HISTORICALLY IMPORTANT EVENTS, DISCOVERIES, AND WORKS IN PROTOZOOLOGY FROM THE MID-17TH TO THE MID-20TH CENTURY*

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SUMMARY

An attempt is made to provide an annotated listing of the major happenings in the development of the field of protozoology from the time of Antony van Leeuwenhoek, father of the field, until roughly the middle of the present (20th) century. Particular attention is paid to the observations of the earliest workers, since they set the stage for further advances in this exiting area of biological inquiry. It is clear that improvements in microscopy have preceded most new discoveries in descriptive and taxonomic protistology (protozoology and phycology). In-depht analyses of the papers and monographs of the "greats" of the past- and, particularly, of various celebrated concepts - could not be undertaken in the present skeletal outline. But numerous direct citations to the vast literature are provided as a foundation for the full, definitive history of protozoology that still awaits doing.

INTRODUCTORY REMARKS

The history of protozoology, as is true for that of any area of human endeavor, abounds in exciting discoveries and in interesting tales of earliest times; and it is replete with events of significance. A full and proper chronicling of the development of this field of scientific inquiry would fill many volumes, a task to which no one yet has had the courage and perseverance to devote himself although there is a crying need for just such an analytic treatment. Cursory overviews or isolated scholarly attempts to portray selected aspects of protozoological history have appeared from time to time over the past 100 years (e.g., see Beltrán, 1977; Bütschli, 1887-1889; Cole, 1926; Corliss, 1978, 1979a,b; Dobell, 1932; Ford, 1991; Garnham, 1971; Goldschmidt, 1956; Kent, 1880-1882; Lechevalier and Solotorovsky, 1965; Wenrich, 1956; Wichterman, 1953, 1986; Woodruff, 1938, 1939). Recently a concerted and admirable effort, under the leadership of bioscience historian F.B. Churchill of Indiana University, was made to prepare a "collective" history with specific respect to the relationship of the protozoa to the Cell Theory (see Churchill, 1989a; and papers by fellow contributors: Corliss, 1989; Jacobs, 1989; Richmond, 1989; Rothschild, 1989). Of Course, via special obituary notices and commemorative eulogies, a few of which are cites in this paper, historically relevant data are numerous, although despairingly scatters, in the biological literature of the past. The present volume of the *Revista de la Sociedad Mexicana de Historia Natural* represents still another attempt to gather together selected aspects in the long and complex history of protozoology (interwined as it is with that of other disciplines), with full credit to Dr. Eucario López-Ochoterena of U.N.A.M. as principal organizer.

Despite all the comments made above, some quite optimistic in their implications, we are obligated to conclude, in agreement with one of the foregoing statements and with Corliss (1989), that the "full, definitive story still awaits doing". The present paper will attempt a conscientious survey of some 300 years of protozoology, with specific citation of several hundred individual discoveries, works, and events of significance. But, once again, it will represent at best a skeletal outline of the whole history of the field: it needs fleshing out at nearly every turn, and critical appraisals of major advances, for want of space, are generally absent from the following pages. Structured, in-depth analyses, as may be found in Churchill (1989, and see the subsequent papers in that volume) are in order: alas, such are beyond the scope of my offering here. At least, my bibliography provides references in sufficient numbers to serve as a helpful guide to the pertinent literature for anyone willing, some day, to rise to the challenge of producing the proper chronicle.

Incidentally, the role of the protozoa in the biotic world may be much greater than is generally realized. They have, and have had, various effects on the welfare of human beings that are far from insignificant; thus, an appreciation of the history of protozoology is not an esoteric consideration. Millions of people around the globe perish each year from the scourge of malaria, a (mostly tropical) disease caused by species of the protozoan genus

Plasmodium. Recall the effect on the world history of the youthful passing of Alexander the Great alone from malaria when he was but 33 years of age.

Other major protozoan afflictions include the trypanosomiases and the leishmaniases, toxoplasmosis, and amoebic dysentery. Protozoan parasite of domesticated livestock, poultry, hatchery fishes, and other such food sources annually wreak havoc on people's health and on their economic welfare.

On the other hand, species of many protozoa, particularly free-living forms, play a major, if unpublicized, role in nature's food chains, both in serving as food for macroorganisms and in mineral recycling and related functions within the water column. Tests of fossil foraminifers serve with precision as indicators of petroleum deposits in the earth's crust. Other protozoa are turning out to be useful in measuring water quality and pollution levels in aquatic systems; still others, as biological control agents of insect parasites and vectors of various diseases. Many species serve us beneficially through their employment in laboratory researches as Model cells" in all sorts of biomolecular and biomedical investigations. There is truly an intimate relationship between and the history of the human race.

Since the early history of many biological fields is concerned with the first descriptive accounts of the organisms involved, and/or with initial attempts at their taxonomic classification, it is natural to wonder who first saw or described protozoan species and when were such. Immediately, in the present case, we must confront the problem of what is a protozoan, a stumbling block that does not exist for such fields as ornithology, for example. If protists *sensu lato* (see Corliss, 1984, 1991a) were to be considered, keeping in mind that they embrace not only the usual protozoan groups but also all of the algae and the "lower" fungal groups as well, than "discoveries" of brown algae, for example, would count: and recall that some such seawees species (giant kelp) grow to lengths exceeding 50 meters, assuring that they must have been known and recognized (or at least seen) thousands of years ago! Even among such single-celled "micro" organisms as the foraminiferans, we must no forget that fossilized forms of extinct species reach sizes more than 15 centimeters in diameter, thus easily visible to the naked eye; and such fossils have long been abundantly available in some parts of the world. Various other species of protozoa reach lengths measurable in millimeters.

Probably it is wiser, with respect to the protozoa *sensu stricto* (protists that are mostly unicellular and mostly microscopic in size, mostly heterotrophic in nutrition (therefore, mostly non-pigmented), mostly independently capable of motility), to start their history with their recognition as an assemblage of unique forms, described and (in due time) classified as such, although the level of their separate taxonomic rank may not have been very high in the beginning. Thus, in the present account of "first" fit protozoology --first discoveries and first events of major importance-- it is reasonable to commence with the well - known "Father of Protozoology", Antony van Leeuwenhoek of Holland (The Netherlands), who in 1674 offered the first description of living forms of protozoa still recognizable today, although he made no attempt to name or classify them (of course, the advent of Linnean taxonomy was not to arrive for another century yet).

Notwithstanding the preceding statement, it would be unfair not to mention the scientific work of Gesner (1565), a century before Leeuwenhoek's time, who described fossil "forams --admittedly as molluscs-- in writing; and the drawing by Hooke (1665), 10 years before the Dutchman's observations on living protozoa, of another fossil foraminifer, still thought of as a microcephalopod. In fact, as late as the early years of the 19th century (e.g., see the taxonomic monograph by d'Orbigny, 1826), the Foraminifera remained as minute molluscs: Dujardin (1841) was the first, I belive, to recognize their protozoan nature.

Here it might be well to remained the reader that the present paper will be focused on the history primarily of the protozoan, not the algal, protists. Thus, in the following pages, citations of purely phycological discoveries will generally be conspicuous by their absence. This is despite my own claim (e.g., in Corliss, 1984, 1991a), and those of others in recent years, that protozoan and algal taxa should not be separated by high-level taxonomic walls, as they conventionally have been, since many of them are closely interrelated phylogenetically and evolutionarily. Many phycologists are quite cognizant of the history of their own speciality groups (e.g., see Round, 1984, on the green algae, and F.J.R. Taylor, 1987, on the dinoflagellates); and workers such as Papenfuss (1955) and Silva (1980) have published papers on the changing algal classification systems over long periods of time. Yet I am not aware of major attempts in recent years to present a story limits to the largely pigmented protists that would parallel mine here on the (largely) heterotrophic forms. See, however, the generally short but pertinent historical accounts by Pappenfuss (1957, 1976) and W.R. Taylor (1969); and Prescott's (1951) scholarly paper deserves special attention despite its age and brevity. It appears from these papers, by the way, that phycologists perhaps have not succeeded in declaring their independence, as it were, from (other) botanists to the extent that protozoologists have been able, over the years, to separate themselves and their discipline from zoology and zoologists.

Recall that several major groups (the “protozoalgal" taxa of Corliss, 1981) have been simultaneously considered

as algae and protozoa and are even subjected (at infrafamilial levels) to separate and differing Codes of Nomenclature (see Corliss, 1990, 1991b; Patterson, 1986; Patterson and Larsen, 1992; Ride and Younés, 1986). The history of these latter taxa (e.g., the dinoflagellates, euglenids, chrysophytes (excluding diatoms), volvocids, and scattered other smaller groups) are generally of concern to me here, as will become evident in citations on following pages.

It may be interest to note, in passing, that textbooks of protozoology and algology (phycology) over the years have seldom attempted to cross over the traditional/conventional plant-animal kingdom boundary, in either direction. In recent times, de Puytorac *et al.* (1987) may be cited as a limited effort to do so; better has been the presentation by Sleigh (1989), who has been well aware of the need --yet the difficulty!-in treating adequately both algal and protozoan protists within the confines of a single book.

Despite the statements made above concerning my deliberate neglect of botanical/phycological "first", more than half a hundred citations to phycological, plus a few mycological papers, books, or monographs are included in appropriate works of such giants in the history of the development of research on the "lower plants" (i.e. algae and fungi) as the Agardhs, de Bary, Beijerinck, Bessegi, Borzi, Chodat, Fritsch, Klebs, Lemmerman, Meunier, Nägeli, Pascher, E.G. Pringsheim, the incredible (ageless!?) Rabenhorst, G.M. Smith, F.K. Parrow, W.R. Taylor, West, Zopf, and Zumstein. Also, I am including at least passing mention of the contributions of such persons of "younger generations" (relatively speaking) as Bold, Chistensen, Copeland, Olive, Papenfuss, Prescot, Round, Silva, Tappan, and F.J.R. Taylor. Than there are the true protistologists who, over the centuries, have worked on both protozoa and algae, such as Belar, Bütschli, Chatton, Deflandre, Diesing, Dujardin, Ehrenberg, Francé, Hall, Hovasse, Janet, Kent, Kofoid, Lwoff, Mast, O.F. Müller, and F. Stein, most of whose cited papers are not included within the 50 mentioned above. Also, recall the contributions of the founding father of both fields, the remarkable Antony van Leeuwenhoek!

