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# Not plants or animals: a brief history of the origin of Kingdoms Protozoa, Protista and Protoctista

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**Summary** In the wake of Darwin's evolutionary ideas, mid-nineteenth century naturalists realized the shortcomings of the long established two-kingdom system of organismal classification. Placement in a natural scheme of Protozoa, Protophyta, Phytozoa and Bacteria, microorganisms that exhibited plant-like and animal-like characteristics but obviously differed in organization from larger plants and animals, challenged traditional classification. The attempts of naturalists to classify these organisms outside the constraints of the plant and animal kingdoms led to concepts of additional kingdoms (Protozoa, Protista, Protoctista, etc.) to accommodate the nature of these organisms as not true plants or animals.

**Key words** Protista–Protoctista · Protozoa concept · Monera · John Hogg (1800–1869) · Herbert F. Copeland (1902–1968)

The greater morphological grouping into kingdoms is, at any one time, a reflection of our understanding of the living world. Prior to the 20th century, concepts of organismal classification had been constrained within narrow boundaries that defined all life as either plant or animal [34, 37]. Nevertheless, there were complex organisms, mainly microscopic and aquatic, with the greater characteristics of greenness of plants and the movement of animals that stretched those plant and animal boundaries. Eighteenth century microscopic investigations into the nature of these organisms regarded them as dissociated cells of plants and animals or at best as imperfect forms of "higher" plants [4]. Technological innovations, such as the achromatic substage condenser in 1838 [3, 35], refined the optics of the light microscope and led the science of microscopy along new paths of investigation into the life histories of microscopic organisms. By the middle of the nineteenth century, the generalized microbial groupings of Protozoa, Protophyta, Phytozoa, and Bacteria placed the organisms in a context of "lower", or intermediate forms in the evolution to "higher" plants and animals [22, 33]. Concurrently, the existing dichotomy of the plant and animal kingdoms became rapidly blurred at its boundaries and outmoded as the organisms in question themselves, by their very plant-like and animal-like nature, clouded any succinct definition of a plant or an animal [34, 37].

## Protozoa as a class, phylum and kingdom

In 1820, German naturalist Georg A. Goldfuss introduced the term "Protozoa" (first, or early animals) into the scientific literature for a class of organisms within Kingdom Animalia that consisted of Infusoria (called ciliates today), Lithozoa (corals), Phytozoa (e.g. *Cryptomonas*), and Medusinae [47]. In 1845 Carl Theodor von Siebold of Germany established a phylum of invertebrate animals within Kingdom Animalia that he named Protozoa [39]. Phylum Protozoa consisted of the classes Infusoria (ciliates) and Rhizopoda (amoebae, foraminifera) and von Siebold regarded these organisms as "unicellular animals", possessing the function and structure of an individual animal cell, not the whole organism [34, 37, 39]. Other investigators, such as naturalist Louis Agassiz, considered the protozoa to be more plant-like than animal-like and did not believe they were part of the animal kingdom [1]. By mid-nineteenth century, microscopic organisms were generally regarded within the generalized groupings of Protozoa (primitive animals), Protophyta (primitive plants), Phytozoa (animal-like plants), and Bacteria (primarly regarded as plants) [1, 22, 33]. No clear consensus existed about the systematic nature of the organisms and their evolutionary relationship to one another or to larger plants and animals [34, 37]. Microscopic life became

increasingly intertwined and constrained taxonomically within the dichotomy of the plant and animal kingdoms.

In 1858, paleontologist Richard Owen (1804–1892) outlined his definition of plants and animals in the context of those "numerous beings, mostly of minute size, and retaining the form of nucleated cells" that demonstrated the "common organic characters" of plants and animals, but without the "superadditions of true plant and animals". He called these organisms Protozoa, defined as a group containing "the sponges or *Amorphozoa*, the *Foraminifera* or Rhizopods, the *Polycystineae*, the *Diatomaceae*, *Desmidiae*, *Gregarinae*, and most of the so-called *Polygastria* of Ehrenberg, or infusorial animalcules of older authors" [31]. In 1860, Owen referred to this grouping as Kingdom Protozoa in his book *Palaeontology* [32].

Those organic characters the Protozoa shared with plants and animals were based upon Owen's definition of a plant and an animal. A plant is "rooted, has neither mouth nor stomach, exhales oxygen, and has tissues composed of 'cellulose' or of binary or ternary compounds" [31, 32]. An animal "receives the nutritive matter by a mouth, inhales oxygen, and exhales carbonic acid, and develops tissues the proximate principles of which are quaternary compounds of carbon, hydrogen, oxygen, and nitrogen" [31, 32]. One could easily recognize plants and animals, according to Owen, when "a certain number of characters concurs in the same organism its title to be regarded as a 'plant,' or an 'animal,' may be readily and indubitably recognized" [30]. On the other hand, the Protozoa were defined by their lack of those certain number of characters, or "superadditions", of true plants and animals.

