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THE KINGDOMS OF ORGANISMS

By HERBERT F. COPELAND

Sacramento Junior College

THIS paper proposes the recognition of certain groups of living creatures as kingdoms in addition to the two which are conventionally recognized.

Revision of the primary classification of organisms is a taxonomic operation, governed by taxonomic principles; it differs from revision of a family or genus only in wider scope. Because of the human need of an arrangement of organisms which will express as fully as possible existing knowledge and opinion concerning them, all groups are always subject to revision. Revision is required whenever the currently accepted groups can be replaced by more nearly natural groups. In practice, a group is held to be natural if each of its members is bound to the others by the whole range of its characters, of which some may be common to the whole group, while those in which there is variation exhibit intergradation. Assuming evolution to be a fact, this continuity of character is interpreted as representing, and the quality of naturalness is regarded as identical with, the possession of a common ancestor. Very many of the accepted taxonomic groups are, so far as knowledge can be positive, positively natural. Others are less positively natural; there is an unbroken transition to acknowledged artificialities, groups maintained for the disposition of races too poorly known as yet to permit of their disposition according to relationship.

The ancestor of a particular group, unless it was the original form of life, must also have had ancestors; and from these, if we go back far enough, we will always find collateral descendants. Accordingly, the limits of each natural group are indefinite at one or more points where there are transitions to related groups. We can give broader limits to any group by taking into account a more distant common ancestor, or narrower limits by considering a more recent one. The limits assigned to a particular group, one which is named, assigned to a definite taxonomic category, and defined by description, are always artificial, arbitrary, decided by convenience. Convenience at this point means something subordinate to the overriding convenience or necessity of recognizing groups which are natural. A conservative element of convenience is familiarity: the taxonomist is loath to propose abandonment of a familiar arrangement unless he can propose one in better conformity to relationship. Another element of convenience lies in the varying inclusiveness proper to groups of different categories: phyla and classes should not be too numerous; families and genera should not be too extensive. A third element of convenience lies in feasibility of definition by description; this is often attained by making limits coincide with "missing links," that is, with breaches of knowledge.

The formulation of a system of classification, then, involves a double set of hypotheses: hypotheses as to the ancestry, origin, and evolution of groups, and hypotheses as to what boundaries will be found expedient. A principle useful in the formulation of hypotheses as to the history of groups may here be discussed. If we find that a group of organisms consists of some which possess a certain positive character and of others which do not, we may most often interpret those having the positive character as a subordinate natural group, that is, as being the descendants of a single individual descendant of the ancestor of the greater group. To this principle, however, exceptions are exceedingly common; the same positive character can often be shown to have appeared more than once in evolution, or to have disappeared more than once. So often are we required, by convincing evidence of relationship, to admit to a group members which do not conform to its formal description that this situation may be regarded as the rule rather than the exception.

The application of these principles to the primary classification of organisms will involve breaches of convenience, particularly in the point of familiarity. It is an ancient and familiar hypothesis, too widely accepted as a law of nature, that every living creature is and must be either a plant or an animal. Judged by knowledge and theory which were available to Linnaeus, this hypothesis is sound; judged by modern knowledge and theory, it seems untenable. It was first challenged by Haeckel, whose *Generelle Morphologie* (43; see Fig. 2), in which he proposed the recognition of a third kingdom, Protista, appeared within a decade after the *Origin of Species*. The knowledge by which a tenable rearrangement of the kingdoms could be formulated was not available when Haeckel first attempted it, and although he subsequently, and more than once, rearranged his kingdom Protista, he never won for it a general acceptance. Various authors more recent than Haeckel have shown a disposition to recognize more kingdoms than two, but none of them, apparently, has formulated a system including all organisms. Pending such an accomplishment, the old system of two kingdoms has persisted for want of a workable substitute.

The scientists who find themselves under pressure to devise a more satisfactory system of kingdoms are those charged with elementary instruction in biology or in one of its main branches, as botany or zoology. The elements of the science include the principles of classification, and the teacher is responsible for presenting kingdoms which are limited in accordance with fact and law rather than with tradition. The one who taught me elementary botany made clear to his freshman students the principles of classification; he has summarized them, essentially as above, in various works on the classification of ferns (21, 23). He made it clear that the limits ordinarily assigned to the plant kingdom fail to include groups which link together the bacteria, the various groups of algae, and the Fungi. Such limits make the kingdom unnatural and are inconsistent with the principles acknowledged. When it became my turn to undertake elementary instruction, my efforts to recognize a series of natural kingdoms led me to distinguish four of them, called Monera, Protista, Plantae, and Animalia. Further reflection and study, extending through about twelve years, have left me confident that this is the best system which can be recognized at the present time. I proceed, therefore, to discuss the four groups as I conceive them, endeavoring to show that each one is acceptable as a unit in a double sense, in evolutionary origin and for purposes of human thought.

THE KINGDOM MONERA

In his *Generelle Morphologie*, Haeckel postulated the existence of a group of organisms without nuclei; he named the group Monera (originally Moneres, but the neuter form used in later works is preferable) and included it in Protista. He is said to have postulated, rather than to have recognized or assembled, such a group, because most of the organisms which he assigned to it, *Protamoeba*, *Protomonas*, and *Vampyrella*, are either nonexistent or false to the definition. Among Haeckel's original examples of Monera, *Vibrio* is the only one representing organisms which actually exist and are interpretable as lacking nuclei.

A few years later, Cohn (19) "with that inspired insight which only unflinching diligence can impart to original genius" (these are the words which Fiske (39) applied to a different scientist and his discoveries) recognized the connection between bacteria and blue-green algae, and combined these organisms in a group which he named Schizophyta ("fission plants"). Earlier scholars (I draw this history from Bergey's *Manual* (5) and from the work of Buchanan (9)) had for the most part regarded bacteria as "animacules," and had given them a place in that group of animals which included the simplest ones and was least definitely defined, namely the Vermes. It may have been the evident relationship of bacteria to blue-green algae that convinced Cohn that they are plants; the group Schizophyta was definitely assigned to the plant kingdom.

Haeckel in his later writings (see his *Wonders of Life* (45)) recognized Cohn's Schizophyta as being the true Monera, and included them, under the latter name, in Protista.

Two authors to my knowledge (22, 106), and doubtless others whom I have overlooked, have published the opinion that the Schizophyta or Monera should be treated as a distinct kingdom. This opinion appears to be correct: I shall present evidence supporting it, but must first discuss the name by which the group is to be called.

Modern usage fixes the application of names by types rather than by descriptions. Under the type system, Monera is the valid name of the group under discussion only if *Vibrio* is recognized as the type, and only if we can attach to the name *Vibrio* some meaning which might have been in Haeckel's mind. The organisms included in *Vibrio* by Mueller, the author of the group, have not been identified. To Haeckel, *Vibrio* seems to have meant bacteria in general. To neither of them could this name have meant the subsequently discovered organism of Asiatic cholera, by which the authors of Bergey's *Manual*, in deviation from their usual nomenclatorial good form, have attempted to typify it. One can perhaps justify Monera as the name of the group now under discussion by the assumption that to Haeckel *Vibrio* meant *V. subtilis* Ehrenberg (*Bacillus subtilis* (Ehrenberg) Cohn, the type of *Bacillus*). If *Vibrio* is not tenable as type of Monera, or if this name is meaningless, Monera becomes a synonym of Rhizopoda, or, perhaps, loses all meaning. No such ambiguity attaches to the name Schizophyta; it means, and has always meant, bacteria and blue-green algae taken together.

It will be well to take into account certain matters which, under the involved niceties of nomenclature, are not entitled to consideration. The names have connotations: Monera should be organisms without nuclei; Schizophyta should be members of the plant kingdom. As Monera is the older name; as the group is to be treated as a distinct kingdom and distinguished by lack of nuclei; as Schizophyta, applied to a group excluded from the plant kingdom, would be a misnomer and a perpetual annoyance; the name Monera will be used.

The Monera are here treated as a kingdom on the basis of two assumptions: that they are the comparatively little modified descendants of whatever single form of life first appeared on earth, and that they are sharply distinguished from other organisms by the absence of nuclei.

The hypothesis that life came into existence just once is perhaps not absolutely necessary to the treatment of this group as a kingdom. The general rule, that a tenable group is bound together by ancestry, is really a matter of convenience; such a group is bound together by the whole range of its characters rather than by a finite number of specific features. If life originated more than once, it might be expedient to make an exception to the rule by gathering into one group all of the original forms and their comparatively little modified descendants. It is possible that this is done in establishing the kingdom Monera; one prefers to suppose that this group, like any other satisfactory taxonomic group, is natural.

This is a supposition regarding events of an antiquity more easily stated than imagined. Definite fossils from time anterior to the Cambrian, which began, probably, about half a billion years ago (cf. Pirsson and Schuchert (97) and Schuchert and Dunbar (103)) are exceedingly scant. The range of pre-Cambrian time has been divided, tentatively, into two eras; Proterozoic, which commenced, perhaps, about a billion years ago, and Archeozoic, including all preceding time of which the earth harbors objective remains. Great deposits of elemental carbon in the Archeozoic seem to constitute definite proof that life was in existence at least a billion and a half years ago, but there is nothing to show what or how many forms of life were in existence. Life as it exists at present exhibits a deep-seated uniformity, bespeaking a unitary origin: all life resides in mixtures of essentially the same materials; all life obtains the energy for its immediate operations by processes of oxidation; all life (with certain puzzling exceptions among Monera; cf. Crow (27, 28) on *Spirulina*, *Arthrospira*, and other blue-green algae, and Ellis (37) on *Leptothrix ochracea*), exhibits cellular organization. Perhaps, once in existence, life spread over the world and so changed it as to prevent a repeated origin. So ancient is life, so extensive has extinction been, that we would not be convinced of its repeated origin by any amount of negative evidence, such as the absence of all trace of lines of descent connecting the various groups of Monera. On the other hand, the existence of organisms which can be interpreted as the surviving traces of lines of descent would be strong evidence of unitary origin. I shall endeavor, by a survey of the groups of Monera, to show that such organisms exist.

The hypothesis that bacteria and blue-green algae are without nuclei (and if this hypothesis is false, the name Monera is inappropriate) involves two ideas; one is morphological, concerning the structure of organisms; the other is a matter of words, and concerns the proper use of the term nucleus. Bütschli (10; see also the textbook by Lutman (84) and the long paper by Dobell (34)) is said to be responsible for two distinct conceptions of nuclei in Schizophyta: that the whole cell of ordinary bacteria is a nucleus, and that in sulfur bacteria and blue-green algae there is a central body which is a sort of incipient nucleus, representing, but not showing all of the features of, the nuclei of higher organisms. Dobell reviewed in detail the work of forty-nine previous authors; on the basis of his own work, he concluded that bacteria definitely possess nuclei. In the following survey of the groups of Monera, I shall refer to what is known of the structure of the cells. I must leave it to the judgment of each reader whether any of the structures encountered is to be considered a nucleus.

MONERA: I. AUTOTROPHIC BACTERIA

Most autotrophic (self-nourishing) organisms, including among Monera the blue-green algae, live by photosynthesis. For this process, it is said that a green pigment, chlorophyll, is necessary: more accurately, two green pigments (forms of chlorophyll) are required, and with these there are always associated other pigments, yellow, brown, red, or blue. All these pigments are highly complicated organic compounds. Photosynthesis uses the energy of light, and accomplishes a single immediate result, the production of organic compounds. The energy for all processes except photosynthesis is obtained by processes (collectively called energesis) in which organic compounds are oxidized and destroyed. We cannot suppose that life as it first came into existence possessed substances as complicated as the photosynthetic pigments, nor that it was capable of as complicated a system of metabolism as this.

Still less can organisms which are dependent on others be regarded as primitive. Most of them can be shown to be descendants of organisms which live by photosynthesis; their metabolic system is essentially that of the photosynthetic organisms, but it has been simplified by degradation, by the loss of capacity for the energy-binding process.

Organisms more primitive than those which are photosynthetic or dependent were first discovered by studies of nitrification, that is, of the natural accumulation of nitrates in the surface of the earth. The scientists of the latter part of the nineteenth century were disposed to blame everything on bacteria; several of them attempted to discover nitrifying bacteria. Success in this attempt came to Winogradsky (126).

Only four species of nitrifying bacteria, all discovered by Winogradsky, are known. Some or all of them occur in all soils fit for agriculture; they are of very great economic importance, but it has not seemed worth while to try to control them, and they have been studied but little. Their cells are minute and presumably of the simplest structure. Their system of metabolism is called chemosynthesis: it consists in the oxidation of inorganic compounds, in this case ammonia and nitrites, and the use of the energy released to make organic compounds from carbon dioxide. Thus, in one operation it effects the results both of the photosynthesis and of the energesis of other organisms. One feels in Winogradsky's original account the bewilderment with which he discovered that the less food he gave his organisms, the better they grew.

Pending a better understanding of the filterable viruses (none of which is known to possess any capacity for making organic compounds from inorganic) the organisms which live by chemosynthesis may be regarded as standing closer to the origin of life than any others yet known. They are, indeed, not very close to the origin of life: they are not intermediate between lifeless matter and living, but are as definitely alive as men. In addition to the nitrifying bacteria, there are other organisms in considerable number which are known or supposed to live by chemosynthesis. Following Bergey's *Manual*, one may treat them as forming three groups (see also Waksman (120)).

Close to the nitrifying bacteria may be placed a sulfur-oxidizing organism of similar character, the *Thiobacillus thioöxidans*, discovered by Waksman and Joffe (121). Here also are placed several genera of obscure organisms which oxidize such substances as hydrogen, carbon monoxide, methane, alcohol, and acetic acid. Several of these are known to be only facultatively autotrophic, and capable of living as saprophytes. These facultatively autotrophic bacteria seem to represent an evolutionary line connecting the purely autotrophic bacteria with the ordinary bacteria of disease and decay.

The order Chlamydobacteria (iron bacteria) includes only about a dozen species (cf. Ellis (37)). Some of these have long been known; the most familiar is *Leptothrix ochracea*, which forms the yellow masses by which we recognize the presence of iron in springs of water. Since the discovery of chemosynthesis, it has been supposed that the iron bacteria live by oxidizing ferrous iron to ferric, but this has apparently not been positively proved.

