EVOLUTION, GENETICS AND RECAPITULATION

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ONTOGENY AND PHYLOGENY

TWO facts are of central importance in Biology. *One*: every living being starts its existence as a single cell, the fertilized egg or zygote. By a series of changes involving division and differentiation, it becomes the adult organism. This is ONTOGENY. *Two*: the species, during the course of its evolution, traces a series of stages in its history beginning with the single-celled animal. This is PHYLOGENY. The striking parallelism between the two,—the history of the individual and the history of the species,—was noticed earlier by several biologists but it was given to Ernst Heinrich Haeckel (1834–1919) to make a comparison and propound a law. The Biogenetic Law or the Theory of Recapitulation states simply and in the fewest of words, 'Ontogeny recapitulates Phylogeny'. Expressed in simple language, 'the embryo in its development retraces its evolutionary path or climbs its family tree from the one-celled ancestor up to the present. The adult stages of ancestral forms are repeated but they are now to be found in the earlier stages of ontogeny'. The embryo of the bird and the mammal show gill slits and these according to Haeckel represent the *adult* fish ancestors in their phylogeny. The zygote was compared to the single celled protozoan ancestor, the blastula to Volvox, the gastrula to Hydra and so on.

Thus was built by Haeckel an edifice of 19th century biology incorporating the remarkable and often incomprehensible phenomena of individual development with the immense data furnished by palaeontology, anatomy and taxonomy as evidences for organic evolution. Charles Darwin's epoch-making book on the Origin of Species had just appeared and the embryologist in Haeckel put the facts of ontogeny into the framework of phylogeny of Darwin.

It was an astounding statement. That the embryos of higher animals record in their development the characters of the *adults* of lower animals and that evolutionary changes are added terminally at the end of development were not only new; they were revolutionary. In Haeckel's own words, "Ontogeny is the short and rapid recapitulation of phylogeny . . . During its own rapid development an individual repeats the most important changes in form evolved by its ancestors during their long and slow palaeontological development" (Generelle Morphologie der Organismen, 1866). It was natural and understandable that it evoked a great deal of discussion and criticism.

HAECKEL AND RECAPITULATION

Haeckel's personal influence was so widespread that his theory found its way into areas far removed from biology. 'Ontogeny recapitulates Phylogeny' came to be an oft-quoted phrase in anthropology, sociology, psycho-analysis, primary education and child development. That the child was closer to the animal and the savage than the adult became acceptable; it became acceptable too that the adults of the lower races of man were like the children of the whites. Haeckel himself believed this and was perhaps one of the earliest apostles of racial purity and supremacy of the white races, which came to assume such hideous manifestations two generations later in Germany. Aggressive and versatile if not profound, domineering and brilliant, Haeckel became a powerful force in the scientific and social scene of 19th century Germany, vanquishing his opponents as much by his ruthlessness as by his evangelic fervour. K. E. Von Baer (1792–1876) stood practically alone to refute Haeckel and argued that the developmental stages of higher organisms display the characters of the embryos of lower organisms (not of the adults) and produced massive evidence against the recapitulation theory. But this was to little avail. Haeckel's enthusiasm and personality prevailed and though his scientific colleagues rejected his theory, the appeal to the general public was so striking that its influence prevailed for a long time. The issue turned into an emotional one and Haeckel became a scientist cast adrift on a sea of metaphysics. Even during his lifetime Haeckel's faith in science waned and as he grew older it gave way to a romantic philosophy. His credibility lost, he was reduced to fulminating against religion, yet unyielding in his belief that his concepts and ideas would finally prevail.

GENETICS AND RECAPITULATION

While it was possible for Haeckel to browbeat and shout down his opponents during his lifetime, as facts of genetics accumulated, as Mendel's findings became known, Haeckel's original assumptions lost much of their validity. Experimental embryology which arrived on the scene at the same time helped drive away recapitulation from the supreme position which the descriptive embryologist in Haeckel had provided for it. Indeed, genetics and experimental embryology rendered Haeckel's recapitulation theory untenable.

It is now 50 years since Haeckel's doctrine has been abandoned and yet a prominent biologist/palaeontologist is prepared to pursue the subject and make a 500 page book out of it. Stephen Jay Gould* does this, not out of any special act of courage or personal interest. He is convinced that the subject is as important today as it has ever been.

Properly restructured, it continues to be the central theme of evolutionary biology, for it illuminates two fundamental issues of contemporary importance: *(a)* evolution of ecological strategies, and *(b)* biology of regulation. The importance of ecology and its control of individual development have been recognized only recently. It is one thing to declare that the embryological structures met with in the development of a higher animal are not the representatives of the adults of lower organisms but of their embryos. It is quite a different thing to explain why they occur at all. Why do gill slits appear during the development of a bird or a mammal? How can we account for the striking parallelism between the individual development of an animal and the evolution in time of the phylum to which it belongs? Haeckel's dictum of Recapitulation may be said to have been laid to rest but the facts revealed during development which struck Haeckel and which led him in the first instance to propound his doctrine are still there and demand an accounting.

Stephen Gould attempts to do just this. He exploits the recent findings of gene function to account for the parallels between ontogeny and phylogeny. He argues that changes in developmental timing (heterochrony) can explain the origin of embryological structures in higher animals reminiscent of those of the lower ones. Gill slits exist in the mammalian embryo because they have never been lost, not because they have in some mysterious way been pushed into the embryo. Understood in terms of genetics, the appearance of gill slits in a terrestrial animal is an indication of the presence of genes that code for them and that these genes have not been eliminated by natural selection. The rejection of Haeckel's dictum is not a repudiation of all embryological evidence for evolution; indeed, in the light of modern genetics, it is an essential testimony of the relationship between ontogeny and phylogeny. To cite a notable example, the understanding that the three disparate adult types,—the free living shrimp, the sessile barnacle and the parasitic Sacculina,—all belong to Crustacea is made available by the presence of the nauplius larva in all the three. Ontogeny is an indication of genetic affinity rather than evidence of resemblance to the adult ancestor.