## John Hogg's Protoctista (1860, 1868)

In 1860 British naturalist John Hogg (1800–1869) wrote an article entitled *On the Distinctions of a Plant and an Animal and on a Fourth Kingdom of Nature* in which he outlined his proposal for "Regnum Primigenum" [19]. Hogg also described this fourth kingdom (the other kingdoms being Plant, Animal, and Mineral, from Linneaus) as the "Primigenal Kingdom", and it was comprised of "all the lower creatures, or the primary organic beings, «Protoctista»" (which he compounded from the Greek, etymologically as "first created beings") [19]. Protoctista were "both *Protophyta*, or those considered now by many as, lower or primary beings; and *Protozoa*, or such are esteemed as lower or primary beings, having rather the nature of animals" [19]. Also included in Regnum Primigenum were sponges, grouped as the Amorphoctista, those "formless or amorphous beings, whether partaking more of a vegetable or of an animal nature" [19].

Hogg's "Primigenal Kingdom" therefore consisted of both multicellular and unicellular organisms as Owen's Kingdom Protozoa did. However, Hogg did not agree with Owen's choice of the term Protozoa, as "naturalists are divided in opinion—and probably will ever continue so—whether many of these organisms, or living beings, are animals or plants", and that the "limits between the animal and vegetable kingdoms are more or less artificial, and cannot be well determined" [20]. Hogg maintained that the term Protozoa "can alone include those that are admitted by all to be animals or «zoa»" and therefore it was an incorrect name for the grouping of organisms that were not unambiguously animals [19]. Hogg was aware that since naturalists cannot agree on the precise characters defining plants and animals (Hogg believed that the defining characteristics of an animal were the "muscular and nervous systems, which do not exist in a plant"), there is no practical solution other than to "place those creatures, or organic beings, whose nature is so doubtful in a fourth kingdom" [19]. Hogg believed that including all these organisms into the Primigenal Kingdom "prevents the unnecessary trouble of contending about their supposed natures, and of uselessly trying to distinguish the Protozoa from the Protophyta" [20]. Hogg more fully described the Regnum Primigenum as containing "those lower organisms, or created beings (*ctista*)… the Desmidiae, some of the Infusoria, and Diatomeae, and doubtful Algae, and other *Protoctista*", and included "all the sponge-beings (Spongioctista), and the like anomalous lower ctista, creatures or organisms" [20].

Hogg's term "Protoctista" was expressive of organisms that came first in evolutionary time, and were diagrammatically represented by Hogg (and originally published in color) [20] (Fig. 1). The Protoctista are depicted as a grouping of organisms having the common characters of both plants and animals. The plant kingdom pyramid and the animal kingdom pyramid merge well before their bases meet. This common area is where the characters of plants and animals become less distinct and where the boundaries between the plant and animal kingdoms are blurred. This merging is representative of the Protoctista (and the embodiment of Regnum Primigenum), those organisms that have intermingled characteristics common to both pyramids or kingdoms. What is significant in Hogg's depiction of the Protoctista is that plants and animals share a common ancestry from the Protoctista.

## Haeckel's Protista (1866)

In 1866, the German naturalist Ernst Haeckel (1834–1919) made the first of many proposals for a third kingdom of life [16]. In his *Generelle Morphologie der Organismen* he named this third kingdom and the organisms contained within it the Protista, "the first of all, primordial" [16, 17]. Haeckel called attention to the problem of classifying "all those doubtful organisms of the lowest rank which display no decided affinities nearer to one side than to the other, or which posses animal