The order Thiobacteria is something of a miscellany; the characters are the accumulation within the cells of granules of sulfur or of salts of calcium or both, or the possession of a red pigment, or both such granules and such pigment. *Beggiatoa*, a colorless inhabitant of sulfur springs, forming filaments which exhibit a writhing movement, has long been known. Winogradsky showed that it lives by oxidation of hydrogen sulfide and elemental sulfur. Gardner (40) described the protoplasm of *Beggiatoa* as forming a network in which a central body is distinguished by greater coarseness of the strands, and apparently also by staining reactions (the preparations which he figured (Fig. 1, q) do not show the latter character). The pigmented Thiobacteria, the "purple bacteria," are, at least in part, saprophytic. They have the property of swimming toward light; it is suspected that they can to some extent use the energy of light, and that they represent a stage in the evolution of photosynthesis.

This is not the proper occasion for putting forward a new taxonomic system of Monera—that would only divert attention from my proper thesis. I have in mind, however, and have been following, a tentative outline which may as well be stated explicitly. The Monera seem not numerous enough for classification in groups of seven ranks as prescribed by the botanical and zoological codes. The category of phyla may be omitted, and the main groups of Monera treated as classes. The groups already described as including organisms which live by chemosynthesis may form a single class of three orders. The remaining Monera may form three classes, embracing respectively the ordinary bacteria or Schizomycetes (orders Eubacteria, Actinomycetes, and Myxobacteria), the spirochaets (a single order), and the blue-green algae (two or three orders).

MONERA: II. ORDINARY BACTERIA

One and only one apparent evolutionary line has been pointed out as leading from autotrophic bacteria into the group here called ordinary bacteria. The latter is a numerous group of parasites and saprophytes, many of which are familiar and of great importance. As the character of the group—physiological dependence—is negative and evidently derived, one can have no confidence that the group is natural; further study may show how to break it up.

The structure of ordinary bacteria is simple. A complete list of the morphological characters in which there are variations usable in classification would include few beyond the following: size and shape of cells; absence or presence and pattern of flagella; production or non-production of spores, gelatinous envelopes, and involution forms; a few staining reactions; characters of colonies. The Myxobacteria, an insignificant group of curiosities, produce comparatively complicated structures which may perhaps be interpreted as highly elaborated colonies.

In physiological characters, as distinguished from morphological, the ordinary bacteria exhibit a remarkable range of variations; the classification is largely based on these.

A note on the position of the nitrogen-fixing bacteria may be included here. They form three distinct groups. One, the species *Clostridium butyricum*, is in Bergey's *Manual* duly placed among ordinary bacteria. The other two, the genera *Rhizobium* and *Azotobacter*, are placed near the nitrifying bacteria. Nitrifying bacteria and nitrogen-fixing bacteria agree in being Monera and in being concerned with the nitrogen cycle. In all other respects they differ; nitrogen fixation is an endothermic process found only in parasites and saprophytes. Places for *Rhizobium* and *Azotobacter*—two different places—should be found among ordinary bacteria.

Among the numerous papers on the internal structure of cells of ordinary bacteria I cite but few. Schaudinn (101) described the exceptionally large *Bacillus Bütschlii* found in the gut of the cockroach (Fig. 1, d–g). He finds the protoplasm finely alveolar and divisible into a central body and an outer part.

When spores are to be formed, a spiral row of granules appears at the outer edge of the central body. This row breaks at the middle, each part migrates to the end of the cell nearer to it, and is involved in the formation of a spore. Each cell, accordingly, forms two spores. In *Bacillus Sporonema*, a smaller organism found as a free-living saprophyte, Schaudinn (102) was unable to find the structures just described. Swellengrebel (111) worked on *Bacillus maximus buccalis* from his own mouth (Fig. 1, a–c). He describes a peripheral spiral filament, which, in each cell division, divides lengthwise, after which the parts separate by sliding past one another as a smaller spring may be pulled out from within a larger one. Swellengrebel's figures support this surprising account, but there are no other reports to confirm it. Dobell (33) described several bacteria from the guts of frogs and toads; among these, *Bacillus flexilis* shows stages quite like those of *B. Bütschlii*, and like it produced two spores from each cell. In *Bacillus Saccobranchi*, which he discovered in the blood of a dead fish (34), he similarly found stainable material appearing either as separate granules or as a crooked, more or less spiral rod (Fig. 1, h–n). The granules or rod, as the case may be, stain as chromatin does.

It may be noted that with the exception of those of Swellengrebel, the results just summarized are drawn entirely from spore-forming rods, the group which forms the genus *Bacillus* as properly construed. Comparatively recent work on this group tends to confirm these results. According to Churchman (57), the outer part of the protoplast is different from the inner; the gram-positive character of the group depends on the outer part. The figures of *Bacillus subtilis* by Knasyi (69) and of *B. Megatherium* by Bayne-Jones and Petrilli (3) seem to show the spiral bodies of the older authors as thickenings of the ectoplasm (this is Knasyi's term; it is preferable to Churchman's "cortex"). These bodies were not found, however, to have

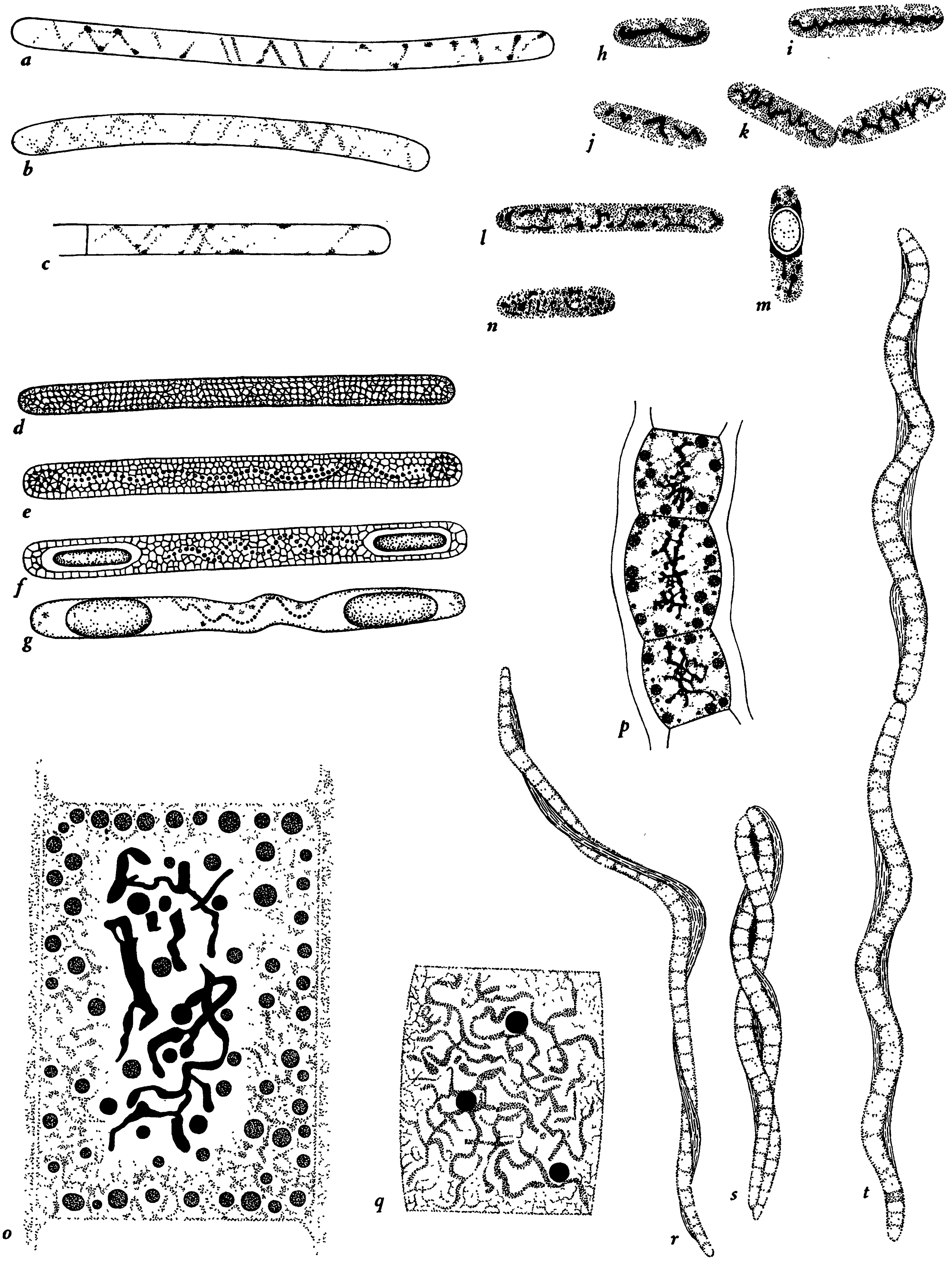

Fig. 1. Cytology of Monera

a–c, *Bacillus maximus buccalis*, after Swellengrebel; d–g, *Bacillus Bütschlii*, after Schaudinn, × 1000; h–n, *Bacillus Saccobranchi*, after Dobell, × 2000; o, *Symploca Muscorum*, after Gardner; p, *Anabaena circinnalis*, after upt, × 2000; q, *Beggiatoa archnoidea*, after Gardner; r–t, *Cristispira Veneris*, after Dobell, × 2000.

an active part in cell division or in spore formation.

MONERA: III. SPIROCHAETS

Spirochaets (the genus *Spirochaeta* and its allies) were first distinguished by Ehrenberg. They include small forms which may be saprophytes in waters, commensals in the alimentary tract of animals (as in the mouth of man and the gut of termites), or parasites in blood, and larger forms of which the most familiar are parasites in mollusks. The group became an object of intense study when Schaudinn showed that one of the species is the cause of syphilis. The character of the group is a spiral body which is flexible. It is a small group, but is so distinct that it must be treated as one of the main groups of Monera.

The cytology is most definitely known in the large forms from mollusks; I describe it primarily from Dobell's account of *Cristispira Veneris* (35; Fig. 1, r–t). The body bears a longitudinal membrane. Internally, it is divided into a series of chambers; if one compares it with filaments of *Spirulina* and *Arthrospira*, one may become uncertain whether it is the whole body or each separate chamber that is to be regarded as a cell. At the margin of each septum between chambers, there is a whorl of granules which stain like chromatin; Dobell interprets these, collectively, as a nucleus. Cell division is transverse; but there is a stage of division during which the two parts of the dividing cell lie side by side; as the free ends separate, they give a false appearance of lengthwise division.

It has been suggested that the spirochaets are related to the trypanosomes, which also inhabit blood and have flexible bodies and lengthwise membranes. This hypothesis served the proper function of hypotheses, that of stimulating investigation, but it should have been abandoned by 1910, when it had become evident that the resemblance extends to no features beyond the ones just stated.

MONERA: IV. BLUE-GREEN ALGAE

Blue-green algae (Myxophyceae Stizenberger 1860; Cyanophyceae Sachs 1874; Schizophyceae Cohn 1879; cf. Setchell and Gardner 104)) are the Monera which possess chlorophyll and live by photosynthesis. They are as common as dirt; they have long been known, but were only gradually recognized, during the latter half of the nineteenth century, as being quite distinct from green algae. As the group is distinguished by positive characters, it is probably natural. It is apparently very ancient; certain species now living build calcareous masses in hot springs, and calcareous masses of similar character are known from the Proterozoic and Archeozoic. I have shown reason, however, for regarding blue-green algae as less primitive than the nitrifying and sulfur oxidizing organisms, and for supposing that they are descended from the latter through the purple bacteria.

The following account of the cytology of blue-green algae is based primarily on the work of Haupt (52; see Fig. 1, p), with consideration of the older accounts of Bütschli (10), Gardner (40; see Fig. 1, o), and Swellengrebel (112).

When cells are studied without sectioning, a central body is evident; sectioning, however, shows that the finely vacuolate protoplasm is uniform throughout the cell. The outer part is distinguished by the presence of pigment in the vacuoles, the inner by the presence of rods and granules, staining like chromatin, imbedded in the protoplasm. The inner part contains also granules which stain red with methylene blue. Gardner calls these "α-granules". They are evidently the same as the "red granules of Bütschli" or metachromatic granules known also from *Beggiatoa*, many ordinary bacteria, and various other organisms. As the cell divides by constriction, the inner part is divided; the rods and granules may be divided, and are distributed at random to the daughter cells.

The above evidence may justify the position (tentative as all scientific conclusions are, yet maintained with confidence) that bacteria and blue-green algae are a natural group, being the forms in which life, since its origin, has undergone least change; that they are distinguishable by lack of nuclei; and that they should be treated taxonomically as a kingdom named Monera.

NUCLEATE ORGANISMS

In all organisms except the Monera, the life of every cell is conditioned by the presence within it of one or more nuclei. The nucleus is a part of the protoplast set apart (at least when it is not dividing) by a membrane. Its most definite character is the process, mitosis or karyokinesis, by which it divides into two. During this process a part of the contents (the chromatin) becomes organized as a definite number of definite bodies called chromosomes, each of which is divided into two parts which are distributed respectively to the two daughter nuclei.

Occasionally, nuclei are found to divide by constriction, without going through the mitotic process. Nuclei formed by definitely non-mitotic divisions are unable to persist without limit; sooner or later, such nuclei always decompose and disappear. Non-mitotic division, either binary or multiple (in the latter form called "formation of chromidia") was formerly supposed to be the normal process in various unicellular organisms, especially certain rhizopods. This has been disproved by Kofoid (70) and his associates.

Typical and durable nuclei can originate not only by division, but also by certain fusions of nuclei, always of just two nuclei, which can differ in their heredity only in minor details. Such fusion is the essential feature of sexual reproduction. It gives rise to diploid stages, stages in which each nucleus has a double set of chromosomes; a life cycle in which it occurs must also exhibit at some point a modification of mitosis called reduction division, or meiosis, in which the chromosomes separate into two groups without splitting lengthwise, so that the original or haploid chromosome number is restored. For reasons which are not clear, the reduction division is usually associated with one or more other nuclear divisions which seem to be essentially ordinary mitotic divisions. In the great majority of nucleate organisms, reduction division is followed by just one other division, so that the whole process yields four haploid nuclei.

The uniformity of mitosis; and, if one denies sexual reproduction as a primitive function of the nucleus, then the capacity of the nucleus to assume identical sexual behavior in groups as diverse as men and diatoms, wheat and wheat rust; furnish evidence that the nucleus has come into existence only once in evolution; that all nucleate organisms are related and constitute a natural group, a super-kingdom. The oldest known remains of nucleate organisms are from the late Proterozoic; they represent Radiolaria, sponges, Foraminifera, and even, apparently, worms. None of these groups can be regarded as including the original form of nucleate life. In attempting to date the origin of the nucleus, one must allow time for the evolution of these groups, perhaps the full length of the Proterozoic, back to a billion years ago. No remains of nucleate organisms older than the groups just mentioned are to be expected. Knowledge of the origin and early evolution of nucleate life must be obtained, if it can be obtained at all, by study of races which survive.

