature, it is always necessary to take up again and again the study of the same materials. Not that the earlier observations are often erroneous, far from it. But ontogenesis is one of the processes of life which is most difficult to integrate in the usual frames of our mentality. With its innumerable problems connected with the physical, chemical, cytological and even philosophical disciplines, it requires a mind specially trained and ever ready to adapt itself to unforeseen facts. The omission or the misinterpretation of the slightest detail may entirely change the significance of a result and thorough reinvestigations are therefore often necessary.

The evolution of descriptive Embryology is, in this respect, characteristic. At the time of the Great War one could, it seemed, consider this science as fully studied. For Invertebrates, as well as for Vertebrates, a series of instructive monographs described accurately, in animals quite representative of each group, the phases of development. In 1919, the late Professor Albert Brachet, under whose guidance it was my privilege to study, was finishing his well-known *Traité d'Embryologie des Vertébrés*. I often heard him express the hope of having built on solid ground and consequently of having achieved a lasting work. After the premature death of that great scientist, my friend Prof. Pol Gérard and myself had to review that treatise for its second edition. We were compelled to modify completely nearly a third of the book (1935), and it now appears that we were not sufficiently drastic. Concerning Invertebrates, the descriptive progress seems less rapid. It is, however, characteristic that, in all species which have been submitted to attentive experimental researches, the authors of these had to amend, correct or complete the classical descriptions of normal ontogenesis.

In experimental matters, the evolution of knowledge is still more rapid. What a magnificent record is that of the achievements of causal Embryology in these last twenty-five years! Although I was then making my first steps in research work, I remember very exactly the ideas that were current, just before the War, in Brachet's laboratory. Without any doubt, the future success of "*Entwicklungsmechanik*" was an article of faith, but Brachet preferred christening the young science "causal Embryology". Certainly, also, the facts of regulation in the first blastomeres, when isolated, of the sea-urchin, the *Amphioxus* and the newt were never lost sight of. The theoretical importance of the conception of "germinal localization", then recently expressed by E. B. Wilson, was, however, often emphasized in opposition to Driesch's discovery. But it was vainly attempted, for the frog's egg, to harmonize the results obtained by destruction of the first blastomeres—and exactly understood, thanks to Brachet himself—with the regulation after reversing the germ, i.e. the experiment of Schultze. In the newt, we did not at all suspect the relation between the processes of regulation in the young stages and the lens-inducing actions of the optic vesicle, demonstrated at that very time by Spemann's epoch-making work. We had, however, the feeling that a new and concrete value was thereby given to the conceptions of self- and dependent-differentiation, a legacy of Roux's prescience. In Fishes, the lesions made by Kopsch at certain places of the blastoporal lip helped to anchor us to the fallacious theory of concrescence. In Birds, defects had been obtained by the same author and American investigators; but the results of these experiments did not at all explain to us the meaning of the primitive streak. This enigmatic feature of early development was erroneously thought by us to be common to all Amniotes, including Reptiles, and we attempted in vain to guess its relation with the gastrulation of Fishes and Amphibians. A fact worthy of special mention is that it became for the first time possible, in those same years 1913–14, to experiment on Mammalian eggs: we wondered at Brachet's successful cultivations *in vitro* of the young blastocysts of the rabbit. Ascidians looked to us, of course, a very strange material: we knew of the definite defects obtained in their case, but this seemed to us really singular. The sea-urchin egg interested us, but more by the then thrilling analysis of its fertilization than by its morphogenesis. We had heard, however, some rumour of the theory of Neo-vitalism. It was generally not sympathetic to our young minds. We attempted to refute it on the grounds that regulation was abnormal and less important than results supporting the mosaic theory.

Very incomplete, indeed, is this sketch of the thoughts prevailing, twenty-five years ago, in a laboratory devoted to causal Embryology. It allows us, nevertheless, to appreciate the progress which has now been made in many directions. Our knowledge, at that time, was altogether rather incoherent and extraordinarily rich in promises. Each of the subjects I have mentioned has been the source of continuous progress and remarkable achievements. The most varied methods have been applied to an ever-increasing number of species. Between the nearly contradictory observations of predictable deficiencies and astonishing regulations a bridge has been thrown by the study of morphogenetic functions. The old struggle between Vitalism and Mechanism has lost much of its acuteness. It has been recognized that it is unnecessary to decide *a priori* if the intimate processes of life are or are not resolvable in terms of our actual physical and chemical knowledge. The problems posed by early development have been faced with a complete spirit of objectivity, a philosophical climate which may be styled a pragmatic Organicism.[1]

