The Origin of Major Invertebrate Groups

Edited by
M. R. House

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Preface

Since it was formed in 1937 the Systematics Association has been a forum for discussion of general theoretical and practical problems of taxonomy and systematics. Advantage has always been taken of the fact that venues in the British Isles normally allow a wide range of British specialists to attend symposia and to contribute to the discussions. Occasionally, finance allows other overseas speakers to be invited to attend and, in addition, overseas participants have always played a significant role in the Association functions.

The theme set for the meeting held from 19–21 April 1978 at the University of Hull, which is recorded in this publication, was a broad one, of interest to most zoologists and geologists. It was deliberately organized to bring neontologists and palaeontologists together, and although the latter outnumbered the former among the formal contributors, in discussion the balance was almost equal. Some selected points arising from the discussions are included in a final section based on recordings of the discussions and written contributions, but this cannot be more than a weak reflection of the informed, lively and witty exchanges which took place, nor does it enlarge on the numerous occasions when it had to be acknowledged that we were in ignorance of so much that was relevant.

How far, it may be asked, is the pursuit of certainty in matters relating to the origin of major invertebrate groups merely the pursuit of a will-o'-th-wisp? The chase, after all, has been going on for long enough, and this is but one of many contributions to it. I think the participants regarded the symposium more as an opportunity to discuss a review of current ideas on origins, and attenders were particularly indebted to the many speakers who were prepared to attempt a synthesis for their approval or criticism. In particular I am indebted to them for accepting my invitation to address the symposium and contribute to this volume.

The symposium was overshadowed by the death of Peter Sylvester-Bradley, who died the day before he was scheduled to give the opening address. This volume is dedicated to him. His loss meant not only that the discussion of Precambrian events lacked the main person who could have contributed so much to the subject, but the whole symposium felt the absence of one whose stimulating ideas and comments have done so much to enliven symposia of this sort in previous years. Dr T. D. Ford, at the shortest notice, gave an address of which he gives a brief report here, and the symposium was especially indebted to him.

The symposium was attended by about 125 participants from some 13 countries. Much of its success is due to the organizational work of Dr and Mrs M. D. Brasier and other staff of the Department of Geology and to the help of a range of others at the University of Hull. To these, and to the contributors and participants, are due the sincere thanks of the Association and not least to the members of Academic Press who have, once more, given great aid in the production of a symposium volume.

March 1979

M. R. HOUSE
President

Contents

1 | Precambrian Prelude

*P. C. SYLVESTER-BRADLEY

Abstract: Although the taxonomic division of all life into two kingdoms, animals and plants, has for a long time been abandoned, a physiological division into *heterotrophs* and *autotrophs* has taken its place. Recent research has shown that even this is an unjustifiable simplification. Since its origin and inception, life has developed more than two ways of capturing its energy.

In this paper, rival theories relating to the ancestry of animals are compared, and tested against available evidence. A model claiming methanogenic bacteria as the most primitive of all organisms is examined in the light of the geological record. Special attention is paid to the origin of sex and its importance with reference to models of diversification. Preference is given to what is termed the "dumb-bell" model (Fig. 1), in which the origin of life brings to an end a period of 1000 m.y. (million years) in which there was a multiplicity of protolife; it is followed by 3000 m.y. characterized by stasigenesis and relative uniformity. Then comes the third period, beginning in upper Proterozoic time and lasting another 1000 m.y., in which the origin of the nucleus is quickly succeeded by the origin of sex, of plants and of the Metazoa. The first example of adaptive radiation takes place, and this is followed by the Phanerozoic explosion of diversity.

THE MOST PRIMITIVE ORGANISMS: BIOLOGICAL EVIDENCE

The division of all life into two kingdoms, Animalia and Plantae, was always based more on their physiological distinction than on their phylogenetic record. For logically it seemed clear that if animals and plants were both derived from a common ancestor, then three kingdoms were necessary, not two, and a glance at any text-book of fifty years ago will show that both kingdoms were regarded as derived from the Protista, which could not therefore be included in either kingdom. "There are some

* Professor Bradley died before the symposium began. This contribution represents the only part of his paper assembled for publication. To this has been appended a list of Professor Bradley's papers in this field. This has been assembled by Dr T. D. Ford.

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types among the simplest and smallest creatures which share animal and plant characteristics, being able both to take in solid food like a typical animal, and to build up food from simple inorganic substances like a green plant. Such examples only show the impossibility of drawing hard and