Among living organisms, the overwhelming majority of macroscopic forms are properly listed, on the basis of relationship, in the kingdoms of plants and animals. Among microscopic organisms likewise many, as rotifers, nematodes, and green algae, are legitimate plants or animals. But many microscopic, and a number of macroscopic, organisms fall into groups which cannot confidently be assumed to be descended from any form which would properly be regarded as either a plant or an animal. One of the objects of this paper is to show that these groups should be treated as an additional kingdom: that they form, if taken together, a natural group, having the original nucleate organism as a common ancestor; and that it is more convenient to maintain this group as a taxonomic entity than to make certain other arrangements which would also be consistent with natural classification.

THE APPLICATION OF THE NAME PROTISTA

The groups which, as here proposed, are to constitute a separate kingdom are those which zoologists treat as Protozoa together with the diatoms, the marine algae, and the Fungi. Before they are considered in detail, it will be expedient to show that Protista is the proper name for the combined group.

Protista is the oldest name after Plantae and Animalia to be published as that of a kingdom. As already mentioned, it was published by Haeckel in his *Generelle Morphologie*, in 1866. The views on classification presented in this work were summarized in a figure which is here reproduced (Fig. 2). The figure is a phylogenetic tree; in fact, it is the original phylogenetic tree, of which all others are modifications. Haeckel was the first to use this familiar device for representing the relationships of taxonomic groups.

The figure is seen to represent three kingdoms. The animal kingdom is arranged as it was understood at the time, except that the sponges and the unicellular "animacules" have been excluded; the Infusoria, however, are not yet recognized as unicellular and are placed among the worms. In the plant kingdom, the new name Archephyta is coined for Chlorophyceae, among which, according to the knowledge of the time, the blue-green algae are included. Red and brown algae are present; so are the Fungi, combined with Lichenes under the name Inophyta. At the summit of the plant kingdom stand the bryophytes and vascular plants, arranged in quite modern fashion.

In the third kingdom, Protista, are the flagellates with *Noctiluca* sharply separated from the others; the diatoms; and the sponges, to which the specialist on marine life has devoted a space out of proportion to their significance. Sporozoa are represented by the gregarines, which are included with certain other organisms in a group called Protoplasta. Aside from these groups, practically all of Haeckel's original Protista are or have subsequently been included in Rhizopoda. This is true of the Myxomycetes; of the Protoplasta, excepting the gregarines; and of the Monera, excepting *Vibrio*.

For the purpose of applying the name Protista, it is desirable to recognize a nomenclatorial type. As we ascend the tree, the first name encountered is that of *Vibrio*, the representative of the bacteria. Since it is clear that Haeckel was but poorly acquainted with bacteria, we would be anchoring the name Protista in a fashion which he could not have intended if we should select *Vibrio* as the type. I think that we may safely select as type of Protista the zoologists' standard example of a rhizopod, the organism commonly known as *Amoeba Proteus* Leidy (for an unusually fine example of the nomenclatorial tangle which can be woven about a familiar species, see the references to this species in the papers of Boeck and Stiles (7) and Schaeffer (100)).

Haeckel's life work subsequent to the

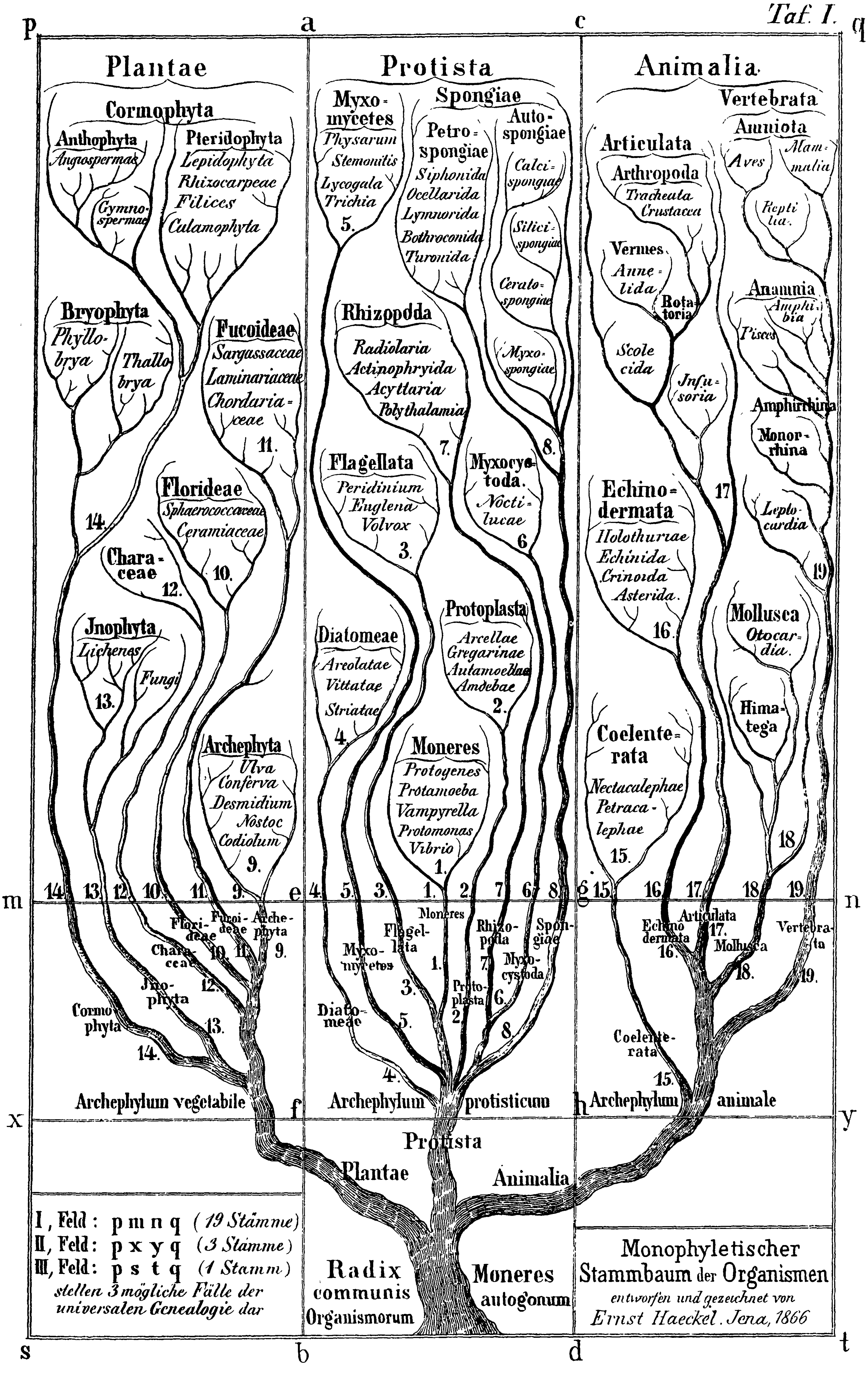

FIG. 2. REPRODUCTION OF PLATE I FROM HAECKEL'S "GENERELLE MORPHOLOGIE," VOLUME 2

publication of the *Generelle Morphologie* consisted in large part in elaborating and refining the ideas expressed in the phylogenetic tree just discussed. In this original tree, he avoided expressing an opinion as to whether life had originated just once or many times: the three transverse lines in the lower part of the figure indicate three levels at which life might have come into existence. He was sufficiently aware of the significance of the nucleus to set apart a group characterized by its absence; he was not sufficiently aware of it to avoid suggesting that life might repeatedly have come into existence equipped with nuclei. In his *History of Creation* (44) he suggested the multiple origin of life and the development of nuclei in several distinct lines. In his late work *The Wonders of Life* (45) he avoided the question by presenting a manifestly artificial "morphological classification" essentially as in the attached table (Table 1).

TABLE 1

Haeckel's "Morphological Classification" (1904)

	"KINGDOM" PROTISTA, (UNICELLULAR ORGANISMS)		"KINGDOM" HISTONA, (MULTICELLULAR ORGANISMS)
	Monera, organisms without nuclei	Nucleate Protista	
Plants.............	Blue-green algae	Green flagellates, diatoms, etc.	Metaphyta
Animals............	Bacteria	Rhizopoda, Infusoria, etc.	Metazoa

By the history just sketched, the name Protista came to have several connotations in the minds, apparently, both of the one author who maintained the group and the many who rejected it. It was conceived as the group representing the most ancient forms of life; the group distinguished by the unicellular character; the group which lies between plants and animals; the group which is essentially a combination of Monera and Protozoa. The use of nomenclatorial types enables one to overlook the connotations, the conflicting supposed definitions, of the name of a group until after the application of the name is determined. If *Amoeba Proteus* is the type of Protista, then whatever kingdom aside from Plantae or Animalia includes this species must be called Protista. On many occasions the results of applying the type system seem outrageous to established conventional usage, but I do not think this will be found true of the present case. The name Protista is here applied to a group considerably amended since it was set up for flagellates, rhizopods, diatoms, and sponges, but the amendments are no greater than one would expect as a result of seventy years' advance in knowledge of the groups concerned. Most of the original Protista retain their place in the kingdom; the group continues to include the common ancestors of plants and animals; it has the common characters of plants and animals in the nucleus and features dependent on the nucleus; it consists chiefly of unicellar organisms. This application of the name Protista to a particular group is qualified, however, by the condition that the group can be justified as natural and convenient.

PROTISTA: I. PIGMENTED FLAGELLATES

Justification of the group involves an enumeration of the subsidiary groups, with a consideration of the origin and characters of each. This survey should begin with the most primitive of nucleate organisms. We cannot as yet recognize, either among living organisms or among fossils, a series connecting Monera with nucleate organisms, nor any very limited race which was the first to possess a nucleus. We can, however, reconstruct to a considerable extent the characters of the original nucleate organism and we can place it in a certain major group of existing organisms.

The original nucleate organism must have been unicellular rather than multicellular, and autotrophic rather than dependent. All autotrophic nucleate organisms live by photosynthesis. As photosynthesis occurs in certain Monera, we may be confident that this function was inherited from Monera by the original nucleate organism. The photosynthetic pigments in nucleate organisms are always confined to certain organelles called plastids. These do not occur in Monera; they were evidently evolved more or less concurrently with the nucleus.

Nucleate unicellular organisms living by photosynthesis are included in the natural groups (commonly construed as orders) called chrysomonads, Heterokontae, cryptomonads, dinoflagellates, chloromonads, and euglenids. (Other organisms with these characters are included among diatoms and green algae; these two groups are evidently derived, and need not be considered in the present connection.)

In the six groups just listed, the typical members are motile by means of flagella. Several if not all of them include, however, forms which lack either or both the characters of flagellation and pigmentation; there are colorless flagellate forms, amoeboid forms, and stationary forms which may be either unicellular, colonial, or filamentous. The amoeboid character appears to be an adaptation for holozoic nutrition, that is, for the ingestion of solid food. It is almost always associated with loss of pigmentation and is obviously a derived condition. The colorless flagellate forms and the colonies and filaments are likewise obviously derived. As to whether possession of flagella is a primitive character in these groups, we may reach a conclusion by considering the alternatives, that flagella of essentially identical character (there are differences in detail, as pointed out by Deflandre (32)) have been developed independently in all six groups, or, on the other hand, that they are inherited from a common ancestor of all six groups, and that the non-motile forms are derived. The latter alternative is surely the sound one. Fagella, like the function photosynthesis, appear to be an inheritance from Monera, and to have been characters of the first organisms that developed nuclei and plastids.

It appears, then, that all organisms which are at the same time nucleate, unicellular, flagellate, and capable of photosynthesis constitute a natural group. It is, however, not expedient to recognize a taxonomic group limited by these characters. In the taxonomic system, as we have seen, organisms as just described are distributed among six groups (or, counting green algae, seven), and to each of these groups are admitted organisms lacking flagella or photosynthetic pigments, or forming bodies of more than one cell. These groups are distinguished by differences in the pattern of flagellation, in the particular pigments present, in storage products, in materials and structure of walls or shells, and in other features. It has been possible only to a very limited extent to show that some of them are derived from others. The chrysomonads are generally supposed to be the most primitive, and Pascher (93, 96) has shown that the Heterokontae (also the diatoms) are related to, and presumably derived from, these. It is evident from the isolation of these groups that they are very ancient, and some authorities have been disposed to raise them to very high taxonomic rank. It is also evident, however, that the six groups taken together are still a natural group, being essentially the sub-class Phytomastigina of zoologists, the division Chrysophyceae of Tilden

(115). All other nucleate organisms may be regarded as derived from this group.

In dealing further with the evolution and groups of nucleate organisms, features of the nucleus will be found significant. Although essentially uniform, the nucleus varies in details; the variations fall into more or less parallel evolutionary lines in the various groups. For the sake of having a definite conception of the starting point of these lines, we need much more knowledge than we have of the nuclei of the pigmented flagellates. In particular, the supposedly primitive chrysomonads are poorly known.