Finally, among these brief introductory remarks, a comment must be included concerning concepts in protozoology. The present paper, with its purposeful emphasis on descriptive "firsts" (primarily of a morphological or taxonomic nature) in the long history of protozoan studies, cannot indulge in discussion of the impact of conceptual pronouncements by the "greats" of the past. This is unfortunate, of course, but meaningful treatment of hypotheses and theories involving the protists would require many times the number of pages already consumed by the present contribution. This is most clearly illustrated by the fact that the recent consideration by Churchill *et al.* (see Churchill, 1989a, and papers following it) of the relationship of the Cell Theory to the protozoa alone occupies 138 pages of a Journal!

Nevertheless, I have attempted to cite direct references to a number of the most significant concepts (generally --but not always!-ill-fated-ideas, though even than stimulating considerable controversy and subsecuent research) at appropriate places on following pages, typing the concept to the name of its principal promulgator. Thus reader will find mention of these major hypotheses, arranged here more or less chronologically: Ehrenberg's Polygastrica Theory, J. Müller's Law (on radiolarian structure), Stein's Acineta Theory, Maupas'Ciliate Life Cycle Concept, Haeckel's "Biogenetic Law", Schaudinn's Binucleata Theory, The "Schaudinn Fallacy" (the malarial life cycle) exposed years later by Garnham, Dogiel's Theory of Oligomerization (and Polymerization) in Evolution, Dobell's Acellularity Hypothesis, Jollos' Dauermodifikationen idea, Chatton's Rule of Desmodexy, Kofoid's Neuromotor Concept and Woodruff's Endomixis Hypothesis. Of course, in the 18th and 19th centuries, protozoa and protozoologists --in one way or another-- were sometimes implicated or involved in (disproving) abiogenesis, the long-time controversial Theory of Spontaneous Generation, Joblot probably being the first microbiologist/protistologist active in such work and Pasteur, some 150 years later, essentially the last.

THE 17TH CENTURY

Leenwenhoek's "firsts" in protozoology and phycology, as well as in parasitylogy and in microbiology generally (not to mention hematology and other sciences), were all dependent on his unique skills as a microscopist (see especially the long account by Dobell, 1932; and, more recently, the book by Ford, 1991), aided and abetted by his insatiable curiosity over tiny forms of life and, I might add, his obviously excellent eyesight. The short paper by Leeuwenhoek (1674) contains his first discovery of protozoa: it is a letter published in volume 9 of *the Philosophical Transactions of the Royal Society* (of London), having been translated into English by Henry Oldenburg, than Secretary of the Society. In this note, the Delft draper described a pigmented species of the flagellate genus *Euglena.* His most celebrated "first letter on protozoa", as many historical references preceding Dobell (1932) have erroneously called it, was long one dated 9 october 1676 and published the next year (Leeuwenhoek, 1677). It contained numerous observations on the microscopic organisms abounding in both natural and experimental

aqueous habitats (see the detailed accounts in Dobell, 1932, and in Schierbeek, 1960).

Leeuwenhoek's first drawings of protozoa appeared in the year 1638; they were of the opalinid *Cepedea* and the ciliate *Nyctotheroides,* both taken from the gut of a frog. Over the years (he lived a long and fruitful life), Leeuwenhoek also probably saw and/or described species of other microorganisms today classified in the protozoan *genera Anthophysa, Bodo, Carchesium, Cercomonas, Chilodonella, Chilomastix, Chlamydomonas, Coleps, Colpidium, Cothurnia, Crithidia, Cyclidium, Dileptus, Eimeria, Elphidium, Euplotes, Giardia, Haemotococcus, Kerona, Monas, Opalina, Oxytricha, Paramecium, Polytoma, Stylonychia, Tetrahymena, Trichodina, Trichomonas, Volvox, and Vorticella* (see Corliss, 1975).

Leeuwenhoek's discoveries were all the more amazing considering the simplicity of his "microscopes" with their single lens, no draw-tube, no mirror, etc., although these small hand-lenses possessed a magnification up to nearly 300X. It should also be noted that his observations were not confined to morphological descriptions alone. He considered the pairing of ciliates to be conjugal in nature; he described reproduction in *Volvox* in some detail; and he commented on the contractility of (the stalk of) *Vorticella.* (Note: Leeuwenhoek's dates of birth and death are not given in this paper, nor are those of the many other "philosophers in little things" mentioned on the following pages, to be consistent. This information (along with photographs) is supplied in Corliss (1978, 1979a) for some 70 distinguished microscopists/protozoologists all of whom are included among the top leaders described in the present paper, so it has seemed unnecessary to further lengthen my accounts here by repeating data below. Photographs of still additional persons, but limited to ciliatologists, appear in Corliss (1979b).)

There were a few other notable protozoological pioneers of the late 17th century. For example, in 1678, Christiaan Huygens described several ciliates and *Astasia,* but in a private letter to his older brother, material not published until 1899 (see the story in Dobell, 1932, p. 164). Buonanni (1691) was the first to publish a drawing of a ciliate (probably a species of *Colpidium);* King (1693) portrayed various free-living protozoa, including a form we now recognize as *Euplotes;* and Harris (1696) rediscovered Leeuwenhoek's *Euglena.*

THE 18TH CENTURY

Throughout the 18th century, with one major exception (O.F. Müller: see below) only scattered descriptive microbiologists/microscopists left accounts that included information on any protozoa. These "firsts" should be recorded here. Recall, however, that the second half of the 1700's was dominated in biological fields by the renowned systematist Linnaeus, the Father of Modern Taxonomy and Nomenclature. Unfortunately, Linnaeus, primarily a botanist, paid little attention to the "lowest animals" (the term "Protozoa" was not coined until the early 19th century: see below). In the well-known 10th edition of his *Systema Naturae* (Linnaeus, 1758: starting date for zoological nomenclature), only the generic name *Volvox* appeared. In the 12th edition (Linnaeus, 1767), *Chaos, Furia* (a name long since dropped), and *Vorticella* were added; several other names available in the literature (e.g., Hill's ciliates of the year 1752: *Cyclidium, Enchelys,* and *Paramecium)* were totally neglected. With respect to algal protists, recall that in Linnaeus (1753), the work that represents the starting date for (most) botanical nomenclature, some 14 genera of algae were listed (recall that he considered *Volvox* as a "zoophyte), although only four *(Chara, Conferva, Fucus,* and *Ulva)* have been accepted as true algae as the group has been redefined since Linnaeus' time.

The isolated studies mentioned above include Joblot's (1718) small but pioneering treatise on microscopes and the tiny organisms made visible through their proper usage. The enterprising Frenchman gave various protozoa vernacular names: for example, his "chausson" has endured as today's "slipper-animalcule", an apt description of *Paramecium.* And he was the first to describe a contractile vacuole. Trembley's (1744) remarkable observations on division in *Stentor* and certain other ciliates also deserve to be remembered, as Tartar (1961) has rightly stressed.

Hill (1752) was the earliest nomenclatural taxonomist of single-celled organisms; as mentioned above, he coined generic names for a number of protozoa. While it is true that such names cannot legally be credited to him --since by the *International Code of Zoological Nomenclature* the starting date for "animals" is 1758, as has been pointed out above-- they could have been used by Linnaeus in his classification of all organisms, and subsequent workers would, quite properly, have credited the Swedish naturalist with them. In his book, the Englishman Hill also included historically valuable notes on microtechniques of the time.

Baker (1753) offered good descriptions of the large and most unusual luminescent marine dinoflagellate later named *Noctiluca* and of the graceful "swan" ciliate *Lacrymaria.* Rösel von Rosenhof (1755) studied a large freshwater amoeba, which Linnaeus (1767) put in the genus *Chaos.* Wrisberg (1765) is said to have been the first to

use the term "Infusoria" for the protozoa (ca.100 years later this name became restricted to the ciliates; now, today, it has fallen into complete disuse as an acceptable taxonomic nomenclatural term). Ellis (1769) experimentally produced the extrusion of a paramecium's trichocysts; and Eichhorn (1781) was apparently the first to offer a recognizable description of an heliozoon (a species of the "sun-animalcule" *Actinosphaerium*). At the end of the century, Guanzati (1796) was the first microscopist to describe a protozoan *cyst* (of a ciliate now concluded to have been an *Amphileptus* species).

Otto Friederich Müller deserves special mention in even a most abbreviated essay on the development of the science of protozoology. A Danish marine invertebrate zoologist of prodigious accomplishments in the areas of ecology and systematics, he was the first biologist to treat microorganisms taxonomically and nomenclaturally in an organized fashion. His culminating massive publication on the protozoa (Müller, 1786), published posthumously and written in Latin, represents the first comprehensive taxonomic treatment of these organisms (and certain other protists plus some prokaryotes --bacteria-- and a few minute multicellular "lower" invertebrates as well) to appear in the scientific literature. All of his forms were placed in a single group, the Infusoria, but that was a very high taxonomic rank in those times. He described, figured, and named some 300 species today representative of many orders and classes of protozoan and algal protists, although he very conservatively assigned them to fewer than a dozen and a half different genera. Recall that his microscope, in magnification and resolution, was hardly superior to the “simple" hand-lens of his predecessor Leeuwenhoek, who had made his observations a full century earlier!

Clear evidence of the high regard in which "O.F.M." is still held today, more than 200 years after his last monographic work had appeared, is to be seen in the persistent use of many of his names and even of some of his original figures. For example, eight of his protozoan genera remain in use: *Gonium and Monas* among the flagellates and *Bursaria, Colpoda, Cyclidium, Enchelys, Kerona,* and *Paramecium* among the ciliates. A number of additional species have survived but with different generic vehicles today, his forms having been transferred out of his unwieldy genera, one of which, for an extreme example, had contained 89 species: the average for a (ciliate) genus in modern classification systems is only five to six (Corliss, 1979b).

Among important specific "firsts" of O.F.M.'s are the following: first to describe, name, or recognize dinoflagellates, parasitic "zooflagellates" (an oral trichomonad), heliozoa, marine sand-dwelling ciliates, scuticociliates, carnivorous gymnostomes, suctoria, tintinnid oligotrichs, the colonial peritrich *Ophrydium,* the noble heterotrich *Stentor,* and the amazing marine loricate heterotrich ciliate *Folliculina.* His drawings, in their very simplicity, were both accurate and full of grace. My favorite is his *"Trichoda S"* (which has become *Metopus es,* a single letter not allowable as specific epithet), his figure clearly portraying the S-shape so characteristic of this particular marine ciliate (see Corliss, 1986a, for reproduction of this and other O.F.M. figures). Müller was also the first to offer remarks on the ecology of planktonic and benthic marine protists.