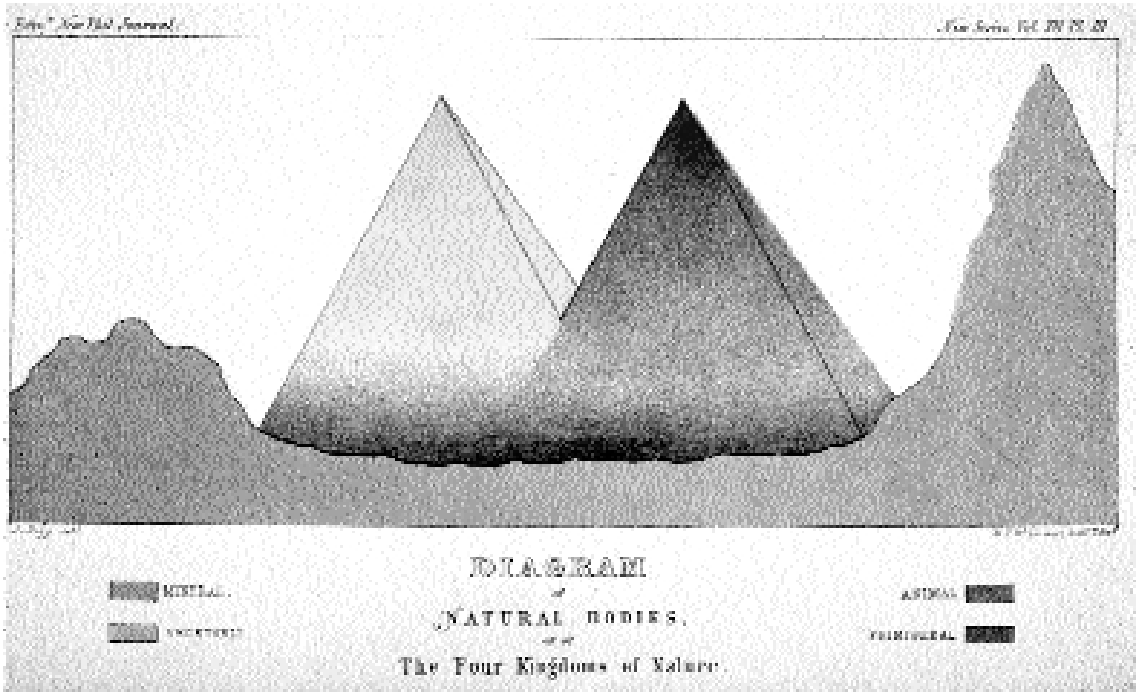


**Fig. 1** Hogg's representation of the "divergency and union of the several kingdoms." From *On the distinctions of a Plant and Animal, and on a Fourth Kingdom of Nature* (1860) Edinburgh New Phil J, NS 12:216–225. Collection of the Linnean Society, London. (With permission.)

and vegetable characters united and mixed" [16, 17]. Unlike Hogg's proposal in which Mineral was a kingdom, Haeckel recognized only Kingdom Plantae and Kingdom Animalia [16]. To Haeckel his third kingdom, Protista ("first of all, primordial"), was "the kingdom of primitive forms", and he regarded the bacteria, or Monera ("simple"), to be Protista as well [17].

Haeckel considered the Protista to be a "boundary kingdom intermediate between the animal and vegetable kingdoms" containing organisms "neither animals nor plants" [16, 17]. Haeckel also regarded the Kingdom Protista as a practical system to "separate the Protista in the system of nature entirely from animals as well as from plants", in the process more clearly defining the characteristics of true plants and animals [16]. However, Haeckel never intended to erect an "absolute wall of separation between the animal and vegetable kingdoms" [17]. Even though Haeckel believed that animals and plants derived their origin from the bacteria, he also considered that the Protista evolved "independent of the lineages of the animal and plant kingdoms", and it was only convenient "on practical grounds to separate the Protista in the system of nature entirely from animals as well as from plants" [17].

Haeckel's aim was for the Protista be considered separately for systematic purposes, not phylogenetic (Haeckel's term) ones [17, 37]. Kingdom Protista contained those organisms generally considered separately by other naturalists as the Protozoa, Protophyta, Phytozoa, and Bacteria; Kingdom Protista was a grouping of both non-nucleated and nucleated organisms [17]. The organisms were systematically arranged by Haeckel into the following Protista phyla: Monera (bacteria, and some cellular slime molds), Protoplasta (amoebae), Diatomaceae, Flagellata (e.g. *Euglena*, *Peridinium*), Myxomycetes (e.g. *Physarum*), Noctilucae (e.g. dinoflagellates), Rhizopoda (cellular slime molds and "radiolarans", e.g. heliozoans, actinopods), and Spongiae [16, 17] (Fig. 2). Kingdom Protista was therefore a grouping of both unicellular and multicellular organisms. Haeckel placed the Infusoria in Kingdom Animalia as he (and other investigators) considered them multicellular animals (until German biologist Otto Butschli demonstrated the unicellular nature of the Infusoria in 1873) [8].

## Haeckel redefines Kingdom Protista

With removal of sponges from Kingdom Protista after he concluded they were animals, Haeckel believed he could now clearly separate Kingdom Protista from true animals and plants in the realization that the defining character of the remaining Protista was the absence of sexual reproduction [17]. Haeckel stated that "all true Protista multiply exclusively by a non-

sexual reproduction (monogamy)" [17]. Basing his groupings of organisms on this criterion, he then moved the phylum Fungi (Inophyta) out of Kingdom Plantae and into Kingdom Protista. The "blue-greens" (known as cyanobacteria today) were also moved from Kingdom Plantae and placed into Kingdom Protista as the phylum Phycochromacea. Phylum Labryinthulea ("slime nets") was moved from the Animal kingdom and placed into Kingdom Protista. Volvocineae (*Volvox*) was moved out of Flagellata in Kingdom Protista and into Kingdom Plantae [17].

Haeckel saw these changes in Kingdom Protista occurring "as our knowledge of one group or another becomes apparently more complete" [17]. In later revision of Kingdom Protista, he founded a two-kingdom concept based upon a morphological division between the Protista ("unicellular plants and animals") and the Histonia (multicellular plants, the Metaphyta, and animals, or Metazoa) [18]. Haeckel maintained that the blastular stage of development was the defining characteristic of an animal, and he saw this characteristic as the fundamental division between animals and the Protista [8, 17, 18]. However, Haeckel's criterion for defining the plant kingdom remained primarily nutritive [17, 18]. Haeckel also returned the terms protozoa ("unicellular animals") and protophyta ("unicellular plants") to the forefront, regarding these groupings as sub-kingdoms of Kingdom Protista [18].