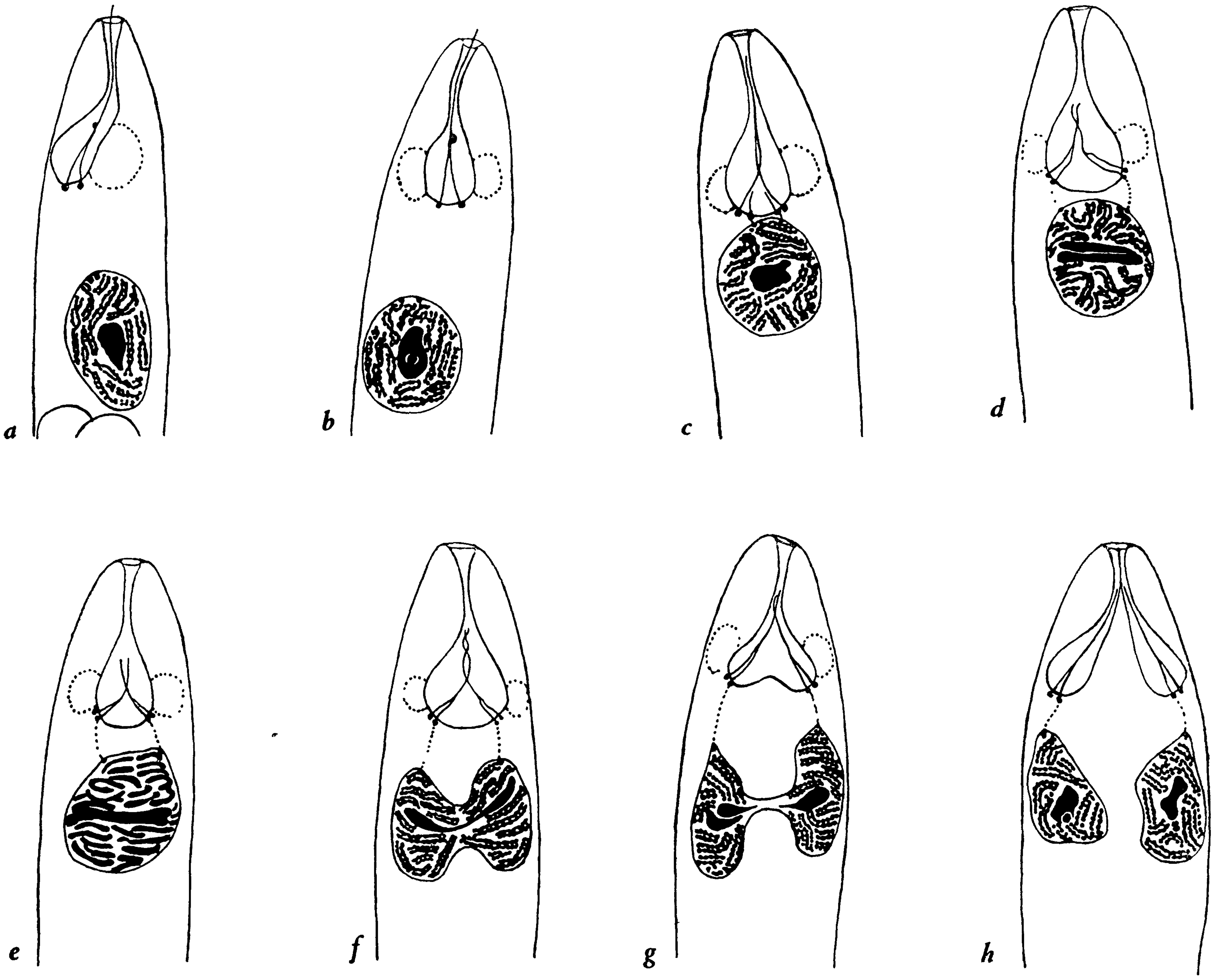

Fig. 3. Nuclear Division in Euglena Spirogyra, after Ratcliffe, × 720

There have been a considerable number of accounts of nuclear structure and behavior among the euglenids. Early observations of *Euglena* revealed a large intranuclear body which divides during mitosis and seems to lead the chromosomes in separating. This body was designated a nucleolo-centrosome; we may for the present call it by the term endosome, which implies an internal body without specifying its nature. Modern work on *Euglena agilis* by Baker (2) and on *Euglena Spirogyra* by Ratcliffe (98; Fig. 3) has shown that the endosome, some time before nuclear division, buds off a body which moves to just within the nuclear membrane and divides.

The term centrosome may be applied to this body and to the two bodies formed by its division rather than to the endosome. As division begins, the nucleus moves forward within the cell and comes into contact with the cell membrane in the bottom of a depression at the forward end. Each centrosome seems to generate, just within the adjacent cell membrane, a body called a blepharoplast; the nucleus then withdraws from the cell membrane, leaving the centrosomes connected to the blepharoplasts through fibers called rhizoplasts. In *Euglena Spirogyra* (the details are different in *E. agilis*) the flagellum, which is attached within the reservoir and already forked at the base, splits lengthwise; a new flagellum grows out from each blepharoplast and becomes fused, not far from the base, with one of the halves of the old one. Meanwhile, within the intact nuclear membrane, the chromosomes and endosome are dividing. The centrosomes are at the sides of the dividing nucleus, not at the poles of a spindle; no spindle has been recognized. Nuclear division is completed by the constriction of the membrane. Subsequently, the centrosomes and rhizoplasts disappear, to be replaced during the next division by new ones.

In the euglenids *Menoidium*, studied by Hall (46), and *Peranema*, studied by Hall and Powell (49) the centrosomes are permanent bodies which divide before the nucleus does and stand at the poles of the dividing nucleus. The dinoflagellates *Oxyrrhis* and *Ceratium* were also studied by Hall (47, 48) and found to agree in general with *Menoidium*, although *Ceratium* lacks the dividing endosome. Hall and Powell are unwilling to accept the features in which *Euglena* is supposed to be different from *Menoidium* and these other genera but the essential agreement of the results of Baker and Ratcliffe is evidence of their accuracy.

Tentatively, in view of the scant data considered, I am disposed to take the system of nucleus and accessory structures in *Euglena* as the most primitive yet known. The chromatin and chromosomes are essentially as in all other nucleate organisms; in the many millions of years since the origin of the nucleus, the chromatin of different organisms has acquired the power of transmitting a bewildering variety of hereditary qualities, but the only visible changes have been fluctuating variations in its arrangement in the resting nucleus, and in the number, size, and shape of chromosomes. The centrosome would appear to be originally a device for the production of flagella, related to mitosis only in that mitosis makes new flagella necessary. The endosome, although it gives rise to centrosomes, is not in itself a centrosome or a nucleolo-centrosome, but it may yet be a nucleolus. The nuclear membrane and nuclear sap, which disappear during division in the nuclei of higher organisms, are here permanent structures, persisting through division and being divided, and the endosome may be a nucleolus with corresponding qualities. Its original significance may be as a guide to the separating chromosomes of organisms so primitive as not to have developed a spindle. It may continue to persist through mitosis after centrosomes have come to occupy the poles of the dividing nucleus, as in *Menoidium* and *Oxyrrhis*, but in *Ceratium*, and, in fact, in all organisms except a very few, it is either absent at all times or disappears during division. The spindle seems to have originated subsequently to polar centrosomes.

PROTISTA: II. ANIMAL-LIKE FLAGELLATES

There exist many flagellates beside those included in the six groups just considered. All these others are dependent (holozoic, saprophytic, or parasitic); they have been arranged in four orders which together form a subclass Zoomastigina.

A few genera whose members are amoeboid constitute the order Pantostomatida.

The Protomonadida, with one or two flagella to each cell, are a varied assemblage. Here are included the Monadidae, the genera of which, as Pascher (94, 95) has shown, would be naturally placed by distributing them among the chrysomonads. Here also are included the trypanosomes—parasites in the blood stream of animals, the most intensively studied of all flagellates—and the choanoflagellates or collared monads, of interest because cells of similar structure are an element in the bodies of sponges.

The Polymastigida have three to eight

flagella per cell (per nucleus, in certain races with multinucleate cells); the Hypermastigida have more than eight flagella per cell. The members of these groups are largely entozoic; the Hypermastigida are confined to insects, particularly termites. They are notable for elaboration of the systems of structures (neuromotor systems) which extend from the nuclei to the flagella and other parts of the cell. Cytologically, as a result of the work of Kofoid and his associates at the University of California, these are the best understood of flagellates.

Kirby's (67) reorganization of the polymastigote family Trichomonadidae gives a convenient view of some of the parts which may make up a neuromotor system, together with some hints as to their evolution.

There is usually a permanent centrosome located just outside the nuclear membrane. Typically, this is connected by a rhizoplast to a blepharoplast or a cluster of blepharoplasts standing near the cell membrane. In *Trichomitus Termitidis* a single body is regarded as a combination of centrosome and blepharoplasts, although one might suspect that by homology it represents only one of them, the other being suppressed. The Hypermastigida, incidentally, although not directly related to *Trichomitus*, resemble this form in having a centroblepharoplast. The blepharoplast or centroblepharoplast, as the case may be, bears several free flagella together with an internal rod which is called the axostyle and is suspected of being homologous with a flagellum. Laterally attached to the blepharoplasts there is in some examples a darkly-staining mass called a parabasal body. One flagellum is usually reversed, trailing behind the cell as it swims; in *Trichomonas* and its immediate allies, this is grown fast to the cell, forming an undulating membrane. Concurrent with the evolution of the undulating membrane has been the evolution of an internal rod attached to a blepharoplast and serving apparently as a mechanical support to the undulating membrane. Kirby, distinguishing this from both the axostyle and the parabasal body, names it the costa.

The features of mitosis in Polymastigida and Hypermastigida may be illustrated by a comparatively simple, and in this respect presumably primitive example, namely, *Trichomonas buccalis* as studied by Hinshaw (54; see Fig. 4). The centrosome, blepharoplast, and rhizoplast divide; the centrosomes remain connected to one another, for a time, by a fiber called the paradesmose. There is no dividing endosome. A spindle is formed within the nuclear membrane between the centrosomes. The nuclear membrane does not disappear; after the chromosomes have separated, it divides

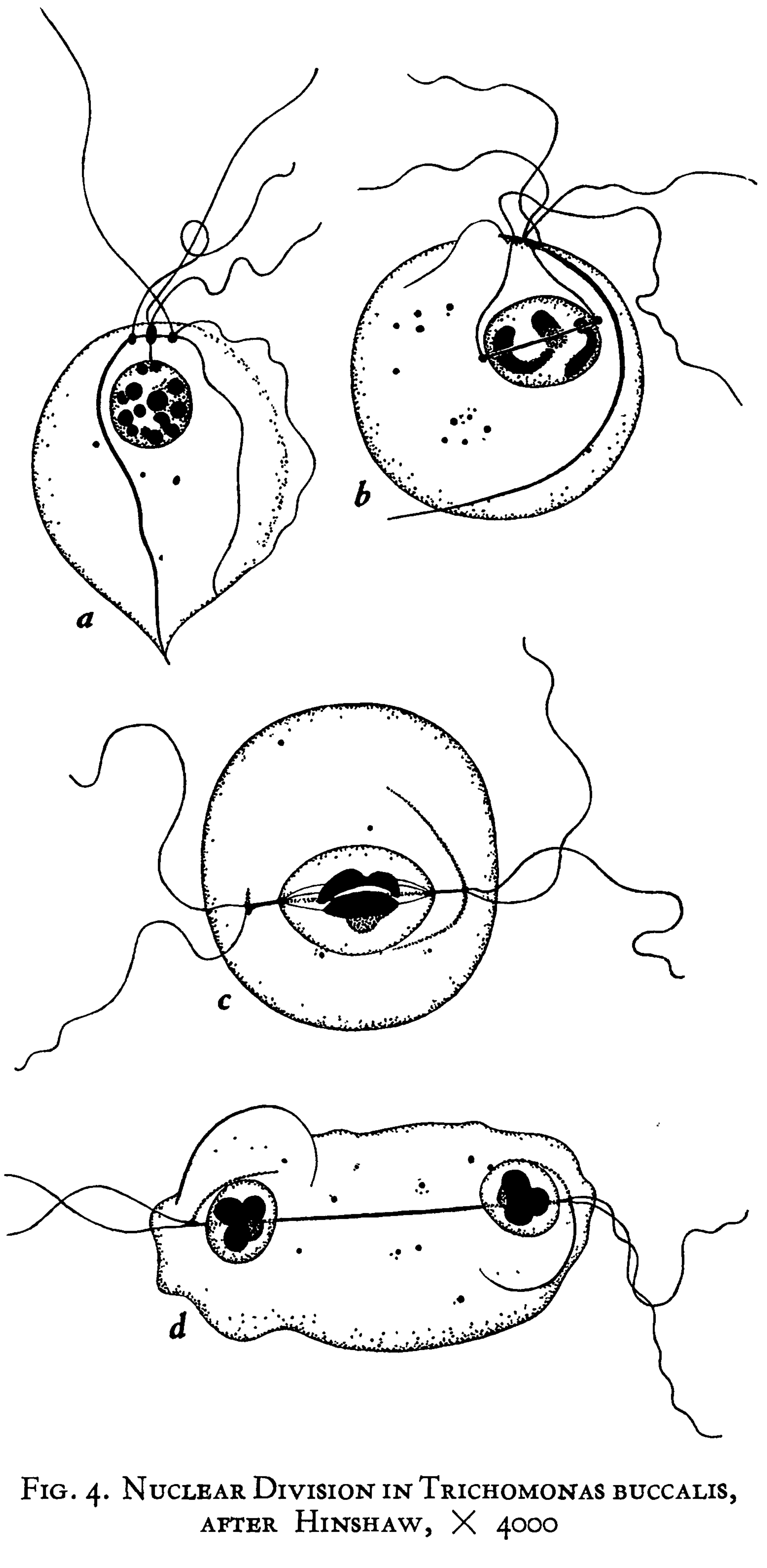

FIG. 4. NUCLEAR DIVISION IN TRICHOMONAS BUCCALIS, AFTER HINSHAW, × 4000

by constriction. The free flagella are divided between the two daughter cells, each of which regenerates the parts of a complete cell which it has not inherited.

Although showing much variation, and in some examples much elaboration, the mitotic process in most Polymastigida and all Hypermastigida is essentially as in *Trichomonas buccalis*.

See, for example, the work of Kofoid and Swezy on *Trichomitus Termitidis* (72), *Chilomastix Mesnili* (75), *Giardia enterica* (77), *Trichonympha Campanula* (73), and *Trichonympha (Leidyopsis) sphaerica* (74); also that of Kirby on *Dinenympha fimbriata* (62), and *Staurojoenina assimilis* (63). A minority of the polymastigotes, including the Oxymonadidae studied by Kirby (65) and Connell (20), and *Streblomastix Strix*, studied by Kidder (61), show deviations profound enough to seem significant of a different evolutionary origin. All, however, have a permanent nuclear membrane, dividing by constriction; and in all in which a spindle is present it is inside the nuclear membrane.

Since many colorless flagellates have been found to belong to typically pigmented groups, it is not to be supposed that the Zoomastigina, being merely the ones not yet so placed, constitute a natural group. The diversity of the group and of its three orders, aside from Hypermastigida, confirms the suspicion that these groups are artificial. The complete breaking up of these groups, by the discovery of the relationships of their members, will be an arduous task, and pending this accomplishment, the groups will have to be allowed a place in the taxonomic system.

PROTISTA: III. DIATOMS

The diatoms are a numerous group of unicellular (less commonly colonial or filamentous) organisms with brown plastids. They have finely, elaborately, and characteristically sculptured shells of silica; the shell of each cell consists of two parts fitting over each other, as the textbooks say, like the parts of a pill-box. The cells may be non-motile, or motile by means of flowing bands of protoplasm which function like endless belts.

The existence of sexual reproduction in the groups just treated as flagellates is questionable; in diatoms it is positively established. Reduction division takes place immediately before the sexual fusion of nuclei; this means that all nuclei of diatoms, except those formed for the purpose of sexual fusion, are diploid. This is a character of groups in which sexual reproduction is ancient and presumably inherited from pre-existing groups; it strengthens the impression made by the other characters of diatoms, that this is a derived, highly specialized group.