Finally, in agreement with his illustrious predecessor of a century earlier, the amateur microscopist A. van Leeuwenhoek (to some of whose protozoa O.F. Müller gave names as he rediscovered them), the gifted Danish protozoologist also correctly interpreted the pairing of ciliates as representing the sexual phenomenon of conjugation, a conclusion rejected for another 100 years by other biologists, who insisted that such ciliates were merely splitting longitudinally in an alternative way of reproducing asexually: but, finally, Balbiani did believe them (see below).

The work of this first and great systematic monographer of the protozoa was not to be extended and improved upon until well into the following century when such giants as Ehrenberg, Stein, Dujardin, Claparède and Lachmann, Haeckel, Kent, Bütschli, and Schewiakoff appeared on the scene, 60-100+ years later. Anker (1950), a modern Dane writing in English, seems to be the first biographer to appreciate fully O.F. Müller's contributions to biology.

NOVEL FINDINGS OF THF 19TH CENTURY

With respect to groups of free-living protozoa, discoveries and advances in the field during the 19th century were principally of two sorts, the first of which --describing scores of new species with considerable precision-- was obviously related to continuing developments and improvements in the sciences of microscopy and microtechnique (Corliss, 1978, 1979a,b; Honigberg, 1967). The second kind of advance was a more conceptual one; that is, it was concerned with the classification of the protozoa into higher taxonomic categories, with attempts to establish separate assemblages based on shared intra- or inter-group characteristics. To recognize diversity --and note how great it has become today with respect to the protists overall (e.g., see Corliss, 1984)!-- one needs to have a "critical mass”, as it were, of different organisms to subject to comparative taxonomic study, a situation that did not exist for the scattered species of protozoa known in the times of Müller and Linnaeus.

With regard to various parasitic (better, symbiotic) protozoa, however, few that were representative of the major groups of such forms known today had been seen by the earliest pioneers in descriptive protozoology (see preceding pages). Thus major "firsts" in this great area are worthy of considering next. Than we shall return to the subject of advances involving mostly the taxa of free-living protozoa protists.

DISCOVERIES INVOLVING PARASITIC PROTOZOA

The single period 1835-1850 seems to have been a rich one with respect to discoveries of important parasitic/symbiotic forms, although several such findings had already been made by either Leeuwenhoek or Müller in preceding centuries (as will be noted below). Purkinje and Valentin (1835) saw and named *Opalina* (recall that our respected friend from Delft had surely seen opalinids *sensu lato* and had drawn a specimen of the closely related *Cepedea);* and Hake (1839) published an account on *Eimeria* from the rabbit (but an oocyst of this coccidian had also been observed by Leeuwenhoek). Donné (1836), a physician, discovered the parasitic *Trichomonas vaginalis* in one of his female patients (but both Leeuwenhoek and O.F.M. had seen members of this or related genera). Gruby and Delafond (1843) detected ophryoscolecid ciliates in the stomach of a rumiant. Gruby (1843), again, and Gluge (1842) and Mayer (1843) --and perhaps others at about the same time-- observed trypanosomes from cold-blooded vertebrate hosts, and Gruby was the one to create the generic name *Trypanosoma;* it would not be for another 35-40 years before mammalian trypanosomes were fully recognized and studied (see below).

Miescher (1843) is credited with description of the first sarcosporidian, found in the muscle of a mouse. Kölliker (1848) and Stein (1848), in the same year, made observations on gregarine sporozoa; but Dufour (1828) had already discovered gregarines from a beetle, 20 years before, in perhaps the first full account of protozoa living within the body of another organism. Leidy (1849), the earliest North American protozoologist of great stature, described the first "true" *Nyctotherus,* a species from the cockroach (Leeuwenhoek's ciliate from the frog was surely a *Nyctotheroides).* Finally, in this rich period of discoveries in the area of parasitic protozoology during the first half of the productive 19th century, mention must be made of Gros (1849) who, working in Russia, was the first discoverer of amoeba living in humans. He studied *Entamoeba gingivalis* from the mouth; it was not until 26 years later that the pathogenic intestinal amoeba, *Entamoeba histolytica,* was detected by Lösch (1875). Incidentally, the generic name *Entamoeba* was not proposed until near the end of the century, by Casagrandi and Barbagallo (1895).

Discoveries of (other) parasitic forms continued into the second half of the past century --and, of course, are still happening today, although most modern findings are, understandably, not such major significance, often being just new species belonging to already well-established genera. Mention of a few more specific 19th century "firsts" is appropriate here, next. The deserving of special attention are the works concerned with what might be termed "medical protozoology", viz., the first studies on the dreadful diseases of human malaria, trypanosomiasis, and leishmaniasis, afflictions still laying waste to millions of people´s lives *every* year: so this topic is addressed in the immediately following section.

Davaine (1854) was the first to observe trichomonad flagellates from the human intestine; and Malmsten (1857) noted the ciliate *Balantidium* from the same general site. The Czech physician Lambl (1859) made a study of the unique flagellate *Giardia* from the small intestine; but recall that Leeuwenhoek had detected this organism in samples of his own fecal material, as described in a letter of 1681 (see Dobell, 1932, p. 224), more than 175 years before! Louis Pasteur (1865, 1866) published his famous papers on the microsporidian *Nosema bombycis,* causative agent of pébrine disease in the silkworm (the protozoan group genus and species had been named a few years earlier, by the phycologist Nägeli, 1857), including practical advice on control and prevention of this otherwise economically disastrous disease. Eimer (1870) made the earliest extensive investigation of coccidians in various hosts; and Schneider (1875), in tribute, gave the name *Eimeria* to what is still today the principal (except for the malarial *Plasmodium)* --and by far the largest (1000 species!)-- genus among the coccidian sporozoa.

EARLY HISTORY OF MAJOR PROTOZOAN TROPICAL DISEASES

A fully chronicle on malariology alone could occupy many volumes; indeed, numerous books have appeared that treat various aspects of its fascinating story. Here, I must limit my account to a mention of only some of the outstanding "firsts" associated with that specialized field of largely medical protozoology. Main sources of the few data I present below are to be found in the delightful and long accounts by Garnham (1966, 1971). Goldschmidt (1956), Lechevalier and Solotorovsky (1965), and Manson-Bahr (1963), books --among still others not cited here-- that I highly recommend to all malaria buffs.

By the way, of the five Nobel Prizes awarded in the period 1902-1908 to persons who had worked with microorganisms (Louis Pasteur would have been a sixth if he had not passed away before the Prizes were established), four went to researchers concerned at least in part with aspects of malariology: Laveran, Golgi, Ross, and Koch (the last was the famed German microbiologist, promulgator of Koch's Postulates, etc., but he did also work a bit in parasitic protozoology: *e.g.,* see Koch, 1899). Fritz Schaudinn, who carried out exemplary research on coccidians not far removed taxonomically from the haemosporidians and who discovered the causative agent of syphilis *(Treponema),* would certainly have been a seventh Nobel Laureate if he had not died before that last discovery of his had been fully recognized and appreciated. And Charles Nicolle, who discovered the exceedingly important related parasite *Toxoplasma* in 1908 (see Nicolle and Manceaux, 1908), did become the eighth medical parasitologist/protozoologist to receive the Nobel Prize (although not until the year 1928). [Additional researchers working at least in part on "protozoan cells" have since received Nobel Prizes, but usually since the year 1950: so mention of their names is generally beyond the scope of the present historical account].

Laveran (1880) was the first investigator to see malarial parasites in human blood, observing the exciting stage of exflagellation in the formation of microgametes. He also discovered all three major species of the malarial parasites of humans. He founded the new field of "comparative haematozoology" and studied other blood-inhabiting microorganisms besides *Plasmodium.* Laveran was truly the greatest pioneer in these new and most significant areas of parasitological protozoology.

Of many other 19th century workers in the field of malariology *sensu lato,* I must at least report the stellar contributions of such investigators as the following three. Danilewsky (1885, and later), worked on avian and reptilian malarial and was proposer of the taxonomic name Haemosporidia for the whole *Plasmodium* group. Golgi (a well-known name in cytology, of course: and it was actually for discoveries in this area that he received --shared with Ramon y Cajal-- the Nobel Prize) produced an instant classic in research on the human malarial (Golgi, 1889). And Ross (1898), made the break-through discovery of the involvement of mosquitoes, as vectors, in the full life cycle of the malarial. He was working at the time with an avian malaria, with a *Culex* vector, but that led immediately to recognition of the role of the female *Anopheles* mosquito in the human malarial.

Research on the other sporozoan blood parasites (flagellates) involved are treated next, below) produced observations relevant to (further) progress in malariology itself. Three outstanding examples deserve special citation: the work by the Roumanian Babes (e.g., 1888), in which the piroplasmid *Babesia* (named in his honor by Starcovici, 1893) who were the first discoverers of the transmission of an infectious protozoan disease (babesiosis) by an arthropod vector (the tick): this set the stage for the subsequent uncovering of the role of tsetse flies in trypanosomiases (see below) and of mosquitoes in the malarial (see above); and that of another American, W.G. MacCallum (1897), who carried out very precise cytological observations on the micro- and macrogametes of *Haemoproteus* in birds and, later of *Plasmodium* in humans. Schaudinn, Chagas, von Prowazek, and several others also merit recognition here for their unusual contributions just before (or slightly after) the turn of the next century (some of their papers are mentioned in later sections, below). Many such works --by these men and others-- are to be found cited in the bibliographies of the references given on malariology at the beginning of this brief section; and see Corliss (1978,1979a), too, where one may also find lists of numerous additional names of early workers in Laveran's "haematozoology" *sensu lato.*

In the vast parallel area (but also part of Laveran's field) of the trypanosomiases and leishmaniases, caused by flagellate blood parasites in humans and other vertebrates (and also some invertebrates and even a few plants), revelations and important advances also occurred towards the end of the 19th and slightly into the 20th century. At least seven names stand out historically, listed here very briefly in chronological order. Lewis (1879, a paper preceded by a couple of preliminary reports elsewhere) first detected *Trypanosoma lewisi* (as the species was later named) in the blood of rats. Evans (1881, 1882) reported "tryps" from horses. Bruce (1895, 1897) studied other trypanosomes from domesticated African mammals, and experimentally showed that the tsetse fly was the insect vector involved. Dutton (1902) recognized that one of the African sleeping sicknesses in humans was caused by *Trypanosoma gambiense.* Donovan (1903) and Leishman (1903) simultaneously discovered that the causative organism of kala-azar in India was (what soon came to be named) *Leishmania donovani.* And, finally, Chagas (1909) described the important South American variety of human trypanosomiasis, later named Chagas' disease: here, the flagellate involved is unique (*T. cruzi),* the vector is a triatomid bug, and the disease is unlike both the African sleeping sicknesses and the two main kinds of leishmaniases known in people.

