PARASITIC PROTOZOA

Edited by JULIUS P. KREIER

I

Taxonomy, Kinetoplastids, and Flagellates of Fish

Parasitic Protozoa

Volume I

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Preface

The parasitic protozoa are a large and diverse group. Many are of interest to physicians and veterinarians because they produce disease in man and his livestock. Others, which seldom produce disease, should be familiar to the practitioner of medicine and to the research scientist because they are present in the animal body and thus must be recognized to avoid a misdiagnosis, while still others, such as the intestinal and rumen protozoa, perform a useful function in the animal's economy, and their presence is an indication of health rather than disease.

I have included in these volumes protozoa parasitic in animals, such as fish and insects, which are not usually included in books on pathogenic protozoa. I did this because I believe veterinary medicine should concern itself with all species of animals, excepting man, whose care falls to the physician. From a more practical standpoint, I feel the inclusion of parasites of diverse species is appropriate in a book on protozoa of veterinary and medical interest because no matter how we set ourselves off from nature we remain a part of it, and thus we inevitably share parasites with the other species with which we live.

Because of the wide range of parasites and the volume of material available, no single author could hope to be qualified to write on all of them, thus I have chosen to have each chapter written by someone qualified in that area. This course of action, while it avoids the problems of the limitations of a single author, has problems of its own, the most serious being the variability in the authors' styles and attitudes which produces uneveness in the treatment of the contributions. For this I accept responsibility as editor. For all that is good and useful in these volumes I thank the authors of the chapters and the staff of Academic Press who have aided in the production of these volumes. I also wish to thank the Army Malaria Project, whose support of my research has made it possible for me to continue my interest in protozoology.

Julius P. Kreier

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VOLUME IV

Contents

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Broad Classification: The Kingdoms and the Protozoans

R. H. Whittaker

I. Introduction

There is a sense in which the protozoans and their photosynthetic relatives are at the hub of the living world. Other major groups can be seen as radiating from them toward simpler structure (the bacteria), on the one hand, and toward the different multicellular organizations of higher plants, higher animals, and higher fungi, on the other hand. This book considers some of the protozoans in their ecological contexts as parasites and symbionts of man and domestic animals. The goal of this chapter is to place the protozoans in their broadest evolutionary context in the systems of kingdoms and phyla by which the living world is classified. I shall consider the merits of three major approaches to the broad classification of organisms, each of which treats the protozoans somewhat differently—the traditional two-kingdom system, the four-kingdom system of Copeland (1956), and the five-kingdom systems of Whittaker (1969) and Margulis (1971, 1974a,b). The following chapter by J. R. Baker discusses further the classification of the protozoans themselves.

II. The Two-Kingdom System

Man is terrestrial, and he sees around him two major groups of organisms of very different adaptation to nutrition on land—the photosynthetic, rooted, higher plants and the food-ingesting, motile, higher animals. So distinct in way of life, direction of evolution, and type of body organization are these groups that a concept of dichotomy (plants versus animals) is almost inescapable if they are considered by themselves. The two groups became the nuclei around which concepts of the plant and animal kingdoms were developed by early naturalists. The kingdoms have been part of the formal classification of living things since Linnaeus.

Mosses, liverworts, and macroscopic algae are clearly plants in their photosynthetic and nonmotile way of life, and (although the photosynthetic process itself was not understood by early naturalists) these forms were grouped with the higher land plants. The higher fungi on land are nonmotile, and their apparently "rooted" manner of growth suggested the plants. It seemed reasonable then to assign the fungi to the plant kingdom, and some students believed that they had evolved from algae. The wealth of unicellular life discovered by microscopists offered greater difficulty. Some forms were motile and ingested food and were naturally regarded as one-celled animals or protozoans. Others were nonmotile and photosynthetic, and hence were considered one-celled plants. There remained a wide range of unicellular forms in which nonmotility and flagellate or pseudopodial motility, and ingestive, photosynthetic, and absorptive nutrition, were combined in various ways that were neither clearly plantlike nor animallike. In a number of cases plantlike and animallike unicells were connected by a series of closely related intergrading forms within the same major taxon. There also remained the bacteria which, although few are photosynthetic and many are motile, seemed better treated as plants because of their walled cells. The plant and animal kingdoms were products of a process of concretion by which groups of organisms that were aquatic, fungal, or microscopic, or more than one of these were added around the nuclear concepts of plant and animal derived from higher land organisms.