Nuclear division in diatoms is best known by the old work of Lauterborn (83). His results, puzzling in many details, were confirmed in most respects by Karsten (58). There is a centrosome at the nuclear membrane (apparently outside). This buds off a ring-shaped structure which enters into the nucleus and by growth becomes a tube extending clear through it. The nuclear membrane disappears early in mitosis, but the nuclear sap remains for a time distinct from the cytoplasm. The chromosomes gather in a mass at the middle of the tubular structure; they then divide into two doughnut-shaped masses which travel to the ends of it. As these masses become organized into new nuclei, the cytoplasm seems to absorb the nuclear sap, and likewise the tubular structure, but not until the latter has budded off a new centrosome from each end.

Lauterborn and Karsten interpreted the tubular structure, in terms of the knowledge of their time, as a central spindle. It seems possible, however, that this structure represents a chromatin-dividing apparatus more ancient than any sort of spindle; perhaps it is homologous with the dividing endosome of the euglenids. Pascher, as already mentioned, has shown that the diatoms are related to the chrysomonads. A confident interpretation of the mitotic process just described will depend on an understanding, yet to be obtained, of the chrysomonads.

PROTISTA: IV, V. MARINE ALGAE

The two great groups of marine algae consist of multicellular organisms, some of which are exceedingly large; they live by photosynthesis and have plastids of other colors than green; they produce no true starch or cellulose. Beyond these characters, they have little in common; they are not closely related.

The brown algae (Melanophyceae Stizenberger 1860; Phaeophyceae Kjellmann 1891; cf. Setchell and Gardner (104)) show an evolution from filamentous forms with a life cycle of similar haploid and diploid stages to thalloid forms with a considerable differentiation of organs and tissues, and whose haploid stages are reduced to the mere gametes. They produce flagellate reproductive cells, each bearing two laterally attached unequal flagella; these cells are so small that the presence of any structures connecting the nuclei with the flagella is doubtful.

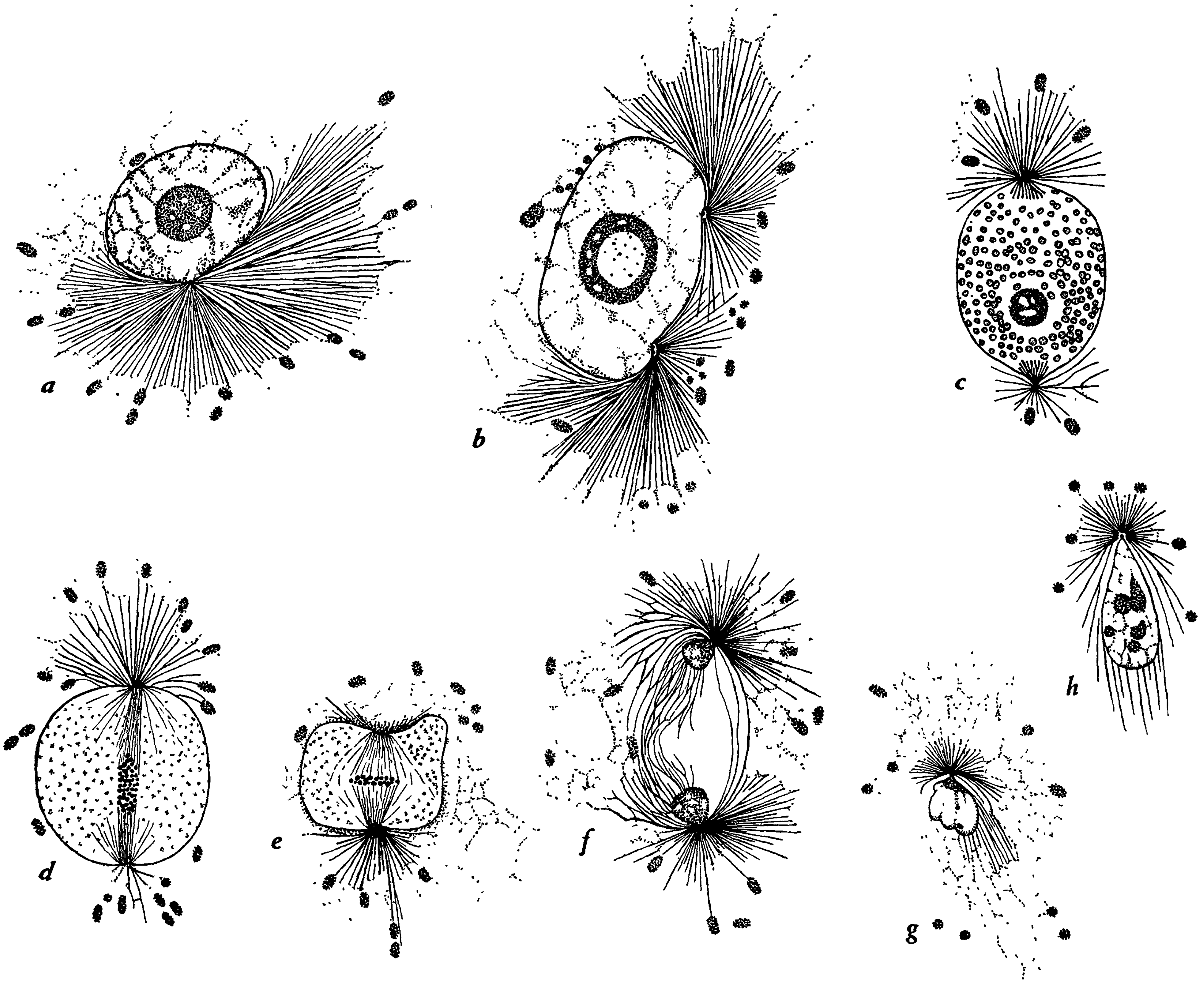

Fig. 5. Nuclear Division in Stypocaulon, after Swingle, × 800

In Sphacelariaceae, among which Swingle (113) studied particularly *Stypocaulon* (see Fig. 5) there is a permanent centrosome located just outside the membrane of each nucleus. It stands at the focus of an aster, a mass of fibers radiating into the cytoplasm; such a structure is found in many groups, including diatoms but apparently not flagellates. Before each nuclear division, the centrosome and aster divide into two, which move apart along the membrane to opposite sides of the nucleus. A spindle forms within the nuclear membrane; it appears as if it were projected from the two centrosomes. The nuclear membrane persists nearly until the end of the mitotic process. Then, as the two groups of chromosomes begin to become organized as daughter nuclei, the distinction between nuclear sap inside the membrane and cytoplasm outside disappears, and the membrane becomes invisible. New membranes form about the daughter nuclei.

The Sphacelariaceae are comparatively primitive brown algae. In other brown algae—*Dictyota* as studied by Mottier (91); *Fucus* and *Cutleria*, by Yamanouchi (129, 130); *Zonaria*, by Haupt (53); *Pterygophora*, by McKay (89)— the centrosomes and asters are absent when the nuclei are not dividing; they appear *de nove* as mitosis commences, and disappear at the end. As an exception, the centrosomes formed during the first or true reducing division in *Dictyota* persist, divide, and function during the immediately following second division. In brown algae in general the nuclear membrane disappears earlier in the mitotic process than it does in *Stypocaulon*.

The descent of brown algae from flagellates is evident. The possession of centrosomes is probably related to the production of flagellate reproductive cells. But those who have studied the groups most closely are unwilling to connect the brown algae with any particular group of flagellates.

The red algae, Rhodophyceae, include certain poorly known organisms of comparatively simple organization; but most of the very large number of species are of complicated structure and exhibit complicated reproductive processes. They produce no motile cells whatever. The cell walls are of a pectinaceous material which appears in commerce in the diverse forms of agar-agar and edible birds' nests.

Features of mitosis in this group were first described by Davis (29), who studied *Corallina;* his results were confirmed and extended by the work of Yamanouchi (127, 128) on *Polysiphonia*.

During most mitoses, centrosomes appear outside of the nuclear membrane at the poles of the intranuclear spindle. There are no asters. As mitosis proceeds, the centrosomes swell, become less stainable, and finally disappear. The old nuclear membrane disappears during the later stages of nuclear division; new ones are formed about the daughter nuclei. The second division of the reduction process, although supposedly essentially an ordinary mitotic process, shows in *Polysiphonia* as in many other organisms certain peculiarities in detail. At the end of the first, or proper, reduction division, the nuclear membrane does not disappear, and does not divide by constriction. No centrosomes appear for the second division, which, taking place within the intact original nuclear membrane, results in four groups of chromosomes in a single tetrahedrally lobed space. The membrane continues to persist where these clumps of chromosomes are against it, but dissolves in the areas between, so that each of the four new nuclei has a membrane which is partly new and partly inherited.

I take the temporary centrosomes of this group to be vestigial structures, indicative of a flagellate ancestry, but there is nothing to connect the red algae with any particular group of flagellates; they are an advanced and highly isolated group.

PROTISTA: VI, VII. RHIZOPODA AND SPOROZOA

The Rhizopoda are nucleate organisms with exposed protoplasm which can be thrust forth in projections called pseudopods. As authority for the name, Siebold, 1845, is cited; Sarcodina of Hertwig and Loesser, 1874 (cf. Stiles and Hassall (110)), was intended to apply to a larger group including this, but must be regarded as a synonym. These organisms were formerly regarded as representative of the starting point of life, and hence as being automatically a natural group. The positive evidence for these views, in the supposed formation of nuclei *de novo* from chromidia, has been discredited; and the evidently derived character of the few known self-nourishing organisms which are amoeboid is convincing evidence to the contrary. Amoeboid forms with flagella are placed naturally among the chrysomonads (*Chrysapsis*) and Heterokontae (*Chloramoeba*); others are conventionally stationed among the Zoomastigina (*Mastigamoeba*) and Sarcodina (*Naegleria*, *Trimastigamoeba*). It will be convenient to call this sort of organisms collectively the amoebo-flagellate complex. Many recognizable natural groups seem to be descended from the amoebo-flagellate complex, and among them are several which are assigned to Rhizopoda; but the Rhizopoda taken together are clearly an artificiality. As various lines of rhizopods have come into existence by loss of characters from organisms which were themselves simple, it will not be easy to find characters indicating their respective true relationships; the group will have to be maintained for some time to come.

The groups included here as orders are Lobosa, Foraminifera, Heliozoa, Radiolaria, and Myxomycetes. All of them appear to be natural except the first. The Foraminifera and Radiolaria, having shells suitable for preservation as fossils, are known to be very ancient, as we might expect in groups having no assignable nucleate ancestors except flagellates.

The best known cytologically, of Rhizopoda as of Zoomastigina, are the entozoic species studied by Kofoid and his associates. The scientists of the California school were not the first to describe a normal mitotic process in amoebas, but in a long series of papers (16, 60, 64, 71, 76, 78, 79, 80, 124) they have shown that typical mitosis is typical of the group. In the resting nucleus, the chromatin is largely or entirely gathered into a single mass called a karyosome. A centrosome, the only remnant of a neuromotor apparatus, is found during mitosis just within the persistent nuclear membrane; it divides, and the parts remain connected by a fiber which, being within the nucleus, is called an intradesmose. A spindle is present; Child (16; see Fig. 6), working on *Endamoeba gingivalis*, found that it forms before the centrosome divides, extending from the centrosome in among the chromosomes which have formed from the karyosome; later, as the two daughter centrosomes move apart along the nuclear membrane, it opens like a jack-knife opening, to form a straight line.

The following are some of the observed chromosome numbers:

Councilmania Decumani	4
C. dissimilis	8
C. Lafleuri	8
C. Muris	6
Endamoeba coli	6
E. dysenteriae	6
E. disparita	12
E. gingivalis	6

In the "*Vahlkampfia* group" the chromosomes are smaller and more numerous, and there are prominent polar caps of stainable material within the dividing nucleus. These polar caps, mistaken for separating masses of chromatin, are largely responsible for the reports of non-mitotic division in amoebas. Within these caps, Kofoid and Swezy (79) first discovered centrosomes in *Karyamoebina falcata*.

In the amoebo-flagellate *Naegleria*,

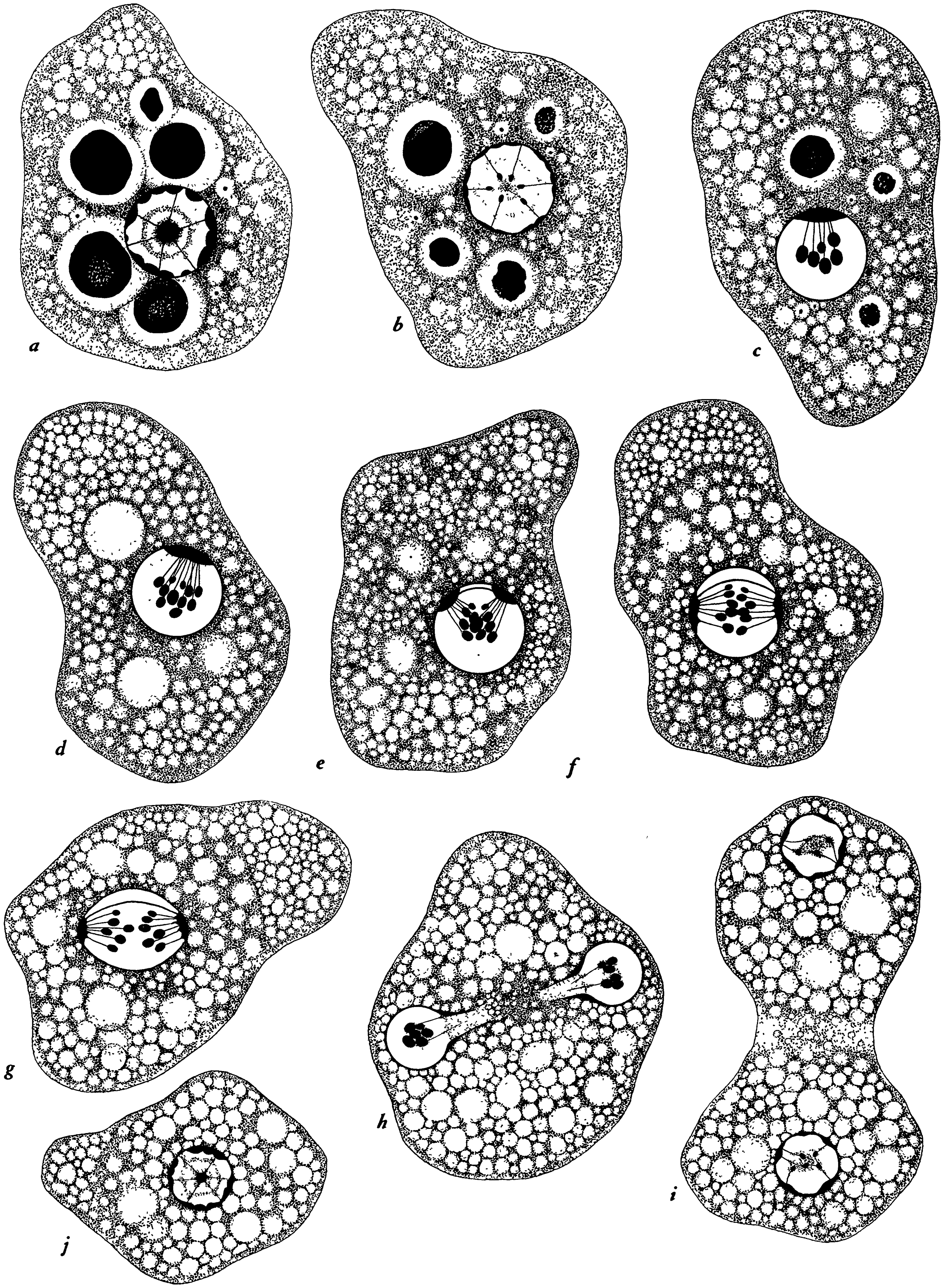

Fig. 6. Nuclear and Cell Division in Endamoeba gingivalis, Original Figures by H. J. Child, × 3750

which is normally amoeboid but readily induced to form a flagellum, Wilson (124) found that mitosis is of the *Vahlkampfia* type. When the flagellum is present, a rhizoplast connects the blepharoplast to the intranuclear centrosome, and another connects this to the karyosome. The extra-nuclear neuromotor apparatus—all of the neuromotor apparatus except the centrosome—is discarded or absorbed before division; it is regenerated from the centrosome, and Wilson was disposed to believe that this emerges from the karyosome.