A large part of this renovation has been due to the discovery of embryonic inductions. The new order of ideas introduced and methodically developed by Spemann's school had been marvellously productive. Avoiding any premature physico-chemical thesis, those investigators have, beyond anything else, accurately registered the answers of the germinal system to logically formulated questions. Realizing organicism in its truest meaning, they have in a few years accumulated a quantity of data, the remarkable

---

[1] Concerning the philosophical interpretations of development, cf. Russel, 1930; Bertalanffy and Woodger, 1933.

outcome of which is plainly established by the recent book of their leader. The American school has not failed to play an indirect but very significant part in this movement. The fine analysis of the relations between the development of the limb bud and the whole embryo, as performed by R. G. Harrison and his distinguished co-workers, has an importance which must at least be emphasized by this very brief allusion. This post-War movement of causal Embryology has taken a rapid extension. Most Chordate germs, those of *Amphioxus* and Tunicates, of Fishes, Reptiles,[1] Birds, and even Mammals, have been examined according to the principles introduced for the Amphibians. In spite of the apparently quite different embryonic forms encountered in Echinoderms, Molluscs, Worms and Insects, skilful and tenacious workers have disclosed to us, at least in its general features, the germinal organization of those Invertebrates.

Such achievements could not fail to attract the attention of embryologists inclined to synthesis. The results gathered up to the end of 1929 have been summarized by Schleip in an incomparable treatise. The extensive textbook of J. S. Huxley and G. R. de Beer, *The Elements of Experimental Embryology*, has discussed primordial ontogeny with the most scrupulous attention. We also have Spemann's memorable book, which was, it must be noticed, already written, for its main part, in 1931, the time of his "Silliman lectures". These excellent contributions are, however, far from making unnecessary an attempt conceived from a rather different angle. In spite of recent advances in causal analysis, the barrier between the normal and experimental data is not overcome in current conceptions. It is of particular difficulty in the cases where *parts of the germ have their fate thoroughly changed with the apparent tendency to restore the normal structure of the whole.* Such processes of *embryonic regulation* may be now considered as of general occurrence. The sole scientific attitude regarding them is to search for an organization of the egg that can account for all results, including the regulation data presented by normal, operated or altered eggs. Normal development (*normogenesis*), anomalies artificially produced (*paragenesis*) and the apparent effort of the germ to build up a normal embryo,

---

[1] Reptiles remain, however, from the experimental viewpoint, an unknown province.

in spite of severe amputations (*regulation*), must receive one common solution. We must know how much such a fundamental organization differs between species of various Classes, Orders, Phyla. We want to understand how it acts from the awakening of the egg by fertilization or activation until the moment where organs are formed and acquire their histological differentiation. This programme is of course an ideal, which can only be progressively fulfilled. I hope to convince my readers that, thanks to the reciprocal illumination of recent descriptive and experimental results, the causality of animal form, which seemed beyond the goal of logical explanation, can now be given a satisfactory interpretation. To bring the subject to that conclusion, it will be necessary to search eagerly for all possible indications concerning the physiological bases of morphogenesis. Normal features must be comparatively considered, paragenesis and regulation must be elucidated, young and later stages must be functionally correlated. In a word, Unity in space and time must be our Ariadne's thread.

REFERENCES, TERMINOLOGY, ACKNOWLEDGMENTS

A detailed account of many researches is to be found in the above cited books and some others.[1] Only recent or specially significant investigations will be referred to at some length. The names of the authors will be generally given in paginal notes. The simple ones concern a quotation of the mentioned fact. Those preceded by "cf." indicate a recent publication which can be used by the reader for the related literature.

The terminology used makes a distinction between the groups of cells and layers still capable of further segregations and those which have reached the end of their embryonic evolution. The former will receive designations with the suffix *-blast*, the latter with the suffix *-derm*. In the case of Chordates, we shall have to consider, at the end of gastrulation, an *ectoblast* which later splits into neural plate (*neuroblast*) and *epiblast*; a *chordo-mesoblast*, soon separated into *chorda* and *mesoblast*, which itself gives the *somites*, the *nephrotomes*, the *coelomic linings* and *mesenchyme*; and an *entoblast*, matrix of the whole digestive and respiratory

---

[1] Cf. Dalcq, 1935 *a*.

tract. In the Amniotes, the outer layer of the didermic stage preceding the primitive streak will be designated as *primary ectoblast*. In Invertebrates, the terms *ectoblast*, *mesoblast* and *entoblast* will be used with their usual meaning.

