Application of the Principles of Phylembryogenesis to the Protista

THE real relation between ontogeny and the adult stages of ancestors (phylogeny) in multicellular organisms (Metazoa and Metaphyta) is now firmly established in the sense that ontogeny is not an abbreviated or modified phylogeny, that is, the stages of development of an individual do not correspond to the adult forms of the ancestors, as was required by the so-called biogenetic law or theory of recapitulation propounded by Ernst Haeckel. All stages of ontogeny are subject to hereditary changes of evolutionary character. Moreover, the greater changes achieved in the early stages of ontogeny, resulting in pædomorphosis and neoteny, appear to be the most important from the point of view of large-scale evolution (macro-evolution). The changes brought about in later stages of ontogeny, resulting in gerontomorphosis, have an adaptive and specialized significance (Garstang, Sewertzoff, de Beer, Hadži).

The question may be asked whether these principles can be applied to the ancestors of the multicellular organisms, that is, to the Protista. In these there is no ontogeny but only a succession of different generations during the life-cycle.

In attempting to answer this question, we have first to compare the life-cycles of Protista with the ontogenies of multicellular forms, in order to establish which phases of the life-cycle of the former correspond to which stages in the individual development of the latter. Next, we must discover whether in the Protista hereditary changes of an evolutionary character make their appearance at all phases of the life-cycle. Analysis and comparison of a few examples selected from among Protista and multicellular forms have revealed which are the corresponding phases in the life-cycle of Protista and in the ontogenies of multicellular organisms.

In the Protista, the chief phases (some of which also comprise sub-phases) take the form of generations, such as the vegetative, progamic, gametic and metagamic generations. The most important phases in the Metazoa are the vegetative and the metagametic (= ontogenetic) phases, while the progamic phase is always enclosed within the gonad. The gametic phase is either free, as in most Protista, and associated with external fertilization, with the exception of the Infusoria; or it remains enclosed within the vegetative phase and is associated with internal fertilization.

Comparisons of the life-cycles of various types of Protista have shown with certainty that evolutionary changes have occurred in all phases or stages of the life-cycles. Larger and more rapid changes involve whole generations, while smaller and slower changes, having the character of adaptations, may be effected within single phases or generations. It therefore seems legitimate to apply the modalities of the development of multicellular organisms (phylembryogenesis of Sewertzoff, pædomorphosis of Garstang, gerontomorphosis of de Beer) to the conditions in the Protista.

In order to illustrate this idea, I propose to take the example of the Euciliate Infusoria as representatives of the Protozoa. Mention should first be made of *Paramecium*, with its rather complex life-cycle. Between the ciliates and the flagellates, which are doubtless their ancestors, there are many differences unbridged to-day by any intermediate forms. The switch-over to a single generation, namely, the vegetative generation, must have occurred by means of a rapid evolutionary change in the history of the ciliates. The remaining three generations, namely, the progamic, gametic and metagamic generations, in the ciliates are enclosed within the vegetative generation and therefore no longer appear as separate entities. Furthermore, the ciliates have become hermaphrodite.

Even the metagamic phase, which corresponds to the ontogeny of multicellular forms, has in ciliates undergone deep change and remains enclosed within the vegetative phase. This metagamic phase is, in fact, changed in so far as the meganucleus of the vegetative phase disappears. During the transition from the Protista to the multicellular condition, the gametic phase became independent and free again as a result of cellularization.

My second example, which I should go so far as to call a case of pædomorphosis, is to be found among the Folliculinidæ (Infusoria, Heterotricha). Here the entire sexual part of the life-cycle (progamic, gametic and metagamic phases) has vanished, and a new, free, vegetative phase has appeared instead, because the old vegetative phase or generation has become sessile.

It is probable that bacteria and viruses may be found to provide examples among the Protista of the applicability of these principles. In such cases, the macro-evolutionary changes would be of a retrogressive character associated with the specialization in adaptation to saprobiotic and parasitic modes of life. The theory of phylembryogenesis might in a general way be applied to viruses and throw new light on their nature and origin. The opinions which microbiologists hold on bacteria and viruses are very divergent; but on the interpretation here suggested, it is possible that viruses may be ascribed to the proper position in the natural system. By comparing the life-cycle, we arrive at the conclusion that viruses were evolved from spore-forming bacteria, in adaptation to conditions of extreme parasitism within the cytoplasm of foreign cells.

In this manner, viruses would reach the level of organization of bacterial spores, decreasing the size of their bodies and simplifying their structure and metabolism. The loss of the entire sexual phase would not in any way invalidate the applicability of the principles and modalities of phylembryogenesis.

I believe that further application of these principles to cases in the Protista will have results as fruitful for the study of Protista as they have already had for multicellular forms.

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'Spiral' Roots in Agar Cultures of *Marsilea*

THE general conditions for the preparation and growth of sterile cultures of the heterosporous fern *Marsilea* have already been described[1-3]. It was shown[3] that, with glucose as carbon source, much better growth was obtained in liquid than on agar media. During further work on this subject an unusual phenomenon was observed in the root system of the agar cultures.

As shown in Figs. 1*a* and *b* and Fig. 2, many roots have pronounced helical ('spiral') growth especially in the more slender regions nearer the tips. In most of the roots the spiral follows the same course, that is, anticlockwise towards the apex, although a few roots have a clockwise spiral. An occasional root, for example, the conspicuous spiral root of Fig. 1*b*,