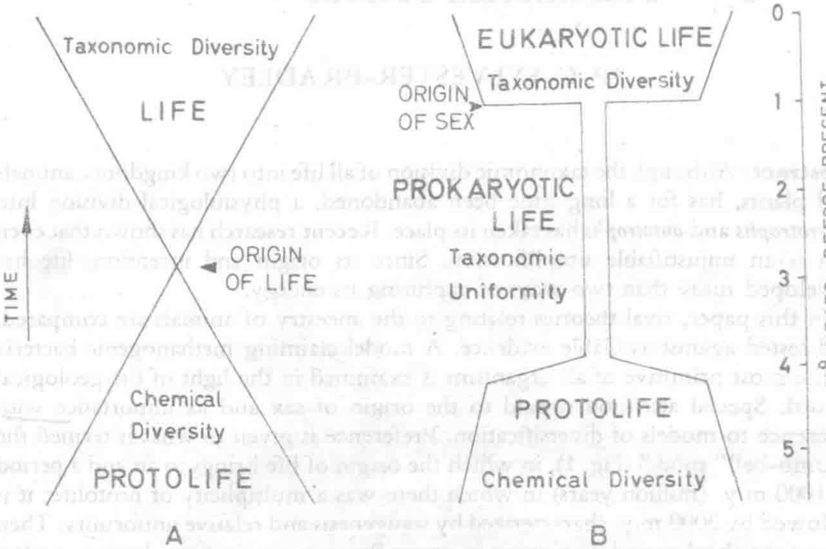

FIG. 1. Diagrams illustrating hypotheses on the early history of life. A, Pirie's hour-glass diagram. B, The dumb-bell model.

fast lines in Nature" (Haldane and Huxley, 1927, p. 5). The idea that the Protista should be regarded as a third kingdom had in fact already been proposed by Haeckel (1866, 1878) when he first introduced the term, and other naturalists of the same period suggested other names for the ancestral kingdom (e.g., "Protozoa", "Protoctista", "Acrita", "Primalia" etc.; see Whittaker, 1959, 1969).

Then, thirty years ago, it became apparent that a much more fundamental distinction could be drawn than that which exists between animals and plants, a distinction which applied not only to the physiology of the organisms concerned, but to the morphology of their very cell. These two divisions consist first of the eukaryotes, which include all animals, plants and protists, composed of individuals whose cells have a nucleus. Secondly, we have the prokaryotes, whose cells have no nucleus; these organisms are represented only by the bacteria and the blue-green algae. Moreover, the prokaryotes are considered not only to be more simply constructed than the eukaryotes, but to be more primitive and, in fact, ancestral to them. The taxonomic significance of this distinction was first recognized by Kluyver and van Niel (1936), and a kingdom for their reception, the "Monera", was adopted in the four-kingdom system of Copeland (1938), with the plants (or Metaphyta), the animals (or Metazoa) and the protoctists as the other three. Further elaborations have been proposed, but the five-kingdom system of Whittaker (1969) and Margulis (1970), in which the eukaryotes are divided into four kingdoms (plants, animals, fungi and protists) and the prokaryotes form just one (the Monera) has, until very recently, become generally accepted.

But now there is some unease. First, it seems that the distinction between the prokaryotes and the eukaryotes is greater than that which exists between any of the four eukaryotic kingdoms. The Monera are cut off from the other four by a gap greater than that which divides the plants from the animals, the fungi, or the protists. There is considerable debate about how this gap was bridged in evolutionary history. Margulis has put forward a convincing theory which postulates that all four eukaryotic kingdoms have been derived from a series of symbiotic associations of various prokaryotic ancestors (Margulis, 1970). Counter theories postulate that the ancestral eukaryote evolved from a single prokaryotic ancestor that was larger in size than normal (Raff and Mahler, 1972). The theories need testing against each other. It is crucial to understand the environment in which the transition from prokaryote to eukaryote took place. Fossil evidence comes down very strongly in favour of a long period of Precambrian time in which only prokaryotes exist. But the evidence is less strong when we come to the recognition of the first eukaryote.

Before we come to this evidence, it is necessary to understand the second cause for the unease in accepting the current division of life into five kingdoms. Should the prokaryotes properly be grouped together in just one kingdom? It is now becoming clear that within the prokaryotes there are several distinctly different groups of organism that differ both in metabolic function and morphological detail (in so far as morphology comprehends the molecular sequences of an organism's genome). Woese and Fox (1977) would separate all life into at least three "superkingdoms" (or "urkingdoms" as they prefer to call them), in which all eukaryotes are grouped together as the "Urkaryotes", and in which the prokaryotes are divided into two groups, the Archaebacteria (composed of the methanogens) and the Eubacteria (the rest of the prokaryotes). Woese and Fox go further. First, they suggest that the Eubacteria and Archaebacteria are equally old, "in that branchings between the two urkingdoms are comparably deep" (see also Fox *et al.*, 1977); secondly, they contend that they are so different from each other that, if they arose from a common ancestor, that ancestor was more primitive than any known prokaryote, and that the prokaryotic level of organization was independently achieved in each branch. Although there is as yet no fossil evidence for the existence of methanogenic bacteria in the Precambrian, the ecological significance of such a possibility is considerable. They are unique in that they are restricted to anaerobic habitats in which they obtain their energy from the oxidation of hydrogen and the simultaneous reduction of carbon dioxide to methane (Bryant, 1974). Comment on Woese and Fox's ideas suggests that the methanogens may have played an important part in the evolution of Precambrian ecosystems (Maugh, 1977; Wilkinson, 1978).