With respect to new names or categories proposed for higher level taxonomic units of (mostly) parasitic protozoa, rather few became available before the 20th century; and some of the ones listed briefly here are now no longer in vogue. The Sporozoa and the Coccidia are both credited to Leuckart (1879); but the names Gregarina and

Acephalina (for one subgroup of the gregarines) sporozoa have been assigned to still earlier workers, viz., Dufour (1828) and von Kölliker (1848), respectively. The Trypanosomata is a name proposed by Kent (1880-1882); and, as mentioned above, the Haemosporidia has long had its authorship assigned to Danilewsky (1885). The name Myxosporidia is first found in Bütschli's (1880-1882) opening volume on the classification of all the protozoa; and Balbiani (1882) erected the Microsporidia. Workers of the 19th century involved in additional names, generally of lower ranks or of lesser importance than the taxa just listed above, include Caullery and Mesnil, Doflein, Delage and Hérouard, Lankester, Schaudinn, and Stolc.

NEW FINDINGS OR IDEAS INVOLVING FREE-LIVING PROTOZOA

As intimated above, the outline of most major groups of the protozoan protists that are predominantly free-living (or symphoriontic in nature, attached to the bodies of other organisms primarily for transport) was established well before the middle of the 19th century, while whole assemblages of the more difficult to study parasitic forms had to await first discovery in the last half of that century. We need, here, to pay special tribute to two outstanding monographers who were publishing on free-living forms in the early 1800's and whose monumental works set the stage for all subsequent protozoological investigations. Even their taxonomic classifications --far more inclusive and comprehensive than O.F. Müller's attempt had been-- were destined to be influential for nearly 50 years, until the appearance upon the protozoological stage of Otto Bütschli, that greatest ever "architect of protozoology" (as Dobell, 1951, saluted him), in the 1880's.

C.G. Ehrenberg is the first of the two “philosophers in little things" to establish the field of protozoology as a legitimate subfield of zoology. Author of several treatises on various protozoa (although ciliates were his favorite objects of study), his major contribution of lasting value was his monograph --written in Latin, German, and French, with pages measuring 19 x 13 inches! -- on protozoa as “vollkommene Organismen" (Ehrenberg, 1838). He included 350 new species in its taxonomic section, and his plates depicted representatives of diverse groups. In the same volume, Ehrenberg propounded his Polygastrica Theory, holding that ciliates, especially, have complete organ systems within their minute bodies; thus, as independent organisms, they approached their multicellular cousins --the animals-- anatomically as well as physiologically. The concept was an euristic one even if inaccurate from a descriptive cytological point of view. Dobell (1911), calling the protozoa “non-cellular” organisms, used it as one of the bases for his vicious attack on the Cell Theory of his time (see Corliss, 1989; Richmond, 1989; and subsequent section --on Dobell-- in the present paper). Ehrenberg (1854, 1875, and other works) should also be hailed as the first “paleoprotistologist”, starting a (sub) science the significance of which is still too often neglected today, 150 years later (but see Deflandre, below, and the excellent modern-times book by Tappan, 1980). [An interesting footnote may be appended here: with the recent fall of the infamous Berlin Wall, Zölffel and Hausmann (1990) have “rediscovered" the burial place of Ehrenberg in (East) Berlin and have taken the occasion to publish an important and well-illustrated tribute to him.

Felix Dujardin was equally productive and influential, but, unlike Ehrenberg, he concentrated much of his own research attention on the amoeboid protozoa (rather than the more obviously structured ciliates). Partly because of the different choice of material to study, he could not support the Polygastrica notion of his German contemporary: indeed, he caused its early downfall. A physiologist as well as morphologist and taxonomist, Dujardin (1838, 1841) first proposed the word "sarcode" for the streaming cytoplasm of (amoeboid) cells. His classification of the protozoa was a sound one. He created the name Rhizopoda for a quite high-level taxon within the later-named "Sarcodina" assemblage; however, technically speaking, he used the term at the family level only and in the vernacular; thus it is customary today to credit van Siebold (1845) with the formal name. The figures in his textbook (Dujardin, 1841), a monograph stylistically not as impressive as Ehrenberg's, were well executed, some of them still taxonomically useful today.

Except for two other compilations (limited in originality) by Perty (1852) and Pritchard (1834-1861, a series of editions remarkable as being the first major books of the 19th century on the protozoa in English), most of the additional works of importance in this century were on specialized groups of (mainly free-living) protozoa and did not appear until well into the second half of the 1800's (see below). An exception is the extensive but often overlooked work on ciliates by the early Russian protozoologist Eichwald (1844-1852). It is also appropriate to mention here that, during the first half of the 1800's, the term Protozoa, with a capital "P", came into existence for the first time. Coined by Goldfuss (1818), it was redefined by von Siebold (1845, 1848) as a group of unicellular animals divided into two classes, the Rhizopoda and the Infusoria. Also, the pioneering efforts of Lamarck (1801,1815) and of Bory de St. Vincent (1826) at classifying microorganisms should not go unnoticed.

THE BURGEONING LITERATURE OF THE SECOND HALF OF THE 19TH CENTURY

In the following paragraphs, brief mention is made primarily of monographic works, although this is not intended to slight the significant discoveries often announced in shorter papers, sometimes by the same authors. Also I am obliged, by space restrictions, to limit my amount to selected citations of a rather few works, since the total number of protozoological publications appearing in the period 1850-1900 --including areas beyond simply descriptive or taxonomic contributions-- is very large in comparison with that of preceding decades and centuries. Finally, this long section on the 19th century is concluded with a tribute to Bütschli, who understood so well the overall relationships of the major protozoan assemblages, parasitic as well as free-living, and who was also a cytologist and cell physiologist of unusual ability.

Johannes Müller (no relative of the great Dane O.F.M.), of Berlin, founded a dynasty of German zoologists and/but was an ardent student of the protozoa, particularly the (until than) largely neglected marine planktonic sarcodinids known, following his publications, as the Radiolaria *(e.g.,* see Müller, 1858). He established "Müller's Law", which refers to the geometrical arrangement of the skeletal spines so characteristic of many radiolarian species. Speaking of "rhizopods", as opposed to von Siebold's "infusorians", one of the earliest American researchers on protozoa, Joseph Leidy of the Philadelphia Academy of Natural Sciences, studied major groups of the fresh-water "sarcodinids". His culminating monograph (Leidy, 1879) represents a landmark in treatment of these non-ciliated, non-flagellated amoeboid protists. Leidy was also a prominent vertebrate paleontologist and a parasitologist as well: recall his discovery of *Nyctotherus,* a symbiotic ciliate, reported on a preceding page (Leidy, 1849).

Still another impressive monograph on "les rhizopodes" (including the foraminifers) –although more than two-thirds of this three-volume work was devoted to "les Infusoires" (including the parasitic ciliate *Balantidium* and the previously neglected suctorians) and to the phenomenon of reproduction in ciliates-- was published in Geneva by Claparède and Lachmann (1858-1861). Claparède had studied under J. Müller in Berlin, and he carried out researches on invertebrate animals as well as the protozoa. Always in poor health, he died at the age of 39, 10 years after the appearance of the monograph just cited.

WORKS ON (MOSTLY) THE CILIOPROTISTS

The ciliated protozoa (today now sometimes referred to as the "cilioprotist", following the proposal of Heywood and Rothschild, 1987, and Rothschild and Heywood, 1987) have long interested microscopist, partly because many of them are relatively large and are quite easily available as free-living forms in fresh and salt-water habitats, and partly because their motility and internally complex bodies are attractive to observe. The history of "ciliatology" has been traced in earlier works by the author *(e.g.,* see Corliss, 1974, 1978, 1979a,b); therefore, we need not go into detail in the present paper. Some of the greatest monographs of the 19th century have been concerned with these protists, however, so the most outstanding ones must receive citation again here. With respect to large and important publications on the flagellates, incidentally, an outstanding example in the second half of the 19th century is the work by Diesing (1866).

On mostly algal protists, the classics of Beijerinck (1890), Borzi (1883, 1895), Francé (1894), and Klebs (1883, 1892) should not be overlooked. Nor should one fail to mention, here, the long-running, truly immemorable, series by (or edited by) Rabenhorst (1844, 1847; 1863, 1870; 1879-1944!) and the still earlier fundamental works by C. A. Agardh (1824) and J. G. Agardh (1842, 1848-1901), father and son, and by Nägeli (1847).

This might also be the place to insert a couple of references to the early pioneering work on some other "non-ciliate" groups of protists. One is the mycetozoa. It was de Bary (1859) who gave these fungus-like "sarcodinids" their long-lasting formal name, the Mycetozoa; and, 25 years later, Zopf (1884) proposed the label "Eumycetozoa", while also naming some subordinate taxa. For a modern authoritative book on many of these forms, see Olive (1975). The other "lower fungal group", the motile zoosporic forms (now also considered to be protists, but completely unrelated to the mycetozoa: see Corliss, 1984, and relevant citations therein), have long been known, too; for relatively recent works containing references to the older literature on them, see Bessey (1950) and Sparrow (1943,1960). Deserving mention here as well, is another major --and/but not closely related to either of the above two phyla—"sarcodinid" group, the Foraminifera, one of the largest taxa in the entire kingdom Protista if one includes (which one should!) its very numerous fossil species. While foraminifers had been seen by Leeuwenhoek

(Elphidium: see above) and by various other workers in subsequent times, it remained for J. J. Lister (1885) to be the first to delineate the full life cycle of one of these amazing marine "rhizopod sarcodinid" heterotrophs. A species of the marine "actinopod sarcodinid" group (a radiolarian), incidentally, was first described by Meyen (1834), early in the century.

Now back to (mostly) ciliates! The great works of Friedrich Stein, with volumes on both ciliates and flagellates (Stein, 1854, 1859, 1867, 1878, 1883), will probably never be surpassed, particularly because of the precision and magnificence of his drawings, but also because of his originality in classifying the ciliates into four major divisions on the basis of the structural diversification and the topographical distribution of their externally borne ciliary organelles. More than 100 years later (e. g., see discussions in Corliss, 1974, 1979b, 1986b), such characteristics are still largely in use as key characters, notwithstanding our growing modern dependence on ultrastructural and molecular features in systematics. Stein also worked on symbiotic forms: "higher zooflagellates" from insects, ophryoscolecid ciliates from ruminants, and others. This modest microscopist/protozoologist from Prague showed but one major error in judgment. He proposed an "Acineta Theory" which held that suctorians were simply larval forms of peritrich ciliates (Stein, 1849). Soon thereafter, however, Lachmann (1856) carefully demonstrated the fallacy of this idea.