The Myxomycetes will be considered separately.

The Sporozoa will merely be mentioned. The group includes very many species, all parasitic in animals. They have complicated life cycles, involving sexual reproduction; they are ordinarily non-motile, but have flagellate or amoeboid stages, indicating descent from the amoeboflagellate complex. They are apparently not a natural group. *Monocystis* was found by Calkins and Bowling (12) to have an extra-nuclear centrosome. This divides during the early stages of mitosis, and a spindle is formed between the daughter centrosomes; the nuclear membrane dissolves, and the spindle is carried laterally in among the chromosomes. The process is very much as in animals.

PROTISTA: VI A. MYXOMYCETES

The Myxomycetes were so named, as a group of Fungi, by Link, 1833. Some twenty-five years later de Bary, recognizing their resemblance to rhizopods, named the Mycetozoa (cf. Macbride and Martin (85)). In their vegetative condition, Myxomycetes are colossal amoebas adapted to life in air; the plasmodium, as the vegetative stage is called, is a naked mass of protoplasm containing thousands of nuclei, moving pseudopodially, and nourishing itself in holozoic fashion. Plasmodia are inconspicuous only because they keep to damp and shaded habitats. In reproduction, the protoplasm builds more or less elaborate structures by secreting pillars, fibers, and walls, of lifeless material, among which it undergoes cleavage into little spores homologous with the cysts of other rhizopods. The germinating spores release amoeboid cells which presently develop flagella.

The nuclei are minute, and the authors who have attempted to study them have found difficulty in recognizing nuclear division in the plasmodium. Just previous to spore formation, and again when the spores are germinating, mitoses are recognizable (see Harper (51) on *Fuligo;* Jahn (56) on *Stemonitis;* Howard (55) on *Physarum;* Gilbert (42) on *Ceratiomyxa*). A sharp-pointed spindle is formed within the nuclear membrane, and definite centrosomes have been recognized at the poles. The nuclear membrane persists for some time, but disappears before the end of mitosis. A nucleolus is present in the resting nucleus, and fades out at about the same time as the nuclear membrane. The nuclear divisions just before spore formation are supposed normally to include a reduction division; in *Ceratiomyxa*, a genus distinguished from other Myxomycetes by a variety of characters, reduction division takes place within the spore, which accordingly becomes 4-nucleate.

Gilbert gives a full description of the formation of flagella in *Ceratiomyxa*.

> The 4-nucleate protoplast escapes from the spore wall; after it has undergone various changes in form, each nucleus divides. While the protoplast is dividing by constriction into eight, each nucleus comes into contact with the cell membrane. The part of each nucleus which comes into contact with the membrane is the part diametrically away from the sister nucleus formed by the preceding division; this is the part where a centrosome, retained since the preceding division, may be presumed to be present. From the

point of contact, a flagellum is suddenly projected beyond the cell membrane; the nucleus then withdraws from the cell membrane and is found to be connected to a blepharoplast at the base of the flagellum by something which looks like a double rhizoplast. The accounts of enflagellation in *Stemonitis* and *Physarum* represent essentially the same process; but Jahn interpreted the structure between the nucleus and the base of the flagellum as a conical region of clear cytoplasm, whose boundaries would appear in optical section as two fibers.

The flagellate cells, in many Myxomycetes if not in all, are gametes; they fuse in pairs. The Myxomycetes are diploid in all stages except spores and gametes. It is not certain whether the amoeboid zygotes can combine with each other in forming the plasmodium, or whether each plasmodium is developed from a single zygote.

The Myxomycetes are evidently a natural group, and are evidently descended from something in the amoebo-flagellate complex.

PROTISTA: VIII. FUNGI

The group called Fungi, as here construed, consists of parasites and saprophytes whose bodies consist of filaments with rigid walls of chitin. They may be arranged in four classes. Two classes, Basidiomycetes and Ascomycetes, are highly developed groups, numerous in species, evidently natural, and showing in their characters some relationship to each other. Zygomycetes are a comparatively small and primitive group, not connected to the others by any forms confidently recognizable as intermediate.

The remaining class, the one usually and properly listed first, is Oomycetes. It embraces a variety of forms so broad that one cannot be positive either that the group is natural or that it is not. The main body of the class, consisting of the orders Saprolegniales and Peronosporales, is a natural group of typical filamentous fungi. They resemble in many respects such green algae as *Vaucheria;* the resemblance is usually taken as indicative of relationship, but is open to interpretation as being a result of parallel evolution.

The order Chytridiales, also included in Oomycetes, has been used as a dumping ground for poorly understood parasites. Here have been placed the intracellular parasites of flagellates, Infusoria, and rhizopods (see Becker (4), Campbell (13), Connell (20), Kirby (66, 68), Kofoid (70), Sassuchin (99)). Some of these, at least, are obvious bacteria. Leaving such things aside, the chytrids can be recognized as having a character of their own. A protoplast, originally naked and flagellate, makes its way into a cell of an alga or higher plant. There it develops a rigid wall, and usually sends out filamentous branches. It becomes multinucleate, and eventually breaks up into naked swimming cells which escape, usually, through a walled tube. Such an organism can be interpreted as a link between the amoeboflagellate complex and the typically fungal Saprolegniales and Peronosporales.

Mitosis is known in several genera of the latter orders (see Davis (31) on *Saprolegnia;* Couch (26) on *Leptolegnia;* Davis (30) and Stevens (107, 108) on *Albugo;* Stevens (109) on *Sclerospora*). It resembles that of Myxomycetes: the sharp-pointed spindle, at the ends of which centrosomes have been detected, is formed within the nuclear membrane. The membrane persists until about the middle of the mitotic process. The nucleolus is rather persistent, and Stevens has in some cases found it to divide into two parts which pass to the poles of the spindle.

Cotner (24, 25) has described the origin of flagella on the swimming cells of several genera. The nucleus is drawn out into a beak which reaches, or nearly reaches, the cell membrane. From the beak, the one or two flagella (the number is constant in each genus) are projected; the nucleus then withdraws from the surface of the cell, but remains connected to the blepharoplasts at the bases of the flagella by one or two rhizoplasts. All this is quite as in *Ceratiomyxa*.

The mitotic processes of Oomycetes have been described chiefly from the reproductive structures; the vegetative nuclei in the filaments are too small, and are not easily enough found in division, for convenient study. The same situation holds in Ascomycetes and Basidiomycetes. The three nuclear divisions, including the reduction division, which lead to spore formation in Ascomycetes have been described by a long series of authors, who consistently confirm Harper's (50) early account of the process as observed in *Erysiphe* (Fig. 7). A centrosome lying next to the nuclear membrane, apparently fused to its outer surface, develops an aster toward the outside and a bundle of spindle fibers toward the inside. The centrosome divides, and as the two daughter centrosomes move apart along the nuclear membrane, the ends of the two parts of the spindle swing apart until they form a straight line. The nucleolus disappears; the nuclear membrane persists until the later stages of mitosis, when it seems to dissolve or collapse, leaving each cluster of chromosomes, while shredding out into a network, to develop a new membrane. The centrosomes persist, dividing at each nuclear division; at the end of the last nuclear division, the nuclei thrust them forth on beaks. These beaks, since the spores are dispersed in air, do not generate flagella; instead, they seem to induce the formation of a spore wall some distance out from and surrounding each nucleus.

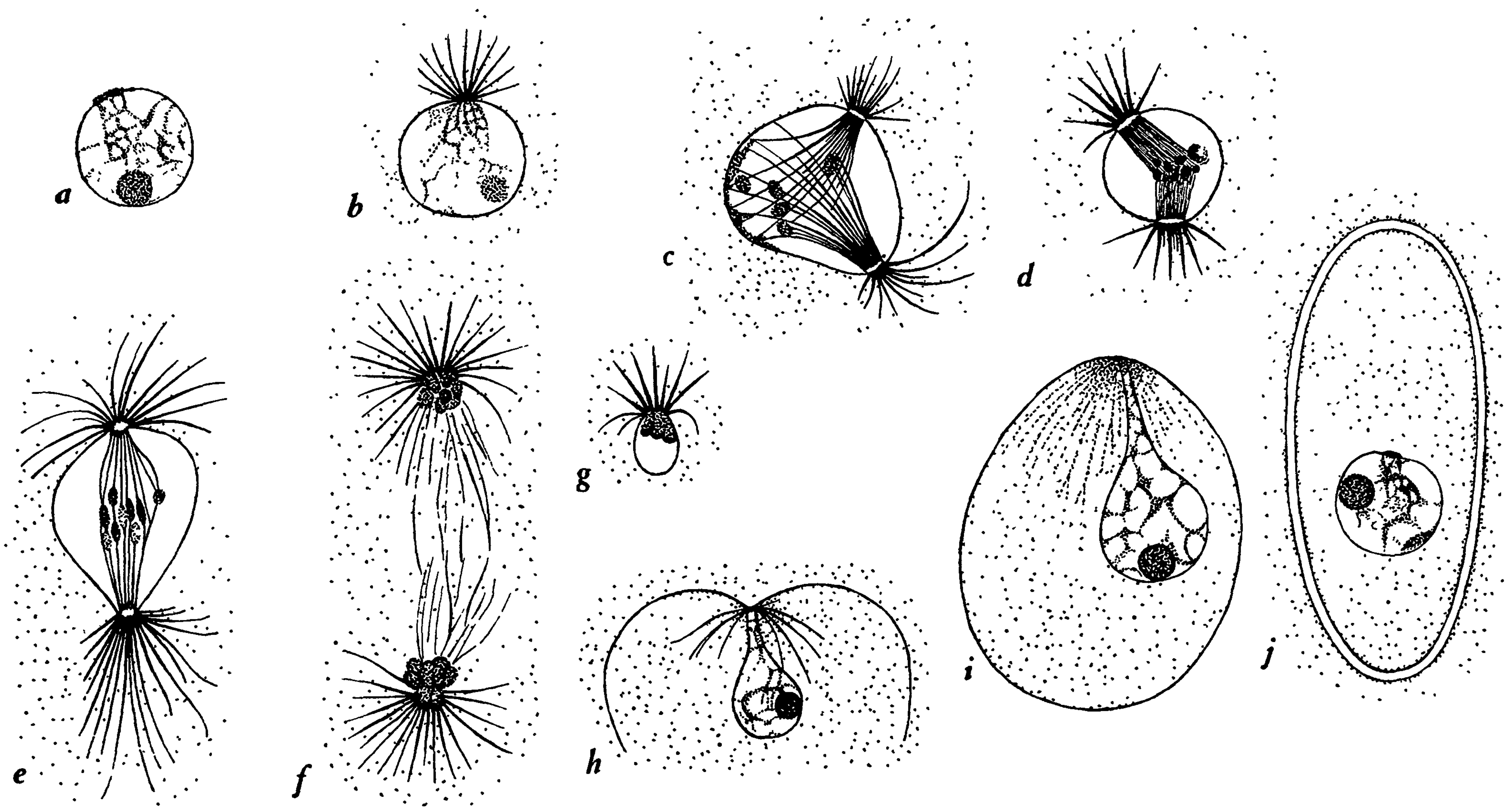

FIG. 7. NUCLEAR DIVISION AND FORMATION OF ASCOSPORES IN ERYSIPHE COMMUNIS, AFTER HARPER

Many studies of Basidiomycetes, of such diverse groups as mushrooms, puffballs, and rusts, have been carried out with the use of technique refined enough to yield chromosome numbers, which are apparently always two or four. The spindle is developed within the nuclear membrane, and is sharp-pointed; Lander's (82) figures of *Scleroderma* show definite centrosomes at the poles. The nuclear membrane seems always to disappear early in the mitotic process, though the nuclear sap may remain distinct from the cytoplasm for some time longer.

The spore-producing organ, the basidium, includes one original nucleus which undergoes a reduction process of two divisions.

In *Coprinus*, Vokes (119) describes the nucleus as moving up to the cell wall; when it withdraws, four points on the wall are found to be connected to one point on the nuclear membrane, where we can imagine a centrosome, by four fibers, possibly homologous with rhizoplasts. The point of attachment seems to divide as nuclear division begins. The spindle is formed within the nuclear membrane, with the points of attachment as poles; the membrane presently disappears, but there are two fibers attached to each pole of the spindle, and, subsequently, to one point on the membrane of each daughter nucleus. The second division goes forward in much the same manner as the first; each of the four resulting nuclei has one fiber attached to it. As the four nuclei are formed, the cell wall grows out, at each point where a fiber is attached, and forms a little cavity at the end of a slender tube; each nucleus moves up the fiber attached to it and into one of the cavities. Each of the resulting bodies—the wall of the cavity and the contained cytoplasm and nucleus—is cut off as a spore.