The present work has been undertaken at the solicitation of Mr C. H. Waddington. His kind request has incited me to an inquiry which has led me much farther than I could foresee. No pleasure is more valued by a scientist than a better comprehension of the field which he is exploring. For having given me this high satisfaction, I heartily thank my distinguished colleague.

I am also deeply indebted to Dr G. Vandebroek for the loan of unpublished results and documents; to Dr E. Van Campenhout, Dr L. Van den Berghe and Dr J. Pasteels for reviewing the manuscript and helping with most valuable suggestions.

CHAPTER II

A brief outline of Organogenesis, especially concerning Chordates

It has long been recognized that the initial processes of animal development show **common fundamental characters.** Their uniformity is nearly complete in regard to meiosis and the growth of the egg. Maturation and fertilization already tend to be more specialized, although not very deeply. Then there always follows a segmentation through karyokineses and—without speaking of other changes inherent to the same period—the blastomeres thus acquire the mobility and laxity that make morphogenetic movements possible. The orientation and chronology of these movements vary according to the species. Everywhere, except in certain Sponges, this period results in the enveloping of cellular groups by an external layer. The uniformity of this phase induced Haeckel to imagine the ancestral type called *gastraea.* If such a being ever really existed, its physiology must have been radically different from that of our actual gastrulae. In fact, these do not constitute a larval stage. Except in the case of some Hydroides, where growth is often extremely precocious,[1] and in that of placentary Mammals, where the elaborated uterine secretion seems to be absorbed by the young blastomeres, the cells of the gastrula do not nourish themselves nor grow noticeably. They divide and they move, and the objective they pursue unceasingly is the construction of the primitive organs. These vary a good deal in the case of Chordates, Worms, Molluscs, Insects, etc., and it will be advisable for the moment to limit ourselves to the first-mentioned group. We shall add the necessary indications when we have to consider other types of ontogenesis.

The termination of gastrulation is, for all Chordates, marvellously uniform. It is the **constitution of a young embryo** provided

---

[1] Cf. Teissier, 1931.

with five or six very characteristic organs, each having its typical form and size (figs. 1, 3, 41). A *neural tube*, swollen at its anterior part into a cerebral vesicle, lies above the *notochord* and protrudes somewhat beyond this, except in the case of *Amphioxus*. These two organs stand over the elongated pocket of *entoblast*, which encloses an archenteric cavity somewhat constricted in its fore-part, the pharyngeal pouch. The *mesoblast* is moulded on the sides of the neural tube, of the chorda and of the archenteron. A continuous *epiblast* surrounds the internal parts.

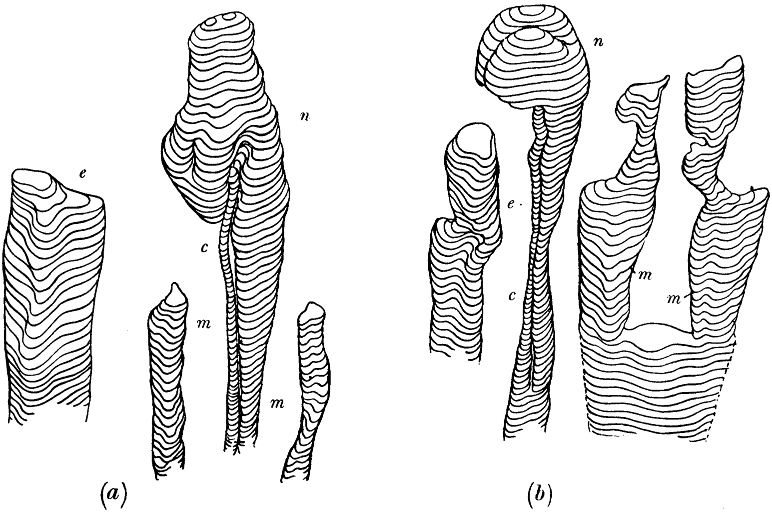

Fig. 1. Reconstruction of the main organs of rabbit (*a*) and tortoise (*b*) embryos, at a comparable stage. *c*, chorda; *e*, entoblast; *m*, mesoblast, mostly somitic; *n*, neural organ.