The Russian worker Shewiakoff may be mentioned next because of his great admiration for Stein (above) and for his valiant attempt to complete Stein's monographic series on the systematics of ciliates, Stein having neglected a detailed treatment of the so-called holotrichous species. Near the end of the century, he succeeded in producing the needed work (Schewiakoff, 1896), still invaluable today. Many years later, the same Schewiakoff (1926) published an authoritative monograph on the fascinating acantharian "sarcodinids", studied mostly from the Mediterranean Sea. Mereschkowsky's (1879) earlier ciliate monograph should be cited here, too.

Another remarkable man who spent a number of years in Russia was the Swiss protistologist Eugène Penard, whose monographs also spanned many decades. Penard (1890, 1902, 1904) treated the rhizopods *sensu lato,* although not the radiolarians and other marine forms; and he (Penard, 1920, 1922) produced similarly authoritative works on the suctorians and the ciliates of fresh water. Working principally under low-power microscopy and mostly with living material, he detected small structures amazingly well: his eyesight must have been comparable to that of the much earlier "philosopher in little things", Antony van Leeuwenhoek!

E. Maupas, professionally a librarian in Algiers, was one of the firsts of a small group to commence serious studies in an area that we would label as "genetics" today: see Maupas (1888, 1889). His observations on conjugation and life cycles in ciliates are still appreciated 100 years later. The "Maupasian life cycle" theory (protozoa pass trough stages of youth, maturity, and old age, with death occurring unless a "rejuvenescence" intervenes), long maligned after its first promulgation (Maupas, 1889), has now --with refinements-- been fully accepted, at least for certain ciliates. Unlike practically all of the other 19th century workers listed in these pages (although Penard would be a major exception), Maupas worked alone, had no large laboratory, had no admiring graduate students or a coterie of "postdocs" surrounding him, etc. He also contributed monographs in the areas of comparative cytology and taxonomy of suctorians and other ciliates: see Maupas (1881, 1883).

Another Frenchman, E. G. Balbiani, was also an early student of sexuality and regeneration in ciliates at the same time as Maupas (see Balbiani, 1888, 1892-1893). He was the first worker to believe and corroborate the shrewd observations and deductions of Leeuwenhoek and O. F. Müller that pairing in *Paramecium* represented a sexual phenomenon, not longitudinal fission. Although primarily an insect embryologist, this fine microscopist also published on the minute parasitic microsporidians (e. g., see Balbiani, 1882), demonstrating his widely ranging interests and abilities. Soon after that, Thélohan (1895) published his important monograph on the myxosporidians, another curious group of totally parasitic protozoa. Fabre-Domergue's (1888) large work should be cited here, too; and that of de Fromentel (1874-1876), as well.

Returning to purely taxonomic monographs on ciliates, and as another of the very few examples of American protozoologists' major involvements before the 20th century (although recall the works of Leidy, Smith, and MacCallum, cited on earlier pages), the pioneering investigations of Alfred Stokes (1888) deserve special recognition. Perhaps here, too, should be inserted reference to two other active and influential North American biologists. H. P. Johnson (1893) produced a large paper on *Stentor.* And even earlier, H. J. Clark (erroneously cited as "James-Clark" in much of the literature) carried out research on various ciliates and flagellates and is credited with the important discovery of the choanoflagellates ("collar-bearing monads"), to which he taxonomically linked the sponges (Clark, 1868), a view strongly supported by Kent (1880-1882).

Richard Hertwig (not to mention his equally well-known brother Oscar) was an experimental embryologist who also became a highly reputable protozoologist, carrying out researches on ciliates, heliozoa, and radiolarians (Hertwig, 1879, 1889, 1899; Hertwig and Lesser, 1874). A student of Haeckel's (see below), he was inquisitive about

reproduction at the cellular level and about the morphogenetic processes taking place at that level: thus, the unicellular protozoa were perfect experimental material for him. Goldschmidt (1956) hails R. Hertwig as the greatest zoological teacher of all time, apparently excelling Haeckel, Bütschli, and the other outstanding German professors of the late 19th and early 20th centuries.

HAECKEL, KENT, AND BÜTSCHLI: LEGENDS IN THEIR OWN TIME

Ernst Haeckel, in my opinion, was surely one of the most, if not the most, exciting and celebrated German biologists of all time (to date). A genius, an artist, a hard-working microscopist, a dedicated Darwinian evolutionist, a popular person fervently full of iconoclastic ideas and concepts (often expressed in pithy aphorisms such as, "Ontogeny briefly recapitulates phylogeny": the "Biogenetic Law" applied with refinements, to ciliated protozoa by mostly French worker some 75 years later: *see* Corliss, 1968) and a taxonomist of precision, Haeckel has left his imprint indelibly on the world of biology. While some of his distinguished contemporaries and a number of leading biologist today consider him a controversial character, Haeckel's published contributions in protozoology/protistology remain of enormous value: see, for example, his beautifully illustrated monographs on the radiolarians, which contain some 3,500 species described as new by him (Haeckel, 1866,1878). In resurrecting his (name and concept) Protista, I have called him the "Father of Protistology" (Corliss, 1986c).

We need to insert here a brief reference to early major investigations on marine protozoa, forms only recently returning to popularity because of belated recognition of their significant role in nutrient recycling *(e.g.,* see the comprehensive review on the ecology of the benthic heterotrophic flagellates and ciliates by Patterson *et al.,* 1989). We may cite, as examples of monographs by late 19th century workers, the following works on ciliates, which contained new species descriptions in abundance: von Daday (1887)' Entz, Sr. (1884: similar fine work was carried out by his son --*e.g.* see Entz, Jr., 1909). Gourret and Roeser (1886), Perejaslawzewa (1886), Quennerstedt (1865-1869), Sterki (1878), and Wrzesuiowski (1870, 1877). It is noteworthy that in "the good old days" both ecological and taxonomic considerations were often included by the same investigator in a single paper on a given group of protists. In many subsequent years, however, the two approaches have become separated (perhaps due to the growing sophistication of each of them?), an obvious disadvantage to advancement in both of these important areas of protistological research. But, today, there is growing hope of a welcome return to the combined approach (see a very recent review of the overall situation by Corliss, 1992a).

This brings us to the work of the Englishman W. Saville Kent (1880-1882), his culminating monograph on the "Infusoria". This masterful three-volume work on flagellates, ciliates, and the then separate suctorians (his Tentaculifera) was the first (Pritchard's earlier compilation, see above, notwithstanding) comprehensive systematic treatment of the protozoa (exclusive of the rhizopods, mycetozoa, and the yet largely unknown sporozoa *sense lato)* in the English language. [A brief section on the sponges is also included]. Kent described many new species, and his third volume consists entirely of plates, 51 in number, of excellent figures, many unsurpassed in subsequent treatises on protozoa. Furthermore, he characterized, and often named as new, the higher-level taxa of the organisms covered; this is particularly true for the choanoflagellates, the peritrichs, and the suctorians. Some of his elegant drawings are still reproduced in books published over 100 years later. In an introductory chapter, Kent offers a most helpful detailed history of protozoology up to 1880; and his bibliography is replete with precise citations to the early literature of the preceding two hundred years.

We come now to Otto Bütschli, long-time Professor of Zoology at the University of Heidelberg: "a giant among giants was he!" (Corliss, 1978). With his own training in chemistry and mineralogy, his studies and views on the nature of protoplasm were ahead of his time (e.g. see Bütschli, 1892) and still referred to by modern cytologists. He, like Maupas and other cited above, was also intrigued by life cycles and sexuality, especially as seen in the ciliates (Bütschli, 1876: see Churchill, 1989b, and Jacobs, 1989, for perceptive analyses of this great study). Finally, his Dobellian label, "Architect of Protozoology" (Dobell, 1951), is most well deserved when considering his encyclopedic compendia on the systematics of all groups of protozoa (Bütschli, 1880-1882, 1883-1887, 1887-1889). He managed to unify the diverse assemblages better than anyone preceding him; and his was the first comprehensive account of all the parasitic "sporozoan" and "cnidosporidian" groups known to that time. Bütschli was superb teacher as well, and he influenced and inspired many young biologists in Germany and abroad to enter the exciting field of protozoology. As was true of Kent's monographs, too, Bütschli's early history of protozoology and his extensive bibliography remain as invaluable source materials for students of the history of science.

Before closing our brief survey of major 19th century contributions to the development and growth of the rapidly emerging biological science of protozoology, two other outstanding works must be mentioned. One of the earliest and most comprehensive studies on behavior and motor responses in the protists was the well-known book by

Vernworn (1889), setting the stage for much research in such areas in the years following that date. An often neglected treatise, a kind of textbook on the cell and, especially, on the protozoa, was the volume produced near the end of the century by Delage and Hérouard (1896). The work includes a well-organized systematic treatment of the classes, orders, families, and genera of the protozoa, while not overlooking their physiology and their reproductive processes. The French authors demonstrate a refreshingly original approach to numerous problems concerning the organization, function, and systematics of the diverse protistan groups covered in their monograph.

EARLY 20TH CENTURY DISCOVERIES OR EVENTS IN PROTOZOOLOGY

A goodly number of the workers cited in preceding sections --or at least their first generation students-- continued to carry out significant work, including the making of new discoveries of importance, on into the present century. These deserve our consideration here, even though it would be impossible to review in this particular paper the entire 91 years of 20th century protozoology that have now passed. Perhaps the single most salient fact about the turn of the 19th century was the advent of protozoological/ protistological research, on a large scale, in the United States of America. This ultimately led to the production of English-language textbooks, the appearance of great centers of research, and the formation of new professionals societies: The Society of Protozoologists (in the year 1947), with its own journal (commencing in the year 1954), and the Phycological Society of America (year 1946) with its journal (1965). The training of many young people commenced, persons stimulated to recognize the protists either as material of interest for their own sake or as ideal models for attacking problems, pure and applied, in cell biology, ecology, conservation, evolution, genetics, taxonomy, and even biomedicine.

