

# THE LOWER METAZOA

**COMPARATIVE BIOLOGY AND PHYLOGENY**

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Edited by ELLSWORTH C. DOUGHERTY, ZOE N. BROWN,  
EARL D. HANSON, AND WILLARD D. HARTMAN

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# The Lower Metazoa

## COMPARATIVE BIOLOGY AND PHYLOGENY

EDITED BY Ellsworth C. Dougherty

IN COLLABORATION WITH

Zoe Norwood Brown • Earl D. Hanson • Willard D. Hartman

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## PREFACE

The present volume traces its origin to the Second Annual Symposium on Comparative Biology of the Kaiser Foundation Research Institute, a meeting almost entirely supported by a grant from the National Science Foundation (G-14066). It was held September 6-9, 1960, at Asilomar, Pacific Grove, California, and September 10, 1960, at the Kaiser Center, Oakland, California. Ellsworth C. Dougherty was expected to be editor of the resulting proceedings, but unforeseen circumstances forced his withdrawal at a crucial time. Editorial work was then undertaken by Dr. B. G. Chitwood, Dr. M. M. J. Lavoipierre, and especially Mrs. Ruth Straus, Editor in the Department of Scientific Publications, Kaiser Foundation Hospitals. Delay due to various difficulties followed, and the Kaiser Foundation Research Institute finally decided to withdraw sponsorship, to return manuscripts to participants, and to release all papers for publication under other auspices at the discretion of the contributors.

At several requests of Symposium participants and other interested persons, Dr. Dougherty and colleagues Mrs. Zoe N. Brown, Dr. Earl D. Hanson, and Dr. Willard D. Hartman undertook to constitute a somewhat comparable volume. This has been accomplished with the result of a book differing only moderately from what the original Symposium would have produced. There have been up-datings or changes of contents of papers by certain workers; a few contributions have been deleted at the decision of the authors; and a few new papers have been inserted. The publication of the volume has been made possible by a generous donation from the Cocos Foundation, Inc., 810 Fletcher Trust Building, Indianapolis 4, Indiana.

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# INTRODUCTION

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By comparison with most other animal groups, the lower Metazoa are relatively neglected. There remains an immense amount of fundamental taxonomic, morphological, and physiological work to be done before we have a reasonably clear picture of their biology. Somewhat more advanced in these connections is the rich and busy discipline of "protozoölogy."<sup>1</sup> Also in the animal sciences there are thriving studies of such advanced forms as vertebrates, arthropods, molluscs, and echinoderms, to name most. But between the "protozoa" and these higher metazoa are diverse assemblages, many of which have been relatively little explored. One must except, to be sure, the parasitic groups, which annoy man enough to be rewarded with a wealth of attention; but, for free-living members of most major taxa that loosely can be called the lower Metazoa, there are comparatively few investigators.

When the meeting that formed the basis of what, after much delay, has become this volume was conceived in 1960, it was not my expectation to see emerge an encyclopedic tome treating all the lower Metazoa equally. Rather I strove for a sampling of work in different disciplines, with a consequent cross-fertilizing of ideas. My reasons for being interested in the lower Metazoa were, first, that for almost a decade and a half much of my own research had been done with certain of them, special concern having thus been evolved; and, second, that I was, and remain, much intrigued with the unresolved questions of their origin *vis-à-vis* the "Protozoa" and of their interrelationships. It was evident, from scanning the literature of recent years, that there was a group of distinguished European phylogeneticists and another group of American and that the latter, at least, had relatively little knowledge of what the former were writing.

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<sup>1</sup> Protozoölogy actually comprehends the study of a *pot pourri* of forms, some of which are shared amicably with the botanists; perhaps a happier alternative would be to eliminate, at the level of unicellular forms and the multicellular algae, the animal-plant distinction and to use instead of a unifying term such as "protist," with words "animal" and "plant" left for the Metazoa and Metaphyta respectively.

So it seemed a felicitous notion to bring together the principal students—those consenting—from both sides of the Atlantic and elsewhere for first-hand discussions. Invitations were extended to the leading authorities, but, of course, could not all be accepted.