## Butschli's Protozoa and Dobell's Protista

The tenet that all microscopic life was single-celled in nature was first brought into prominence by von Siebold some twenty years earlier and became reinforced by the German zoologist Otto Butschli (1848–1920) in the 1880s [8, 21]. Butschli's concurrent rejection of the concept of a third kingdom entirely was based upon his belief that the Protista, especially with inclusion of the bacteria, was too polyphyletic in nature to be considered a single kingdom [21, 22, 37]. Butschli's grouping of Protozoa was defined as consisting of only nucleated, unicellular animal-like organisms; bacteria as well as the protophyta were considered as a separate grouping [21]. Consequently, Butschli's influence strengthened the von Siebold concept of protozoa as single-celled animals and the protophyta as single-celled plants [13, 21]. The German naturalists and their academic institutions asserted an authoritarian view over the rest of the worldwide scientific community, and by the turn of the century the definitions of these organisms as unicellular animals and unicellular plants had become solidly established [13, 36].

However, British biologist C. Clifford Dobell (1886–1949) in 1911 redefined the concept of unicellularity, and in doing so reinterpreted the definition of Protista as "acellular" instead of unicellular [14]. Dobell argued that the function and organization of the unicellular protistan organism, or "protist" (Dobell's term), is equivalent to the entire ensemble of cells constituting a plant or an animal. Calling the Protista "acellular" was Dobell's manner of calling attention to the fact that the Protista as organisms were organized quite differently from that of "cellular" plants and animals. Dobell asserted that "the great importance of the Protista lies in the fact that they are a group of living beings which are organized upon quite a different principle from that of other organisms" [14]. Dobell's concept of acellularity laid the foundation of the study of "Protistology", as coined by Dobell [13, 14, 36]. Investigation of the Protista in the light of acellularity was the beginning of a shift away from the dogma of German cell theory of the late 1800s and its concept of the Protista as "unicellular" [21, 36]. From the early 1900s and into the 1920s and 1930s, for lack of a viable alternative, Haeckel's Kingdom Protista became increasingly regarded as a makeshift classification too polyphyletic to represent a coherent evolutionary look at the organization of life on Earth [29, 37]. The Protista began to be regarded more in terms of evolutionary systematics rather than in a phylogenetic classification of protist taxa, although the Protista as an evolutionary grouping remained varied in interpretation [34].

## Copeland's Kingdoms Protista and Protoctista

In 1938, American biologist Herbert F. Copeland (1902–1968) at Sacramento Junior College in California, proposed a four-kingdom classification of life in a article entitled *The Kingdoms of Organisms* [9]. Copeland's aim was to present a taxonomy that systematically reflected the diversity of the living world beyond the boundaries of the plant and animal kingdoms. The primary basis for Copeland's four-kingdom concept was his conclusion that the "establishment of several kingdoms of nucleate organisms in addition to plants and animals is not feasible; that all of these organisms are to be treated as one kingdom" [9]. What led him to this conclusion was the extreme difficulty of teaching biology based upon Haeckel's system, and that "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" [9].

In Copeland's proposed four kingdom reclassification of life (Kingdom Monera, Kingdom Protista, Kingdom Plantae, Kingdom Animalia), the foundation was in the exclusion of the bacteria and the "blue-green algae" (cyanobacteria) from Haeckel's Kingdom Protista into a separate kingdom he named Monera. Copeland regarded the bacteria to be so different in organization from nucleated cells that this difference was of central importance to his proposed four-kingdom system of life, in that "the organisms thus set apart