We should not fail to point out that the 20th century marked the time of the rise of interest in the protozoa in many other non-European countries or part of the world as well: the Orient, India, Israel, New Zealand, Mexico, South America, etc. But elsewere the growth was not on the scale witnessed in the U.S.A., with its greater population of scientists interested in research in areas of cell biology and microscopy and microbiology generally. The often close association of Americans with various European laboratories long devoted to carrying out protozoological investigations was another factor favoring the rapid increase in work on this side of the Atlantic Ocean.

RESEARCH IN GERMANY AND THE REST OF EUROPE

Germany protozoologists still dominated the field at the turn of the century, both conceptually and in production of taxonomic and other monographs in areas including both free-living and symbiotic groups. As implied above, many such investigators (some from countries other than Germany) were trained by the earlier leaders already mentioned on proceeding pages, particularly Bütschli, Haeckel, and Hertwig. Space permits only briefest mention of selected persons. In parasitological areas, Doflein worked on a variety of protists; but he will be remembered longest for his production of a most authoritative edition on protozoan parasites, first of its kind (Doflein, 1901; with the 6th and last edition published as Doflein and Reichenow, 1949-1953, long after his death). Reichenow, 10 years Doflein's junior, produced brilliant studies on the life cycles and phylogeny of the coccidian haemogregarines and haemosporidians *(e.g.,* see Reichenow, 1910, 1921, 1940), among other parasitological investigations, and kept up the invaluable "Doflein and Reichenow" after the senior author's passing in 1924. Mention of Auerbach's (1910) work might be appropriate here: he published a lengthy monograph on the still rather new group of intriguing protozoan parasites (mostly of insects and fishes) than known as the Cnidosporidia.

The versatile von Prowazek, called a "walking encyclopedia of protozoology" by Golschmidt (1956), worked on many different (including free-living) groups of microorganisms in his short lifetime, ending up as an authority on tropical medicine and viral diseases (see Prowazek, 1898-1903, 1910, 1912, 1913, selections from among his 200+ publications: and recall that he died at age 39!).

Fritz Schaudinn, noted briefly on an earlier page of this paper, was a man of energies and breath that matched those of his colleague von Prowazek (who succeeded him at Berlin and at the celebrated Hamburg Institute of Tropical Diseases). He was a prolific producer of major works on many microscopic forms, including the coccidians *(e.g.,* see Schaudinn, 1900; Schaudinn and Siedlecki, 1897), entamoebae, trypanosomes and spirochaetes (Schaudinn, 1903), etc. One of his papers (Schaudinn, 1905), incidentally, put forward his mostly flawed Binucleata Theory, in which he concluded (among other ideas) that trypanosomes had two (different kinds of)-nuclei, considering the (now well-known) kinetoplast as one of them. He also worked on malarial species: for example, see Schaudinn (1902), the work in which he made, alas, a second error in observation, his false but long surviving and influential claim of witnessing direct entry of a sporozoite into a human erythrocyte. However, among his many positive contributions, before he passed away at the tender age of 34, Schaudinn founded, in 1902, the first (and still

goings journal of protozoology, protistology, the celebrated *Archiv für Protistenkunde.*

A few years later, Dogiel established a school of protistology in the U.S.S.R., with considerable emphasis on symbiotic forms but also on life cycles of protozoa generally, and including some novel evolutionary concepts (see Dogiel, 1925, 1927, 1929, 1951; and Poljansky and Cheissin, 1962, 1965, for the continuation of his 1951 book, which rivalled Doflein's voluminous publication cited above). Poljansky, one of Dogiel's most outstanding student and still publishing today, has also been very active in research mostly, but not exclusively, on symbiotic ciliates *(e.g.,* see Poljansky, 1926, 1934; Poljansky and Strelkow, 1938). At the conceptual level, one of Poljansky's most stimulating contributions has been an expansion and extension of Dogiel's (1954) idea of organ(elle) oligomerization and polymerization in evolution (see convenient review in Poljansky and Raikov, 1976). Considerably earlier, the Russian protozoologist Awerinzew (1906) had produced a masterful work on the Rhizopoda.

In Czechoslovakia and Poland, somewhat similar events were occurring --although at much later dates-- under the leaderships of Jírovec and Raabe, respectively; but the emphasis was far less than Doflein's on protozoa of medical importance (see Jírovec, 1951, 1966; Jírovec *et a*l., 1953, 1962; and Raabe, 1947, 1964, 1967-1972, 1971). Raabe was also the founder and first editor the noted Polish journal *Acta Protozoologica,* starting in the year 1963. And Jírovec was a principal organizer of the First International Congress of Protozoology, convened in Prague in 1961 (and meeting every four years since that date in various other parts of the world: it will be in Berlin in 1993).

In Hungary, the great cytologist and ecologist --a unique combination! -- J. von Gelei *(e.g.* 1932, 1934, 1950, 1954) was becoming active on various protozoological problems involving free-living forms; he had studied abroad in Hertwig's laboratory, and had a number of outstanding students of his own (see commemorative papers in Bereczky, 1986). In nearby Austria, Bruno Klein, working alone (in fact, he never left the vicinity of Vienna throughout his lifetime), was producing numerous works on free-living ciliates using a novel method of silver impregnation; his interest were not in taxonomy or ecology but morphogenesis (Klein, 1927, 1932,1943). Finally, in Roumania, J. Lepsi *(e.g.,* 1926) carried out ecological and taxonomic researches on ciliates and produced the first textbook in his language (Lepsi, 1965).

In the meantime, activity was continuing/growing in France in parasitological researches. For example, see Brumpt's (1910) widely known and heavily used *Précis de Parasitologie,* which ran into many later two-volumed editions (last: Brumpt, 1936). And recall such monographs as Caulery and Mesnil (1905), Cépède (1910), Cuénot (1901), Laveran and Mesnil (1904, 1912), Léger and Dubosq (1909, 1910), and Naville (1925, 1931).

In Great Britain, researchers such as the highly self-disciplined yet irascible scholar Dobell, various of whose writings have been cited in preceding sections of the present paper (and see the thorough obituary notice by Mackinnon and Hoare, 1952), became leaders in parasitic protozoology. Dobell's monographs on pathogenic amoebae alone established his reputation for all time (e.g. see Dobell, 1919, and Dobell and O'Conner, 1921), not to mention his elegant series on intestinal protozoa of monkeys and man (Dobell, 1928-1943). And his classic (Dobell, 1925) on the life cycle and cytology of the coccidian *Aggregata eberthi* is still cited today by cytologists and developmental biologists. Dobell's (1911) "Acellularity Concept" (as it came to be known) --a scathing attack on the German "Cell Theory" of the time-- has recently been treated in detail by historians Jacobs (1989) and Richmond (1989). As I have pointed out (Corliss, 1989), the terms "cell" and "organism" are not mutually exclusive words, and consideration of protozoa as acellular organisms is unnecessary --in fact, the concept is no longer and acceptable one.

The Britisheres Muriel Robertson and E.A. Minchin worked on trypanosomes of Africa shortly after the turn of the century; and Minchin (1903, 1912) was also broadly interested in sporozoan and even groups of non-symbiotic protozoa. Moving briefly into more recent times, the englishman C.A. Hoare, who studied under Dogiel in Russia and authored a textbook on medical protozoology (Hoare, 1949), was an expert on, especially, the mammalian trypanosomes (e.g., see his culminating monograph, 1972); but also note his doctoral work on ciliates (Hoare, 1927). P.C.C. Garnham (1966, 1980, and many more papers before and since those dates: he is still active today) is the leading world authority in the overall research field of malariology and an inspirational teacher as well (see Canning, 1981). It was his classic paper (Short and Garnham, 1948) that first toppled the "Schaudinn Fallacy" (see an earlier page, above), demonstrating that there is an E-E (exoerythrocytic) stage in mammalian malarial before entry of the parasites into the erythrocytes of the circulating blood.

Working before 1950, the noted parasitologist Wenyon is best remembered for his ever-useful two-volume compendium on all the protozoa (although emphasizing forms of medical and veterinary importance), which was published over 65 years ago (Wenyon, 1926). He was also an expert on leishmaniases and intestinal protozoa of humans (see references in Wenyon, 1926). Fellow countryman Sandon (1927) stands out as unique monographer on a completely non-parasitic subject, protozoa of the soil (for a superb modern review of that still neglected area of

research, see Foissner, 1987). Several other works on free-living forms may be mentioned here briefly. A thorough and exiting book on the structure and reproduction of algal protists, by Fritsch (1935, 1945), is still consulted today. And West's *(e.g.,* 1916) compilations on the algae remain valuable as well. Back closer to the turn of the century, we find the notable series by J. Cash and colleagues on the taxonomy and ecology of fresh-water rhizopods, including the heliozoa (Cash and Hopkinson, 1905, 1090; Cash and Wailes, 1919, 1921; Cash *et al.,* 1915).

Let us return to the German schools and, now, to brief mention of (generally) early 20th century workers there who were not principally involved in parasitological researches. For example, Hartmann and Jollos (Hartmann, 1909, 1928, 1952; Hartmann and Jollos, 1910; Jollos, 1921, 1934) were deeply involved in study of life cycles and sexuality in flagellates and ciliates: Jollo's "Dauermodifikationen" concept stimulated much research in many laboratories of the world. Hartmann was also long-time editor of the *Archiv für Protistenkunde.* In areas ranging from cytology and laboratory cultivation to the systematics and field ecology of diverse protozoan/protistan groups, papers, books, and monographs were being published by such workers as Brandt (1907), von Daday (1910), Haecker (1908), Hamburger and Buddenbrock (1911, 1913), Kahl (1930-1935), Lauterborn (1908), Lemmerman (1908, 1910), Maier (1903), Pascher (1913-1936, 1914, 1917, 1927, 1937-1939), Pringsheim (1928, 1930, 1946, 1956, 1963), Wetzel (1928), and Zumstein (1900). Poche's (1913) work represents the first book-length paper ever devoted solely to nomenclatural aspects of the taxonomy of the protozoa; he included a complete classification of these protist as known up that time, proposing new names for various taxa at different hierarchical levels. In separate publications, Poche emended the taxonomic names of other groups as well; in all cases, he did not know the organisms from First-hand study. So, over time, in the field of zoology he has gained the rather non-complimentary title of "armchair systematist".

Deserving praiseworthy attention are the works by Karl Belar (not a German, but trained in their laboratories), whose contributions to our knowledge of the protistan nucleus culminated in a slim but fact-packed authoritative (still today) book (Belar, 1926). Tragically killed in an automobile accident in the southwest U.S.A. at the age of 36, this brilliant microscopist and cytologist will also be remembered for his ability in microtechniques (see Belar, 1928).