Maybe there are other divisions within the prokaryotes, as important as those which divide the eukaryotes into kingdoms. For example, Lewin (1976) has demonstrated that a newly discovered kind of alga, symbiotically associated with ascidians, although certainly prokaryotic, cannot be regarded as one of the cyanophytes (blue-green algae), as their chlorophyll constituents have more in common with the eukaryotic algae. He has proposed they should be regarded as a new class, the Prochlorophyta. But a new class of what phylum, what kingdom? Do they form a link between the prokaryotes and the eukaryotes? It is easier to pose the questions than to supply the answers. As Stanier and Cohen-Bazire (1977) have shown, we have something more exciting to debate than any taxonomic conclusion. We have evidence in the Prochlorophyta of the polyphyletic origin of chloroplasts. Perhaps the Chlorophyta and Rhodophyta represent two separate phyla of Protists that have been independently derived, through endosymbiosis, from two separate phyla of Eubacteria, one a prochlorophyte, the other, one of the Cyanobacteria.

These new discoveries have not only complicated our simple classical picture of life divided into just two categories, animals and plants. They have also demonstrated that we can no longer rely even on the simplicity of the physiological distinction between autotrophs and heterotrophs, for life has developed more than two ways of capturing its energy. There is some suggestion that even from the earliest days there was heterotrophy of at least two kinds, represented by the Archaebacteria and the Eubacteria. Likewise there seem to be at least two kinds of autotrophy, each using a different kind of chlorophyll. But these complications have been introduced by the study of living representatives of primitive organisms. It is time to turn to the geological evidence.

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2 | Precambrian Fossils and the Origin of the Phanerozoic Phyla

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Abstract: Spheroidal and filamentous algae, some found in stromatolites, demonstrate the presence of Protistan life forms throughout much of Precambrian time. None can be shown to be ancestral to the late Precambrian Ediacaran fauna. Now known from many trace-fossils this appears to include primitive coelenterates, annelids, arthropods and other organisms of uncertain affinity, though proof of the assignations to these phyla is lacking and links to their Cambrian descendants are minimal.

INTRODUCTION

The Phanerozoic Phyla must have had ancestry in the Precambrian, and the purpose of this paper is partly to update those of Glaessner (1962, 1966), Cloud (1968, 1976), Hofmann (1971), Grabert (1973) and Schopf (1975, 1977, 1978) and partly to provide a basis for the discussions which follow. This paper has been hurriedly prepared and I apologize for its shortcomings. Professor Peter Sylvester-Bradley, whose death robbed us of having his thoughts on the origin of the Phyla, had prepared but a few pages of his address, and these are produced as Chapter 1: they deal largely with the origin of life and particularly with the environments and significance of such prokaryotes as methanogenic bacteria and their successors, the early eukaryotes. The evidence is mostly biochemical or by analogy with modern bacteria and algae. My task is to look at the fossil evidence itself. Professor Sylvester-Bradley has been a stimulus for many years, and it is

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a matter of regret that pressure of work in other fields prevented me from approaching this review earlier and more thoroughly.

Some hundreds of Precambrian fossils have now been named and described in the literature, more are as yet nameless. They fall into the following categories:

1. Organic microfossils
2. Stromatolites
3. Trace fossils
4. Dubio-fossils
5. Pseudo-fossils

The last two categories can be disposed of rapidly; dubio-fossils are those features of rocks or rock surfaces where there is doubt as to whether the feature is of organic origin or not. If this can ever be provided then the fossil will be transferred to another category. Pseudo-fossils are those which are now regarded as of inorganic origin though they were once described, and sometimes named, as true fossils. The names may be in the literature but they no longer have significance.

Body fossils such as shells, carapaces and coral structures are so far absent from Precambrian records; we are thus largely restricted to a survey of organic microfossils, stromatolites and a miscellany of impressions, the traces of the former presence of soft-bodied life forms.

ORGANIC MICROFOSSILS

Spheroidal and filamentous nannofossils of organic composition are now known from all the continents and from almost the whole range of Precambrian time. Reviews have been provided by Downie (1967); J. M. Schopf (1969); J. W. Schopf (1975 and in Ponnamperuma, 1977) J. W. Schopf *et al.* (1971, 1973); Schopf and Oehler (1976). The earliest claimed so far are from cherts in the Onverwacht Formation of the Barberton Mountains in South Africa (Brooks and Shaw, 1971). Dated at some 3300 m.y. (million years before the present), they are very small spheroids only a few microns in diameter. Cloud (1976) is less certain of the organic origin (but see Muir *et al.* in Ponnamperuma, 1977). Slightly later rocks, The Fig Tree Series, in the same area, have yielded rod-shaped and filamentous bodies, now reasonably well accepted as organisms (Barghoorn and Schopf, 1966; Schopf and Baarghoorn, 1967). Dated at some 3100 m.y. they have been compared with algae and bacteria.

A much more diverse flora occurs in the Gunflint Formation of the Lake