In this view of the kingdoms it was natural to recognize one phylum of animals defined by unicellular organization: the Protozoa. Although their evolutionary relationships were obscure, the protozoans were generally grouped into five classes, each characterized by a single major morphological or life cycle feature: flagella (class Mastigophora or Flagellata), cilia (Ciliata), pseudopods or protoplasmic extensions (Sarcodina), suction tubes for predation (Suctoria), or sporulation (Sporozoa). (The Suctoria, because of their ciliated stages, were later grouped with the ciliates in the Ciliophora, and in many treatments the sporozoans were divided into the Sporozoa, in a narrower sense, and the Cnidosporidia, which possess polar filaments.) The intergradation between animallike and plantlike forms occurred primarily among the Mastigophora or flagellates, and many of these organisms were claimed for both the plant and the animal kingdoms. The slime molds were also claimed for both kingdoms because of their mixtures of animallike and funguslike features. It was recognized by all that the two-kingdom system came into difficulties in its treatment of some of the lower organisms. The system seemed, however, a reasonable treatment of the living world in terms of two kingdoms and evolutionary directions (Fig. 1). In time the system seemed not reasonable but axiomatic; suggestions of other kingdoms were regarded as the idiosyncrasies of individuals. Such suggestions were made, how-

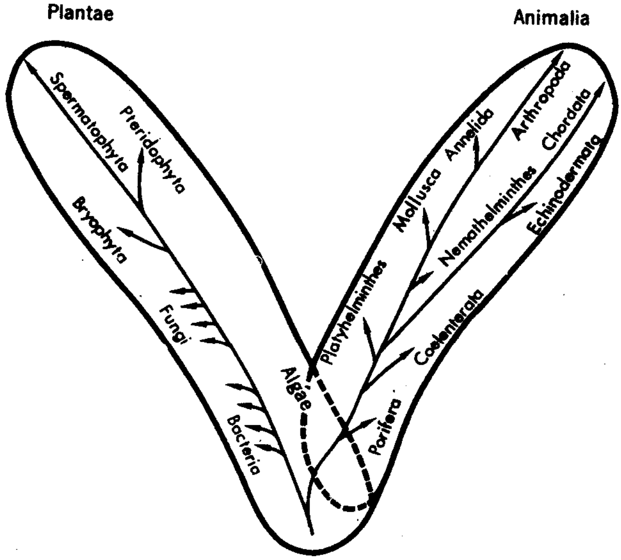

Fig. 1. A simplified evolutionary scheme of the two-kingdom system as it might have appeared early in the century. The plant kingdom comprised four divisions—Thallophyta (algae, bacteria, fungi), Bryophyta, Pteridophyta, and Spermatophyta. Only major animal phyla are indicated. (Whittaker, 1969.)

ever, as the limitations of the two-kingdom system became more evident. Early proposals for other kingdoms were reviewed by Whittaker (1959).

III. Limitations of the Two-Kingdom System

The difficulties of the two-kingdom system can be summarized in relation to four points.

A. The Protists

The most obvious difficulty is that for which we use *Euglena* and its relatives as the exemplar for students—the intergrading combinations of plant and animal characters, the fusion of the kingdoms, among unicellular organisms. Because of the impossibility of clear division of the unicells into plants and animals, a number of authors suggested third kingdoms of lower organisms. Hogg (1860) observed the intergradation of plants and animals among lower forms and proposed for them the Regnum Primigenum and the term "Protoctista." Haeckel (1866) proposed separating the lower organisms as the kingdom "Protista." Haeckel included the sponges in this kingdom in one treatment (1866) and the fungi in another (1878), but the kingdom comprised primarily, and in later treatments (1894, 1904) only, the unicellular organisms.