Terminal Addition of characters is one of the necessary laws of recapitulation. Haeckel argued that new evolutionary features are added at the end of ancestral ontogenesis so that adults of earlier animals become pre-adult *stages of the descendents.* It was essential for Haeckel's theory that the evolution of higher animals over the lower, lay in the 'terminal addition' of features exclusive to the former over those of the latter. We now know that genes act at any time, not terminally. Evolution is not by superposition. It is organic change in phylogeny.

STRUCTURAL AND REGULATORY GENES

Structural genes are important but even more important to the process of evolution are the genes that regulate their activity. Regulatory genes hold the key not only to morphological diversity but to the entire instability and non-equilibrium in the biological world. Gould's book draws attention to genetic regulation as none else does, indeed perhaps as no publication on genetics does, for while regulation is interesting to the geneticist, it is to the student of evolution that it has the supreme message. The student of comparative anatomy and embryology is struck not only by the variety of structures he meets with in his studies but also by the timings of their appearance during development; and while Haeckel and his supporters could not offer an explanation, modern genetics is able to account for them. Changes in the relative time of appearance and rate of development of characters should adequately explain the variations in morphology of organisms. The *young* of the chimpanzee resembles man most, the *adult* least, due to negative allometry of the brain and positive allometry of the jaws. Humans and chimpanzees are almost identical in structural genes: the difference lies in the regulatory system that slows down the general rate of development and the introduction of heterochrony. The parallels between ontogeny and phylogeny which Haeckel regarded as recapitulation are really the effects of differences in developmental timing.

Most evolutionary events are controlled by regulatory genes and regulation is the most important factor in evolution, the major stuff of evolutionary change. The displacement in time of the appearance and development of one organ with reference to another

* *Ontogeny and Phylogeny* by Stephen Jay Gould (Harvard University Press, Cambridge), 1977, Pp. ix+501. Price: $ 18·50.

is of the greatest importance. This is the major contribution of modern genetics to biological evolution.

Gould's emphasis on regulation of gene activity in no way minimises the origin of new characters. Indeed, he recognises that evolution is under the influence of two major events: (*a*) introduction of new characters accounted for by structural genes, and (*b*) changes in the characters already present brought about by changes in developmental timing, due to regulatory genes. The relative importance of these two in the process of evolution has been Gould's major concern. Indeed 'Ontogeny and Phylogeny', is a critical exposition of genetic regulation and not merely a reassessment of Haeckel's Recapitulation theory. It is a profoundly important discussion on the concepts of evolution in the light of modern knowledge, not merely a re-examination of the relationship between ontogeny and phylogeny. It is also a historical assessment of the Biogenetic Law, a judicious examination of what can be salvaged from the original formulation of Haeckel and what needs to be altered and conditioned in the light of modern ideas in biology. A major book.

A COMPARATIVE STUDY ON ACETYLCHOLINE AND ACETYLCHOLINESTERASE DURING DEVELOPMENT OF THE LEPIDOPTERAN *PHILOSAMIA RICINI* AND THE DIPTERAN *SARCOPHAGA RUFICORNIS*

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ABSTRACT

Acetycholinesterase activity and acetycholine content in the larvae, pupae and adults of both sexes of *P. ricini* and *S. ruficornis* have been studied and their physiological role in cholinergic system discussed.

INTRODUCTION

DETECTION of several insect neurosecretory substances distinct from those connected with growth and metamorphosis has recently been made. The most well known among them being acetylcholine and acetylcholinesterase.

Acetylcholine is considered as a neurotransmitter having a role in adrenergic transmission[1] and in general oxonic transmission[2]. The latter role, however, has been challenged or modified by others[3].

Insect neurosecretory compounds have been the topic of several reviews[4,5] and recently Smallman and Mansingh[6] summarized the existing data on the distribution of acetylcholine in various insect tissues and at different stages of development. However, lack of information on the neurotoxicology of the lepidopteran *P. ricini* and the dipteran *S. ruficornis*, both of considerable importance, prompted the study on the two neurosecretory compounds during development of these insects.

MATERIALS AND METHODS

Rearing of *P. ricini* and *S. ruficornis* were carried out as described by Pant and Agrawal[7] and Pant and Kumar[8] respectively.

6 hour starved larvae, pupae and adults were randomly selected from colonies of known age and homogenized to 10% (w/v) tissue concentration as described by Pant and Morris[9].

Acetylcholinesterase activity and acetylcholine content were assayed by the method of Hestrin[10] as modified by Metcalf[11].

All assays were made in duplicates on three individual homogenates prepared from 10 insects each and the average values were calculated.

RESULTS AND DISCUSSION

Acetylcholinesterase activity in the lepidopteran *P. ricini*, during fifth instar development, gradually declined but on commencement of spinning increased three-fold. During larval–pupal transformation from day 2 onwards till day 5, 90% activity of the enzyme was lost thereafter, it maintained a very low activity all through the quiescent pupal development (Fig. 1).

Acetylcholine, on the other hand, maintained nearly a constant concentration till spinning commenced but gradually got depleted till day 5 and remained steady in the metamorphosing pupa till 15th day (Fig 1). In the newly emerged both acetylcholinesterase activity and acetylcholine concentrations increased significantly. All along development, acetylcholine maintained a marked higher level than the esterase.

In the dipteran *S. ruficornis* both acetylcholine and acetylcholinesterase activity (Fig 2) increase during