A prime feature of the meeting was a round table discussion where opposing views were argued on the origin of the Metazoa and allied problems. For suggesting this we are indebted to Dr. Earl D. Hanson. Otherwise the persons invited were free to talk about any subject, including ones transcending the lower Metazoa, provided that the latter organisms were basic to the discussion. It was originally hoped to see represented the taxa (phyla) Porifera, Mesozoa, Platyhelminthes, Rhynchocoela (Nemertinea), Coelenterata (Cnidaria), Ctenophora, Acanthocephala, Aschelminthes, and Entoprocta. In this volume one or more aspects of all groups save the last are treated, and the list has been extended to the Ectoprocta with the insertion of Dr. Dietrich Schneider's paper, which was not on the original program.

Although the book that is finally emerging largely coincides with the addresses at the meeting, several papers were withdrawn because of delay in publication. But a number of contributions offered in substitution have been included. The original tenor of the meeting has thereby been largely retained. A detailed summary and synthesis based on the diversity of papers that follow would be beyond the scope of a short introduction. Rather than offering further, necessarily superficial review of the contents of this volume, I feel it more useful to take this opportunity to formulate a generalizing idea, much of which the meeting brought into focus.

The concept revolves about the time-honored problem of homology *vs.* analogy in biology. For the most part we know perfectly well what we mean when we use these terms. The wing of a bird is homologous with the pectoral fin of a fish, but merely analogous (convergent in function) with the wing of a butterfly, in the latter instance because the similarly named bird and butterfly appendages are flying organs without phylogenetic connection as usually reckoned. But I should like to interject a concept that, if it has any virtue at all, may help resolve some of the argumentation about the significance of homology *vs.* analogy in the never-never land between protist and metazoön (and in other biological domains as well).

As a working hypothesis I suggest that most of the crucial evolutionary "ideas," both structural and biochemical, were evolved very early, and, once realized, have, by a sort of "principle of genetic parsimony," never really been discarded even though we may lack, at our present stage of knowledge, either morphological or physiological evidence of certain features in the life cycle of a given organism today. What has primarily happened is that, where a basic attribute is not expressed, genetic information has been merely shuffled about and put to other use, but remains in the genome of the organism and, under appropriate situations, is ready for utilization—given time to be genetically mobilized, of course.

This concept can lead to seemingly far-fetched speculations. For example, I wonder if the sort of genetic information that enables serial replication to give, say, a string of bacteria is not called upon (with added genetic ammunition, of course) to make possible serial replication at much higher levels: cestode strobilization; metamerism generally; and so forth. If the living world is looked at through the eyeglass of such a principle of genetic parsimony, many things that seem convergent or parallel (and are so in the sense they are generally conceived) have an

element of homology. If you recoil at conceiving of *homology* between linear sequences of bacteria and cestode strobili, we can perhaps compromise with a different word—*metalogy*, let us say.

For ultimate testing of the concept of metalogy, those that must be asked are not we more or less orthodox invertebrate zoölogists (who are in no position—so far as I can see—to test such a hypothesis), but the geneticists and molecular biologists. They are the ones that might ultimately provide the DNA blueprints, if such exist. The question really is: is novel genetic information, once acquired, too precious to be thrown away; may it perhaps be shifted about and put to seemingly different use, but, like the genie in the bottle, remain to emerge again in its earlier form and so engineer the repetition of conditions that by most usual conventions would be termed non-homologous?

If this is a valid idea, then a great deal of the argumentation on homology vs. analogy in phylogeny at the metazoan level really misses the mark. The answers lie not in relatively recent (I mean 600,000,000-year-old) events, but two billion or more years earlier when basic genetic ideas were first really formulated; thereafter they have kept cropping up—*inter alia* to bedevil today the phylogeneticist trying to make sense out of a metalogy that is far more archaic than he may imagine.

More than a year ago I went to a doctoral oral examination on some serpentine gymnostomatous ciliates. If I had not been forewarned, I should have thought that at one point I was seeing slides depicting the anterior end of gastrotrichs and, from the view of the posterior end of the same animalcules, of nematodes. It made me ask myself: are these mere examples of convergence (in the traditional sense) or are they metalogous—that is, have our modern aschelminths brought into use genetic information that was fashioned two billion or more years earlier by organisms much further down the evolutionary scale?