It was long ago suggested that the Fungi are not a natural group; that the Ascomycetes may be placed near the red algae, and the Oomycetes and Zygomycetes broken up and distributed near various groups of green algae. Traces of this arrangement remain in the recent classification of Fungi by Clements and Shear (18). Gäumann (41) accepts most of the Fungi as a natural group derived through Saprolegniales from green algae, but derives some of the chytrids from the rhizopods. Martin (87) maintains that the whole range of Fungi, including Myxomycetes, is a natural group. The evidence seems to me not strongly con firmatory of any of these views. For the present it will be convenient to assume that Martin's view is correct; that Fungi proper and Myxomycetes represent parallel lines of development from more or less the same member of the amoebo-flagellate complex. Under this assumption, natural classification would permit the treatment of Myxomycetes either as a group of Fungi or as a separate group. The more convenient alternative is the treatment of Myxomycetes as a separate group, or their assignment to Rhizopoda, since this facilitates the descriptive definition of the group to which the name Fungi is applied.

PROTISTA: IX. INFUSORIA

Infusoria are distinguished by the possession of cilia, structures typically shorter in proportion to the size of the body than flagella, more numerous, and distributed generally over the surface. The Infusoria reach fairly large sizes, and may be individually visible to the naked eye; they are common, numerous in species, and familiar, and are notable for an elaboration of the structure of the individual cell exceeding that of other organisms. A mouth and gullet (more technically cytostome and cytopharynx) are adaptations for holozoic nutrition. The bases of the cilia are linked together by an elaborate neuromotor apparatus; this does not, however, come into contact with the nuclei. In most Infusoria there are two kinds of nuclei, both represented in every cell; in other words, each cell contains at least two nuclei which are not alike.

Nuclei of the more conspicuous kind, called macronuclei, divide by a non-mitotic process; and, at intervals, they dissolve and disappear, to be replaced by new ones originating by the division of micronuclei. This process is called endomixis. There is a sexual process in which pairs of cells form a junction without losing their individuality. The macronuclei dissolve, while the micronuclei undergo three or four divisions including a reduction process (since reduction takes place just before sexual fusion, all nuclei except those capable of fusion are diploid). Each cell receives one of the nuclei formed by reduction division in the other; this unites with one of those formed by reduction division in its own body; the remaining haploid nuclei degenerate and disappear. The cells separate, and in each of them the fusion nucleus divides once or more than once; macronuclei and micronuclei arise by the differentiation of the nuclei formed by these divisions. It is evident that only micronuclei retain the genetic powers of proper nuclei.

It has long been known that micronuclei divide mitotically, and that their membranes do not disappear but undergo constriction at the end of the process. Turner (117), working on *Euplotes Patella*, discovered in the micronucleus an endosome which divides during mitosis, the parts remaining connected for some time by a fiber. The daughter endosomes seem to accompany, rather than to lead, the separating chromosomes; they may be comparable with the endosomes of *Euglena* rather than with centrosomes.

The Infusoria are evidently a natural group. Like red algae, they are a highly evolved group of unknown origin, and an evolutionary blind alley which has led to nothing higher.

PROTISTA: DISCUSSION

A great number of nucleate organisms have now been surveyed under the assumption that they constitute a kingdom Protista. They have been arranged in nine groups which may be construed as phyla or divisions. Some of these are manifestly artificial, but I have tried to show that the whole assemblage is a natural group, that all of these organisms are derived from the one original nucleate organism by lines of descent which lie entirely within the divisions considered (see Fig. 8). If the whole assemblage is a natural group, the question of recognizing it as a taxonomic group, a kingdom, is one of convenience.

One element of convenience, as already mentioned, lies in the feasibility of definition by description. As the Protista are separated from Monera by a broad evolutionary gap, it is easy to distinguish them from Monera by a character, namely, the presence of nuclei. From plants and animals, Protista can to some extent be distinguished by primitive features of the nucleus. The apparently most primitive of known nuclei have a membrane which does not disappear during mitosis, but divides by constriction. Centrosomes, and spindles formed within the intact nuclear membrane, are features of very primitive, if not of the most primitive nuclei. We may regard the permanent nuclear membrane, the centrosome, and the intranuclear spindle, as the positive characters of typical Protista. All these characters fade out in the evolution of various lines: we find the nuclear membrane disappearing at earlier and earlier stages in brown algae and in Fungi; the centrosome, permanent in the lowest brown algae, is present only during mitosis in the higher brown algae; is absent during the second division of the reduction process in *Polysiphonia;* has not been detected in many Basidiomycetes. The spindle originates in the cytoplasm of the sporozoan *Monocystis*. And, while the characters of typical Protista are absent from the higher Protista, they are to some extent present, as would be expected, in the lowest plants and animals.

The kingdoms of plants and animals, being derived groups, are distinguished respectively by combinations of positive characters pecular to themselves. The Protista may be distinguished by the absence of these characters, but it is to be remembered that organisms can be retained as plants or animals even if by degenera-

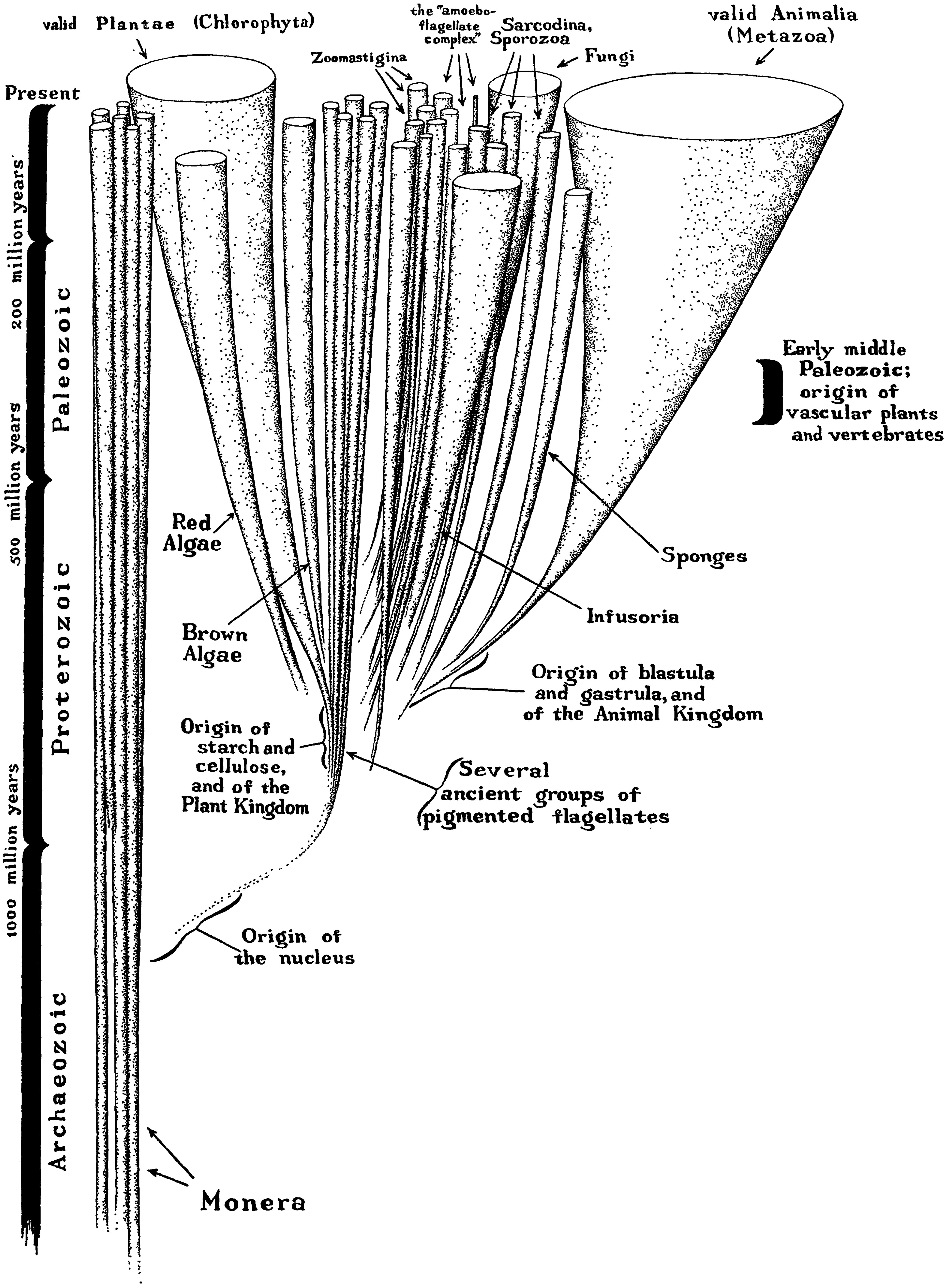

FIG. 8. DIAGRAM OF THE GENERAL PHYLOGENY OF ORGANISMS AS PRESENTED IN THE PRESENT PAPER

tion they lose the characters of the kingdoms to which they belong. Ultimately, it is not by characters but by relationship that groups are defined, and the more extensive the group, the more numerous will be the exceptions to the formal descriptive characters.

We may with equanimity abandon the attempt to define Protista by characters, positive or negative, which will not admit of exceptions. The convenience of the group will appear most definitely by contrast with alternative dispositions of the included organisms.

The traditional disposition of these organisms has been by partition (apparently with a subconscious attempt at equity) between plants and animals. The plant kingdom resulting from this partition, as presented in the text books, includes a group Algae, divided into classes distinguished by pigmentation, as blue-green, green, brown, or red, and a group Fungi, including bacteria and Myxomycetes. It is obvious that by this treatment neither Algae nor Fungi nor the plant kingdom is a natural group. Toward the end of the nineteenth century, Engler and Prantl (38) attempted to correct this situation by annexing the whole group of flagellates. Not all botanists welcomed this proposal; Thaxter (114), an outstanding authority on Myxobacteria, Zygomycetes, and Laboulbeniales (organisms having little enough in common with proper plants) characterized the annexed group as "a menagerie of organisms whose zoology is orthodox to a degree." The real objection in natural classification to the Englerian system is not the orthodox zoology of the flagellates, but the appearance that annexations were not carried far enough. In order to link the Fungi and Myxomycetes into the plant kingdom, we need also the Rhizopoda, and as the annexation of this group leaves the Infusoria and Sporozoa at loose ends in the animal kingdom, we might as well take these groups with the others. This is, indeed, not the only way of setting up a natural system of two kingdoms: the zoologists can keep the Protozoa in their kingdom, if they are willing to accept along with them the Monera, the diatoms, the marine algae, and the Fungi. These groups move as a block; an equitable partition which is at the same time natural is, to present knowledge, an impossibility.

Recognizing the extreme inconvenience of throwing the whole range of Protista (and the Monera along with them) into either Plantae or Animalia, and recognizing also the impossibility of distributing these organisms between the two kingdoms, some authors have proposed to recognize, in place of the one kingdom Protista here described, a series of several kingdoms. This is, for example, the position of Smith (106), who, having distinguished six phyla of algae, remarked that "in reality, the six divisions listed above represent six kingdoms. Five of these kingdoms would have but one division each." Similarly, such a treatment might be satisfactory to Martin (87), who remarked that "Myxomycetes, Phycomycetes, Ascomycetes, and Basidiomycetes . . . together constitute a phylum, to be included among plants as a matter of convenience, but in reality neither plants nor animals, but an independent group of organisms, one of several such." This multiplication of kingdoms is not in itself inconsistent with natural classification, but neither now nor in immediate prospect would it be found practical, in such a multiplication of kingdoms, to make them all natural. A system granting regnal rank to such petty groups as cryptomonads, and to such artificialities as Zoomastigina and Sporozoa, is scarcely desirable. Natural classification permits all these groups to be treated as one unit, and it is more convenient to do so than to treat them as a dozen or more units.

The balance of authority has been strongly against the recognition of a kingdom Protista. The objection advanced with most show of reason states that the line between plants and animals is recognized with difficulty, and that the establishment of a group placed between them will increase the difficulty by requiring the recognition of two vague lines instead of one. Here I may introduce an analogy. It seems that mankind, for the most part, consists of three races. Imagine that by immemorial tradition mankind has been held to consist of two races: the line between them will be a constant source of difficulty, but the difficulty will become inconsiderable whenever science is persuaded to recognize two lines instead of one. It will presently be shown, of the kingdoms left as plants and animals by the exclusion of Protista, that each of these groups can be defined by positive characters to which exceptions are reasonably few, and that each kingdom is quite definitely limited by its characters to certain subordinate groups. The situation to which objection is made is imaginary.

In undertaking actually to use Protista as a taxonomic entity, I recognize a difficulty which did not concern the authors who refused to do so. Organisms previously within the jurisdiction of two different nomenclatorial codes are to be placed in a group for which no code has been framed: the result may be nomenclatorial confusion. We need not take this difficulty too seriously. The art of nomenclature rests as much on antiquarian as on biological science. We have seen enough nomenclatorial confusion, in the realms governed by codes, to know that biology, and even taxonomy, can survive it. Meanwhile, I have taken advantage of the escape from codes to apply consistently the practice of Linnaeus in capitalizing all specific epithets which are proper nouns.

PLANTS

Such is the concept of Protista, as it has just been formulated, that an account of the characters and limits of Plantae and Animalia will complete the characterization and limitation of Protista, and will, in fact, complete the limitation of kingdoms which is the object of this paper.

The limits of the plant kingdom are those which will include the two groups Chlorophyceae (green algae) and Embryophya (higher plants). The positive characters are the possession of chloroplasts, that is, of plastids containing the four pigments Chlorophyll A, Chlorophyll B, carotin, and xanthophyll (and no others), and the production of two specific carbohydrates, true starch and true cellulose. Some of these characters appear to some extent among Protista. The plastids of Heterokontae, chloromonads, and euglenids can scarcely be called anything but chloroplasts, though they may differ from those of proper plants in the relative abundance of the different pigments. The carbohydrates starch and cellulose have been reported from various Protista. Blackman's (6) account of the dinoflagellate genus *Pyrocystis* refers to a cellulose which does not give a blue color with zinc chlor-iodide, and to a starch which does not give a blue color with iodine. Maltaux and Massart (86) refer without qualification to starch as occurring in the cryptomonad *Chilomonas*. There are other such reports, and it is not improbable that some of them are correct. But no organisms except proper plants show the complete combination of plant characters.