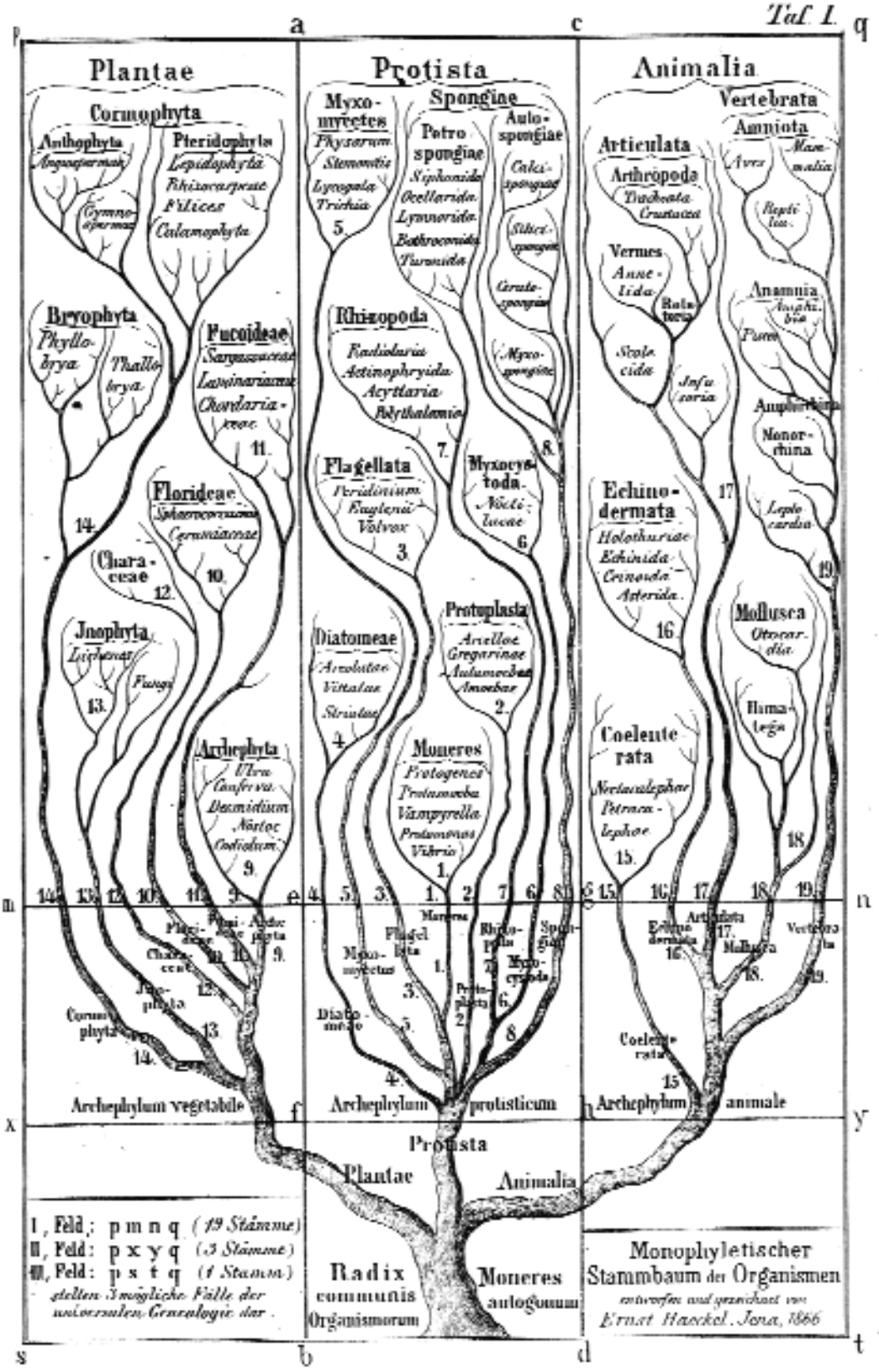


**Fig. 2** Haeckel's three kingdoms of life. From *Generelle Morphologie der Organismen.* Vol II. (1866). Berlin: Georg Reimer. Collection of Amherst College Library, Massachusetts, USA. (With permission.)

are evidently to be treated as a kingdom: they are different from plants and animals in greater degree than the latter are different from each other" [9].

In 1947, Copeland chose to call this fourth kingdom Protoctista (which he defined etymologically as "first established beings") instead of Protista [10, 11]. Copeland did not believe that it was appropriate to use Protozoa based upon Hogg's objections to the term, as well as the fact that Protozoa had been used previously not only for a kingdom (Owen) but also as a class (Goldfuss) and a phylum (von Siebold) [10, 11]. Copeland utilized the term Protoctista as inclusive of the protophyta and protozoa as Hogg did for organisms not true plants or animals. Although Haeckel defined the Protista in the same way, Copeland chose Protoctista for a kingdom name based on the fact that after Kingdom Protozoa, the term Protoctista had priority [10, 11]. Since Copeland recognized the primary cellular difference between anucleate and nucleate organisms, he regarded Protista unfit to use any longer as the name for his kingdom due to the fact that in all Haeckel's versions of Protista the anucleate bacteria were always included with nucleated organisms [11].

In 1956, Copeland presented a more detailed taxonomic view of his four-kingdom system in his book *The Classification of Lower Organisms* [11]. Copeland's definition of Kingdom Protoctista relied upon a sharp limitation of the plant and animal kingdoms. Kingdom Plantae was defined to contain organisms demonstrating the "presence of chlorophyll *a* and *b*, carotene, xanthophyll, and the production of starch" [11]. This group of organisms included all plants, as well as the green algae. Photosythetic organisms that did not meet these criteria were the brown and red algae. Kingdom Animalia was defined (after Haeckel) by the presence of the multicellular blastular stage of development [11]. What remained of these organisms, on the surface the "miscellany [of] the kingdom Protista of Haeckel", consisted of "nucleate organisms not of the characters of plants and animals" [10, 11]. Thus the Protoctista were those nucleate organisms, either unicellular or multicellular with or without photosynthetic pigments but not of the type in plants; without a blastular stage, and consisting of the broad groups red algae, brown algae, fungi, and protozoans [11]. Copeland also realized that so many unicellular organisms have multicellular descendants that a unicellular/multicellular dichotomy is invalid [11]. Even though Copeland recognized the fact that the organisms of Kingdom Protoctista were "an unfamiliar assemblage and undeniably heterogeneous" and may be distinguished as a group by the absence of true plant and animal characteristics, he nonetheless believed it is "not by characters but by relationship that groups are defined, and 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" [9].