Towards the end of the first half of the 20th century, we find a number of new and active biological centers developing in various universities and other research institutions in Germany. A protozoological one that attracts our special attention is the laboratory established at Tübingen under the leadership of Karl Grell, a man still very productive today. Grell, like Hartmann before him, has had a great interest in protozoan life cycles and sexuality (including those of the little-studied foraminiferans: see references to his series of papers in Grell, 1973), was long the editor of the *Archiv für Protistenkunde,* and has produced an outstanding and beautifully illustrated textbook (Grell, 1956, 1968, and an edition in English, 1973) widely still in use some 20-25 years later. A specialist on groups ranging from gregarines and forams and radiolarians to hypotrichs and suctorians and an expert in electron microscopy and microcinematography, Grell has trained a number of students in the cytology of the protozoan cell, persons now leaders in their own right. His interest in the protozoan nucleus is reminiscent of Belar's *(e.g.* see review by Grell, 1953, 1964, 1967, and references to many of his own fine works therein).

In France (and nearby Belgium and Switzerland), numerous papers on the ecology, systematics, and culturing of flagellates and ciliates, especially, were appearing in the first half of the 20th century: works by Chodat (1913), de Saedeleer (1934), Janet (1912, 1922, 1923), Meunier (1910), and Roux (1901) may be cited as examples. The excellent papers of young Bernard Collin (1911, 1912) on the perplexing suctorians merit special attention because he was probably the first protozoologist ever to make thorough use of reproductive and morphogenetic phenomena in drawing phylogenetic and taxonomic conclusions about his organisms. Dying at the age of 34, he left in his area of research a void that was unfilled for many years (but see the immediately following section) In Denmark, towards the middle of the century, the stimulating work of the phycologist Christensen (e.g., see 1926) on algal systematics deserves insertion here.

CHATTON AND FAURÉ-FREMIET CILIATOLOGISTS SANS PEERS

The two persons who were to come to dominate research on the protists in France for many years were born in the same year, 1883. While both working mostly on ciliates, E. Chatton (often with his young colleague Nobel Laureate A. Lwoff) and E. Fauré-Fremiet seemed to have tacitly had an understanding: *viz.*, their subareas of research seldom overlapped. But both employed, with great effectiveness, the Chatton-Lwoffsilver technique; and both were an inspiration to many graduate students, of their own and around world. Both were men of ideas as well as being "fact-finders" equally comfortable working at the laboratory bench or collecting out in the field. Among their many conceptual contributions must be mentioned at least Chatton's celebrated Rule of Desmodexy, his postulation of two modes of protistan fission (*viz.*, homothetogenic and symmetrogenic) and his belief in the autonomy, genetic

continuity, and pluripotency of kinetosomes, Fauré-Fremiet adopted and extended these, applied a refinement of Haeckel's "Biogenetic Law" to ciliate evolution and phylogeny, and offered additional hypotheses on morphogenesis, with particular emphasis on stomatogenesis (new mouth-formation) in diverse ciliophorans groups.

Chatton concentrated mostly on marine symbiotic forms (including unusual dinoflagellate groups as well as ciliates), and Fauré-Fremiet on fresh-water free-living forms. Chatton takled problems of life cycles and effects on hosts, often studying interrelationships within major groups; he also (Chatton, 1925, a long overlooked paper) was the first biologist to recognize the evolutionarily significant differences between bacteria and all the other ("higher") organisms, even creating the now universally accepted terms "prokaryote" and "eukaryote" long before their application, nearly 40 (!) years later, by microbiologists such as Stainer and van Niel (1962).

Fauré-Fremiet worked more from comparative cytological and morphogenetic approaches and drew phylogenetic conclusions from inter-group comparisons. A few examples representative of the contributions of both of these great men may be seen in the following references: Chatton (1920, 1952, 1953: last two published posthumously), Chatton and Lwoff (1935, 1936, 1949-1950: last one posthumous), Chatton and Pérard (1921), Chatlon and Séguéla (1940); Fauré-Fremiet (1910, 1924, 1945, 1948, 1950, 1967a,b, 1970, 1984: last one posthumous).

Long tributes to these two productive leaders, Chatton and Fauré-Fremiet, may be found, respectively, in Lwoff (1948), published in the year following Chatton's too early passing; and in Corliss (1972), after "F-F's" death, wich occurred much later than Chatton's. Also see the discussions by Corliss (1956, 1961, 1979b) of the lasting impact of the researches of both men on ciliate systematics overall.

Incidentally, Chatton's brilliant young colleague André Lwoff, still active at the time of this writing, gained world-wide leadership, towards the end of the first half of the present century, in studies on the physiology (nutrition) and biochemistry of protozoa (Lwoff, 1923) should also be remembered specifically as the first person to stablish a ciliated protozoon *(Tetrahymena pyriformis)* in axenic culture, a feat that opened the door to hundreds upon hundreds of subsequent publications on the biochemistry, genetics, and molecular biology of this protist so ideal as a laboratory experimental cell/organism.

Three French contemporaries of the preceding remarkable trio of (mostly) ciliate protozoologists deserve mention, too. P.-P Grassé investigated the symbiotic flagellates of termites, especially; and he will perhaps be longest remembered as the hard-working editor of a most ambitious project, production of the *Traitè de Zoologie* (see Grassé, 1952, 1953, 1984, for the completed tomes on the protozoa). In fascicules 1 and 2 of the first volume may be found major contributions authored by himself as well as references to many of his original papers. Grassé, an influential leader and indefatigable researcher and author, trained many students --especially in areas of symbiotic protozoology-- most of whom are still active today. He was also one of the founders of the Groupement des Protistologues de Langue Française, in 1961, and of its journal, *Protistologica,* which ran from 1966 through 1986 (having been replaced by the new *European Journal of Protistology,* Managing Editor Klaus Hausmann of Berlin, in 1987).

G. Deflandre worked in the area of paleoprotistology (recall that Ehrenberg founded this field: see above), specializing on fossil dinoflagellates and silicoflagellates in particular; but he published on testaceous rhizopods and occasionally ciliates, too. Deflandre also edited an ill-fated French protistological journal, *Annales de Protistologie,* that appeared in the years 1929-1936. For some of his major works, see Deflandre (1928, 1952a-d, 1953a,b), with still others cited in the bibliographies of various chapters in the Grassé *Traite* volumes mentioned above.

Finally, colleague R. Hovasse carried out mainly cytological studies on such groups as dinoflagellates and radiolarians. He was a keen authority on extrusomes and on endosymbiotic relationships; and he trained a number of excellent students in protistology over the years, many of whom are leaders today in their own right. In Hovasse (1923, 1932, 1965, 1984a,b) may be found references to still other important papers of his.

RESEARCH IN AMERICA

In America, great centers of protozoology were commencing to appear not long after the run of the century. Not surprisingly, their leaders --at least some of the first ones-- were often educated, at least in part, in the great European (generally German) laboratories. In another paper in these proceedings (Corliss, 1992b), I have treated, albeit rather briefly, the development of protozoology in the U.S.A.; I have added a little more information below, including citation of further papers of significance. The three earliest, and long strongest, graduate training centers

were located at Columbia University, under the leadership of G.N. Calkins, the first (and only?) American to occupy formally a Chair of Protozoology (his title, Professor of Protozoology); at Johns Hopkins University, with diverse leaders H.S. Jennings, R.R. Hegner, and S.O. Mast, joined eventually by M.M. Metcalf; and at the University of California (Berkeley), under C.A. Kofoid (later joined by Kirby who, much later, was succeeded by Balamuth).

Soon thereafter, L.L. Woodruff, Calkins'first Ph. D. student and only 10 years his junior, established a center at Yale University. Still later, we find strong graduate programs in protozoology at Illinois (Kudo, also Levine; and, much later, Corliss as Kudo's successor), Philadelphia (University of Pennsylvania: Wenrich, than Diller; Temple University: Schaeffer and Wichterman), New York University (Hall), Chicago (Taliaferro), Wisconsin (Noland), Stanford (Taylor), Indiana (Sonnerborn and van Wagtendonk), Harvard (Cleveland and Cushman), Iowa (King), Iowa State (Becker), North Carolina (Beers and Olive), Syracuse (Manwell), and California, Los Angeles (Jahn, Ball and Furgason), to mention the principal ones.

I have not attempted to include major centers of phycological, or mycological, research in America in the brief list above although studies of protists *sensu lato* were beginning apace there, also. And in considering textbooks, below, I have not given ones in phycology: bull will mention here that G.M. Smith's (1933, 1950) was one of the first authoritative books on the algae in America and is still a widely respected work. Among the many fine texts available today, let me cite but one, Bold and Wayne (1985), which has an admirably comprehensive coverage of algal structure and reproduction and has a bibliography rich in citations to much of the important phycological literature of the 20th century. Here, too, allow me to insert references to the indispensable marine algal monographs by W.R. Taylor (1937, 1960, 1962: last is a revised edition of the 1937 work) and the convenient "overview" book on all algae by Prescott (1968).

Textbooks of protozoology soon became available in English: Calkins' (1901) was the first to appear, in any language (later editions, 1909, 1926, 1933). A text by Kudo (1931, and fifth and last edition, 1966) became the most popular --by translations, thorough the world-- for many years. The books produced by the Britishers Minchin (1912) and, later, Wenyon (1926) were also appreciated by numerous biology students of English-speaking countries. The first general protozoology text in Spanish, incidentally, was produced by E. Fernández Galiano (1921) in Madrid. Beltrán's (1948) book, published in Mexico, was the first in that language in the area of protozoan parasites of humans.

Jahn and Jahn's (1949: second edition, Jahn et *al.,* 1979) highly popular (and inexpensive!) little book, *How to know the Protozoa,* appeared next. It was followed by scholarly text by Hall (1953), which offered the first real competition to Kudo's books; and it apparently stimulated production of a rash of sometimes excellent teaching manuals in English in the 1960's and 1970's and beyond (all post-1950 works, therefore not appropriate for citation here). Hall, by the way, like Pringsheim of Germany and Lwoff of France (see references on earlier pages), and fellow American colleague Hutner (see below), was a pioneer in study of the physiology of the unicellular protist (pigmented flagellates and, later, the ciliate *Tetrahymena),* using "puree --better, anexic-- cultures of his experimental organisms (see Hall, 1941, and references therein). A student of C.A. Kofoid's, R.P. Hall had many graduate students himself, his first and probably most productive being the inimitable T.L. Jahn.