The lowest group in the plant kingdom

as here construed is the order Volvocales. In an evolutionary sense, this group and its descendants, as distinguished from all other organisms, are plants. The Volvocales have the characters of flagellates, and are by zoologists regularly listed as the order Phytomonadida of class Mastigophora. This disposition of the group is in quite as good accord with natural classification as the botanical treatment which places the Volvocales among green algae: we have here a perfect example of an evolutionary link between two groups. The botanical treatment is followed here as being the more convenient, in emphasizing the positive characters, the chloroplasts, starch, and cellulose, of the Volvocales.

We have in Kater's (59) account of *Chlamydomonas* a thoroughly satisfactory description of the nucleus and mitosis of a primitive and typical example of the Volvocales. With this as a starting point, we can make out the course of the evolution of the nucleus in plants: a matter which is of interest as tending to confirm the interpretation of the evolution of the nucleus already given in connection with Protista.

Chlamydomonas (Fig. 9) has a neuromotor system of two flagella, a blepharoplast, a rhizoplast, and an intranuclear centrosome.

During mitosis, all of these are cast off or dissolved except the centrosome; the nucleolus also dissolves, as in higher plants. The dividing centrosome forms an intradesmose, and a spindle forms within the nuclear membrane with the daughter centrosomes as poles. The nuclear membrane persists until mitosis is nearly complete, but eventually dissolves instead of undergoing constriction. The neuromotor systems of the daughter cells are formed as outgrowths from the centrosomes. The whole process is of great interest as being intermediate between what we observe in flagellates and what we observe in higher plants. As in most flagellates, but not the primitive euglenids, the centrosomes have become division centers and the nucleolus dissolves instead of dividing. There has possibly been a stage resembling what we find in the trichomonad flagellates, in which the neuromotor system and nuclear membrane are permanent, being divided and inherited at each division. The dissolution of these parts seems to be a matter of degeneracy of the neuromotor system, but it is a preliminary to advance in the evolution of the organism as a whole.

The Volvocales, with several other orders, belong to the class Isokontae. This is the most significant of the classes of green algae, as being the most numerous in species, and as including both the most primitive green algae and those which come closest to the higher plants. No other Isokontae seem to be as well understood, cytologically, as *Chlamydomonas.* From several genera (see Allen (1) on *Coleochaete;* Timberlake (116) on *Hydrodictyon;* von Cholnocky (17) on *Ulothrix*) there have been reports of granules at the poles of the mitotic spindle; these may be recognized as centrosomes. They are found most usually during the divisions preceding the formation of flagellum-bearing swimming cells.

Among green algae belonging to minor groups—classes apparently derived from Isokontae and leading to nothing further —the genus *Spirogyra* has been the most studied. There is a recent precise account of the behavior of the nuclear membrane and spindle during division by McAllister (88).

The spindle appears first in polar positions outside the nuclear membrane; subsequently it extends within, not breaking through the membrane in any crudely mechanical fashion, but being extended beyond it. The part first formed, outside the membrane, becomes invisible while the part inside persists and functions. The nucleus becomes football-shaped; the membrane remains intact for some time, but eventually, as in *Chalmydomonas*, it disappears, and new membranes are formed about the daughter nuclei. No trace of centrosomes remains; this is perhaps associated with the complete absence of flagellum-bearing cells in the group represented by *Spirogyra.*

It is possible for an organism to retain the occasional habit of producing flagellum-bearing cells after losing all trace of centrosomes, though this situation is not usual. It is exemplified by *Oedogonium*, which represents another evolutionary side-line among green algae. In this genus, Ohashi (92) finds that there is no centrosome. The nuclear membrane disappears early in the mitotic process. When a cell is to develop flagella, a number of granules appear *de novo* in the cytoplasm. They move to the cell membrane and arrange themselves in a ring where the flagella are to form.

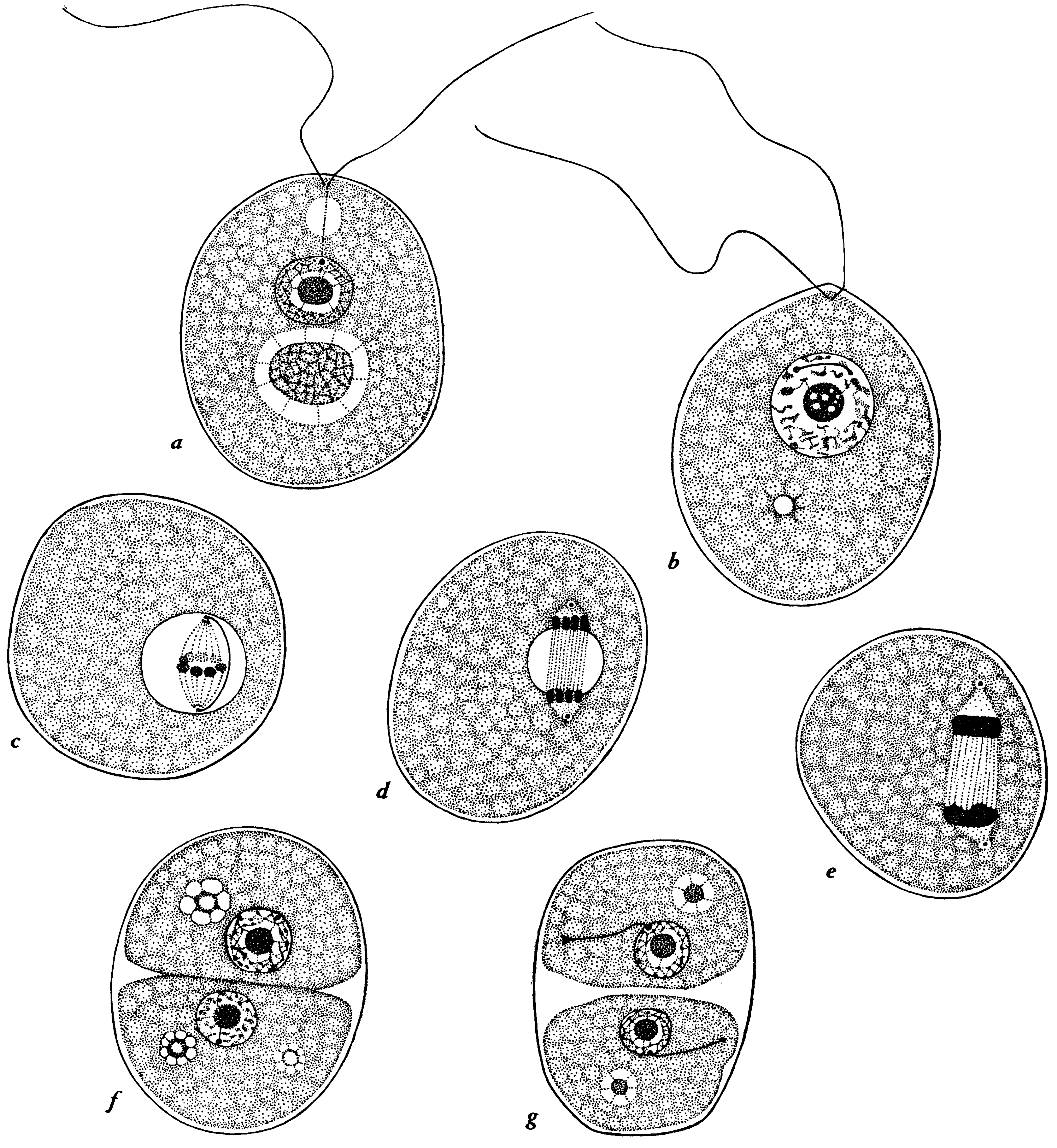

FIG. 9. NUCLEAR AND CELL DIVISION IN CHLAMYDOMONAS NASUTA, AFTER KATER, × 2567

As we turn from green algae to higher plants, we find that many of the latter produce male gametes which are motile by means of flagella. In liverworts, mosses, and some of the fern allies, the sperms are biflagellate, apparently as an inheritance from the Isokontae; in ferns, cycads, and the maidenhair tree, they bear many flagella, apparently as a modification of the biflagellate condition. The flagella born by sperms of these higher plants arise always from granules which stand at the poles of the spindle during the mitoses by which the sperm nuclei are formed.

There is a considerable literature (cf. Sharp (105)) concerning these granules; they may be absent during all mitoses except those by which the sperm nuclei are formed, or may appear during a few previous mitoses; or, in liverworts, there may be traces of them elsewhere in the body (see Chamberlain (15) on *Pellia* and Van Hook (118) on *Marchantia*). Following Chamberlain (14) and Sharp, we may accept these bodies as being centrosomes, though not all authorities have done so. The additional term blepharoplast, coined by Webber (122), has been found useful in dealing with organisms whose neuromotor apparatus includes a flagellum-bearing structure distinct from the centrosome.

In the highest plants, the conifers and the angiosperms, there are no flagellate cells whatever. There are no traces of centrosomes; nuclear membranes disappear at the beginning of mitosis; spindles originate in the cytoplasm. These nuclear features typical of plants, then, are fully developed only in the highest plants, and are the outcome of a long evolutionary process.

ANIMALS

The only known organisms not accounted for in the foregoing treatment of Monera, Protista, and Plantae, are those which the zoologists call Metazoa. To these, by the present treatment, the kingdom Animalia is limited. All are multicellular, holozoic in nutrition (with exceptions), and (again with exceptions) diploid as to all cells except the gametes. The bodies include freely wandering amoeboid cells. The sperms bear flagella. These characters indicate an amoebo-flagellate ancestry, like that of the Fungi and the various groups of Rhizopoda (as the amoebo-flagellate complex is not in itself a natural group, there is nothing to indicate that the animals, Fungi, and Rhizopoda are related through any ancestor more recent than flagellates).

Centrosomes are present, outside of the nuclei, in the cells of animals; at each mitosis they divide; the spindle is formed between the daughter centrosomes, and enters in among the chromosomes only as the nuclear membrane dissolves.

There are also embryological characters which bind together the great majority of the species. The developing individual passes through a stage in which it is a closed hollow sphere of a single layer of cells, a blastula. The blastula, by one series of stages or another, develops into a more or less spherical body whose wall is a double layer of cells pierced by an opening to the interior; this is a gastrula. An adult *Hydra* is a slightly modified gastrula; a man or a beetle is, in individual development and in evolution, a profoundly modified gastrula. So far as these characters extend, there is a pervading uniformity to animals, marking the group as obviously natural.

Doubt must be acknowledged as to the position of one group. Porifera (sponges) are the most primitive of the groups regularly included in Metazoa. This is the one phylum of organisms whose assignment to a kingdom is made here without confidence. The sponges are clearly descended from the amoebo-flagellate complex, and are in many ways intermediate between the amoebo-flagellate complex and typical animals. It is, however, not certain that they can be construed as exhibiting the embryological characters of typical animals, and if not, it is possible that their evolutionary origin may have been independent of that of typical animals. If this possibility is the truth, the sponges should be placed among Protista, as in Haeckel's original account of that kingdom, but one tends to assume that they represent a stage in the evolution of typical animals, and are legitimate members of the animal kingdom.

CONCLUSIONS

The evidence and argument presented have been to the effect that organisms can be arranged, naturally and more conveniently than in the past, in four kingdoms, as follows:

1. Monera (Haeckel). Organisms without nuclei, the cells solitary or physiological independent. Groups included, bacteria and blue-green algae. Ancestral form, the original form of life; it is believed to be most nearly represented among living organisms by the nitrifying bacteria. Nomenclatorial type, *Bacillus subtilis*.

2. Protista, Haeckel. Organisms, largely unicellular, with nuclei; typically with permanent nuclear membranes, centrosomes, and intranuclear spindles, though all of these may be lost in evolution; lacking the combinations of characters to be listed as characteristic of plants and animals. Groups included, Flagellata (construed as excluding Volvocales), Rhizopoda, Sporozoa, Infusoria, diatoms, red algae, brown algae, and Fungi. Ancestral form, the first nucleate organism; this is presumably most nearly represented among living forms by the Chrysomonadida. Nomenclatorial type, *Amoeba Proteus*.

3. Plantae, Linnaeus. Organisms (with few and derivative exceptions) having plastids containing the four pigments chlorophyll A, chlorophyll B, carotin, and xanthophyll, and producing true starch and cellulose. The primitive members are motile, unicellular, and have nuclei much as in Protista; the higher are non-motile and of elaborate structure and have no centrosomes nor intranuclear spindles. Groups included, Chlorophyceae and Embryophyta. Ancestral group, Volvocales.

4. Animalia, Linnaeus. Organisms which are multicellular, typically diploid and holozoic, passing through blastula and gastrula stages in development. Centrosomes are present; spindles are generally formed outside the nuclear membrane, and enter the nucleus only as the membrane dissolves. Groups included, the Metazoa as usually construed (except possibly Porifera, which might fall into Protista). Ancestral group, Porifera; or, if that be excluded, Coelenterata.

ACKNOWLEDGEMENTS

Acknowledgements of more than one kind may be in order. The standard taxonomic revision is the work of an expert in the group concerned; it cites all pertinent literature; it is received with respectful interest (never with complete acquiescence) by the author's fellow experts in the same group, and is more or less annoying to others who have to take it into account, as requiring revision of familiar ideas of the limits of groups and the application of names. The present paper, on the contrary, issues from no expert; there lives now no Aristotle or Linnaeus, no one who is an expert on the whole range of life. Accordingly, it may perhaps be an annoyance to all who take cognizance of it. But one who thinks as a taxonomist is unable to withhold his hand from what appears to be an opportunity to make the taxonomic system more natural.

Associated with the fact that this is not the work of an expert is the fact that the bibliography is fragmentary. The literature pertinent to the present subject is a major fraction of the whole literature of life. I have studied what literature was readily at hand; I have leaned heavily on the advanced textbooks (5, 9, 11, 18, 36, 57, 81, 84, 85, 90, 97, 103, 105, 106, 123, 125); the original contributions consulted have been largely recent and largely American. I regret having overlooked many pertinent contributions, which it would have been only just to have

cited, but I believe that the evidence assembled is typical of the whole body and makes a strong case.

No part of the data presented is my own discovery. Of the ideas, I can claim as my own only the delimitation of the kingdom Protista. The remaining ideas are assembled from many sources—from reading, from conversation, from instruction. My teacher, in principles of classification, has been my father, Dr. E. B. Copeland; in cytology, Dr. C. E. Allen; in the science of algae, Dr. G. M. Smith. I am keenly aware of my indebtedness to them, and again to my father, and to my colleagues, Dr. H. J. Child and Dr. H. C. Day, for interest during the preparation of this paper and for searching criticism of fact, of inference, and of presentation. But no responsibility for the outcome is to be attributed to any of these gentlemen.

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