## The Five-Kingdom system of classification

In 1957 Robert H. Whittaker (1924–1980), a biologist at Brooklyn College in New York City, began a reassessment of Copeland's four-kingdom system from an ecologist's point of view [43]. Whittaker, who studied the New Jersey pine barrens, recognized an ecological division of the living world by distinction between autotrophs and heterotrophs [43]. This outlook did not correspond to Copeland's four-kingdom concept or to the two-kingdom system of plants and animals [43]. Whittaker detailed his own four-kingdom system of Protista, Fungi, Plantae, and Animalia in his 1959 article, *On the Broad Classification of Organisms* [44].

Whittaker based his kingdom groupings upon the three main modes of nutrition in natural communities: absorption, ingestion, and autotrophy [43, 44]. He also credited the evolutionary sequence of unicellular to multicellular with central importance to his classification scheme [44]. Utilizing these criteria as the basis for classification, Whittaker returned the bacteria to Kingdom Protista (also based upon their unicellular nature) and placed all algae (green, brown, and red) into Kingdom Plantae [44]. The protozoa of Copeland's Protoctista were reassigned by Whittaker to his Kingdom Protista. Whittaker's primary phyletic interest overall was, however, in establishing a separate kingdom to contain macroscopic fungi [44]. In particular, Whittaker observed the absorptive role of the fungi in the natural environment. He rejected the common belief that the superficial resemblance of fungi to plants, with their non-motile habit and cell walls, made them true plants [44]. Whittaker did not believe that the fungi were derived from algae, but rather he thought they evolved from "colorless, flagellated protist ancestors" [44].

In 1969 Whittaker published a revision of his four-kingdom system to expand it to five kingdoms, now including a separate bacterial kingdom named Monera in recognition of the fundamental division of life as "prokaryotic" versus "eukaryotic" (as Copeland did, but expressed as "anucleate" and "nucleate") [45]. This distinction was first conceived by French protozoologist Edouard Chatton (1883–1947) in 1925 in an article entitled "*Pansporella perplexa*: Amoebien a Spores Protégées Parasite des Daphnies. Réflexions sur la Biologie et la Phylogenie des Protozoaires", (*Ann Sci Nat Sér X (Zool)*, **8**:5–84, cited by Ragan [35]) and again in 1938 in his own bound works entitled *Titres et Travaux Scientifiques* [7, 26, 34, 35, 41]. Whittaker noted that this concept was now more evident due to the writings of microbiologist Roger Y. Stanier in 1962 and 1963 [41, 42] and that this evolutionary divergence in cellular structure had to be accounted for by the recognition of Kingdom Monera [45]. Otherwise, Whittaker's reasoning remained the same for retaining the other four kingdoms in this Five Kingdom system. He reasserted his ecological model as well as the belief that inclusion of multicellular organisms into Kingdom Protista would make the Five Kingdom system an evolutionarily unnatural, heterogeneous grouping [45]. The central characteristic of Protista: unicellularity, remained

diagnostic of the group, the same as Haeckel's Protista was known at the turn of the century.

In 1968, just prior to Whittaker's publication of his five-kingdom classification, biologist Lynn Margulis at Boston University proposed a four-kingdom system based upon the model of Copeland, who was at the time the only researcher to offer a detailed taxonomic work that recognized the biological discontinuity between prokaryotic and eukaryotic organisms [23]. Differing from Copeland's Protoctista, Margulis' Kingdom Protoctista included the green algae, which she did not consider plants; this change was considered in light of the theory of bacterial endosymbioses in the evolution of the Protoctista [23]. Increasing evidence of genetic and ultrastructural nature of mitochondria and plastids showed these eukaryotic cell organelles having independent bacterial genomes, and consequently plants and animals themselves were regarded by Margulis as evidencing a polyphyletic nature, evolving from protoctist ancestors [23].

After Whittaker's publication of his five-kingdom concept, Margulis incorporated the phylogenetics of her system with the five-kingdom system and accepted the kingdom name of Protista instead of Protoctista [24]. However, Margulis' Kingdom Protista differed from Whittaker's in that hers contained all algae (green, brown, red), limiting Kingdom Plantae to the botanical phylum Embryophyta [24]. These modifications were in direct consideration of endosymbiotic evidence that "protozoans and nucleate algae represent a large group of organisms with flagellated heterotrophic eukaryote ancestors" [24]. Margulis further viewed the Protista as a heterogeneous grouping of unicellular and multicellular eukaryotes representing "polyphyletic evolutionary 'experiments' leading toward the ultimate establishment of mitosis and regular meiosis" [24].