An early American --in fact, largely, midwestern American (as opposed to domination by the east- and west-coast schools of Calkins and Kofoid)-- multiauthored production that included nearly 200 pages of text and figures on protozoa and algae was Ward and Whipple's (1918) *Fresh-Water Biology.* But the single volume that lent the greatest impetus to (further) development of protozoological research in the United States was Calkins and Summers (1941), an heuristic collection of chapters (by some 20 American specialist-authorities) to which I have paid tribute in my paper referred to above (Corliss, 1992b). Preceded by Hegner and Andrews (1930) and eventually followed by Chan (1967- 1972), the impressive "blue bible" of Calkins and Summers nevertheless stood --and survives-- as a most unique publication, truly one of a kind.

Citation of specific papers of all of the American workers mentioned in the preceding paragraphs is not in order here. But a few of the outstanding or landmark works of the older leaders --*viz*., Calkins, Cleveland, Cushman, Hegner, Jennings, Kofoid, Kudo, Mast, Metcalf, Schaeffer, Taliaferro, Taylor, Wenrich, and Woodruff-- will be helpful in indicating the diversity of areas covered by them and developed still further by their students (and the students of those!) in the second half of the present century. Many of them also fit one of the themes of this paper, "firsts" in protozoology, although that is not explicitly pointed out in each case below. For example, than, see Calkins (1902a,b, 1919, 1930a,b; Calkins and Cull, 1907); Cleveland, (1949, 1956); Cushman (1928, 1948); Hegner (1927, 1938); Hegner and Taliaferro (1924); Jennings (1904, 1920, 1929, 1931); Kofoid (Kofoid and Campbell, 1929, 1939; Kofoid and MacLennan, 1930; Kofoid and Skogsberg, 1928; Kofoid and Swezy, 1919, 1921; not to mention his pre-1900 single-authored works on the plankton of the Illinois River, culminating monographically in Kofoid, 1903, 1908; and see Sharp, 1914, for the first account on the eventually ill-fated "neuromotor apparatus" or Cytobrain); Kudo (1920,

1924, 1959); Mast (1911, 1914); Metcalf (1909, 1923, 1940); Schaeffer (1920, 1926); Taliaferro (1929); Taylor (1920, 1928, 1941); Wenrich (1935, 1944, 1954; Wenrich and Diller, 1950); Woodruff (1905, 1912; Woodruff and Erdman, 1914: this last paper included the concept and cytological descriptions of "endomixis", an alleged nuclear reorganization phenomenon in ciliates such as *Paramecium* that was later shown to be totally non-supportable, both cytologically and genetically; but, alas, LLW went to his death-bed some 33 years later still stoutly insisting on the validity and importance of the concept).

Numerous additional influential works on the cytology, taxonomy, ecology, physiology, morphogenesis, immunology, behavior, parasitism, nomenclature, phylogeny, evolution, sexuality, genetics, biochemistry, and molecular biology of numerous protist species and higher-level groups have been published by (other) American --not to mention non-American!-- researchers before or at mid-20th century, people whose papers generally have not yet been cited in the present historical account. As stated above, many such investigators are/have been students of the leaders who are considered on preceding pages, and very often the research projects of this "younger generation" have continued well beyond my arbitrary cut-off date of 1950.

Nevertheless, to tie the works of the past, to some extent at least, to those of the second half of the current century, I am going to offer next --arranging my presentations alphabetically-brief consideration of the researches of a deliberately selected group of eight persons who, by chance, represent quite a diversity of fields of interest (see the following paragraphs). Generally, not more than four or five publications (often bearing dates beyond 1950) will be given for each individual, plus a very brief comment about the researcher's impact on advances in his or her areas(s) of investigation.

First, a separate, quite unusual case --often overlooked-- deserves at least passing mention in any history of early American protozoology. Under the mentorship of the great parasitologist, Minnie Watson (later Minnie Watson Kamm) single-handedly, and under sole authorship, produced a pair of monographs on the bionomics of gregarines (Kamm, 1922; Watson, 1916) that stand as a lasting major contribution to the systematics of a group of "lower" Sporozoa previously known almost exclusively from the European literature.

Now to the eight other, mostly mid-century, American workers, many of whose major papers have admittedly appeard since 1950 and/but are continuing to elicit a high level of research productivity among numerous younger folk in the U.S.A. and elsewhere.

Libbie Henrietta Hyman has been a strong influence on "whole organism" research primarily through her scholarly series of stimulating volumes on the invertebrate animals, admirably produced without co-authors. Original ideas and important information on the protozoa are included in Vols. 1 and 5 (Hymen, 1940, 1959). Her own research papers, mostly on the physiology of amoebae, reflect her training at the University of Chicago under the noted embryologist C.M. Child *(e.g.,* see Hyman, 1917, 1936). Seymour Hutner, at times as iconoclastic as Dobell though much more lovable, has long been the American "André Lwoff" of physiological protistology *(e.g.,* see Hutner, 1936, 1964; Hutner *et al.,* 1972; Hutner and Lwoff, 1955; Lee, Hutner, and Bovee, 1985; Levandowsky and Hutner, 1979-1981). His Haskin-Pace laboratory in New York City has become a mecca for junior bug-lovers from far and near. Many colleagues have profited from his ready wit and profound wisdom.

Harold Kirby, who was surely C.A. Kofoid's most outstanding student and who met a most untimely death (heart attack when on a hike with boy scouts) at the age of 52, rapidly became a world authority on the cytology, taxonomy, morphogenesis, and evolution of flagellates symbiotic in termites. He was also an expert on protozoological techniques and an excellent teacher (at the University of California, Berkeley), with wide interests in the biology and symbiology of diverse protists. Of his many published papers, meticulously prepared, a representative few are the following: Kirby (1941a,b, 1944a,b, 1949 --last of an impressive series, 1950a,b). Norman D. Levine, American Dean of Coccidiology and producer of the apt name "Apicomplexa" for the (former) Sporozoa *sensu stricto,* has published hundreds of authoritative papers and books in his field *(e.g.,* see Levine, 1972, 1973, 1985a,b, 1988; Levine *et al.,* 1980). Levine, long active in affairs of the Society of Protozoologists, was one-time editor of the *Journal of Protozoology.* He has trained numerous graduate students in parasitology, and many of them are now very active in research across the country.

Lowell E. Noland, a sterling product of the Birge-Juday school of limnology/ecology at the University of Wisconsin, was above all a great and gentle --and inspiring-- teacher for half a century at Wisconsin. With broad interest and abilities even beyond the sciences, Noland's personal researches on the protozoa were primarily concerned with the ecology and systematics of the ciliates, as reflected in the following short list of selected papers: Noland (1925, 1937, 1959), Noland and Finley (1931), Noland and Gojdics (1967). Dorothy R. Pitelka, an early most effective user of the electron microscope with protozoan material (Pitelka, 1949; Pitelka and Schooley, 1955), 30 years ago produced an outstanding book (Pitelka, 1963) that heralded the advent of the Age of Ultrastructure in

protozoological research. Pitelka's subsequent chapters (Pitelka, 1969, 1974) in books edited by others further confirmed her leadership in an area so significant in modern protozoological investigations of many kinds.

Tracy M. Sonneborn, Jennings' most gifted student at Johns Hopkins in the 1930's, made breaks-through discoveries in the genetics and cytogenetics of ciliates, especially of members of the *Paramecium aurelia* complex (Sonneborn, 1937, 1950, 1957, 1970, 1974, 1975). Sonneborn established a flourishing school of ciliate genetics at Indiana University that has produced half a dozen of the top leaders in areas of ciliate genetics and morphogenesis in the world today. He was a stimulating and highly knowledgeable teacher who exuded infectious enthusiasm over any topic under discussion. William Trager, a student of the rigorous taskmaster L.R. Cleveland at Harvard, was early interested in insect physiology and tissue culture, and he found a way to apply his technical abilities in work on cultivation of protozoan parasites. Using sophisticated physiological approaches --plus a great deal of care, patience, and common sense-- he was the first to discover ways of culturing the blood stages of human malarial in the laboratory, opening the door to research by many groups who are attempting to develop a vaccine against the number 1 killer of human beings in the world today (Trager, 1934, 1942, 1964, 1982, 1988; Wager and Jensen, 1980). Wager served many years as the first editor of the *Journal of Protozoology,* establishing it as an outlet for top quality research papers; and he has long been interested in the field of symbiotic associations involving protists as one of the partners.

Incidentally, it has not seemed appropriate in the present account to treat as a separate subject the role of women in the historical development of protozoology --in the U.S.A. or in other countries of the world (although note references to Americans Hyman, Pitelka, and Watson-Kam, above). As is not surprising, considering the male domination in the sciences in general, women's pre-20th century contributions have not been conspicuous. In fact, single- or senior-authorships by women hardly (if) ever appear in the protozoological/algal literature of the 1800's, despite the explosion of interest in studies of microscopic organisms in that highly productive period. But it should be noted that with the turn of the century --and especially since 1950-- we have seen an ever-increasing and often independent involvement of female workers in protozoological researches of significance. The topic is deserving of special consideration, but space restrictions demand that worthwhile task be carried out properly, in due time, elsewhere that in the present paper (see preliminary note by Corliss, 1992c, an abstract in press).

WHAT OF THE FUTURE?

Progress in protozoology since the times of the last groups of researchers considered in immediately preceding pages has been, once again, tied largely to advances in microscopy --for example, the widespread application of transmission and scanning electron microscopy to protozoological problems. But progress is also often due to the increased usage, in study of protozoan material today, of the sophisticated biochemical and molecular techniques currently so very commonly employed in cell biology.

As indicated by the title of this paper, discoveries and events of significance in the explosive post-1950 era of protozoological research are largely beyond coverage here, as well as mention of the new principals and principles involved. From a conceptual point of view, the recent advent and increasingly widespread acceptance of a "protist perspective" (see Corliss, 1986c; Margulis *et al.,* 1990; and of earlier historical importance, Copeland, 1956; Whittaker, 1969) have altered the long held conventional notion of what comprises "the Protozoa". This has particularly affected the systematics and classification of these eukaryotic microorganisms; and results of molecular approaches are having profound effects on our ideas of the evolutionary and phylogenetic interrelationships among major assemblages assigned to the neoHaeckelian kingdom Protista.

Suffice it to say, events in the times that lie ahead of us will surely be as exiting and intriguing in this area of biological inquiry --protozoology/protistology-- as have been those of the past 300 years!

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