Although the content of the third kingdom of lower organisms and the use of the terms "Protoctista" and "Protista" have varied, two principal possibilities can be distinguished. Either the lower kingdom comprises only unicellular organisms (including those forming colonies of unicells or simple syncytia), the kingdom Protista of Haeckel and others, or the lower kingdom comprises the unicells plus other organisms that lack the kind and degree of tissue differentiation characteristic of higher plants and animals, thus including fungi and most or all algae, the kingdom Protoctista of Hogg (1860) and Copeland (1956). (In either of these concepts bacteria and blue-green algae may be excluded as indicated below.)

Some authors prefer the term "Protista" for the second concept also. Different interpretations of the Protista are possible from Haeckel's own treatments of the kingdom. Protists are conceived (Haeckel, 1866, 1894) as unicellular and as organisms that form no tissues [in a later statement by Haeckel (1904), ". . . organisms which as a rule remain unicellular throughout life (monobia), less frequently they form loose cell communities (coenobia) by repeated cleavage, but never real tissues."]. They are contrasted with the tissue-forming organisms of the kingdom Histonia, comprising the Metaphyta (including higher fungi, higher algae, and higher land plants) and Metazoa (multicellular animals).

From this contrast of unicellular and tissue-forming conditions, the difficulty has resulted. Kingdoms defined by the unicellular condition and by somatic tissue differentiation exclude a broad middle ground occupied by organisms that lack evident somatic tissue differentiation but are clearly multicellular or multinucleate as organisms, as indicated by cell differentiation and interdependence (sponges), or somatic organ differentiation (higher algae, mosses), or differentiation of reproductive tissues and organs (higher fungi). I suggest in consequence that the Protista can be best defined not by lack of tissue differentiation but by lack of tissue formation—absence of integration of cells (or nuclei and cytoplasm) into the one or more tissues of a multicellular (or multinucleate) organism. Tissue differentiation in some lower multicellular and multinucleate organisms (some algae, fungi, and sponges) is limited to a single somatic tissue plus reproductive cells, tissues, or organs distinct from it. For clarity and consistency terms and concepts for the lower kingdoms are distinguished throughout this chapter. The kingdom Protista comprises organisms which are unicellular or unicellular–colonial and which form no tissues. The alternative kingdom is conceived, as by Copeland (1956), as a broader kingdom of unicellular, multicellular, or multinucleate organisms that mostly lack somatic tissue differentiation, including higher algae and fungi [but excluding the higher fungi in the classification of Margulis (1974a,b)]. I shall follow Copeland in terming this grouping the kingdom Protoctista.

B. The Monerans

Haeckel (1966, 1878) regarded the bacteria and blue-green algae as protists without nuclei and placed them in the group Moneres or Monera, subordinate to the kingdom Protista. Recent work has made more evident the profound differences of organization between bacterial cells and those of other organisms (Stanier *et al.*, 1963; Margulis, 1974a,b; McLaughlin and Dayhoff, 1970, 1973). Cells of bacteria and blue-green algae lack mitochondria and plastids, nuclear membranes and mitotic spindles, the endoplasmic reticulum and Golgi apparatus, vacuoles, and advanced (9+2 strand) flagella, among the organelles characteristic of the cells of other organisms. Nuclear material is probably a single strand of DNA without histones, dividing by means other than mitosis; sexual reproduction is apparently both infrequent and incomplete in the sense that only partial recombination of genetic material of cells may result from bacterial conjugation and other processes. Bacteria and blue-green algae also resemble one another and differ from other organisms in biochemical characteristics, including their method of ornithine synthesis, the ap-