Relying more upon morphological and ultrastructural comparisons within the Protista, Margulis departed from Whittaker's nutritional and unicellular morphological criteria of the Protista, and led her to accept the kingdom name Protoctista from Copeland. Plants became defined as the group of organisms that develop from a multicellular embryo retained in maternal tissue, then, animals develop from a multicellular blastular stage, fungi as organisms that develop from spores and lack flagella (today termed as undulipodia) at any stage of life history. Protoctista were eukaryotic organisms either unicellular or multicellular that are not plants, animals or fungi [46]. Margulis also introduced the term "protoctist" to refer to an individual organism of the Protoctista, whether unicellular or multicellular [46]. Defining the Protoctista by exclusion was the extension of sharply defining, or limiting, the characteristics of organisms in kingdoms Plantae, Animalia, and Fungi. The fact remained, however, that as a grouping the organisms of Protoctista had more in common with each other than to the larger plants, animals, or fungi. Increased research combining genetic (16S rRNA comparisons), biochemical, and ultrastructural observations of protoctists has evidenced the Protoctista as a grouping of independent lineage, some of which evolutionarily led to plants, animals and fungi and some did not [25]. Protoctists could be recognized more clearly as organisms in their own right, not in terms of being "lower", or intermediate solely leading to "higher" organisms [27].

## A return to Kingdoms Protozoa and Protista

John Corliss, protozoologist at the University of Maryland, has reinterpreted the taxonomy of Kingdom Protista of Whittaker and Kingdom Protoctista of Margulis based primarily, but not exclusively, upon unicellularity [12]. He draws a line of demarcation regarding "differentiated, functional tissues" of multicellularity, similar to concerns Whittaker had voiced [12]. Corliss in turn describes plants and animals by the presence of more than a single tissue and "protists, while showing multicellularity to varying degrees in certain groups, and occasionally even huge body size, again fail to demonstrate the organization of cells into two or more clearly differentiated tissues" [12]. To Corliss, red and brown algae appear not to have the complexity of tissues as true plants and animals and therefore can not be seen in the same light of plant and animal multicellularity; they are placed within the Kingdom Protista primarily on this basis [12]. Corliss also defines plants and animals upon mode of nutrition (autotrophy and heterotrophy, respectively), which are invalid distinctions as there are phototrophic animals (e.g. *Convoluta roscoffensis*) and fully heterotrophic plants (e.g. *Monotropa*) [26]. Corliss, who bases his four eukaryotic kingdoms (Animalia, Plantae, Fungi, Protista) on degree of cellular organization also overlooks the fact that multicellular, differentiated organisms are known in all four eukaryotic kingdoms and in Kingdom Monera (e.g. cyanobacteria) [26, 38].

Corliss takes the issue with the "major high-level taxonomic and nomenclatural problems presented in recognition of a kingdom Protista", and his main concern is that "proponents of a separate kingdom of protists have characterized it in a negative fashion" [12]. Corliss has weighed this concern in his taxonomic arrangement of protists to "stress major uniqueness, emphasizing the presence rather than the absence of a structure or function" [12]. However, Copeland maintained that absence of positive characters in the definition of the Protista is not a detriment to classification as a coherent grouping: it is not the presence or absence of animal and plant characters that define the kingdom but by relationship between organisms within the greater grouping [8].

Corliss has advocated adopting the term Kingdom Protista instead of Protoctista, as his opinion is that Protista is more popular and etymologically simpler [12, 13]. He also advocates usage of the term protist to denote all forms of Protista, both unicellular and multicellular. However, the term protist, as coined by Dobell, was defined by Dobell in reference to the Protista possessing the "unicellular type of organization" [14].

**Table 1** Concepts of Kingdoms Protozoa, Protista, and Protoctista (1860–1998) discussed in the text

| Kingdom Protozoa | Kingdom Protista | Kingdom Protoctista |
|---|---|---|
| Owen (1860)* | Haeckel (1866, 1869, 1905) | Hogg [Regnum Primigenum] (1860, 1868) |
| Cavalier-Smith (1983, 1998) | Copeland (1938) | Copeland (1947, 1956) |
| | Whittaker (1957, 1959, 1969, 1978) | Margulis (1968, 1970, 1990, 1996, 1998) |
| | Margulis (1970) | |
| | Corliss (1984, 1986) | |

* Years correspond to works cited in the list of References.

Protoctist, a term recovered by Margulis, has always referred to both unicellular and multicellular eukaryotes within the Kingdom Protoctista [26, 46].