This stage, common to all Chordates without exception, is moreover of a short duration. Among Prochordates, the Ascidiae immediately show a scission of the mesoblast in *mesenchyme* and *myoblast*, containing the future muscular cells.[1] In *Amphioxus*, the same mesoblast remains partly continuous with the archenteric wall; it takes the aspect of the well-known saccules, at first symmetrically disposed; later, when these saccules have been pinched off, the perfect symmetry is modified by the appearance

[1] The "caudal mesenchyme" is simply a posterior group of less differentiated cells, later transformed into muscle cells.

of diverticles of the future pharynx, a larger right one displacing the right saccules slightly backwards. In the young embryos of Vertebrates, cephalic neural crests appear on each side of the brain, while the cerebral vesicle constricts in three distinct parts, the anterior one expanding laterally into primary optic vesicles. A loose mesoblast, mostly of mesenchymatous aspect, fills up all the free spaces of the now quite distinct head. In the trunk, the dorsal mesoblast (epimere) shows a caudally progressing segmentary constriction into somites, which later on become entirely free from one another. The intermediate part (mesomere), corresponding to some of the first somites, forms a small block of cells, dorsally indented by the somitic segmentation. This rudiment of the pronephros preserves its continuity with the ventral mesoblast (hypomere), which fills the space between the lateral wall of the archenteron and the epiblast. The material of the *lateral plates* is soon separated, by a new arrangement of its cells, into an external and an internal layer, the *somatopleure* and *splanchnopleure*, forming the *coelomic linings*. The entoblast is now distinctly divided into a pharynx, the lateral wall of which is pushed outside in two, three or four branchial pouches, and a broader, nearly tubular enteron. The primordial organs, when fully constituted, are remarkably similar throughout Chordates (figs. 1, 41).

This accomplishment of a uniform result is, however, attained by a development which is clearly subject to considerable **variation according to the zoological position** of the species.

Between Prochordates and Vertebrates, we first notice that, at the blastula stage, the cells of the former are placed in a cuboid or cylindrical epithelium, while those of the latter, especially in Anamniotes, are arranged in a pluristratified wall (fig. 2). Such a difference is not only quantitative but also indicates that, in the second case, cleavage has been more pronounced before the appearance of the formative movements. Another contrast, much more important, consists in the position occupied, relatively to the axis of the egg, by the materials which are to form the various organs. But it would be premature to discuss this matter before having studied the functional features of the presumptive territories in the whole Phylum.

Considering the Vertebrates, the quantity and the density of the vitelline reserves affect the development in a marked way. It causes cleavage to be partial in the case of all telolecithic eggs and considerably complicates their gastrulation. But it is well known that Sauropsides present embryonic aspects (fig. 5) which are extremely different from those of Teleosts or Selachians (fig. 3). The site of the invagination, the appearance of the first visible structures, and the chronology of the processes are all affected, and an interpretation will only be possible by the judicious combination of the cytological and vital staining methods. It will, however, be convenient to examine separately the mode of **formation of the entoblast**. This question has been recently solved, in my opinion, by the study of serial sections. Its consideration will clear the way for a more general analysis.

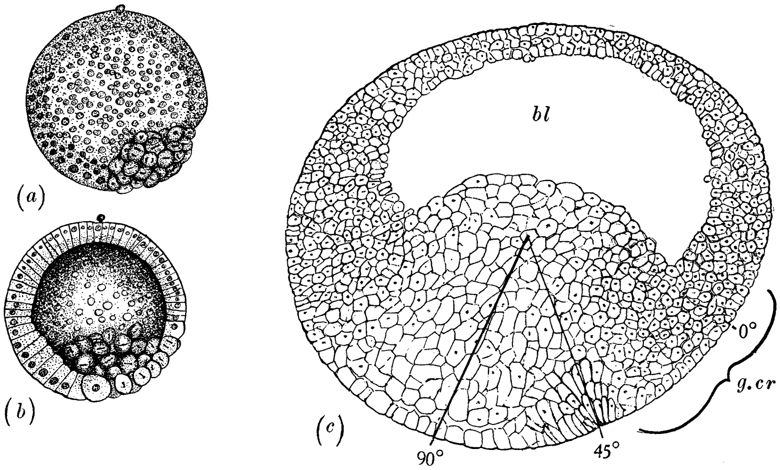

Fig. 2. Difference in the arrangement of the cells, at the incipient gastrula stage, between Prochordates and most of Vertebrates. (*a*) and (*b*) Very young gastrula of *Amphioxus*, whole mount seen from the left side (*a*) and in optic sagittal section (*b*). The conspicuous rounded cells, many of which are in division, are the mesoblastic ones. Redrawn from Conklin, 1932. (*c*) Early gastrula in *Discoglossus pictus*. The exactly sagittal section shows the place where invagination begins, exactly at equal distance from the equatorial plane and the vegetative pole. *g.cr*, average position of the gray crescent. *bl*, blastocoel.

In the case of Amphibians, it is perfectly evident that the entoblast is represented by the vegetative blastomeres. The