# **I. Comparative Morphology and Phylogeny**

## **A. GENERAL ORIGIN AND AFFINITIES**



# 1 ♦ Homologies and the Ciliate Origin of the Eumetazoa

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The elucidation of phylogeny is dependent on the identification of homologies (Remane, 1956). In an earlier paper (Hanson, 1958), reviewing the problem of the phylogenetic origin of the Eumetazoa, it was shown that the acele Turbellaria share many similar features with certain gymnostomatous ciliates. On the basis of these similarities—homologies were, at that time, specifically avoided—it was concluded that there could exist a phylogenetic relationship between aceles and ciliates such that a ciliate-like form was ancestral to both groups. This conclusion, based simply on similarities, has been criticized as having an insufficient basis for phylogenetic speculations (Grimstone, 1959; Nursall, 1959; Dr. Rudolph Jander, through personal discussions). The purpose of this presentation is to reexamine the data presented in the paper just alluded to, and determine if any of the similarities noted there are indeed homologies.

The most significant analysis of the problem of homologies is that of Remane (1956). This eminent morphologist has developed criteria that can be used to identify homologous structures and at the same time exclude parallelisms and convergences that have been mistaken for homologies. The major part of this paper will be devoted to an examination of the Remanian criteria of homology and their application to the possible ciliate origin of the acele Turbellaria. First, however, there must be presented, at least briefly, arguments in favor of the primitive nature of acele organization, as opposed to its interpretation as being secondarily reduced, for, if the Acoela are not the most primitive of the free-living flatworms, there would be no point in comparing them to the ciliates for phylogenetic purposes.

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This paper was written while the author was a fellow of the John Simon Guggenheim Foundation for 1960–1961.



### The Primitive Nature of the Acoela

This problem can be approached by listing three features typical of forms usually widely accepted as showing structural and functional reductions. These are often parasitic forms (*e.g.*, cestodes) or sessile forms (*e.g.*, tunicates).

1. Reduction is the result of adaptation to a special mode of life.
2. Not all characters of the organism are reduced; certain are of continuing significance to the biology of the organism and hence are preserved without reduction and often evolve to a more specialized level.
3. Embryologically there is often evidence of reduction through the transitory appearance of embryonic structures that are suggestive of a more complex ancestral form.

Taking these three points in order, we see, first, that there is no evidence that the simplicity of the aceles relative to other Turbellaria is the result of adaptation to a mode of life conducive to the reduction of body parts. Aceles are herbivores, carnivores, and ecto-commensals. There are also benthic and pelagic forms. All of these forms, pursuing very different modes of living, show a characteristic acele organization, and to argue that in all cases the postulated reduction is an adaptatively significant change is simply not convincing.

Next, we note that those favoring the secondary reduction of acele characters argue that *all* major structures—epithelium, gut, excretory apparatus, genitalia, nerve net, contractile fibers, etc.—are reduced. Not a single organelle system remains that is not affected. This is not the case in well-established examples of reduction.

Third, there is only one embryonic character in the Acoela that suggests the possibility of reduction, and that is the occurrence of cellular blastomeres in the early cleavage. These cell boundaries disappear when the young worm hatches or shortly thereafter. Another explanation for this phenomenon is, however, possible—namely, that this is the only way the fertilized egg can develop. Such a suggestion will be inconceivable to those convinced by the biogenetic law that metazoan embryogenesis must always recapitulate something, and that the cells in early acele embryos are such a recapitulation. This point is discussed again later in the context of the origin of acele embryogenesis; further details are therefore deferred until that discussion.

In brief, no convincing argument for reduction is possible. To compare acele structures with their counterparts in other turbellarians and then simply “interpret” the differences as reduction is to argue without explicit criteria. When, however, such criteria are used, as above, the conclusion in favor of reduction of structures remains unfounded. On the other hand, to argue for the primitive nature of these structures is to argue for a lack of excessive specialization. Excessive specialization can result in highly complex structures or in much simplified ones. The first are relatively obvious and do not constitute a problem in the Acoela. The second are the same as reduction and can be recognized by the criteria suggested above. In the case of the Acoela, lack of fulfillment of these criteria and the absence of structures of obvious evolutionary complexity exclude the possibility of consider-