Other researchers are primarily concerned by the lack of physiological and morphological features that fail to unite the Protoctista into natural, or monophyletic classification [2, 6, 35]. Since the late 1970s and widespread use of the techniques and concepts of Woese et al. [48] there has been greater focus upon 16S rRNA sequence comparisons and cellular architecture, with less integration of biochemical and morphological characteristics [2, 6, 35]. Tom Cavalier-Smith, botanist at the University of British Columbia, Canada, has argued for a six-kingdom system of classification that emphasizes monophyly [5, 6]. The basic outline of his classification contains the Kingdoms Bacteria (prokaryotic kingdom), Protozoa and Animalia (two eukaryotic "zoological" kingdoms), and Fungi, Plantae, and Chromista (e.g. oomycetes, xanthophytes), the three eukaryotic "botanical" kingdoms [6]. Cavalier-Smith's dispersion of the Protista/Protoctista throughout his five eukaryotic kingdoms presents an evolutionary look at life that is less polyphyletic. The goal of monophyly neglects the endosymbiotic history of eukaryotes [25]. In his search for ultrastructural similarities between organisms, the overt morphological distinctions that define plants and animals are seemingly lost; animals are instead defined as "ancestrally phagotrophic multicells with collagenous connective tissue between two dissimilar epithelia", and plants defined as organisms with "plastids with double envelope in cytosol; starch; no phagocytosis" [6].

Cavalier-Smith also considers that there is value in holding on to the term Protozoa for a Kingdom name, "very similar in composition to Owen's (1858)" for eukaryotic organisms "more primitive form of life than animals, plants, or fungi" [6]. He believes that retaining the term protozoa (which he terms a kingdom of "lower" organisms) is justified because the term has been so widely used by biologists since the nineteenth century, and that "there is real value in keeping as close as possible to the historically dominant meaning" [6]. However, this historical meaning can be misleading, as Hogg himself pointed out in 1860 [19]. Cavalier-Smith also retains the terminology of "lower" and "primitive" in describing the evolutionary context of the organisms [6]. As far back as 1911 Clifford Dobell wrote that "simple, lower, unicellular, or primitive… are terms that have arisen chiefly through misconceptions involved in the cell theory and the theory of organic evolution" [14]. These labels can also be seen as more of a holdover from the Victorian age and its prevailing idea of ascension up the ladder of progress leading to perfection rather than reflecting any meaningful quality of evolutionary history of organisms [15].

A brief account of the different names used by some authors is indicated in Table 1. The years in the Table correspond to the works cited in the list of References.

## The three-domain system of life

In the late 1990s it is becoming more tempting for biologists and scientists of different disciplines alike to give more weight to a completely non-morphological system of organismal classification as advocated by bacteriologist Carl Woese [48, 49]. Woese does not share in common with most biologists the recognition that the living world is primarily classified by a dichotomy of prokaryotic and eukaryotic cellular organization [48, 49]. He has instead presented an argument for life on earth being composed of three primary divisions, or domains: Archaea (archaebacteria), Bacteria (eubacteria), and Eucarya (all eukaryotes) [48, 49]. This concept sketches out a basic evolutionary perspective between the two prokaryotic domains (Archaea and Bacteria) and the domain of Eucarya. Relying upon 16S rRNA gene sequences and to a lesser extent lipid content in order to determine evolutionary relationships between organisms, Woese neglects any evolutionary significance of endosymbioses in eukaryotic cell evolution [25]. What may be regarded on one hand as being more scientifically "precise" (and certainly, fashionably reductionist), is on the other hand expressive only of relative change for a single gene over evolutionary time. Furthermore, in nature it is not molecules but populations of whole organisms that are selected [25]. Still, Woese considers his system to reflect the "evolutionary *process*,

not its outcomes" [49]. Yet the greater morphological, biochemical and even ultrastructural, distinctions between organisms are no longer considered, blurring the boundaries of how even plants and animals are defined.

Harvard University zoologist Ernst Mayr takes umbrage at Woese's manner of classification as not adequately expressing the phenotypic diversity of living organisms, asserting that to "claim that the difference between the two kinds of bacteria is of the same weight as the difference between the prokaryotes and the extraordinary world of the eukaryotes strikes me as incomprehensible" [28].

Utilizing the same techniques of Woese, Mitchell Sogin (Woese's former student) of the Marine Biological Laboratory at Woods Hole, has focused upon the small and large subunit rRNA gene sequencing of protoctist Eukarya [40]. When taking into account the endosymbiotic life histories of the organisms, Sogin finds protoctists to be a collection of independently evolved lineages of tremendous diversity [40]. However he does not take into account phenotypic differences in his classification, "since the rate of genotypic change is not necessarily linked to phenotypic variation, measures of genetic similarity between protists cannot be determined from traditional studies of morphology, physiology, or biochemistry" [40].

Clearly, biological classification is at a crossroads. Technology is providing a new manner of systematic investigation and evolutionary interpretation, much the same way microscopic investigation in the 1850s was intensified by the improved optics of the light microscope and the intricacies of cellular ultrastructure became uncovered by electron microscopy beginning in the 1950s [2]. However defined, the diversity of life is evidenced by our changing interpretation of the system of living organisms, never set in stone, ripe for revision in response to the changing light of biological investigation.

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